MEMORANDUM OF UNDERSTANDING
Among
EGLIN AIR FORCE BASE (Air Force Development Test Center),
BLACKWATER RIVER STATE FOREST (Florida Department of Agriculture and Consumer Services-Division Of Forestry),
NORTHWEST FLORIDA WATER MANAGEMENT DISTRICT,
CONECUH NATIONAL FOREST (National Forests in Alabama),
CHAMPION INTERNATIONAL CORPORATION,
THE NATURE CONSERVANCY (Florida Regional Office, Alabama Field Office, Florida Natural Areas Inventory, Alabama Natural Heritage Program), and CHOCTAWHATCHEE NATIONAL FOREST (National Forests in Florida)

THIS MEMORANDUM OF UNDERSTANDING (hereinafter referred to as "MOU" or "Understanding") is made and entered into on the 8th day of March 1996, among Eglin Air Force Base (Air Force Development Test Center), Blackwater River State Forest (Florida Department of Agriculture and Consumer Services, Division of Forestry), Northwest Florida Water Management District, Conecuh National Forest (National Forests in Alabama), Champion International Corporation, The Nature Conservancy (Florida Regional Office, Alabama State Office, Florida Natural Areas Inventory, Alabama Natural Heritage Program), and Choctawhatchee National Forest (National Forests in Florida), and hereinafter referred to as "parties."

The parties have responsibilities on and collectively own and manage approximately 840,000 acres in the ecosystems of the region (see Attachment). These acres comprise the largest remaining nearly contiguous blocks of longleaf pine uplands in the southeastern U.S. and include portions of four major watersheds, including the Escambia-Conecuh, Blackwater, Yellow, and Choctawhatchee river drainages.

The purpose of this MOU is to develop and implement a voluntary and cooperative stewardship strategy to sustain the long-term viability of native plants and animals, the integrity of ecosystems, the production of commodities and ecosystem services, and the human communities that depend upon all of them.

The general goals of this MOU include the following:

-To assist, share information and coordinate efforts with the other parties in fulfilling the purposes of the MOU.

-To provide a model for local, state, federal, and private entities working together to fulfill the purpose of the MOU.

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DTIC QUALITY INSPECTED 1

The Nature Conservancy®

Gulf Coastal Plain Ecosystem Partnership

APPENDIX E.

Gulf Coastal Plain Ecosystem Partnership

Steering Committee Meeting # 1

Bear Lake Recreation Area, Blackwater River State Forest
December 1-2, 1998

Research, Scientific and General Information

DISTRIBUTION STATEMENT A:
Approved for Public Release -
Distribution Unlimited

Groundcover Restoration
Exotics
Longleaf Pine Genetics
Endangered Species
Prescribed Burning
Game Species
Aquatics, Wetlands
General

Champion International • 4025 Highway 178 • Jay, Florida 32565 • 850 675-5760 • FAX 850 675-5756

recycled paper

-To communicate to the public success in meeting both individual and common goals related to the MOU.

-To cooperate with:

- U.S. Fish and Wildlife Service
- The National Biological Service
- The U.S. Environmental Protection Agency
- The Florida Department of Environmental Protection
- The Florida Department of Transportation
- The Alabama Division of Game and Fish
- The Florida Game and Fresh Water Fish Commission
- The Southern Leadership Longleaf Pine Restoration Strategy Group
- The Longleaf Pine Alliance
- Southeastern State Foresters

This MOU recognizes that the individual parties (public and private) have legitimate and varied management goals ranging from military training and weapons testing, to producing forest commodities, providing recreational opportunities, protecting water quality, and conserving native species and ecosystem integrity. This MOU is in no way intended to limit or constrain the parties' individual goals.

This MOU is entered into pursuant and subject to all applicable federal, state, and local laws. This MOU is not entered in the interest of obtaining advice or recommendations for any office or agency of the federal government and nothing herein shall be construed, nor is intended to state or imply, that this MOU establishes a federal advisory committee or that the Federal Advisory Committee Act (5 U.S.C. Appendix 2) shall apply.

IN ORDER TO FULFILL the stated purpose and intent of this MOU, the Parties agree in principle to the following:

1. To develop jointly a voluntary strategy, to be reviewed and updated annually, that will document critical ecosystem elements, processes, and interactions, identify priority ecosystem goals and objectives, both individually and jointly, and measure progress in attaining goals and objectives.

2. To develop jointly a voluntary red-cockaded woodpecker management strategy, and strategies for other listed species as appropriate, to be reviewed and updated annually, that will coordinate objectives and management efforts among the parties toward the mutual goal of recovering the red-cockaded woodpecker and other listed species.

3. To develop jointly a voluntary longleaf pine restoration strategy, to be reviewed and updated annually, that will coordinate objectives, strategies and actions among the parties and other efforts toward the mutual goal of recovering representative and ecologically functional examples of the longleaf pine ecosystem.

4. To share and exchange relevant information and technology as appropriate and needed to compile and implement the above strategies.

5. To develop specific agreements and working plans for individual projects considered by all or some of the parties hereto to have mutual interest. Such agreements and working plans will be developed whenever deemed appropriate by the relevant parties.

6. To consider entering into specific agreements among all or some of the parties and/or third parties, as occasion demands, for the use of specialized equipment, transfer of funds, purchasing of supplies, and other matters pertaining to the general purposes of management agreed upon by all or some of the parties hereto. Any allocation of responsibilities and liabilities, including limitation of expenditures under this Understanding, will be as set forth in specific working agreements entered into by the relevant parties.

7. To hold at least one meeting per year and more often as required to discuss management opportunities and coordinate management and monitoring efforts and to keep written records made under this Understanding.

8. To make this Understanding effective as of the date it is executed by the last party and continuing for a term of one year and renewing automatically on an annual basis unless terminated in writing by one or more of the parties hereto pursuant to paragraph 9 below.

9. To terminate this Understanding at any time by mutual agreement by all parties with any party having the right to withdraw from this Understanding by giving the other parties 30 days notice.

10. To amend this Understanding as necessary at any time to incorporate new parties, new information or changes in any parties' authorities, policies, directives, or goals, subject to concurrence by all parties.

Nothing in this Understanding shall be construed to place financial commitment upon any of the parties. Actions taken and funds expended to implement this Understanding are contingent upon appropriations, priorities, and other constraints.

IN WITNESS WHEREOF, the parties hereto have executed this Memorandum of Understanding as of the first date above written.

EGLIN AIR FORCE BASE

By: _____
Air Force Development Test Center Commander

Date: Mar 8, 1996

FLORIDA DEPARTMENT OF AGRICULTURE AND CONSUMER SERVICES

By: _____
Director, Div. of Administration

Date: May 10 1996

NORTHWEST FLORIDA WATER MANAGEMENT DISTRICT

By: _____
Executive Director

Date: 05.07.96

NATIONAL FORESTS IN ALABAMA

By: _____
Forest Supervisor

Date: 26 April 1996

CHAMPION INTERNATIONAL CORPORATION

By: _____
General Manager-Western Florida Region

Date: 22 March 1996

THE NATURE CONSERVANCY

By: _____
Chief Conservation Officer

Date: 5/31/96

NATIONAL FORESTS IN FLORIDA

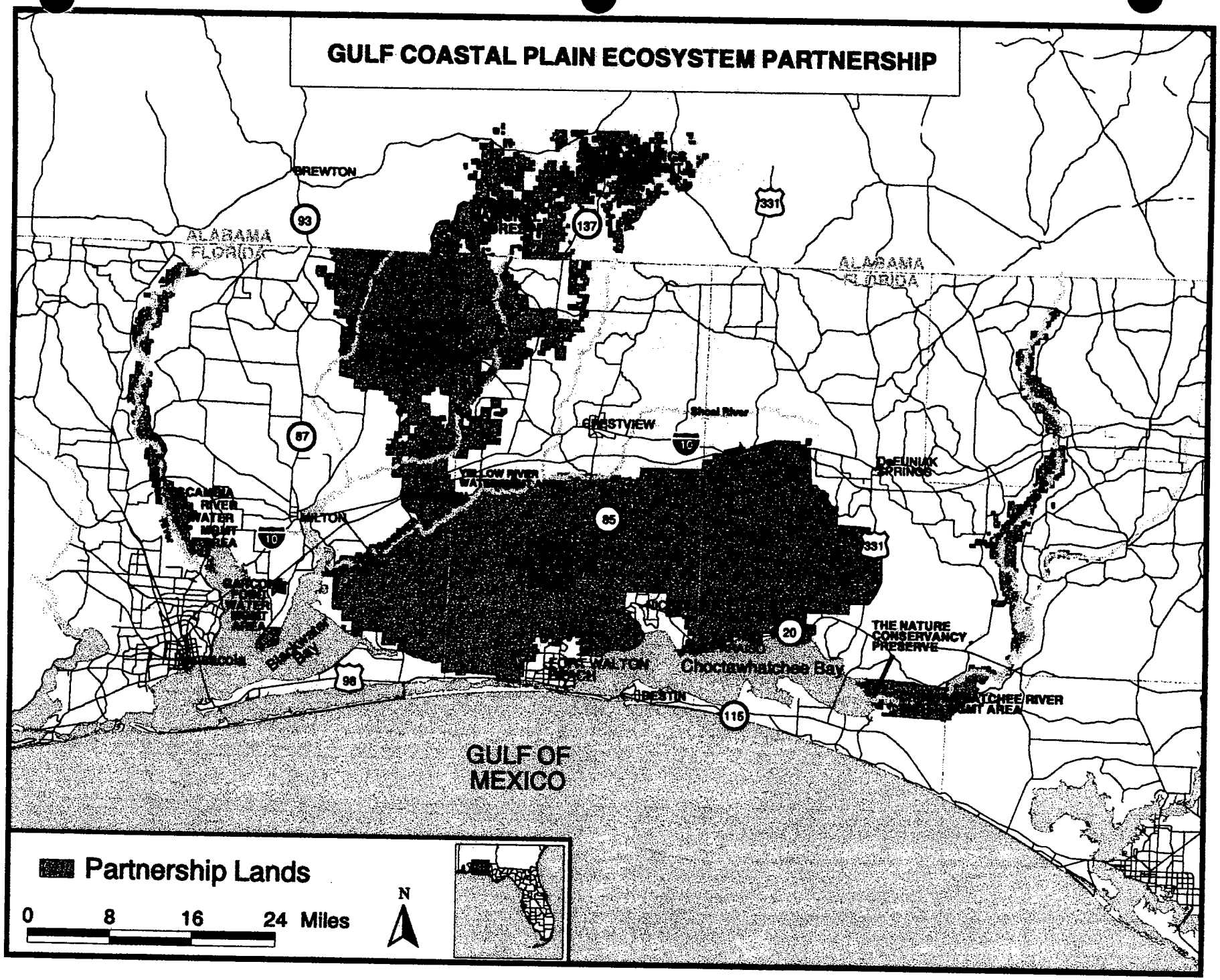
By: _____
Forest Supervisor

Date: 5/3/96

ATTACHMENT

Ownerships included in Memorandum of Understanding:

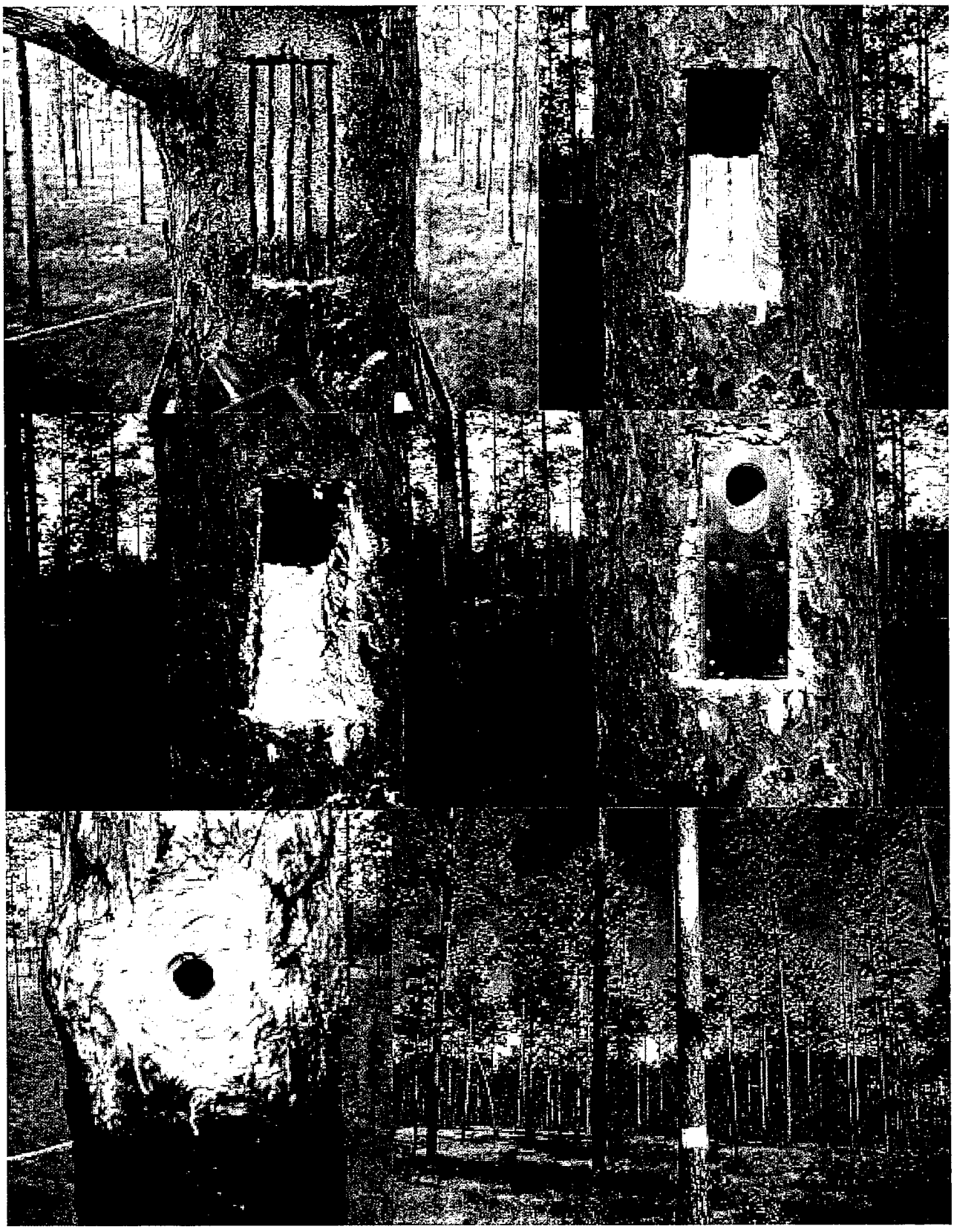
Owner/manager	Name of property	Acreage (approx.)
DEPARTMENT OF DEFENSE	Eglin Air Force Base	463,441 acres
FLORIDA DIVISION OF FORESTRY	Blackwater River State Forest	183,670
NW FLORIDA WATER MANAGEMENT DISTRICT	Garcon Point, Yellow River, Choctawhatchee River, and Escambia River Water Management Areas	95,467
NATIONAL FORESTS IN ALABAMA	Conecuh National Forest	83,790
CHAMPION INTERNATIONAL CORPORATION	Connector parcel	7,550
THE NATURE CONSERVANCY	Choctawhatchee River Delta Preserve	2,750
NATIONAL FORESTS IN FLORIDA	Choctawhatchee National Forest	1,114


GULF COASTAL PLAIN ECOSYSTEM PARTNERSHIP
BREWTON
93
ALABAMA
FLORIDA
137
331
ALABAMA
FLORIDA
87
CRESTVIEW
Shoal River
10
DeFUNIAK SPRINGS
CANOE RIVER WATER MGMT AREA
10
85
331
20
THE NATURE CONSERVANCY PRESERVE
Choctawhatchee Bay
98
115
GULF OF MEXICO
Partnership Lands
0 8 16 24 Miles
N

GULF COASTAL PLAIN ECOSYSTEM PARTNERSHIP—PARTNER CONTACTS (as of Nov. 23, 1998)

	CONTACT	ALTERNATE
Blackwater River State Forest	**Dennis Hardin** Phone: 850-414-8293 Fax: 850-488-0863 Florida Division of Forestry 3125 Conner Blvd. Tallahassee, FL 32399	**Tom Serviss** Phone: 850-957-4201 Fax: 850-957-4203 Florida Division of Forestry 11650 Munson Highway Milton, FL 32570
Champion International	**Arden Shropshire** Phone: 850-675-0929 ext.113 Fax: 850-675-0938 Champion International Corporation 4025 Highway 178 Jay, FL 32565	**Ad Platt** Phone: 850-937-4830 Fax: 850-968-3027 Champion International Corporation 117 Pace Parkway P.O. Box 875 Cantonment, FL 32533-0875
Conecuh National Forest	**Rick Lint** Phone: 334-222-2555 Fax: 334-222-6485 Conecuh National Forest Rt. 5, Box 157 Andalusia, AL 36420	**Gary Taylor** Phone: 334-222-2555 Fax: 334-222-6485 Conecuh National Forest Rt. 5, Box 157 Andalusia, AL 36420
Eglin Air Force Base	**Rick McWhite** Phone: 850-882-4164 Fax: 850-882-5321 Natural Resources 107 Highway 85 North Niceville, FL 32578	**Carl Petrick** Phone: 850-882-4164 Fax: 850-882-5321 Natural Resources 107 Highway 85 North Niceville, FL 32578
National Forests in Florida	**Andy Colaninno** Phone: 850-643-2282 Fax: 850-643-2284 National Forests in Florida P.O. Box 579 Bristol, FL 32321	**Art Rohrbacher** Phone: 850-942-9300 Fax: 850-942-9305 **Kathleen Atkinson** Phone: 850-942-9347 Fax: 850-942-9305 National Forests in Florida 325 John Knox Rd., Suite F100 Tallahassee, FL 32303
NW Florida Water Management District	**Steve Brown** Phone: 850-484-5125 Fax: 850-484-5133 NW FL Water Mgmt. District 2261 W. Nine Mile Rd. Pensacola, FL 32534-9416	**Mark Herndon** Phone: 850-539-5999 Fax: 850-539-4380 NW FL Water Mgmt. District Rt. 1, Box 3100 Havana, FL 32333
The Nature Conservancy	**Jeff Hardesty** Phone: 352-392-7006 Fax: 352-846-1344 The Nature Conservancy Dept. of Botany/Univ. of FL P.O. Box 118526 Gainesville, FL 32611	**Chris Oberholster** Phone: 205-251-1155 Fax: 205-251-4444 The Nature Conservancy 2821-C 2nd Ave. S. Birmingham, AL 35233
PROJECT DIRECTOR	**Vernon Compton** Phone: 850-983-7414 Fax: 850-983-8456 Gulf Coastal Plain Ecosystem Partnership P.O. Box 785 Milton, FL 32572-0785	Fed Ex/UPS Address: 303 Conecuh Street Milton, FL 32570 email: comptonv@bellsouth.net

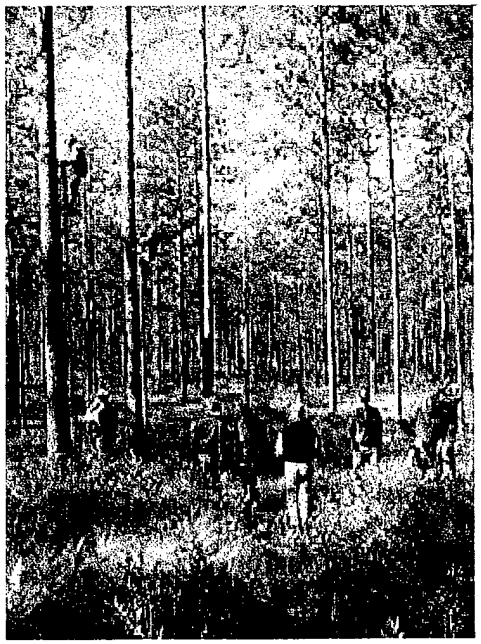
Blackwater River State Forest
Red-cockaded Woodpecker Artificial Cavity Installation



Red-Cockaded Woodpecker
Cavity Insert and Banding Program
on Blackwater River State Forest
a project of the

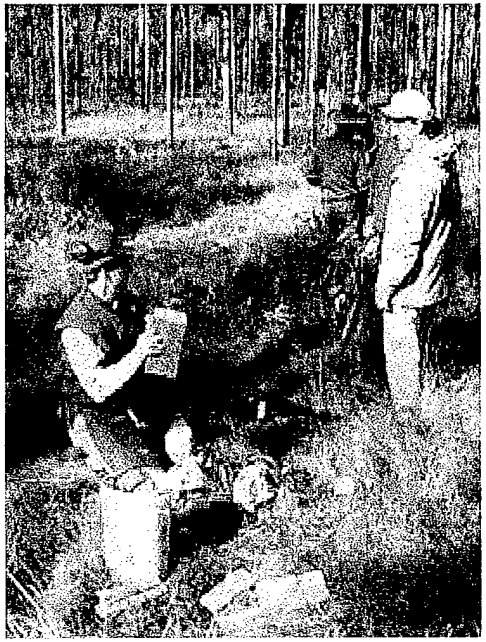
Gulf Coastal Plain Ecosystem Partnership

Members Assisting
National Forest of Alabama
(Conecuh National Forest)
National Forest of Florida
(Apalachicola National Forest)
Blackwater River State Forest
Eglin Air Force Base
January 23 - 24, 1998

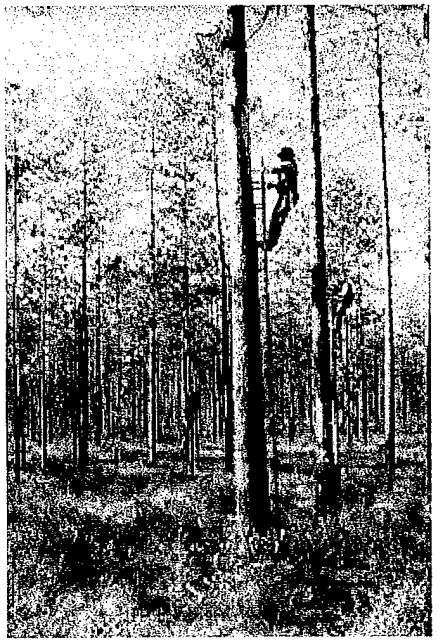














Post-Treatment Analysis of Restoration Effects on Soils, Plants, Arthropods, and Birds in Sandhill Systems at Eglin Air Force Base, Florida

Principal and Co-Principal Investigators:
Jeffrey L. Hardesty, The Nature Conservancy, CO-PI, Project Director
Louis Provencher, The Nature Conservancy, PI
George W. Tanner, University of Florida, PI
Doria R. Gordon, The Nature Conservancy, CO-PI
Leonard A. Brennan, Tall Timbers Research Station, CO-PI

Prepared by[1]:
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Krista E. M. Galley, The Nature Conservancy, Entomologist
Brenda J. Herring, The Nature Conservancy, Botanist
James Sheehan, Tall Timbers Research Station, Ornithologist
Nancy M. Gobris, Tall Timbers Research Station, Ornithologist
Doria R. Gordon, The Nature Conservancy, CO-PI
George W. Tanner, University of Florida, PI
Jeffrey L. Hardesty , The Nature Conservancy, Project Director
H. LeRoy Rodgers, The Nature Conservancy, Botanist[2]
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Longleaf Pine Restoration Project
The Nature Conservancy–University of Florida–Tall Timbers Research Station
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[1] Citation: L. Provencher, K.E.M. Galley, B.J. Herring, J. Sheehan, N.M. Gobris, D.R. Gordon, G.W. Tanner, J.L. Hardesty, H.L. Rodgers, J.P. McAdoo, M.N. Northrup, S.J. McAdoo, and L. A. Brennan. 1998. Post-treatment analysis of restoration effects on soils, plants, arthropods, and birds in sandhill systems at Eglin Air Force Base, Florida. Annual report to Natural Resources Division, Eglin Air Force Base, Niceville, FL. Public Lands Program, The Nature Conservancy, Gainesville, FL.

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Post-Treatment Analysis of Restoration Effects on Soils, Plants, Arthropods, and Birds in Sandhill Systems at Eglin Air Force Base, Florida

Executive Summary

We evaluated techniques for extensive restoration of a fire-suppressed regional longleaf pine (*Pinus palustris*) landscape. We tested for variable response to experimental methods for reducing midstory hardwood dominance in a large-scale, long-term study. We also compared variable response between restoration and relatively high quality sites. We stress that we are presenting initial results from a five-year project. This report primarily focused on the ecological responses to treatments prior to fuel reduction burns in 12 plots that were implemented during winter and spring 1997, thus these conclusions and our assessment of management implications may change.

Methods. The response of soil chemistry, plant densities, tree densities and size distributions, arthropod densities and biomasses, and breeding bird detection rates were compared among and within four woody species removal treatments in mixed hardwood-longleaf pine community types (hereafter named restoration plots) and within one mixed sand pine (*Pinus clausa*)-hardwood-longleaf community type (hereafter named sand pine removal plots). Hardwood reduction treatments were growing season burning, hexazinone (ULW®) herbicide application, chain saw felling/girdling, and no removal in the former community type, and sand pine harvest in the latter community type. Treatments were 81 ha (200 acres) each with six replicates distributed among six block of a completely randomized block design. Restoration effectiveness will be judged through comparison of response variables to no-treatment controls and to a restoration "model" derived from replicated higher quality, frequently-burned reference sites.

Pre-treatment Soil Analyses. We determined soil chemistry and soil texture from the pre-treatment phase of this study to examine the similarity among the 36, 81-ha (200-acre) plots described above. Using correspondence analysis to group similar plots based on variation among soil chemistry and texture variables, we found that total Kjeldahl N positively segregated plots and that Al, Fe, sand of 0.125 mm, sand of 0.063 mm, and silt negatively influenced the position of plots in multivariate space on the first axis of the ordination. Ca was the only element that separated plots on the second axis of the ordination. Mg, K, P, Cl, pH, percent organic matter, percent clay, percent total sand, and percentages of all other sand size classes had no influence on plot ordination. We found no significant correlation between percent silt in the upper soil horizon and the depth of the argillic layer, but the slope at the location of an auger sample was positively and significantly correlated to percent sand. Soil chemistry and texture variables were correlated to pre-treatment densities of plant species and basal areas of tree species. The number of plant species was positively and significantly explained by percent silt and by the percent of extreme sand size classes, and negatively explained by the 0.25 mm sand size class (dominant sand size).

Significant correlation between soil chemistry variables with plant species densities and tree species basal area were generally less than the absolute value of 0.2 and never exceeded the absolute value of 0.31. Correlation between soil texture variables and the same plant and tree variables were greater than for soil chemistry and generally greater than the absolute value of 0.2. The following common species were more abundant on soils with less silt: turkey oak (*Quercus laevis*), bluejack oak (*Q. incana*), sand live oak (*Q. geminata*), catbrier (*Smilax auriculata*), weeping haw (*Crataegus lacrimata*), arrowfeather (*Aristida purpurescens*), wireweed (*Polygonella gracilis*), and bracken fern (*Pteridium aquilinum*). We suggest that the positive correlation between silt and plant species richness should be considered by Eglin Air Force Base's land managers if they include plant species richness as a metric of ecological condition.

Vegetation Responses to Treatments. Restoration treatments significantly decreased canopy cover compared to the control in 1995 and 1996. Canopy cover was decreased the

Sminthurus carolinensis (Collembola: Sminthuridae) and the flatid planthopper *Metcalfa pruinosa* (Homoptera: Flatidae) were more abundant in burn plots.

We regressed nine arthropod order densities against variables describing midstory structure and groundcover composition. During the pre-treatment period of this study, we found no significant dependence of arthropod densities on a subset of eight uncorrelated independent variables measuring groundcover plant composition and tree species basal area. One year after treatment application, homopterans and thrips densities were the only arthropod orders that were significantly explained by a multiple regression model composed of six uncorrelated independent variables. Homoptera density was positively explained by graminoid cover and negatively by the density of longleaf pine juveniles. Graminoid cover was significantly and positively correlated to woody groundcover species cover, plant species richness, and the basal area of longleaf pine. There was a negative correlation between longleaf pine juveniles and bare ground cover and a positive one to woody species cover. Overall, these results support the idea that fire shaped the variation in homopteran density. The basal areas of turkey oak and sand live oak, respectively, negatively and positively explained thrips density. Because the basal area of sand live oak was highest in burn plots, we again suggest that fire influenced thrips densities. We conclude that land managers seeking to enhance arthropod diversity would benefit from the positive effects that growing season burning has on some arthropod taxa.

Overall, results indicate that growing season burning increased arthropod density and biomass more than that of other treatments. Because northern bobwhite quail (*Colinus virginianus*), wild turkey (*Meleagris gallopavo*), red-cockaded woodpeckers (*Picoides borealis*), and other wildlife feed heavily on arthropods, especially during the breeding season, we suggest that managers could burn to increase arthropod availability. Continued sampling and comparisons of these results to treatment effects on trees and plants will provide broad criteria for judging the cost and benefits of different restoration techniques.

Bird Response to Treatments. Of 18 common breeding bird species tested, only red-cockaded woodpeckers and pine warblers *(Dendroica pinus)* significantly responded to treatments the second year post treatment. Detection rates for the red-cockaded woodpecker were significantly greater in ULW® than other treatments and marginally significantly greater in felling/girdling than burn plots. Compared to controls, pine warblers achieved a 4-fold increase in detection rates in felling/girdling plots and a 2-fold increase in ULW® and burn plots. Pine warblers responded positively to a reduced midstory.

Foraging observations of common wintering birds reflected known habitat associations. Carolina chickadees (*Parus carolinensis*), tufted titmice (*Baeolophus bicolor*), ruby-crowned kinglets (*Regulus calendula*), downy woodpeckers (*Picoides pubescens*), and palm warblers (*Dendroica palmarum*) exhibited higher use of hardwoods relative to pines. The red-cockaded woodpecker, brown-headed nuthatch (*Sitta pusilla*), and pine warbler used longleaf pine nearly exclusively, although pine warblers also foraged on hardwoods. Woodpeckers foraged mainly on tree boles and branches, while the smaller passerines mainly searched from twigs, needles, leaves, and branches, consistent with their respective foraging guilds. Birds used longleaf pine more than all other tree species in both treatment and reference sites. We suggest that pine warblers would be good indicators of ecological change due to their abundance, known habitat and foraging preferences, and rapid responsiveness to habitat modification.

Evaluation of treatment success remains premature, because treatment application has continued into 1997, and we primarily reported here on results that were not affected by this latter change. We suggested that felling/girdling achieved the best primary restoration goal of midstory hardwood reduction compared to growing season burn and ULW®. While stimulating arthropod biomass and plant species richness, growing season burns alone were least effective for rapid midstory reduction.

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We regressed nine arthropod order densities against variables describing midstory structure and groundcover composition. During the pre-treatment period of this study, we found no significant dependence of arthropod densities on a subset of eight uncorrelated independent variables measuring groundcover plant composition and tree species basal area. One year after treatment application, homopterans and thrips densities were the only arthropod orders that were significantly explained by a multiple regression model composed of six uncorrelated independent variables. Homoptera density was positively explained by graminoid cover and negatively by the density of longleaf pine juveniles. Graminoid cover was significantly and positively correlated to woody groundcover species cover, plant species richness, and the basal area of longleaf pine. There was a negative correlation between longleaf pine juveniles and bare ground cover and a positive one to woody species cover. Overall, these results support the idea that fire shaped the variation in homopteran density. The basal areas of turkey oak and sand live oak, respectively, negatively and positively explained thrips density. Because the basal area of sand live oak was highest in burn plots, we again suggest that fire influenced thrips densities. We conclude that land managers seeking to enhance arthropod diversity would benefit from the positive effects that growing season burning has on some arthropod taxa.

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PROCEEDINGS OF THE INTERNATIONAL CONFERENCE ON FOREST VEGETATION MANAGEMENT

ECOLOGY, PRACTICE AND POLICY

APRIL 27 - MAY 1, 1992

AUBURN, ALABAMA, U.S.A.

Cosponsored By

School of Forestry
Alabama Agricultural Experiment Station
Auburn University

and

International Union of Forestry Research Organizations
Subject Group P1.13-00 Forest Weed Management

Auburn University
School of Forestry Report 1993:1
E.F. Thompson, Dean

Dean H. Gjerstad, Editor

Wiregrass cover following site preparation of sandhills

KENNETH W. OUTCALT
USDA Forest Service, Southeastern Forest Exp. Stn.
P. O. Box 14524, Gainesville, FL 32604

Wiregrass (*Aristida stricta* Michx.) is a keystone species in the longleaf pine (*Pinus palustris* Mill.) community of the southeastern Coastal Plain, USA, providing the fuel for recurring ground fires. This survey assessed the impact to wiregrass cover of different site preparation techniques. All sandhills sites regenerated to longleaf pine in the past 5 years on the Ocala National Forest, Florida were sampled. Hexazinone applied at rates up to 2 kg/ha, did not adversely impact wiregrass cover on sandhills sites. Areas treated with hexazinone and a double drum chopper had about half the wiregrass cover found on untreated or hexazinone only areas. In an operational comparison of Garlon with single chopping, single chopping treatments had less than one third the wiregrass cover found on herbicide treated areas. Double chopped sites averaged less than 2 percent wiregrass cover. Thus, herbicide treatments appear superior to chopping for reducing woody competition while maintaining wiregrass in sandhills longleaf communities. If chopping is used, it should be a single chop plus a herbicide rather than double chopping.

Introduction

Wiregrass or pineland threeawn (*Aristida stricta* Michx.) is a major understory species in the slash pine (*Pinus elliottii* Engelm.), South Florida slash pine (*P. elliottii* var. *densa* Little and Dorman), longleaf pine (*P. palustris* Mill.) - slash pine, longleaf pine, and longleaf pine - scrub oak types of the Atlantic coastal plain (Eyre 1980). It is most prevalent on infertile sands ranging from poorly-drained soils, typified by the Leon series (sandy, siliceous, thermic, Aeric Haplaquod) to excessively-drained soils like Lakeland (thermic, coated Typic Quartzipsamment). Pine - wiregrass communities once covered more than 10 million ha, from North Carolina to Florida (Southern Section SRM 1974). Although the overstory was southern pines, wiregrass was a critical component of the ecosystem. Fire was a frequent natural occurrence across much of the area, maintaining the pine - wiregrass communities (Christensen 1981). The accumulation of dead wiregrass furnished the fuel necessary to carry these ground fires. Thus, wiregrass significantly influenced the natural fire regime and thereby the plant community (Clewell 1989). Some land managers have recognized wiregrass as an important fuel source for prescribed fires (Christensen 1981). These fires reduce the risk of damaging wildfires and control the invasion of pine - wiregrass areas by hardwood species (Komarek 1977). In longleaf pine stands fires also control brown spot needle blight (*Scirrhia acicola* (Dearn.) Siggers), which can severely limit growth and survival of seedlings (Boyer 1975). In addition, the understory of wiregrass maintains a more favorable soil environment by improving soil structure and water and nutrient holding capacity (Snedaker and Lugo 1972).

Its ability to develop a dense root mat just below the soil surface makes wiregrass a strong competitor during the pine regeneration phase (Haines et al. 1975). This competition can be especially severe on dry sites where wiregrass can significantly reduce pine seedling survival (Scheer and Woods 1959). Numerous mechanical systems have been tested for reducing the amount of wiregrass competition when pine stands are being regenerated. Single treatments with a single drum chopper disturb but do not seriously affect wiregrass (Grelen 1959, Sheer and Woods 1959). Two passes with a double drum chopper, will nearly eliminate the wiregrass component (Grelen 1962) on dry sandhills sites and greatly reduces it on flatwoods sites (Moore 1974). It is similarly reduced on flatwoods sites by other dual mechanical site preparation treatments such as disking and bedding and reduced further by the triple treatment of disking and double bedding (Schultz and Wilhite 1974). Since wiregrass is a key species in the community, land managers need site preparation techniques which only temporarily reduce wiregrass cover. This means limiting the destruction of wiregrass clones or bunches, because reproduction from seed is rare (Clewell 1989). This survey was to gain insight into the impact to wiregrass cover on sandhills sites of different site preparation systems.

Materials and Methods

The study was conducted on the Ocala National Forest located in the central highlands region of Florida, USA. Most of the forest is covered by deep sandy soils from relic dunes formed during the Pleistocene as sea level rose and fell. Sand pine scrub, a mixture of sand pine and shrubby hardwoods with sclerophyllus leaves, is the most prevalent community type on the forest. Within this matrix of sand pine scrub exist islands of longleaf pine growing in open stands with scattered clumps of understory oaks and a ground cover dominated by wiregrass. A portion of this longleaf area on the forest needs restoration to eliminate off site pines, to reduce the hardwood component and to reestablish longleaf pine. Some sites have slash pine

plantations on them, while others have been invaded by sand pine or scrub oaks during a 30 year era of fire exclusion.

All of the 53 sandhills wiregrass - longleaf sites on the forest regenerated between 1985 and 1990 were sampled. Wiregrass cover was assessed during the late summer and autumn of 1990 along 30-m line transects by the line-intercept method (Mueller-Dombois and Ellenberg 1974). A total of 12 transects were established from random starting points in each area. The number of 15-cm segments containing wiregrass were counted and recorded for each transect. Ocala National Forest records were searched to determine date and method of site preparation and method of planting. Wiregrass cover data were also collected from 31 uncut mature natural longleaf stands. These stands were a stratified random sample of all sandhills longleaf stands on the forest greater than 50 years old.

Four study sites had received no site preparation before regeneration (Table 1). Hexazinone was used on 47 of the sites with 22 treated with liquid and 25 with the granular form. The liquid was applied using either a boom sprayer or backpack sprayer while granules were spread with an Omni air spreader. The boom sprayer gives broadcast coverage. A spot gun was used with the backpack sprayer with spots spaced on a 2 meter square grid. Application rates varied from 1 to 2 kg/ha of active ingredient for liquid treatments and from 1.1 to 1.7 kg/ha with the granular form of hexazinone. Ten sites treated with granules and 12 with liquid hexazinone were also given a single pass with a double drum chopper 5 to 6 months following herbicide application. Two sites received no herbicide treatment, but were chopped twice within a 3 to 6 month period. On two areas half of the site was chopped and the other broadcast sprayed with Garlon™ [triclopyr (3,5,6-trichloro-pyridinyloxyacetic acid)] at a rate of 4.5 kg/ha active ingredient. Machine planting was used to establish longleaf seedlings on allregenerated sites. On ten sites a V-blade scalped about a half meter strip during planting.

Table 1. Number of stands and total area by treatment

Treatment	Number of Stands	Area Treated (ha)
Uncut stands	31	735
Harvest only	4	50
Hexazinone liquid	10	210
Hexazinone granular	15	270
Hexazinone liquid & chop	12	190
Hexazinone granular & chop	10	105
Chop & chop	2	30

Table 2. Wiregrass cover by treatment for selected longleaf stands on the Ocala National Forest, Florida.

Treatment	Wiregrass Cover	
	Range	Mean and CI*
	(percent)	
Uncut stands	10-81	42+/-2.1
Harvest only	28-64	47+/-3.2
Hexazinone (liquid)	21-73	42+/-2.3
Hexazinone (granular)	18-68	36+/-1.8
Hexazinone (liquid) and chop	2-67	27+/-2.1
Hexazinone (granular) and chop	1-20	14+/-1.5
Chop and chop	0-1	1+/-0.3

*Mean and the 95 percent confidence interval.

Results and Discussion

There was a considerable range in wiregrass c[illegible] (10 to 81 percent) in mature uncut stands (Table 2). Site prepared areas had the same general range of values except the hexazinone and chop and the double chop sites, which both had lower maximum values. The range in wiregrass cover in uncut stands results largely from differences in past burning regimes and location relative to sand pine stands. Areas burned more often have less cover from competing oaks and other shrubs and consequently more wiregrass cover. Stands adjacent to sand pine scrub, have been invaded by sand pine and the shrub understory of that community. Competition from these species will eliminate wiregrass from a significant portion of the site. Thus stands that burned very infrequently and were next to sand pine scrub, now have low wiregrass cover.

Statistical comparisons of site preparation treatments are not valid because most site preparations were not assigned at random. However, comparisons of treatment averages do suggest treatment effects. Areas regenerated without site preparation appear to have the same average wiregrass cover as uncut stands or harvest only areas (Table 2). Sites prepared with liquid hexazinone also appear to have nearly the same cover as untreated stands. It appears [illegible] granular form of hexazinone may have caused [illegible] decline in wiregrass cover. The average wiregrass cover on areas chopped after spraying with liquid hexazinone was less than for uncut stands. Stands

treated with granular hexazinone and then chopped now have only about one third the wiregrass cover of uncut stands. Only two sites had been double chopped, but both now have very little wiregrass cover.

It appears liquid hexazinone applied at the rates and by the methods used here should not adversely impact wiregrass cover on sandhills wiregrass - longleaf sites. Individual wiregrass bunches have responded to the reduction in competition, as they would following a fire, and have flowered abundantly. The small apparent decline with granular hexazinone agrees very closely with the estimated 5 percent loss in wiregrass noted by Duever (1989). Vegetative reproduction of wiregrass should be able to replace this small decline in cover. Also this is a one time herbicide treatment to reduce competing oaks, which can then be easily maintained with prescribed fire.

This does not mean hexazinone will not kill wiregrass. At higher rates, which can occur if application strips overlap, mortality may be higher (Duever 1989). This can be avoided by using spot gun applications which virtually eliminate overlap. The lower application rate of 1.1 kg/ha appears adequate for competition control and should be favored.

Since liquid hexazinone alone caused no decline in wiregrass cover, chopping after herbicide treatment must have caused the wiregrass mortality. The magnitude of the present difference in wiregrass cover, between chopped and uncut sites, is comparable to the 23 percent decline from chopping alone reported for a west Florida sandhills site (Outcalt and Lewis 1990). The combined effect of granular hexazinone and chopping also appears harmful to wiregrass. Thus, even a single pass with a double drum chopper should be avoided on sandhills sites which contain wiregrass. As shown previously (Outcalt and Lewis 1990) two passes with a double drum chopper will nearly eliminate wiregrass from the site.

Only two sites were treated with Garlon but it was done so statistical comparisons could be made. Both sites had a lot of oak competition before treatment, and thus low wiregrass cover. Two years after site preparation the Garlon treatments had 18 percent wiregrass cover while the chopped treatments had significantly less at 6 percent (s.e of 2.63). As with hexazinone, chopping was much more detrimental to wiregrass than the herbicide. Further study is needed comparing wiregrass cover before and after treatment with Garlon before wide scale use can be recommended.

Conclusion

With selective herbicides, sandhills sites can be site prepared and planted to longleaf pine without adversely impacting the critical species wiregrass. If the site has a heavy invasion of sand pine (Figure 1a), it should first be prescribed burned. Prescribed burning should be followed by a spring application of liquid hexazinone at a rate of 1 to 1.5 kg/ha active ingredient. Herbicide should be applied with a spot gun with spots spaced on a 2 meter grid. This treatment will reduce woody competition without materially damaging the wiregrass (Figure 1b). Sites can then be planted with machine or by hand (Figure 1c). This should result in a good stand of longleaf seedlings and an abundant cover of wiregrass three to four years after planting (Figure 1d). Any sand pine seedlings in the stand can be mechanically removed using brush saws. In a few years when the longleaf are large enough, a prescribed fire carried by the wiregrass will reduce oak sprouts and other woody competition. From this point forward a fire cycle of 3 to 5 years with the majority during the growing season will mimic the natural fire regime, restrict sand pine invasion, keep woody competition in check and help maintain the vigor of the wiregrass ground cover.

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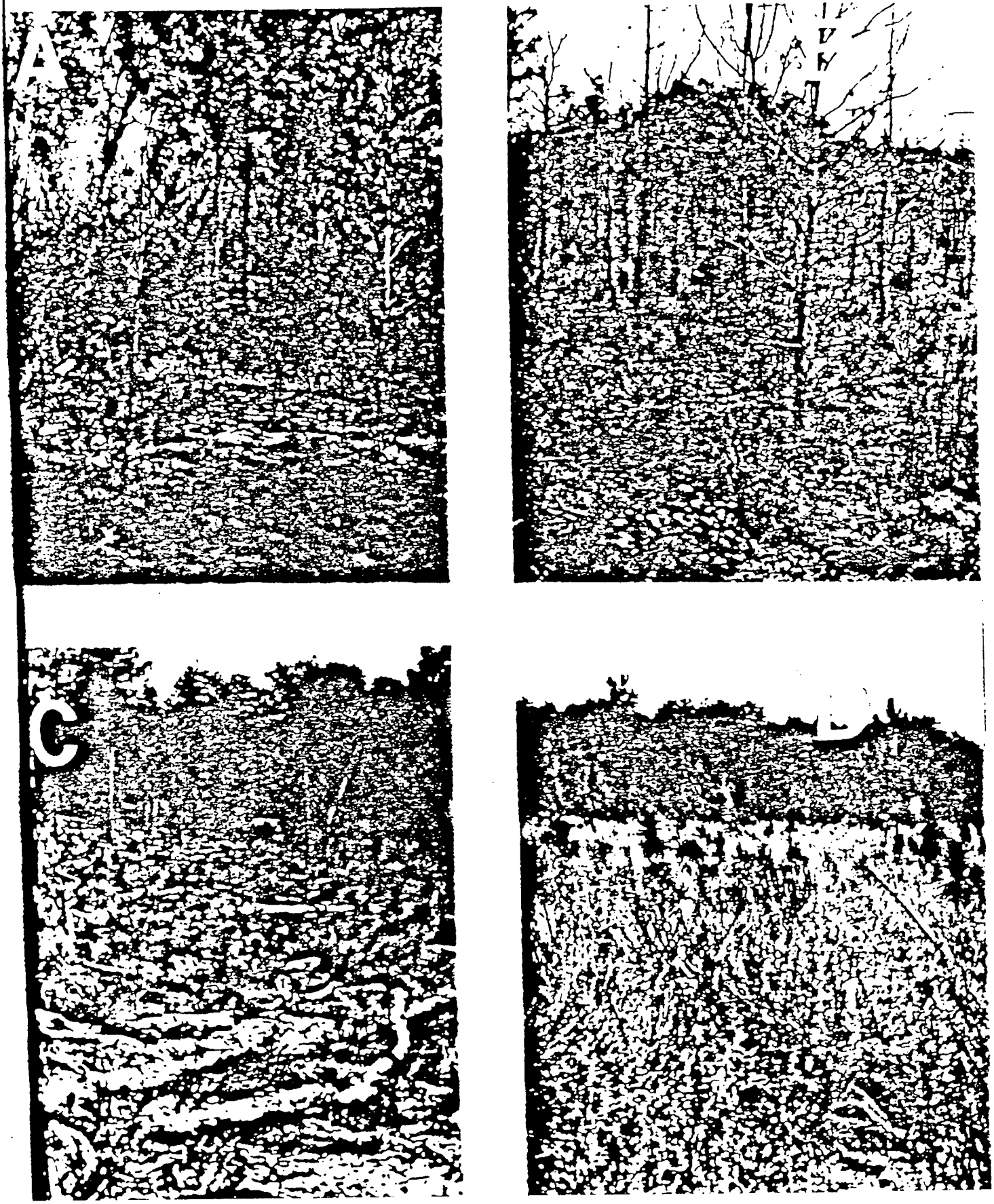
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Figure 1. Adjacent sandhills areas on the Ocala National Forest, Florida, at different stages of restoration with hexazinone. (a) Two months after August prescribed burn. (b) Five months after May application of hexazinone by spot gun. (c) Six months after May hexazinone treatment and 2 months after V-blade planting of longleaf seedlings. (d) Four years after hexazinone and planting operations.



natural nectars were tested. Fluorescence was directly proportional to concentration in dilute samples. The presence of sugars did not interfere with the calculation of amino acid concentration. Because different amino acids fluoresce at different intensities, this method provides only an approximation of amino acid concentration. Nonetheless, the magnitude of error caused by the differential fluorescence is relatively small. Fluorescamine is sufficiently sensitive for use with dilute, small-volume nectar samples. This method allows rapid intraspecific and interspecific comparisons of plant nectar composition.

OUTCALT, KENNETH W. and DALE G. BROCKWAY. USDA For. Serv., P.O. 14524, Gainesville, FL 32604, and Ft Collins, CO. 80526, USA Response of wiregrass to hexazinone treatments on Florida sandhills.

Previous evidence indicates the herbicide hexazinone may be useful for restoration of longleaf wiregrass communities. The study objective was to access the impact of hexazinone on wiregrass (Aristida stricta Michx.) growth. Hexazinone was applied in granular (0.9kg/ha) or liquid form (0.9 and 1.8 kg/ha) to plots in five longleaf pine (Pinus palustris Mill.)sites on the Ocala National Forest in May, 1991. Before treatment, 46 percent of the wiregrass biomass was living green tissue. Five months after treatments, September, 1991, the proportion of biomass from green tissue had declined to 35 percent with no differences between treated and control plots. Prior to treatment above-ground wiregrass biomass ranged from 135 g/square m on control and high rate liquid hexazinone plots to 191 on the plots treated with granular hexazinone and 272 on low rate liquid treated plots. The first fall following treatment above-ground wiregrass biomass was the same as before treatment on all but the plots given the high rate of liquid hexazinone. On this treatment wiregrass biomass nearly doubled. Thus, at low rates, hexazinone could be used to reduce woody competition on sandhills sites without reducing wiregrass biomass nor the percentage of living tissue, and certain treatments can actually increased wiregrass.

OVERTON, JACOB McC. University of California, Los Angeles, CA 90024 USA. The influence of dispersal on mistletoe infection patterns.

The influence of dispersal patterns on the distribution and abundance of two species of mistletoes, Phrygilanthus sonorae (Loranthaceae) and Phoradendron californicum (Viscaceae), was investigated. At several sites in Baja California, mistletoe and host distributions were mapped. Dispersal patterns were determined by bird observation and the locations of dispersed seeds. The two species of mistletoes differ dramatically in the the manner in which birds handle fruits and disperse seeds. Within sites, both intensity and prevalence of mistletoe infections increase with host size. Differences between sites in overall infection rates and the rates at which prevalence and intensity increase with host size can be explained by differences between sites and species in the dispersal efficiency and the proportion of mistletoe seeds dispersed off of the parent host tree. Other explanations for differences in infection patterns, including differences in mistletoe establishment success, adult mistletoe mortality and host turnover are also investigated.

PADILLA, DIANNA K. University of Wisconsin, Madison, WI, 53706, USA Costs and consequences of feeding morphology plasticity in an herbivorous gastropod, *Lacuna*.

Although radular shape in molluscs is generally stereotypic, I have found that species of *Lacuna* have variable tooth shapes that can be induced by dietary changes. *L. variegata* is primarily found in grass beds feeding on epiphytes, and generally has blunt teeth. *L. vincta* primarily lives on and consumes macroalgae, and generally has pointed teeth. However, both species are found in both habitats. To determine the potential efficiencies of different tooth shapes, short term feeding experiments were conducted with *L. vincta* (pointed cusps) and *L. variegata* (blunt cusps) on both kelp and epiphyte-covered sea grass. *L. vincta* consumed significantly more kelp than *L. variegata*. *L. variegata* consumed most of the epiphytes while not damaging the grass. *L. vincta* was less effective at removing epiphytes and damaged the grass. These results support the prediction that blunt teeth are more effective for grazing epiphytes, whereas pointed teeth are more effective at excavating the surface of a macrophyte. These results are used to calculate costs and potential efficiency increases of having fixed versus plastic tooth morphology in a variable environment.

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MAINTAINING THE NATIVE PLANT COMMUNITY DURING LONGLEAF PINE (*Pinus palustris* Mill.) ESTABLISHMENT

KENNETH W. OUTCALT

USDA Forest Service, P.O. Box 14524, Gainesville, FL, USA 32604

SUMMARY

Site preparation treatments were evaluated to determine which were useful for establishing longleaf pine seedlings without excessive long-term damage to the native understory. Hexazinone treatments of 1.1 to 2.2 kg/ha were sufficient to reduce woody competition and allow the successful establishment of longleaf seedlings using hand planting of containerized stock. Hexazinone at rates of 2.2 kg/ha followed by strip scalping and machine planting resulted in slightly higher seedling survival rates. Although there was some initial exposure of soil and a decline in grass cover, the understory soon recovered. Thus, this treatment can be used to re-establish longleaf without undue damage to the understory.

INTRODUCTION

Longleaf pine is the key tree species in a complex of fire-dependent ecosystems long native to the southeastern United States (1). It once occupied perhaps as much as 25 million hectares, stretching from southeastern Virginia south to central Florida and west into eastern Texas (2). These forests have been intensively exploited since colonial times with little regard for regeneration. Currently only 1.3 million hectares of longleaf pine forest remain. The continuing reduction of this important forest type carries with it a risk to the myriad of life forms characteristic of and largely dependent on longleaf pine ecosystems. The diversity of ground cover plants per unit area places longleaf pine ecosystems among the most species-rich plant communities outside the Tropics. Extreme habitat reduction is the main cause for the precarious state of at least 191 taxa of vascular plants (3).

The need to re-establish longleaf on former sites is now widely recognized. It is believed that native understory grasses, especially wiregrass (*Aristida stricta*) and woody shrubs can be strong competitors during the regeneration phase. Numerous mechanical site preparation systems have been used to reduce competition prior to planting longleaf seedlings. These were quite effective in increasing seedling survival but they also resulted in significant reductions in the native understory grasses. Two passes with a double drum chopper, for example, will nearly eliminate wiregrass from dry sites (4) and will severely reduce it on wet flatwoods sites (5). All soil-disturbing site preparation methods reduce wiregrass cover, and it does not seem to recover even after long periods of time (6). Using selective herbicides for site preparation appears to cause less long-term damage to the understory (7). The purpose of this study was to evaluate site preparation treatments to determine if alternative techniques could be found which were successful in both re-establishing longleaf and maintaining the native understory plant community.

METHODS

Site preparation treatments were applied at three dry sandhills sites on the Ocala National Forest in central Florida. These sites were former longleaf stands with a dense cover of scrub oaks and a good intact understory of wiregrass and associated species. Treatments consisting of liquid hexazinone at 1.1 kg/ha a.i., liquid hexazinone at 2.2 kg/ha, granular hexazinone at 1.1 kg/ha, and an untreated control were randomly assigned to 0.25-ha plots at each site. The liquid hexazinone was applied on a 2-by-2m grid with spot guns and the granular herbicide was broadcast. Treatments were applied in May and all plots were hand planted with containerized longleaf seedlings the following winter. An operational treatment consisting of liquid hexazinone at 2.2 kg/ha applied by spot gun and machine planting of containerized longleaf in a scalped strip about 1-m wide was used to plant the remainder of each site.

Prior to treatment, ten 15-m transects were established in each of the operational portions of the sites. Cover by species was collected from these transects before site preparation treatments. All transects were surveyed again at the end of the first, second, and third growing seasons since site preparation. Two growing seasons after planting, longleaf seedling survival was determined on 100 planting spots in a ten-by-ten configuration in the center of each treatment plot. Seedling survival and cover data for major understory species were analyzed with analyses of variance after transformation of percents.

RESULTS AND DISCUSSION

Two years after treatment seedling survival was lowest on the untreated control sites at 55 percent, while the operational treatment had the highest survival of 72 percent. Liquid hexazinone treatments were not significantly different from the operational treatment, with mean survival rates of 66 percent. The granular treatment had a lower seedling survival of 62 percent. No understory plants were selectively eliminated by the operational herbicide and strip scalping treatment. This treatment did, however, significantly reduce the cover of turkey oak (*Quercus laevis*); the primary woody competitor on the sites (Table 1). The scalping in the operational treatment exposed bare soil on 32 percent of the area. Vegetation rapidly recolonized these strips, and 3 years after treatment bare soil occurred on only a small portion of the site. This scalping also caused wiregrass, the dominate grass species, to initially decline on operational sites. It soon recovered, however, and at the end of the third growing season after treatment there was more wiregrass cover than had existed prior to treatment.

Table 1. Effect of operational hexazinone application and V-blade planting on major understory species and bare soil on sandhills sites in Florida.

	Time since treatment			
Species	Pretreatment	1 year	2 year	3 year
Aristida stricta	52 b*	36 a	49 b	58 c
Quercus laevis	11 a	0.5 b	0.5 b	1 b
Bare soil	0 a	32 c	7 b	4 b

* Row means sharing common postscripts are not significantly different (P<0.05)

Thus, it is possible to re-establish longleaf without drastically changing the understory community. Managers who want treatments with low risk to the understory and very little visible evidence of impact can utilize low rate hexazinone treatments and hand planting. Those mangers who wish to utilize machine planting can do so by using a combination of hexazinone and planting in scalped strips. Although this treatment exposes some bare soil and causes some disturbance of the understory, the effect is only temporary as the understory will recover rapidly.

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Restoring longleaf pine wiregrass ecosystems: plant cover, diversity and biomass following low-rate hexazinone application on Florida sandhills

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Restoring longleaf pine wiregrass ecosystems: plant cover, diversity and biomass following low-rate hexazinone application on Florida sandhills

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Abstract

A longleaf pine wiregrass ecosystem in the sandhills of north central Florida, upon which turkey oak gained domi. following a wildfire, was treated with low-rate (1.1 or 2.2 kg/ha) applications of the herbicide hexazinone during the 1991 growing season. All applications successfully reduced oak in the overstory and understory, mortality ranging from 83 to 93%. The declining competition from oaks was associated with progressive increases in foliar cover of wiregrass, all graminoids and forbs over time. Plant species diversity declined in the initial year, but recovered by the second growing season. Species richness increased overall, while evenness declined with the continuing expansion of wiregrass. Initial increases in the standing biomass of wiregrass did not persist beyond the second growing season. The broadcast application method exposed a greater number of understory plants to contact with hexazinone, resulting in initial declines in forb cover, species richness and diversity. Although recovery was noted in subsequent years, because of lower selectivity this broadcast application method is not recommended as a restoration technique. Spot application of liquid hexazinone was generally more selective in its effect upon the plant community. The 1.1 and 2.2 kg/ha application rates, while producing an initial year reduction in diversity and evenness, resulted in increases in the cover of all graminoids and forbs and the highest species richness. While both application rates are useful, the 2.2 kg/ha application is most effective in controlling woody plant competition and stimulating increases in wiregrass and is therefore recommended for restoring xeric sandhills and similar longleaf pine wiregrass ecosystems. © 1998 Elsevier Science B.V.

Keywords: *Pinus palustris* Mill.; *Aristida stricta* Michx.; *Quercus laevis* Walt.; *Sporobolus curtissii* (Vasey) Small ex. Scribn.; *Andropogon virginicus* L.; Herbicide

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Introduction

Longleaf pine (*Pinus palustris*) forests became established in northern Florida about 7800 yr ago (Watts et al., 1992) and during the ensuing 4000 yr spread throughout the southeast (Delcourt and Delcourt, 1987). The native range of longleaf pine encompasses an area along the Gulf and Atlantic Coastal Plains from Texas to Virginia, extending well into central Florida and the Piedmont and mountains of northern Alabama and Georgia (Stout and Marion, 1993). Throughout its range, longleaf pine occurs in forests, woodlands and savannas on a wide variety of sites, ranging from wet poorly-drained flatwoods to xeric sandhills and rocky mountain ridges (Boyer, 1990). In the western Gulf Coastal Plain, longleaf pine understories are commonly dominated by bluestem grasses (*Andropogon* spp. and *Schizachyrium* spp.) and, from Florida eastward, longleaf pine is typically associated with wiregrass (*Aristida stricta*), otherwise known as pineland threeawn, a prominent bunchgrass. A distinguishing characteristic of these ecosystems is an open, park-like stand structure (Harper, 1914; Laessle, 1942; Edmisten, 1963), known commonly as 'pine barrens' (Bartram, 1791). The plant communities contain few shrubs or hardwood trees, because of the attributes of understory grasses that facilitates the ignition and spread of fire during the growing season (Landers, 1991). In these ecosystems, longleaf pine and bunchgrasses function together as keystone species that facilitate but are resistant to fire (Platt et al., 1988; Noss, 1989). They exhibit substantial longevity and demonstrate nutrient and water retention to a degree that reinforce their site dominance and minimize change in the plant community following disturbance (Landers et al., 1995).

Longleaf pines rarely achieve their biological potential of 500 yr, because the longleaf pine wiregrass ecosystem evolved in an environment influenced by catastrophic disturbance, such as damaging tropical storms. Lightning is an important agent in individual tree mortality and the creation of small scale disturbance in longleaf pine stands (Komarek, 1968; Taylor, 1974). The rich biological diversity in this ecosystem is maintained by a combination of disturbance events and site factors. Variation in lightning strikes, tree mortality and animal interactions at local scales and wind storms, soils and hydrologic regimes at broader scales influence the landscape mosaic. Such disturbances across site gradients provide large living trees, snags, coarse woody debris, forest openings and hardwood thickets. Numerous organisms, including many species of plants, mammals, birds and reptiles are adapted to this disturbance-prone, yet largely stable ecosystem. The resulting high diversity of understory plants per unit area makes this one of the most species-rich plant communities outside the tropics (Peet and Allard, 1993).

Longleaf pine forests were at one time among the most extensive ecosystems in North America (Landers et al., 1995). These forests occupied over 37 million hà in the southeastern United States prior to European settlement (Frost, 1993). Since then, this ecosystem has undergone a progressive decline in occurrence to 8 million ha in 1935 (Wahlenberg, 1946), 2 million ha by 1975 and 1.5 million ha in 1985 (Kelly and Bechtold, 1990), with current levels estimated at less than 1.2 million ha. Several factors are responsible for this long-term decline, including clearing land for crops and pasture (Ewel, 1990) and conversion of longleaf pine forests to other southern pines such as loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii*). Another major factor contributing to this decline has been interruption of natural fire regimes, resulting from forest fire protection policies implemented during the 1920s. This interruption impeded natural regeneration of longleaf pines and allowed invasion of longleaf sites by hardwood trees and more aggressive southern pines, including loblolly pine, slash pine and sand pine (*Pinus clausa*). Area reductions are continuing for stands in every diameter class below 41 cm (Kelly and Bechtold, 1990), therefore, most remaining longleaf pine forests appear to be aging without replacement. With this ecosystem now occupying only about 4% of its original extent, habitat reduction has resulted in the increased rarity of 191 taxa of vascular plants (Hardin and White, 1989; Walker, 1993) and several terrestrial vertebrate species.

Concern about loss of these unique forests (Means and Grow, 1985; Noss et al., 1995) has stimulated discussion regarding how to effectively restore the longleaf pine wiregrass ecosystem. Since longleaf pine still occurs over most of its natural range, albeit in isolated fragments, it is reasonable to conclude

that restoration of this ecosystem is feasible (Landers et al., 1995). Success in such an endeavor will depend on identification of the ecological processes needed to create favorable conditions for a gradual expansion of longleaf pine and wiregrass occupancy. The use of fire as an ecological process necessary for the maintenance of fire-dependent natural communities, especially growing season fires where appropriate to promote diversity and stability, has been suggested (Frost, 1990; Streng et al., 1993). Natural regeneration methods employing a regime of frequent fire are compatible with maintenance of the longleaf pine wiregrass ecosystem (Boyer and White, 1990). Mechanical site preparation methods have also been proposed, but must be carefully applied to avoid adverse effects upon wiregrass (Clewell, 1989; Outcalt and Lewis, 1990; Outcalt, 1993). Herbicide application has also been suggested as a means of selectively reducing competing vegetation, favoring expansion of longleaf pine and wiregrass, minimizing physical disturbance of the soil and avoiding displacement of site nutrients (Wilkins et al., 1993a,b; Outcalt and Brockway, 1993; Brockway and Outcalt, 1994).

Longleaf pine wiregrass ecosystems in xeric sandhills, commonly referred to as 'high pine land,' grow on deep coarse textured soils with limited available water and nutrients (Kalisz and Stone, 1984; Myers, 1990). In central Florida, much of this type has been converted to citrus groves (Myers and White, 1987; Ewel, 1990), and elsewhere, pine cutting has left much of the area occupied by turkey oak (*Quercus laevis*) and related scrub oaks (Burns and Hebb, 1972; Myers and White, 1987). Harvest of longleaf pine timber and fire suppression have also encouraged invasion by sand pine and associated scrub oaks (Myers, 1990). The sandhills component of the longleaf pine wiregrass ecosystem is regarded by many as an endangered community (Means and Grow, 1985). The remaining longleaf pine wiregrass sites in the sandhills typically occur as 'pine islands' (Rawlings, 1933; Laessle, 1958) surrounded by a landscape dominated by sand pine forests or lands converted to agriculture and urban development (Kalisz and Stone, 1984; Myers, 1990). Many of these islands contain degraded longleaf pine wiregrass lands currently occupied by oaks and could benefit substantially from restoration treatments.

A degraded longleaf pine wiregrass ecosystem, that had been invaded by turkey oak and scrub oaks following timber harvest and wildfire in the sandhills of north central Florida, was treated with low-rates of hexazinone. In measuring the post-treatment changes in vascular plant cover, diversity and productivity over several years, the objectives of this study were to (1) Evaluate hexazinone as a selective agent for controlling competition from invasive woody vegetation (primarily oaks), (2) Measure the effects of hexazinone on non-target plant species (principally wiregrass, other grasses and forbs), (3) Quantify differential effects resulting from the methods of hexazinone application, and (4) Determine whether low-rate application of hexazinone can serve as a viable treatment for restoring longleaf pine wiregrass ecosystems in sandhills and similar environments.

2. Methods and materials

2.1. Study site

This experiment was conducted on the Lake George Ranger District of the Ocala National Forest in Marion County, north central Florida. The study site is located on Riverside Island (29°28′N, 81°50′W), one of largest remaining longleaf pine wiregrass areas along the Mount Dora Ridge (Laessle, 1958). The climate is humid subtropical (Chen and Gerber, 1990). Annual precipitation is abundant, averaging 1300 mm, with more than half of this arriving during the June to September season (Aydelott, 1966). Average monthly temperatures range from 21°C to 28°C for the April to October period and from 14°C to 19°C for November to March (NOAA, 1930–1985).

The study area is approximately 49 m above sea level in a sandhill landscape with rolling topography, devoid of surface drainages and characterized by closed depressions. Surface slopes at the study site range from nearly level (0 to 2%) to moderately inclined (up to 8%). The surface geology is underlaid by a bedrock of Ocala Limestone, a relatively pure calcium carbonate deposit dating to the Eocene, approximately 40,000,000 yr old (Brooks, 1972). This limestone, also known as the Crystal River Fo

tion, is largely responsible for the karst nature of the locale, forming numerous sinkholes and large springs (Brown et al., 1990). Above this limestone is the Citronelle Formation (Laessle, 1958), which occurs continuously throughout the central ridge of Florida over a distance of 240 km (Pirkle et al., 1963). The Citronelle Formation is composed of sand and gravel intermixed with clay (Brooks, 1972). Over this formation are aeolian dunes which developed during periods of climate and sea level fluctuation in the Pleistocene (Kalisz and Stone, 1984). Lands higher than 30 m above mean sea level remained above the ocean surface during the entire Pleistocene (Alt and Brooks, 1965).

Surface deposits are dominated by sands 2 to 3 m thick overlying the stratified sand, gravel and kaolinitic clays of the Citronelle Formation (Laessle, 1958). Soils developed in parent materials devoid of easily weathered primary minerals and consist of quartz sand with small amounts of iron and titanium (Kalisz and Stone, 1984). Clay-sized particles are primarily quartz, kaolinite, hydroxy-aluminum interlayered minerals and gibbsite (Carlisle et al., 1978). Soils present on the site are excessively drained sols and typically exhibit little if any profile elopment (Brown et al., 1990). The predominant soil is the Astatula series (Typic Quartzipsamments, hyperthermic) which is low in organic matter, nutrients and water holding capacity (Aydelott et al., 1975). The terms 'wet desert' and 'desert in the rain' are commonly used to describe this environment since, while precipitation is abundant, this soil can become extremely dry within one week without substantial rainfall (Outcalt, 1993).

Vegetation on this 'high pine' sandhills area was previously dominated by an overstory of longleaf pine, within a larger matrix of sand pine (Laessle, 1958; Myers and White, 1987; Myers, 1990). Evidence suggests that these have been the two principal ecosystems in this locale for the past 5000 yr (Watts, 1971; Watts and Hansen, 1988). However, the degraded nature of the study site was reflected in the absence of longleaf pine and predominance of turkey oak with lesser amounts of sand pine, Chapman oak (*Quercus chapmanii*), sand live oak (*Quercus geminata*) and myrtle oak (*Quercus myrtifolia*). Associated understory shrubs included dwarf live oak (*Quercus minima*), saw-palmetto (*Serona repens*), scrub palmetto (*Sabal etonia*), rosemary (*Ceratiola ericoides*), crookedwood (*Lyonia ferruginea*), wax myrtle (*Myrica cerifera*), prickly pear (*Opuntia humifusa*), shiny blueberry (*Vaccinium myrsinites*), gopherapple (*Licania michauxii*), Adam's needle (*Yucca filamentosa*) and coontie (*Zamia pumila*). Wiregrass, Curtiss dropseed (*Sporobolus curtissii*), broomsedge bluestem (*Andropogon virginicus*), lopsided indiangrass (*Sorghastrum secundum*), panic grass (*Panicum* spp.), sandgrass (*Triplasis* spp.) and yellow nutsedge (*Cyperus recurvata*) were among the prominent graminoids. Forbs commonly observed included partridge-pea (*Cassia chamaecrista*), treadsoftly (*Cnidosculos stimulosus*), doveweed (*Crotan argyranthemus*), buckwheat (*Eriogonum tomentosum*), dogfennel (*Eupatorium compositafolium*), milkpea (*Galactia* spp.), St. Johnswort (*Hypericum* spp.), wild indigo (*Indigofera caroliniana*), silverthread goldaster (*Pityopsis graminafolia*), wireweed (*Polygonella gracilis*), blackroot (*Pterocaulon virgatum*), dollarweed (*Rhynchosia* spp.), blue-eyed grass (*Sisyrinchium solstitiale*) and queens delight (*Stillingia sylvatica*).

2.2. Site history and experimental treatments

The study area was occupied by a second-growth longleaf pine forest that was harvested for timber and replanted with longleaf pine seedlings in 1971. During the winter of 1989, the young longleaf pine trees were killed by a lightning-ignited wildfire. The numerous oaks present vigorously resprouted and, in the absence of a longleaf pine overstory, quickly gained dominance on this site. It was soon obvious that this longleaf pine site would be lost to rapidly growing turkey oak.

In April 1991, a randomized complete block experimental design was established on the study site. Four experimental treatments were replicated in five blocks distributed across the 230 ha study area. Each 1 ha (100 m × 100 m) block contained four 0.25 ha (50 m × 50 m) plots. All treatments were one-time applications of hexazinone applied in May 1991 following initiation of plant growth. Treatments included (a) 1.1 kg a.i. hexazinone/ha applied as a granular formulation that was broadcast evenly upon the soil, (b) 1.1 kg a.i. hexazinone/ha applied as a liquid that was sprayed in a 2 m × 2 m spot-grid on

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the ground, (c) 2.2 kg a.i. hexazinone/ha applied as a liquid that was sprayed in a 2 m × 2 m spot-grid upon the soil and (d) control that received no hexazinone. Since liquid hexazinone applied at these low rates may not give the desired level of oak reduction during dry periods, treatment was timed so that rainfall occurred within two weeks following application, to facilitate efficient uptake by the widely spreading root systems of woody plants. In February 1992, longleaf pine seedlings were planted by hand on the site to promote the eventual development of a longleaf pine overstory and recovery of the ecosystem.

Hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1*H*,3*H*)-dione] is one of several herbicides currently registered for forestry use in the United States and is commercially available as Velpar ULW™, Velpar L™ (E.I. Du Pont De Nemours) and Pronone 10G™ (Pro-Serve). Recommended application rates for site preparation range from 2.0 to 6.7 kg hexazinone/ha (E.I. Du Pont De Nemours). Rates used in our study are quite low and similar to those used to restore understory plants elsewhere in xeric sandhills (Wilkins et al., 1993b). These are characterized as trial rates for selective uses (Beste, 1983).

Hexazinone is a triazine herbicide that is absorbed from soil solution by plant roots and distributed through the transpirational stream to its site of action in the chloroplasts (Ashton and Crafts, 1973). There the compound binds to a specific protein and inhibits its ability to mediate electron transport, the Hill reaction (Van Rensen, 1989). This results in a build-up of triplet state chlorophyll which generates singlet oxygen (Dodge, 1982). Singlet oxygen peroxidizes cell membrane lipids and the affected plant dies from oxidative stress (Balke, 1987; Bartels, 1987). Some species have greater abilities to metabolize the compound before it reaches the site of action (McNeil et al., 1984; Jensen and Kimball, 1990), thereby imparting some degree of tolerance. While blueberries are fairly tolerant (Zutter and Zedaker, 1988), oaks, sweetgum (*Liquidambar styraciflua*) and sumac (*Rhus* spp.) are quite susceptible to hexazinone (Neary et al., 1981; Griswold et al., 1984; Miller, 1984; Zutter and Zedaker, 1988).

Hexazinone is highly soluble in water (33,000 ppmw at 25°C) and is potentially very mobile in subsurface solution (Neary et al., 1983; Bouchard et al., 1985). Following applications of 1.68 kg a.i./ha, off-site movement of hexazinone has been observed to be minimal and of low toxicity risk to adjacent aquatic ecosystems (Neary et al., 1983). Aquatic macroinvertebrates did not exhibit major changes in community composition (Mayack et al., 1982). Following hexazinone applications of 2 kg/ha on sandy loam sites in Arkansas, off-site movement was 2–3% and < 0.1% of that applied was returned to the forest floor upon oak defoliation (Bouchard et al., 1985). Persistence in forest soils is relatively short-lived (Lavy et al., 1989). Half-lives of hexazinone in silt loam soils in Delaware, Illinois and Mississippi have been reported at 1, 2 and 6 months, respectively (Rhodes, 1980). In Alabama, half-lives were 4–6 weeks in clay soil and < 4 weeks in loamy sand (Sung et al., 1981).

2.3. Measurements

In May 1991, plant cover and biomass were measured on all plots to assess the pretreatment stat the plant community. Repeated post-treatment measurements were then completed in September 1991, 1992 and 1993 to ascertain the ecological changes resulting from hexazinone application. Total foliar cover (vertical projection of canopy) of all plant species was measured by line-intercept method along two permanent 20 m line transects (oriented north and south) within each treatment plot. Identification and nomenclature for plant species were consistent with taxonomic authorities (Fernald, 1950; Gleason, 1952; Hitchcock, 1971; Duncan and Foote, 1975; Bell and Taylor, 1982; Wunderlin, 1982; Clewell, 1985; Kurz and Godfrey, 1986; Godfrey, 1988; Foote and Jones, 1989; Grimm and Kartesz, 1993; Hall, 1993). Wiregrass biomass was measured on two randomly selected 1 m × 1 m (1 m^2) sampling subplots within the larger treatment plots. The standing biomass of all wiregrass was destructively sampled by clipping at the groundline and placing samples in paper bags.

All wiregrass samples were sorted into living (green) and nonliving (brown) components, dried to a constant mass in a force draft oven at 85°C for 24 h and weighed. These data were then used to construct productivity estimates for wiregrass relati

hexazinone treatment. Data on the foliar cover of each species were summarized as estimates for each plot and analyzed by hexazinone treatment and change over time. Foliar cover data were used as importance values to compute numerous diversity indices (Ludwig and Reynolds, 1988).

Species richness (total number of species present) and evenness (how abundance is distributed among species) are the two principal components of diversity. Species richness is frequently characterized by the number of species present (N_0), abundant species (N_1), very abundant species (N_2). Margalef species richness (R_1) and Menhinick species richness (R_2). Evenness (approaching one when all species are of equal abundance and declining toward zero when few species dominate) can be described by the evenness index of Pielou (E_1), evenness index of Sheldon (E_2), evenness index of Heip (E_3), evenness index of Hill (E_4) and the modified ratio of Hill (E_5). Diversity indices combine species richness and evenness components into a single numeric value. The most commonly used indices of diversity are the diversity index of Shannon (H') and the diversity index of Simpson (λ).

All data for dependent variables were summarized as estimates of the mean for each experimental plot. Each plot mean was then used to estimate the mean and variance for each of the four hexazinone treatments. For each dependent variable, a comparison of differences among experimental treatments and over the time sequence of repeated measurements was then undertaken. A repeated measures ANOVA, using initial conditions as covariates, was used to evaluate time and treatment effects and interactions. Treated responses were compared to the untreated response using a set of three pairwise contrasts. The trend over time after treatment was analyzed using orthogonal polynomials. Because initial conditions were not significantly correlated to the post-treatment response of woody plants, an analysis of the time and treatment interaction was substituted for the analysis of covariance. Statistical analysis of the time and treatment interaction for computed diversity indices was completed using the bootstrap technique PROC MULTTEST in SAS (Efron and Tibshirani, 1993; Westfall and Young, 1993; SAS Institute, 1996). Adjusted p-values, which maintain a constant Type I error across the full range of comparisons, were used to determine significant differences among means (10,000 bootstrap iterations were used). Except otherwise noted, a probability level of 0.05 was used to discern significant differences reported.

3. Results

3.1. Foliar cover changes

The foliar cover of turkey oak declined dramatically during the 1991 growing season following hexazinone treatment (Fig. 1). The broadcast and liquid spot 1.1 kg/ha applications caused an average 83% decrease in turkey oak cover and the liquid spot 2.2 kg/ha treatment resulted in a 92% decline (Table 1). These foliar cover reductions for turkey oak persisted throughout the 1992 and 1993 growing seasons without evidence of any significant recovery relative to the control. During this same period, turkey oak on control plots continued to extend its dominance, doubling its foliar cover. A similar pattern was noted for all oak species combined. Hexazinone application significantly reduced the foliar cover of all oaks, while their cover essentially doubled on untreated plots. The effects of hexazinone treatment on shrubs were less pronounced. Only the 2.2 kg/ha application rate caused a significant decline in shrub cover. Overall woody plant cover on the control plots increased by 175% between 1991 and 1993. All hexazinone application rates appear to have curtailed the rapid ascent of oaks. However, only the liquid spot 1.1 and 2.2 kg/ha treatments resulted in significant reductions of total woody plant cover 2 yr after application.

Foliar cover of wiregrass increased following hexazinone application at all rates (Table 1). While wiregrass cover on control plots expanded only 18% during the 1991 growing season, increases in wiregrass cover on liquid spot treatment plots ranged from 29 to 58%. Although wiregrass cover increased over time more rapidly on hexazinone treated plots than on untreated plots, when adjusted for initial conditions these differences were not significant and thus, largely time driven ($p < 0.05$). The 20% increase on broadcast plots was not significant when compared with controls.

During the 1992 and 1993 growing seasons, wiregrass cover continued to expand, showing increases

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Fig. 1. Contrast in overstory oak cover between hexazinone treated area (foreground) and untreated control area (background) two growing seasons following treatment.

for all hexazinone treatments. While wiregrass cover was nearly comparable on all applications, ranging from 60 to nearly 70% foliar cover, the largest overall increase (89%) and only significant increase ($p = 0.09$) was observed for the 2.2 kg/ha treatment. By the second and third growing seasons, wiregrass on plots receiving the broadcast 1.1 kg/ha treatment expanded to coverage comparable to that found on the other treatments. The smallest increase in wiregrass cover was noted on control plots where oak canopies continued to expand.

The foliar cover response pattern for all graminoids combined corresponds to that of wiregrass (Table 1). Significant linear increases in cover occurred over time; however, there were no significant differences among hexazinone treatments. Following application, grasses expanded into growing spaces adjacent to and beneath the skeletal crowns of dead trees and shrubs. Significant increases through time in the foliar cover of forbs were observed, but no significant differences among hexazinone treatments were noted. During the 1991 growing season, the broadcast 1.1 kg/ha application caused a 56% decline in forb cover. However, during the 1992 and 1993 growing seasons, forb cover recovered on this treatment to the highest overall levels, approaching 15%. The liquid spot 1.1 and 2.2 kg/ha treatments resulted in progressive increases in forb cover during all three growing seasons, eventually exceeding 10%.

3.2. Plant diversity dynamics

A total of 87 plant species were found on the Riverside Island study plots (Table 2). With few tree species present in this plant community, turkey oak dominated both overstory and understory prior to hexazinone application. Following treatment, no tree species was dominant in the overstory. Longleaf pine seedlings planted during the winter of 1992 appeared positioned to eventually form the new overstory in the absence of substantial competition from the declining oaks. Although there was a moderate number of shrubs on the site, turkey oak sprouts dominated this layer prior to hexazinone application. Following treatment, the most prominent shrubs were rosemary, crookedwood, shiny blueberry and gopherapple. The variety of graminoids was obvious; however, only a few such as *Andropogon*, *Aristida* and *Sporobolus*

Table 1
Foliar cover response to hexazinone application (% cover)

Hexazinone (kg/ha)	0.0	1.1 broadcast	1.1 spot	2.2 spot	Adjusted Mean[a]
Turkey oak					
Spring 1991	5.5	6.2	12.2	13.6	
Fall 1991	5.6	0.6	2.2	0.9	3.3[d]
Fall 1992	5.0	1.0	1.1	1.7	3.2[d]
Fall 1993	10.4	1.6	1.3	2.4	4.9[d]
Adjusted Mean[a]	10.8	1.1[b]	1.6[b]	1.7[b]	
All oaks					
Spring 1991	5.6	6.2	12.5	14.0	
Fall 1991	5.7	0.6	2.3	2.1	3.7[d]
Fall 1992	5.1	1.0	1.1	1.8	3.3[d]
Fall 1993	10.6	1.6	1.9	3.6	5.5[d]
Adjusted Mean	11.3	1.1[b]	1.8[b]	2.5[b]	
All shrubs					
Spring 1991	4.4	6.6	8.5	11.9	
Fall 1991	4.4	5.4	4.1	3.3	5.0[d]
Fall 1992	5.5	6.3	7.5	3.9	6.4[d]
Fall 1993	7.0	8.4	7.7	5.5	7.8[d]
Adjusted Mean	8.7	7.5	6.0	3.4[b]	
All woody plants					
Spring 1991	11.4	14.8	22.3	26.8	
Fall 1991	11.1	9.0	8.6	7.5[b]	
Fall 1992	12.5	11.8	11.0	12.1[b]	
Fall 1993	28.0	18.8	13.5[b]	16.3[b]	
Wiregrass					
Spring 1991	54.9	48.5	44.0	36.1	
Fall 1991	64.7	58.6	56.3	56.1	58.9[d]
Fall 1992	65.3	64.8	59.5	62.9	63.1[d]
Fall 1993	67.4	68.5	62.9	67.1	66.5[d]
Adjusted Mean	57.8	61.7	61.2	70.7[c]	
All graminoids					
Spring 1991	58.8	54.8	50.4	51.0	
Fall 1991	68.0	67.2	64.1	65.6	65.8[d]
Fall 1992	69.6	72.5	73.5	76.1	72.5[d]
Fall 1993	72.7	74.0	74.5	75.7	73.8[d]
Adjusted Mean	65.6	70.1	74.5	72.7	
All forbs					
Spring 1991	4.5	7.2	5.0	3.0	
Fall 1991	7.3	3.2	8.5	5.3	6.1[d]
Fall 1992	9.3	12.8	10.0	9.1	10.3[d]
Fall 1993	7.4	14.8	10.8	10.1	10.8[d]
Adjusted Mean	8.6	7.7	9.6	10.3	

[a]Post-treatment mean adjusted by analysis of covariance.
[b]Significantly different from untreated control plots. $p \leq 0.05$.
[c]Significantly different from untreated control plots. $p \leq 0.10$.
[d]Significant linear change through time following application. $p \leq 0.05$.

Table 2
Plant species pr

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Trees	P
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Shrubs	A
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Table 2
Plant species present on the Riverside Island study site, Ocala NF

	Scientific name	Common name
Trees	*Pinus clausa*	sand pine
	Pinus palustris	longleaf pine
	Quercus chapmanii	Chapman oak
	Quercus geminata	sand live oak
	Quercus laevis	turkey oak
	Quercus myrtifolia	myrtle oak
Shrubs	*Asimina incarna*	pawpaw, polecat bush
	Asimina obovatum	flag pawpaw
	Baccharis haliminifolia	groundsel tree
	Ceratiola ericoides	rosemary
	Garberia fruiticosa	garberia
	Licania michauxii	gopherapple
	Lyonia ferruginea	crookedwood
	Myrica cerifera	wax myrtle
	Opuntia humifusa	prickly pear
	Quercus minima	dwarf live oak
	Sabal etonia	scrub palmetto
	Serona repens	saw-palmetto
	Smilax auriculata	greenbrier, catbrier
	Smilax bona-nox	greenbrier, catbrier
	Vaccinium myrsinites	shiny blueberry
	Vaccinium darrowii	groundbush blueberry
	Yucca filamentosa	Adam's needle
	Zamia pumila	coontie
Graminoids	*Andropogon floridanus*	Florida bluestem
	Andropogon gyrans	bluestem
	Andropogon tracyi	Tracy's bluestem
	Andropogon virginicus	broomsedge bluestem
	Aristida lanosa	woolysheath threeawn
	Aristida purpurescens	arrowfeather threeawn
	Aristida stricta	wiregrass, pineland threeawn
	Bulbostylis warei	hairsedge
	Cyperus recurvata	yellow nutsedge
	Digitaria villosa	shaggy crabgrass
	Hypoxis spp.	star grass
	Panicum spp.	panic grass
	Rhynchospora spp.	beakrush
	Scleria spp.	nutgrass
	Sorghastrum secundum	lopsided indiangrass
	Sporobolus curtissii	Curtiss dropseed
	Sporobolus junceus	pinedrop threeawn
	Triplasis spp.	sandgrass
Forbs	*Agalinus fasciculata*	figwort
	Balduina angustifolia	yellow buttons
	Baptisia lecontei	false indigo
	Bonamia grandiflora	bonamia
	Cassia chamaecrista	partridge-pea
	Cladonia spp.	lichen, reindeer moss
	Clitoria mariana	butterfly pea
	Cnidosculos stimulosus	treadsoftly

Table 2 (continued)

Scientific name	Common name
Conyza canadensis	Horseweed
Coreopsis spp.	tickseed
Crotalaria rotundifolia	rattelbox
Croton argyranthemus	doveweed
Croton punctatus	beach tea
Desmodium spp.	tick trefoil
Eriogonum tomentosum	buckwheat
Eupatorium album	white thoroughwort
Eupatorium compositafolium	dogfennel
Euthamia minor	false goldenrod
Galactia elliottii	milkpea
Galactia regularis	milkpea
Galactia volubilis	milkpea
Hieracium gronovii	hawkweed
Hypericum spp.	St. Johnswort
Indigofera caroliniana	wild indigo
Lactuca spp.	wild lettuce
Lechea spp.	pineweed
Lespediza hirta	bush clover
Liatris spp.	blazing star
Linaria spp.	toadflax
Lycopodium spp.	clubmoss
Lygodesmia aphylla	roserush
Palafoxia feayi	palafoxia
Palafoxia integrifolia	palafoxia
Pityopsis graminafolia	silverthread goldaster
Polygala lewtonii	batchelor's button
Polygonella gracilis	wireweed
Pterocaulon virgatum	blackroot
Rhynchosia difformis	dollarweed
Rhynchosia reniformis	dollarweed
Silphium asteriscus	rosin-weed
Sisyrinchium solstitiale	blue-eyed grass
Solidago spp.	goldenrod
Stillingia sylvatica	queens delight
Tragia urens	tragia
Trichostema dichotomum	blue curls

Total plant species = 87.

appeared to be abundant. Yellow nutsedge, panic grass and sandgrass were well represented on some portions of the site. Forbs seemed to be present in great variety, but they typically persisted at low levels, approximating 5% cover, prior to hexazinone treatment.

During the first growing season following application, species richness (N_0) was generally unaffected by hexazinone, with nonsignificant increases in the number of plant species observed on control plots

Table 3
Plant species richness, diversity and evenness responses to hexazinone application

Hexazinone (kg/ha)	0.0	1.1 Broadcast	1.1 Spot	2.2 Spot
Number of species				
Spring 1991	15.0	18.2	16.0	17.0
Fall 1991	17.4	13.2[a]	19.6	17.6
Fall 1992	18.4	17.6	20.8	21.6
Fall 1993	17.8	18.2	20.4	21.2
Shannon's index				
Spring 1991	1.11	1.50	1.51	1.51
Fall 1991	1.03	0.99[a]	1.29	1.20
Fall 1992	1.23	1.37	1.54	1.44
Fall 1993	1.33	1.39	1.47	1.43
Hill's index				
Spring 1991	0.60	0.59	0.64	0.69
Fall 1991	0.61	0.69	0.59[b]	0.58[b]
Fall 1992	0.56	0.63	0.56[b]	0.55[b]
Fall 1993	0.61	0.62	0.57[b]	0.54[b]

[a]Significantly different from untreated control plots, $p \leq 0.05$.
[b]Significant change through time following treatment, $p \leq 0.05$.

and those receiving the liquid spot treatments (Table 3). However, the 1.1 kg/ha broadcast treatment resulted in a significant 28% decline in richness, from 18 species to 13 species in this period. During the 1992 and 1993 growing seasons, plant species richness had fully recovered on the broadcast treated plots and continued to increase on the liquid spot treated plots, exceeding 20 species present. Plots receiving the 2.2 kg/ha treatment contained as many as 22 species, while control plots typically supported no more than 18 species. Computations for the Margalef richness (R_1) and Menhinick richness (R_2) indices closely corresponded to these trends, as do the indices for abundant species (N_1) and very abundant species (N_2).

All hexazinone treatments caused a decline in plant species diversity during the first growing season following application (Table 3). The largest and only significant decrease in the Shannon diversity index (H'), from 1.50 to 0.99, was observed on the broadcast treated plots. Alpha diversity declines for the liquid spot applications were typically from 1.51 to 1.25. Broadcast values were comparable to those on control plots and liquid spot values exceeded those on controls. During the 1992 and 1993 growing seasons, species diversity recovered on all hexazinone treated plots, approaching values between 1.37 and 1.54. While diversity on the controls continued to rise over time from an initially low value of 1.11, Shannon index values approaching 1.33 remained less than those on hexazinone treated plots. The Simpson diversity index (λ), a reciprocal computation, showed an overall similar trend.

Hexazinone application also appeared to affect plant species evenness during the first growing season following application (Table 3). The broadcast treatment caused a nonsignificant increase in the Evenness Index of Hill (E_4), from 0.59 to 0.69. The liquid spot treatments resulted in a significant decline in evenness, from 0.64 to 0.59 for the 1.1 kg/ha application and from 0.69 to 0.58 for the 2.2 kg/ha application. During the 1992 and 1993 growing seasons, evenness declined on the broadcast treated plots to levels comparable to those on controls. The liquid spot treatments, however, produced significant declines in plant species evenness that continued throughout the study period. Computations for the other evenness indices (Pielou, E_1; Sheldon, E_2; Heip, E_3; Modified Hill, E_5) indicated similar trends.

3.3. Wiregrass biomass

Standing biomass values for wiregrass were highly variable over the period of study and thus, the trends reported are largely nonsignificant (Fig. 2). Pretreat-

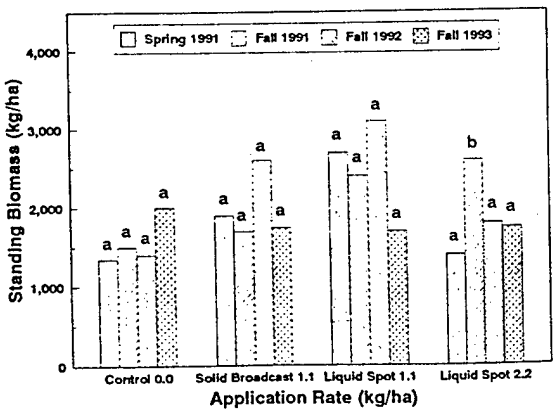
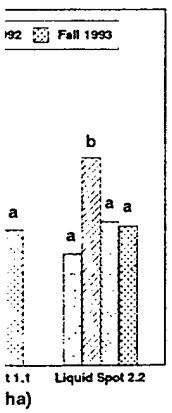


Fig. 2. Standing biomass of wiregrass following hexazinone application (means within the same treatment associated with a different letter are significantly different at the 0.05 level).

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ment biomass typically ranged from 1400 to 1900 kg/ha; however, 2700 kg/ha was present on the liquid spot 1.1 kg/ha treatment plots. During the first growing season following application, only the liquid spot 2.2 kg/ha treatment produced a significant increase in wiregrass biomass. This increase, from 1400 to 2600 kg/ha, represented an 86% rise in wiregrass biomass during 1991. In the 1992 growing season, wiregrass biomass increased to 2600 kg/ha on the broadcast treatment and to 3100 kg/ha on the liquid spot 1.1 kg/ha treatment. However, these trends were not significant. During this season, biomass on the liquid spot 2.2 kg/ha treatment declined to approximate pretreatment levels. By the end of the 1993 growing season, biomass on all hexazinone treatments approximated that on controls, about 2000 kg/ha or less. The proportion of living green tissue (as contrasted with dead brown tissue) declined overall from a pretreatment value of 46% to a post-treatment level of 35%. There were, however, no significant differences among treatments.

4. Discussion

4.1. Foliar cover changes

Low-rate hexazinone application on these xeric sandhills nearly eliminated the turkey oak and related oaks that had begun to dominate this longleaf pine wiregrass ecosystem. This result is similar to that reported for higher-rate hexazinone applications of 1.7, 3.4 and 6.8 kg/ha in sandhill environments (Wilkins et al., 1993a) and low-rate applications of 0.3, 0.6 and 0.9 kg/ha on well-drained uplands (Long and Flinchum, 1992). Turkey oak mortality rates ranging from 83 to 93% indicate that low-rate hexazinone application may be a useful treatment in selectively shifting the balance of competition for water and other site resources to favor desirable plant species in the understory and developing overstory (Wilkins et al., 1993b; Brockway and Outcalt, 1994). While shrub cover was unaffected by all but the highest treatment rate, the overall decline of woody plants appeared to have created opportunity for expansion of plants already occupying the site and liberated microsites where additional species might colonize subsequent to successful dispersal and germination.

The method of hexazinone application (broadcast vs. spot-grid) may have had some degree of differential effect on understory plant species. While not impairing the growth response of wiregrass or other graminoids, the broadcast application method appears to have adversely affected forb cover during the first growing season, causing a 56% decrease. The broadcast method distributes granules of hexazinone evenly upon the ground across the entire plot. This places nearly all plants growing on the plot in direct physical contact with hexazinone, thus, a higher probability of assimilation and mortality. However, in subsequent years forb cover recovered to the highest observed levels, reaching nearly 15%. Thus, low-rates of hexazinone applied by the broadcast method may initially depress and subsequently, stimulate the growth of some understory plants.

In contrast, the spot grid application method deposits a 2 ml dose of liquid on the soil surface in a 2 m × 2 m grid pattern, thus creating numerous large interstitial zones that are free of hexazinone. As th crowns and root systems are typically not wide spreading, the probability of any individual plant being directly 'hit' by the spot is quite low, thus most understory plants escaped the effects of this type of herbicide treatment. Individual clusters of wiregrass contacted by spot treatment, were noted to decrease their proportion of green to brown tissue. However, rarely was an entire cluster observed to completely succumb to the herbicide. The overall danger to understory plants when using the spot-grid application technique is lower, yet the mortality of targeted overstory species, because of their widely spreading root systems, is at least as great as that resulting from the broadcast application method.

Spot treatments resulted in progressive linear increases in wiregrass, all graminoids and forb cover throughout the first, second and third growing seasons following application. The highest mortality rate for turkey oak and the largest proportional and only significant increase in wiregrass cover were observed on plots receiving the 2.2 kg/ha treatment. This relationship is indicative of wiregrass having been released from competition with the declining turkey oak. Progressive increases in grass and forb cover on plots receiving 1.1 and 2.2 kg/ha identif

both liquid spot application rates as useful treatments for ecosystem restoration.

4.2. Plant diversity dynamics

Sandhills have been characterized as ecosystems dominated by scrub vegetation of low species diversity, whose structure and function reflect adaptations for survival in an environment characterized by seasonal water deficits, periodic fires and low soil fertility (Snedaker and Lugo, 1972). However, the presence of 87 plant species on this site is typical of the high vascular plant diversity of longleaf pine ecosystems (Peet and Allard, 1993). Plant species diversity is largely determined by interspecific competition interacting with site productivity, microsite heterogeneity and disturbance regimes (Tilman, 1982). Herbaceous plant diversity is reported to initially increase and subsequently decline to predisturbance levels on sites disturbed by prescribed fire, tree harvest or site preparation (Swindel et al., 1984; Lewis et al., 1988). The action of hexazinone, causing selective mortality among different plant groups, altered the competitive relationships among species and thus, plant diversity dynamics.

The significant decline in plant species diversity during the first growing season following broadcast treatment was no doubt a result of the application method, which brought hexazinone into close physical contact with nearly all plants on the treated plot. This initial year decrease in diversity was closely related to the decline in plant species richness and can be largely attributed to decreases in turkey oak and several forbs. The corresponding increase in species evenness indicated that the fewer species remaining, and available site resources, were more equitably distributed across the site. Thus, the effect of broadcast applied hexazinone on the plant community appeared generalized over the entire plot during the first growing season following treatment. The subsequent recovery of species richness and diversity was largely related to the resurgence of forb species during later growing seasons. Species evenness was seen to decline as wiregrass increased during the 1992 and 1993 growing seasons. This overall response pattern is similar to that reported for single applications of herbicide used in site preparation, where initial depression of diversity is followed by recovery along a trajectory similar to that of an untreated site (Neary, 1991).

Nonsignificant declines in plant species diversity were observed for both liquid spot hexazinone treatments during the initial growing season following application. Species richness was unaffected by treatment, due to the non-uniform manner in which spot application distributes hexazinone, thus, impacting fewer understory plants than broadcast application. The diversity decline was largely attributed to significant decreases in evenness among plant species. Declining plant species evenness resulted from the increasing dominance of wiregrass following reduction of turkey oak. Increases in plant species diversity in subsequent growing seasons was largely a product of increasing species richness. Over time, increasing forbs and grasses accounted for this trend on the 1.1 and 2.2 kg/ha treatments, where forbs persisted at about 4% cover prior to application. This progressive response by forbs is unlike that reported in other xeric sandhills ecosystems where higher application rates (1.7, 3.7 and 6.8 kg/ha) resulted in declining herbaceous plant diversity (Wilkins et al., 1993b). Plant species evenness for the liquid spot treatments continued to significantly decline, as wiregrass and other grasses gained increasing dominance over the course of study. These findings concur with reports of plant species numbers being unchanged or slightly higher during the second and subsequent growing seasons following herbicide application (Blake et al., 1987).

4.3. Wiregrass biomass

The highly variable response of wiregrass to hexazinone application appears characteristic of a plant species with xerophytic adaptations that allow it to persist in the droughty sandhills environment (Stalter, 1984). A slow growth rate and limited investment in propagules constitute a conservative strategy that contributes to long-term survival (Grime, 1979). The 1.1 kg/ha applications, whether by broadcast or spot method, appeared insufficient to stimulate significant increases in wiregrass biomass. Neither the decline in turkey oak cover (83%) or forb cover (56%) during the first growing season affected biomass production. This finding is not surprising, considering the naturally slow growth rate of wiregrass. The

nonsignificant increases during the 1992 growing season may be attributed to lag-time effects, with wiregrass requiring at least two seasons to respond to reduced competition. However, declining biomass during the 1993 growing season indicates the absence of a genuine growth response by wiregrass to hexazinone applications at this low-rate.

By contrast, the 2.2 kg/ha treatment stimulated a significant increase (86%) in wiregrass growth during the initial growing season following application. The significant reduction (93%) in turkey oak cover very likely contributed to this increase in wiregrass standing biomass. Considering the typically slow growth rate of wiregrass, it is surprising that such a response was observed during the first post-treatment growing season. However, wiregrass is known to respond relatively quickly to the increased availability of site resources (Parrott, 1967).

4.4. Restoring the ecosystem with hexazinone

Decades of logging, reduction of regeneration by hogs, interruption of natural fire regimes and introduction of frequent low intensity winter burning which eliminated pine seedlings but failed to kill oaks has resulted in the creation of an extensive area of turkey oak dominated sandhills that once supported longleaf pine forests (Myers, 1985; Myers and White, 1987; Rebertus et al., 1989a; Myers, 1990). The close association of longleaf pine wiregrass communities with periodic fire has been long recognized (Cary, 1932; Garren, 1943; Bruce, 1947; Veno, 1976; Christensen, 1981; Wright and Bailey, 1982; Abrahamson, 1984) and need for frequent growing season burning to restore and sustain this ecosystem has become more recently understood (Noss, 1989; Rebertus et al., 1989b; Landers et al., 1990; Wade and Lundsford, 1990; Streng et al., 1993; Landers et al., 1995). The pattern of diversity in this ecosystem is largely a product of such natural periodic disturbance. However, under circumstances where fire cannot be effectively utilized, other techniques may prove useful in restoring such underrepresented or declining ecosystems.

A wide variety of methods are potentially available for restoring ecosystems. Physical techniques such as irrigation, tillage and mechanical manipulation of vegetation can be useful, but sometimes cause excessive site disturbance or may not be economical. Biological techniques such as species introduction, though often effective, are costly and can produce uncertain results. Chemical techniques such as application of fertilizer or herbicide and use of prescribed fire also have advantages and disadvantages related to cost, safety and potential impacts upon non-target species. Prescribed fire is perhaps the most frequently suggested restoration method, because periodic fire is an essential ecological process for maintenance of longleaf pine wiregrass ecosystems. However, on degraded longleaf pine wiregrass sites, treatments such as selective herbicide application, planting seedlings or mechanical removal of competing vegetation may be required to achieve more prompt ecosystem restoration than could be realized by use of fire alone. Restoration efforts currently underway in the sandhills of northwestern Florida use a combination of treatments to achieve multiple management objectives (McWhite et al., 1993).

Among the many beneficial roles herbicides may play in ecosystem management are (a) Restoration of damaged landscapes, (b) Control of alien and or undesirable plants and (c) Creation and maintena. of desired habitats (McMahon et al., 1993). Whe properly applied to longleaf pine sites which have been degraded through oak invasion, hexazinone has potential to provide these benefits, while causing minimal adverse impact to native plant diversity. When fuels present on a degraded site are insufficient to sustain a prescribed fire or too heavy to burn without risking destruction of desirable plant species or social constraints preclude the use of fire, hexazinone application may be considered.

Hexazinone application also provides the added benefit of time efficiency to longleaf pine wiregrass restoration efforts. At least three biennial spring burns are required to significantly reduce oaks on sandhills sites (Glitzenstein et al., 1995). Many cycles of prescribed fire, over a period of several decades, may be required to attain an oak mortality rate of 83 to 93% and corresponding increase in desirable understory plants. A single low-rate hexazinone application achieves this condition in a very brief period, thus, greatly shortening the timeframe required for restoration (phase I). The restored site can then be more quickly scheduled for fire maintenance (phase II). The second phase of this continuin

study will examine the differential recovery effects resulting in longleaf pine wiregrass ecosystems treated with hexazinone followed by prescribed burning as contrasted with those resulting from treatment with prescribed fire alone.

5. Conclusion

Within the first three growing seasons following treatment, single low-rate applications of hexazinone caused substantial changes in a former longleaf pine forest that had become dominated by turkey oak after a wildfire. All hexazinone treatments resulted in significant reductions in the foliar cover of turkey oak and other oaks during the first year. The resulting decline in competition from oaks produced progressive increases in foliar cover of wiregrass, other graminoids and forb species over time. Plant species richness generally increased, while species evenness declined over time, with the continued expansion of wiregrass on treated plots. Standing biomass of wiregrass initially increased then declined to pretreatment levels.

The broadcast 1.1 kg/ha treatment produced non-significant declines in forb cover and significant decreases in species richness and diversity during the first post-treatment growing season. Although these variables recovered in subsequent years, broadcast application may be a less desirable restoration method because pellets are widely distributed on the site, bringing the rooting zone of nearly all understory plants into close contact with herbicide. The possible overlap of edges during strip application may also create local areas where hexazinone dosages exceed prescribed rates. The risk to non-target plant species may therefore be unacceptably high.

The liquid spot 1.1 and 2.2 kg/ha applications caused declines in species diversity, which can be largely attributed to significant decreases in evenness resulting from the progressive expansion of wiregrass during the initial post-treatment growing season. Our overall findings suggest that these treatments resulted in increases in the cover of all graminoids and forbs and in the highest species richness. In addition, these treatments were highly effective in decreasing the dominance of turkey oak and other oaks. However, the 2.2 kg/ha treatment proved most effective in controlling all woody plants and producing significant increases in wiregrass. Therefore, while both application rates are useful, we recommend the liquid spot 2.2 kg hexazinone/ha application be used for restoration of xeric sandhills and similar longleaf pine wiregrass ecosystems.

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Cogongrass
Problem and Solutions



Newly established cogongrass in natural loblolly pine stand in Bay Minette, Alabama



Cogongrass flowers

Cogongrass (*Imperata cylindrica*), also known in Alabama as Japgrass, was introduced in the United States in Gainesville, Florida and Grand Bay, Alabama in the early 1940s as a soil erosion control plant and as a possible forage. Native to Southeast Asia, this grass does not work well as a forage plant but does work well for soil erosion control. Similar to another plant introduced in the 1940s—kudzu—it has become naturalized and is very difficult to stop. In Florida it has spread throughout the state, and in Alabama it has spread roughly 120 miles from Grand Bay. Using Interstate 10 as a corridor, it has spread along the coast of both Mississippi and Louisiana. Along Interstate 65, it has reached the Atmore exit.

Cogongrass creates problems for foresters and land managers with natural regeneration, particularly in longleaf stands. It also creates a severe fire hazard, especially when mixed with other volatile fuels such as waxmyrtle, gallberry and young pines. It also ruins the habitat for gopher tortoises and indigo snakes, which are both threatened species in the area.

Cogongrass is an exotic, perennial, rhizomatous grass and has colonized large tracts of natural and disturbed ecosystems. It grows in loose to compact tufts, producing creeping, scaly rhizomes. The leaves are 1/2 to 3/4 inches wide, up to 4 feet long, with an off-center midrib and rough edges. The seedhead is a white, fluffy spike. Cogongrass spreads by both seed and rhizomes, and once established has the ability to dominate and limit species diversity in forests, rangelands, roadways, and reclaimed mined lands.

Previous attempts to control cogongrass have proven insufficient due to its large rhizome reserves and quick recovery following tillage, burning, or herbicide treatments. Ultimately, if an ecological niche filled by cogongrass is not replaced with another plant species following control, cogongrass will reinvade. An integrated management strategy utilizing all available methods of control is needed to effectively manage cogongrass.

Mechanical Control

Mowing and tillage are tools which have been used effectively for management of many perennials. Mowing of cogongrass may be an effective management strategy if time is not limiting. One mowing alone has little effect on subsequent regrowth, due to large rhizome reserves which quickly produce new growth. However, sequential mowings over two or more years will eventually deplete rhizome reserves. Discing has a dual effect of knocking down shoot growth and damaging rhizomes by chopping and desiccation. As with mowing, regrowth occurs and numerous tillage operations may be necessary for complete control. Cogongrass rhizomes have

difficulty producing shoots from depths of greater than 6 inches, thus deep tillage is important.

Chemical Control

Only a few herbicides have shown promise for cogongrass control. Imazapyr (Arsenal) at 0.75 lbs ai/A and glyphosate (Roundup) at 2.0 lbs ai/A provide 70 to 80 percent control up to 12 months after treatment, but both herbicides are nonselective and imazapyr has considerable soil residual activity. Consequently, establishment by other plant species could be inhibited when Arsenal is used. Fluazifop (Fusilade 2000 - 0.7 lbs ai/A) and glufosinate (Ignite - 1.0 lbs ai/A) provide good control for up to 3 months. Timing of herbicide application is also important, and a September or October application (if before a killing frost) provides longer cogongrass suppression than a spring or summer application. Once again, 100% control has not been achieved with a single application of any herbicide. As part of any control strategy, check with your county extension agent or other expert to consider legal and technical issues.

Competition

The long-term control of cogongrass can only be achieved by changing the ecology of an area to a competitive, diversified plant community. Establishing new species in cogongrass infested areas is difficult due to the chemicals exuded by cogongrass that are toxic to other plants, the extensive rhizome system, and the dense canopy of cogongrass which allows only limited light penetration. Plants which show promise in competing with cogongrass include hairy indigo (and possibly other legumes) bermudagrass, and bahiagrass. Establishment of native species in cogongrass infested areas is difficult due to a lack of experience in the management of most desired species.

Integrated Management

Reliance on a single means of control will generally result in failure to effectively manage cogongrass. Integrated management, including burning, tillage, mowing, chemical, and cultural control will increase the likelihood of cogongrass suppression. Burning, which removes old growth and dead biomass, has two benefits. One, the rhizomes are forced to reallocate starch storage reserves to produce new shoot growth, thereby weakening the rhizomes. Second, removal of the substantial biomass improves other management practices, tillage operations are more effective and once regrowth occurs, greater herbicide coverage of actively growing tissue is achieved. Allowing regrowth after burning and tillage, followed by a proven herbicide, is the most effective management program. When the above ground tissue is young and actively growing, the rhizomes have been weakened, and if timed correctly (September/October application), the rhizomes may be very strong photosynthetic sinks.

After suppression of cogongrass, the establishment of desirable plant species is essential for long-term control of cogongrass. The essence of our strategy is to replace cogongrass, not just kill it. If a replacement plant species does not fill the niche occupied by cogongrass after suppression, then cogongrass will simply refill the niche. Presently, improved forage species such as bermudagrass or bahiagrass have been successfully utilized to fill the cogongrass niche. Various practices such as fertilization and mowing have been shown to encourage the competitiveness of the desirable species. Practices that will encourage native species establishment and persistence are presently being investigated.

Ultimately the effective displacement of cogongrass using the aforementioned integrated approach should be successful albeit costly. In many areas the cost is justified; however in others this is not the case. Nevertheless, cogongrass is established and continues to spread into many low maintenance areas where cost constraints preclude the aforementioned approach. Therefore, as part of the overall strategy, some form of classical biological control will be essential. Without some form of widespread management, a continuous source of seed and rhizomes will persist. Consequently, no matter how effectively we control cogongrass in some areas, spread and reinfestation will continue. When dealing with a noxious and invasive plant such as cogongrass, a regional or national strategy is essential. Effective management of cogongrass will only be successful if cooperation is achieved between many groups, organizations, and involved states.

Editor's Understory

Continued from page 6

developing the overall garden tour; and helping train the garden's many volunteer guides.

Bill was the leader in developing the CBER. Garden founders knew this element of the facility was critical because it would raise the Huntsville Botanical Garden from a garden of local appeal to one of national interest. The mission of the CBER is to increase knowledge and understanding of closed ecological systems (biospheres), both natural (such as Earth itself) and manmade (a space station or a base on the moon or Mars).

Because of his work at Marshall, Bill was able to bring current and retired scientists and researchers from NASA and the Marshall Space Flight Center (MSFC) and other members of the aerospace community together to design the CBER program. Many of these people were and are the masterminds behind some of the United States space programs in recent decades.

Bill and this group managed to obtain a "surplus" full-size mockup of a piece of the International Space Station from NASA/MSFC. The garden transformed the "node" into a Lunar Greenhouse, and it is proudly housed in the new CBER building.

Also located in the complex is "Ground Truth Site," a research station monitored by NASA from a space satellite and from the ground by local high school students. Test results are compared to see if data from space and from the ground match.

"Biological Laboratory for Student Research" is also part of the space thrust at the garden. It is a space lab manned by college students. Their first shuttle flight experiment flew successfully aboard Columbia in October 1992.

As Jeanie and Bill walk through the garden they never fail to speak to staff members and workers, calling them by name and making comments on the jobs they are doing. The Snoddys speak with pride of the accomplishments at the garden and each new thing stirs an air of excitement. And they should be proud and excited. It is through their dedicated work and commitment, along with many others just like them, that the Huntsville-Madison Botanical Gardens became a reality.

Biological Sciences

COGONGRASS (*IMPERATA CYLINDRICA*) CONTROL WITH GLYPHOSATE[1]

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ABSTRACT: *A stand of cogongrass was burned in February 1983, and the regrowth sprayed with 0.5, 1.0, and 2.0% solutions (v/v) of glyphosate in either April, August, or November of the same year. Plant density was estimated immediately before each treatment and again in July 1984 and 1985. Plant control with the 2% glyphosate treatment differed significantly ($p<0.05$) from the 0.5 and 1.0% solution treatments only after the November application date. Glyphosate as a 2% solution appeared to control cogongrass satisfactorily for at least 2 yr (91% mortality), while control after the August application never exceeded 40%. Controlling cogongrass in forests will be required to effectuate adequate natural regeneration of pines or survival of planted seedlings and to maintain natural diversity of plant species.*

COGONGRASS (*Imperata cylindrica* (L.) Beauv.) is rapidly becoming a serious weed problem in some southeastern states. Since its accidental introduction near Mobile, AL in 1911, cogongrass has established itself throughout southern Alabama, Mississippi, and in at least 27 of Florida's 67 counties (Tanner and Werner 1986).

Cogongrass propagates rapidly, both vegetatively by developing an extensive rhizome mat and by wind-blown seed. This species has been planted along highways and canals where it is an effective soil-stabilizing grass. However, small colonies have begun to invade undisturbed sites in native pastures and forest land from the nearest highways (source). The wind evidently disperses the light, villous seeds long distances over the open, flat landscape. Once a stand of cogongrass is established, our observations are that few herbaceous or woody plant seedlings can invade or survive in these locations. The spread of cogongrass must be controlled promptly and effectively.

Although cogongrass has been controlled in agricultural fields by deep plowing (Hartley, 1949), stands of this grass in forest understories or in open range areas are managed best with herbicides. The most extensively tested and recommended herbicides for cogongrass control are Dalapon, (2,2-dichloropropanoic acid), and glyphosate, [N-(phosphonomethyl)glycine] (Dickens and Buchanan, 1975). Of these two herbicides, glyphosate is more effective on sandy soils (Yeoh and Pushparajah, 1976) that characterize most of Florida's soils where cogongrass has invaded. Additionally, effectiveness of glyphosate is greater in shaded sites (Moosavi-Nia and Dore, 1979; Wong, 1981), such as under forest canopies.

The objective of this study was to test the efficacy of glyphosate in controlling cogongrass when applied seasonally at three rates.

[1]This is a contribution to the Florida Agricultural Experiment Station Journal Series No. 8469.

MATERIALS AND METHODS—This study was established in a longleaf pine-turkey oak (*Pinus palustris* Mill.-*Quercus laevis* Walt.) forest near Brooksville, FL, in Hernando County. Although the mature pines (*ca* 200 yr old) were tapped for turpentine production, no active timber harvesting has ever occurred on this forest tract. Soil series at the study site are primarily Arredondo fine sand of the loamy, siliceous, hyperthermic Grossarenic Paleudults. The annual, frost-free growing season averages 312 days, and average annual precipitation is 137 cm.

An experiment was designed to test the effectiveness of four application rates of glyphosate (0.0, 0.5, 1.0, and 2.0% (v/v) solutions of a 430 gm/L commercial formulation) applied at three times of the year (April, August, and November 1983) on cogongrass control. Applications were made on a spray-to-runoff basis, i.e., until solution was observed dripping off of leaves. A backpack sprayer with a hand-controlled nozzle was used. The spray solution concentrations used were those the manufacturer recommended (Anonymous, 1983); a 1.0% solution is recommended for most circumstances, but a 2.0% solution is recommended for some perennials.

At the time of the study several solid stands of cogongrass, 0.5 to 2 ha in size, were located within the forest. The experimental study site was placed within one of these homogeneous stands. The study site received a prescribed fire in February 1983 to remove senescent plant material and to stimulate plant regrowth. At each of the three times of application, four replicates of each of the four herbicide treatments were allocated within a 7 plot by 7 plot grid using a completely random experimental design. Each square plot was 4 m on a side and was separated from adjacent plots by 1-m borders of untreated vegetation.

Cogongrass tillers were counted in two, permanently-marked, 0.9-m^2, circular quadrats located within each experimental plot. Counts were made immediately prior to each treatment and again in August 1984 and July 1985, following 1 and 2 growing seasons, respectively. Percent mortality associated with each treatment was estimated by comparing pre- and post-treatment tiller counts within the permanently-marked quadrats.

Because the completely randomized study design was replicated by time of application (but not space), the data were analyzed as a series of experiments (Cochran and Cox, 1950). Count data were transformed by the square root procedure. Both count data and tiller mortality rates were compared among the herbicide treatments using analysis of covariance, with the 1983 pretreatment counts as the covariable. Least-square-mean, pair-wise comparisons were used to determine the effectiveness of the four herbicide rates. Only the unadjusted tiller mortality means are reported because the mortality trends were statistically the same as those of the transformed and adjusted, least-square data.

RESULTS AND DISCUSSION—After the February 1983 fire, cogongrass plant density in the check plots (0.0 % treatment) increased from April 1983 (average=71 plants/m^2) to August 1984 (average=82 plants/m^2), but then declined in November 1985 (average=65 plants/m^2) (Table 1). Plant density on the check plots at this study was much lower than the densities of 1000-1200/m^2 reported on road sides in southern Alabama (Dickens and Buchanan, 1975). Low plant densities at this study may have been due to the partial shading of overstory pines and oaks, a relationship demonstrated by Eussen (1976), or to the prescribed fire.

Percent mortality of cogongrass plants one growing season after herbicide application in the spring was significantly greater in the 1.0 and 2.0% treatments than in the 0.0 and 0.5% treatments (Table 1). After two growing seasons natural mortality (32%) in the check plots (April application) was still less than mortality in the other three treatments. There was no significant difference among the mortality rates in 0.5, 1.0, and 2.0 treatment rates.

Glyphosate applied in summer resulted in little to no reduction in cogongrass plant density, regardless of application rate or time since treatment (Table 1). Plots receiving the 0.5% rate actually showed an increase in plant density in comparison to check plots.

TABLE 1. Mean number of living congongrass plants immediately before three rates of glyphosate application on three dates, and the percent mortality one and two growing seasons later, Hernando County, FL.

Glyphosate treatment		Sampling date[a]		
		Before treatment	Aug. 9, 1984	July 29, 1985
	Rate (%)	Live plants (no./M²)	Mortality (%)	Mortality (%)
April 13, 1993	0.0	72	16*	32*
	0.5	83	15*	46
	1.0	57	49	46
	2.0	71	54	56
		Avg. 71		
August 23, 1983	0.0	84	18*	38
	0.5	76	+12*	10*
	1.0	73	27	37
	2.0	94	39	39
		Ave. 82		
November 18, 1983	0.0	57	+13*	16*
	1.0	73	13*	33*
	1.5	64	51*	63*
	2.0	65	80	91
		Avg. 65		

[a]Mean mortality values within a column for each separate treatment date followed by an asterick are significantly lower ($p<0.5$) than the label-recommended, 2.0%-application rate according to pair-wise comparison *t*-tests.

Cogongrass plant mortality was highest following the November application time (Table 1). Mortality continued to increase at all three rates of application between the first and second post-treatment growing seasons. At both post-treatment sampling dates, tiller mortality in plots receiving the 2.0% application rate was significantly greater than in the other three treatments with only 9% of the tillers surviving after two growing seasons.

Due to the ability of cogongrass to spread rapidly from rhizomes, all tillers and rhizomes must be killed before control can be considered successful. In this study even the highest level of mortality (91% following 2% glyphosate treatment) would require sequential treatments to eliminate the grass completely. However, this high level of initial stand reduction would reduce the cost of follow-up treatment.

Burning the test plots before the herbicide treatment removed all standing dead cogongrass and stimulated regrowth. Succulent cogongrass regrowth was hypothesized to be more susceptible to glyphosate action at reduced concentrations. However, glyphosate concentrations of less than the recommended label rate for perennials (2.0% v/v) did not kill succulent regrowth effectively. The net direction of carbohydrate translocation, though not measured in this study, may have been a critical factor in reducing the amount of herbicide translocated to the rhizo-

CONCLUSIONS—Given that cogongrass is a relatively tall (1.0-1.5 m), mat-forming grass that is well adapted to the environment of the southeastern United States, control of its current and future spread is needed to protect the ecological integrity of this region's forest and range lands. Results of this study indicate that glyphosate, when applied in a 2.0% (v/v) solution in the fall following a spring burn, will give good to excellent control for at least 2 yr. Continued treatment of residual living plants, however, will be necessary to assure long-lasting eradication of this species. Burning, or some other type of top removal, of cogongrass stands to remove standing dead plant material prior to herbicide application, should reduce the total amount of herbicide needed to treat a stand of grass.

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Influence of Herbicide Combinations and Application Technology on Cogongrass (*Imperata cylindrica*) Control[1]

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Abstract: Field experiments were conducted to evaluate various herbicides and application technologies for the control of cogongrass. Imazapyr at 0.8 kg ae/ha provided the highest cogongrass control, followed by glyphosate (3.4 kg ae/ha) and sulfometuron (1.1 kg ai/ha) when applied as a single application. When sequential applications were evaluated, glyphosate plus imazapyr provided the best control. Sulfometuron could be applied sequentially after imazapyr or glyphosate with no loss of control, but control was less if sulfometuron was the initial herbicide. Tank mix combinations of glyphosate and imazapyr (100% rate at 3.4 and 1.1 kg ae/ha, and subsequent rates of 0 + 100, 25 + 75, 50 + 50, 75 + 25, and 100 + 0% of each herbicide, respectively) provided similar cogongrass control regardless of rate. Control using imazapyr improved from 20 to 40% with 234 L/ha diluent volume when compared to 46 L/ha. Glyphosate at either of these volumes provided from 0 to 21% inhibition of cogongrass. A 50% concentration of imazapyr applied twice with a ropewick provided greater control than a 33% concentration with one pass or either concentration of glyphosate with one or two passes. Efficacy with glyphosate applied using a ropewick was not affected by concentration or number of passes.

Nomenclature: Imazapyr, (±)-2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid; sulfometuron, 2-[[[[(4,6-dimethyl-2 pyrimidinyl)amino]carbonyl]-amino]sulfonyl]benzoic acid; cogongrass, *Imperata cylindrica* (L.) Beauv. #[3] IMPCY.

Additional index words: Low-volume applications, methods of control, ropewick, sequential herbicide combinations, tank-mix.

Abbreviation: CRBD, completely randomized block design.

INTRODUCTION

Cogongrass is a serious perennial pest throughout the subtropical and tropical regions of the world (Holm et al. 1977). It ranks as the seventh most troublesome weed worldwide, spreading by both seed and rhizomes. Cogongrass has been reported to adversely affect banana (*Musca paradiscaca* L. var.), citrus (*Citrus* spp.), coconut (*Cocus nucifera* L.), oil palm (*Elaeis guineensis* Jacq.), pasture, pineapple [*Ananas comosus* (L.) Merr.], pine (*Pinus* spp.), rubber (*Hevea brasiliensis*), and tea (*Camellia sinensis*). In addition, cogongrass has become a problem in many noncrop areas, such as forests, roadsides, reclaimed mined areas, recreational areas, and natural ecosystems. It has little utility except for thatch, forage production, and soil stabilization. Cogongrass research has been geared toward short-term control, and long-term control of this species has proven extremely difficult. Slash-and-burn and shifting agriculture has resulted in transient control, usually allowing only a year or two of crop production before reinfestation. By eliminating natural vegetation that competes effectively with cogongrass and concomitantly distributing seeds and rhizomes, these control strategies have increased the area of cogongrass infestation (Prommool 1984).

At least 30 herbicides and hundreds of combinations have been evaluated and reported for cogongrass control (Bacon 1986; Dickens and Buchanan 1975; SEAWIC 1988). Of these herbicides, dalapon (2,2-dichloropropanoic acid), glyphosate [*N*-(phosphonomethyl)gycine], and imazapyr have shown the greatest activity on cogongrass with the fewest adverse effects (i.e., bioaccumulation of heavy metals, extending periods of soil sterilization, nontarget species injury, or applicator injury). In most situations, long-term control or complete control has not been achieved from a single application of any of these compounds. Repeat applications have been nec-

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[3] Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Revised 1989, Available from WSSA.

essary to kill or deplete rhizomes. Long-term control can be achieved only if rhizomes are controlled.

Various innovations in application technology have also been tested to improve the activity of these herbicides on cogongrass. Low- and ultralow-volume (ULV) applications (usually in the range of 20 to 100 L/ha diluent volume) have been reported to enhance the activity of glyphosate on selected annual grasses (Buhler and Burnside 1983), common bermudagrass [*Cynodon dactylon* (L.) Pers.] (Jordan 1981), quackgrass [*Elytrigia repens* (L.) Nevski] (Sandberg et al. 1978), but control of johnsongrass [*Sorghum halepense* (L.) Pers.] was equal for various herbicides at spray volumes of 94 and 374 L/ha (McWhorter and Hanks 1993). The use of low-volume technology with glyphosate and imazapyr on cogongrass has been reported (Townson and Price 1987). However, results have been variable and not definitive as to the enhancement of activity or long-term control.

Townson and Butler (1990) evaluated "cloth-wiping" and "rope-wicking" of imazapyr and glyphosate on cogongrass, and reported that ropewick wipers were more effective for both herbicides, but that imazapyr concentration must remain below 10 g ae/L to be effective. The authors also reported that increasing imazapyr concentration reduced imazapyr translocation, while the reverse was true for glyphosate.

The concept of control has been frequently defined as the initial effects of the herbicide treatment. Research that provides the most useful information (i.e., long-term efficacy) about cogongrass and other perennial weed control allows sufficient time following treatment before evaluation (Dickens 1973). Short-term evaluation of herbicide efficacy on perennial species can often be misleading (Shilling and Haller 1989). The most accurate measure of perennial weed control is the inhibition of regrowth from perennating organs. This measure can be accomplished by harvests of foliage regrowth and the amount of productive perennating tissue remaining after an extended period of time (i.e., one growing season following application).

Because herbicides have not provided effective cogongrass control, an experiment was initiated to develop a program that would provide long-term control using herbicides applied alone or in combination, sequential herbicide programs, and application methodology (i.e., low volume and ropewick applications).

MATERIALS AND METHODS

Sequential Herbicide Applications. Sequential herbicide applications for cogongrass control were evaluated over a 3-yr period (1986 to 1988) at Chiefland, FL. The area was located in a flatwoods, noncropped field, and the soil type was a Sparr fine sand (Loamy, Siliceous, Hyperthermic, Grossarenic, Paleudults) heavily infested with cogongrass.

The herbicides and rates applied were: (a) dalapon, 16.8 kg/ha; (b) glyphosate, 3.4 kg/ha; (c) imazapyr, 0.8 kg/ha; (d) sulfometuron, 1.1 kg/ha; and (e) untreated control. Initial herbicide applications were made to cogongrass foliage 60 to 90 cm tall and the second treatment of the sequential program was made to regrowth 60 to 120 cm tall. Treatments were applied using a CO_2-pressurized backpack boom-sprayer delivering 280 L/ha at 210 kPa. Treatments were arranged as a 3 by 5 factorial using a completely randomized block design (CRBD) (initial treatments of glyphosate, imazapyr, and sulfometuron and second treatments of dalapon, glyphosate, imazapyr, and sulfometuron, or untreated) with three replications on 1.8- by 4.6-m plots. Sequential applications for the first experiment were made on July 9, 1985 and September 19, 1986, respectively. Treatments were made July 9, 1985 and September 19, 1986 in the first experiment and September 19, 1986 and October 8, 1987 in the second experiment. In January 1986 and 1987, cogongrass was mowed to 2 cm in both experiments. This allowed the sequential applications to be made to regrown foliage without any interception by dead foliage. A substantial regrowth period was necessary to provide an accurate assessment of the long-term effects of herbicide treatments for cogongrass control. To accomplish this, a 1.8-m-wide swath was mowed through each plot. From this area, foliage regrowth within a 0.25-m^2 (reported on a 1.0-m^2 basis) quadrat was harvested. In addition, rhizome biomass was determined by harvesting six random samples (182 cm^2 diam soil cores to a depth of 12 cm; 4,710 cm^3 total volume; reported on a 1.0 m^3 basis) within each plot. Foliage and rhizome tissue was dried at 60 C for 72 h and dry weights were determined.

Plots for the initial and sequential herbicide applications, low- and conventional-volume applications of glyphosate and imazapyr, and the ropewick applications of glyphosate and imazapyr experiments were mowed in January 1987 for the first experiment and in January 1988 for the second experiment. These plots were then harvested in September 1987 and June 1988 for the first and second experiments, respectively.

Plots for the first and second glyphosate and imazapyr tank-mix combination experiments were mowed in January 1986 and 1987 and harvested in September 19[illegible] and June 1987, respectively.

Tank-Mixed Glyphosate and Imazapyr. Glyphosate and imazapyr were tank-mixed and applied as a single application to cogongrass foliage on July 9, 1985 (first experiment) and on September 16, 1986 (second experiment). Applications were made using the CO_2-pressurized boom system previously described. The 100% rate of each herbicide was designated as 3.4 and 1.1 kg/ha for glyphosate and imazapyr, respectively. From this rate, glyphosate and imazapyr mixtures of 0 + 100, 25 + 75, 50 + 50, 75 + 25, and 100 + 0% were formulated. The experimental design was a randomized complete block with three replications on 1.8- by 4.6-m plots. Cogongrass was mowed in January 1986 and 1987 for the first and second studies, respectively, and the foliage regrowth was harvested in September 1986 and June 1987 for the first and second studies, respectively.

Spray Volume Applications of Glyphosate and Imazapyr. The influence of carrier volume on the efficacy of glyphosate and imazapyr was evaluated in two experiments over a 3-yr period. In the first experiment, applications were made using a tractor-mounted boom sprayer traveling at 6.4 km/h. To deliver 46 L/ha, the boom was equipped with 11001LP[4] flat fan nozzles calibrated at 124 kPa. To deliver 234 L/ha, the boom was equipped with 11005 flat fan nozzles calibrated at 276 kPa. In the second experiment a CO_2-pressurized backpack boom sprayer was used. With this system, 46 L/ha was applied by using TX-6[5] hollow cone nozzle calibrated at 207 kPa and traveling at 8 km/h while 234 L/ha was applied by using 11003[4] flat fan nozzles calibrated at 221 kPa traveling at 4.8 km/h. Glyphosate and imazapyr were applied in 46 and 234 L/ha at two rates.

Treatments were applied on July 8, 1985 (first experiment) and September 16, 1986 (second experiment). The experimental design was a CRBD with treatments arranged in a 2 by 2 by 2 factorial with three replications. Plots were 3.0 by 6.1 m in the first experiment and 1.8 by 4.6 m in the second experiment. In January 1987 and 1988 cogongrass was mowed. Regrown foliage and soil-rhizome cores were obtained, as previously described, in September 1987 and June 1988 for the first and second experiment, respectively.

Ropewick Applications. Ropewick applications of glyphosate and imazapyr were evaluated for cogongrass control. Glphosate and imazapyr (33 and 50% v/v, respectively) were applied once or twice (in opposite directions). The study was conducted twice in consecutive years. The ropewick apparatus used was 2.1 m long with a reservoir capacity of 17.3 L. Two rows of half-overlapping Pistachios[5] rope (nine sections per row 20 cm long) were attached using rubber bushings within a screw-cap compression fitting, the body of which was glued to the PVC reservoir, creating 1.8 m of wicking surface. Two sets of ropewicks were constructed, one for each herbicide. Applications were made by two people carrying the ropewick through the plot at 4.8 km/h with the wicking surface held horizontally to the ground approximately 20 cm below the leaf apex.

The experimental design was a CRBD using a two (glyphosate and imazapyr) by two (33 and 50% concentrations) by two (one or two passes) factorial arrangement with three replications in the first experiment and four replications in the second experiment. The plot size in both experiments was 1.8 by 4.6 m. Applications were made on July 9, 1985 for the first experiment. In the second experiment, glyphosate was applied October 2, 1986 and imazapyr was applied October 3, 1986. In both experiments, cogongrass was 60–90 cm tall at the time of application. In January 1987 and 1988 plots were mowed. Regrowth foliage was harvested as previously described in September 1987 and June 1988 for the first and second year, respectively.

Analysis of variance was used to test for main factor effects and interactions, and means were separated using the appropriate Fisher's least significant difference (SAS Institute 1989). There were no year-by-treatment interactions ($P > 0.05$) in any study; consequently, the data were pooled across years.

RESULTS AND DISCUSSION

Sequential Herbicide Applications. Cogongrass shoot regrowth and rhizome biomass were affected differently by herbicide treatments (Table 1). Using data from single applications the herbicidal activity ranked as follows (high to low): imazapyr (76 and 34% inhibition of shoot and rhizome growth, respectively), glyphosate (61 and 34% of shoot and rhizome growth, respectively), sulfometuron (38 and −22% inhibition of shoot and rhizome growth, respectively). Regardless of the order of application, all combinations of glyphosate and imazapyr provided the best control.

Sequential applications of imazapyr plus glyphosate controlled cogongrass as well as or better than when each herbicide was followed by dalapon or sulfometuron. Sequential applications of imazapyr or glyphosate following sulfometuron provided excellent control (greater than 90%) of shoot regrowth. Sulfometuron by

[4] Spraying Systems Co., North Avenue, Wheaton, IL 60188.
[5] Gulf Rope and Cordage Inc., P.O. Box 5516, Mobile, AL 36605.

Table 1. The effect of sequential herbicide treatments on cogongrass regrown shoot and rhizome dry weight from 1985 to 1988.

Sequential application (kg ha)	Initial application					
	Imazapyr (0.8 kg/ha)		Glyphosate (3.4 kg/ha)		Sulfometuron (1.1 kg/ha)	
	SDW[a]	RDW[a]	SDW	RDW	SDW	RDW
	% inhibition[b]					
Dalapon (16.8)	74	47	95	58	52	−5
Glyphosate (3.4)	88	67	87	48	94	−13
Imazapyr (0.8)	99	64	98	69	94	16
Sulfometuron (1.1)	62	60	37	43	−6	−38
Untreated	76	34	61	34	38	−22

[a] Regrowth shoot dry weight (SDW) and root-rhizome dry weight (RDW) harvested 10 mo after sequential treatment.

[b] $LSD_{(0.1)}$ = 14 and 20 for SDW and RDW row comparisons, respectively; $LSD_{(0.1)}$ = 18 and 25 for SDW and RDW column comparisons, respectively. Inhibition values were computed using untreated areas that contained 128 g/m² (harvested from 0.25 m²) and 860 g/m³ (harvested from 4,170 cm³) of foliage and rhizome tissue, respectively.

itself, or preceding dalapon, provided little or no control of cogongrass shoots or rhizomes.

Tank-Mixed Combinations. Tank-mixed combinations of glyphosate and imazapyr provided the same level ($P > 0.1$) of control regardless of the rate combination (data not shown); however, all combinations significantly ($P < 0.05$) reduced cogongrass shoot biomass 70% and rhizome biomass 39%. Therefore, either of these two herbicides can substitute for the other in a single tank-mix application, and are at least as effective applied alone. This flexibility could provide possible economic and environmental advantages. By increasing the proportion of glyphosate in the tank-mix, a cost savings could be realized. In addition, decreasing the proportion of imazapyr would reduce the time interval before revegetation could be reduced. Conversely, if longer term bare soil were desired, imazapyr would be the herbicide of choice due to soil residual activity. Imazapyr could be an effective herbicide choice if tolerant plant species were desirable vegetation.

Spray Volume Applications of Glyphosate and Imazapyr. Herbicides (glyphosate and imazapyr), herbicide rates (half or full rate), and carrier volumes (46 or 234 L/ha) affected cogongrass control interactively ($P < 0.05$) as measured by shoot regrowth (Table 2). Imazapyr provided significantly greater cogongrass control (20 to 70%) than did glyphosate at both rates when applied at 234 L/ha. Imazapyr rate did not influence control. Both rates of glyphosate resulted in poor control (0 to 21%). Imazapyr provided a greater level of control when applied at the higher volume. This may indicate that in dense stands of cogongrass greater coverage is more important than diluent concentration (Townson and Butler 1990).

Table 2. The effect of carrier volume and imazapyr and glyphosate rate on cogongrass shoot dry weight.

Carrier volume (L/ha)	Imazapyr		Glyphosate	
	0.4 kg/ha	0.8 kg/ha	1.7 kg/ha	3.4 kg/ha
	% inhibition[a]			
46	33[b]	48[c]	16	21
234	73[b,c]	71[b,c]	−10[c]	12[c]

[a] Inhibition values were computed using untreated areas that contained 99 g/m² of foliage (harvested from 0.25 m² area).

[b] Indicates a significant ($P < 0.05$) volume effect baesd on ANOVA.

[c] Indicates a significant ($P < 0.05$) herbicide effect based on ANOVA.

Ropewick Applications of Glyphosate and Imazapyr. There was a significant ($P < 0.05$) three-way interaction betwen herbicides, percent solution, and number of passes (Table 3). Control with glyphosate (both shoot and rhizome dry weight) was unaffected by solution concentration and number of passes with the ropewick applicator. Control from imazapyr applied in a 33% solution was not affected by the number of passes and was not significantly greater than control observed from glyphosate at either solution concentration. Imazapyr provided better control at a 50% solution than at a 33% solution. Control based on shoot regrowth was not affected by the number of passes, whereas two passes provided significantly greater control of cogongrass rhizomes than a single pass. Boerboom and Wyse (1988) speculated that the reason for poor control of Canada thistle [*Cirsium arvense* (L.) Scop.] achieved using ropewick-applied glyphosate was that the concentration applied was greater than the optimum level needed for

Table 3. The effect of ropewick applications of imazapyr and glyphosate rate on cogongrass shoot and rhizome dry weight.

Solution	Passes	Imazapyr		Glyphosate	
		SDW[a]	RDW[a]	SDW	RDW
%	no.	% inhibition[b]			
33	1	67	−17[c]	55	17
33	2	68	11[c]	65	31
50	1	76[d]	24[c,e]	38[d]	28
50	2	78[d]	45[c,e]	60[d]	27

[a] Regrown shoot dry weight (SDW) and rhizome dry weight (RDW), respectively.

[b] Inhibition values were computed using untreated areas that contained 174 g/m² (harvested from 0.25 m²) and 1,390 g/m³ (harvested from 4,170 m³) of foliage and rhizome biomass, respectively.

[c] Indicates a significant ($P < 0.05$) % solution effect within herbicides and passes based on ANOVA.

[d] Indicates a significant ($P < 0.05$) herbicide effect within % solutions and passes based on ANOVA.

[e] Indicates a significant ($P < 0.05$) number of passes effect within herbicides and % solutions based on ANOVA.

maximum translocation to the roots. Geiger and Bestman (1990) determined that glyphosate lowered photosynthesis and limited import into developing sink leaves of sugar beet (*Beta vulgaris* L.). In essence, by overdosing the leaf tissue, glyphosate provides more contact activity, to the detriment of systemic activity. Therefore, the use of concentrations of more than 33% glyphosate would be economically unsound. In fact, the use of concentrations lower than 33% may provide as much, if not more, control of cogongrass. Imazapyr at the 50% concentration provided better control of cogongrass shoot regrowth than did glyphosate. The highest level of control was achieved at 50% v/v applied twice. These data would seem to indicate that imazapyr absorption and/or translocation is not as sensitive to high concentrations as glyphosate. However, Townson and Butler (1990) reported that ropewicked imazapyr concentrations above 10 g ae/L reduced radiolabeled imazapyr movement in cogongrass. The use of two passes at the 50% concentration provided the highest level of control of any of the treatments. Although 100% control was not achieved with either herbicide, multiple ropewick applications of glyphosate or imazapyr may be a viable alternative for cogongrass control in situations where broadcast applications are not desirable.

None of the treatments provided 100% control of cogongrass. The best control was achieved with sequential applications of glyphosate or imazapyr. Varying the concentrations of imazapyr and glyphosate in a tank-mix application while maintaining the same level of control offers flexibility to vegetation managers. Less imazapyr in the mixture reduces soil residual activity, and earlier revegetation of an area would be possible. More imazapyr in the mixture offers a longer period of complete vegetation control. Glyphosate and imazapyr are also interchangeable in sequential applications, offering the same type of management flexibility. Application techniques such as reduced carrier volume, ropewick, and tank-mixes did not enhance the activity of these herbicides on cogongrass. If, for economic or site considerations, ropewick or high-diluent-volume application technology are used, then imazapyr could provide better control.

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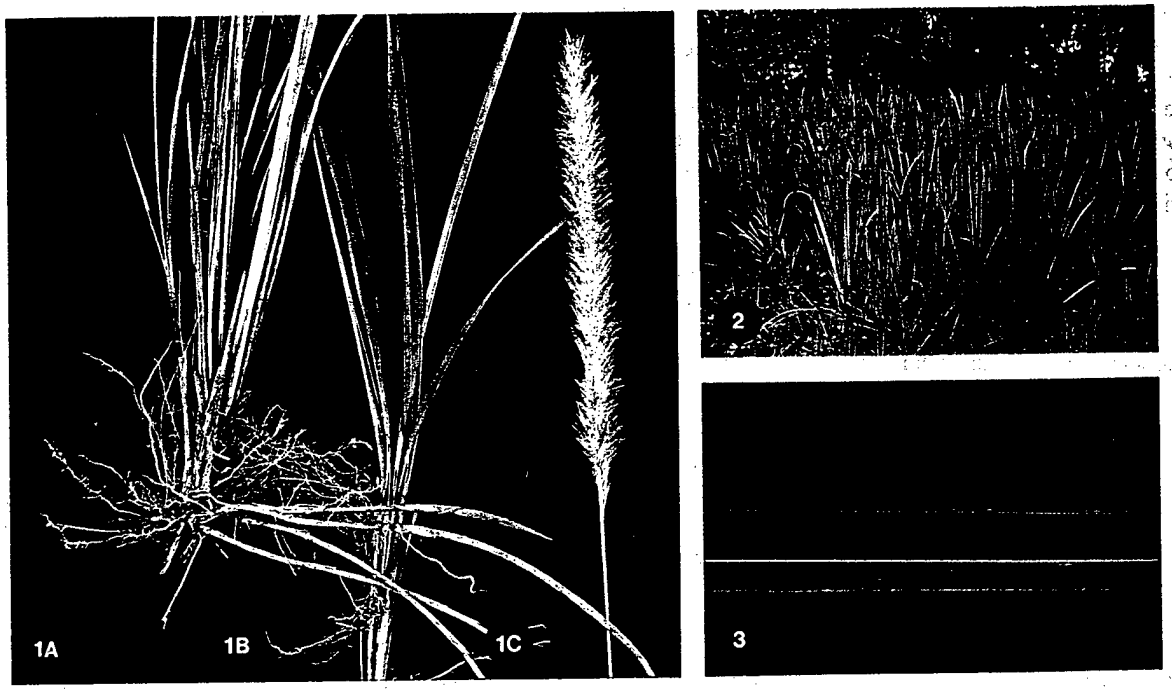
Cogongrass, *Imperata cylindrica* (L.) Beauv.: A Good Grass Gone Bad![1]

Nancy C. Coile[2] and Donn G. Shilling[3]

INTRODUCTION: Cogongrass was imported into Florida at Gainesville and Brooksville in the 1940s in hopes that it would be a good forage grass and would help control soil erosion (Hall 1983; Willard 1988). As with many too-good-to-be-true cases, cogongrass proved to be unsuited for forage and its ability to spread and displace desirable vegetation outweighed any soil erosion control considerations.

Cogongrass has features that minimize herbivory. The rough edges of mature leaves cause mammals to avoid chewing the foliage. In fact, the leaf edges may cause abrasions on persons who walk barelegged through a patch of cogongrass. Silica bodies throughout the leaves add to the unpalatabilty for grazing animals.

Cogongrass responds to stress by producing underground stems (rhizomes) and stress induces flowering. Rhizomes allow for spread and the production of additional plants with the same genetic makeup. Dense stands of cogongrass crowd out other species in the area. Rhizome production allows cogongrass to proliferate to the point where it has been designated the worst perennial grass weed of southern and eastern Asia and one of the 10 worst weeds worldwide (Holm *et al.* 1977).



Figures 1-3. *Imperata cylindrica* (L.) Beauv., Cogongrass. **Fig. 1.** A) portion of a stem with attached roots and four elongated rhizomes; B) stem with leaves; C) the plume-like inflorescence composed of many paired flowers. **Fig. 2.** Note the flowering plant at the center back. **Fig. 3.** Portion of a leaf blade, showing the off-center midrib and the scabrous leaf margins. (Photography credits: Luanne M. Marsh, Fig. 1; Jeffery W. Lotz, Figs. 2 & 3).

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Cogongrass has an allelopathic effect on other plants -- chemicals produced by cogongrass inhibit growth of other plants (Hussain *et al.* 1992). This suppressive feature may be another reason there are monotypic stands of cogongrass.

Cogongrass has the very efficient C_4 type of photosynthesis (the process of converting the energy of sunlight into food energy). Corn and several other C_4 plant species with this type of photosynthesis are usually better able to survive in hot and/or dry climates than are the more common C_3 plants.

With all these features for endurance, it is no wonder that cogongrass has proved to be a pest. In addition, cogongrass has few, if any, competitors or other control species to slow its growth and spread outside its native area. There are many plants, insects, nematodes, and pathogens which hold cogongrass in check in the Old World tropics, where it is native. To use the vernacular phrase, cogongrass has "gone bad" in Florida and in many other areas.

In the United States, cogongrass has been documented in Louisiana, Mississippi, Alabama, South Carolina and Florida (Bryson and Carter, *in press*). Cogongrass is listed by the USDA Animal and Plant Health Inspection Service, Plant Protection and Quarantine and the Florida Department of Agriculture & Consumer Services, Division of Plant Industry as a noxious weed. Cogongrass threatens pine plantations, pastures, range, and natural habitats.

DESCRIPTION: In Florida, cogongrass is most noticeable as luxuriant stands of yellowish-green grass growing along the roadsides and usually in full sun. There are many scattered patches of cogongrass along I-75, US 441, and other highways through central and north Florida. Cogongrass extends from these highways into lightly wooded stands, pastures, range, and reclaimed phosphate mine areas. Cogongrass may form large stands in the phosphate mine reclamation sites and other disturbed areas.

The growing tip of the rhizome is very sharp and may grow through the roots of other plants. The rhizomes (Fig. 1, A) of cogongrass, like those of Johnsongrass, *Sorghum halepense* (L.) Pers., have many scale-like, non-green leaves called cataphylls. Most grasses do not have such obviously scaly rhizomes.

Root systems (Fig. 1, A) of cogongrass are efficient at extracting water and minerals; they may extend to 2 meters (about 2 yd) deep. Cogongrass survives in dry, barren areas where other plants have difficulties.

Plants are usually about 1 meter tall (3 ft), but very rarely may grow to 3 m (9 ft) tall. Plants are similar to Johnsongrass. However, cogongrass leaves are longer than Johnsongrass; the stems (Fig. 1, B) are not as evident because the leaves obscure the stem; and the seedheads are covered with silky hairs. The basal leaves may be 1 m long and are much longer than the leaves higher up on the stem. In Australia, a common name for cogongrass is "blady grass" which is descriptive of the plant's leafy appearance. Leaves are up to 18 cm (about one-half inch) wide.

The leaf margins (Fig. 3) are scarious (translucent, dry) and are scabrous (rough). These rough edges will slice through skin like the leaves of *Leersia*, a grass found in the wet areas and commonly called cutgrass. The abrasions caused by the scabrous edges of cogongrass have caused some to incorrectly call the leaves saw-toothed. Gary L. Henry (Florida Department of Transportation, personal communication) has observed pigs with bloody chests and shoulders after running through cogongrass.

A quick identification feature for cogongrass is the off-center placement of the midrib, which is whitish. The off-center midrib is more apparent toward the tips of the leaves (Fig. 3).

The flowers (spikelets) are grouped into a large panicle (Fig. 1, C) about 10-20 cm (5 inches) long. Each tiny flower (spikelet) has a fuzzy, plume-like structure which can float the seed through the air. These hairy structures are shiny and give the panicle a silky appearance. When viewed with magnification, it is apparent that the spikelets are paired and one of the pair has a longer stalk. Each spikelet has two stamens and two feathery stigmas.

In Florida, cogongrass usually flowers late winter into May (Dickens and Moore 1974) or in the fall following frost (Willard 1988). Year-round flowering may occur in central and south Florida (Willard 1988). Stress, drought, cool temperatures and mowing, can force the plants into bloom at any time. It is not known whether the seed produced due to stress are capable of germination.

Variation in the plants, with as many as 17 biotypes (Charles Bryson, USDA, personal communication), indicates a species with strong adaptive potential. One variant of cogongrass is Japanese bloodgrass, whose red pigmented leaves have been praised by landscapers. Unfortunately, this red pigmentation is probably due to stress (e.g., cold) and is not consistent. The red coloration will revert to the normal green hue. These plants demonstrate the same aggressive growth features that ordinary cogongrass possesses. Since cogongrass is listed as a noxious weed, all subdivisions of the taxon (variants, subspecies, varieties, cultivars, etc.) are prohibited by both federal and State of Florida law.

CONTROL: Control of cogongrass in Florida is still problematic. Several herbicides have been tested on cogongrass, including glyphosate, paraquat, imazapyr, fluazifop, and sulfometuron (Dickens and Buchanan 1975; Buhler and Burnside 1983; Boonsritat *et al.* 1985; Lee 1985; Dean *et al.* 1988; Willard 1988; Townson and Butler 1990; Tanner *et al.* 1992; Akobundu 1993). Glyphosate or imazapyr are probably the best for Florida cogongrass where it can be applied. However, several treatments are necessary for effective control. Please refer to the control measures described in the IFAS publication "Cogongrass (*Imperata cylindrica* (L.) Beauv.) Biology, Ecology and Control in Florida" by Colvin *et al.* (*in press*).

Application of herbicides to kill cogongrass along roadsides does not present a problem of off-target drift. However, in wooded areas, care must be used to avoid herbicides which harm trees.

The dead leaves of cogongrass remain upright and do not decay easily. Dead leaves prevent herbicides from being effectively absorbed. For effective control, herbicides should be applied to green leaves. Living leaves allow the herbicide to be transported to rhizomes. When a herbicide reaches the rhizomes better control results.

The timing for application of herbicides is critical. Late fall is an excellent time to apply herbicides because plants are then sending carbohydrates into the roots and rhizomes for storage. Along with the carbohydrates, the herbicides will be translocated to rhizomes. If cogongrass is to be controlled, the rhizomes must be killed.

Cultivation can be part of control for cogongrass (Wilcut *et al.* 1988). However, cultivation alone can do more harm than good because a single disking often simply spreads the rhizomes. For more effective control, it is essential to apply a herbicide after cultivation or burning (Willard *et al.* 1990).

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The Response of *Imperata cylindrica* to Chemical Control Followed by Revegetation with Desirable Species

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Summary

Studies were conducted in 1993 and 1994 in central Florida, United States, to determine the influence of chemical and cultural control strategies on *Imperata cylindrica* management. An area with an established *I. cylindrica* population was initially burned and six weeks later herbicides were applied to regrown shoots. Fertilizer treatments were applied and the area disced and *Indigofera hirsuta*, *Lolium perenne*, *Panicum virgatum*/*Cassia fasciculata*, or *Paspulam notatum* seeded. In 1994, *Cynodon dactylon* substituted for *L. perenne*. A combination of *I. hirsuta* and imazapyr provided excellent control of *I. cylindrica* 12 months after treatment (MAT) in 1993. In the 1994 study, *I. hirsuta* became established in the imazapyr-treated plots and *C. dactylon* became established in the glyphosate-treated plots. However, by 12 MAT, neither species had persisted and *I. cylindrica* control was minimal. Overall, integration of competition provided by desirable species after initial suppression with glyphosate or imazapyr has the potential to provide the most sustained control of *I. cylindrica*.

Introduction

Imperata cylindrica (L.) Beauv. is an invasive, noxious, rhizomatous grass in natural and disturbed sub-tropical and tropical ecosystems. Chemical control has been reported using fluazifop (Akobundo, 1993), glyphosate and imazapyr (Akobundo, 1993; Boonsritat et al., 1985; Lee, 1985; Mabb and Price, 1986; Townson and Butler, 1990). Combinations of chemical and mechanical control have also been reported to be effective (Willard et al., 1996). However, repeat applications are necessary for complete control (ie. long-term control). The bare soil, which results when chemical control is successful, may lead to soil erosion and the potential for reinfestation. Thus, simply suppressing *I. cylindrica* with a herbicide will not prevent reinfestation and may have undesirable consequences.

Little regard has been given to revegetation of infested areas, and the long-term control of *I. cylindrica* in range-land and forest situations can only be achieved by changing the vegetation from a dominant monoculture of *I.* cylindrica to a competitive, diversified plant community. Replacing *I. cylindrica* would require integrating chemical suppression with biological suppression. If managed properly, plant species used to suppress *I. cylindrica* could could eventually replace it. Plants used as cover crops, smother crops, or green manure have the potential to increase soil nitrogen, improve soil properties, increase biological activity in the soil, and control weeds (Akobundo, 1992; Buckles, 1995; Sanchez and Benites, 1987). For example, *Mucuna* spp. is a vigorous, climbing legume which has been used for centuries as a cover crop and green manure in the tropics (Buckles, 1995).

Akobundo (1992), in Ibadan, Nigeria, reported that *Mucuna pruriens* (L.) Var *utilis* (Wight) Burck, *Pueraria phaseoloides* (Roxb.) Benth., *Centrosema pubescens* Benth, and *Psophocarpus palustris* Desv. used as live mulches prevented erosion, added organic matter to the soil, reduced the need for nitrogen fertilizer, suppressed weed growth and depleted the soil weed-seed bank. In Yurimaguas, Peru, *Pueraria phaseoloides* was used as a fallow crop to preserve agroecosystem diversity, limit weed pressure, and sustain production in humid tropic oxisols and ultisols (Sanchez and Benites, 1987).

In the southern United States, *I. cylindrica* has invaded rangelands, roadsides, forests, and reclaimed mining sites. Little attention has been given to maintaining these areas free of *I. cylindrica* once initial control measures have been implemented. Therefore, the objective of this study was to determine if the integration of several control methodologies could provide sustained long-term control of *I. cylindrica*.

Materials and Methods

Studies were conducted in central Florida from 1993 to 1995 on reclaimed phosphate strip-mined land. In 1993 the study was located at a reclaimed phosphate mining site on which the original top soil had been returned (IMC-Agrico Mining). The soil before mining was a sandy, silacious haplaquad (97.5% sand, 2.2% silt, 0.3% clay) (USDA/SCS, 1990). The area was a *Paspulam notatum/Indigofera hirsuta* (L.) pasture which had become severely infested with *I. cylindrica*. In 1994 the study was located on a reclaimed clay "settling pond." Waste clays are a by-product of phosphate mining and are pumped into impoundments (settling ponds). These soils are classified as hydraquents and are approximately 85% montmorillonite, kaolinite, and illite clay, 10% silt and 5% sand. The soil was poorly drained and some areas of the study site were subjected to seasonal flooding.

The studies were arranged in a 2 by 3 by 5 factorial, split-split plot design with four replications on 6 by 6 m plots. Main plots consisted of fertilizer [450 kg/ha of N(10)-P(10)-K(10)] or no fertilizer, sub-plot treatments were glyphosate (as Roundup, 360 g ai/l, Monsanto Agricultural Co.), imazapyr (as Arsenal, 240 g ai/l, American Cyanamid Co.), or an untreated control, and the sub-subplots were revegetation species (*Indigofera hirsuta* (L.), *Lolium perenne* (L.), *Paspalum notatum* Flugge, *Panicum virgatum* (L.)/*Cassia fasciculata* Michx., and an unseeded control). In 1994, *Cynodon dactylon* (L.) replaced *L. perenne*.

In 1993, herbicides (2240 and 840 g a.i./ha of glyphosate and imazapyr, respectively) were applied to *I. cylindrica* on 25 July, and on 17 September the area was mowed, main plots fertilized, the entire area disced, and desirable species seeded to designated sub-subplots. In 1994, the area was burned in May, herbicides applied (1993 rates) to regrowth on 01 June, and subsequent fertilizing and seeding completed on 29 June 1994. Herbicides were applied using a CO_2-pressurized back-pack sprayer and hand-held boom equipped with 8003 flat fan nozzle tips delivering 280 l/ha at 210 kPa pressure. Above-ground biomass was collected from a 1 m^2 area within each plot 12 months after the final treatment (MAT), sorted into seeded species and *I. cylindrica*, dried and weighed. Data were subjected to analysis of variance to test for main effects and interactions. Means were calculated and are presented with standard errors. Data from each year are presented separately.

Results

1993 season

In 1993 *Indigofera hirsuta* was the only species to establish uniformly and data are not shown for the others. A species by herbicide interaction existed for biomass of seeded species in 1993 at the $p<0.01$ level (Table 1). *Indigofera hirsuta* was the most competitive of all species evaluated

in 1993 regardless of herbicide used, producing 395, 654, and 297 g/m^2 of above-ground biomass in combination with glyphosate, imazapyr and an untreated control, respectively. These same treatments provided 63, 100, and 53% control, respectively, of *I. cylindrica* relative to the untreated/unseeded control. The interaction occurred because imazapyr was the most effective herbicide for *I. cylindrica* control and *I. hirsuta* is relatively tolerant of imazapyr. Thus, the greatest *I. hirsuta* growth, and, consequently, the least *I. cylindrica* growth, occurred with the imazapyr/*I. hirsuta* combination. *Indigofera hirsuta* is an annual legume native to tropical Africa and Asia, growing erect, and is adapted to well-drained, somewhat dry, sandy soils. It is an excellent green manure and provides high quality forage when immature (Baltensperger et al., 1985.). A mixture of *C. fasciculata* and *P. virgatum* after imazapyr treatment provided 86% control of *I. cylindrica* at 12 MAT (data not shown). Although no *C. fasciculata* or *P. virgatum* biomass was measured at 12 MAT, both species had emerged and grew in the year of seeding and control was likely due to this growth and residual activity of imazapyr. These species are Florida natives (Hall, 1978), *C. fasciculata* found in open woodlands, prairies, and occasionally along streambeds on poorly-drained soils, and *P. virgatum* found anywhere from pond margins and wet prairies to *Quercus* ridges. As native, wild species, they are suitable for reclamation of natural ecosystems, but uniform germination and seedling establishment are difficult due to dormancy mechanisms and non-viable seed. Combinations of imazapyr and *P. notatum*, a perennial, tropical forage grass, or *L. perenne*, a perennial, cool-season grass, provided less control than imazapyr alone. *Lolium perenne* may be useful as an initial revegetation species for the cool season of the sub-tropics, but will not survive extreme temperatures of summer. *Paspalum notatum* is slow to establish and may be limited in use for revegetation where *I. cylindrica* remains competitive.

Regardless of species seeded, imazapyr provided superior control to glyphosate (Table 1). Although biomass data was collected only up to 12 MAT, plots treated with imazapyr and seeded with *I. hirsuta* remained free of *I. cylindrica* 24 MAT, apart from some encroachment from adjacent plots. Poor establishment of the seeded species was attributed to two factors. One, most grew slowly and were not able to overcome *I. cylindrica* interference even after suppression with glyphosate. Two, imazapyr provided longer term suppression of *I. cylindrica*, but soil residual activity prevented growth of all but *I. hirsuta*.

1994 Season

A species by herbicide interaction ($p<0.1$) existed for *I. cylindrica* biomass in 1994. The greatest control (55%) of *I. cylindrica* was achieved with a combination of imazapyr and an *P. notatum* (data not shown), followed by imazapyr and the unseeded check (40% control) (Table 2). *Cynodon dactylon* was the only species established in any plots at 12 MAT, but control achieved with it and imazapyr was only 13%. Once again, an interaction occurred because *C. dactylon* is more tolerant of glyphosate than imazapyr and grew well, adding to long term *I. cylindrica* control. Because persistence of the seeded species was poor or nonexistent, suppression of *I. cylindrica* in 1994 may be attributed more to the herbicide. However, most seeded species grew well during the first 3 months after seeding and may have hindered re-establishment of *I. cylindrica* in the early stages.

Combinations of glyphosate and revegetation species were not significantly different from the untreated control. *I. hirsuta*, which grew vigorously in 1993 on well-drained sand, grew well and formed a canopy in some areas in the year of seeding in 1994, but did not re-establish the following season. By 12 MAT only a few *I. hirsuta* plants remained. *C. dactylon*, an unimproved forage species, likewise started well from seed but by 12 MAT only plots on higher, more thoroughly-drained ground contained a strong stand. As a result, although growth of *C. dactylon* cover was impressive and *I. cylindrica* absent in some areas, the results were inconsistent.

Table 1. Above-ground biomass of *Imperata cylindrica* and *Indigofera hirsuta* as influenced by herbicide in 1993 (12 months after treatment).

	Seeded with *I. hirsuta*	Unseeded
	Biomass of *Imperata cylindrica (g/m2)*	
Glyphosate	66 ±27	108 ±34
Imazapyr	0 ±0	77 ±28
Untreated	85 ±32	179 ±37
	Biomass of *Indigofera hirsuta* (g/m2)	
Glyphosate	395±94	-
Imazapyr	654±62	-
Untreated	297±80	-

Table 2. Above-ground biomass of *Imperata cylindrica* and *Cynodon dactylon* as influenced by herbicide in 1994 (12 months after treatment).

	Seeded with *C.dactylon*	Unseeded
	Biomass of *Imperata cylindrica (g/m2)*	
Glyphosate	322±59	370±46
Imazapyr	272±83	186±55
Untreated	349±53	312±43
	Biomass of *Cynodon dactylon* (g/m2)	
Glyphosate	30±30	-
Imazapyr	46±31	-
Untreated	37±37	-

Control provided by both herbicides and all herbicide/species combinations was poor in 1994 (Table 2). Most species emerged and developed in the summer of seeding but died-back or did not re-seed the following year. Numerous factors may have contributed to poor control of *I. cylindrica* and limited growth of revegetation species. The stand of *I. cylindrica* on the 1994 site was more dense, with a biomass of 499 g/m^2 compared to 179 g/m^2 of above-ground biomass in the 1993 untreated checks. Rhizomes developed only in the top 10 to 15 cm of soil at the 1993 site. Rhizomes on the clay settling pond (1994 site) were consistently found at depths of 80 cm. Finally, the high clay content of the soil in 1994 probably contributed to greater binding and less residual activity of imazapyr, relative to the sandy soil of 1993. The imidazolinone family of herbicides, of which imazapyr is a member, become somewhat less biologically available as clay content increases (Mangels, 1991).

Discussion

Revegetation with desirable species after chemical suppression of *I. cylindrica* is necessary for sustained, long-term control. This study emphasizes the importance of choosing plant species suitably adapted for specific situations, and with adequate tolerance to the herbicides commonly used for *I. cylindrica* management. Imazapyr, while providing greater control of *I. cylindrica* than glyphosate, is generally nonselective and has soil residual activity. Glyphosate has no residual activity and could offer flexibility in timing and species selection for revegetion. *Indigofera hirsuta* performed well on a well-drained, sandy soil but grew poorly on a heavy clay soil. Only *I. hirsuta* in 1993 became established, and in 1994 no desirable plant species grew well. Characteristics of species to be considered for future revegetation of clay settling ponds include tolerance of poor drainage, and the ability to establish quickly due to the vigor of *I. cylindrica* on clay. Effective, sustained suppression of *I. cylindrica* is possible as demonstrated in 1993 with imazapyr and *I. hirsuta*.

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Factors Limiting the Distribution of Cogongrass, *Imperata cylindrica*, and Torpedograss, *Panicum repens*[1]

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Abstract. Greenhouse, growth chamber, and laboratory studies were conducted to determine anatomical and morphological characteristics and cultural practices limiting the distribution of cogongrass, torpedograss, and johnsongrass in the United States. Cogongrass did not produce axillary buds along most of the rhizome nor regenerate when apical six-node-long rhizome segments were buried deeper than 8 cm. Both torpedograss and johnsongrass produced axillary buds along the entire lengths of their rhizomes. Torpedograss shoot emergence decreased at burial depths between 8 and 16 cm. Shoot emergence from johnsongrass rhizomes was not affected by burial as deep as 16 cm. Rhizomes of all three species were tolerant of desiccation. Cogongrass grew better in soil at pH 4.7 than in soil at pH 6.7, whereas torpedograss and johnsongrass grew equally well in either pH. It is postulated that cogongrass spread is limited by lack of axillary bud formation on most of the rhizome and the inability of rhizomes to send up new shoots if buried deeper than 8 cm. These factors could account for the intolerance of cogongrass to cultivation. Torpedograss appears to spread only vegetatively due to the lack of viable seed production. Nomenclature: Cogongrass, *Imperata cylindrica* (L.) Beauv. #[3] IMPCY; torpedograss, *Panicum repens* L. # PANRE; johnsongrass, *Sorghum halepense* (L.) Pers. # SORHA.
Additional index words. Replacement series, temperature, *Sorghum halepense*, PANRE, IMPCY, SORHA.

INTRODUCTION

Cogongrass and torpedograss are perennial, rhizomatous, C_4 grasses introduced into the United States in the late 19th and early 20th centuries. Currently, both are serious weeds in certain areas of Florida and along the Lower Coastal Plains of Alabama and Mississippi (2, 5, 11, 22).

Cogongrass spreads by rhizomes and seed (4, 11, 12). A single plant may produce as many as 3000 seed (8). The small, plumed, one-seeded spikelets may be carried great distances by wind but average flight is approximately 15 m (9). Seed are capable of germinating immediately. Cogongrass seed does not require an afterripening period (3). It germinated best (>70%) in light at about 30 C and remained viable for at least 1 yr under laboratory conditions. The spread of cogongrass from coastal areas inland in Asia appears to be by seed, primarily along rights-of-way bordering highways and railways (9). The distribution and spread of cogongrass northward in Alabama from 1973 to 1985 appears to have been due to the northeasterly prevailing winds off the Gulf of Mexico along Interstate 65 (22).

The ready production of rhizomes by cogongrass plants facilitates rapid spread at new colonized sites. In controlled-environment experiments, it was found that cogongrass started from rhizome fragments could produce up to 168 new rhizomes in 87 days (11). When plants were started from seed, rhizome production began within 30 to 40 days (11).

Cogongrass is controlled by cultivation (7, 13) and hence is rarely found in cultivated fields (13). Little regrowth from cogongrass rhizomes occurs under simulated cultivated field conditions (13). This was attributed to a lack of adaptation to regeneration from cultivation. Also there was reported difficulty in regenerating plants from rhizome fragments unless individual plantlets were planted (13). However, even small fragments of cogongrass rhizomes could produce new plants (9). New plants were produced from terminal sections of rhizomes (12). Peng (13) and Hubbard (9) failed to report whether the rhizome fragments they used were terminal sections. Most viable buds are located at the nodes on the apical portion of the rhizome (17).

In the United States, torpedograss is believed to spread only by rhizomes. In Taiwan, torpedograss does not produce viable seed (13), but in Portugal, torpedograss is spread by seed[4]. In Florida, torpedograss reportedly can spread by both seed and rhizomes (19). However, no citations or data are presented to substantiate this claim. Unlike the situation with cogongrass, moderate cultivation fails to control torpedograss; rather it may accelerate its rate of spread (13). This is attributed to a lack of apical dominance of torpedograss rhizomes, a high rhizome regeneration rate, and the ability of the plant to absorb and store water and nutrients during periods of environmental stress.

The relative competitive abilities of weed and crop species are not constant but vary with environmental conditions, including soil pH (1, 15, 23). Weed competitive ability varied with both soil pH and the competing species (21). Decreasing soil pH might result in gradual, long-term changes in weed species composition through competitive interactions. This may be an important factor in weed ecology because soil acidification is increased by the use of acid-forming nitrogenous fertilizers (21).

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[3]Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

[4]Moreira, I. 1978. Propagation of *Panicum repens* by seed. Weeds and herbicides in the Mediterranean Basin. Proc. Mediterr. Herb. Symp., Madrid, Spain. Ministerio de Agricultura. Vol. 1:1–7.

The objectives of this research were to determine: a) whether torpedograss produces viable seed; b) how cogongrass is controlled by cultivation; and c) whether soil pH affects the relative competitiveness of cogongrass, torpedograss, and johnsongrass (included for comparative purposes).

MATERIALS AND METHODS

Plant collection and growing conditions. Plants and seed of cogongrass were collected from Grand Bay, AL; torpedograss plants and seed were collected from Pascagoula, MS; johnsongrass seed and rhizomes were supplied by Dr. Gene Wills, Delta Branch Experiment Station, Stoneville, MS. The grasses were planted and maintained in flats in a greenhouse to produce a source of rhizomes for the experiments. The plants received natural light, and temperatures ranged from 15 to 40 C.

Torpedograss seed germination study. Mature seed of torpedograss were collected from Pascagoula, MS, in August of 1982 and 1983. The seed were air dried and stored in polyethylene bottles at room temperature.

For all experiments, lots of 50 torpedograss seed were placed on two layers of Whatman No. 1 filter paper moistened with 9.0 ml of distilled water or test solution in 9-cm-diam petri plates. Seed were recorded as germinated if after 14 days the radicle extended 2 mm through the pericarp. A completely randomized design was used for each experiment with four replications for each treatment, and each experiment was repeated three times. The germination experiments were conducted within 4 months of seed collection and were repeated 1 yr later for seed collected in August 1982.

Temperature and light. Seed were placed in either continuous light or dark, or in a 16-h photoperiod at continuous temperatures of 15, 20, 25, and 30 C or at alternating 30/25 and 25/20 C. The high temperatures in the alternating temperature regime coincided with the 16-h photoperiod. Complete darkness was obtained by wrapping the petri dishes in four layers of aluminum foil.

Scarification. Germination was measured after two different seed coat scarification methods: seed soaked in concentrated sulfuric acid for 5, 10, 15, or 20 minutes, then rinsed with three changes of water; and seed tumbled in a sandpaper-lined drum for 10, 20, or 30 s. Seed were then placed in continuous light or darkness or in a 16-h photoperiod at 25 C or 25/20 C.

Chemical stimulators. Germination was measured after two different potential chemical stimulation tests: GA_3 treatment at 1.0×10^{-8} M, 1.0×10^{-6} M, or 1.0×10^{-4} M; and seed treated with KNO_3 at 1.0×10^{-4} M, 1.0×10^{-2} M, or 1.0 M solutions.

Rhizome desiccation study. Apical, six-node-long rhizome sections were excised from plants and allowed to air dry at room temperature to various percentages (35 to 60%) of the initial fresh weights. Following desiccation, rhizomes were planted 2 cm deep in commercial potting soil[5] in 15-cm-diam pots (volume 1.6 L, one rhizome section per pot). Five replicates of each treatment for each species were used, with the experiment repeated twice. All pots were watered just to excess daily with demineralized water. Shoot emergence was recorded 30 days later.

Rhizome depth-of-emergence study. Apical, six-node-long rhizome sections were planted at depths of 2, 4, 8, and 16 cm in the commercial potting soil[5] which had been watered to field capacity and placed inside 15-cm-diam plastic pipe sections (30 cm long) standing upright on aluminum plates. One rhizome section was used per pipe section. Pipe sections were weighed and watered daily to maintain the soil at field capacity.

The experiment was conducted in a growth chamber for a 30-day period with a 16-h photoperiod and a day/night temperature regime of 29/21 C. Photosynthetic photon flux density (PPFD) at the top of the pots was 450 $\mu E \cdot m^{-2} \cdot s^{-1}$. Cylinders were arranged in a randomized complete block, each block of three species at each of the treatment planting depths was replicated four times, and the experiment was performed four times. The number of emerged aerial shoots after 30 days was recorded for each species. At the start of each experiment, an additional four, six-node-long, apical rhizome sections of each species were oven dried for 48 h at 60 C, and weighed, and mean dry weights per section were calculated.

Germination of rhizome sections. Apical rhizome sections (10 cm long) were excised from vigorously growing plants of each species. The apical 2 cm was excised from one-half of these sections to give 8-cm-long sections without apices. Both decapitated and intact rhizome sections were planted 2 cm deep in commercial potting soil[5] in 15-cm-diam pots (volume 1.6 L, one rhizome section per pot). All pots were watered just to excess daily with demineralized water.

The experiment was conducted in a greenhouse with an average day/night temperature regime of 32/21 C. Thirty days after planting, shoot emergence was recorded.

Pots were arranged in a randomized complete block, each block of six treatments (three species with two rhizome lengths) was replicated 15 times, and the experiment was repeated three times.

Location of axillary buds on rhizomes. Intact rhizomes and cross-sections of the nodal regions of rhizomes of each species were examined for the presence of axillary buds with a dissecting microscope. The same rhizome sections and nodal cross-sections were fixed in FAA, dehydrated through an alcohol series, and transferred to amyl acetate. Next, the specimens were critical-point dried in a pressure bomb by replacing the amyl acetate in the tissue with liquid CO_2 and then increasing the temperature and pressure of the system until all the CO_2 present simultaneously entered the gaseous phase. This method produces dry specimens undamaged by the effects of surface tension (14). Specimens were mounted on aluminum stubs with double-stick tape, coated with gold-palladium, and examined with a

[5] Pro-mix. Capitol Agric. Serv. and Supply Co., Montgomery, ...

scanning electron microscope[6] at 5 kV to confirm the light microscope findings.

Soil pH and interference. A greenhouse study was conducted to investigate the effects of soil pH and inter- and intraspecific plant interference on the growth and relative competitiveness of cogongrass, torpedograss, and johnsongrass. The plants received natural light supplemented with 16 h of incandescent light (10 $\mu E \cdot m^{-2} \cdot s^{-1}$ PPFD) for photoperiod control only. Temperatures varied between 14 and 41 C with an average temperature of 34 C day and 22 C night. The soil was fertilized before the start of the experiment as prescribed for forage production by the Alabama Cooperative Extension Service. Thirty days before the start of the experiment, 2.0 g $CaCO_3$/296 g soil was added to some of the soil (Rhodic Paleudult) and watered daily with demineralized water. This 30-day period permitted soil pH level to stabilize before planting. The two soil pH levels were 4.7 and 6.7, representing typical pH's for uncultivated and cultivated soil in the Southeastern United States.

The experiment was arranged as a randomized complete block experiment with a factorial arrangement of treatments, combining two soil pH levels [untreated soil (pH 4.7) and $CaCO_3$-adjusted soil (pH 6.7)] each with three interference levels (nine treatments) giving a total of 18 treatments. The nine interference treatments were obtained through the use of a modified replacement series design (15) and were grouped into three levels. The first level of three treatments had no competition (plants of each species growing with one plant/pot). The second level had three treatments with intraspecific competition (each species growing in monoculture at a density of two plants/pot). The third level consisted of three treatments with interspecific competition (cogongrass with johnsongrass, cogongrass with torpedograss, torpedograss with johnsongrass) with one plant of each species/pot. Treatments with one plant/pot (first level of treatments) provided a check for the effect of intraspecific and interspecific competition. The six treatments with two plants/pot (second and third levels of treatments) can be interpreted as three interlocking replacement series, one for each of the three possible pairs (6). Each block of nine interference treatments was replicated six times at each of the soil pH levels. The entire experiment was repeated. Six-node-long apical rhizome sections were planted 2.5 cm deep in 15-cm-diam pots (volume = 1.6 L) containing 1.2 L of soil. All pots were watered just to excess with demineralized water each morning. To minimize interference between plants in different pots, a bench area of 0.4 m^2 was allocated to each of the nine pots.

Plants were harvested after 56 days and roots and rhizomes were washed free of soil. Plant height (to the tip of the longest extended leaf) and leaf area were measured. Plants then were separated according to species, treatment, and plant part (leaves, stems, or roots and rhizomes). The plant parts were oven dried for 48 h at 60 C. Leaf, stem, root-rhizome, and total dry weights were recorded. At the start of the experiment, an additional 10, six-node-long, apical rhizome sections of each species were dried for 48 h at 60 C, and mean dry weights/section were calculated to determine average initial dry weights.

Analyses of variance were performed with selected comparisons of treatment means made by analysis of variance partitioning of degrees of freedom with single degree of freedom contrasts. Data from duplicate experiments were combined because results of the replicate experiments did not differ significantly according to analysis of variance.

RESULTS AND DISCUSSION

Torpedograss seed germination study. Torpedograss seeds failed to germinate with any of the germination-inducing treatments (data not shown). These results support Peng's Taiwan findings (13) that torpedograss does not produce viable seed. Thus, torpedograss apparently spreads only vegetatively in the lower coastal plains of the United States. However, since no vital test, such as tetrazolium, was performed, the possibility of deep dormancy cannot be discounted. Both cogongrass and johnsongrass growing in this area produce viable seed (data not shown).

Rhizome desiccation study. Air-drying of cogongrass, torpedograss, and johnsongrass rhizomes to 35 to 60% of initial fresh weight had no effect on subsequent regrowth (data not shown). The marked tolerance to desiccation of all three species would suggest that cogongrass intolerance to cultivation probably is not due to desiccation following exposure of previously buried rhizomes.

Rhizome depth-of-emergence study. Emergence of cogongrass and torpedograss was significantly reduced at burial depths greater than 4 cm, but the emergence reduction for cogongrass was much greater than for torpedograss (Table 1). Johnsongrass emergence was not significantly reduced at any burial depth. The reduced emergence of cogongrass when rhizomes are buried deeper than 4 cm may partially explain why this grass is controlled by cultivation (7, 13).

Table 1. Effect of planting depth on the emergence of cogongrass, torpedograss, and johnsongrass shoots.

Planting depth	Shoot emergence from 16 rhizomes after 30 days[a]		
	Cogongrass	Torpedograss	Johnsongrass
(cm)	(no.)		
2	15 a	14 a	15 a
4	15 a	16 a	15 a
8	3 b	11 c	14 a
16	0 c	4 b	13 a

[a]Treatments sharing the same letter within each row and column are not significantly different at the 5% level (selected comparisons made by analysis of variance partitioning of degrees of freedom with single degree of freedom contrasts).

[6]Model ISI SS-40. Internation Scientific Instruments, Massan, South Korea.

Table 1. Effect of removing the apical 2 cm of rhizomes of cogongrass, torpedograss, and johnsongrass rhizomes on shoot emergence.

Species	Shoot emergence from 30 rhizomes after 30 days[a]	
	Apex removed	Apex intact
	(no.)	
Cogongrass	1 a	29 b
Torpedograss	28 b	29 b
Johnsongrass	29 b	28 b

[a]Treatments sharing the same letter within each row and column are not significantly different at the 5% level (selected comparisons made by analysis of variance partitioning of degrees of freedom with single degree of freedom contrasts).

Germination of rhizome sections. The removal of the apical 2 cm of a 10-cm-long apical rhizome section generally prevented new shoot regrowth from cogongrass rhizomes but not from johnsongrass and torpedograss rhizomes (Table 2).

Location of axillary buds on rhizomes. An investigation of the whole rhizome systems of cogongrass showed an interesting developmental pattern. During the process of aerial shoot formation the rhizome apex grew upwards, and axillary buds at that site grew out to form new rhizomes. However, rhizome nodes further from the apex lacked axillary buds. Investigation of those nodes by stripping away the leaf sheath and observing the rhizome surface with the SEM (Figure 1) failed to disclose any evidence of axillary bud formation.

Generally, disconnection and fragmentation of a rhizome into nodal segments induces activation of buds in many rhizomatous grasses (10). Based on these observations, it would appear that much of the cogongrass rhizome system fails to produce axillary buds. Both torpedograss (Figure 2) and johnsongrass (Figure 3), however, produce axillary buds along the entire lengths of their rhizomes. Figure 2 is a scanning electron micrograph of an axillary bud on a rhizome node of torpedograss. Growth of these axillary buds leads to the subsequent production of numerous aerial stems. Figure 3 shows a surface view of an axillary bud at the node of a johnsongrass rhizome.

Restriction of axillary bud formation to the apical region of cogongrass is probably of major importance in slowing the spread of the species. Absence of axillary buds along the rest of the rhizome length, together with the inability of terminal rhizome fragments to grow if buried deeper than 4 cm, could explain why cogongrass is controlled by cultivation (7, 13). Fragmentation of the cogongrass rhizome system by cultivation would produce many rhizome fragments, but only a few apical pieces would be capable of producing aerial shoots. This lack of regrowth potential, plus the deep-turning action of a moldboard plow burying



Figure 1. A scanning electron micrograph (SEM) of a node of cogongrass at some distance from the site of aerial shoot formation. The leaf sheath has been partially removed. No axillary bud is present. LS = leaf sheath. Bar equals 0.5 mm.



Figure 2. SEM of a rhizome node of torpedograss. An axillary bud associated with trichomes is evident. AB = axillary bud, AR = adventious root, T = trichome. Bar equals 0.5 mm.

Table 3. Effects of soil pH and species interference on dry matter production, height, and leaf areas of cogongrass.

Species	Competitor	Dry matter production[a]		Plant height[a]		Leaf area[a]	
		Soil pH					
		4.7	6.7	4.7	6.7	4.7	6.7
		(g/plant)		(cm)		(cm^2/plant)	
Cogongrass	None	5.8 a	4.4 b	24.9 a	23.7 a	460 a	330 b
	Cogongrass	2.9 bc	2.2 c	19.8 a	19.7 ac	210 b	160 c
	Torpedograss	3.5 b	3.3 bc	20.2 a	17.1 bc	260 bd	240 d
	Johnsongrass	2.3 c	2.3 c	13.5 b	13.9 b	160 c	160 c

[a]Treatments sharing the same letter within each species, row, and column are not significantly different at the 5% level (selected comparisons made by analysis of variance partitioning of degrees of freedom with single degree of freedom contrasts).

the cogongrass rhizomes, would effectively reduce regrowth. The lack of extensive axillary bud formation by cogongrass may provide an explanation for the contradictory findings of Peng (13), who reported no sprouting from rhizome fragments, and of Hubbard (9) who reported that even small rhizome fragments can generate new plants. Neither scientist reported whether apical portions were among the rhizome sections used.



Figure 3. An axillary bud at the node of a johnsongrass rhizome. AB = axillary bud. Bar equals 0.5 mm.

In contrast, mechanical cultivation of johnsongrass or torpedograss would produce numerous fragments, most of which would bear axillary buds capable of producing aerial shoots even if buried relatively deeply in the soil.

Soil pH and interference. Soil pH treatments never affected dry matter production (DMP) and height, or biomass partitioning in torpedograss or johnsongrass (data not shown) and rarely in cogongrass. Cogongrass DMP (Table 3) in the absence of interference was lower at the higher pH level of 6.7. The reduced cogongrass DMP at pH 6.7 may be in part the result of reduced cogongrass leaf areas (Table 3) at pH 6.7, both in the absence of interference and with intraspecific interference. However, cogongrass leaf weight ratios (LWR) (Table 4) were lower at pH 4.7 than at pH 6.7 in the presence of intraspecific interference or interspecific interference from johnsongrass. Cogongrass root-rhizome weight ratios (RRWR) (Table 4) were lower at pH

Table 4. Effects of soil pH and species interference on biomass partitioning in cogongrass[a].

Species	Competitor	Root-rhizome weight ratio[b]		Leaf weight ratio[c]	
		Soil pH			
		4.7	6.7	4.7	6.7
		(g/g)			
Cogongrass	None	0.45 a	0.40 b	0.42 a	0.45 ab
	Cogongrass	0.44 a	0.38 b	0.41 a	0.46 b
	Torpedograss	0.46 a	0.40 b	0.38 a	0.46 b
	Johnsongrass	0.47 a	0.38 b	0.41 a	0.46 b

[a]Treatments sharing the same letter within each species, row, and column are not significantly different at the 5% level (selected comparisons made by analysis of variance partitioning of degrees of freedom with single degree of freedom contrasts).

[b]Root-rhizome weight ratio (RRWR) = root-rhizome dry weight/total dry weight, (g/g).

[c]Leaf weight ratio (LWR) = leaf dry weight/total dry weight, (g/g).

6.7 regardless of presence or type of interference. Teem et al. (20) found that a low soil pH reduced the elongation of primary roots of three weed species (prickly sida, *Sida spinosa* L.; sicklepod, *Cassia obtusifolia* L.; and tall morningglory, *Ipomoea purpurea* (L.) Roth.) to different extents. Previous research (18) has shown that cogongrass grows better in acid soils.

Generally, johnsongrass and torpedograss competition reduced DMP and height of cogongrass about equally. Johnsongrass usually reduced cogongrass leaf area more than torpedograss. There were no consistent effects of interference on biomass partitioning in any species. Soil pH treatments affected biomass allocation more than competition treatments (Table 4).

The slight but significant changes in growth (DMP and height) with changes in soil pH suggest that the gradually decreasing soil pH in agricultural fields, from frequent applications of acid-forming nitrogen fertilizers, may result in long-term changes in weed species composition through gradual competitive interaction effects (1, 21). Research (16) has indicated that plant dry matter production may be a more accurate indicator of the influence of environmental and competitive interactions than other growth parameters.

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Note

Cogongrass (*Imperata cylindrica*) Distribution on Florida Highway Rights-of-Way[1]

TOMMY R. WILLARD, DAVID W. HALL, DONN G. SHILLING, JAMES A. LEWIS, and WAYNE L. CURREY[2]

Abstract. A survey of Florida highway rights-of-way was conducted during 1984–85 to determine the occurrence and severity of cogongrass infestation. Florida Department of Transportation district maintenance engineers surveyed 8,200 km of limited-access and other major highways (22% of highway system). Cogongrass was distributed widely from the north central region southward through the central Florida ridge north of Lake Okeechobee. Highest frequencies were in counties where cogongrass was used for forage and soil stabilization during the 1950s. The large, widely scattered cogongrass infestations probably were established during extensive roadway construction and routine maintenance which used rhizome-contaminated fill soil. Nomenclature: Cogongrass, *Imperata cylindrica* (L.)Beauv. #[3] IMPCY.

Additional index words: Weed dispersal, utility turf, plant introduction, IMPCY.

Indroduction

The FDOT[4] maintains 45,326 ha of roadside vegetation along 18,500 km of highway. Maintenance practices, which include mowing, fertilization, tree and brush removal, wildflower management, and selective herbicide treatments are necessary to create safe, aesthetically pleasing roadways for the resident and tourist populations (4). The FDOT allocates approximately $20 million annually for these activities.

Environmental conditions that favor establishment of turfgrass species on these rights-of-way also favor the establishment of tall undesirable perennial grasses. Glyphosate [*N*-(phosphonomethyl)glycine], dalapon (2,2-dichloropropanoic acid), and hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1*H*,3*H*)-dione] have been used to control perennial grass weeds on Florida highway rights-of-way although control is not always satisfactory (6).

In 1981, the FDOT Bureau of Maintenance cited cogongrass among nine grassy weed species requiring additional efforts beyond those needed to maintain desired turf species. Selective control of cogongrass is difficult because this weed and the desired turf species are all warm-season perennial grasses.

Cogongrass is a serious problem throughout the subtropical regions of the world as well as in Florida and other parts of the southeastern United States (9). Cogongrass adversely affects several crops and certain pasture grasses and is ranked as the seventh most troublesome weed worldwide (5). It has little utility except for thatch, short-term forage production, and soil stabilization.

Materials and Methods

This survey of Florida highway rights-of-way was conducted in 1984–85 to determine the occurrence and severity of cogongrass. FDOT maintenance engineers were involved in roadway selection, survey format, and conducting the survey while the authors verified and compiled the data. The survey area included all limited access roadways including interstate highways and the Florida Turnpike; and, where possible, at least one north-south and one east-west roadway in each county. Urban sections of roadway were excluded from the survey.

The survey data for each roadway consisted of county name, section number, roadway number, kilometer marks, and an infestation estimate based on a 0 to 3 rating scale where 0 = not present, 1 = sparse infestations, 2 = frequent infestations, and 3 = numerous large infestations. Surveyors also noted any unusual conditions favoring cogongrass growth and precise locations of major infestations.

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[3]Letters following this symbol are a WSSA-approved computer code from the Composite List of Weeds, Revised 1989. Available from WSSA, 309 W. Clark St., Champaign, IL 61820.

[4]Abbreviations: FDOT, Florida Department of Transportation; DMI, distance measuring instrument; I-75, Interstate Highway 75; I-10, Interstate Highway 10.

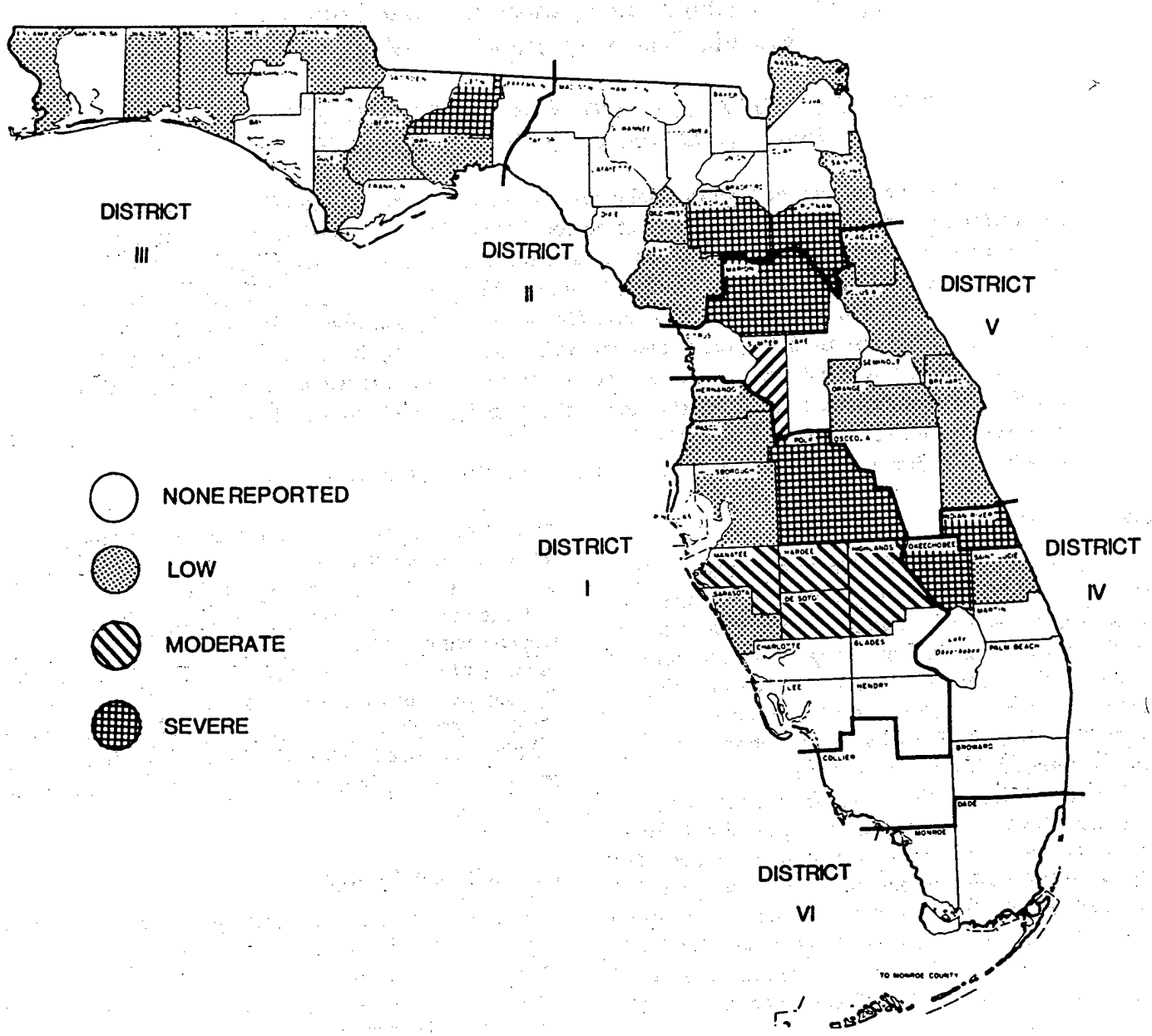


Figure 1. Occurrence and severity of *Imperata cylindrica* on Florida highway rights-of-way.

The relative intensity of cogongrass in each county was determined as follows: 1 to 5 infestations of 100 m^2 or greater–1 (low), 6 to 15 infestations–2 (moderate), and greater than 15 infestations–3 (severe).

Training seminars were conducted to acquaint personnel with the survey format and identification of cogongrass. Trial surveys of selected roadways also were conducted. Surveyors were given 18 mo to complete their surveys of assigned roadways and to recheck mowed or reconstructed areas.

Districts IV and VI surveyors (Table 1) did not use the survey form but used a K-5000 Nu-Metrics[5] DMI[4]

[5]Nu-Metrics Instrumentation, Cedar Valley Bldg., Box 471, Vanderbilt, PA 15486-0471.

Table 1. Rights-of-way distance surveyed by district in 1984–85 for perennial grass weeds by the Florida Department of Transportation.

District	Geographic region	Counties	Distance surveyed	Centerline surveyed[a]
		no.	km	%
I	SW Gulf Coastal through S Central	14	2182	28.1
II	N Central through N Atlantic Coastal	18	1709	21.4
III	West Florida (Panhandle)	16	1377	18.5
IV	SE Atlantic Coastal	7	1078	21.0
V	Central through Central Atlantic Coastal	10	1415	21.3
VI	Everglades (Monroe and Dade Counties	2	473	22.5
Statewide total		67	8200	20

[a]Percentage of centerline distance computed by dividing the kilometers surveyed by 2 to account for surveying each shoulder and dividing that value by total kilometers of rights-of-way in the district.

and printer. This instrument continuously monitored kilometers traveled. Each infestation was entered and was printed with the kilometer mark.

Results and Discussion

The geographical scope of the survey by district is presented in Table 1. Approximately 8,200 km of Florida highway rights-of-way were surveyed, representing about 92% of that designated for survey.

Rights-of-way in the north central region (Districts II and V) and the south central region (Districts I and IV) were severely infested with cogongrass (Figure 1). Historical records indicate that these locations correspond to intentional propagation of this species for forage and soil stabilization during the 1940s and 1950s (3, 7). Points of introduction in Florida include Gainesville (University of Florida Experiment Station), Brooksville (USDA Plant Introduction Station), and Withlacoochee [Soil Conservation Service reclamation area (10)].

Once introduced, cogongrass can be dispersed by two methods [seeds and rhizomes (9)]. Infestations on Florida highway rights-of-way tend to be isolated areas occurring at irregular intervals which suggests that movement of rhizome-contaminated soil during road construction and maintenance may be a major means of dispersal in Florida. Cogongrass will expand laterally 25 to 40 cm per year from established infestations (1). This may have occurred on I-75[4] and U.S. 441/301. These two roadways which traverse Alachua (District II), Marion, Sumter (District V), Polk, Highlands (District I), and Okeechobee (District IV) counties are heavily infested with cogongrass (Figure 1).

District III (covering western Florida) reported several isolated infestations. These infestations occurred on highways U.S. 90 and I-10[4]. During the 1940s cogongrass was removed from university experiment stations without authorization. An estimated 400 ha were planted in western Florida during this period (8). Transport of cogongrass no doubt occurred on U.S. 90 which was the major east-west corridor before I-10 was completed in the 1970s. Dickens (2) reported movement of cogongrass from Florida to Alabama.

West to east movement of cogongrass also may have occurred via U.S. 90 and I-10 (which parallels U.S. 90) as these two roadways pass through Grand Bay and Mobile, AL, which have been infested with cogongrass since the 1940s (7). However, observations of cogongrass along I-10 from Grand Bay to Pensacola, FL, in 1988 showed that Alabama infestations ended 15 to 25 km west of the state line and Florida infestations began approximately 15 km east of the state line (data not shown).

Tallahassee (Leon County, District III) is a major transportation hub because of the convergence of I-10, U.S. 90, and U.S. 19/27. The interchanges surrounding Tallahassee are heavily infested with cogongrass. This reinforces the hypothesis that roadway construction and maintenance may have played a major role in the distribution of cogongrass in Florida.

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The influence of growth stage and mowing on competition between *Paspalum notatum* and *Imperata cylindrica*

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Abstract

Greenhouse experiments were conducted to evaluate competition between cogongrass (*Imperata cylindrica*) and bahiagrass (*Paspalum notatum* var. *saurae* 'Pensacola') as affected by growth stage and mowing. Cogongrass ramets propagated from rhizomes were grown in pure stand and in mixture with seedling and established bahiagrass, the latter, with and without mowing. Cogongrass was more competitive than seedling bahiagrass but much less competitive than established bahiagrass. Mowing slightly increased the relative competitiveness of established bahiagrass. When grown in pure stand, two mowings caused an 8% and 21% decrease in the foliage weight of cogongrass and established bahiagrass, respectively. However, when the two species were grown in a 50:50 mixture, two mowings caused a 45% and 13% decrease in the foliage weight of cogongrass and bahiagrass, respectively. These data indicate that under conditions of no nutrient or water stress cogongrass effectively competed with seedling bahiagrass but not with established bahiagrass.

Resumen

Se realizaron experimentos en invernadero para evaluar la competencia entre Imperata cylindrica *(pasto congon)* Paspalum notatum *var. saurae 'Pensacola' (pasto bahía) influenciados por la etapa de crecimiento y corte. Clones de* I. cylindrica, *reproducidos a partir de rizomas, fueron establecidos como cultivos puros y en asociación con* P. notatum *ya establecido y en fase de plántula. Dicha asociación fue sometida a tratamientos con y sin corte.* I. cilindrica *fue mas competitivo que las plántulas* P. notatum, *pero mucho menos agresivo que* P. notatum *establecido. El corte incrementó ligeramente la competencia relativa de* P. notatum *ya establecido. En los cultivos puros, dos cortes ocasionaron una disminución de 8 y 21% en el peso del follaje de* I. cilindrica *y* P. notatum *establecido respectivamente. Sin embargo, cuando se cultivaron las dos especies en una asociación de 50:50 los dos cortes causaron una reducción de 45 y 13% del peso del follaje de* I. cylindrica *y* P. notatum *respectivamente. Estos datos mostraron que, bajo condiciones no deficientes de agua o nutrientes,* I. cylindrica *podría competir efectivamente con las plántulas de* P. notatum, *pero no cuando este se encuentra ya establecido.*

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Introduction

Cogongrass (*Imperata cylindrica*) has been reported to be a weed problem in many annual and perennial crop species (Eussen 1979; Eussen *et al.* 1976). Competition for light, water, and nutrients, physical plant injury (caused by the rhizome apices penetrating crop roots), and allelopathy have been reported to be mechanisms of cogongrass interference (Boonitee and Ritdhit 1984; Eussen and Soerjani 1975). Cogongrass infests 200 million ha in southeast Asia, several thousand ha in the southern United States, and over 500 million ha worldwide; consequently, cogongrass is considered one of the world's worst weeds (Falvey 1981; Dickens 1974; Holm *et al.* 1977).

In Florida, bahiagrass (*Paspalum notatum*) is the predominant grass used on rights-of-way and in pastures due to drought tolerance, lack of insect and disease problems, and responsiveness to fertilizer (Beard 1973). Establishment and mowing are the two major cultural practices used

for bahiagrass management on highway rights-of-way (J.A. Lewis, personal communication). In Florida, cogongrass has become a serious pest along roadways. Willard (1988) hypothesized that cogongrass has become a problem due to movement and use of rhizome-contaminated soil during bahiagrass establishment following roadway construction. However, the spread of cogongrass into undisturbed, established bahiagrass appeared to be rather slow regardless of management practices. Therefore, research was conducted to determine the influence of bahiagrass stage of development and mowing on its interaction with cogongrass.

Materials and methods

Preliminary experiments were conducted to determine the effect of population density and fertility on cogongrass and bahiagrass growth for this system. Utilizing this data, all subsequent studies were conducted using 1) a population density that would insure interspecific competition (*i.e.* yield that was independent of density) and 2) a soil fertility level that both maximized yield and alleviated interspecific competition for nutrients.

Seedling bahiagrass and emerging cogongrass competition study

The interaction of seedling bahiagrass and emerging cogongrass ramets was studied under greenhouse conditions using a replacement-series experimental design (de Wit 1960). This design allows a determination of the relative competitiveness of two plant species as affected by different factors. Cogongrass was propagated for this study from cleaned, de-scaled rhizome segments. Multi-node segments were placed horizontally in trays covered with vermiculite located in a growth chamber. The environmental conditions were: 16-hr light/8-hr dark photoperiod with a light intensity of 20 $\mu E/m^2/s$ and temperature of 30 °C. Two weeks after planting, single nodes that had produced a two-leaf shoot were cut from the multi-node rhizomes. Bahiagrass 'Pensacola' was established by overseeding and then thinning the seedlings to the desired population density. Seed of bahiagrass and cogongrass shoots were planted at the same time in 2.8 l pots containing 50% fumigated Arredondo fine sand (loamy, siliceous, hyperthermic Grossarenic Paleudult) and 50% vermiculite on a volume basis.

There were five treatments consisting of varying ratios of bahiagrass and cogongrass: pure bahiagrass (100:0), predominantly bahiagrass (75:25), equal species mixture (50:50), predominantly cogongrass (25:75), and pure cogongrass (0:100). Population densities for bahiagrass were 100, 75, 50, 25, and 0 plants per 31.4 cm^2 and for cogongrass 0, 4, 8, 12, and 16 plants per 31.4 cm^2.

All pots were watered daily and fertilized weekly with 500 ml of nutrient solution (Hoagland and Arnon 1950). The experiment was conducted in a greenhouse with the following environmental conditions: 16-hr light/8-hr dark photoperiod, daytime temperature of 30 ± 5 °C, night time temperature 25 ± 5 °C, and a mean light intensity at noon of 900 $\mu E/m^2/s$.

Eight weeks after planting, leaf dry weight, height of each species, and rhizome dry weight of cogongrass were determined. Relative yield, based on leaf dry weight, for each species was obtained by dividing the absolute yield at each ratio by the yield of each species in the pure stand. Relative yield totals were determined by adding the relative yield of each species within each ratio. Relative crowding coefficients based on leaf dry weight were determined for each species as described by Harper (1977). Briefly, the relative crowding coefficients were calculated for each species, (whose yield was determined on a per plant basis), by determining the quotient of the yield of species A (species for which the relative crowding coefficient is desired) in each mixture divided by the yield of species B (the competing species) in each mixture and the yield of species A in pure stand divided by the yield of species B in pure stand. Relative crowding coefficients were calculated for each species at three mixtures (*i.e.* species ratios): 25:75, 50:50, and 75:25.

Established bahiagrass and emerging cogongrass competition under the influence of mowing

To determine the influence of cogongrass on established bahiagrass as affected by mowing frequency, another replacement-series type experiment was conducted. The main difference to the previous experiment was that bahiagrass was established prior to planting cogongrass.

Bahiagrass was planted in 2.8 l pots at densities of 25, 50, 75, and 100 plants per 31.4 cm^2. After

Table 1. The interaction of seedling bahiagrass (B) and emerging cogongrass (C) as measured by height, foliage dry weight, and rhizome dry weight

Plant Species	Species Ratio 100B 0C	75B 25C	50B 50C	25B 75C	0B 100C
			Height (cm)		
Bahiagrass	38.2 (1.5)[1]	38.0 (1.4)	33.1 (1.7)	28.9 (1.2)	—
Cogongrass	—	54.8 (3.2)	58.8 (3.2)	65.1 (3.9)	64.5 (2.9)
			Foliage Dry Weight (g)		
Bahiagrass	24.8 (1.6)	15.2 (1.6)	10.3 (1.9)	4.6 (1.0)	—
Cogongrass	—	7.1 (1.2)	11.2 (1.4)	19.4 (1.6)	23.3 (2.3)
			Rhizome Dry Weight (g)		
Cogongrass	—	4.1 (0.8)	5.6 (0.8)	10.6 (1.2)	15.8 (1.4)

[1] Standard error of the mean.

eight weeks of growth, bahiagrass foliage above 10 cm was removed by clipping. At this time, three sets (one for each of three mowing treatments) of replacement-series treatments, similar to those previously described, were established. Single-node cogongrass rhizome segments that had produced a two-leaf shoot were planted into the bahiagrass sod to establish densities of 0, 4, 8, 12, and 16 plants per 31.4 cm^2. The cultural conditions were similar to the previous experiment.

There were three mowing treatments: no mowing, mown at 10 cm at 4 weeks, and mown at 10 cm at 4 and 8 weeks. All treatments were harvested to ground level at 12 weeks.

At each mowing, leaf dry weight of material clipped from each species was determined. At 12 weeks, leaf dry weight and height of each species and the rhizome dry weight of cogongrass were determined. Total leaf dry weight of each species was determined by adding the weight harvested at each clipping to the final weight. Relative yields, relative yield totals, and relative crowding coefficients were determined as described previously.

Experimental design and analysis

All experiments were conducted twice using a randomized complete block design with four replications. An analysis of variance was conducted to determine if the influence of single factors (species, ratios, growth stages, mowing regimes, and experiments) and interactions between these factors significantly influenced yield components (Helwig and Council 1982). Because there was no interactions between experiments and the other independent variables ($P > 0.05$), mean values were averaged across experiments and presented together with standard errors.

Results

Cogongrass maintained a height advantage over seedling bahiagrass regardless of the species mixture (Table 1). Even when seedling bahiagrass represented 75% of the species mixture, the height of cogongrass was only slightly reduced compared to its height in pure stand. Further, cogongrass reduced the foliage dry weight of seedling bahiagrass to a greater extent than bahiagrass did cogongrass. This effect was greatest for the lowest proportion of cogongrass (25%). Each produced about the same amount of foliage in pure stand.

For all species ratios, the relative crowding coefficients of cogongrass were larger than those of seedling bahiagrass (Table 2). A value of one indicates that the two species are equally com-

Table 2. The interaction of seedling bahiagrass (B) and emerging cogongrass (C) as measured by relative yield total (RYT), and relative crowding coefficient (RCC) using leaf dry weight produced by each species

	Species Ratios 100B 0C	75B 25C	50B 50C	25B 75C	0B 100C
RYT	1.00	0.90	0.88	1.01	1.00
RCC_B	—	0.67	0.86	0.67	—
RCC_C	—	1.49	1.16	1.50	—

petitive (Harper 1977). As the competitiveness of a species increases its relative crowding coefficient increases concomitantly. Regardless of species ratio cogongrass was at least 35% more competitive than seedling bahiagrass.

On the other hand, cogongrass was less competitive than established bahiagrass (Tables 3 and 4). With no mowing and bahiagrass representing just 25% of the species mixture cogongrass rhizome and foliage dry weight was reduced by 96 and 93%, respectively, whereas bahiagrass foliage dry weight was only reduced by 14%. In this experiment bahiagrass had a higher foliage weight in pure stand. In contrast to cogongrass, established bahiagrass was more affected by mowing than by the presence of cogongrass. Two mowings resulted in a reduction in foliage weight of 21% in pure stand compared with only a 8% reduction in cogongrass. Height and rhizome dry weight of cogongrass were more affected by mowing than foliage weight.

There was a significant interaction ($P < 0.05$) between mowing and growth in mixture for both species. As the number of mowings increased the growth of cogongrass in mixture decreased (Table 3). In the 50:50 mixture there was a 42 and 77% reduction in cogongrass rhizome dry weight in response to one and two mowings, respectively, and about a 45% decline in foliage weight to either one or two mowings. In contrast, established bahiagrass foliage weight when in a 50:50 mixture was only reduced by 13% by two mowings (Table 4). Nevertheless, the absolute effect (*i.e.* weight loss due to mowings) on bahiagrass was greater than that on cogongrass.

The relatively large relative crowding coefficients of established bahiagrass indicate a lack of cogongrass competitiveness regardless of the mowing treatment (Table 5). Mowing did not substantially increase the relative crowding coefficients of cogongrass regardless of species ratio.

Table 3. The influence of mowing and established bahiagrass competition on cogongrass height, foliage dry weight, and rhizome dry weight

Cogongrass Ratio	Height	Rhizome Dry Weight	Foliage Dry Weight
	(cm)	(g)	(g)
	No Mowings		
25	45.0 (1.3)[1]	0.16 (0.05)	1.3 (0.19)
50	40.8 (1.3)	0.52 (0.19)	2.9 (0.66)
75	49.3 (6.1)	0.63 (0.2)	4.0 (0.60)
100	91.4 (5.7)	15.80 (1.5)	56.6 (6.4)
	1 Mowing		
25	40.5 (1.8)	0.13 (0.08)	1.0 (0.21)
50	51.0 (4.1)	0.30 (0.1)	1.7 (0.33)
75	51.3 (1.5)	0.31 (0.1)	2.7 (0.52)
100	80.4 (5.2)	11.90 (1.8)	57.2 (3.5)
	2 Mowings		
25	38.0 (0.8)	0.14 (0.04)	1.3 (0.17)
50	40.8 (1.9)	0.12 (0.03)	1.6 (0.18)
75	45.3 (3.7)	0.31 (0.11)	2.6 (0.51)
100	62.9 (2.9)	9.60 (1.0)	52.3 (4.9)

[1] Standard error of the mean.

Table 4. The influence of mowing and cogongrass competition on established bahiagrass height and foliage dry weight

Bahiagrass Ratio	Height	Foliage Dry Weight
	(cm)	(g)
	No Mowings	
25	50.0 (2.5)[1]	82.3 (7.1)
50	49.2 (2.2)	85.8 (3.3)
75	52.8 (3.4)	85.4 (6.5)
100	49.1 (1.7)	99.8 (6.2)
	1 Mowing	
25	58.2 (3.1)	77.2 (9.7)
50	56.5 (3.5)	78.6 (4.2)
75	52.0 (3.9)	77.8 (3.3)
100	58.4 (3.6)	76.9 (4.1)
	2 Mowings	
25	51.0 (2.4)	70.6 (9.3)
50	50.2 (2.1)	74.9 (5.4)
75	51.0 (1.0)	68.9 (6.7)
100	49.5 (2.5)	78.6 (5.2)

[1] Standard error of the mean.

Table 5. The influence of mowing on the interaction of established bahiagrass (B) and emerging cogongrass (C) as measured by relative yield total (RYT) and relative crowding coefficient (RCC) using leaf dry weight produced by each species

	Species Ratio				
	100B 0C	75B 25C	50B 50C	25B 75C	0B 100C
	No Mowings				
RYT	1.00	0.88	0.93	0.90	1.00
RCC_B	—	12.4	16.8	35.0	—
RCC_C	—	0.08	0.06	0.03	—
	1 Mowing				
RYT	1.00	1.03	1.05	1.03	1.00
RCC_B	—	19.3	34.5	63.8	—
RCC_C	—	0.05	0.03	0.02	—
	2 Mowings				
RYT	1.00	0.90	0.99	0.93	1.00
RCC_B	—	11.8	31.2	54.1	—
RCC_C	—	0.08	0.03	0.02	—

However, both mowing and species ratio influenced the relative crowding coefficients of established bahiagrass with one mowing maximizing its competitiveness.

The overwhelming effect of growth stage on competition between cogongrass and bahiagrass is shown in Figure 1. The shapes of the relative yield curves for emerging cogongrass and seedling bahiagrass indicate that cogongrass was more competitive than seedling bahiagrass (Harper 1977). Cogongrass yielded relatively more than seedling bahiagrass at all species ratios and therefore contributed more to the relative yield total (Table 2). Cogongrass was less competitive than established bahiagrass regardless of the number of mowings (Fig. 1). The convex shape of the relative yield curve for established bahiagrass shows that it contributed a disproportionately large amount of the relative yield total compared to cogongrass. Mowing had only a minor effect when bahiagrass was already established.

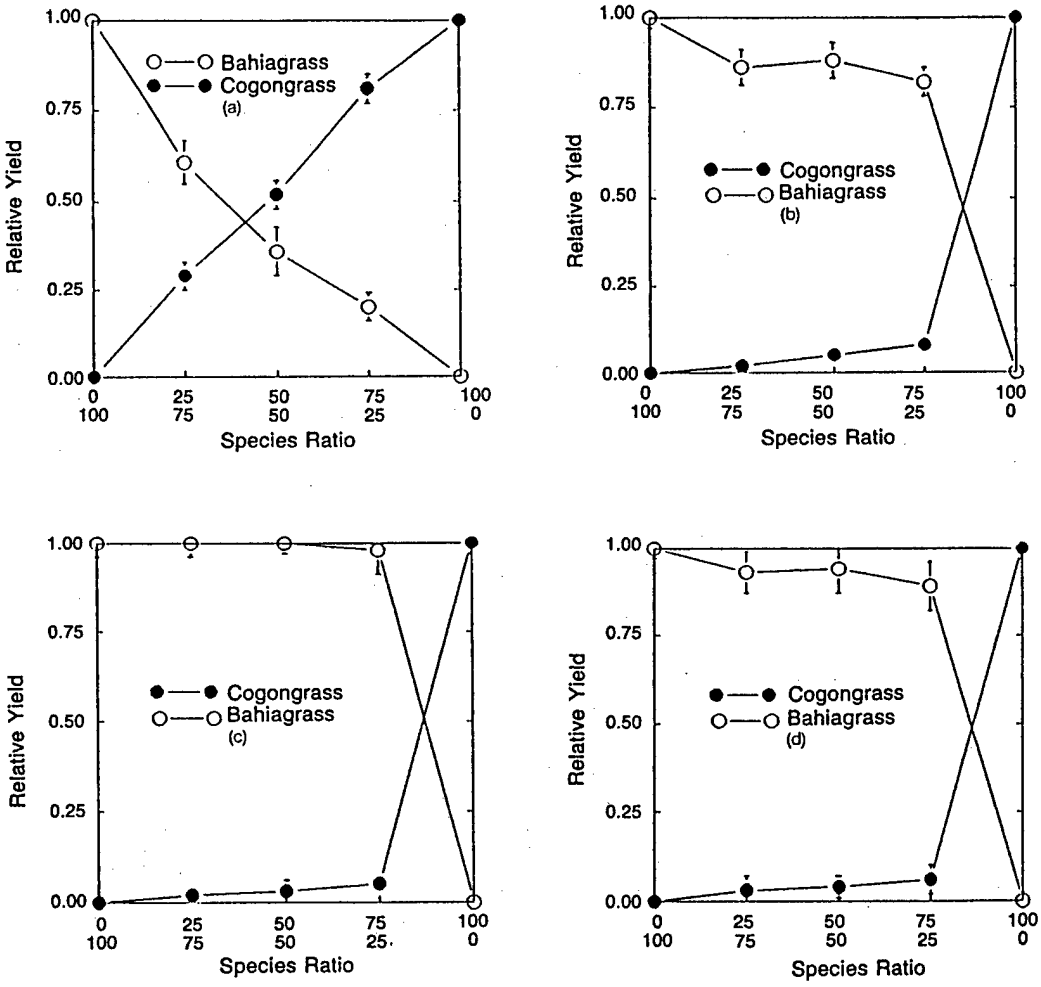


Figure 1. The influence of growth stage and mowing on interaction of cogongrass and bahiagrass measured as the relative yield of each species (based on leaf dry weight produced by each species): (a) seedling bahiagrass and emerging cogongrass; established bahiagrass and emerging cogongrass with (b) no mowings; (c) one mowing; and (d) two mowings.

Discussion

These studies were conducted using a technique that allows a determination of the relative competitiveness of two plant species. This classical de Wit method is based on plants competing at the same physiological stage of development. Therefore, prudence should be exercised when drawing conclusions based on strict theoretical interpretation of these data because cogongrass and bahiagrass were competing at different stages of development. However, from a practical point of view these data are useful if utilized to address the question of whether fragments of cogongrass can effectivenly compete with seedling or established bahiagrass.

Cogongrass ramets were shown to be relatively more effective in competing with seedling bahiagrass than with established bahiagrass. These findings support studies conducted in southeast Asia which found that cogongrass does not become dominant until disturbance releases it from competition of overstory or sub-story species (Eussen 1979; Eussen and Soerjani 1975). When these sites are disturbed by man or nature, cogongrass has the ability to compete with and eventually displace species that are at a comparable development stage. These studies also support the hypothesis of Willard (1988) as to how cogongrass became a problem along roadways. It was proposed that cogongrass became a problem in bahiagrass dominated areas through the introduction and/or distribution of cogongrass rhizomes during roadway construction which is then followed by bahiagrass seeding. These events would allow cogongrass to compete effectively with seedling bahiagrass and thereby become effectively established.

These studies also have implications as to the effects of mowing on cogongrass. Roadside vegetation management is accomplished primarily by mowing. These data indicate that mowing bahiagrass infested with cogongrass may reduce the spread of cogongrass. This would probably occur due to the re-allocation of carbohydrates used to produce new leaf tissue at the expense of rhizome growth. Decreased rhizome growth would result in decreased spread.

These short-term studies were conducted under optimal moisture and nutrient regimes which could have favoured bahiagrass. Consequently, under long-term natural conditions competition for limited moisture and nutrients may influence bahiagrass-cogongrass competition and therefore the outcome of their interaction.

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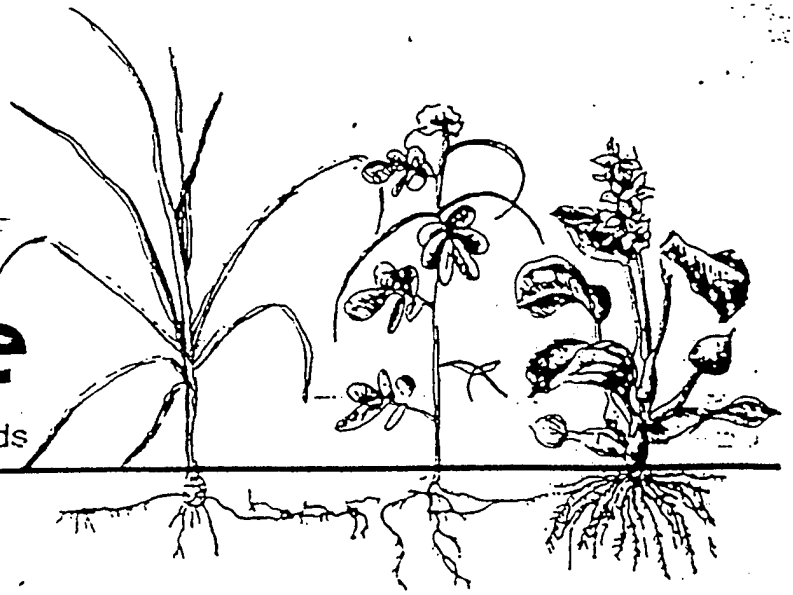
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Weeds in the Sunshine

Information for control of Florida weeds



Florida Cooperative Extension Service
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COGONGRASS

(*Imperata cylindrica* (L.) Beauv.)

BIOLOGY, ECOLOGY AND CONTROL IN FLORIDA -- 1994

D. L. Colvin, J. Gaffney and D. G. Shilling

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HISTORY

Cogongrass is an aggressive, rhizomatous, perennial grass which is distributed throughout the tropical and subtropical regions of the world. It has become established in the southeastern United States within the last fifty years, with Alabama, Mississippi, and Florida having extensive acreage of roadway and pasture infested with cogongrass. Cogongrass first appeared in the area around Grand Bay, Alabama as an escape from Satsuma orange crate packing in 1912. It was intentionally introduced from the Phillipines into Mississippi as a possible forage in 1921. Cogongrass was introduced into Florida as a potential forage and for soil stabilization purposes; subsequently, cogongrass was spread by illegal plantings, and inadvertent transport in forage and in soil during roadway construction. It cannot survive in cultivated areas but establishes itself along roadways, in forests, parks, and mining areas. It is now found from the panhandle region well into south Florida.

TAXONOMY

Cogongrass is a perennial grass that varies greatly in form, growing in loose to compact tufts with slender, erect leaves from long, tough, extensively creeping scaly rhizomes. The seedhead is branched but compacted into a dense, white, fluffy spike-like head. The plant is for the most part stemless with one to eight erect slender leaves originating from near ground level. The leaves are 1/2 to 3/4 of an inch wide, up to 4 feet long and taper to a stout point. It has a prominent white midrib that is slightly off-center (Figure 1). The leaf margins are finely serrated which makes it undesirable as a forage. The seeds are small and are attached to a plume of long hairs which facilitate long distance wind dispersal.

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ECOLOGY

Cogongrass is a native of southeast Asia and covers millions of acres of plantation and agricultural land. It is now found on every continent, although it does not tolerate cool temperatures. In the United States, cogongrass only extends as far north as South Carolina. In Florida, cogongrass has invaded ditch banks, pastures, golf courses, and forests. In central Florida, monocultures of cogongrass have become established on hundreds of acres of reclaimed phosphate mining areas. Soil type is of little consequence, as cogongrass thrives on fine sand to heavy clay and does well on poor soils of low fertility. Attempts at finding natural pests of cogongrass have met with limited success. Pathogens have been isolated but have not been developed for effective control. Cogongrass does not tolerate shade well. In Asian rubber plantations, cogongrass dies-back upon canopy formation. Reports of invasion into old growth forests in Florida suggest a more shade-tolerant eco-type has developed.

The rhizomes are responsible for the survival and short-distance spread of cogongrass. Established stands may produce over three tons of rhizomes per acre. The specialized anatomy of the rhizome allows for water conservation within which enables the rhizome to penetrate down to four feet in the soil, although the majority of rhizomes remain in the top six inches. Burning has little effect on the rhizomes of cogongrass. The duration and intensity of a fire are well below that needed to reduce the water content of the rhizomes to a lethal level. The sheer mass and persistence of rhizomes is not the only factor contributing to the ability of cogongrass to dominate an area. It has also been reported that these rhizomes exude allelopathic substances which inhibit growth of other plants. Seedhead formation is sporadic and seems to be induced by mowing, burning, or fertilization. The leaves are persistent after winterkill and are a substantial fire hazard. These factors in addition to its prolific seed production enable cogongrass to become established in many areas. As the density increases, all other vegetation may be excluded and normal succession of species will not occur.

FORAGE VALUE

Herbage yield, palatability, and nutritive value must be considered when discussing the forage value of a plant. Cogongrass has been utilized in southeast Asia as a forage due to the fact that it is the dominant vegetation on over 300 million acres. In these areas it was found that only very young shoots should be grazed or cut for hay. At this stage, the leaves lack the sharp points and razor-like leaf margins. Crude protein rarely attained the minimal 7% level needed to sustain cattle. Cogongrass yields are relatively low, even under heavy fertilization, and usually do not exceed five tons per acre. The nitrogen, phosphorus, and energy content of cogongrass is very low making supplementation essential.

CONTROL

Extensive research has been conducted in southeast Asia and the United States on the control of cogongrass. Burning, cultivation, competition, and herbicides have been used with varying degrees of effectiveness. To eliminate cogongrass the rhizomes must be destroyed or regrowth will take place quickly. Cultivation and herbicides have been the two control strategies used most

often with varying degrees of success. One of the oldest and most successful of these is to deep plow or disk several times during the dry season to desiccate the rhizomes and exhaust the food reserves held within. It is essential to cut to a depth of at least six inches to insure most, if not all the rhizomes have been cut. Results from these practices are evident when observing cogongrass growing up to the edge of a cultivated field with no evidence of spread into the field itself.

The use of herbicides for control of cogongrass began in the 1940's. Today only a handful of the hundreds of herbicides tested are effective against cogongrass. In non-crop areas such as rights-of-way and fence rows the so-called soil sterilants such as Pramitol, Spike, and Arsenal will give excellent control, however areas treated with these materials will be free of any vegetation for six months to a year. Often these conditions promote erosion and are unacceptable. In crop production areas the current chemical control alternatives are very limited. Roundup applied at 3-4 quarts per acre will substantially reduce cogongrass stands following multiple applications. However, Roundup is a non-selective herbicide and as such will control all vegetation present at the time of treatment. Subsequent to application, crops can be planted immediately because Roundup has little or no residual soil activity. If high rates (4-5 quarts) of Roundup are used, slight soil residual may exist in Florida soils; therefore a 10-14 day waiting period should be observed before revegatating with tender seeds or seedlings. Arsenal is also very effective for the control of cogongrass but has even more limitations than Roundup because of long-lived soil residual activity. Fusilade 2000 at 2 pints per acre suppresses cogongrass and is a selective grass herbicide allowing more flexibility when crops are present for revegetation. For exact rates and times of herbicide application, consult the herbicide label for most current legal information. Increasing efficacy of these herbicides may be possible with burning or mowing. While burning or mowing have little adverse effect on rhizomes and subsequent regrowth of cogongrass when used alone, they remove dead biomass. After regrowth, more thorough herbicide coverage on actively growing leaves can be achieved. Where burning is possible, a spring burning, a 3 to 4 month regrowth period, and an early-autumn herbicide application may be most effective. If burning or mowing is not possible, early autumn may remain as the most effective time of herbicide application. New, active regrowth is at its maximum at this time and interception of herbicide by dead leaves will be minimized. As is the case with tillage, repeated application of any herbicide is needed for complete control. Elimination of cogongrass using these materials alone may be realistically and/or economically impossible.

A combination of burning or mowing, tillage, and repeated herbicide applications appears to be the most viable solution to controlling cogongrass. By reducing the rhizome system with plowing or disking, or removing dead biomass with burning or mowing, treatment of regrowth with herbicides is much more effective and economical.

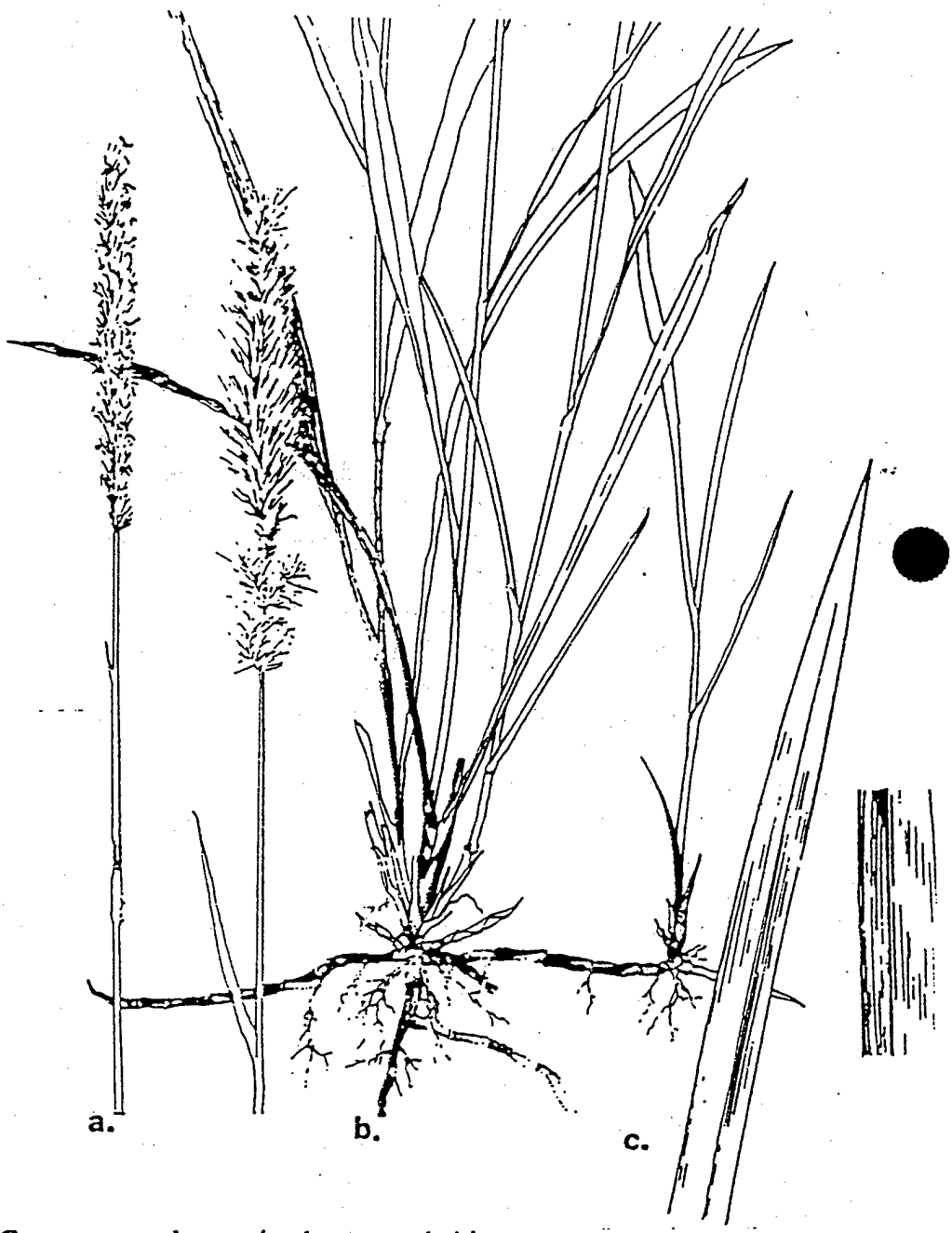
It is important that cogongrass not be allowed to continue its spread. Allowing cogongrass to grow unchecked ensures its continued spread along roadways and into pastures, mining areas, forest land, parks and

other recreation areas. If you have any questions concerning the identification and/or treatment of cogongrass contact your county extension agent or the Herbarium at the University of Florida. Line drawings that follow should assist in identification.

The use of product trade names does not constitute a guarantee or warranty of the products named and does not signify approval to the exclusion of similar products.

Prepared by: D. L. Colvin, Extension Weed Specialist, J. Gaffney, Ph.D. Graduate Student, and D. G. Shilling, Weed Scientist, University of Florida, Gainesville, FL.

Figure 1.



A. Cogongrass seedhead; B. Cogongrass plant w/scale covered rhizome system; C. Cogongrass leaves w/offset midrib.

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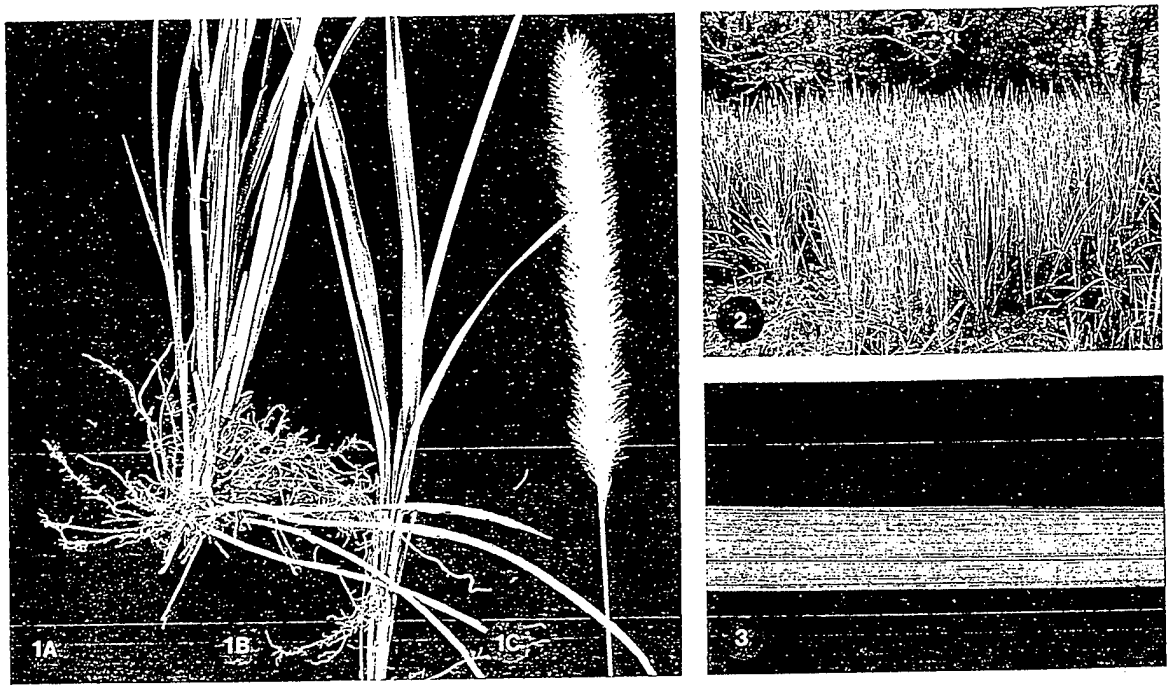
Cogongrass, *Imperata cylindrica* (L.) Beauv.: A Good Grass Gone Bad![1]

Nancy C. Coile[2] and Donn G. Shilling[3]

INTRODUCTION: Cogongrass was imported into Florida at Gainesville and Brooksville in the 1940s in hopes that it would be a good forage grass and would help control soil erosion (Hall 1983; Willard 1988). As with many too-good-to-be-true cases, cogongrass proved to be unsuited for forage and its ability to spread and displace desirable vegetation outweighed any soil erosion control considerations.

Cogongrass has features that minimize herbivory. The rough edges of mature leaves cause mammals to avoid chewing the foliage. In fact, the leaf edges may cause abrasions on persons who walk barelegged through a patch of cogongrass. Silica bodies throughout the leaves add to the unpalatabilty for grazing animals.

Cogongrass responds to stress by producing underground stems (rhizomes) and stress induces flowering. Rhizomes allow for spread and the production of additional plants with the same genetic makeup. Dense stands of cogongrass crowd out other species in the area. Rhizome production allows cogongrass to proliferate to the point where it has been designated the worst perennial grass weed of southern and eastern Asia and one of the 10 worst weeds worldwide (Holm *et al.* 1977).



Figures 1-3. *Imperata cylindrica* (L.) Beauv., Cogongrass. **Fig. 1.** A) portion of a stem with attached roots and four elongated rhizomes; B) stem with leaves; C) the plume-like inflorescence composed of many paired flowers. **Fig. 2.** Note the flowering plant at the center back. **Fig. 3.** Portion of a leaf blade, showing the off-center midrib and the scabrous leaf margins. (Photography credits: Luanne M. Marsh, Fig. 1; Jeffery W. Lotz, Figs. 2 & 3).

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Cogongrass has an allelopathic effect on other plants -- chemicals produced by cogongrass inhibit growth of other plants (Hussain *et al.* 1992). This suppressive feature may be another reason there are monotypic stands of cogongrass.

Cogongrass has the very efficient C_4 type of photosynthesis (the process of converting the energy of sunlight into food energy). Corn and several other C_4 plant species with this type of photosynthesis are usually better able to survive in hot and/or dry climates than are the more common C_3 plants.

With all these features for endurance, it is no wonder that cogongrass has proved to be a pest. In addition, cogongrass has few, if any, competitors or other control species to slow its growth and spread outside its native area. There are many plants, insects, nematodes, and pathogens which hold cogongrass in check in the Old World tropics, where it is native. To use the vernacular phrase, cogongrass has "gone bad" in Florida and in many other areas.

In the United States, cogongrass has been documented in Louisiana, Mississippi, Alabama, South Carolina and Florida (Bryson and Carter, *in press*). Cogongrass is listed by the USDA Animal and Plant Health Inspection Service, Plant Protection and Quarantine and the Florida Department of Agriculture & Consumer Services, Division of Plant Industry as a noxious weed. Cogongrass threatens pine plantations, pastures, range, and natural habitats.

DESCRIPTION: In Florida, cogongrass is most noticeable as luxuriant stands of yellowish-green grass growing along the roadsides and usually in full sun. There are many scattered patches of cogongrass along I-75, US 441, and other highways through central and north Florida. Cogongrass extends from these highways into lightly wooded stands, pastures, range, and reclaimed phosphate mine areas. Cogongrass may form large stands in the phosphate mine reclamation sites and other disturbed areas.

The growing tip of the rhizome is very sharp and may grow through the roots of other plants. The rhizomes (Fig. 1, A) of cogongrass, like those of Johnsongrass, *Sorghum halepense* (L.) Pers., have many scale-like, non-green leaves called cataphylls. Most grasses do not have such obviously scaly rhizomes.

Root systems (Fig. 1, A) of cogongrass are efficient at extracting water and minerals; they may extend to 2 meters (about 2 yd) deep. Cogongrass survives in dry, barren areas where other plants have difficulties.

Plants are usually about 1 meter tall (3 ft), but very rarely may grow to 3 m (9 ft) tall. Plants are similar to Johnsongrass. However, cogongrass leaves are longer than Johnsongrass; the stems (Fig. 1, B) are not as evident because the leaves obscure the stem; and the seedheads are covered with silky hairs. The basal leaves may be 1 m long and are much longer than the leaves higher up on the stem. In Australia, a common name for cogongrass is "blady grass" which is descriptive of the plant's leafy appearance. Leaves are up to 18 cm (about one-half inch) wide.

The leaf margins (Fig. 3) are scarious (translucent, dry) and are scabrous (rough). These rough edges will slice through skin like the leaves of *Leersia*, a grass found in the wet areas and commonly called cutgrass. The abrasions caused by the scabrous edges of cogongrass have caused some to incorrectly call the leaves saw-toothed. Gary L. Henry (Florida Department of Transportation, personal communication) has observed pigs with bloody chests and shoulders after running through cogongrass.

A quick identification feature for cogongrass is the off-center placement of the midrib, which is whitish. The off-center midrib is more apparent toward the tips of the leaves (Fig. 3).

The flowers (spikelets) are grouped into a large panicle (Fig. 1, C) about 10-20 cm (5 inches) long. Each tiny flower (spikelet) has a fuzzy, plume-like structure which can float the seed through the air. These hairy structures are shiny and give the panicle a silky appearance. When viewed with magnification, it is apparent that the spikelets are paired and one of the pair has a longer stalk. Each spikelet has two stamens and two feathery stigmas.

In Florida, cogongrass usually flowers late winter into May (Dickens and Moore 1974) or in the fall following frost (Willard 1988). Year-round flowering may occur in central and south Florida (Willard 1988). Stress, drought, cool temperatures and mowing, can force the plants into bloom at any time. It is not known whether the seed produced due to stress are capable of germination.

Variation in the plants, with as many as 17 biotypes (Charles Bryson, USDA, personal communication), indicates a species with strong adaptive potential. One variant of cogongrass is Japanese bloodgrass, whose red pigmented leaves have been praised by landscapers. Unfortunately, this red pigmentation is probably due to stress (e.g., cold) and is not consistent. The red coloration will revert to the normal green hue. These plants demonstrate the same aggressive growth features that ordinary cogongrass possesses. Since cogongrass is listed as a noxious weed, all subdivisions of the taxon (variants, subspecies, varieties, cultivars, etc.) are prohibited by both federal and State of Florida law.

CONTROL: Control of cogongrass in Florida is still problematic. Several herbicides have been tested on cogongrass, including glyphosate, paraquat, imazapyr, fluazifop, and sulfometuron (Dickens and Buchanan 1975; Buhler and Burnside 1983; Boonsritat *et al.* 1985; Lee 1985; Dean *et al.* 1988; Willard 1988; Townson and Butler 1990; Tanner *et al.* 1992; Akobundu 1993). Glyphosate or imazapyr are probably the best for Florida cogongrass where it can be applied. However, several treatments are necessary for effective control. Please refer to the control measures described in the IFAS publication "Cogongrass (*Imperata cylindrica* (L.) Beauv.) Biology, Ecology and Control in Florida" by Colvin *et al.* (*in press*).

Application of herbicides to kill cogongrass along roadsides does not present a problem of off-target drift. However, in wooded areas, care must be used to avoid herbicides which harm trees.

The dead leaves of cogongrass remain upright and do not decay easily. Dead leaves prevent herbicides from being effectively absorbed. For effective control, herbicides should be applied to green leaves. Living leaves allow the herbicide to be transported to rhizomes. When a herbicide reaches the rhizomes better control results.

The timing for application of herbicides is critical. Late fall is an excellent time to apply herbicides because plants are then sending carbohydrates into the roots and rhizomes for storage. Along with the carbohydrates, the herbicides will be translocated to rhizomes. If cogongrass is to be controlled, the rhizomes must be killed.

Cultivation can be part of control for cogongrass (Wilcut *et al.* 1988). However, cultivation alone can do more harm than good because a single disking often simply spreads the rhizomes. For more effective control, it is essential to apply a herbicide after cultivation or burning (Willard *et al.* 1990).

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Mechanical and Chemical Control of Cogongrass (*Imperata cylindrica*)[1]

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Abstract. Field studies were initiated in 1985 and 1986 to evaluate the effects of dalapon, glyphosate, imazapyr, and sulfometuron applications to established cogongrass alone or in combination with either mowing or discing. Mowing and discing treatments were performed 4 mo before and 8 months after the herbicide treatments in the 1985 experiments and 2 months before and 7 months after the herbicide treatment in the 1986 experiments. When applied alone, glyphosate at 3.4 kg ai/ha and imazapyr at 0.8 kg ai/ha caused the greatest reduction in shoot and rhizome biomass about 2 yr after application. However, the rhizome infestation was reduced only 43% by glyphosate and 51% by imazapyr, as compared to the nontreated control. With no herbicide, two mowings or discings were generally more effective than a single mowing or discing treatment. The reduction in shoot and rhizome biomass for two mowings without herbicide was 65 and 38% and for two discings, 73 and 66%, respectively. Acceptable (> 80%) levels of cogongrass control, based on reductions in rhizome biomass occurred only when applications of dalapon, glyphosate, or imazapyr were made in combination with two discings despite the fact that mowing before and after treatment reduced shoot biomass by at least 89%. **Nomenclature:** Dalapon, 2,2-dichloropropanoic acid; glyphosate, *N*-(phosphonomethyl)glycine; imazapyr, (±)-2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-3-pyridinecarboxylic acid; sulfometuron, 2-[[[[(4,6-dimethyl-2 pyrimidinyl)amino]carbonyl]amino]sulfonyl]benzoic acid; cogongrass, *Imperata cylindrica* (L.) Beauv. #[3] IMPCY.

Additional index words: Discing, mowing, perennial, tillage, weed control combinations.

INTRODUCTION

In the South Pacific and Southeast Asia cogongrass (known as alang-alang or lalang-alang) infests several million hectares (7). These regions do not have the resources to effectively control cogongrass on a large-scale basis (6). Therefore, localized efforts relying on slash-and-burn, grazing, and tillage are the most widely used control methods. Studies on the effectiveness of these techniques have indicated that: 1) shifting agriculture, in which a fallow of local plant species is maintained, may provide control long enough to produce one or two crops prior to reinfestation often at higher populations, 2) repeated burning followed by grazing will marginally support animal production, but provides little control, and 3) intensive tillage has repeatedly shown to be an effective method for cogongrass management, however the availability of implements, soil type, climatic conditions, and terrain limit its use in Southeast Asia (4, 9, 11).

Several herbicides are available for control of cogongrass (1). Much of the chemical control revolves around the use of dalapon, paraquat (1,1′-dimethyl-4,4′-bipyridinium ion), and glyphosate applied with knapsack sprayers or antiquated high-volume spray systems (5, 8, 13, 14, 15). Multiple applications are expensive, but necessary to achieve significant control and even then long-term control is seldom realized.

The integration of tillage and herbicides has been used in the United States for the control of several perennial weeds. Programs using tillage either prior to or following glyphosate applications have been used for control of Canada thistle (*Cirsium arvense* L.) (18), johnsongrass (*Sorghum halepense* L.) (16), and quackgrass (*Elytrigia repens* L.) (3).

Cogongrass has spread throughout much of Florida and is also found in other gulf-coast states (17). Many of these areas include highway rights-of-way, forests, and pastures that are routinely mowed (17). Other areas of infestation

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[3]Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, revised 1989. Available from WSSA, 1508 West University Ave., Champaign, IL 61821-3133.

include natural ecosystems, state and national parks, and reclaimed phosphate mines. Mowing has only short-term effects on perennial grass growth and little is known regarding the impact of mowing on cogongrass. Objectives of these studies were to determine the interactive effects of mowing or discing and selected postemergence herbicides on cogongrass control.

MATERIALS AND METHODS

Two studies were conducted at Chiefland, FL. One involved mowing and herbicide treatments and one discing and herbicide treatments. Mowing and discing experiments were conducted during the period 1985 to 1987. The experiments were duplicated during the period 1986 to 1988. The site for the experiments was a noncropped field heavily infested with cogongrass, and the soil type was a Sparr fine sand (loamy, siliceous, hyperthermic Grossarenic Paleudults).

The experimental design was a split-plot with mechanical treatment (mowing or discing) as the main plot and herbicide treatment as the subplot. Treatments were factorially arranged. Three input levels of mechanical treatment were used: 1) no mechanical treatment, 2) mowing or discing before herbicide treatment, and 3) mowing or discing before and after herbicide treatment. Herbicide treatments included dalapon at 16.8 kg ai/ha, glyphosate at 3.4 kg/ha, imazapyr at 0.8 kg/ha, sulfometuron at 1.1 kg ai/ha, and a nontreated control. In 1985 each treatment was replicated three times on 1.8 m by 3.7 m plots. In 1986 each treatment was replicated four times on 1.8 m by 4.6 m plots.

Mowing was done with a tractor-mounted horizontal impact-mower[4] set to remove all but the lower 10 to 15 cm of the 70-cm tall cogongrass shoots. Areas designated for discing were first mowed to ground level before being subjected to repeated discing to a depth of 10 to 15 cm. In the discing treatments, all above-ground vegetation was destroyed. Due to the dense rhizome layer, 8 to 10 passes per treatment were required. Herbicides were applied using a CO_2-pressurized backpack sprayer calibrated to deliver 280 L/ha at 207 kPa.

In the initial experiments, mowing and discing were performed on July 5, 1985 with herbicide treatments being applied on Nov. 5, 1985. Follow-up mowing and discing was performed on July 29, 1986. When the study was repeated, the initial mowing and discing was performed on Sept. 16, 1986, herbicides were applied on Nov. 14, 1986, and follow-up mowing and discing was performed on June 25, 1987.

Cogongrass control was determined on Sept. 17, 1987 and on June 23, 1988 (about 2 yr after the herbicide treatment) by harvesting the shoots from a 0.25-m^2 area in the center of each subplot. A soil-rhizome core was also extracted from this area at the time of harvest by inserting a bucket auger with a 180 cm^2 surface area to a depth of 20 cm. Rhizomes that were not decayed were removed from the cores. Shoot and rhizome samples were dried at 60 C for 72 h. Cogongrass control was based on percent reduction in biomass determined by using the dry weights of samples removed in a similar fashion from plots that received no chemical or mechanical treatment. Data were subjected to analysis of variance to test for single factor effects and interactions. There were no treatment by year interactions ($p > 0.1$) for either study; therefore, data were pooled over years for each study.

RESULTS AND DISCUSSION

There was a significant ($p < 0.1$) interaction between mowing and herbicide treatments based on the biomass of both the shoot regrowth and rhizomes (Table 1). Mowing impacted cogongrass control with and without herbicides. In the absence of any herbicide, cogongrass control increased as the number of mowings increased. One and two mowing treatments reduced shoot biomass 20 and 65%, and rhizome biomass 22 and 38%, respectively. Mowing probably affected rhizomes by depleting carbohydrate reserves as shoot regrowth occurred (12). In addition, young, succulent shoot tissue present following mowing may have been more sensitive to herbicide treatments.

Dalapon and sulfometuron provided little or no control (< 28%) when applied to cogongrass that was not mowed (Table 1). Dalapon, unlike sulfometuron, caused necrosis of the shoot tissue present at the time of treatment (data not shown). Mowing increased the effectiveness of dalapon and sulfometuron, but the magnitude of the response varied. Dalapon in combination with mowing influenced cogongrass control in an additive manner by increasing cogongrass control of shoot biomass by 36% and rhizome biomass by 16%. Sulfometuron increased cogongrass control of shoot biomass by 44% and rhizome biomass by 30% when used in combination with mowing. A second mowing in the year following herbicide application resulted in a

[4]Bush Hog Manufacturing, Inc., Selma, AL.

Table 1. The effect of mowing and herbicide on the biomass of cogongrass shoots and rhizomes.

Herbicide	Rate	Mowing regime[a]					
		0		1		2	
		Shoot	Rhizome	Shoot	Rhizome	Shoot	Rhizome
	kg/ha	% control[b,c,d]					
Dalapon	16.8	28	3	64	24	89	50
Glyphosate	3.4	56	33	73	58	96	61
Imazapyr	0.8	79	48	75	56	94	62
Sulfometuron	1.1	−6	−6	38	24	78	61
Nontreated	—	0	0	20	22	65	38

[a]0 indicates herbicide application to undisturbed cogongrass, 1 indicates mowing 2 to 4 mo before herbicide treatment, and 2 indicates a second mowing in June of the following year.

[b]Control is based on percent reductions in shoot and rhizome biomass when compared to a nontreated check whose shoot and rhizome biomasses averaged 220 g/m^2 and 2420 g/m^2, respectively.

[c]$LSD_{(0.1)}$ 11 and 13 for determining mowing effects based on shoot and rhizome biomass, respectively.

[d]$LSD_{(0.1)}$ 14 and 17 for determining herbicide effects based on shoot and rhizome biomass, respectively.

further increase in shoot and rhizome control with both herbicides.

When applied without mowing, glyphosate and imazapyr reduced shoot biomass by 56 and 79% and rhizome biomass by 33 and 48%, respectively (Table 1). When based on reductions in shoot biomass, cogongrass control with glyphosate was improved with each mowing, but when based on rhizome biomass, no additional control was provided by the second mowing. Two mowings were necessary to improve control with imazapyr regardless of the parameter measured. One possible explanation for the response to only the second mowing is that imazapyr provided such good long-term control (i.e., suppression of shoot regrowth) that at the time of the first mowing little regrowth had occurred. Consequently, the first mowing did not result in a further depletion of rhizome reserves.

A significant ($p < 0.1$) discing by herbicide treatment interaction was also obtained. Based on shoot and rhizome biomass, cogongrass responded similarly to discing or discing-herbicide combinations (Table 2). In the absence of herbicide, two discings were required to reduce shoot biomass; rhizome biomass was reduced by one and two discings. In this study, the interval between discing and harvest is one year more for the one discing treatment than the interval for the two discings treatment. Hence, differences in evaluation intervals probably contributed to the poor results obtained from one discing in reducing shoot biomass. In the case of rhizome biomass, reductions were seen following one discing because carbohydrate reserves were depleted below a level that would otherwise have been present to support the increased shoot growth resulting from the initial discing. Control was increased with the second discing because rhizome reserves had been depleted sufficiently to hinder recovery.

When used alone, glyphosate and imazapyr provided at least a 70% reduction in cogongrass shoot biomass and a 52% reduction in cogongrass rhizome biomass in the discing study (Table 2). With one exception, discing prior to the application of glyphosate and imazapyr did not improve the control of cogongrass. Control provided by these herbicides without discing was already at 50% or greater, leaving little room for improvement. However, two discings enhanced control.

Sulfometuron alone resulted in an increase in both cogongrass shoot and rhizome biomass. This could have been due to the release of cogongrass from interspecific competition when sulfometuron controlled the broadleaf species present. Sulfometuron may have also broken apical dominance in cogongrass and released dormancy of axillary buds in the rhizomes thus stimulating growth of cogongrass shoots. When sulfometuron was used in combination with one discing, the control of cogongrass shoots and rhizomes was greater than that obtained with either of the two inputs alone (Table 2). Sulfometuron and two discings improved both shoot and rhizome control relative to sulfometuron and one discing, but control was equal to two discings without any herbicide. Evidently, discing had a much greater impact on cogongrass than did sulfometuron. Combining one discing and dalapon resulted in reductions in biomass of both shoots and rhizomes that was greater than the reductions associated with the inputs alone. Cogongrass control was further increased when treatment

Table 2. The effect of discing and herbicides on the biomass of cogongrass shoots and rhizomes.

Herbicide	Rate	Discing regime[a]					
		0		1		2	
		Shoot	Rhizome	Shoot	Rhizome	Shoot	Rhizome
	kg/ha	% control[b,c,d]					
Dalapon	16.8	31	10	65	56	96	85
Glyphosate	3.4	70	52	76	68	92	89
Imazapyr	0.8	77	54	78	64	94	90
Sulfometuron	1.1	−23	−13	32	46	80	66
Nontreated	—	0	0	−2	27	73	66

[a]0 indicates herbicide application to undisturbed cogongrass, 1 indicates discing 2 to 4 mo before herbicide treatment, and 2 indicates a second discing in June of the following year.

[b]Control is based on percent reductions in shoot and rhizome biomass when compared to a nontreated check whose shoot and rhizome biomasses averaged 70 g/m^2 and 2500 g/m^2, respectively.

[c]$LSD_{0.1}$ 11 and 13 for determining discing effects based on shoot and rhizome biomass, respectively.

[d]$LSD_{0.1}$ 14 and 17 for determining herbicide effects based on shoot and rhizome biomass, respectively.

with dalapon was preceded and followed by discing. Enhanced control from the discing pretreatment could have occurred from improved herbicidal activity that resulted from an increase in shoot to rhizome ratio caused by fragmentation of the rhizomes (2, 10). The presence of more shoots and the greater demand for energy resulting from the breaking of apical dominance along the rhizome following discing could have allowed more herbicide to be absorbed and translocated resulting in a greater concentration in the rhizome buds.

Long-term control of a perennial weed like cogongrass is dependent upon the elimination of rhizomes. Basing perennial weed control evaluations on foliar responses alone can cause an overestimation of long-term treatment efficacy. This is caused by the abundance of subterranean tissue that has regrowth potential. In these studies, glyphosate and imazapyr controlled cogongrass more effectively than did dalapon and sulfometuron in the absence of a mechanical pretreatment, but rhizome biomass was reduced an average of only 43% by glyphosate and 51% by imazapyr. Two thorough discings without the compliment of herbicides provided 66% rhizome inhibition, and continued discing may have eventually depleted rhizome reserves.

Acceptable (> 80%) reductions in cogongrass rhizome biomass was achieved only where a treatment with glyphosate or imazapyr was preceded and followed by discing. Dalapon also provided similar levels of control, but it is no longer available in the United States. None of the mowing-herbicide treatments provided greater than 62% control of rhizomes. Because none of the treatments evaluated in this study provided complete control, follow-up applications of glyphosate or imazapyr and, where practical, discing and mowing should be part of any cogongrass management program.

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Systems of Weed Control in Wheat in North America

The WSSA announces publication of the most comprehensive monograph ever published on wheat production practices and methods of managing weeds in wheat in the United States. *Systems of Weed Control in Wheat in North America* contains 22 chapters that total 487 pages and was prepared by 26 weed scientists who have specialized in weed management in cereals. The monograph documents spring and winter wheat production practices in different regions of North America, weed problems, and methods of managing weeds using herbicides and cultural practices.

The monograph is divided into three parts. In the first part, the distribution of weeds of wheat in North America and yield loss assessment are summarized. In the second part, wheat production practices and weed control systems are reviewed for the following regions of North America: the Canadian Prairie Provinces, the Northern, Central, and Southern Great Plains, the Northeast, the Southeast, the Pacific Northwest, and California and Arizona. Finally, the use of the following herbicides in wheat is reviewed: barban, bromoxynil, clopyralid, diclofop, difenzoquat, flamprop, picloram, propanil, substituted triazines, triazinones, and urea herbicides, sulfonylurea herbicides, triallate, and trifluralin. Each chapter on wheat herbicides summarizes knowledge of weed control, application methods, spray additives, crop response, environmental effects on weed control, combination treatments, and environmental fate.

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C[illegible]grass Control Requires Integrated Approach (F[illegible]a)

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Cogongrass (*Imperata cylindrica*), a perennial grass native to southeast Asia, has become a serious problem in the southeastern United States. It spreads by both seed and rhizomes and, once established, has the ability to displace other vegetation on forests and rangelands, as well as on reclaimed phosphate mines and other disturbed areas. Others (Tanner *et al.*, 1992; Willard, 1988; Lee, 1986; Eussen and Soerjani, 1975) have had some success controlling cogongrass for short periods of time. Nonetheless, our experience indicates that only a combination of techniques, applied in an integrated way, can effectively control cogongrass.

Mowing and tillage have been used to manage many perennial species and may be effective in controlling cogongrass. Mowing cogongrass, however, must be done consistently over two or more years to deplete the starch reserves that support the growth of new shoots. We suspect that most managers will find that such a strategy causes budgetary or logistical problems. Tilling, on the other hand, both knocks down new shoots, and cuts and helps dry out the rhizomes. Deep tillage is important since cogongrass rhizomes rarely resprout from depths greater than 15 c[illegible]). Complete control of cogongrass requires repeated tilling until there is no regrowth—typically three tillings every year for three years.

Only a few herbicides have proven effective in controlling cogongrass. We found that an application of imazapyr (*Arsenal*) at 0.84 kg/ha (0.75 lb/A) or glyphosate (*Roundup*) at 2.24 kg/ha (2.0 lb/A) in September provided 70-80 percent control up to one year after a single treatment. Both of these herbicides have some drawbacks, however. Both kill all plants in the treated area, and *Arsenal* can remain active in the soil for long periods of time, where it inhibits the establishment of desirable species. Our studies using Fluazifop (*Fusilade 2000*) and glufosinate (*Ignite*) indicate that those herbicides suppress cogongrass for only three months, after which regrowth occurs. Complete control requires repeated and often costly applications of all these herbicides, and is rarely achieved.

We feel that the key to long-term control of cogongrass is replacing it with a competitive plant community capable of closing ranks and resisting re-invasion. Establishing new species in cogongrass-infested areas is difficult because cogongrass secretes allelophathic chemicals, has an extensive system of rhizomes, and creates a dense canopy. We have, however, found several exotic species that show promise in competing with cogongrass including [illegible] indigo (*Indigofera hirsuta*), Bermudagrass (*Cynodon dactylon*), and bahiagrass (*Paspalum notatum*). These species seemed to grow best when we added 22.5 kg (50 lbs.) per acre of 10-10-10 fertilizer and mowed once a month. We have also begun tests to determine whether similar practices will encourage the establishment and growth of native species. We expect, however, that native plants will be more difficult and costly to work with and be less effective at competing with cogongrass.

We believe that ultimately the best way to control cogongrass is by following an integrated approach that employs a variety of management techniques. For example, burning followed by tilling and herbicide applications should contain cogongrass long enough to give restorationists a chance to establish species chosen to compete successfully with cogongrass over the long-term. Regardless of its potential for success, we suspect that this strategy may be somewhat expensive with replacements using horticulturally-altered exotics costing hundreds of dollars per acre, and restorations with native species costing even more—perhaps thousands of dollars per acre. In many areas the cost of this integrated approach is justified. In areas where it cannot be justified for financial or other reasons, some form of classical biological control that would include introduced insects or pathogens will be necessary. It is also essential that the conservation organizations and state agencies develop a regional strategy to discourage the spread of cogongrass while restorationists and others begin the work of suppressing this nuisance species.

Acknowledgment

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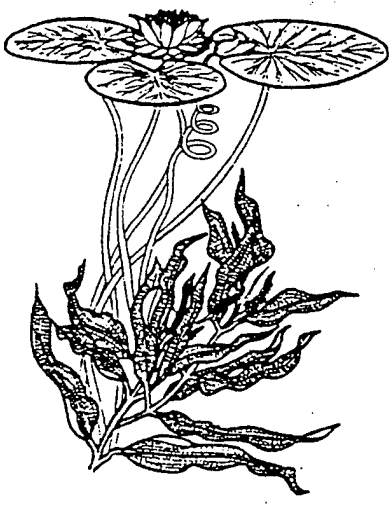
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Cutting Queen Anne's Lace Reduces Seed Supply (Wisconsin)

Martha and Bill Kilgour, 332 Marston Avenue, Madison, WI 53703; 608/255-4947

Tolerated by some restorationists and despised by others, Queen Anne's lace (*Daucus carota*) frequently invades prairie plantings in the upper Midwest. A deep-rooted biennial, which is also capable of producing thousands of seeds, it often displaces prairie seedlings.

Wayne Pauly, Dane County Parks naturalist, wanted to find a way to control Queen Anne's lace other than pulling it. Together with him, we set up an experiment on Schumacher Farm



Chinese Tallow
(*Sapium sebiferum*)

by

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CHINESE TALLOW
(*Sapium sebiferum*)

INTRODUCTION

In 1988, an article entitled "Another Exotic Nuisance- The Chinese Tallow Tree" published in The Palmetto (Florida Native Plant Society newsletter), referred to *Sapium sebiferum* as the "north Florida melaleuca", in reference to "chilling" similarities to the south and central Florida pest: its potential for rapid expansion; its promotion by beekeepers as a honey plant; and its ability to spread widely from a single parent tree, especially in moist areas (Farnsworth, 1988). "This tree (*Sapium*) stands now where melaleuca and Brazilian pepper were in the 1950's- small, localized populations that, in another ten years, are apt to explode into an intractable problem of major proportions", writes Farnsworth." Cameron and Spencer (1989) describe *S. sebiferum* as an exotic tree from the far-east that invades lake and river margins and wetlands in Florida.

Sapium sebiferum (L.) Roxb. is a member of the Euphorbiaceae, a family of more than 1,000 species and varieties, many of which are classified as poisonous. The genus *Sapium* consists of approximately 100 species. Although the Chinese tallow tree has been considered toxic by some authorities on poisonous plants, Russell, (1969) does not consider Chinese tallow to be toxic. Common names of *S. sebiferum* in the United States include the popcorn-tree, Florida aspen, Chinese tallow, and the Chinese tallow-tree (Godfrey and Wooten, 1981). The latter names arise from the fact that the outer layer of the seed can be used to obtain solid vegetable tallow. The plant is known as the popcorn-tree because of the appearance of white seeds when the capsule splits open (Godfrey, 1988).

DISTRIBUTION

S. sebiferum is a native of China, where it has been cultivated for at least 14 centuries as a seed-oil crop (Seibert et al., 1986; Jones and McLeod, 1989). Chinese tallow has been introduced to various subtropical parts of the world as an ornamental plant, including the American sunbelt.

Chinese tallow is considered a weed in some other warm regions of the world. It is a "common" weed in Taiwan, i.e, very widespread in many crops or regions, requiring constant effort and expense to hold at bay (Holm et al., 1979). It is present and behaves as a weed in the U.S., but its rank of importance relative to other weeds is unknown (Holm et al., 1979).

Earliest accounts by Hunt (1947) reported that *S. sebiferum* was introduced into Charleston, South Carolina in the late 1700's. It was introduced to the U.S. gulf coast in significant numbers in the early 1900's by the Foreign Plant Introduction Division of the United States Department of Agriculture, Bureau of Plant Industry. The primary thrust for this introduction was to establish local soap industries based upon the large amounts of vegetable tallow found around the seed (Jamieson and McKinney, 1938). Since the initial introductions, it has spread into coastal prairie habitats (Cameron and Spencer, 1989). It is now naturalized in the southern coastal plain from South Carolina south to Florida and west to Texas.

In Gulf areas such as Galveston, Texas, *S. sebiferum* is one of a number of nonnative plantings in residential yards. McDonald (1989), commented that, "Because of human intervention, cultivated landscapes have replaced native Gulf coastal plant communities".

Chinese tallow in Florida is distributed from the Florida/Alabama border (Escambia County) eastward to Jacksonville and south as far as Tampa (Hillsborough County). According to the most recent survey (Figure 1) conducted by the Department of Natural Resources, the plant can presently be found in 38 of the 67 Florida counties (55%). Of that total, 25 counties (37%) have trees that are primarily associated with ornamental landscapes; occasional outlier trees can be found, but the densities are low (5 trees per a single observation point). Thirteen counties (19%) have numerous populations of trees present that are outside of the ornamental landscape and

number at least 50 trees per cluster. To date, there have been no verified sightings of *Sapium* in 29 counties (45%). Trees found outside of ornamental landscapes are found adjacent to wetlands and in disturbed sites. It is commonplace to find trees 15-20 feet tall (4.5-6.5 m), with some older sites having plants at heights of 30-40 feet (9-12 m).

Chinese tallow is rapidly invading wild areas where it has not been seen before. Farnsworth (1988) gives as an example, Paynes Prairie near Gainesville, where he found *S. sebiferum*, miles from human habitation, where it had previously not been present. James Weimer, DNR Parks Biologist at Paynes Prairie, documented in excess of 10,000 trees in 1992 (pers. comm., 1992). As well as finding it in upland habitats, he also found it in the ecotone between cattail (*Typha* spp.) and maidencane (*Panicum hemitomon*). In Paynes Prairie Chinese tallow is expected to take over all higher ground from native species unless action is taken to control it.

While surveying with Beth Morford, District 1 Biologist (DNR), several *Sapium* trees, approximately 8 feet in height, were discovered growing amongst *Cladium jamaicense* (sawgrass) along the shore of Grand Lagoon, a moderately saline bay located at St. Andrew's State Park, Panama City Beach. According to Godfrey (1988), Chinese tallow typically thrives in upland, well-drained areas near human habitation, as well as natural, undisturbed areas such as closed canopy forests, in bottomland hardwood forests, on shores of waterbodies and sometimes on floating islands.

DESCRIPTION AND IDENTIFICATION

S. sebiferum is a small to medium-sized tree with a milky sap that is putatively poisonous. Chinese tallow is a popular ornamental because of its fast growth and attractive foliage which becomes yellow to red in the fall, and is resistant to pests. As a young plant, it flowers and fruits from the time it is about 3 feet (1 m) high (Godfrey, 1988). Leafy twigs are basically herbaceous early in the season, and the bark turns a tan color later. Leaf scars are shield-shaped with three vascular bundle scars.

Leaves are simple, alternate, deciduous, and as broad or broader than long (Godfrey and Wooten, 1981). Blades are pinnately-veined and broadly ovate, about 1-2.5 inches (3-6 cm) wide with broadly rounded bases (Godfrey, 1988). Apices are abruptly acuminate and margins are entire (Fig. 2). Petioles are slender, mostly about 1-2 inches (2-5 cm) long.

Inflorescence on some plants are solitary terminating branchlets, each narrowly cylindrical, 2-8 inches (6-20 cm) long, bearing pistillate flowers proximally, each in the angle of a bract, and staminate flowers distally in many short fascicles of up to 15 flowers each (Godfrey, 1988). On other plants, the inflorescence is branched, the central terminal branch elongate and usually wholly staminate. Each pistillate flower has three styles and lacks petals. The fruit is usually three-lobed with one seed in each lobe (Cameron and LaPoint, 1978). Each fruit is about 0.4 inch (1 cm) long and broad; it dehisces to leave 3 dull, ovoid to globose white seeds that stay attached to the plant for a period of time, and superficially resemble popcorn (Singh and Pal, 1990). Seeds are covered with vegetable tallow, a white waxy coating.

In India the plant is called khinna (Ansari and Nand, 1987) and in Pakistan, wilati shishum or the churbi plant (Aziz, 1987). The nominal taxa *Croton sebiferum, Stillingia sebifera,* and *Triadica sebifera* (L.) Small are synonyms (Bonner, 1974).

The national champion is located in Travis County, Texas, and is 10 feet (3 m) in circumference, 52 feet (16 m) in height, with an 86 foot (26 m) spread (Godfrey, 1988).

BIOLOGY

In the southern coastal plain of Texas, new growth of *S. sebiferum* begins in February and flowering lasts from March through May (Cameron and LaPoint, 1978). In the coastal plain from South Carolina to Florida to Texas, Oklahoma, and Arkansas, the plant usually flowers after three years, and fruit ripens from August to November

(Bonner, 1974). During late summer the capsule husks drop, leaving the seeds exposed. The plant is deciduous, losing leaves during autumn. Maximum life-span is probably less than 100 years, however, root stocks may live much longer (Jones and McLeod, 1989). Typical trees live only 15 - 25 years (Whitcomb, undated). Growth during the first 5 - 10 years is very rapid. Young tallow seedlings quickly produce a taproot system and are able to withstand extended periods of drought (Scheld and Cowles, 1980).

The plant possesses the classical characteristics of most exotic pest species: It grows quickly, fruits when young, produces abundant seeds, is resistant to native pests, grows in a wide range of soils, invades undisturbed habitats, and has traits that are found to be attractive by man and are therefore promoted and distributed. In many cases, Chinese tallow has invaded Florida's ecosystems as a result of human introductions.

It has been introduced repeatedly to the United States as an ornamental or potential oil crop species (Jones and McLeod, 1989). The fruit of the tree contains high-quality drying oil, tallow, and protein, in addition to fibers and hulls. The oil, known as stillingia oil, can be extracted from the seed and has been thoroughly investigated as an ingredient for varnishes and paints. Stillingia oil has been considered poisonous, but Bailey (1938) indicated that the oil was not toxic to rabbits. Chinese tallow produces heavy seed crops. The amount of oil concentrated in the seed averages 20% by weight, but varies widely according to location and cultivation of the tree (Rielly, 1947). The seed contains the greatest concentration of oil when grown in water-rich soils, such as lowlands near the coast.

The primary vectors for seed dispersal are birds (Jones and McLeod, 1989) and moving waters. Weimer (pers. comm. 1992) reported observing pileated woodpeckers (*Dryocopus pileatus*) eating the seed. It is expected that boat-tailed grackles (*Quiscalus major*) also contribute to the movement of the seed. Preliminary studies at the DNR Aquatic Plants Laboratory indicate that these seeds are quite capable of floating for several weeks while maintaining their viability. The species also regenerates from stump sprouts and is easily propagated by cuttings (Jones and McLeod, 1989). *S. sebiferum* expands over the landscape at a high rate. In Texas, Scheld and Cowles (1981) reported that seedlings planted at a 2 foot x 2 foot (0.6 m x 0.6 m) spacing produced more than 5 dry tons of biomass/acre at the end of the second growing season, and more than 7 dry tons/acre on coppiced plots. The plant could possibly out-compete the lower productivity of wild Florida flora.

To illustrate *S. sebiferum* domination of a lowland area, plants were quantified at a site in Leon County, Florida. The site, on the southeast shore of Megginnis Arm, Lake Jackson, is a basin that has been affected by surrounding urban development and by partial impoundment of water from 1970 until the present. It is believed to be the oldest stand of Chinese tallow on the lake; trees present are 18 - 22 years of age (based on tree ring counting and R. Presnell, pers. comm., 1992). Most Chinese tallow at the site appear to fall into various younger age classes, probably because older age classes have been greatly reduced by extreme water-level fluctuations.

In April 1992, point-quarter sampling of trees and quadrat sampling of young plants were conducted along lowland transects within 25 m of shore in Megginnis Arm. The point-quarter method was used to obtain data on density, areal coverage, and frequency of large plants, without requiring sampling plots (Brower et al., 1990). Quadrat sampling was used to obtain data on more closely spaced young individuals under large *S. sebiferum*, in order to assess the degree of ongoing reproduction.

To obtain point-quarter data, a transect rope was laid parallel to the southeast corner of Megginnis Arm. The transect was sampled randomly at one point every 2 - 4 m, excluding locations recently disturbed by nearby construction and foot-traffic. At each of these points, the surrounding area was divided into four equal-angle quadrants (Brower et al., 1990). In each quadrant, the distance from the chosen point to the center of the nearest plant greater than breast height (1.5 m tall) was recorded. Then the plant's species and diameter at breast height (dbh) were recorded. Sampling was repeated perpendicular to transect #1, in the smaller available habitats of transects # 2 and 3.

The number of young propagules produced around large Chinese tallow adults, the former were quantified by quadrats in the same lowland area as the large plants. Three transects were laid in approximately the same locations as in point-quarter sampling, and random points were chosen. At each point, a 1-m^2 quadrat was placed around the base of the nearest *S. sebiferum* that was greater than 3 cm dbh. The number of seedlings and root sprouts of each plant species encountered and scored, and a visual estimate of percent ground cover was recorded.

For both point-quarter and quadrat data for each transect, the plant density, coverage, and relative frequency were calculated (Brower et al., 1990), along with the means and standard deviations over all transects (Tables 1 and 2). Multiple comparisons were run to determine whether measures of abundance of *S. sebiferum* were greater than measures of abundance of other species. Prior to these comparisons, when variances of data were nonhomogeneous, data were transformed. SQRT(data + 0.001) transformations were applied to density data because they proved more effective in producing homogeneous variances than did LOG(data + 1) transformations (Zar, 1984). ARCSIN(SQRT(data)) transformations were applied to coverage and relative frequency data because this transformation tends to normalize such percentages or proportions. Means of transformed data were compared by Tukey's test because it compensates for multiple comparisons, yet still retains good pairwise testing power.

Table 1. Measures of abundance of Chinese tallow (*S. sebiferum*) and other species taller than breast height, Megginnis Arm, Lake Jackson, on April 23, 1992. Measures in which species means are not significantly different from one another have the same superscripts (P>0.05; see text). Means and SD values (in parentheses) were calculated over n=20, 8, and 8 points along each of transects 1, 2, and 3, respectively.

Species	Density (m^{-2})	Coverage (cm^2 m^{-2})	Relative freq.
Sapium sebiferum	0.452^{a} (0.074)	6.69^{ab}(4.31)	0.636^{a} (0.027)
Liquidambar styraciflua	0.055^{b} (0.005)	12.34^{a}(2.58)	0.185^{b}(0.040)
Salix nigra	0.025^{bc}(0.021)	6.61^{ab}(6.37)	0.103^{bc}(0.090)
Sambucus canadensis	0.014^{bc}(0.014)	0.01^{b}(0.02)	0.066^{bc}(0.089)
Cornus foemina	0.002^{c} (0.004)	0.07^{b} (0.12)	0.010^{c} (0.018)
Total	0.548	25.72	1.000

Results indicated that *S. sebiferum* plants of 1.5 m height or greater were abundant along transects. This species had the greatest density of any tree or bush (Tukey comparisons of SQRT[data + 0.001], P 0.05, Table 1). Furthermore, in spite of arriving only 18 - 22 years before, it was already in the top three species in terms of level of coverage, based on dbh. It also had a higher relative frequency than the other species (Tukey's test of untransformed values, P>0.05).

Table 2. Abundance of seedlings plus vegetative sprouts of *S. sebiferum* and all other plant species under large *S. sebiferum* (greater than 3 cm dbh), Megginnis Arm, Lake Jackson, on April 24, 1992. Measures in which species means are not significantly different have the same superscripts (P>0.05; see text). Means and SD values (in parentheses) were calculated over n = 25, 6, and 7 m^2-quadrats along each of transects 1, 2, and 3, respectively.

Species	Density (m^{-2})	Cover (%)	Relative freq.
Sapium sebiferum	14.600[a](10.49)	7.92[a] (3.98)	0.684[a]0.274)
Liquidambar styraciflua	*1.242*[b] (1.156)	0.33[b] (0.31)	0.245[ab](0.213)
Quercus sp.	0.122[b] (0.147)	0.02[b] (0.02)	0.044[b] (0.040)
Sambucus canadensis	*0.053*[b] (0.092)	0.03[b](0.05)	0.009[b] (0.016)
Cephalanthus occidentalis	*0.013*[b] (0.023)	0.01[b] (0.02)	0.009[b] (0.016)
Sesbania sp.	0.013[b] (0.023)	0.01[b] (0.02)	0.009[b] (0.016)
Total	16.043	8.32	1.000

Chinese tallow reproduced prolifically compared to other species in the same area. There was an average of 14.6 seedlings plus vegetative sprouts in the m^2 area below large *S. sebiferum* (Table 2). This density was greater than the density of *Quercus* sp. and *L. styraciflua* propagules in the same area (Table 2). Similarly, percent cover by *S. sebiferum* was significantly greater than cover by *L. styraciflua* and *Sambucus canadensis*. The relative frequency of Chinese tallow propagules was greater than that of all other species in the quadrats except *L. styraciflua*. Thus, after *S. sebiferum* individuals became well established and grown, their propagules expanded rapidly beneath them.

Scheld and Cowles (1981) reported that within aquatic habitats, the plant survives well in both poorly drained freshwater and saline soils. In flood-tolerance experiments on seedlings in South Carolina, Chinese tallow had lower mortality than the highly flood-tolerant species, water tupelo (*Nyssa aquatica*; Jones and Sharitz, 1990). Growth reductions during flooding were similar for both species under 20% of full sunlight, but greater for *S. sebiferum* than for tupelo in 100% light.

S. sebiferum is expanding its range in low-lying areas along the U.S. gulf coast, where it can dominate and radiate along roadside ditches and into areas where the soil stays wet (Cameron and LaPoint, 1978). High flood tolerance and sensitivity to root competition with other species may explain why seedlings are concentrated in low wet areas of floodplain forests (Jones and Sharitz, 1990).

Jones and McLeod (1989) experimentally demonstrated that in 5% sunlight, *S. sebiferum* exceeded sycamore (*Platanus occidentalis*) and cherrybark oak (*Quercus falcata*) in dry mass production and photosynthesis. They noted that these results were consistent with the observation that the plant could easily establish under closed canopies and grow rapidly in full sunlight.

Jubinsky and Oliver (1990) performed experiments to provide a screening of the potential of *S. sebiferum* for invading various types of Florida aquatic habitats. They found that a high percentage of plants could survive when inundated with freshwater, and when raised in soil wetted with brackish water (simulated 1/2-seawater), but not when inundated with brackish water. These experimental tank results are consistent with field observations of Scheld and Cowles (1981), mentioned above. Thus, the plant could invade freshwater lakes, rivers, and other wetland zones in Florida, as well as tidal estuarine and coastal wetlands.

Part of the flood tolerance in seedlings may be due to heavy growth of lenticels and adventitious roots, and the production of thicker feeder roots. These traits are related to an ability to oxidize root regions, and are typical of woody plants capable of surviving prolonged flooding and low soil redox potentials (Hook, 1984; Jones and Sharitz, 1990).

Tolerance of warm-temperate winters allows *S. sebiferum* to spread in climates typical of north Florida. The plant is restricted only if temperatures drop below about -18 C (Whitcomb, undated).

The growth of *S. sebiferum* can increase in the presence of symbiotic root fungi. When grown on nitrogen deficient upland substrate, seedlings inoculated with nitrogen-fixing endomycorrhizal fungi grew faster than when not inoculated, whether or not the substrate was low in phosphorus (Davies and Call, 1990).

S. sebiferum can have significant effects on surrounding ecosystems. Cameron and Spencer (1989) concluded that these plants may increase eutrophication in systems to which they have been introduced by adding (actually recycling) nutrients, via a rapid decay of leaves. Decay of *S. sebiferum* leaves was much more rapid (k = -4.33) than native *Salix nigra* (k = -0.35) and other deciduous leaves (k = -0.77). Furthermore, the plant produces tannins, which are known to inhibit the feeding of isopod and amphipod invertebrates of aquatic systems (Cameron and LaPoint, 1978). This factor may have contributed to the fluctuations in isopod density and reproductive potential that were seen in *S. sebiferum* forests (Miller and Cameron, 1983).

More significantly, the plant produces toxic organic chemicals capable of stupefying fish. Bradley,(1956) reported that tannins extracted from leaves of congeners of *Sapium sebeferum* are toxic to vertebrates. It produces skin-irritating and tumor-promoting diterpene esters of the tigliane type (Seip et al., 1983). The latex is acrid and a powerful vesicant. Cytotoxic activity has been traced to a *S. sebiferum* constituent, gallic acid (Liu et al., 1988). Floridian biota are not adapted to these powerful chemical defenses and would, in many cases, be repressed by them.

IMPORTANCE

Sapium sebiferum is sold commercially as an ornamental plant throughout the gulf coast states. Residents of Florida and other states can currently buy plants from a number of nurseries under various trade names, i.e., Florida aspen, popcorn-tree, and Chinese tallow-tree. A telephone survey of three north Florida wholesale nurseries indicated that, since 1987, wholesale production averaged between 3000- 5000 trees per year, with a general downward trend in sales. All wholesalers indicated that the majority of their stocks were sold out of state, as a function of demand.

Studies by Russell et al. (1969) indicated that leaves and fruits of *S. sebiferum* caused severe diarrhea, accompanied by weakness and dehydration in steers within 12 to 14 hours after the plant material was first given. One steer died after being fed the plant for five consecutive days. At the end of the experiment, another steer had lost 20 kg. (44 pounds) in body weight.

In some warm-weather regions, *S. sebiferum* is a major resource for commercial honey. In Louisiana in 1968, *S. sebiferum* was the sixth most important plant species for the production of honey (Lieux, 1975).

Recently, chemicals have been extracted from leaves of the plant for testing for possible anti-cancer activity (Liu et al., 1988). For centuries, leaves have been used in China for dye production (Aziz, 1987). Root bark has been used as a purgative and diuretic in China and is reported to be effective against the parasite *Schistosoma japonicum* (Seip et al., 1983).

The outer solid tallow has been reported to contain tumor-promoting and irritant compounds, so it is not appropriate as a food, in spite of the name "Chinese vegetable tallow" (Seip et al., 1983). This tallow is used candles, cosmetics, and soaps (Seip et al., 1983). Oil from inside the seed, known as stillingia oil, has been investigated as a drying ingredient in paints and varnishes. The oil contains 5 percent of the conjugated deca-2, 4-dienoic acid as triglycerides, making it comparable to linseed oil in drying capacity (Aziz, 1987).

In India, the plant has been used for stupefying and harvesting fishes, by putting the crushed leaves and fruits in aquatic habitats (Ansari and Nand, 1987).

MANAGEMENT OPTIONS

• Herbicides

A number of woody plant species can be controlled by herbicides. In appropriate habitats, the herbicide Garlon (triclopyr) is extremely effective for removing *S. sebiferum*. Herbicide trials conducted by the Department of Natural Resources are being conducted in the Megginnis Arm site, using Garlon 4 and the surfactant (JLB Oil Plus), and glyphosate. Preliminary results suggest an 11% triclopyr solution with JLB Oil Plus controls trees with dbh cm (6 inches); trees with dbh 15 cm. appear to have been successfully controlled with a 20% solution.

• Mechanical

The vegetative propagation potential of *S. sebiferum* increases dispersal and survival, and makes the plant less vulnerable to mechanical control. For example, cutting of horizontal shoots results in the immediate production of small independent plants. Thus vegetative reproduction makes mechanical control impractical. This method of reproduction also could decrease the efficacy of herbicidal control. Of course, additional reproduction by seeds increases dispersal and makes the problem worse.

• Habitat Manipulation

Habitat manipulation may help to control the plant. In native coastal grasslands in Texas, overgrazing and the cessation of fires had resulted in decreases in the major grass species and prairie plants, and an allowed invasion by *S. sebiferum* and other plants (Munroe, 1981). Biologists planned to restore and manage the system by summer burning to eradicate *S. sebiferum* and other brush plants, and to encourage established grasses. They then planned to manage native grasses by haying every year and by doing maintenance burns, every third winter. It is not yet known whether this method would work in Florida ecosystems. A proposal to evaluate control burning of *Sapium* is proposed for the spring of 1995 at St. Andrew's State Recreation Area.

• Biological Control

In places where appropriate, control by domestic animals might be used to decrease levels of *S. sebiferum*: Sheep and goats have been known to eat the leaves (Ansari and Nand, 1987). However, the plant's toxicity to cattle decreases the possibility of effective control by grazing (Russell et al., 1969).

The plant apparently lacks serious insect biocontrols or pathogens in the United States (Jones and McLeod, 1989). It experiences low herbivory compared with, e.g., green ash (*Fraxinus pennsylvanica*), and this is in keeping with other observations that tallow foliage is particularly resistant to attack by native insects or pathogens. However, it does have some insect pests such as the bagworm *Eumeta* from Japan (Nishida, 1983). Other herbivores from Japan and China, which have adapted to the plant's chemical defenses, could be tested as biocontrols, provided that are monophagic.

SUMMARY

Chinese tallow *S. sebiferum* is a nonnative ornamental tree that has been spreading across the southern coastal plain of the United States, including Florida. It is a physically attractive horticultural plant that is resistant to native pests, and can produce numerous seeds in about three years. Vegetative reproduction makes it hard to control, as does its tolerance for shade, bright sun, and various soil conditions. Sexual reproduction makes matters worse, by allowing the species to survive and return, and to adapt to environmental changes. Unfortunately, the seeds have some value as a wildlife food which has apparently aided Chinese tallow in its dissemination.. Such factors make the plant a serious threat to native Florida flora and associated ecosystems.

Prospects for herbicidal control are currently being systematically evaluated. Mechanical methods are not likely to be very effective because of resprouting. Burning or grazing may help in some circumstances, and no effective biocontrols are known at this time. Based on the current distribution map of the species, if *S. sebiferum* is left unchecked, it is likely to be present and potentially dominate large areas of the state, including wetlands, bottomland hardwood forests, closed canopy forests, and the shores of lakes and rivers.

S. sebiferum tends to take over large areas (Bonner, 1974). The tendency to monopolize space leads to a reduction in physical habitat for native Florida plants. Data from this study indicate that the density and relative frequency of occurrence of large *S. sebiferum* at a lakeshore site in April, 1992, were 0.452 m^{-2} and 0.636 respectively, greater than any other tree or bush species present. The density of *S. sebiferum* seedlings plus vegetative sprouts beneath large plants of the species (3 cm dbh) was 14.6 m^{-2}. Thus *S. sebiferum* can colonize a lowland area, become abundant, and produce numerous propagules.

S. sebiferum competes with native plants that provide preferred cover and food for native fauna. Thus the plant could have a negative economic impact on leisure-time trips to observe and photograph nature, as well as on other outdoor recreational activities. In general, the high content of allelopathic chemicals in *S. sebiferum* makes it dangerous to native fish and other macrofauna. High concentrations of tannins are toxic to some invertebrates, and complex organics in leaves and fruits are toxic to fish.

S. sebiferum can proliferate to the detriment of native plants (Jones and McLeod, 1989). In marshes, it is replacing native graminoids, thus changing the form of these areas. "Unless root competition, cold temperatures, or something else limits establishment and growth of [the] tallow tree, this species will likely invade and persist in many of the floodplain forests of the coastal Southeast" of the United States (Jones and McLeod, 1989), including Florida.

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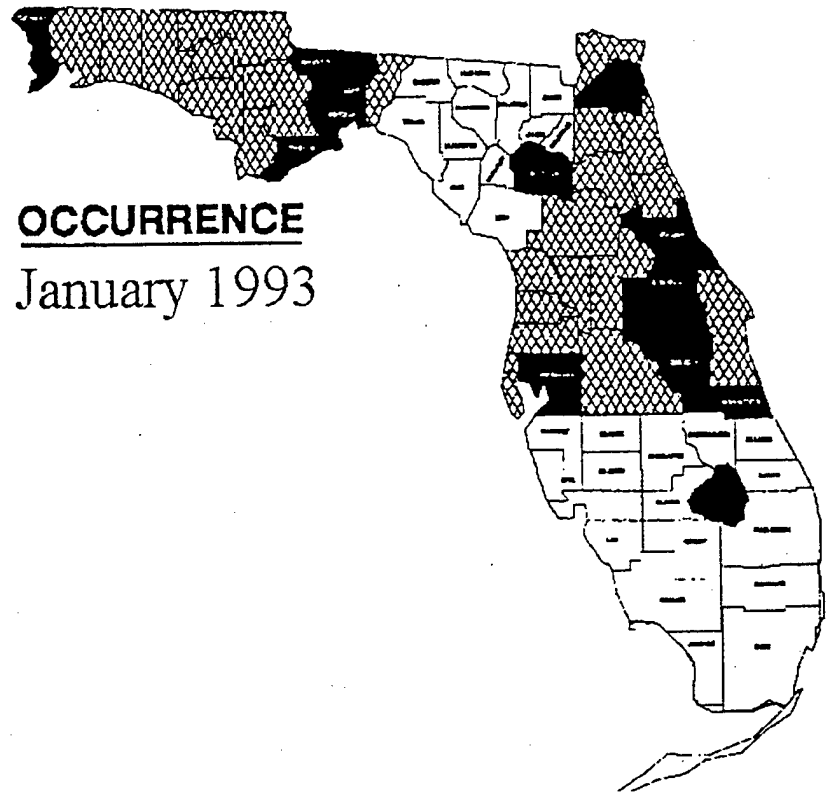
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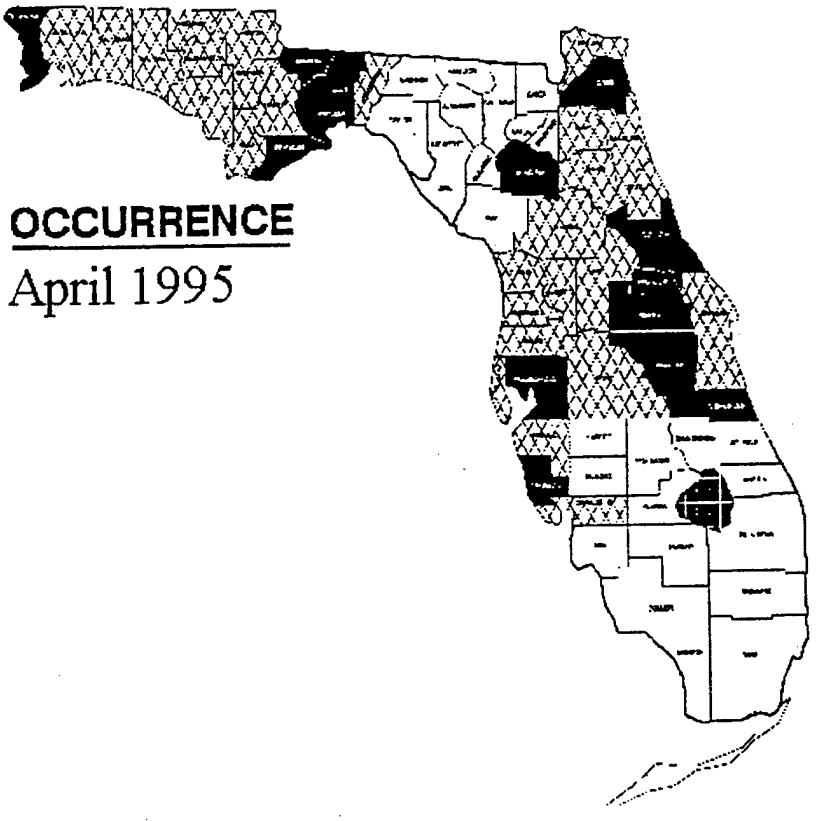
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Figure 1. Distribution of naturalized Chinese tallow (*Sapium sebiferum*) in Florida from 1993 - 1995. (Jubinsky, 1995)





CATEGORY # 1
Trees frequently found outside of ornamental landscapes; clusters with > 50 trees per cluster

CATEGORY # 2
Trees found primarily in ornamental landscapes; occasional "wild" sightings (< 5 trees per observation point)

No verified sightings

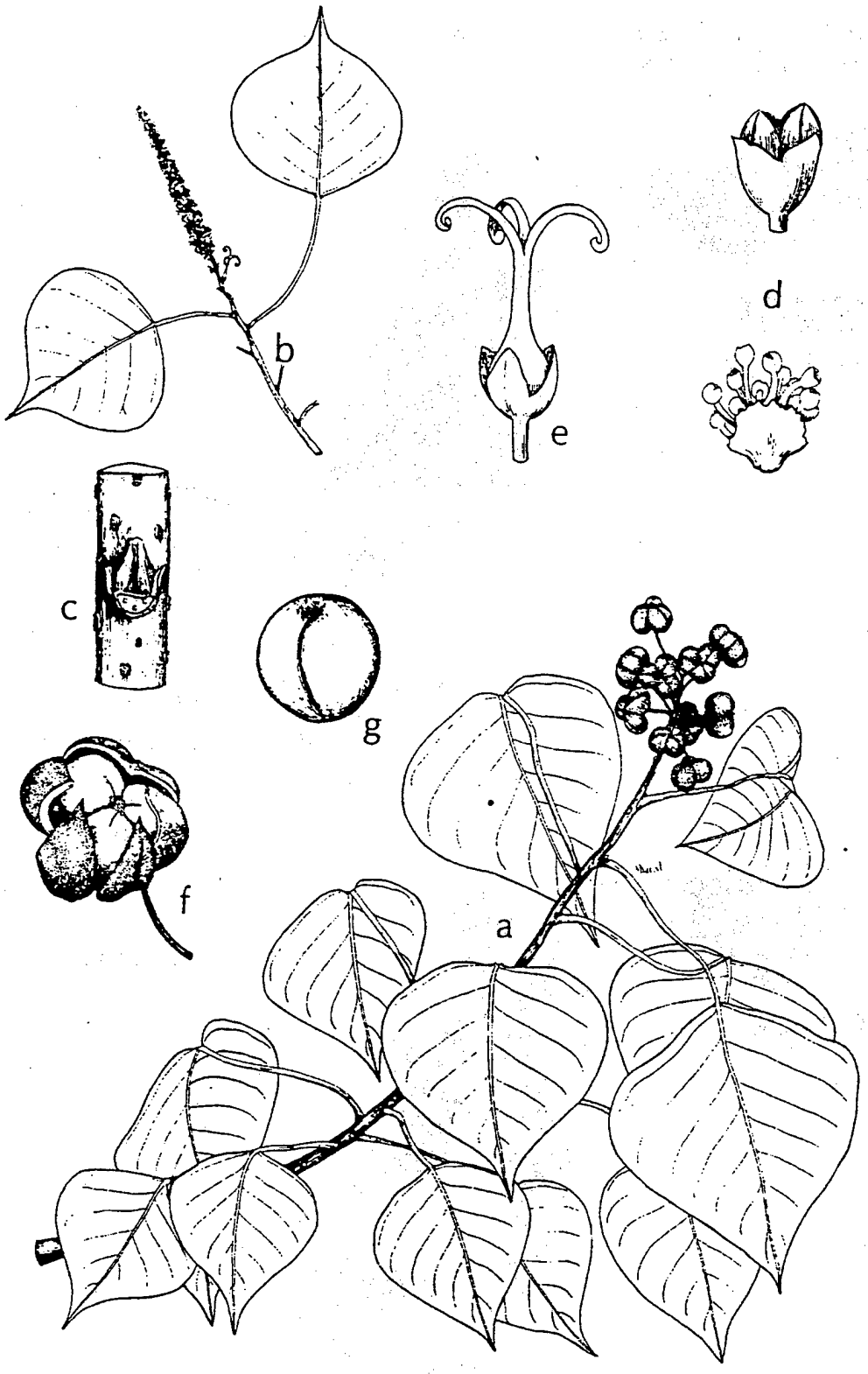


Figure 2. *Sapium sebiferum*: a, fruiting branch; b, flowering branch; c, leaf scar; d, staminate flowers, including a close-up, above; e, pistillate flower; f, dehisced capsule; g, seed. (Reprinted from Godfrey, 1988, Fig. 133, with permission of the author, the artist [Melanie Darst], and copyright University of Georgia Press. Trees, Shrubs, and Woody Vines of Northern Florida and Adjacent Georgia and Alabama).

EGLIN FACT SHEET

Exotic Plants

Exotic plants have been brought to the U.S. from other places. Many exotic plants are useful for food crops or other purposes, but others are weedy or invasive. Unleashed in new places, invasive exotic plants are a threat to native plants and wildlife.

Some exotic plants invade areas that we depend on for natural resources. Exotic plant invasions are changing native ecosystems, harming the environment around the world.

The 79 most invasive exotic plants have caused over $97 billion in damages, according to the U.S. Office of Technology Assessment. The top 15 invaders will cause over $134 billion in damages to natural areas, agriculture, industry, and human health in the future. These damages do not even include losses in tourism or scenery!

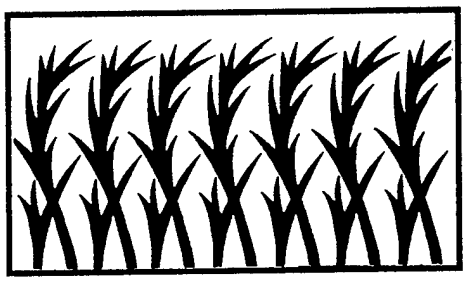
Scientists recognize exotic plants as a grave threat to native ecosystems in parks and forests around the U.S. Invasive exotic plants now are blamed for the loss of more native species than any other factor except development by humans.

In the U.S., the states of Florida, Hawaii, and California are hardest hit. For example, in Florida, Australian punk *(Melaleuca)* and Brazilian pepper have invaded over a million acres of the Everglades ecosystem, a large area of sawgrass marshes that provides clean water and wildlife habitat.

Dangers of Exotic Plants

Over 4,000 types of exotic plants have been introduced into the U.S. Now, nearly a third of the plants growing in the U.S. are from elsewhere. Of the 300 most invasive exotic plants in the U.S., 150 species have escaped from yards and gardens. Other invasive exotics were imported as crops, to control erosion, or by accident.

Once a natural area becomes dominated by one kind of invasive exotic plant, the system has less diversity because a variety of native plants and animals have been



pushed out. Invasive exotic plants harm nature in various ways, such as:

- ▲ crowding out native plants and animals
- ▲ poisoning soils so natives can't grow
- ▲ drinking up surface and ground water
- ▲ increasing erosion
- ▲ making land more or less prone to fire
- ▲ inbreeding with native species
- ▲ changing grasslands to thickets or forests
- ▲ covering open-water marshes
- ▲ smothering native trees with heavy vines

The biggest threat of invasive exotic plants to our natural systems is a reduction in the diversity, or variety, of native forms of life. Healthy, diverse natural systems are valuable because they provide us with:

- ▲ clean air and water
- ▲ natural resources like timber and game
- ▲ medicines and chemicals
- ▲ recreational areas and scenic beauty

Diversity provides a buffer for nature to survive unexpected changes. If we allow our natural systems to become too simple, they may stop working and we may not be able to continue to have clean water or other resources. Because healthy native ecosystems are an investment in the future, it's easy to see why we want to keep a "diversified portfolio" -- to keep as many of the native life forms as possible and prevent invasive exotic plants from taking over.

Control of Invasive Exotics

Invasive exotic plants sneak up on us. At first an invasive plant appears to spread slowly, then the population explodes and control becomes difficult and costly. It is important to take action early. Invasive exotic plants must be stopped at our borders and eliminated around our homes, schools, and businesses, *before* they take over our natural areas.

Exotic Pest Plant Councils (EPPCs) in several states are working to prevent the spread of invasive exotic plants. The EPPCs define *Category I* exotics as plants that are invading and disrupting native plant communities, and *Category II* exotics as plants to watch out for in the future. Florida has 61 *Category I* and 55 *Category II* invasive exotic plants. Many counties in Florida have prohibited some of these exotic plants. The Florida Legislature and U.S. Congress have adopted lists of "Noxious Weeds" that are illegal to grow or sell.

Exotic Plants on Eglin

As more people move to the Florida panhandle, Eglin's forests and wetlands are facing an increased threat from invasive exotic plants. So far, 15 EPPC *Category I* exotic plants have been found on Eglin Air Force Base:

- ▲ Chinese tallow (Popcorn tree)
- ▲ Cogongrass
- ▲ Tropical soda apple
- ▲ Japanese climbing fern
- ▲ Air potato vine
- ▲ Kudzu vine
- ▲ Japanese honeysuckle
- ▲ Torpedo grass
- ▲ Nandina (Heavenly bamboo)
- ▲ Lantana
- ▲ Hedge privet
- ▲ Chinaberry tree
- ▲ Camphor tree
- ▲ Water hyacinth
- ▲ Hydrilla

Eglin Natural Resources Branch ● Jackson Guard Building
107 Highway 85 North ● Niceville, FL 32578 ● 904-882-4164

EGLIN FACT SHEET

An Ounce of Prevention is Worth a Pound of Cure

Eglin's Action Plan

In 1994, the federal government established a policy to landscape with native plants at all new developments. The policy recognizes that native plants grow well, provide attractive landscapes, require little care, provide wildlife habitat, and use less water and fertilizer because they are adapted to local soils and weather. Most new government landscaping on Eglin is being done with native plants. Eglin's Grounds and Urban Forestry Plans promote landscaping with noninvasive plants for base housing.

Eglin's Natural Resources Branch is taking action to control invasive exotic plants in Eglin's forests and wetlands by:

- ▲ replanting native trees and plants in damaged ecosystems
- ▲ reintroducing natural disturbances, such as fire
- ▲ reducing unnatural disturbances to soil, like unnecessary roads
- ▲ controlling invasive exotics by removal or chemical treatment

To better understand invasive plants, scientists are working to identify characteristics that signal future problems. They have observed that invasive exotic plants:

- ▲ grow in a wide range of soils and climates
- ▲ produce lots of seeds or berries
- ▲ grow rapidly and reproduce early
- ▲ easily spread seeds by animals, birds, wind, or water
- ▲ reproduce by both seed and sprouting
- ▲ resist pests, fires, storms and disturbances

Controlling Invasive Plants at Home

The best control methods for Eglin-area homes, schools, neighborhoods, and businesses include:

- ▲ hand pulling to minimize soil disturbance in yards and gardens
- ▲ tool cultivation for pulling out masses of vines or roots
- ▲ girdling trees
- ▲ mulching to prevent seed from sprouting
- ▲ mowing repeatedly before invasive exotics flower
- ▲ tilling of already cultivated areas
- ▲ herbicides as a last resort (new earth-friendly, soap-based herbicide formulas are safer for home use)

What you can do:

1. Recognize that exotic plant problems involve everyone.
2. Learn to identify and prevent invasive exotic plants. Replace invasive exotics in your yard with native or noninvasive plants.
3. Don't plant, grow, or give away suspected invasive exotic species.
4. Remind your local nursery to provide only non-invasive plants.
5. Contact Eglin's Grounds Section for landscape suggestions (904-882-8179). Contact your county extension agent or the Florida Game Commission's Wildlife Education Section to learn about backyard wildlife habitat plantings (904-488-4676).
6. Contact Eglin's Natural Resources Branch if you see invasive exotic plants in Eglin's forests (904-882-4164).

Replace the Invasive Exotic Plants in Your Landscape

Invasive Exotic Plant	Reason for Introduction	Preferred Native or Noninvasive Plants
Chinese tallow (Popcorn tree) *(Sapium sebiferum)*	Fast growing tree with fall leaf color and fruits attractive to birds	Shumard and other native oaks, tupelo, red maple, sourwood, ornamental cherry or crabapple, hackberry, mulberry, persimmon
Cogongrass *(Imperata cylindrica)*	Thick grass with plume-like seed heads	Native grass or grass-like plants such as dropseed, muhly, wiregrass, broomsedge, bluestem, star-rush, switchgrass, sea oat, nutsedge, beakrush, iris, yellow-eyed grass, coontie, yucca, fern
Japanese climbing fern *(Lygodium japonicum)*	Climbing fern with fine foliage	Native ground ferns, resurrection fern
Hedge privet (*Ligustrum* species)	Evergreen hedge with small leaves and fruits attractive to wildlife	Native viburnums such as black haw or possumhaw, wax myrtle, hawthorn, chickasaw plum, sumac, huckleberry, dwarf live oak
Japanese honeysuckle *(Lonicera japonica)*	Woody vine/shrub with fragrant spring flowers	Coral honeysuckle, yellow jasmine, trumpet vine, cross vine, climbing aster, native azalea, cultivated camellias or azaleas
Lantana *(Lantana camara)*	Flowering shrub attractive to insects and hummingbirds	Native azalea, cultivated camellias or azaleas, coral honeysuckle, butterfly milkweed, buttonbush, sweet shrub, oak-leaf hydrangea
Heavenly bamboo *(Nandina domestica)* Ardisia *(Ardisia elliptica)*	Ornamental shrubs with compound leaves and colorful berries attractive to birds	American beautyberry, coralbean, elderberry, sumacs, deerberry, yaupon or dahoon holly, hybrid roses, bunchberry, winterberry, palmetto, sparkleberry, buckthorn, blueberry
Chinaberry *(Melia azedarach)* Mimosa *(Albizia julibrissin)*	Trees with compound leaves and interesting flowers	Honey locust, Florida soapberry, staghorn sumac, sourwood, fringetree, dogwood, redbud
Camphor tree *(Cinnamomum camphora)*	Fragrant tree	Sassafras, pine, Southern redcedar, cypress, Florida anise (shrub)

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Prepared by Dr. S.K. Jacobson and S.B. Marynowski of the University of Florida's Department of Wildlife Ecology and Conservation for Eglin's Natural Resources Branch.

EGLIN FACT SHEET

Wild Hogs

Florida's Wild Hog

The wild hog, or feral pig, is descended from European wild boar and escaped farm pigs. Wild hogs are exotic animals and are not native to the United States.

Thirteen hogs were released in Florida by Hernando DeSoto in 1539, and by the next year there were over 300 wild hogs. Since that time, the wild hog has become widespread in Florida and other parts of the U.S. Wild hogs are one of the most common exotic animals in southeastern pine woods. Florida and Texas combined have two-thirds of the wild hogs of the southeastern U.S.

Wild hogs are managed by some agencies as a game species, and they are a popular game food item. However, many other land agencies manage wild hogs as exotic animals, and seek to remove them from parks and forests because of the negative impacts wild hogs have on natural systems.

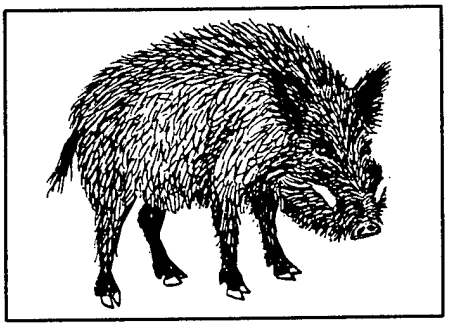
Wild Hog Biology

Wild hogs weigh about 100 pounds, with the largest on record weighing 575 pounds. They have sparse, bristly hairs which form a ridge along the back. Adults vary in color from gray to black, with some having a white blaze on their snout.

It's no wonder DeSoto's hogs were able to spread throughout Florida! Wild hogs have a high reproductive rate. They begin breeding at 6 months of age with an average litter size of four or more piglets. Wild hogs occupy an average home range of 1.5 square miles, and up to 23 hogs may occupy a square mile.

Wild hogs occur in a wide variety of habitats. Open land or pasture supports low to medium populations. Higher populations are found in pine woods mixed with cypress swamps and oak hammocks, like the forests on Eglin Air Force Base. Wild hogs thrive in forested areas with dense cover. Hogs do not have sweat glands, so they must wallow in cool, moist areas during hot weather.

Wild hogs eat a diet of 55% plants, 40% roots, 3% fruit, and 2% animals and insects. Plants make up the bulk of hogs' diet, with



mast (acorns and pine seeds) being more important in fall and winter and foliage (herbs and grasses) being more important in spring and summer.

Effects of Wild Hogs on Natural Systems

Wild hogs compete with native wildlife for food and alter habitats that are important for native fish and wildlife:

- Wild hogs compete for acorns with turkeys, deer, bears, and other animals.
- Wild hogs destroy nests and eat eggs of turkeys, quail, and other ground nesters.
- Small mammals and insects that live in leaf litter disappear from areas disturbed by wild hogs, thus limiting food sources for animals like quail and turkey.
- Wild hog digging along streams reduces water quality and fish habitat.

The digging of wild hogs damages ecosystems that humans depend on for natural resources and economic benefits:

- Wild hogs eat pine seeds and seedlings -- in some areas wild hogs are responsible for the failure of pines to regrow.
- Wild hogs have significantly damaged agricultural land and crops, forests, roads, pastures, and fences on every continent.
- Wild hogs' disturbance of native vegetation opens the way for exotic plants to invade.
- Wild hog digging contributes to dune erosion in coastal areas by destroying stabilizing plants.

Wild hogs carry a number of dangerous diseases which can be spread to livestock and humans:

- In Florida, 99% of wild hogs carry ticks.
- Wild hogs can carry and spread the diseases Leptospirosis, Brucellosis, Trichinosis, Pseudo-rabies, Bovine Tuberculosis, Hog Cholera, Foot and Mouth Disease, African Swine Fever, Anthrax, and Rinderpest.
- Wild can hogs carry and spread parasites like tapeworms, kidney worms, lungworms, roundworms, and hookworms.
- The transfer of wild hogs from one area to another spreads diseases and parasites.

Wild hogs are not picky eaters. Their appetite, their habit of digging, and their wallowing behavior can change natural areas:

- By digging for food, wild hogs change the kinds of plants that grow in an area.
- Wild hogs reduce the number and diversity of flowering plants.
- Only deep-rooted plants or plants able to reproduce after being dug up remain where wild hogs dig for food.
- Over time, wild hogs have an impact on the kinds of trees that grow in a forest.
- Wild hogs alter soil and nutrient cycling in the forest.

Wild hogs also are destructive to habitats of rare and endangered species on Eglin:

- Wild hogs' digging has damaged and destroyed endangered plants in many areas.
- Wild hogs' wallowing and digging severely degrades moist areas such as bogs which provide habitat for the pitcher plants and other rare plant species.
- Wild hogs in coastal areas destroy up to 80% of endangered sea turtle nests.
- Wild hogs prey on rare reptiles such as indigo snakes and Florida pine snakes, and the nests of some reptiles.

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EGLIN FACT SHEET

Management of Wild Hogs

How Public and Private Agencies Manage Wild Hogs

Management practices for wild hogs differ from site to site. The Florida Game and Fresh Water Fish Commission classifies wild hogs as a game species, which applies to all Wildlife Management Areas in Florida. Wild hogs are valued by some hunters as a game food item.

In Florida's state parks, wild hogs are eliminated as undesirable exotic animals. The National Park Service has a similar approach, killing all wild hogs found in parks. The U.S. Forest Service defines wild hogs as "livestock trespassing on National Forests in Florida," and attempts to have the animals removed by their "owners." Private conservation organizations such as The Nature Conservancy recommend eradicating wild hogs from preservation areas where there is no hunting, and controlling numbers of wild hogs in hunting areas to reduce the impacts caused by the animals.

Trapping, hunting, and fencing are the main ways of controlling wild hogs. It is usually necessary to use two or more of these methods together to control wild hogs. The traditional practice of moving wild hogs to other areas now goes against public policy restricting the introduction of exotic animals on public lands.

Hunting alone is not commonly used as a wild hog control method, but rather as a recreational and food-gathering activity. Fall is the recommended time to harvest wild hogs, and they can be hunted indefinitely without an impact on populations.

Research has shown that fall hunting does not reduce wild hog populations. Fall harvest of wild hogs reduces competition for acorns, which makes remaining hogs healthier and actually *increases* the number of young born the next year. Where wild hog populations need to be controlled, hunting may take place during the breeding season or all year to reduce the number of potential offspring and the overall number of hogs.

Wild Hog Management on Eglin

At present, Eglin's wild hogs are classified as a game species and are included as a prey item in Eglin's recreational hunting program. There is no limit on the size or number of hogs hunters may take during Eglin's archery, muzzleloading, or general gun seasons. However, wild hogs on Eglin are competing with other game species for limited resources and are damaging some of Eglin's sensitive ecosystems. Eglin wildlife biologists have begun to monitor wild hog populations and their impacts to determine whether control may be necessary in the future.

Learn More About Eglin's Wild Hogs

- Refer to Eglin's *Outdoor Recreation, Hunting, and Fresh Water Fishing Map and Regulations* for further information about hunting wild hogs.
- View Eglin's captive wild hogs at the Jackson Guard building on Highway 107 in Niceville.
- Look for wild hogs, or signs of their wallowing and digging behaviors, in Eglin's forests. Their narrow hoofprint is easy to spot in Florida's sandy soil.
- Direct further questions about wild hogs to Eglin's Natural Resources Branch at 904-882-4164.

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LONGLEAF PINE GENETICS

R.C. Schmidtling, USDA Forest Service, Southern Institute of Forest Genetics, Saucier, MS

There has been a movement of late toward the use of natural regeneration for longleaf pine (*Pinus palustris* Mill.) as well as for other forest tree species. If you have a good natural stand, and have plenty of time, natural regeneration will result in a suitable stand, and genetics is not relevant.

Using natural regeneration can be risky, however. A good example is from the Southwide Southern Pine Seed Source Study (SSPSSS), longleaf phase, established in the early 1950's (Wells and Wakeley 1970). The stands and trees from which seed was collected were carefully chosen to be representative of the genetic resource of the area. One of the seed sources, from southeastern Louisiana performed much below expectations in growth and survival after 10 years. Upon investigation, Wakeley found that the area had been clear-cut in 1905, and that the stand seeded in from three, possibly four residual trees. Allozyme analysis later showed that the source was indeed genetically challenged (Schmidtling and Hipkins 1998).

If you don't have an existing stand of longleaf, or if that stand is genetically suspect (established with an unknown and perhaps foreign seed source, or from only a few residual trees), then some form of artificial regeneration is necessary, and genetics is relevant.

TREE IMPROVEMENT

Every important characteristic in longleaf pine is heritable to some degree. Genetic variation in longleaf pine follows the pattern for other southern pines for most traits, making it suitable for genetic improvement. There are tree improvement programs for longleaf pine in the NC State, Florida, and Western Gulf (TX A & M) cooperatives as well as in the US Forest Service (R-8), but these programs are minor compared to the effort in loblolly (*P. taeda* L.) and slash (*P. elliottii* Engelm.) pines.

Traditional tree improvement programs involve selecting "plus" trees in the forest based on size, form, and branch characters. Age is determined by increment cores taken at breast height (4.5 ft) for comparison to similar-aged trees in the same stand. This system works very well for slash and loblolly pines, producing significant genetic gains in the first round of selection. It is not very suitable for longleaf pine, however, since variation in the "grass" stage makes it impossible to tell the true age of the tree, and therefore its true growth potential.

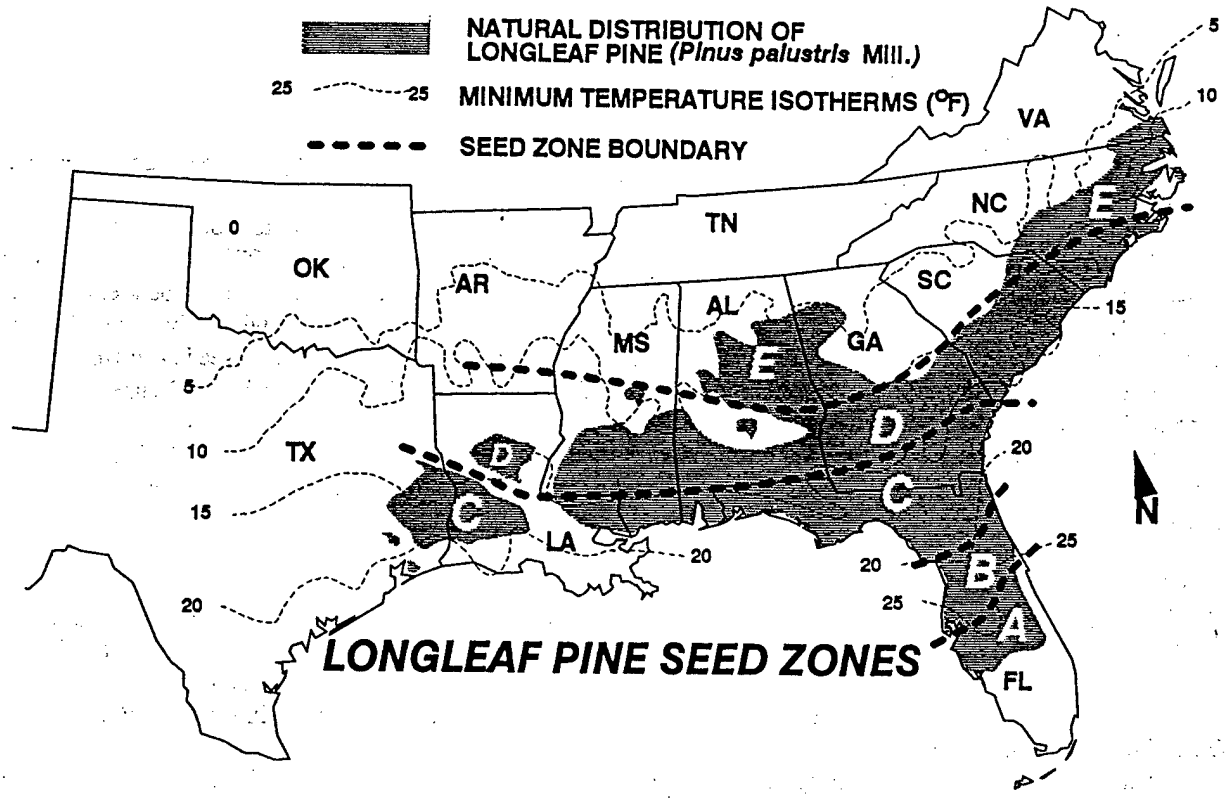
The "grass" stage is quite important genetically as well as silviculturally, and complicates the tree improvement program. Most of the tree improvement programs in longleaf have shifted to a progeny test approach. Selection criteria are relaxed so that many vigorous, well formed trees are included. Open pollinated seed are collected from these selections, and replicated plantings of seedlings are established to determine growth potential, including duration of the grass stage. These plantings are then rogued and thinned to convert them to seed orchards. This is a much more precise way of determining genetic potential and producing genetic gain, but takes a great deal of time to produce improved seed.

Early growth and survival is largely determined by the two most important inherited traits in longleaf, the duration of the grass stage, and resistance to brown-spot disease (*Mycosphaerella dearnessii* Barr). Both of these traits are strongly inherited, with heritabilities around 50% (Snyder et al. 1977). Progeny testing for these traits is also simple, because the traits can be evaluated in open-pollinated seedlings within 3 or 4 years from seed, and most tree improvement programs emphasize these traits.

Duration of the grass stage and brown-spot disease are obviously related, as severe brown-spot infection will prevent height growth, sometimes for many years. Thus, there is a strong **phenotypic** or environmental correlation between brown-spot disease and duration of the grass stage. The **genetic** correlation between the two traits, on the other hand, is very low. This means that you can select and breed for one of the traits without affecting the other.

There are several different strategies, therefore, for overcoming the problems associated with the grass stage. You can breed for early height growth, and ignore brown-spot. If height growth occurs before brown-spot build-up, then there is no problem. Or, you can breed for brown-spot resistance, and height growth will not be delayed.

One danger in breeding for early height growth, is the possibility of incorporating loblolly pine genes. Longleaf pine hybridizes naturally with loblolly pine, the resulting hybrid is referred to as a Sonderegger pine (Chapman 1922). The hybrid seedlings begin height growth almost immediately after germination, and early growth is much better than for longleaf pine. The hybrid possesses many of the undesirable characteristics of loblolly pine, however, such as poor form and susceptibility to fusiform rust disease (*Cronartium quercuum* f. sp. *fusiforme*). Any longleaf seedling that begins height growth in the nursery is surely a hybrid. Breeding for early height growth subsequent to outplanting, however, can be accomplished without favoring loblolly genes (Lott et al. 1996).



SEED SOURCES

Unfortunately, only limited quantities of genetically improved longleaf pine are available. This is due to the small size and immaturity of longleaf pine tree improvement programs as well as the sporadic nature of good cone crops, a problem in the orchards just as it is in the forest. The most conservative approach to reforestation would be to use seed collected from healthy, vigorous local stands. There is little risk involved in using non-local seed, however, if certain guidelines are adhered to.

The most important factor influencing growth and survival in longleaf pine is climate, specifically average yearly minimum temperature (Schmidtling 1997, Schmidtling and Sluder 1995). This parameter has been used, not coincidentally, to determine plant hardiness zones (USDA 1990).

There is no ecotypic differentiation in the species, ie, stands from deep sand sites differ little genetically from stands on heavier soils. Unlike loblolly pine, there are no important differences between eastern and western sources. This basic difference between longleaf and loblolly pines is probably rooted in the Pleistocene geologic era. During the height of the Wisconsin Ice Age, 14,000 years before present, the south was occupied by a boreal forest. Patterns of genetic variation in allozymes indicates that longleaf resided in one refuge in south Texas/ north Mexico and migrated northward and eastward when the ice retreated (Schmidtling and Hipkins 1998). It is probable that loblolly pine originated from two refugia, one in the southwest near longleaf pine, and one in south Florida/ Caribbean.

The lack of east-west differences in longleaf pine simplifies seed transfer guidelines. I have divided the natural range of longleaf pine into five collection/ planting zones (Figure). Seed may be collected from anywhere within a zone for planting in this zone. Seed from one zone warmer will result in an increase in growth, whereas seed from one zone colder will result in a decrease in growth compared to local sources. Seed should not be used from more than one zone distant.

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Red-cockaded Woodpecker

Picoides borealis FRENCH: *Pic à face blanche*



The Red-cockaded Woodpecker, one of nine species within the genus *Picoides* in North America, depends on old growth southern pine forests for food and habitat. As a result of this dependence, its populations have been vulnerable to elimination, fragmentation, or modification of those forests by man. Conversion of favored longleaf pine (*Pinus palustris*) forest to slash pine (*P. elliottii*) has also been linked to population declines in this woodpecker.

Once considered common in the South, the Red-cockaded Woodpecker has disappeared from much of its range and has been considered Endangered since 1968 (U.S. Dept. Interior 1968). This status, as well as its continued broad distribution (albeit of small and declining populations) in the southeastern United States and its occurrence on many federal lands, has made the Red-cockaded Woodpecker the subject of intensive study since the early 1970s. Indeed, it may well be the most studied woodpecker species in the world. Jackson's (1981) annotated bibliography of the species includes 1,790 entries, Marion and Hagedorn's (1991) review covers selected literature through 1990, and three symposia since 1971 have focused on this woodpecker (Thompson 1971, Wood 1983a, Kulhavy et al. in press).

The Birds of North America
Life Histories for the 21st Century

Like most of its congeners, the Red-cockaded Woodpecker is rather sedentary and not known to migrate, although on occasion individuals may wander far, perhaps a result of habitat destruction. Unlike its North American congeners, this is a social species that lives in family groups, often

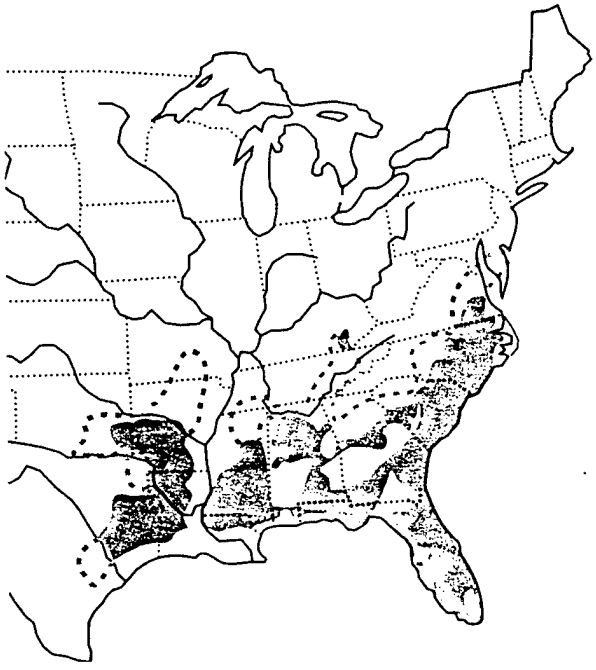


Figure 1.
Approximate current breeding range of the Red-cockaded Woodpecker. Within this range populations are exceedingly fragmented (see text). Probable 20th century breeding range is indicated by areas within dashed boundary lines. Text discusses additional extralimital records.

called clans, with a cooperative breeding system. The cluster of cavity trees used by the family group and the group itself led early observers to refer to this species as "colonial" and to the cavity tree cluster as the "colony site." These misnomers have died hard and given casual observers a false sense of the species' abundance. Throughout this account the site of the cavity tree or trees occupied by a family group will be referred to as the "cavity tree cluster."

Unlike most woodpeckers, the Red-cockaded typically excavates nest and roost cavities in living trees (several pine species), cavities that may be used for decades. Above and below each cavity the birds also excavate tiny holes—resin wells—from which resin exudes, apparently protecting the birds and their nests from climbing rat snakes (*Elaphe obsoleta, E. guttata*). Their social system, unusual cavity sites, and resin wells are hallmarks of a species so different among woodpeckers that a unique vocabulary has become associated with it (Jackson and Thompson 1971).

DISTINGUISHING CHARACTERISTICS

Small (20–23 cm) black-and-white woodpecker with a ladder back and large white auricular patches. White "cheeks" separate Red-cockaded from all other species in range. Black above with white bars on back and wings, white outer rectrices with black bars, white to gray-white breast and belly with distinctive black spots along the sides of breast tending to bars on flanks. Narrow white line above eye, white-gray-buff nasal tufts. Adult male has a tiny streak of red on each side of the nape within the black cap and near the junction of the black cap and white auricular patch (see cover photo). This is rarely visible on adults in the wild and they cannot be reliably sexed without capture. Legs and feet gray, bill black.

DISTRIBUTION

THE AMERICAS

Breeding range. Populations highly fragmented within the se. U.S. north to se. Oklahoma, s.-central Kentucky, and se. Virginia (Fig. 1), primarily concentrated on extensive old-growth pine forests of federal and state lands (Jackson 1971, 1978a, Hooper et al. 1980, Lennartz et al. 1983).

Winter range. Same as breeding. Occasional individuals have recently wandered as far north as s. Ohio (Peterjohn 1989).

OUTSIDE THE AMERICAS

Not recorded outside North America.

HISTORICAL CHANGES IN DISTRIBUTION

Dramatic declines, including contraction and extreme fragmentation of populations, have occurred this century with accelerated fragmentation in recent decades (Jackson 1971, 1978a). Nineteenth century records beyond current range include n. New Jersey and se. Pennsylvania (Stone 1894). The species was last seen in Missouri in 1946 (Robbins and Easterla 1992), in Maryland in 1976 (Devlin et al. 1980), and in n. Mississippi in 1977 (Jackson et al. 1977). The Tennessee population is on the verge of extinction—one bird known in 1992 (JAJ); Kentucky and Virginia populations perilously low (JAJ); Virginia has only 5 family groups, entirely on private lands (Beck 1991).

Well-documented losses have occurred throughout the species' range, including steady precipitous declines in recent decades on National Forests throughout the South (Costa and Escano 1989). The most dramatic loss was decimation of the then largest known, healthiest population on the Francis Marion National Forest, S. Carolina, by Hurricane Hugo in September 1989.

FOSSIL HISTORY

There is a single record reported by Woolfenden (1959) from the late Pleistocene, Rancholabrean (North American Land Mammal Age, 0.6 million years before present), Rock Springs, Orange Co., Florida.

SYSTEMATICS

GEOGRAPHIC VARIATION

Larger (mass, wing, tail) in northern interior areas to smaller in southern and coastal areas, varying clinally through its range (Mengel and Jackson 1977). Short (1971) suggests size limits and some special characters of Red-cockaded a result of interaction with Hairy (*Picoides villosus*) and Downy (*P. pubescens*) woodpeckers.

SUBSPECIES

Two subspecies recognized (Am. Ornithol. Union 1957): *P. b. borealis* ranging from n. Florida northwards, and *P. b. hylonomus* ranging from n.-central to s. Florida. The validity of the latter subspecies, described by Wetmore (1941) on the basis of average smaller size of birds from peninsular Florida, has been questioned by Todd (1946), Jackson (1971), Mengel and Jackson (1977), and Short (1982). Mengel and Jackson (1977) analyzed geographic variation in the species and found it to be smoothly clinal for wing, tail, and bill measurements, the largest birds occurring in Kentucky, the smallest in s. Florida. No distinctive geographic variation in plumage color pattern.

RELATED SPECIES

Nuttall's (*Picoides nuttallii*) and Ladder-backed (*P. scalaris*) woodpeckers were considered to be the closest relatives of the Red-cockaded by Voous (1947) and Mayr and Short (1970). Short (1982) considers the Red-cockaded closest to the "*Picoides scalaris - nuttallii-pubescens* complex" on the basis of similarity in plumage and vocalizations, and in part on habitat segregation with Downy and a lack of habitat segregation with Hairy woodpeckers in Louisiana (reported by Morse 1972). Contrary to the latter, Downy Woodpeckers are quite common in Red-cockaded Woodpecker habitats throughout the range of the species; the two may forage within a few meters without interaction (JAJ), or the Red-cockaded may drive a Downy away (Ligon 1968a). My observations at a Downy nest within 12 m of a Red-cockaded nest revealed no interaction. Hairy Woodpeckers are notably uncommon in the Southeast. Agonistic encounters with both species reported (see Behavior: social and interspecific). Perhaps in support of an ancestral tie with the Downy Woodpecker, I enticed a juvenile Downy Woodpecker in Mississippi into a mist net by the playback of the greeting call of a Red-cockaded Woodpecker.

As an alternative ancestry hypothesis, Jackson (1971) argued that the Red-cockaded Woodpecker had its origins from an ancestral Hairy Woodpecker stock in insular Florida during higher sea levels of a Pleistocene interglacial. Evidence supporting this hypothesis includes: (1) barring on the back of some Hairy Woodpeckers in several peripheral, isolated populations; (2) the reduction of red on eastern male Hairy Woodpeckers to two lateral nape spots; (3) more extensive white on the cheeks of some Hairy Woodpeckers from the Bahamas than from mainland populations (JAJ); (4) relative rarity of Hairy Woodpeckers within the range of the Red-cockaded, and specifically its rarity in pine forest habitats of the Southeast; and (5) the near restriction of Hairy Woodpeckers to pine forests in the Bahamas, suggesting that perhaps their scarcity in pines on the adjacent mainland may be a result of competitive exclusion.

MIGRATION

This species does not migrate.

HABITAT

BREEDING RANGE

In general, extensive mature open pine forest maintained naturally by frequent (1–5 yr interval) lightning-started fire during the summer (Jackson et al. 1986; Fig. 2). Species occasionally persists for a time in stands that are younger or where hardwood encroachment is dense, and rarely in bald cypress (*Taxodium distichum*) adjacent to pines. An extremely tenacious species, probably the result of the lengthy period needed for cavity excavation and the persistence and reuse of cavities. Quite often the birds will not abandon a cavity tree cluster even though much of the surrounding forest has been clearcut. This should *not* be construed as the species' acceptance, tolerance, or ability to survive in such modified habitats. Population responses to habitat alteration are often delayed 6–10 yr or more; short-term persistence is not meaningful (Conner and Rudolph 1989, 1991, Jackson and Parris in press). Leaving cavity tree clusters without quality foraging habitat and corridors linking adjacent populations may transform the cavity tree cluster into an ecological sink.



Figure 2. Typical habitat of the Red-cockaded Woodpecker —a longleaf pine forest in Talladega National Forest, Alabama. The woodpeckers use these pine trees for nest sites and feeding. Lightning-caused fires help to maintain longleaf pine forests by preventing hardwoods from invading; the pines are quite resistent to fire. Photo by S. G. Maka, Wildlife Photography.

Uses longleaf, loblolly (*Pinus taeda*), slash, shortleaf (*P. echinata*), Virginia (*P. virginiana*), pond (*P. serotina*) and pitch (*P. rigida*) pines. Some argue that longleaf is the preferred species, although many populations exist well north of the range of longleaf pine.

Extremes of habitat can be found at the extremes of the species range: scattered slash pine stands mixed with baldcypress and grassy wetlands in s.

Florida (Patterson and Robertson 1981) and upland pitch pine in s.-central Kentucky (Jackson et al. 1976). Even within a pine species, there is great diversity in the habitat the Red-cockaded Woodpecker uses. For example, the longleaf pine forests of coastal S. Carolina can include trees in excess of 30 m tall, whereas trees of the same species and age in the flatwoods of central Florida may barely reach 10 m and half the trunk diameter. To be sure, with such variation in habitat, there is also variation in available food resources—the bigger trees have greater foraging surface available. Thus one cannot simply define habitat needs by the number of "stems" available, as done in the current Recovery Plan for the species (Lennartz and Henry 1985; see Conservation and Management).

SPRING AND FALL MIGRATION

Not applicable.

WINTER RANGE

Habitat same as breeding range.

FOOD HABITS

FEEDING

Main foods taken. Adults, larvae, and eggs of tree surface and subsurface arthropods; to a much lesser extent various seeds and fruits.

Microhabitat for foraging. Males forage primarily on branches and upper trunk of pines; females primarily on trunk, often below lowest branches (Ligon 1968a, Ramey 1980, Jackson and Parris in press). Report of no differences in foraging sites of sexes (Morse 1972) was based on study of unmarked birds; identification of sexes of unmarked birds is not reliable. About 90% of foraging is on pines; 10% on hardwoods; varies with available habitat and season (Ramey 1980).

Larger pines favored over smaller ones (e.g., Ramey 1980, Bradshaw 1990), probably a function of available surface area per tree and looser and larger bark plates on older trees which likely provide greater diversity and abundance of arthropod prey.

Will forage in corn fields on corn earworms (*Heliothis zea*) when within range (Dingle 1926, Baker 1971).

Food capture and consumption. Characteristically forages with group; may join or be joined by mixed flocks of passerines, especially in winter. "Scales" loose bark from pines to reveal arthropods underneath. Bark plates are flicked from the tree with an upward or sideways movement of the bill, or pulled loose with the bill. Less often, and more commonly with females, the bird may pull bark loose with its feet (Ligon 1968a). The presence of the birds high in a tree is often evidenced by bark chips falling to the ground. The group so thoroughly scales trees within its range that the resulting smooth, reddish trunks are good cues that the stand is within the foraging range of a family group (Jackson 1978c). Probes crevices, branch stubs, and needle and cone clusters, especially on younger trees with more adherent bark; excavates in rotting wood. Rarely comes to feeders for suet.

DIET

Major food items. At times, ants (Hymenoptera) comprise as much as 70% of the Red-cockaded's diet (Beal et al. 1916). However, a captive female (Jackson 1983a) not only refused to eat ants, but would not tolerate them in her cage; she relished termites (Isoptera). Adults and larvae of southern pine beetles (*Dendroctonus frontalis*) and bark beetles (*Ips* spp.) frequently taken. Most frequent foods brought to young include insect larvae, wood roaches (Blattidae), and centipedes (JAJ, Mississippi; Harlow and Lennartz 1977, S. Carolina). Vegetable material includes seeds of pine (*Pinus* spp.) and fruits of wild cherry (*Prunus serotina*), pokeberry (*Phytolacca americana*), grape (*Vitis* spp.), magnolia (*Magnolia grandiflora*), poison ivy (*Rhus toxicodendron*), blueberry (*Vaccinium* spp.), blackgum (*Nyssa sylvatica*; Beal et al. 1916, Baker 1971).

Quantitative analysis. Beal et al. (1916) examined 99 stomachs from six states and found 86% arthropods, 14% plant; ants about 52% of annual diet, beetles about 18%.

NUTRITION AND ENERGETICS

Food consumption of captive female fledgling increased to a maximum of 54 crickets/d during molt and declined following molt (Jackson 1983a). This was supplemented with a small quantity of fruit (perhaps as much as one grape and a 0.5 cm slice of banana) and about 12 mealworms per day. Later maintenance diet of captive female included mealworms, termites, crickets, a peanut butter-cornmeal mixture, scrambled egg, grapes, banana, apple, and occasionally other arthropods and fruit. Water has always been provided ad lib. To date its weight and health have been maintained for 12 yr.

METABOLISM AND TEMPERATURE REGULATION

See Behavior: self-maintenance.

DRINKING, PELLET-CASTING, AND DEFECATION

Rarely comes to the ground, but drinks from water-filled tree cavities or depressions on horizontal limbs. Also takes water from dew- or rain-laden leaves or needles. Not known to cast pellets. Generally defecates in flight, but may defecate while foraging on a vertical trunk or limb by leaning to the side and raising the tail 3–4 cm from the surface to eject the excreta away from the tree (Jackson 1983a).

Feces collected during banding operations often contain fragments of arthropods and occasionally undigested seeds (e.g., *Rhus*; JAJ).

FOOD SELECTION AND STORAGE

Laying females will cache bone fragments (Repasky et al. 1991).

SOUNDS

VOCALIZATIONS

It was the constant chatter of bands of Red-cockaded Woodpeckers that led Alexander Wilson (1810) to describe the species as "*Picus querulus*." Wilson suggested that the voice of the Red-cockaded Woodpecker "greatly resembles the chirping of young nestlings." Most descriptions anecdotal. Winkler and Short (1978) provide sonographs and compare vocalizations with other *Picoides* spp.

Development. At hatching, and for about 4 d thereafter, chicks are nearly silent except for the strident, rasping squeak of begging calls. By day 4, adults begin leaving chicks for several minutes at a time, leaving the chicks huddled together, facing one another on the nest floor, each with its neck propped up on its siblings. At such times chicks produce a constant, low-intensity, rhythmic peeping sound that suggests "contentment." This Contentment Peeping ("Soft Note" of Winkler and Short 1978) continues through at least day 10, about the time a chick's eyes open. From day 4 to day 10, the intensity of the Contentment Peeping increases to the point that a human can sometimes hear it from the base of the nest tree. Periodically and for no apparent reason one or more chicks may give a brief begging call, but in the absence of an adult, it settles back into the Contentment Peeping.

For about the first 10 days, the stimulus that elicits a begging call is the change in light intensity from light to dark when an adult sticks its head in the entrance. A passing cloud, the shadow of a wind-blown branch, or a human hand held up to the entrance can elicit the same response. By day 15, chicks begin to produce the Chirp Call and transitions to the Call Note and Short Rattle. Ligon (1971) noticed transition to adult calls beginning about day 11. Within 2 d of fledging a chick begins to wait at the entrance of the cavity, often silently, but will occasionally give *sklit* or *churt* notes or "Short Rattle" calls. As an adult approaches, either of these quickly changes to excited begging. At fledging the chick is capable of producing the array of adult vocalizations, but is much less vocal than adults, often silently waiting nearly motionless for 20 min or more for a nearby adult to bring food. Some dependence on the adults for food and reduced frequency of vocalization (compared to adults) may continue into fall.

Vocal array. As might be expected of a more social species, the Red-cockaded Woodpecker seems to have a greater variety of vocalizations than its North American congeners. Winkler and Short (1978) document the greatest number of vocalizations, provide sonographs, identify seasonality and contexts, and compare vocalizations with those of congeners.

Churt Note. This call, described mnemonically by Ligon (1970), is the normal "call note" of the species. It is characteristically given at 2–4 s intervals as a bird flies into the cavity cluster area—when it is unaware of human presence. I have only heard it given by a bird in flight. If human presence or other disturbance is known, the birds give the *sklit* note, which is the call for which the species is best known.

Sklit Note. Winkler and Short (1978) refer to this call as the "Call Note" of the species and did not distinguish between it and the "Churt." The *sklit* note is more emphatic, a call given in a state of excitement, as opposed to the "non-excited," but equally loud Churt. Latham (1822) indicated that the bird was called "Sklit" in Louisiana as a result of this characteristic call. Other mnemonics for it include: *szrek* or *shrit* (Ligon 1970). It may be given by a bird in flight or perched. What Winkler and Short recorded seems to have been the *sklit* call which they found to have a pitch lower than that of the Downy Woodpecker and similar to that of the Hairy Woodpecker. The duration of the *sklit* note of the Red-cockaded is the longest "call note" (Winkler and Short 1978) known for *Picoides*; it averages nearly twice that of the Hairy Woodpecker. This is the most frequent vocalization noted by humans, it is given all year, and given by nestlings near fledging. In most contexts it is a call given when the birds are disturbed, such as by human presence.

Scolding. See Figure 3b. Not recorded for Red-cockaded, but "scolding" mentioned by Crosby (1971). *Sklit* notes given in situations where other species scold.

Rattle Call. Figure 3c. Resembles that of Hairy Woodpecker, descending at the end; juvenile rattle a different pitch and variable in length (Winkler and Short 1978). Often given as an adult flies into cavity tree cluster or towards nest.

Short Rattle. Characteristic of young near or just following fledging, but also given by adults during disturbance at nest; similar to Call Note, but given in a quick series; shorter than Rattle. Mnemonics: *wa-a-a* or *whe-he-he* (Ligon 1970).

Kweek. Shrill, uttered singly or in short string; sometimes transitions to Call Note. Given following feeding of young, but heard year-round.

Wicka Call. Mnemonics: *wicka* (Winkler and Short 1978); *wic-a* (Ligon 1970). A call given by an excited bird, described by Ligon as given by a male calling to female while defending nest from a Red-bellied

Woodpecker (*Melanerpes carolinus*). Treated by Winkler and Short (1978) as synonymous with She-u Call.

She-u Call. Mnemonics: *she-u, che-u, whe-u* (Ligon 1970); *tsi-voo* (Winkler and Short 1978). Treated as synonymous with *Wicka* Call by Winkler and Short. An excited call given during intraspecific territorial encounters; usually accompanied by open wing display and erratic flight (Ligon 1970, JAJ). Often given in series and in several social contexts: following feeding of young or when adults are close to one another, often when one adult flies to another.

Chortle Greeting. Figure 3a. Not described by Winkler and Short (1978). A somewhat melodious, soft chortling given by one or, more frequently, by two or more birds as they hitch close to one another while foraging (JAJ). This may be the same call described by Ligon with the mnemonic *whu-whu*; context and function match but, to my ear, the mnemonic does not. Ligon refers to it as: "soft notes uttered when the birds are calm and feeding near others of their group." Captive female would give Chortle Greeting when I came very close to its cage. From the context of the call, it seems both a greeting and, at times, a gentle admonition not to come any closer.

Twitter. Mnemonics: *tyet*. Often given in series of 2–6 notes. May occur with *Kweeks*. Given by parent flying to feed young; a bird flying from excavation activity, adults approaching fledglings (Winkler and Short 1978).

Wad. Recorded once; resembles call of Ladder-backed Woodpecker (Winkler and Short 1978).

Contentment Peeping. "Soft note" of Winkler and Short (1978); Contentment Peeping more descriptive. See Development, above.

Chirp Call. This is an anticipatory begging call of older nestlings given when an adult has just arrived at the nest, or sometimes spontaneously. These are the "soft begging calls" of Ligon (1970).

Loud Chirp Call. A loud, excited begging call given by nestlings as an adult enters the nest or arrives at the nest when young are in the entrance; also given at times when a shadow passes the entrance to a cavity containing young < 11 d old. Differs from Chirp Call by having broadened introductory element (Winkler and Short 1978). Mnemonic: *whew-whew* (Ligon 1970).

Squeak Call. Seems to be an exagerated Loud Chirp Call resulting from the stress of constant begging (JAJ); Winkler and Short (1978) describe it from fledglings.

Zrip. Described by Ligon (1970) as a soft note given at the cavity just before a bird goes to roost.

Deedle-Deedle. Described (Ligon 1970) as rarely given by a bird hovering before the cavity entrance before entering to roost. Seems similar or related to Chortle Greeting.

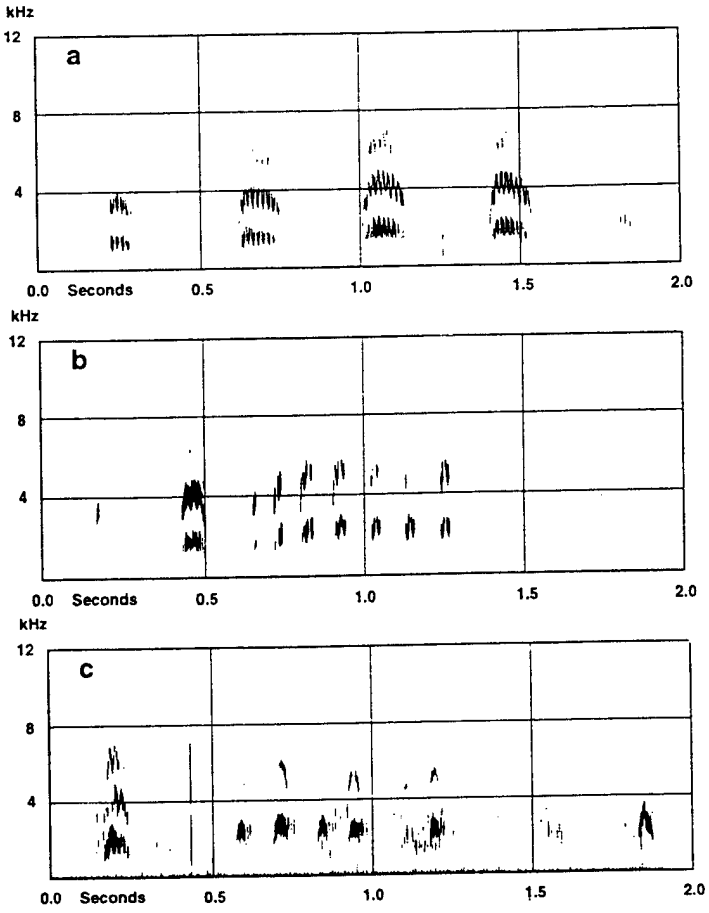


Figure 3. Common vocalizations of the Red-cockaded Woodpecker, recorded in Lean Co., FL, and produced by the Borror Laboratory of Bioacoustics (BLB), Ohio State University. (a) Chortle Greeting (BLB #4470); (b) Scolding; (c) Rattle Call (BLB #3774).

Shurz-U. Described by Ligon (1970) as a soft warning call given when a hawk flew near. Typically given as the Red-cockaded quickly hitches to the opposite side of the tree (JAJ).

Chit. A low, single note uttered at intervals by a Red-cockaded that has intruded on another group's territory and is being chased by them (Ligon 1970); given during Flutter Aerial Display (see Behavior: Agonistic; JAJ).

Distress Cry. Loud screams with regular frequency modulation of 55–63 kHz given by captured bird (Winkler and Short 1978).

Phenology. An extremely vocal species at all times of year. Clan maintains integrity through constant vocalization. On a seasonal basis, most evident in early spring; least evident during incubation and early brooding.

Daily pattern of vocalizing. Most vocal upon leaving roost in morning and upon return to cavity tree cluster in late afternoon. Group travels together and vocal exchanges are constant.

NONVOCAL SOUNDS

Array of sounds. *Tapping.* Communicative tapping not known. *Drumming.* By adults of either sex, especially breeding male in spring on pine trunk

(Ligon 1970) or less often on resonant branch; usually within or near the cavity tree cluster; neither common nor particularly loud (JAJ). Not used for long distance communication. TONGUE DRUMMING. Soft drumming-like sound produced by rapid vibration of the tongue on tree surfaces (JAJ). Observed in both captive and wild birds during mild states of excitement; may be related to foraging. The sound is reminiscent of the rattling of a rattlesnake. WING WHULL. Mnemonic: *whull* sound made with wings during Flutter Aerial Display (see Behavior: Agonistic). Ligon (1970) refers to this as "Wing Fluttering" or a "galloping" sound and indicates that it occurs when an agitated bird flies to its mate.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Hops on ground or along horizontal branches. In hitching upwards, the bird lunges forward using the upper body as well as legs, its tail serves as a spring helping to propel it upward and inward. As it lunges upward, the grasp of the feet on the trunk is released and the feet are brought forward (upward) together to gain a new grasp. The tail, momentarily away from the trunk, regains contact, preventing downward regression. Downward pressure flexes the tail and again it functions as a spring to assist the next hitch upwards. In hitching downward, the tail is lifted and quickly returned to the trunk, allowing the bird to drop slightly, but braking its downward movement.

Flight. In taking flight from a vertical position on a tree surface, the bird leans outward and with feet and tail propels itself away from the tree with folded wings. Once away, it drops, then opens its wings to take flight. Normal flight is that typical of other woodpeckers, slightly undulating, with wings held against the body in downward segment of undulation. Flight often below the canopy when moving short distances, but for longer distances may be above the canopy. An exaggerated "Flutter Aerial Display," similar to that described for other *Picoides*, is common early in the breeding season and apparently serves both agonistic and courtship functions (JAJ). See Agonistic behavior.

SELF-MAINTENANCE

Maintenance behaviors described for captive and wild birds by Jackson (1983a).

Preening, head-scratching, stretching, bathing, anting, sunbathing, etc. During molt, preening increases in frequency; captive juveniles eat some small feathers. Head-scratching done directly with no associated wing movement; only digit 3 seems to make contact with the head. Common during head molt. Captive birds also rub head on bark and cage wire during molt. Preening seems socially facilitated; when one bird begins to preen, other group members preen.

Captive birds bathe regularly, but only in fresh water; a wild bird seen bathing in shallow depression on a limb following rain. Behavior seems ritualized: initially bird dips beak in water, gently flicking drops upwards; this increases in vigor and each time the beak is dipped deeper until the head is nearly submerged. Simultaneously the wings are drooped and feathers of the head, neck, and back erected. Finally the bird enters the water completely, with all body feathers raised; flicking with the beak and slight splashing with the wings completes the bath within seconds and the bird emerges to shake, fluff body feathers, and preen in the sun.

Sunning occurs with or without a prior bath and is usually associated with preening and done in full sun on a branch that is horizontal to (more commonly) about 60° above horizontal. The bird typically fluffs body feathers, lowers the wings to the tree surface, fans the tail against the surface, and remains immobile in the sun for 5–10 min, after which preening may resume. I have observed involuntary sunning (Hauser 1957) in captive birds.

Stretching behavior is common and includes maximum extension of the manus, ulna, and humerus outward, slightly back, and down at about a 45° angle from the body. This is accompanied by fanning of the rectrices and occasionally backward and outward extension of the leg on the same side of the body as the wing being stretched. Nearly always (138 of 140 observations) a stretch is followed within 3–20 s by a lifting of both wings over the back with the manus and ulna in a folded wing position; simultaneously the bird hunches slightly forward with a lowered head (Jackson 1983a).

Sleeping and roosting. Typically solitarily (or with nestlings) in a cavity excavated by a Red-cockaded Woodpecker in a living pine. May continue to use the cavity after the tree dies if suitable replacement cavity unavailable. May use cavity of another species or a natural tree cavity. If a cavity is not available, roosts under a limb or other protected site. When sleeping the head is turned so that bill including nostrils can be buried under scapular feathers. Normally only one adult roosts per cavity.

Daily time budget. Usually leaves roost 10 min before to 20–30 min after sunrise, later on overcast days; group members gather for a few minutes in cavity tree cluster area, then depart to forage through the day; may occasionally return to cavity tree cluster during day, especially during inclement weather or following encounter with a raptor; direct return to cavity tree cluster 15–40 min before sunset; resin well maintenance most common in late afternoon before going to roost; usually enter roost 30 min

before to 30 min after sunset, earlier on overcast or inclement days (JAJ, Wood 1983b).

AGONISTIC BEHAVIOR

Physical interactions. Both members of a pair (Ligon 1968b) and occasionally helpers (JAJ) may attack an intruder. A Red-cockaded Woodpecker's wings are typically extended and raised, then closed rapidly as the attacking or defending woodpecker jabs at its opponent with its bill (Ligon 1970, JAJ). A Flutter Aerial Display similar to that described for Downy and Hairy woodpeckers (Short 1971: 78–79) is common during breeding season. In this display one individual chases another at canopy level, often for 15–30 min, with wings held in an exaggerated position above the horizontal (JAJ). I have watched birds involved in Flutter Aerial Display continue until, obviously exhausted, both birds landed in a tree panting. They resumed the chase up the tree trunk with wings spread as they hitched spiraling around the trunk. Kilham (1962, 1966) described Flutter Aerial Display (= Moth Flight, Floating Flight, or Flutter Flight of Kilham) in Downy and Hairy as courtship, but Short (1971) provides data to contrary. In Red-cockaded, both courtship (pair bond maintenance) and agonistic functions are apparent. At least 3 birds usually present, one of which (sometimes identified as female, never as male) does not participate. Both sexes observed in chases. Flight attitude of the Flutter Aerial Display produces the Wing *Whull*. *Chit* Call often heard during this display.

Communicative interactions. Raised crest, wings raised high over back, and bill pointing express agitation or aggression; see above: physical interactions. Raised crest also evident in sexual encounters.

Spacing. Individual distance greatly reduced with group members often foraging within 3–5 cm of one another; perhaps facilitated by reduced and usually concealed red on head of males. Individuals roost solitarily.

Nature and extent of territory. Ligon (1970) considers the territory of a Red-cockaded Woodpecker family group to be the "Type A" of Hinde (1956), encompassing all activities of the birds. Because of the very large home ranges characteristic of the species, boundaries can obviously not be constantly defended and the functional territory is one that shifts with the daily movements of the group. Home ranges of adjacent clans frequently overlap. See Demography and Populations: home range.

Interspecific territoriality. None known.

SEXUAL BEHAVIOR

Mating system. Monogamous. Monogamy confirmed by examination of parentage via DNA profiles (Haig et al. 1993, Haig et al. in press).

Pair bond. *Courtship Displays.* See Flutter Aerial Display under Agonistic behavior.

Nest-Showing Displays. None known.

Copulatory Displays. Often none evident. Copulation observed at any time of year, increasing in frequency in late spring prior to nesting. Crosby (1971) describes female as instigator, calling to male. Ligon (1970) observed erratic "corkscrew" flight associated with *szrek* call prior to copulation.

Duration of Pair Bond. Often mates for life, but may change mates between years (Walters et al. 1988, JAJ).

Extra-pair copulations. Rare, one record (Haig et al. in press).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Highly developed social system, birds living in family groups often called clans, usually including 2–5 individuals and only one female prior to breeding. Group size greater with addition of fledglings. Males dominate females to the extent that if insufficient roost cavities are available in a cavity tree cluster, the breeding female may lose her cavity to a hatching year male (JAJ). Birds forage together, often within a meter or less. When one moves to another tree, they all generally move.

Play. Not known.

Interactions, other than predation, with members of other species. Agonistic ("usurping foraging locations, chasing, open-wing displays, etc.") toward Hairy Woodpecker and Blue Jay (*Cyanocitta cristata*; Wood 1983b); aggression reported towards Downy Woodpecker when foraging close (Ligon 1968a, 1970, Nesbitt et al. 1981, Wood 1983b), but these species sometimes forage close with no aggression (Crosby 1971, JAJ).

The cavities of Red-cockaded Woodpeckers provide nest and roost sites for numerous vertebrate and invertebrate species (Dennis 1971, Jackson 1978d, Everhart 1986). During the breeding season, Harlow and Lennartz (1983) found 28–56% of Red-cockaded cavities in S. Carolina occupied by other species, yet some cavities unoccupied; minimal evidence suggests adverse influence on Red-cockadeds. In Texas, 46% of cavities were occupied by other species, but Red-cockaded Woodpeckers did not roost in the open or in suboptimal cavities as a result, thus competition not apparent (Rudolph et al. 1990b). However, Red-bellied Woodpeckers may physically pull Red-cockaded from a cavity (Ligon 1971, JAJ). A Great Crested Flycatcher (*Myiarchus crinitus*) nesting in an abandoned Red-cockaded cavity physically attacked and gave chase to a Red-cockaded that ventured near (Crosby 1971). Interactions at cavities reported with many species. Cavities enlarged by Red-headed (*Melanerpes*

erythrocephalus) and Red-bellied woodpeckers are often reused by Red-cockaded. Those enlarged by Northern Flickers (*Colaptes auratus*) or Pileated Woodpeckers (*Dryocopus pileatus*) are generally not used again by Red-cockaded.

Cavity dispersion is likely important to group success. Clustering of cavities may reduce interspecific competition via intraspecific territorial behavior of competitors; more dispersed cavities may increase competition (Jackson 1978d).

Foraging flocks of other pine forest birds often associate with Red-cockaded Woodpeckers. Eastern Bluebirds (*Sialia sialis*; Beckett 1971) and Brown-headed Nuthatches (*Sitta pusilla*; Jackson 1983c) feed commensally with Red-cockaded, capturing arthropods dislodged by woodpecker scaling.

PREDATION

Climbing rat snakes (*Elaphe obsoleta*) prey on nestlings, probably on eggs, possibly on adults. The corn snake (*Elaphe gutatta*) is a likely predator. Fresh gum exuding from resin wells forms an effective barrier against snakes (Jackson 1974, Rudolph et al. 1990); dried gum does not (Jackson 1978b, Summerour 1988). Regular abandonment of enlarged cavities likely a result of threat from avian predators such as Eastern Screech-Owls (*Otus asio*) and American Kestrels (*Falco sparverius*). Remains of Red-cockaded found beneath Eastern Screech-Owl roost (JAJ). American Kestrel will chase Red-cockaded (Wood 1983b, Jackson and Parris in press). Red-bellied and Red-headed woodpeckers rarely remove and eat eggs and small nestlings, generally in the process of usurping the cavity. Southern flying squirrels (*Glaucomys volans*) may eat eggs and small nestlings. Red-cockaded responds immediately to appearance of Sharp-shinned (*Accipiter striatus*) or Cooper's (*A. cooperii*) hawk by giving *Shurz-u* Call and quickly moving to side of tree, out of sight of hawk. The group may then leave the area quickly, often returning to the cavity tree cluster (JAJ).

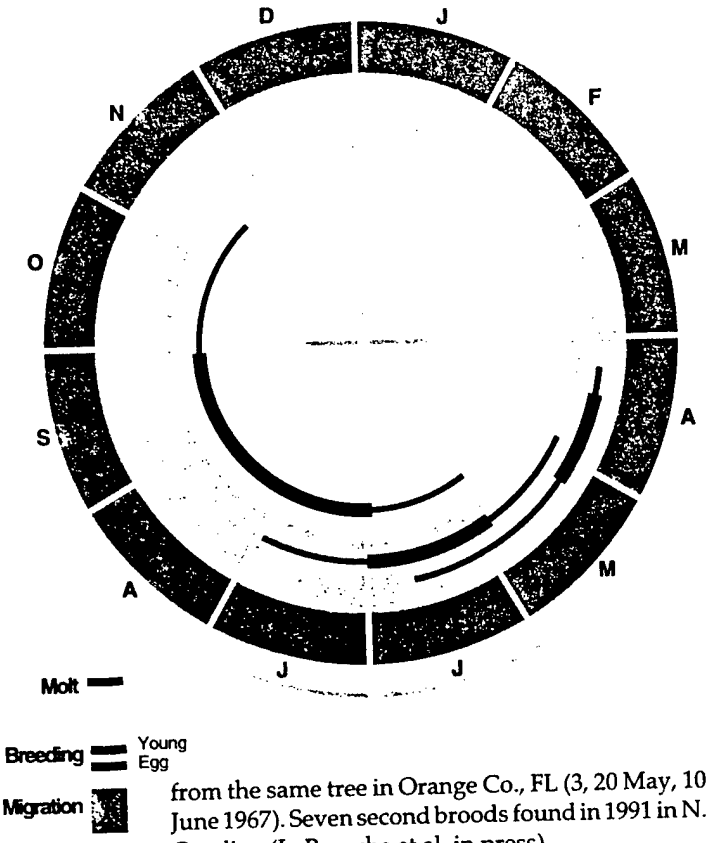


Figure 4. Annual cycle of breeding and molt for the Red-cockaded Woodpecker. This species does not migrate. Thick lines show peak activity, thin lines off peak.

BREEDING

PHENOLOGY

Pair formation. Figure 4. Anytime, upon arrival of a female at a cavity cluster lacking a female; usually early spring.

First brood per season. Usually eggs by late Apr, young by first week in May; groups within a region are often quite synchronous; little variation among years.

Second brood per season. Rare; a clutch or brood lost early may result in renesting (61% of such groups in N. Carolina; LaBranche and Walters in press). C. E. Carter (oological data, Western Foundation of Vertebrate Zoology) took three clutches from the same tree in Orange Co., FL (3, 20 May, 10 June 1967). Seven second broods found in 1991 in N. Carolina (LaBranche et al. in press).

NEST SITE

Selection process. Nest is in the roost cavity of the breeding male; this cavity typically is most recently excavated one and has the greatest gum flow of cavities in the cluster.

Site characteristics. Nest and roost cavities are characteristically excavated in a mature pine (longleaf = about 100 yr; other species = ca 80+ yr; Jackson et al. 1979), below the lowest branch (Conner and O'Halloran 1987). Cavity excavation is typically associated with the presence of red heart fungus (*Phellinus pini*) which enters the tree through naturally pruned branch stubs (Jackson 1977a, Conner and Locke 1982). Cavities generally open to the west or south (Locke and Conner 1983, Wood 1983b). If cavity does not face west to south, it usually faces in the most open direction. Rarely a cavity is excavated in a vertically growing branch.

Determining the status of a cavity tree or specific cavity is often important in determining the status of a family group. This can be done using characteristics of cavity trees resulting from recent activity by the birds (Jackson 1977b, 1978c). The outer color of pine bark is generally brown, whereas removal of bark flakes reveals a distinctly redder color. This brighter color fades within about 8 mo; presence of the reddish color over the general cavity tree surface, and specifically at the edges of resin

wells, is indicative of recent activity. Gum flow, per se, does not indicate Red-cockaded Woodpecker activity, since it can be caused by work of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) or other injuries.

NEST

Dimensions. Cavity height can be from < 1 m to nearly 100 m above ground. Most are from 10–13 m and are located just below the lowest branches. The horizontal diameter of the entrance tunnel of newly-excavated active cavities averages 57.1 ± 18.0 mm and of active cavities 70.6 ± 19.2 mm (Jackson 1978d). The entrance tunnel angles slightly upward and goes through the sapwood, often 6–9 cm until the decayed heartwood is reached. From the bottom of the entrance tunnel the cavity usually extends downward at least 17–18 cm and reaches a diameter of 9–10 cm at mid-point. The cavity may also extend upwards from the entrance hole, often far enough for a bird to take refuge from a predator reaching in and down. Cavity shape and size varies somewhat, following the contour of heartrot and increasing with years of use and occasional use by other species. Each evening the Red-cockaded occupying a cavity pecks at resin wells and at an increasingly large bare area surrounding the cavity entrance. This bare area, the "plate" is characteristic of long-used cavities. At such cavities, the lower lip of the entrance tunnel also becomes quite beveled, making vertical diameter measurements difficult.

Microclimate. Generally opens to south or west; eggs laid on a layer of wood chips left from excavation at the bottom.

Maintenance or re-use of nests, alternate nests. Nest sites typically reused so long as the same male is the breeder and the cavity has neither been enlarged nor usurped. Same nest cavity used for more than one season 66% of time; reuse more likely if previous nest was successful (Harlow 1983).

EGGS

Shape. Sub-elliptical to oval (Bent 1939).

Size. *P. b. borealis*; length = 24.28 (23.04–25.80) mm, breadth = 17.81 (17.15–18.57) mm (n = 7 clutches, 25 eggs). *P. b. hylonomus*; length = 23.31 (21.37–24.97) mm, breadth = 17.42 (16.84–18.28) mm (n = 7 clutches, 22 eggs; Western Foundation of Vertebrate Zoology). Average dimensions of 50 eggs reported by Bent (1939): 24.04 x 17.86 mm. Ramey and Jackson (1979) found a clutch in Mississippi which included one egg larger and three smaller than any previously reported for the species. Extremes were: 26.8 x 17.6 mm and 16.0 x 13.3 mm. None of the eggs hatched.

Color. Shiny white.

Surface texture. Smooth and glossy.

Egg laying. At 1 d intervals.

INCUBATION

Onset of broodiness and incubation in relation to laying. May begin with next to last egg.

Incubation patch. One large patch on both breeding adults; lesser development on helpers (JAJ).

Incubation period. Among the shortest known: 10–11 d (Ligon 1970, Crosby 1971).

Parental behavior. By both parents and less frequently by helpers; breeding male incubates at night. In absence of helpers male and female share duties during day.

HATCHING

Generally asynchronous, most young hatch the same day, one or two may hatch the next day (Ligon 1971, LaBranche 1992).

YOUNG BIRDS

Condition at hatching. Altricial and nidicolous; no down; body skin bright pink, transparent; legs and feet very pale pink/white; "heel" pads very large; nails tiny, white; eyes and ear openings closed; maxilla pink/white narrower at base and slightly shorter than mandible; mandible pink/white with prominent white oral flanges curving upwards to "seat" maxilla; glossy white egg tooth remains on upper bill to gradually disappear through wear before fledging; 10 tiny white "points" where rectrices will emerge; 3.2–3.3 g (JAJ, Ligon 1970).

Growth and development. Weight changes from hatching (3.3 g) to fledging (about 42–45 g; Ligon 1970). Asymptotic weight may be reached 3–4 d before fledging and decline before fledging. Hatched naked. By day 4 (JAJ) or 5 (Ligon 1970) gray Juvenal feather tracts visible. By day 7–8 red color of spot on forehead of male nestlings is often detectable, although tips of red feathers may not emerge for 2–3 d (JAJ). Eyes open about day 10. Details of growth and development in Ligon (1970, 1971). Comparison of male and female sibling nestlings of varying ages from S. Carolina, Mississippi, and Louisiana revealed females lighter mass in 19 of 24 comparisons (JAJ). Lesser weight of nestling females may put them at a competitive disadvantage, resulting in a disparate sex ratio (favoring males) of nestlings and fledglings as found by Gowaty and Lennartz 1985). Walters (1990) and LaBranche (1992) found no sex ratio bias among nestlings.

Limited thermoregulatory ability beginning on about day 4; well-developed by day 13–15 (JAJ).

Young remain in bottom of nest until about day 15. Until day 10, young face one another in the bottom and intertwine necks. Chick that is fed is the first to put head down, others continue begging such that "hungriest" is last to lower head; result is that when an adult next arrives, that chick will be the first to raise its head to beg. During hot weather, older chicks will sprawl along sides of cavity. During

last 3–5 days chicks will begin clinging to and climbing cavity walls.

Injured fledglings found and kept in captivity by Jackson (1983a) were found to have a pathological calcium deficiency, possibly a result of infection by a mosquito-borne virus (H. Gerlach pers. comm.). Studies in S. Carolina, Georgia, Mississippi, and Louisiana (JAJ) have revealed the frequent presence of a mite (specimens in the Zoological collections, Dep. Biol. Sci., Mississippi State Univ.) associated with the base of the two central rectrices.

PARENTAL CARE

Brooding. By both parents and by male and rarely female helpers; begins at hatching and is nearly constant for first 4 d; decreases in frequency slowly through about day 10, infrequent during the day thereafter. The male broods at night but may roost elsewhere just prior to fledging.

Feeding. By both parents and by male (rarely female) helpers.

Nest sanitation. At first fecal sacs may be eaten by the adults, later they are removed when a chick is fed. Within a few days of fledging they are often not removed by the parents, but the nest remains relatively clean; it is possible they are eaten by the nestlings. Captive injured fledglings ate their feces for several days. Both parents and helpers may remove fecal sacs, although the parents seem to remove most.

Parental carrying of young. Live young not known to be carried. Dead nestlings are removed by adults and young dead chicks have been carried 100 m or more from the nest before being dropped (JAJ).

COOPERATIVE BREEDING

Characteristic of the species (Jackson 1987, Walters et al. 1988, Walters 1990). At the beginning of nesting, a group includes one breeding pair and may also include one to four helpers. Helpers are generally male offspring of the pair from previous breeding seasons. Females rare as helpers (about 5% or fewer of helpers) in Mississippi (Ramey and Jackson 1979), N. Carolina (Walters 1990), and S. Carolina (Lennartz et al. 1987), but were 30% of helpers in central Florida (DeLotelle and Epting 1992). Groups with helpers at the nest tend to fledge more young (S. Carolina, x = 2.05 vs. 1.40, Lennartz et al. 1987; Florida, x = 2.0 vs. 1.4, Ligon 1970)—but not always (Florida; DeLotelle and Epting 1992). One or more nonbreeding, non-helping birds, "auxillaries," may forage with the group and roost in the cavity cluster.

BROOD PARASITISM

Not known.

FLEDGLING STAGE

Departure from the nest. Most young fledge at 26–29 d (Ligon 1971). Fledging success, defined as ≥ 1 young from breeding effort, high (e.g., 86.8% in N. Carolina, Carter et al. 1983).

Growth. Rectrices not fully emerged from sheaths at fledging; weight less than adult. Development of post-fledging captives described by Jackson (1983a).

Association with parents or other young. Remain partially dependent on parents for 2–5 mo, but young independent of one another; by 5 mo hatching year (HY) male may usurp after hatching year (AHY) female's roost cavity if cavities are limited. DeLotelle and Epting (1992) found that 94% (n = 534) of Jun feedings of fledged young were by breeding male; later, proportion by breeding male declined, by helpers increased; fledglings fed 7.8 times/h through Sep, 2.0 times/h during Oct. See Demography and Populations: range/dispersal.

Ability to get around, feed, and care for self. Short flights the day of fledging, but thereafter flight abilities strong; take some food independently within days of fledging, but may be fed occasionally by adults as much as 5 mo post fledging.

IMMATURE STAGE

Normally remain with group into fall, males longer.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Can breed at 1 yr. Generally first breeding of males is delayed as males serve as helpers in natal group. May breed annually, although not all clans breed each year.

Clutch. 2–5 eggs, usually 3–4; x = 2.9 (n = 16, central Florida, DeLotelle and Epting 1992), 3.27 (n = ± 665, N. Carolina, LaBranche and Walters in press).

Annual and lifetime reproductive success. Within a population not all groups produce nestlings in a given year. In the most detailed study, LaBranche and Walters (in press) found that 9–25% of N. Carolina groups did not nest in any given year. Annual rates of nestling production include: n. Florida, 70% of groups (Hovis 1982); south Florida, 81%, (Patterson and Robertson 1981); Oklahoma, 62% (Wood 1977). Brood reduction is common. In N. Carolina, a mean clutch of 3.27 eggs produced a mean of 2.31 nestlings and 1.88 fledglings (LaBranche and Walters in press).

LIFE SPAN AND SURVIVORSHIP

A captive female has lived 13 yr and banded wild birds have lived at least 12 yr (JAJ). Seven month

survivorship of juveniles in central Florida was 73%; of breeding males and females, 90% and 93% (DeLotelle and Epting 1992).

RANGE

Natal philopatry. Exceptionally strong in males; females typically disperse.

Fidelity to breeding site and winter home range. Strong so long as roost/nest cavity tree remains; may continue after tree dies, at times even after cavity tree is removed. Strongest in males.

Dispersal from breeding site or family group. Females normally disperse from their natal group during their first winter. Males may disperse at this time if roost cavities in the natal cavity tree cluster are limited or if the male has located a mate elsewhere. If a suitable roost cavity is available in an adjacent cavity tree cluster, a young male may roost with that group and return each day to forage with its natal group. Young males characteristically remain as helpers. Walters et al. (1992) view dispersal and non-dispersal of young males as alternative life history strategies and found that evolutionary fitness of those that remain as helpers can exceed that of those that disperse early. I view these strategies as a function of cavity and habitat conditions and early dispersal as indicative of less optimal conditions. Adults sometimes disperse following mate loss or failed nesting attempts. Mean (median) dispersal distances: fledgling females, 4.7 (3.2) km; adult females, 2.1 (1.3) km; fledgling males, 5.4 (4.5) km; adult males, 1.8 (1.3) km (N. Carolina; Walters et al. 1988). One female dispersed 90 km (Walters et al. 1988). Dispersal frequency may reflect local population density, habitat quality, or disturbance to habitat; e.g., a male in poor habitat and low population density resided in five different cavity clusters (Jackson 1990).

Home range. Home range of the group is least when there are nestlings (Skorupa and McFarlane 1976, Jerauld et al. 1983, Bradshaw 1990, JAJ), likely a function of the time/energy costs associated with travelling farther to obtain food for the chicks. Once the chicks have fledged, the group often forages at the extremes of its home range (JAJ, Ramey 1980). The extended home range is used through the fall and winter, although only portions of it may be used on a single day. At times daily movements can take the birds 2 km or more from their cavity tree cluster.

Home ranges often exceed 80 ha (Nesbitt et al. 1978, 1983, Hooper et al. 1982, DeLotelle et al. 1983, Bradshaw 1990, Jackson 1990), and may exceed 400 ha in very poor habitat (S. Carolina, Jackson 1987; Louisiana, Jackson and Parris in press). Home range data in the literature include diverse areas and habitats and a broad range of values (e.g., Skorupa and McFarlane 1976, Sherrill and Case 1980, Hooper et al. 1982). It is very important, however, that the available home range data not be simply accepted and taken to indicate differing needs of the birds. Home range data should be carefully scrutinized for the nature of the effort made to obtain it. Only by frequently following a group from dawn to dark at all seasons of the year can the true extent of the home range be understood.

Efforts to monitor home range via telemetry should be viewed with some skepticism since there have been several negative effects of transmitters reported, including birds having difficulty flying and excessive mortality (e.g., Jackson et al. 1977, Odom et al. 1982). Home ranges of groups in dense populations may be constrained by neighboring groups and groups in less dense populations may tend to range farther from their cavity clusters. Reported figures must be taken as "minimum home range." Comparisons among studies must consider season, habitat, cavity cluster dispersion, and researcher effort.

POPULATION STATUS

Estimates or counts of density. Rangewide estimates of numbers have consistently been within the range of 3,000–10,000 birds (Jackson 1971, 1978a, Hooper et al. 1980), although previously unknown clusters have been found and substantial losses have been documented. Available data are fraught with problems of misidentified cavity cluster status, presence of lone males, and occasional double-counting such as when land management/use responsibilities are shared by different agencies. Most remaining large populations are on Federal lands (Lennartz et al. 1983); largest populations on state lands are in Florida (Wood and Wenner 1983) and N. Carolina (Carter et al. 1983). Large populations on private lands include mainly hunting preserves in S. Carolina (JAJ), s. Georgia, and n. Florida (Baker et al. 1980).

Census data documenting declines and status on National Forests provided by Costa and Escano (1989) and Alcock (1990). Long-term studies on military and private lands in N. Carolina have monitored population changes (e.g., Carter et al. 1983, Reed 1990). Data for lesser populations include: Arkansas (Burnside 1983); Georgia (Baker 1981); s. Florida (Patterson and Robertson 1981, Murhpy 1982, Robertson and Patterson 1982); Kentucky (Jackson et al. 1976); Oklahoma (Wood and Lewis 1977); Tennessee (Nicholson 1977); Texas (Ortego and Lay 1988, Conner and Rudolph 1989); Virginia (Miller 1978, Bradshaw 1990, Beck 1991).

Population numbers. Jackson (1971) estimated the species numbered about 3,000, but "probably ... not as many as 10,000 birds." With improved data (*not* population growth), Jackson (1978a) estimated the species to total 3,473 active colonies, with 84% of the population on federal lands. With further

refinement of data, Lennartz et al. (1983) estimated 2,677 ± 456 active cavity tree clusters (= family groups) on federal lands. Only 3 of 37 federal properties (Francis Marion, Appalachicola, and Kisatchie National Forests) had populations of 250+ groups. Costa and Escano (1989) tallied 2,115 active cavity tree clusters on National Forests in 1986.

Population regulation. This is a species that seems to fit the model for a K-selected species, i.e., one whose populations, under natural conditions, remain at or near carrying capacity. Development of new groups and cavity tree clusters are rare events limited by the lengthy time required for cavity construction, and, today, the availability of suitable trees for cavity excavation, adequate habitat for foraging, and surplus females in the population to replace breeding females.

New group formation is very rare and usually occurs in the vicinity of established groups, with a young male excavating a cavity at a new site while roosting with its natal group.

CONSERVATION AND MANAGEMENT

Two recovery plans for the Red-cockaded Woodpecker have been written (Jackson et al. 1979, Lennartz and Henry 1985). The former was never implemented; the latter was prepared by a U.S. Forest Service employee at a time when his Agency was under a jeopardy opinion ruling for adverse affects of Forest Service management on the species. The 1985 plan deleted some components of the 1979 plan (e.g., establishing habitat corridors along interstates to link populations (cf. Jackson 1976) and provides for only minimum needs for the species based primarily on findings of Forest Service biologists working with the then largest, healthiest population, that on the Francis Marion National Forest. The 1985 plan came under severe criticism from a committee appointed by the American Ornithologists' Union (Ligon et al. 1986); as of 1993 the plan has not been revised.

Devastation of the Francis Marion National Forest population by Hurricane Hugo (September 1989) was the stimulus that put experimental artificial cavity construction and translocation of birds into common management practice. The stimuli for greater protection and more aggressive management efforts on federal lands include realization, after Hurricane Hugo, of the species' vulnerability. Without question, however, the major stimulus that has precipitated federal action has been the verdict of a Texas federal judge that the species was declining as a result of Forest Service management. Jackson (1986) discusses problems thwarting conservation efforts and contributing to continued species decline on federal lands. McFarlane (1992) provides details of the development of recovery plans and legal cases involving the species. Decreased genetic heterozygosity has been found in smaller populations (Stangel et al. 1992) and is likely a result of increased isolation via habitat fragmentation, and maintenance of large populations is considered important to the species survival. The current Recovery Plan for the species (Lennartz and Henry 1985) bases management decisions on a calculated, genetically-based minimum viable population size of 500 breeding birds. Reed et al. (1988) argued that the figure should be 1,018 breeding birds, which would require an estimated 25,450 ha of pine forest habitat. With further refinement of the model, Reed et al. (1993) suggest 310 to 390 breeding pairs are needed for an effective population size of 500. Walters (1991) eloquently debunks the Recovery Plan figure, noting that "genetic models are too imprecise to be useful in making management and policy decisions..." And that "This is an example of the premature application of ecological theory in management, resulting in an illusion of rigor that disguises the arbitrariness of individual decisions and inhibiting use of more reasonable approaches..."

Three innovations have allowed major breakthroughs in Red-cockaded Woodpecker management in recent years. (1) The use of cavity restrictors (Carter et al. 1989)—metal plates which restrict the size of a cavity opening—have made some previously enlarged cavities useable and have prevented the enlargement of others. (2) The movement of young females from their natal site to groups lacking a female has provided a mechanism for reducing extinction of isolated groups and for maintaining genetic diversity in isolated populations (DeFazio et al. 1987). (3) The development of artificial cavity construction techniques has allowed enhancement of cavity tree clusters and even the establishment of new groups (Copeyon 1990, Allen 1991, Walters et al. in press). While of great significance to the conservation of the species, it is critical that these techniques be treated for what they are—time and dollar expensive tools to assist a seriously troubled species. They are not substitutes for quality habitat.

As of 1993, very intensive and costly efforts are being made to manage the species on federal lands. These include widespread translocation efforts and extensive removal of hardwood understory to correct years of habitat neglect. Basic conservation issues that have not been resolved include: (1) the question of even-aged (clear-cutting) versus uneven-aged (selective cutting) management; (2) the use of late winter prescribed burns versus summer burns; (3) the extent of hardwood removal that is needed to manage for the species; (4) the nature of management of southern pine beetle infestations near cavity tree clusters; (5) the amount and nature of habitat to

provide per group; (6) the management of groups and cavity tree clusters on private lands; and (7) the nature of enforcement of endangered species laws on public and private lands. To date, on National Forests and National Wildlife Refuges, clear-cutting is considered the basic management "tool;" to provide habitat for the species, winter burns predominate, total hardwood removal is prescribed for cavity tree cluster sites, extensive clearcutting of buffers around cavity tree clusters is done to "protect" the birds, management on private lands is ignored or inadequate, and enforcement is highly selective and infrequent. In my professional opinion these are the mistakes and weaknesses in current management efforts to restore the species to a non-endangered status.

Because of the habitat needs of the Red-cockaded Woodpecker, court rulings that have favored the bird, the extent of forest industry holdings in the Southeast, the reliance of mills on trees from public lands, and the reliance of local communities on revenues resulting from the sale of forest products, it is no wonder that the Red-cockaded Woodpecker has been called the "Spotted Owl" (*Strix occidentalis*) of the Southeast.

EFFECTS OF HUMAN ACTIVITY

The greatest impacts of human activity on the birds are cavity tree loss and foraging habitat loss or degradation due to short rotation, even-aged forest management, conversion of forest to non-forest habitats, or elimination or limitation of fire in the ecosystem.

Novel noise, one to which the birds have not regularly been exposed, such as sudden loud music or a chainsaw operating nearby may keep birds away from a nest. However, the birds acclimate to loud noise that continues over a long period (Jackson 1983b).

In general this species is quite tolerant of human activities so long as suitable habitat is available. Many groups have persisted on golf courses, interstate rights-of-ways, and in suburban communities.

MANAGEMENT

Most written about this species in the past two decades has been related to management and, since 1992, we have begun to see reversal in some population trends as a result of management. In managing for the species only one thing is important: provide for *all* of its needs. The general "bureaucratic" approach has been to search for a "magic bullet"—a simple cookbook method that can be applied across the range of the species with positive results. This approach has not and will not work. Counting the number of pine stems per unit area (as suggested in Lennartz and Henry 1985) may be useful in managing two different group ranges in S. Carolina, but applying the same numbers to the flatwoods of Florida or the rugged hills of Kentucky makes no biological sense.

APPEARANCE

MOLTS AND PLUMAGES

Hatchlings. Naked.

Juvenal plumage. Growth visible by day 4 or 5. Compared to Definitive plumage, it is more lax and fluffy, duller in color, white cheek patches have considerable gray in them, and P10 wider, longer and less pointed. Often have white flecks at base of bill on forehead (particularly females), though sometimes present in adults as well. Males have red spot in middle of forehead that is replaced by black in first Prebasic molt. P1 is much smaller than P2–9.

Basic I plumage. Prebasic I molt complete, except for secondaries, which are retained. Secondaries are not molted and second year birds can often be aged by the presence of a uniform set of old secondaries. When compared to new primaries, the white spots are often quite scalloped (worn) on the secondaries and are not at all scalloped on the primaries. Late May through mid-Nov. Primaries molted from innermost to outermost, beginning with P1 either before or shortly after fledging. About 2 mo after primary molt begins, rectrices (R2–R6) begin molting more or less in order 2–6–3–5–4, followed last by R1 (this is an adaptation which maximizes available tail support while molting). Gray in cheek and red spot or white flecks on forehead among the last feathers to be replaced.

Definitive Basic plumage. Definitive Prebasic molt includes all body plumage, primaries, rectrices, and some to all secondaries; occurs from early Jul through early Oct. Flight feathers molted from innermost to outermost. Some secondaries may be replaced in an irregular fashion.

Male: Crown and nape deep, somewhat glossy, black; black elsewhere is less intense. About 12 white transverse bars on back. Nasal tufts white/gray. Wings black with white spots on periphery of both vanes of remiges (none on primary 10 and alular feathers); spots arranged such that the extended wing shows 5–6 broken bands sweeping outward and forward from the tertiaries to primary 9. Greater primary coverts black, often faded to brown. Other upper wing coverts with central white spot near tip. Underwing coverts and feathers on patagium white-gray with diffuse black. Breast white-gray; black extends from malar to sides of breast where central elongate black spots on white feathers extend along sides to diffuse black barring on flanks. Rectrices 1–2 black, 3 inner half black, outer half white with one black spot at tip, 4–5 white

with black spots in both vanes, sometimes forming a bar distally; 5 sometimes lacking black. Cockades begin at side of crown behind the eye and extend slightly downward and backward to near the white of the cheek patch; these include 12–16 small red feathers which are usually concealed by black crown feathers.

Female: Same as male, but lacking red cockade feathers.

ABERRANT PLUMAGE

Only one aberrantly plumaged Red-cockaded Woodpecker has been reported (Lennartz and Lee 1983), and none was among 800+ specimens examined in North American museums (JAJ). The aberrant bird, an adult male, appeared to have reduced melanin with normally black flight and contour feathers "pale Salmon" and the crown "a slightly darker Cinnamon or pale Tawny" (*sensu* Smithe 1975).

BARE PARTS

Bill. Black.

Iris. Hatchlings have buff-yellow (color names from Smithe 1975) ring around a dull brown iris. The yellow component usually disappears by Sep. At least occasionally this ring will only fade to a smoke-gray (Smithe 1975) ring that can be retained until 15 mo. Adult eye is dark chestnut. (gray-yellow in some older adults). Iris often has a lighter halo around darker center; somewhat variable and not quantified (JAJ).

Bare skin on head. Bare skin around eye gray.

Legs and feet. Gray, nails black.

MEASUREMENTS

Linear. Geographic variation in linear measurements is clinal with decreasing size from northern to southern populations (Mengel and Jackson 1977). Tail length, as in other woodpeckers, varies greatly as a result of wear. No significant differences between the sexes in wing or tail length. Mean culmen length of 266 males (22.6 + .05 mm) was significantly ($P < .001$) greater than that of 164 females (21.8 +.08 mm). Pizzoni-Ardemani (1990) found a similar pattern of variation using data collected from live birds by several researchers.

Mass. Mass probably varies in parallel with linear measurements, but pattern may be obscured by variation with time of day at which weights taken (average about 8% less at dawn than at dusk; JAJ), recent weather, age of bird, and with habitat quality. Table 1 summarizes mass data for adult birds captured as they went to roost in the evening at Noxubee National Wildlife Refuge, Mississippi; Ft. Polk, Louisiana; and Savannah River Plant (SRP), S. Carolina. They were weighed on the same triple-beam balance to the nearest 0.1 g. Habitat at both Ft. Polk and SRP included a few relict pines scattered within otherwise very young and patchy forest, i.e., poor habitat. That at Noxubee included open mature (100 year+) forest that would be considered very good habitat. At all sites males averaged significantly heavier than females. The difference between sexes was greatest at the poor sites, suggesting that lack of large trees in foraging habitat may have a differentially negative influence on females, a conclusion supported by known foraging site differences between the sexes (see Food Habits, above).

Table 1. Mass (g) of adult male and female Red-cockaded Woodpeckers (*Picoides borealis*) captured as they went to roost in the evening. See text for locality descriptions.

Locality	Sex	*n*	Mean	SD	P
Noxubee Natl. Wildl. Refuge, MS	M	22	49.8	1.78	.031
	F	13	48.2	2.19	
Ft. Polk, LA	M	26	48.5	2.46	.048
	F	16	46.9	2.46	
Savannah River Plant, SC	M	32	48.1	1.81	.012
	F	8	45.9	3.18	

Other mass data have been presented without details of date, time of day, or age of birds, or vary in scale accuracy. They are thus valid only for gross comparison but do indicate something of the geographic variation in the species. As examples, these include: Florida, 5 males, x = 42.4 g; 4 females, mean = 45.3 g (Hartman 1955); Kentucky, 3 adult males, mean = 52.2 g; 5 adult females, mean = 48.8 g (Mengel 1965); N. Carolina, 61 males, mean = 49.6; 36 females, mean = 47.6 (Pizzoni-Ardemani 1990).

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SPECIES-CENTERED ENVIRONMENTAL ANALYSIS: INDIRECT EFFECTS OF FIRE HISTORY ON RED-COCKADED WOODPECKERS

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Abstract. "Species-centered Environmental Analysis" (SCEA) is a procedure for diagnosing species-specific environmental factors that limit the size of a population. It attempts to identify presently recognized biotic and abiotic limiting factors. Then, through comparisons and applications of the principles of experimental design, it evaluates the relative importance of the factors and searches for new ones. The advantage of SCEA is that it frames ecological hypotheses in a context that spans population-, community-, and ecosystem-level processes while keeping the research focused on ecological factors that directly or indirectly affect the size of a focal population. In the case of the endangered Red-cockaded Woodpecker (*Picoides borealis*), which lives in mature pine forests of the southeastern United States, four types of environmental factors have been shown to limit its numbers, even on public land: (1) insufficient habitat due to hardwood midstory encroachment, (2) a shortage of suitable cavity trees, (3) loss and fragmentation of habitat, and (4) demographic isolation.

As part of the research to identify other potentially limiting environmental factors in the Apalachicola National Forest of northern Florida, we studied a sample of 87 social units (each unit usually a mated pair of birds with or without helpers, but sometimes a single bird). Each unit was defending a cluster of cavity trees and a foraging territory of open longleaf pine (*Pinus palustris*) forest. We then developed regression models for predicting within-population variation in the size, density, and productivity of social units from data on habitat variation. We found that variation in the bird variables was not significantly related to the sizes or densities of pine trees in these territories. It was, however, highly significantly related to the ground cover composition and the extent of natural pine regeneration, both of which are indirect indicators of local fire history. This suggests that, in addition to the four main causes, environmental processes driven by the history of fire are also limiting the Red-cockaded Woodpecker population. Additional support for this idea comes from the fact that female Red-cockaded Woodpeckers on the Apalachicola Ranger District tend to lay larger clutches of eggs in the first breeding season after their territories have been burned.

Because fire history affects soil nutrient dynamics, which in turn affect ground cover composition, our present hypothesis is that nutrient dynamics are affecting the health of animal populations in the system, including that of the Red-cockaded Woodpecker. The path by which this process operates, the particular nutrients involved, and its importance relative to other factors that limit the population need to be addressed experimentally. If nutrient dynamics are a previously unrecognized limiting factor for animal populations in this ecosystem, then the role of fire is not restricted to its ability to reduce vegetation in the midstory, and managers should acknowledge that different regimes of prescribed fire are likely to have different effects on animal, as well as plant, populations.

Key words: Apalachicola National Forest; fire; indirect effects; longleaf pine; multiple regression; Red-cockaded Woodpecker; Species-centered Environmental Analysis (SCEA).

INTRODUCTION

There is substantial interest now among biologists, including foresters, in the development of forestry practices by which trees can be harvested and, simultaneously, natural forest processes and former species diversity can be restored (Aplet et al. 1993, Alverson et al. 1994). We think that this development should include research on mechanisms by which ecosystem-level processes limit populations of some of the species that are typical of the association being restored. In other words, ecosystem management should not be viewed as an alternative to single-species management; it should be underlain by research in single-species ecology and population regulation of component species at the level of individual social units and individual territories. In this paper, we suggest a procedure for such analysis and we use the Red-cockaded Woodpecker (*Picoides borealis*) in the longleaf pine (*Pinus palustris*)/wiregrass (*Aristida stricta*) association as an example of at least preliminary steps in this direction.

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PLATE 1. Longleaf pine–wiregrass association in the Apalachicola National Forest in northern Florida. This site had been subject to five prescribed fires in the previous 18 yr.

Species-centered Environmental Analysis

We combine the ideas of Grinnell (1917, 1924), Andrewartha and Birch (1984), Caughley and Gunn (1996), and James and McCulloch (1995) into a set of recommendations for the identification of causes of limitation in animal populations, and we term the process "Species-centered Environmental Analysis" (SCEA). Grinnell (1917) emphasized the importance of comparing the species-specific behavior of animals in many different situations to determine what combinations of environmental factors were consistently present (see also James et al. 1984). Andrewartha and Birch (1984) constructed one-directional flow diagrams (envirograms) to help the researcher organize explicit summaries of environmental processes believed to affect, directly and indirectly, the number of individuals in present and future populations. Caughley and Gunn (1996) insisted on incorporating principles of experimental design even into descriptive comparisons, to help reject hypothesized alternative explanations. James and McCulloch (1995) showed how, in observational studies, it is possible to increase the strength of inferences about causes by moving through a sequence of comparisons toward more powerful types of quasiexperimental designs. Steps to decrease levels of uncertainty in stochastic models of alternative management strategies (Nichols et al. 1995) and direct experimental approaches to testing alternative explanations (Walters 1986, Walters and Holling 1990, Potts and Robertson 1994, Caughley and Gunn 1996) are the final stages of the process.

Red-cockaded Woodpeckers in the longleaf pine/wiregrass ecosystem

The relationship between the biology of the Red-cockaded Woodpecker in the southeastern United States and the restoration of the classical, highly diverse longleaf pine/wiregrass ecosystem is used here as an example. The geographic ranges of these three species are not coincident. The Red-cockaded Woodpecker occurs in longleaf pine forests beyond the range of wiregrass (e.g., in southern Florida, Louisiana, and Texas) and in scattered loblolly and shortleaf pine forests from Texas and Oklahoma to Virginia), but the three species are widely associated in the uplands of the Atlantic and Mississippi coastal plains from North Carolina to Mississippi, in fragments of the originally widespread longleaf pine/wiregrass ecosystem. All three species declined sharply during the 20th century (Wahlenberg 1946, Jackson 1994, James 1995).

After the major harvest of old-growth longleaf pine forests early in the 20th century, changing patterns of land use, replanting with slash (*P. elliotii*) and loblolly (*P. taeda*) pine, and modern short-rotation forestry practices further reduced the acreage of even seminatural longleaf pine forests (Hermann 1993). At present, longleaf pine is estimated to occupy $\leq 3\%$ of its former geographic range (Frost 1993, Ware et al. 1993), of which <400 ha are in old-growth forest with trees >300 yr old (Means 1996). Woodpecker populations today are mainly on national forests and military bases in areas that are being managed for pine saw timber (Lennartz et al. 1983, Costa and Escano 1989). These areas do not necessarily qualify as old-growth forest; they just have those few characteristics of old-growth forest required by a Red-cockaded Woodpecker population. These characteristics include enough old pine trees to enable the birds to maintain cavities as needed, and sufficient open pine habitat for foraging.

Wiregrass is a perennial bunchgrass that flourishes in well-burned open pine forest, especially if fires have occurred in spring or summer (Platt et al. 1988, Streng et al. 1993). In presettlement times, natural ground fires ignited by lightning burned large areas of the longleaf pine/wiregrass habitat every few years (Wahlenberg 1946), and the Red-cockaded Woodpecker was a common resident in this system (Audubon 1839).

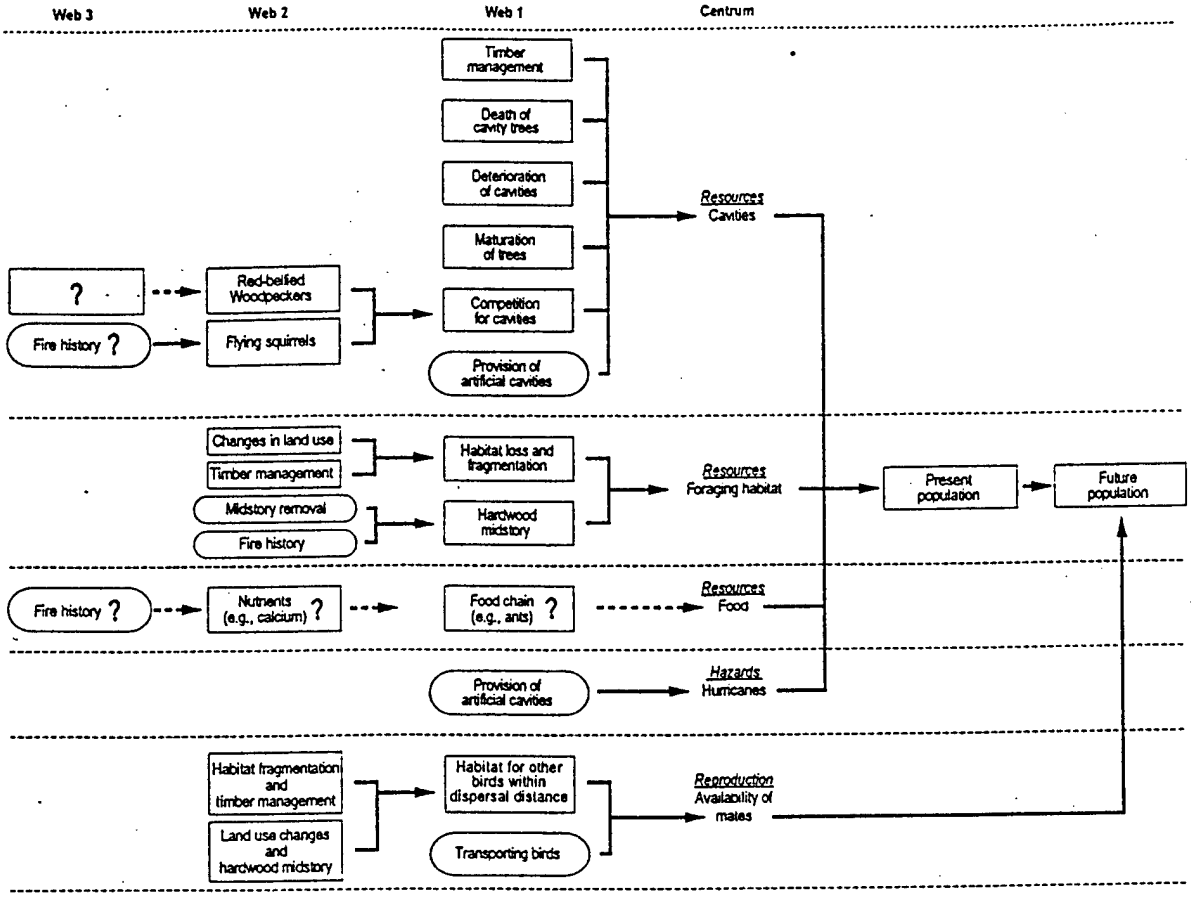


FIG. 1. Envirogram for the Red-cockaded Woodpecker. The centrum gives environmental factors that, if their levels were changed, would be expected to affect the numbers of birds directly. The webs give factors that, if their levels were changed, would affect secondary and tertiary (i.e., indirect) processes. Current management practices are noted in ovals rather than rectangles. The envirogram format is modified from Andrewartha and Birch (1984).

Causes of decline in the Red-cockaded Woodpecker

The recently approved plan for the management of the Red-cockaded Woodpecker in national forests (USDA 1995) gives four reasons why many populations have continued to decline, even on public lands where they have maximal protection. First, loss of habitat due to hardwood midstory encroachment causes abandonment of cavities (Hooper et al. 1980, Conner and Rudolph 1989); second, the rate of loss through natural mortality of old trees suitable for cavity construction is not being offset by increasing stand age; third, timber management practices fragment the habitat (Conner and Rudolph 1991); and fourth, demographic isolation in sparse populations lowers the chances that young birds can find mates (Walters et al. 1988, Walters 1991). To alleviate these problems, the Forest Service plans to reduce the hardwood midstory, lengthen the rotation age for saw timber, provide artificial cavities, restrict the sizes of areas to be regenerated with pine trees, and translocate individual birds from larger to smaller populations. The Forest Service also recommends a 2- to 5-yr prescribed-burning cycle in longleaf pine stands and encourages growing-season burning, a policy justified largely by fuel reduction and the need to limit midstory encroachment by hardwoods. In this paper, we incorporate these management practices into the envirogram for the Red-cockaded Woodpecker (see ovals in Fig. 1) and ask whether processes other than the four listed contribute to the species' decline.

Red-cockaded Woodpeckers in the Apalachicola National Forest

The Apalachicola National Forest in northern Florida encompasses ≈243 000 ha (600 000 acres) and supports an estimated 15% of all remaining Red-cockaded Woodpeckers (James 1995). The large subpopulation on the western Apalachicola Ranger District (ARD) is apparently stable on its own (supporting ≈500 active territories; S. Fitzgerald, USDA Forest Service, *personal communication*) and is even used as a source of birds for transport to other populations (Hess and Costa 1995). In contrast, the subpopulation on the eastern Wakulla Ranger District (WRD) has been declining

(supporting ≈150 active territories; S. Fitzgerald, *personal communication*). The forest supports one large population, but the birds on the two ranger districts, which are separated by a river and a strip of private land ≈8 km wide, have undergone different management histories. Dispersal between the two districts may be limited.

As elsewhere in its geographic range, the male Red-cockaded Woodpecker in the Apalachicola National Forest is very site faithful. Generations of birds inherit cavities at their native site. Only occasionally are new social units established by budding at the periphery of established territories (Walters et al. 1988, Walters 1991). On the ARD, after four years of intensive work with a population of 160 social units, Hess found only four successful cases of budding and no cases of new social units established beyond the borders of monitored territories. On the WRD, the tendency for sites to be abandoned is not balanced by either reoccupation of inactive sites or establishment of new sites elsewhere (James 1991; G. Hagan, USDA Forest Service, *personal communication*).

The management program in the Apalachicola National Forest to supply artificial cavities encouraging the establishment of new sites and the reoccupation of abandoned sites has been partially successful. In this program, >125 artificial cavities have been inserted into longleaf pine trees since 1991 (S. Fitzgerald, *personal communication*). Of the 40 artificial cavities added in the ARD before October 1994, 28 were occupied by Red-cockaded Woodpeckers in the breeding season of 1995, and two new social groups had been established. Of 27 artificial cavities added to seven new sites in the WRD before 1 January 1995, one became a nest cavity in 1995 (G. Hagan, *personal communication*).

In the Apalachicola National Forest, irregularly shaped, 0.8-km radius territories defended by Red-cockaded Woodpeckers consist mostly of even-aged timber stands of open pine woods, in which most trees are ≥25 cm diameter at breast height. Porter and Labisky (1986) reported that mean home-range size is 129 ha and preferred foraging stands have a mean basal area of 16.1 m^2/ha. Some stands contain scattered remnant trees >100 yr old, which the woodpeckers are using for cavities (Hovis and Labisky 1985; F. C. James, *unpublished data*). In the forest as a whole, >40% of the area managed for timber is in dense stands of *P. elliottii* <30 yr old. These areas are unsuitable for both cavity trees and foraging.

In the last 15 yr, large management compartments that often include more than one foraging territory have been burned an average of once every 5 yr on the ARD and once every 7 yr on the WRD. This program of prescribed fire has been more extensive than in other national forests. Many prescribed fires cover areas >400 ha (≈1000 acres). Since the late 1980s, some of these prescribed fires have occurred in the growing season for plants (April–July). Most natural fires have been put out. There was no clear-cutting in the Apalachicola National Forest between 1989 and 1995.

METHODS

Species-centered Environmental Analysis

The steps in Species-centered Environmental Analysis are as follows:

1) Prepare a formal envirogram summarizing prior information about environmental factors that, if their levels were changed, would be expected to affect the present or future numbers of the focal species. The objective of the envirogram is to help the researcher organize prior knowledge and limit the questions to be asked. On the basis of species-specific aspects of the species' ecology, include in the centrum those environmental factors that may directly affect its numbers, and include in a series of webs those successively less direct factors that affect processes in the centrum. The envirogram contains submodels for limiting resources and hazards.

2) Study the species and its environment in many places so that comparisons can be made between its status and levels of the environmental factors. If the entire population of interest cannot be measured, use random sampling.

3) Incorporate principles of experimental design (randomization, replication, control) into a plan for making comparisons that help evaluate, and perhaps eliminate, some alternative explanations.

4) Use modeling to characterize environmental processes affecting population regulation and, if possible, test alternatives experimentally.

Field methods for the Red-cockaded Woodpecker

From USDA Forest Service records of territories that were occupied by Red-cockaded Woodpeckers in 1981, we randomly drew 100 territories from the WRD and 50 from the ARD. Mostly because of the declining population on the WRD, difficult access, and problems with past record keeping, only 87 of these 150 territories were occupied by an average of more than a single bird between 1992 and 1995. For this sample of 87 social units, we banded adult and nestling birds, tracked the annual productivity of pairs, documented the cavities in which birds were roosting, and tracked dispersal behavior.

The bird variables used in the present analysis are the mean number of adults in a social unit or clan (ADUL) for 1992–1995, the number of other active social units within 1.6 km in 1993 (DENS), the mean number of eggs laid in the first clutch for 1992–1995 (EGGS), and the mean number of fledglings produced for 1992–1995 (FLEG) (Table 1). Sample sizes are 87 for the first two variables and 74 for the second two, because EGGS and FLEG were calculated only for groups that had an average of at least two birds per group. The field work was conducted by C. A. Hess

TABLE 1. Variables for birds and foraging habitat used in Species-centered Environmental Analysis of the Red-cockaded Woodpecker.

Variable	Definition
a) Birds	
ADUL	Mean no. adult birds in the social group, 1992–1995
DENS	No. active units within 1.6 km (1 mile) in 1994
EGGS	Mean no. eggs laid in the first nesting attempt, 1992–1995
FLEG	Mean no. young fledged 1992–1995
b) Foraging habitat within 0.8 km of cavity trees†	
WIGR	Percentage wiregrass (*Aristida stricta*) in the ground cover
GALB	Percentage gallberry (*Ilex glabra, I. coriacea*) in the ground cover
PALM	Percentage saw palmetto (*Serenoa repens*) in the ground cover
ROAK	Percentage runner oak (*Quercus minima, Q. pumila*)
NPRG	Area of forest stands‡ that have natural pine regeneration
AHAB	Area of forest stands‡ with some trees ≥25 cm dbh
AGED	Area of stands‡ with some trees ≥33 cm dbh
ATRE	Index of density of trees 10–18 cm dbh
BCTR	Index of density of trees 18–33 cm dbh
DETR	Index of density of trees >33 cm dbh

† Averaged over all pine stands with some trees ≥25 cm (10 inches) dbh; conventional criterion for suitable habitat (USDI 1985, USDA 1995).

‡ Stands are management units of a few hectares to 60 ha each within the Apalachicola National Forest, usually even-aged pine plantations.

and assistants on the ARD and by G. Hagan, F. C. James, D. Kufrin, and coworkers on the WRD, in cooperation with the Forest Service.

Field methods for habitat analysis

Red-cockaded Woodpeckers rarely forage >0.8 km from their cavity trees, and management of their foraging habitat in the current recovery plan (USDI 1985) is based on units (not necessarily circular) within 0.8 km of the cavity trees. For each of the 87 active territories, we surveyed the habitat that had pine trees ≥25 cm dbh within 0.8 km (0.5 mile) of the cluster of cavity trees (Table 1). Because the forest has been managed in fairly uniform stands of even-aged trees, we sampled by stands and weighted data for stands according to their proportional contribution to the area within 0.8 km that was suitable foraging habitat (usually regarded as having some pine trees ≥25 cm dbh). That procedure excluded swamps, dense hardwood forest, unthinned pine plantations <30 yr old, and fallow plowed fields.

Trees were sampled in each stand by random selection of two to eight 0.04-ha (0.1-acre) samples per stand. The species of trees were identified and assigned to 8 cm diameter size classes (Table 1). Ground cover was sampled by 50 sightings through an ocular tube (James and Shugart 1970) along two transects in each stand, according to the categories in Table 1. For each stand, we recorded the presence or absence of natural pine regeneration at 2 m height and of trees ≥25 cm dbh. One variable (AHAB) was the total area within 0.8 km of the cluster of cavity trees that was suitable for foraging (with some pine trees ≥25 cm dbh); another variable (AGED) was the area that had some trees ≥33 cm dbh. In the course of the project, after we realized that the results suggested a probable close relation between fire history and the indicators of the health of the Red-cockaded Woodpecker population (bird variables), we reviewed Forest Service records for recent fire history of each of the 87 sites.

RESULTS

The envirogram

In the envirogram for the Red-cockaded Woodpecker (Fig. 1), management practices designed to increase the numbers of birds are enclosed by ovals rather than rectangles, and dashed lines separate compartments of the model. Progressively more indirect effects appear in the columns of the web. For example, in the submodel for cavity availability, if the number of potential cavity trees is limiting, the rate of death of old cavity trees and natural deterioration of the quality of cavities (rotting) must be balanced by the maturation rate of trees to the point at which they are suitable for cavity construction by the birds. However, cavities in good condition are often usurped by other species, such as Red-bellied Woodpeckers (*Melanerpes carolinus*) and flying squirrels (*Glaucomys volans*). Such indirect factors may, in turn, be affected by the history of fire.

Even if the land is being managed for timber, short-rotation forestry practices and fragmentation of habitat into stands that are unsuitable for foraging cause habitat loss for the Red-cockaded Woodpecker. The extent of hardwood encroachment into the midstory depends on the history of ground fires in the system and also on whether managers have removed the hardwood midstory mechanically or with chemical treatments.

Cavity shortages and destruction of cavity trees by hurricanes can be alleviated by provision of artificial cavities. Sometimes single male birds in isolated territories can be provided with immature females as mates, clearly a desperation measure.

TABLE 2. Basic statistics for 87 territories of Red-cockaded Woodpeckers and their foraging habitat within 0.8 km (0.5 mile) in the Apalachicola National Forest. Habitat values are rounded to the nearest whole number, except for tree density indices (ATRE, BCTR, and DETR).

Variables†	Mean	1 SD	Minimum	Maximum
a) Birds (1992–1995)				
ADUL	2.4	0.6	1.3	4.0
DENS	5.1	2.7	1.0	12.0
EGGS‡	3.3	0.9	0.0	5.0
FLEG‡	1.4	0.7	0.0	3.3
b) Foraging habitat (1994–1995)				
WIGR	33.0	18.0	1.0	78.0
GALB	18.0	11.0	0.0	46.0
PALM	18.0	8.0	0.0	40.0
ROAK	11.0	9.0	0.0	36.0
NPRG	111.0	65.0	0.0	371.0
AHAB	176.0	69.0	64.0	371.0
AGED	139.0	72.0	0.0	371.0
ATRE	2.1	0.4	1.1	3.0
BCTR	2.2	0.5	1.0	3.0
DETR	1.4	0.8	0.2	3.0

† See Table 1 for definitions of variables.
‡ Sample size for EGGS and FLEG is 74, all social groups with an average of at least two adult birds from 1992 to 1995.

TABLE 3. Spearman correlations (a) among bird variables; (b) between bird and habitat variables other than tree density; and (c) between bird variables and tree density variables by size class. In sections (a) and (b), values between −0.20 and 0.20 are omitted, so the variables AHAB, AGED, and ROAK do not appear. Correlations >0.32 are significant at $P = 0.05$ with a Bonferroni adjustment for 12 simultaneous tests.

	ADUL	EGGS	FLEG	DENS
a) Correlations among bird variables				
ADUL		0.77	0.81	0.43
EGGS			0.85	0.37
FLEG				0.35
b) Correlations between bird and ground cover variables				
WIGR	0.38	0.34	0.31	0.46
GALB	−0.48	−0.24	−0.22	−0.27
PALM		−0.25		
NPRG	0.34		0.27	0.23
c) Correlations between bird and tree density variables				
ATRE	−0.07	−0.18	−0.23	−0.12
BCTR	−0.11	−0.09	−0.10	−0.03
DETR	−0.13	−0.20	−0.08	−0.16

Note: Variables are defined in Table 1. Sample sizes are as in Table 2.

Red-cockaded Woodpecker population and habitat statistics, and individual territory variation

For 87 territories of Red-cockaded Woodpeckers representing a random sample of territories in the entire forest, each of which had a mean of more than a single bird for 1992–1995, mean group size varied from 1.3 to 4.0 birds. Therefore, the largest social units had a mean of one pair with two helpers (male offspring that had not dispersed from their natal territory). Variation in territory density was estimated on the basis of the number of active clusters of cavity trees within 1.6 km of each social unit in the sample. Some clusters had no neighbors within this distance, and others had as many as 12 other social units. For the 74 clusters with a mean of at least one pair of birds, the mean first-clutch size varied from 0 to 5 eggs, and the mean number of young fledged per breeding season varied from 0 to 3.3 fledglings. Overall, there is substantial variation in all four bird variables at the level of the individual territory.

Of the dominant plant species in the ground cover, the greatest variation among territories was in wiregrass (0–78% cover). Gallberry, palmetto, and runner oak varied from 0% to ≈40% cover. All territories contained pine trees in three major size classes (Table 2), but the area of foraging habitat within 0.8 km (AHAB) varied from 26 to 150 ha (64 to 371 acres). In some territories, there was no natural pine regeneration (NPRG); in others, all 150 ha of habitat had natural pine regeneration (Table 2).

Correlations

Spearman correlations among the bird variables indicate that pairs of birds in larger social units (ADUL) (those with more helpers) produce more eggs (EGGS) and fledglings (FLEG). In addition, these three variables are significantly positively related to the local density of social groups (DENS) (Table 3a).

Several of the correlations among bird variables and ground-cover variables are highly significant. Most

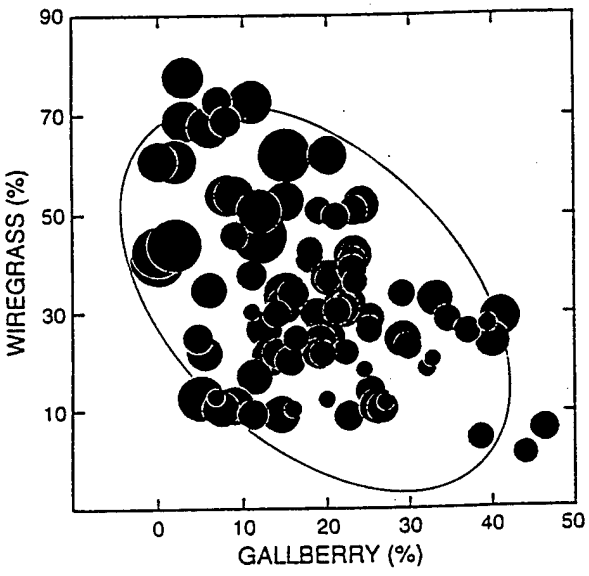


FIG. 2. Percentages of wiregrass (*Aristida stricta*) and gallberry (*Ilex glabra* and *I. coriacea*) in the ground cover of 87 Red-cockaded Woodpecker territories in the Apalachicola National Forest. Circle sizes are proportional to the average number of adult birds in each social group (range 1.3–4 adults) during 1992–1995. Note that group size tends to increase with high wiregrass and low gallberry in the ground cover. The 90% concentration ellipse shows the negative relationship between these two variables.

TABLE 4. Multiple regressions of bird variables on habitat variables.† Variables included in the analysis that were not included in any of the final models were AHAB, AGED, ATRE, BCTR, and DETR. The best regressions (highest adjusted R^2; equations 4, 6, 11, and 13) are in boldface type.

	Regression model	R^2	Adj. R^2	MS	N	P
1	ADUL = 2.9 − 0.03 GALB	0.21	0.20	0.30	87	0.000
2	ADUL = 1.9 + 0.02 WIGR	0.19	0.18	0.30	87	0.000
3	ADUL = 2.0 + 0.003 NPRG	0.14	0.13	0.32	87	0.000
4	**ADUL = 2.4 + 0.01 WIGR − 0.02 GALB**	**0.27**	**0.26**	**0.28**	**87**	**0.000**
5	ADUL = 2.5 + 0.002 NPRG − 0.02 GALB	0.26	0.24	0.28	87	0.000
6	**EGGS = 2.7 + 0.02 WIGR**	**0.10**	**0.08**	**0.68**	**74**	**0.008**
7	EGGS = 3.0 + 0.01 WIGR − 0.01 PALM	0.10	0.08	0.68	74	0.022
8	FLEG = 1.0 + 0.01 WIGR	0.10	0.08	0.41	74	0.007
9	FLEG = 1.1 + 0.003 NPRG	0.09	0.08	0.41	74	0.008
10	FLEG = 1.7 + 0.01 GALB	0.05	0.04	0.43	74	0.058
11	**FLEG = 0.89 + 0.01 WIGR + 0.002 NPRG**	**0.15**	**0.13**	**0.39**	**74**	**0.003**
12	DENS = 6.3 − 0.07 GALB	0.07	0.06	6.70	87	0.014
13	**DENS = 2.5 + 0.08 WIGR**	**0.27**	**0.26**	**5.29**	**87**	**0.000**
14	DENS = 2.8 + 0.07 WIGR − 0.01 GALB	0.27	0.25	5.34	87	0.000
15	DENS = 2.4 + 0.07 WIGR + 0.002 NPRG	0.27	0.25	5.34	87	0.000

† Variables are defined in Table 1.

striking are the positive correlation between the density of territories (DENS) and the percentage of wiregrass (WIGR), and the negative correlation between the size of the social unit (ADUL) and the percentage of gallberry (GALB). The percentages of wiregrass and gallberry in Red-cockaded Woodpecker territories are negatively related (Fig. 2). The area within a territory that has natural pine regeneration shows the same positive relationship with the bird variables as does the percentage of wiregrass in the ground cover (Table 3b).

Rather surprisingly, the structure (density and size class distribution) of pine trees is negatively, and not significantly, related to the bird variables. Woodpeckers on territories with fewer trees tend to have larger group size, lay more eggs, bring off more fledglings, and have more neighboring social units (Table 3c).

Multiple regression models

To explore these relationships further, we used multiple regression analysis to predict each bird variable from combinations of habitat variables. The most highly significant models retained only the following four variables: wiregrass, gallberry, palmetto, and natural pine regeneration (Table 4). None of the other variables contributed to the improvement (higher adjusted R^2) of the models. In fact, the best models (boldface type in Table 4) used only wiregrass, gallberry, and natural pine regeneration to account for 10–27% of the variation in the bird variables, and all models were highly significant. In predicting the number of young fledged per year (FLEG), wiregrass and natural pine regeneration respectively account for 10% and 9% of the variation when considered separately, but 15% when considered jointly. On the other hand, wiregrass alone can account for 27% of the variation in the local density of territories, and neither gallberry nor natural pine regeneration adds to its predictive power.

Fire history

Because the ratio of herbaceous to woody vegetation in the ground cover and the presence of natural pine regeneration are known to respond positively to fire, variation in density of the woodpecker social units, in social unit size, and in number of eggs laid and young fledged may be indirectly affected by fire history in the woodpecker territories (Table 3). As an independent check of this idea, we report the recent total numbers of fires (from Forest Service records) for the stands of trees that contain clusters of cavity trees, and give the average percentages of wiregrass, gallberry, and palmetto and the likelihood of finding natural pine regeneration in these stands (Table 5). The largest differences are in the positive relationship between the number of fires and the likelihood of natural pine regeneration.

We also review variation in the number of eggs laid in the first clutch (EGGS) in the breeding season before and after a dormant-season burn (October–March, 1992–1995). For the 23 cases in which clutch size data and Forest Service data on fire history were available,

TABLE 5. Mean percentage of wiregrass (WIGR), gallberry (GALB), and palmetto (PALM) in the ground cover, and the probability of natural pine regeneration (NPRG) in the forest stand with cavity trees, in 79 cluster sites† of Red-cockaded Woodpeckers in the Apalachicola National Forest, grouped and ordered by the total number of times they were burned in the last 18 yr.

	No. fires 1977–1995 (no. cases)		
Variable	<3 (30)	3–5 (39)	6–8 (10)
WIGR	21	26	33
GALB	18	17	18
PALM	20	14	11
NPRG	0.54	0.68	1.00

† Cluster sites are the pine stands with cavity trees. In each case, they are the core of a territory.

TABLE 6. A comparison of descriptive statistics for bird and habitat variables in the Wakulla (WRD) and Apalachicola (ARD) Ranger Districts. The *t* tests are for independent samples, and the probabilities for variables are not corrected for simultaneous tests.

Variables†	Wakulla Ranger District (n = 43)‡ Mean	1 SD	Apalachicola Ranger District (n = 44)‡ Mean	1 SD	P
a) Bird variables (1992–1995)					
ADUL	2.15	0.56	2.60	0.58	0.00
DENS	3.67	1.89	6.48	2.60	0.00
EGGS	2.87	1.10	3.56	0.44	0.00
FLEG	1.23	0.69	1.61	0.61	0.02
b) Habitat variables (1994–1995)§					
WIGR	21.0	10.0	44.0	17.0	0.00
GALB	20.0	11.0	16.0	10.0	0.08
PALM	20.0	8.0	17.0	7.0	0.07
ROAK	14.0	10.0	7.0	7.0	0.00
NPRG	102.0	62.0	120.0	67.0	0.19
AHAB	162.0	71.0	190.0	65.0	0.06
AGED	140.0	83.0	142.0	62.0	0.00
ATRE	2.3	0.5	2.0	0.3	0.00
BCTR	2.3	0.5	2.1	0.4	0.08
DETR	1.9	0.9	1.1	0.5	0.00

† See Table 1 for definitions.
‡ Sample size for EGGS and FLEG are for groups with an average of at least two adults: 31 for WRD and 43 for ARD.
§ WIGR, GALB, PALM, and ROAK are plants <1 m high; NPRG is for young pines ≥2 m high.

clutch size was higher after the burn in 12 cases, the same in eight cases, and lower in three cases. If the eight ties are ignored, the probability of 12 of 15 cases being higher by chance is 0.018. In other words, unless there are confounding factors, burning the habitat must improve resources for this population, as reflected in a tendency for the birds to have an increased clutch size in the subsequent breeding season. Data for growing-season burns are insufficient to justify performing the analogous test.

Because the two management districts of the forest have been managed independently and have had different histories of prescribed fire, we report descriptive statistics for bird and habitat variables for the districts separately (Table 6). Note that the density of trees (ATRE, BCTR, DETR) is higher on the WRD, as are the percentages of gallberry, palmetto, and runner oak in the ground cover. On the ARD, where the woodpeckers are thriving, average values of all other habitat variables are higher.

DISCUSSION

Alternative causes of population regulation

How should results reported here be interpreted in light of the four currently accepted reasons for the continued endangered status of the Red-cockaded Woodpecker on public lands, where the only recent population increases have been associated with provision of artificial cavities (Kulhavy et al. 1995)? First, the fact that artificial cavities are readily occupied in the ARD, which is deemed to have a healthy and stable Red-cockaded Woodpecker population of ≈500 groups, shows that cavity limitation is severe, even there. The availability of relict trees is undoubtedly a limitation, but does not fully account for the reluctance of birds to establish new groups unless artificial cavities or start holes are provided (Walters et al. 1992, 1995). Fragmentation of habitat may be causing demographic problems on the WRD, where ≈150 groups are sparsely distributed in certain areas, and birds may have trouble finding mates. The tendency of birds in other populations to abandon cavities in stands where a hardwood midstory approaches cavity height is unlikely to be a cause of population regulation in the Apalachicola National Forest. The more frequent prescribed burning in this forest has prevented the development of midstory encroachment, except in those few areas designated as wilderness. There has been no mechanical removal of midstory in the Apalachicola National Forest, because virtually no midstory exists in Red-cockaded Woodpecker habitat.

None of these processes accounts for our finding that within-population (and within-district) variation in group size and reproductive success of the woodpeckers is related to within-population variation in recent fire history, as evidenced by ground cover composition. Social groups of birds with high percentages of wiregrass and low percentages of gallberry in the ground cover of their territories, and with larger areas of natural pine regeneration, have more adults and more neighboring groups, and produce more young than do other groups. Variation in these habitat variables is a function both of how the land was prepared when the pine trees were planted, and of the recent history of prescribed fire. Because this habitat variation is unlikely to affect the birds directly, it is logical to attribute

it to indirect processes involving nutrient cycling in the longleaf pine ecosystem. It raises the additional question of whether the quantity and quality of items in the diet of the Red-cockaded Woodpecker are a function of fire history. It suggests that the role of prescribed fire in conservation of the Red-cockaded Woodpecker is still a poorly understood phenomenon, and that the physical presence of hardwoods in the midstory in infrequently burned areas in other populations is only part of the story.

Does the diet of the Red-cockaded Woodpecker vary with fire history?

Graveland and Van Gijzen (1994) have shown that the nutrient content of caterpillars, beetles, and aphids in the Netherlands is responsive to the levels of nutrients in the soil, and that calcium limitation in songbirds can limit clutch size. Such results suggest to us that nutrient limitation in the longleaf pine ecosystem may extend beyond the vegetation (Boyer and Miller 1994) to the animal populations. This hypothesis is currently under investigation.

C. A. Hess and F. C. James (*unpublished manuscript*) have recently found that the diet of adult Red-cockaded Woodpeckers in the Apalachicola National Forest is dominated by arboreal ants. *Crematogaster ashmeadi* and three other species of ants comprise a higher percentage of the biomass of the stomach contents (58%) than does any of the other major components (other arthropods, 17%; fruits and seeds, 16%; wood, 9%). *C. ashmeadi* alone accounted for 43% of the total biomass of the stomach contents, and this species was found to be abundant throughout the geographic range of the Red-cockaded Woodpecker, from North Carolina to Texas. Poorly burned areas of the Apalachicola National Forest had higher densities of *C. ashmeadi*, and well-burned areas had a higher diversity of arboreal ants. Whether or not the nutritional value of ants varies with fire history is unknown.

Relevance of fire ecology to management

As recently as 1989, the Red-cockaded Woodpecker population in the Apalachicola National Forest was viewed as one population (Costa and Escano 1989), but the new Forest Service guidelines consider the ARD and WRD populations separately, and no longer consider the latter one of the 12 Forest Service populations designated for official recovery status (USDA 1995: xii). The districts have approximately equal areas and levels of standing timber, and approximately equal histories of plowing in connection with site preparation for the planting of trees, but evidence of the abandonment of many former territories on the WRD (James 1991) and higher cavity turnover rates (James et al. 1995) suggest that the population there should receive a higher intensity of management. One of the major differences between the districts has been in the frequency and intensity of past burning regimes. In particular, management compartments in the northern section of the ARD have been burned to encourage the fresh growth of grass for cattle, and growing-season burning has been used in the southern section to encourage herbaceous diversity in open pine savannas. Although it is difficult to sort out the relative importance of various factors in the history of these two districts, their differences in fire history support the hypothesis that ecosystem-level processes related to fire, other than midstory encroachment, can be limiting to a Red-cockaded Woodpecker population. Possibly confounding correlations between fire history and site quality or soil moisture can be addressed with further work, but are unlikely to account fully for our results.

In the longleaf pine ecosystem, generally, the species of hardwoods, shrubs, and ground cover are different in wet flatwoods sites, dry sandhills sites, and clay hills (Peet and Allard 1993), but prescribed burning always promotes the grasses and herbaceous components of the flora (Boyer 1990). Even so, the underlying mechanisms are poorly understood (Christensen 1993). A promising topic for experimental investigation would seem to be the passage of nutrients through the soil, plants, and arthropods on the living pine trees, and finally to the diet of the Red-cockaded Woodpecker. Another topic that would lend itself to experimental investigation is whether or not the history of fire is important to the rival, more frugivorous, Red-bellied Woodpecker (*Melanerpes carolinus*), a serious competitor of the Red-cockaded Woodpecker for cavities (Kappes and Harris 1995). Male Red-bellied Woodpeckers can displace male Red-cockaded Woodpeckers from their cavities prior to the nesting season, causing the latter to fail to nest that year (C. A. Hess, *unpublished field notes*). Question marks in the envirogram (Fig. 1) emphasize topics we think need further investigation.

The continued use of prescribed fire is acknowledged to be important to the survival of the Red-cockaded Woodpecker (USDA 1995:53) and to numerous other endangered and threatened species in the longleaf pine ecosystem (Robbins and Myers 1992, Costa 1995). However, until the mechanisms are better understood, we are unlikely to discover the most efficient management strategies. The common view, that the role of prescribed fire in the management of Red-cockaded Woodpecker habitat is to reduce the development of midstory vegetation, does not account for the results reported here.

Modeling in ecology

Although we have not developed a specific modeling approach to Species-centered Environmental Analysis (SCEA), and we have not conducted the experiments or made the comparisons necessary to estimate the relative importance of different causal factors, we introduce it here as a strategy for the diagnosis of environmental factors that limit the numbers of a focal species.

In most cases, a complex combination of processes will be involved, and sorting out their relative importances in specific cases will be difficult. Even so, we view SCEA as supplementary to the several other approaches that have the same objective. These include (1) key factor analysis (Royama 1996); (2) the exponential growth models of Caswell (1989), Lande (1987), and Lebreton et al. (1992); (3) population viability analysis (Boyce 1992); and (4) the spatially explicit models of Pulliam and others (Pulliam et al. 1992). Predictions based on these methods depend heavily on the estimation of age- or stage-specific demographic parameters for which reliable estimates are very difficult, and sometimes impossible, to obtain (Pulliam et al. 1992). This dependence has been problematic (Eberhardt 1987, Newton 1991, Boyce et al. 1994). For example, Ruckelshaus et al. (1997) show with sensitivity analysis that errors of >2% in estimates of mortality during dispersal can make predictions from spatially explicit models unreliable. Some of the advantages of SCEA are that (1) it focuses the research on environmental limiting processes without relying heavily on estimating demographic parameters; (2) it keeps individual investigations in the context of present knowledge about all environmental factors that limit a focal population; and (3) it attempts to evaluate the relative magnitude of traditionally recognized and newly proposed environmental factors.

At the other end of the modeling spectrum, the term "indirect effects" is now being used in ecology to mean complex interspecific interactions, involving more than two species (Miller and Kerfoot 1987, Strauss 1991, Wootton 1994). These models focus on certain biotic interactions within communities of organisms, and they usually ignore abiotic processes. Optimization models of complex systems of simultaneous interactions (Heppell et al. 1994) can be useful for selecting among simultaneous and partially conflicting management objectives (Nichols et al. 1995), but they are unlikely to reveal new causal ecological mechanisms in the systems they address.

If the natural units in ecological systems are individuals and populations, then focusing on processes that affect these units as response variables, even in community, landscape, and ecosystem studies, is the most powerful way to discover causal phenomena. If we bypass studying the dependence of individual organisms on specific subsets of the resources in their environments, we forgo essential aspects of causal analysis.

In summary, for the Red-cockaded Woodpecker population in the Apalachicola National Forest, we report two new findings: (1) in the ARD, females lay larger clutches of eggs in the first breeding season after their territories have been burned; and (2) approximately one-fourth of the variation in social group size can be accounted for by variation in the composition of the ground cover, which is <1 m high and is highly sensitive to the local fire history. Neither of these findings is predicted by the four environmental processes generally viewed as causes of population decline in this endangered species. The birds rarely come to the ground, so their relationships with fire history and ground cover must be indirect. Our current hypothesis is that because burning affects the mobilization of nutrients in the plant community, it also may affect the quantity and quality of arboreal arthropods in the birds' diet. Regardless of whether or not future work supports this hypothesis, the management of Red-cockaded Woodpecker foraging habitat should emphasize a vigorous prescribed fire regime, not just to reduce midstory vegetation, but also to improve other ecosystem processes that are not fully understood at present.

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THE ECOLOGY AND MANAGEMENT OF THE GOPHER TORTOISE IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT: Recent research on the gopher tortoise (*Gopherus polyphemus*) has indicated its ecological importance, revealed reasons for its decline, and suggested management strategies. It is generally associated with the sandhill community but occurs in a variety of other natural and ruderal habitats. Limiting factors include well-drained sandy soil, adequate herbaceous food, and sunlit nesting sites. Tortoise densities and movements are related to herbaceous biomass. As the principal sandhill grazer, the gopher tortoise serves as a seed dispersal agent for native groundstory plants. The burrowing habits of the gopher tortoise return leached nutrients to the surface and the burrows provide refuges for many other species. Female gopher tortoises reach sexual maturity at 10–20 yr of age and produce a single annual clutch of about six eggs. Recruitment is reduced by heavy egg and hatchling predation. The major reasons for the decline of the gopher tortoise are habitat destruction, habitat degradation, and human predation. Recommended conservation measures include prescribed burning of sandhill habitat, establishment of preserves, protection from over-harvest, restocking, and public education.

Key words: Reptilia; Testudines; Testudinidae; *Gopherus polyphemus*; Gopher tortoise; Ecology; Management; Sandhill

ONE of four North American tortoise species, the gopher tortoise (*Gopherus polyphemus*) occurs in the southeastern Coastal Plain from South Carolina to Louisiana (Auffenberg and Franz, 1982). Recent concern over the decline of the gopher tortoise has prompted research and conservation programs in several states. Increasing requests from land managers and wildlife policy makers for information on the species necessitate a synthesis of research findings. This paper discusses

the factors affecting the gopher tortoise, summarizes current knowledge on its ecology and management, and proposes conservation measures.

Ecology

Like the other North American tortoises, the gopher tortoise inhabits a xeric environment; however, the aridity is a reflection of edaphic rather than climatic factors. Gopher tortoises are generally associated with well-drained sandy soils which support a variety of vegetational communities. Auffenberg and Franz (1982) listed four major tortoise habitats in Florida: longleaf pine (*Pinus palustris*) and oak (*Quercus* spp.) uplands, xeric hammock, sand pine (*P. clausa*) and oak ridges (including beach scrub), and ruderal communities (e.g., roadsides, grove edges, fencerows, clearings, and old fields). Tortoises also occur in pine flatwoods, dry prairies, and mixed hardwood-pine communities in Florida.

Besides edaphic and vegetational parameters, seasonal and annual climatic variations may also affect tortoise habitat utilization. During a severe drought in 1981, I observed tortoise burrows at the edge of a cypress (*Taxodium distichum*) swamp and in a low sawgrass (*Cladium mariscoides*) area in southern Florida. Although tortoises have been observed swimming (Brode, 1959; P. Moler, personal communication), they are not usually associated with wetland habitats in the southeastern Coastal Plain.

Throughout its geographic range, the gopher tortoise usually frequents sandhill or longleaf pine-turkey oak (*Q. laevis*) habitat (Auffenberg and Franz, 1982). This community is a fire subclimax which develops into a xeric or evergreen oak hammock in the absence of fire (Laessle, 1942, 1958). Natural fires during summer occurred once every 5–10 yr (Wharton, 1978). Frequent burns favor the fire-adapted longleaf pine and wiregrass (*Aristida stricta*), creating an open savanna-like habitat. Removal of the pines and the absence of fire produce a thick turkey oak forest with a sparsely vegetated understory (Campbell and Christman, 1982; Harris, 1980; Snedaker and Lugo, 1972).

The gopher tortoise responds not to a particular plant association, but rather to the physical characteristics of the habitat (Campbell and Christman, 1982). For this reason, the gopher tortoise may be found in a number of habitat types. Limiting factors include well-drained loose soil in which to burrow, adequate low-growing herbs for food, and sunlit nesting sites (Auffenberg and Franz, 1982; Hallinan, 1923; Landers, 1980).

The availability of forbs and grasses affects tortoise density and movements. The home range of the gopher tortoise is inversely related to the amount of herbaceous ground cover (Auffenberg and Iverson, 1979). Studies in southern Georgia revealed that herbaceous biomass was 2.3 times as great and tortoise density 3.1 times as great in a frequently burned slash pine (*P. elliottii*) plantation as in an adjacent unburned natural sandhill area where longleaf pine had been harvested (Landers and Speake, 1980). Umber and Harris (1974) also noted that tortoises "seemed to prefer" plantations over natural sandhills in central Florida. Wright (1982) reported that tortoise densities in South Carolina were lower in turkey oak-dominated areas than in pine-turkey oak habitat and suggested that an abundance of hawthorn (*Crataegus* sp.), a low sprawling bush, inhibited herbaceous growth.

Landers (1980) indicated that the tortoise is the primary sandhill grazer. Principal food items in southern Georgia included broadleaf grasses (Poaceae) and legumes (Fabaceae), although wiregrass was taken in the early spring and fall (Garner and Landers, 1981). Wright (1982) reported that wiregrass comprised the major part of the tortoise's diet in South Carolina. Auffenberg (1969) discussed the tortoise's role as a seed dispersal agent for native grasses.

The burrowing habits of the gopher tortoise are particularly important to the xeric communities. In constructing its subterranean tunnels, the gopher tortoise, like the fossorial pocket gopher (*Geomys pinetis*), returns leached nutrients to the surface (Auffenberg, 1969; Kalisz and

Stone, 1984; Landers, 1980). The tortoise burrow averages about 4.5 m in length (Hallinan, 1923; Hansen, 1963) and protects the tortoise from temperature extremes, desiccation, and predators. The burrow secondarily serves as a refuge for a variety of species: e.g., the eastern indigo snake (*Drymarchon corais couperi*), the Florida mouse (*Peromyscus floridanus*), and the gopher frog (*Rana areolata*) (Auffenberg, 1969; Brode, 1959; Hallinan, 1923; Hubbard, 1893, 1894; Hutt, 1967; Landers and Speake, 1980; Woodruff, 1982; Young and Goff, 1939).

In the Florida sandhills, the mounds created by the gopher tortoise and pocket gopher may serve as localized islands in areas of wiregrass and thus provide the necessary conditions for the reptilian "sand swimmers", such as the sand skink (*Neoseps reynoldsi*) and the mole skink (*Eumeces egregius*) (Campbell and Christman, 1982). Additionally, these mounds afford a foothold for young plants (Laessle, 1942).

The placement and depth of gopher tortoise burrows vary with soil type and geographic location. Burrow depth has generally been considered a function of ground water levels (Hallinan, 1923; Hansen, 1963; Young and Goff, 1939). Auffenberg (1969) described a population in coastal Florida where tortoises construct shallow pallets rather than burrows, because burrowing at this location is apparently difficult due to limestone bedrock near the surface and is not essential because of the mild year-round temperatures. In southern Florida, Kushlan and Mazzotti (1984) noted the scarcity of burrows within 10 m of the beach and suggested that tortoises avoided digging burrows in areas subject to flooding by overwash. However, Means (1982) reported the use of flooded burrows by gopher tortoises during the winter months in northern Florida. Means also hypothesized that the autumn migrations of some tortoises from xeric to mesic soils (McRae et al., 1981) may be due to a preference for moister overwintering burrows. McRae et al. (1981) explained this migration tendency as a response to food depletion on xeric sites and speculated that burrows in mesic soils were possibly better insulated against extremes of winter temperature.

The gopher tortoise exhibits deferred sexual maturity, low fecundity, and a long life span (Iverson, 1980; Landers, 1980; Landers et al., 1980). Female tortoises in southwestern Georgia reach sexual maturity at 19–21 yr of age (250–265 mm carapace length) and produce a single annual clutch averaging seven eggs (Landers et al., 1980, 1982). Iverson (1980) estimated sexual maturity at 10–15 yr of age in the northern Florida peninsula; mean clutch size was 5.2. At two study sites in northern Florida, I found similar results: the smallest mature female was 232 mm carapace length; estimated age at sexual maturity was 14–15 yr, and mean clutch size (n = 99) was 5.8. Wright (1982) reported a mean clutch size of 3.8 in South Carolina. Turner et al. (1984) recently reported that some desert tortoises (*Gopherus agassizii*) lay more than one clutch per year; to date, no evidence exists to indicate multiple clutches in *G. polyphemus* (Iverson, 1977, 1980; Landers et al., 1980).

Nests are generally constructed in the burrow mound from mid-May to mid-June (Iverson, 1980; Landers et al., 1980). The incubation period varies latitudinally: 110 days in South Carolina (Wright, 1982), 102 days in southwestern Georgia (Landers et al., 1980), and 80–90 days in northern Florida (Iverson, 1980). Landers et al. (1980) found that 87% of the nests were depredated within a few weeks after laying and estimated that a female gopher tortoise would produce a successful hatch only once in about 10 yr. Auffenberg and Iverson (1979) described colonies in northern Florida in which no young were produced for as long as 7 yr. Wright (1982) reported that 74% of the eggs were destroyed on his South Carolina site during a 2-yr study; the predation rate on hatchlings was 70% the first year and 41% the second year. Based on burrow counts in northern Florida, Alford (1980) estimated that from the time of egg laying through the first year, the recruitment potential can be reduced by about 94%. The most important egg and hatchling predator appears to be the raccoon (*Procyon lotor*)

(Landers, 1980); however, a variety of mammalian, avian, and ophidian predators have been noted (Causey and Cude, 1978; Douglass and Winegarner, 1977; Fitzpatrick and Woolfenden, 1978; Landers and Garner, 1981; Landers et al., 1980; Wright, 1982).

Reasons for Decline

The major reasons for the decline of the gopher tortoise are habitat destruction, habitat degradation (fire exclusion), and human predation (Auffenberg and Franz, 1982; Landers and Garner, 1981; Lohoefener and Lohmeier, 1984; Wright, 1982). Auffenberg and Franz (1982) estimated that these factors have reduced the original number of gopher tortoises by about 80% over the last 100 yr.

No other southeastern state rivals Florida in the magnitude of urban development. Heavy human migration into Florida is the primary reason for increased urbanization (Fernald, 1981) and the associated destruction of tortoise habitat. Lohoefener and Lohmeier (1984) cited human migration from urban to rural areas as a reason for tortoise habitat loss in Louisiana. Landers and Garner (1981) noted that the construction of housing projects and reservoir dams adversely affected tortoise populations in southern Georgia.

In Florida, the gopher tortoise is a prime candidate for mitigation efforts at urban development sites. Tortoise relocation is advocated by environmental consultants and regional planning councils with little thought to biological impacts. In recent years, state and local parks have often served as dumping grounds for displaced tortoises (Diemer, 1984).

The clearing of land for agricultural purposes has also contributed to the loss of gopher tortoise habitat (Auffenberg and Franz, 1982; Landers and Garner, 1981; Lohoefener and Lohmeier, 1984). Florida is again noteworthy due to the thousands of hectares of sandhill habitat that have been converted to citrus groves. Lohoefener and Lohmeier (1984) cited conversion of land to row crops and pasturage as a major reason for habitat loss in Mississippi; most of the remaining tortoise populations in Mississippi are located within Desoto National Forest.

Gopher tortoises are often considered pests on livestock and field crop production areas (Auffenberg and Franz, 1982). Local tortoise hunters are often enlisted to remove the tortoises in fields and pastures.

Livestock grazing may affect desert tortoise populations in the southwestern United States (Berry, 1978), but it does not appear to be a major problem for the gopher tortoise (Auffenberg and Franz, 1982). Moreover, the once free-ranging cattle and past "let burn" fire policies were important in retaining proper open areas for gopher tortoises (H. Stahls, personal communication).

The effects of pesticides and herbicides on gopher tortoise populations are unknown, but Landers and Garner (1981) and Lohoefener and Lohmeier (1984) listed these chemicals as potential threats. A recent tortoise die-off in southern Alabama may have been the result of herbicides (J. Dobie, personal communication).

Mortality on highways also decreases gopher tortoise populations both in urban and rural areas (Franz and Auffenberg, 1978; Landers and Garner, 1981; Lohoefener, 1982). Landers and Buckner (1981) cited vehicular traffic as the greatest mortality factor on their study area in rural Georgia.

To a lesser degree, mining activities have affected tortoise habitats (Auffenberg and Franz, 1982; Landers and Garner, 1981). Phosphate stripmining in central Florida has destroyed many thousands of hectares of sandhill and scrub habitat and has created a mosaic of disturbed wetlands and uplands over a vast area. Information regarding tortoise recolonization of mined lands is minimal. Schnoes and Humphrey (1980) cited tortoise utilization of unreclaimed pits and spoil piles 5–30+ yr after mining. Prior to 1975, reclamation of mined lands in Florida was not required; however, stringent regulations are now in effect.

In the southeastern Coastal Plain, large

tracts of land originally in sandhill habitat have been converted to pine plantations. Clearcutting, site preparation, and plantation management may negatively affect gopher tortoises (Auffenberg and Franz, 1982; Landers and Garner, 1981; Lohoefener, 1982; Lohoefener and Lohmeier, 1981, 1984; Wright, 1982). On the other hand, selective cutting and prescribed burning are beneficial to tortoises because they stimulate higher yields of tortoise food plants (Auffenberg and Franz, 1982; Landers and Buckner, 1981; Landers and Speake, 1980).

Of particular concern are the extensive areas of planted sand pine in the Florida Panhandle. This species' fire intolerance and limby growth-form result in a dense forest with little or no understory (Landers and Buckner, 1981). Tortoise densities are exceedingly low in these areas. Similarly, Lohoefener and Lohmeier (1984) reported that extensive, thickly planted (1–1.5 m between trees) stands of loblolly pine (*P. taeda*) have contributed to the tortoise's near extinction in Louisiana.

The use of heavy machinery to reduce logging debris in preparation for planting may be detrimental to tortoises (Auffenberg, 1978; Auffenberg and Franz, 1982; Lohoefener and Lohmeier, 1981; Wright, 1982). Tanner and Terry (1981) cited burrow destruction from chopping treatments, but they did not follow up on the fate of the tortoises. Landers and Buckner (1981) and Diemer and Moler (1982) demonstrated that gopher tortoises are able to dig out following chopping treatments on deep sandy soils. Tortoise response to more intensive site preparation techniques (shearing, windrowing, root-raking, bedding) may vary markedly. Windrows of unburned debris may hamper tortoise movements in slash pine plantations (Lohoefener and Lohmeier, 1981), but Landers and Speake (1980) favored retention of windrows on regularly burned sites as foraging and hiding areas for indigo snakes.

Human predation on the gopher tortoise is well documented (Alberson, 1953; Auffenberg and Franz, 1982; Hutt, 1967; Jennings and Fritts, 1983; Landers and Garner, 1981; Lohoefener and Lohmeier, 1984; Roosevelt, 1917; Thomas, 19[illegible] Wright, 1982; see Taylor, 1982 for additional references). Taylor (1982) reported that the species has been exploited in Florida for over 4000 yr. The gopher tortoise was a major food source for many families during the Depression, as reflected in the name "Hoover Chicken" (Hutt, 1967).

Human predation usually does not remove every individual from the population. "Gopher pulling" (using a long flexible rod to pull the tortoise from its burrow) removes an average of 20% of the larger tortoises, and one-time harvest is not necessarily the "death knell" for a colony (Taylor, 1982). Intensive predation pressure sustained over a long period could, however, seriously impact local populations (Landers, 1980; Landers and Garner, 1981; Taylor, 1982). For example, tortoise populations in the Florida Panhandle appear to be depleted as a result of sustained heavy human exploitation (Auffenberg and Franz, 1982), and Panhandle tortoise hunters now travel to Georgia or the Florida peninsula to obtain tortoises.

Lohoefener and Lohmeier (1984) reported the taking of tortoises as pets [illegible] curiosities in Mississippi. This practice h[illegible] also been observed in Florida, but it is not considered to be a significant impact on tortoise populations. The collection of desert tortoises, however, once was a major reason for the decline of this southwestern species (Bury and Marlow, 1973; Coombs, 1977).

In Georgia and Florida, some populations of gopher tortoises have been affected by the collection of individuals for use in tortoise races. Organized races to benefit charities have been in existence for several decades (Diemer, 1984). In the late 1970's, it was not uncommon for 100 or more gopher tortoises to be captured in Georgia and transported to Florida for a single race (R. Stratton, personal communication). Concerns include population disruption, gene pool mixing, parasite or disease transmission, and the ethics of using these reptiles for such purposes in the first place (Diemer, 1984).

MANAGEMENT

Specific recommendations to maintain or enhance gopher tortoise populations have been recently proposed by Landers and Speake (1980) for Georgia, Wright (1982) for South Carolina, Lohoefener and Lohmeier (1984) for Louisiana, Mississippi, and western Alabama, and Auffenberg and Franz (1982) for the entire range of the species. Important conservation measures include habitat management, establishment of preserves, protection from overharvest, and public education (Landers, 1980).

Auffenberg and Franz (1982) presented a detailed description of gopher tortoise response to natural and human-caused succession, stating that tortoise densities are highest in grassy, open canopy associations, whether intermediate successional stages or fire-adapted savanna-like habitats. To promote these optimal conditions in natural longleaf pine-turkey oak stands, Landers and Speake (1980) recommended judicious thinning of scrub oaks, reestablishment of the pine component (to aid in carrying fire), and prescribed burning at least every 5–10 yr where summer burns are feasible or every 2–4 yr if winter burns are used.

Gopher tortoise management in commercial pine stands should include less intensive site preparation (burning, anchor chaining), pine thinning, planting a fire-tolerant species like longleaf pine, and annual or biennial prescribed burning (Landers and Buckner, 1981; Landers and Speake, 1980). Landers and Buckner (1981) reported that gopher tortoises in southwestern Georgia are commonly found in seedling and pole stage slash pine plantations on sandhills; however, tortoises abandon the dense sapling stage plantations and move to roadsides where they are more vulnerable to human predation and highway mortality. Forest management also influences gopher tortoise reproduction. Female tortoises in dense scrub oak stands and sapling plantations move to open roadsides and firelanes to find sunlit nesting sites.

Florida's sand pine scrub habitats are adapted to and maintained by fire; however, the manner in which this association burns is quite different from the sandhill (Snedaker and Lugo, 1972). The cool ground fires characteristic of the grassy sandhills seldom occur in the thick woody sand pine scrub. Instead, catastrophic crown fires destroy the above ground system. The extreme heat also releases the sand pine seeds from the serotinous cones, thereby regenerating the community (Campbell and Christman, 1982; Snedaker and Lugo, 1972). Although human intervention has largely excluded fire from the scrub, the clearcutting and even-age management of sand pine in the Ocala National Forest in some ways mimics the natural situation of infrequent crown fires and appears to provide the variety of successional stages necessary to maintain the native herpetofauna (Campbell and Christman, 1982). Although gopher tortoise densities are generally relatively low in sand pine scrub habitats, tortoises are most often associated with ecotones, clearcuts, and young plantations rather than mature stands (Auffenberg and Franz, 1982; Campbell and Christman, 1982; Logan, 1981). Thus, the forest management practices described above should benefit the gopher tortoise. However, additional research on tortoise management in scrub is needed. Preliminary data indicate that the herbaceous biomass is increased by prescribed burning of coastal scrub (without sand pine) habitat (D. Breininger, personal communication).

The minimum number of tortoises or amount of habitat necessary to maintain a viable colony is unknown (Auffenberg and Franz, 1982). Gopher tortoise movements include short (<30 m) feeding forays as well as longer movements associated with breeding behavior (Douglass, 1976; McRae et al., 1981). Infrequent long-range movements (0.8–4.8 km) also occur, and some tortoises exhibit homing ability (Diemer, 1984; McRae et al., 1981). The normal yearly movements of an average colony (approximately 10 adults) in sandhill habitat occur in an area of less than 4 ha, suggesting that viable populations could be maintained in relatively small

management units (Landers and Speake, 1980). Larger areas (several hundred hectares) would, however, reduce the impacts of emigration and highway mortality.

Other suggested conservation measures include nest protection and predator-proof enclosures for hatchlings (Wright, 1982), control of nest predators through hunting or trapping (Landers, 1980), and the restocking of tortoises on available lands on which they been severely reduced or extirpated (Diemer, 1984; Landers, 1980; Lohoefener and Lohmeier, 1984; Wright, 1982). Little information exists on the fate of relocated gopher tortoises; similarly, experiments involving desert tortoise relocation (e.g., Berry, 1975*a*,*b*) were inconclusive, because many transplanted tortoises simply disappeared. Landers (1981) estimated that approximately 41% of introduced gopher tortoises remained in the vicinity of release sites 3 yr later. In a separate study, 29% of relocated tortoises were recaptured 5 yr following release (Diemer, 1984). Lohoefener and Lohmeier (personal communication) noted reduced migration away from the relocation site when tortoises were initially penned; their observations, however, were based on only one activity season. The relocation sites of the above three studies, as well as the methods employed during release and follow-up, differed greatly, and comparison of the results is difficult. Landers (1981) proposed releasing twice as many tortoises as desired and suggested that migration away from the restocking site may be reduced by first establishing a group of females and then introducing males during the breeding season. Lohoefener and Lohmeier (personal communication) recommended that the sex ratio of relocated tortoises be 1:1 and that the tortoises be penned for at least 1 wk on the restocking site. The identification of biologically suitable and secure relocation sites remains a major obstacle in Florida (Diemer, 1984). Reclaimed mining lands may serve as tortoise restocking areas in the future. However, before additional relocations are undertaken on reclaimed sites, radiotelemetry studies should be conducted to gather data on dispersal and survival of transplanted tortoises.

Auffenberg and Franz (1982) recommended the prohibition of gopher tortoise races. Public sentiment has resulted in some races being discontinued. The Florida Panhandle, however, remains a stronghold for these traditional charity events. If the existing annual tortoise races are allowed to continue, they should be clearly and uniformly regulated. One person or group should be responsible for the capture, handling and release of tortoises each year. Ideally, the tortoises should be trapped and released in the same area, with consideration given to minimally affecting their reproduction.

The problems facing the gopher tortoise are varied and complex. Research is needed to determine the minimum size of habitat preserves, the optimal season and frequency of prescribed burning on sandhills, and alternate habitat management techniques in areas where burning is not feasible. As mitigation for the destruction of tortoise habitat, developers could be required to contribute funds for the purchase of tortoise preserves. Educational efforts should strongly emphasize that xeric habitats, as well as wetlands, have an aesthetic and biological value. Additionally, information on tortoise habitat management should be distributed to land managers. In conclusion, research should provide the information—and public concern the impetus—to insure that quality gopher tortoise habitat is available in the future.

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The Status of The Gopher Tortoise in Florida

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Abstract

Data regarding gopher tortoise (*Gopherus polyphemus*) status and distribution in Florida were gathered through field surveys from 1981-1987 and questionnaires sent in 1979 and 1987. The gopher tortoise remains widely distributed in Florida, occurring in all 67 counties. Tortoise utilization of pine flatwoods and dry prairies is much more common than previously reported. Tortoises are rare in extreme southern Florida and fairly common to uncommon elsewhere in the state. Many populations are declining due to urbanization, agriculture, phosphate mining, forestry practices, fire exclusion, or human predation. Overharvest has depleted tortoise populations in the Florida panhandle. Peninsular populations that are currently stable will be affected by increasing development pressures. Gopher tortoise decline, coupled with the species' low fecundity, necessitates further evaluation of tortoise harvest regulations. Stronger legislation to protect upland habitats in Florida is required.

The only North American tortoise occurring east of the Mississippi River, the gopher tortoise (*Gopherus polyphemus*) is restricted to portions of 6 states in the southeastern Coastal Plain (Auffenberg and Franz 1982). In the early 1970's, Auffenberg and Franz (1982) conducted a status and distribution survey of this reptile. Although it remained unpublished for nearly a decade, this survey focused attention on the range-wide decline of the gopher tortoise and induced detailed studies in several states (Landers 1980). Subsequent status surveys were conducted by Landers and Garner (1981), Wright (1982), Jennings and Fritts (1983), Lohoefener and Lohmeier (1984), and Spillers and Speake (1986). Lohoefener and Lohmeier's (1984) findings prompted the U.S. Fish and Wildlife Service to list the gopher tortoise in 1987 as a threatened species west of the Tombigbee-Mobile drainage.

The legal status of the gopher tortoise varies among the 6 states where the species occurs. Georgia and Alabama list the gopher tortoise respectively as a protected non-game species and a game species with no open season. Mississippi and South Carolina consider it endangered, whereas Louisiana affords the tortoise no protection. In Florida, the gopher tortoise is a species of special concern. Regulations include a possession limit of 2, a 3-month open season, and a ban on commercial sale and certain capture methods. Additionally, tortoise harvest is prohibited in the southern third of the peninsula and in Florida's 3 national forests. Florida also prohibits the introduction of gasoline or other toxic substances into tortoise burrows.

This paper presents the results of a comprehensive status survey conducted by the Florida Game and Fresh Water Fish Commission (FGFWFC). Appreciation is extended to FGFWFC personnel who returned questionnaires and assisted in field surveys. Special thanks go to R. Stratton for contributing invaluable information regarding gopher tortoise harvest and for generously donating his time to collect tortoises. Other tortoise hunters who provided field data on harvest success include M. Bush, L. Smiley, W. Corbin, and J. Hamilton. C. Maloy and R. McWhite arranged access into the bombing ranges at Eglin Air Force Base. R. Wilkerson and A. Beck provided tortoise distribution data and field assistance in conjunction with their tick surveys. T. Steele and J. Hamblen typed the manuscript, and C. Moore provided statistical assistance.

Methods

Data regarding gopher tortoise status and distribution were gathered from 1979-1987 in conjunction with a long-term FGFWFC tortoise research project. Information was derived from a variety of sources: questionnaires, soils and vegetation maps, field surveys, harvest violation records, and interviews with tortoise hunters, biologists, wildlife officers, foresters, and landowners.

In 1979, a questionnaire was sent to FGFWFC biologists and wildlife officers requesting information on relative tortoise abundance, population trends, reasons for population trends, illegal commercialization, and management recommendations. In 1987, a follow-up questionnaire was sent to FGFWFC biologists and wildlife officers requesting similar information. Two additional questions in the 1987 survey addressed tortoise habitat utilization.

One hundred fifty-six questionnaires were returned in 1979; the number of questionnaires originally sent in 1979 is not available. Of 424 questionnaires sent to FGFWFC personnel in 1987, 248 (58%) were returned.

General soils maps for the 67 Florida counties were used in the broad delineation of tortoise habitat. Additional information was obtained from detailed county soil surveys; however, these surveys were available for only 30-35 counties. Tortoise habitats were classified according to the Soil Conservation Service's (1981) ecological communities map and descriptions.

Tortoise hunters were questioned regarding tortoise population status and trends, preferred hunting locations, tortoise sex ratios and size, and harvest success.

Data regarding harvest success (tortoises obtained/burrows attempted) and tortoise sex ratios were gathered during field surveys with experienced tortoise hunters. Carapacial measurements were taken on harvested tortoises. Interviews with wildlife officers and hunters, in addition to questionnaire responses and harvest violation records (1980-1987), provided information on unlawful possession and commercialization of tortoises.

Field surveys were undertaken to update tortoise distribution data and to determine the location and magnitude of impacts on tortoise populations. Distribution surveys focused on those counties reported by Auffenberg and Franz (1982) to have minimal or no tortoise populations. Status surveys emphasized the southern peninsula and the panhandle, areas of reported tortoise decline (Auffenberg and Franz 1982). Numerous development sites were visited to determine the magnitude of the impact on tortoises and to formulate mitigation and management strategies. To compare tortoise populations on Eglin Air Force Base sites open to the public with those on closed sites (bombing ranges), spot checks (Lohoefener and Lohmeier 1984) were used in lieu of transects (Auffenberg and Franz 1982). Overall, more than 65 trips to numerous sites in Florida were made from 1981-1987.

Results and Discussion

Distribution

The gopher tortoise remains widely distributed in Florida, occurring in all 67 counties. However, its current range in southern Florida is restricted due to unsuitable habitat and increased urbanization.

Auffenberg and Franz (1982) presented a detailed description of tortoise distribution in the state and provided population estimates on a county by county basis. Additional distribution and census information was provided in Logan's (1981) tortoise survey of federal lands in Florida. Nineteen federal areas were found to support tortoises; 5 of 17 surveyed areas contained estimated populations of over 400 tortoises (Egmont Key, Merritt Island, St. Marks National Wildlife Refuge, Everglades National Park, and Ocala National Forest) (Logan 1981). The Everglades National Park population occurs on Cape Sable and represents the southernmost colony of *G. polyphemus* (Auffenberg and Franz 1982, Kushlan and Mazzotti 1984).

Auffenberg and Franz (1982) reported no tortoise populations in 2 southern peninsular counties. Interviews with entomologists studying the distribution of a burrow arthropod revealed tortoises in the northwest corner of Hendry County (A. Beck, pers. commun.). Colonies have also been located in the dry prairies of Okeechobee County. Disjunct tortoise colonies were found in Dade (North Miami and Cutler), Broward (Ft. Lauderdale Executive Airport) and Baker counties (oak hammocks, within Osceola National Forest and sandhills south of the St. Marys River).

Auffenberg and Franz (1982) provided a detailed description of tortoise distribution in relation to physiography and noted that tortoises were widespread on the prominent ridges (relict dunes) that occur on a north-south axis in the peninsula. Tortoise colonies do not occur within the Everglades proper; however, sightings of individual tortoises on canal berms have been reported.

Throughout much of its range, the gopher tortoise is generally associated with well-drained sandy soils (Diemer 1986). In Florida, over 80 individual soil series, ranging from somewhat poorly-drained to excessively-drained, are capable of supporting tortoises. However, Breininger et al. (1986) found higher tortoise densities in poorly-drained soils than moderately well-drained soils on the Kennedy Space Center.

Based on Davis' (1967) vegetation map, Auffenberg and Franz (1982) listed 4 major tortoise habitats in Florida: longleaf pine (*Pinus palustris*) and oak (*Quercus spp.*) uplands, xeric hammock, sand pine (*P. clausa*) and oak ridges (including beach scrub), and ruderal (man-produced) communities. The latter category includes roadsides, grove edges, fencerows, clearings, and old fields. Classified according to the Soil Conservation Service's (1981) ecological community map and descriptions, tortoise habitats include the following: North Florida Coastal Strand, South Florida Coastal Strand, Sand Pine Scrub (includes oak scrub), Longleaf Pine and Turkey Oak (*Q. laevis*) Hills, Mixed Hardwood and Pine, Upland Hardwood Hammocks, Oak Hammocks, North Florida Flatwoods, and South Florida Flatwoods (includes dry prairies) (Diemer 1986).

In 1987, questionnaire recipients were asked to indicate in which of 6 habitats (3 natural and 3 ruderal) they had observed tortoises and/or burrows (Table 1). Of those respondents who answered the question, more reported seeing tortoises or burrows in sand pine-oak scrub and sandhill than in old fields, roadsides, and planted pine areas. The higher percentage in sand pine-oak scrub than in sandhill may be due in part to misinterpretation of the habitat classification. True sand pine scrub is much less widely distributed than sandhill in Florida (Soil Conservation Service 1981). In some portions of the panhandle with little or no natural sand pine scrub habitat, some respondents had circled this response. "Sand pine-oak scrub" may have been interpreted as identical to "pine-scrub oak" (another name for sandhill habitat). Another possible explanation is that tortoise burrows were seen in (or more likely, along the edge of) planted sand pine areas in the panhandle.

Table 2 lists 2 natural and 3 ruderal habitats heretofore considered to be unoccupied or only marginally occupied by tortoises. Of 233 respondents who answered the question, 77% had observed tortoises and/or burrows in pine flatwoods. Breininger et al. (1986) reported an overall mean density of 1.3 tortoises/ha in scrub and flatwoods habitats on the Kennedy Space Center and

compared it with Auffenberg and Franz's (1982) overall mean density of 0.9 tortoises/ha in Florida sandhill habitats. The field surveys also indicate that tortoise utilization of scrubby flatwoods, pine flatwoods, and dry prairies is much more common than originally thought. Additional surveys are needed to determine whether these heretofore "marginal" areas constitute major habitats for the gopher tortoise in central and southern Florida. Other natural habitats in which tortoises or burrows had been observed by questionnaire respondents included the following: mesic hammock, river swamp, hydric hammock, high mangrove islands, dry ponds, edges of cabbage palm (*Sabal palmetto*)-live oak (*Q. virginiana*) hammocks, and scrubby flatwoods. Other ruderal habitats listed by the respondents included railroad edges, powerlines, canal banks, rye plots, lawns, gardens, mining spoil, vacant lots, unimproved groves and pastures, and the Lake Okeechobee dike.

Status

Tortoise Abundance and Population Trends—Perceptions of relative tortoise abundance were compared for 1979 and 1987 (Table 3). Respondents' perceptions of relative tortoise abundance in their area were significantly different between the 2 surveys ($X^2=11.33$, $df=4$, $0.025>p>0.01$). In both years, however, 62% of the respondents who answered the question considered tortoises to be "fairly common" in their area. The "abundant" category was also similar in the 2 surveys. Differences arose in the "uncommon" and "rare" categories. These percentage shifts may be due to the subjectivity of abundance categories or they may reflect a greater awareness of tortoise presence over the 8-year period. Respondents from the 5 FGFWFC administrative regions were equally represented (approximately 20% for each region) in 1979 and 1987, so the differences in perceived tortoise abundance between the 2 surveys can not be attributed to a shift in regional representation. Tortoises were deemed "not present" in the Keys and in portions of 3 Everglades counties. Figure 1 indicates relative gopher tortoise abundance for the 67 Florida counties based on questionnaire responses.

Respondents' perceptions of tortoise population trends (declining, increasing, or stable) in 1979 and 1987 (Table 4) were not significantly different at the $p \leq 0.05$ level ($X^2=2.20$, $df=2$). The 1979 tortoise population trend percentages are comparable to those reported in Landers and Garner's (1981) Georgia questionnaire survey for the period 1978-1980 (declining—52%, stable—45%, and increasing—3%).

In both 1979 and 1987, questionnaire recipients were requested to provide their recommendations and comments regarding gopher tortoise management, harvest regulations, etc. Respondents who commented on the harvest regulations were divided into 3 categories: those who advocated prohibiting tortoise harvest, those who favored increased restrictions (i.e., reduction in possession limit and/or season), and those who thought the current regulations were adequate. Despite the fact that more restrictive harvest regulations were implemented between 1979 and 1987 (see Table 6), 68% of those who addressed the harvest issue in 1987 favored complete protection, as compared with only 26% in 1979 (Table 5). Differences in the distribution of responses in these 3 categories were highly significant between the 2 years ($X^2=51.0$, $df=2$, $p<0.001$).

The majority of recommendations in 1979 were related to tortoise harvest regulations. Increased education, termination of tortoise races, and restocking depleted populations were suggested in both 1979 and 1987. In 1987, establishing preserves, implementing tougher development regulations, identifying restocking sites, and burning habitat at regular intervals (1-3 years) were considered management priorities.

Human-Related Impacts on Tortoise Populations.—Of those questionnaire respondents indicating a negative population trend, 57% in 1979 and 68% in 1987 attributed tortoise decline to habitat loss. Seventeen percent in 1979 and 10% in 1987 considered tortoise harvest to be the major impact, while 26% (1979) and 23% (1987) attributed the negative trend to both habitat loss and harvest in their area. Perceptions regarding reasons for tortoise decline in 1979 and 1987 were not significantly different at the $p \leq 0.05$ level ($X^2=3.23$, $df=2$). Although many respondents merely cited habitat loss as a factor in tortoise decline, some specified development, agriculture, mining, timber, and improper burning. Reasons given for a positive population trend included the closure of national forests, season and bag limit restrictions, cropland allowed to go fallow, education of pullers, and the release of confiscated tortoises. One respondent who indicated stable tortoise populations commented that the loss of tortoise burrowing habitat to development was being offset by the creation of new burrowing habitat (canal berms) due to drainage.

No other southeastern state rivals Florida in the magnitude or urban development. In 1980, Florida's human population was approaching 10 million; demographers predict that the population will reach 12-15 million by the year 2000 (Fernald 1981). Heavy human migration into Florida and intrastate residential mobility (movement from a more populated to a less populated area) are the major reasons for increased urbanization (Fernald 1981) and the associated destruction of tortoise habitat. By the year 2000, continuous urbanization is expected on the east coast from Miami to Jacksonville, the southwest coast from Naples to Crystal River, and in the area along Interstate 4 between Tampa and Daytona Beach (Fernald 1981). This urbanization has serious implications for the future of the gopher tortoise in Florida (Auffenberg and Franz 1982).

Field surveys on the southeast coast revealed continuing destruction of sand pine scrub habitat despite preservation efforts by local and regional planning councils. State parks and federal refuges are

receiving increased pressure to take the tortoises displaced by urbanization. The manifold problems associated with gopher tortoise relocation are reviewed elsewhere (Diemer 1984, 1987).

The increasing proximity of human residences to tortoise colonies has resulted in numerous incidents of dog predation. Causey and Cude (1978) described feral dog predation on tortoises in Alabama. Hawkins and Burke (1987) cited dog predation on relocated tortoises in north-central Florida.

Increased urbanization has also increased the chances of tortoise highway mortality. It would be difficult to assess the number of tortoises killed on highways. On a single July day in 1981, 7 road-killed tortoises were observed along the Florida turnpike (southbound lane only); 3 of the dead tortoises were found in a 5-km stretch north of Orlando.

The clearing of the land for agricultural purposes has also contributed to tortoise habitat loss (Auffenberg and Franz 1982). Thousands of hectares of longleaf pine-turkey oak habitat in central Florida have been converted to orange groves. Rapid urbanization of the older citrus growing areas has caused a gradual southward shift of the citrus industry (Fernald 1981).

Production of field crops and livestock also adversely affects tortoise populations (Auffenberg and Franz 1982). The watermelon industry in north-central Florida and soybean industry in the panhandle have resulted in extensive land clearing. The key to tortoise persistence in livestock production areas appears to be landowner tolerance. Numerous interviewees have reported tortoises being killed by farmers or ranchers who feared crop damage by tortoises or livestock injuries from the burrows. Local tortoise hunters are often enlisted to remove tortoises from fields and pastures (Diemer 1986).

One questionnaire respondent in 1979 referred to "thousands" of tortoises being "killed by poison" in watermelon fields in central Florida. The type or source of this poison was not specified. The effects of pesticides or herbicides on tortoise populations is unknown. Indications are that a similar tortoise die-off in southern Alabama may have been the result of herbicides (J. Dobie, pers. commun.).

Livestock grazing does not appear to be a major problem for the gopher tortoise (Diemer 1986). Tortoises co-exist with cattle on portions of the southern dry prairies and in pine plantations in northern Florida. Tortoise burrow entrances are occasionally occluded by cattle activity but are later reopened by the occupants. The once free-ranging cattle and past "let-burn" fire policies were important in retaining proper open areas for tortoises (H. Stahls, pers. commun.).

In central Florida, phosphate stripmining has had a major impact on the gopher tortoise (T. Gilbert, pers. commun.). From 1880-1980, approximately 750 km² were mined in the northern portion of the phosphate mining area (Schnoes and Humphrey 1980). As these northern reserves are depleted, a shift toward the southern parts of the district is expected (Schnoes and Humphrey 1980). This mining activity has destroyed many square kilometers of sandhill and scrub habitat and has created a mosaic of disturbed wetlands and uplands over a vast area (Diemer 1986). Information regarding tortoise recolonization of mined lands is minimal. Schnoes and Humphrey (1980) noted tortoise utilization of unreclaimed pits and spoil piles 5-30+ years after mining.

Since 1975, reclamation of mined lands has been required by state law (Schnoes and Humphrey 1980). International Mineral and Chemical has established several sand pine scrub restoration areas. Native and exotic grasses and legumes have been introduced, as well as seedling pines and oaks. One hundred thirty-four tortoises have been relocated from 2 development sites to 1 of the reclaimed scrub sites; radiotelemetry and periodic burrow surveys are being used to monitor tortoise movements and determine relocation success (Godley 1987).

In northern Florida, timber production has altered large tracts of land originally in sandhill habitat. Clear-cutting, site preparation, replanting, and plantation management may negatively affect tortoise populations (Auffenberg and Franz 1982). On the other hand, selective cutting and prescribed burning improve conditions for tortoises by opening the canopy and stimulating higher yields of legumes and other preferred foods (Landers and Speake 1980, Landers and Buckner 1981, Auffenberg and Franz 1982).

Tortoise populations may also be affected by the species of pine planted on a particular site (Landers and Buckner 1981). Field surveys in the panhandle have revealed extensive areas of thickly planted sand pine (Diemer 1986). This species' fire intolerance and "limby" growth form result in a dense forest with little or no understory (Landers and Buckner 1981). Tortoise density is related to herbaceous biomass (Auffenberg and Iverson 1979); therefore, tortoise densities are exceedingly low in these plantations (Diemer 1986).

The use of heavy machinery to reduce logging debris in preparation for planting has been deemed detrimental to tortoises (Auffenberg 1978, Lohoefener and Lohmeier 1981, Auffenberg and Franz 1982, Wright 1982). Tanner and Terry (1981) cited burrow destruction from chopping and web plowing on a dry prairie, but they did not follow up on the fate of the tortoises. Diemer and Moler (1982) used radiotelemetry to investigate tortoise response to site preparation on a sandhill site. The results of this study substantiated earlier findings by Landers and Buckner (1981) in Georgia that gopher tortoises are able to dig out following chopping treatment on deep sandy soils. Additionally, a subadult tortoise which had been radio-instrumented in conjunction with a tortoise movements study dug out following bedding treatment in a plantation (Diemer, unpubl. data).

In 1982, 7 northern Florida paper companies and the U.S. Forest Service were contacted to inquire about site preparation methods. This survey revealed that chopping

was the preferred treatment on xeric sites. Although chopping is less costly and less detrimental to top soil, some companies still use the more intensive shearing, windrowing, rootraking, or bedding. More recent conversations with foresters in the Ocala National Forest (which contains Florida's largest area of sand pine scrub) revealed that chopping was being replaced by the use of a Bracke seeder. This machine turns the topsoil, clears brush, and plants the pine seeds. Tortoises in these areas should be minimally impacted by this less disruptive site preparation method.

Gopher tortoise populations are also affected by the exclusion of fire from xeric habitats. Many areas that appear to be "good" tortoise habitat (i.e., longleaf pine-turkey oak) actually support very low tortoise densities due to increasing canopy closure, shrub density, and ground litter. Sandhill habitat is a fire-subclimax; without fire, it gradually succeeds to an evergreen hardwood community (Wharton 1978). A detailed description of varying tortoise densities in response to natural and man-caused succession is presented by Auffenberg and Franz (1982).

Organized tortoise races to benefit charities have occurred for decades in Florida (Diemer 1984). In the late 1970's, 100 or more gopher tortoises were captured annually in Georgia and transported to Florida for a single race (R. Stratton, pers. commun.). In recent years, many races have been abolished due to adverse public sentiment. Prior to FGFWFC intervention, treatment of race tortoises was often less than satisfactory (Dietlein and Smith 1979, Diemer 1984). Other concerns include population disruption, gene pool mixing, and disease or parasite transmission (Diemer 1984). In 1985, tortoise race guidelines were issued to govern the capture, maintenance, and release of the tortoises. Following the race, all tortoises must be returned to the capture site.

The gopher tortoise has been exploited in Florida for over 4000 years (Taylor 1982). In the late 1800's, barrels of tortoises were a common sight on the sidewalks of Pensacola (Matthews 1979). Cuban schooners visited the Naples coast in the 1920's and returned to Cuba with hundreds of gophers (Trowbridge 1952). The tortoise was a food source for many families in Florida during the 1930's and 1940's (Hutt 1967, Taylor 1982, Mickler 1986). Its importance to Floridians during the Depression is reflected in names like "Hoover Chicken" (Hutt 1967).

The FGFWFC first began regulating tortoise harvest in 1972 by prohibiting sale and export of the species. Table 6 summarizes the history of gopher tortoise regulations from 1972-1986. With 2 exceptions, regulations have become more restrictive in the 12-year period. In 1979, the tortoise was reclassified from threatened to species of special concern when the state's status categories were modified. The newly created species of special concern category was considered more suitable for the widely distributed tortoise. In 1982, the prohibition on export of tortoises was deemed unnecessary and was therefore deleted from the regulations.

Tortoise populations on Eglin Air Force Base (which covers 188,000 ha in 3 panhandle counties) appear to be severely depleted due to overharvest. During field surveys on Eglin, areas open to the public were compared with areas closed to the public. On 8 open sites checked by a 2-person team, only 5 tortoise burrows (3 appropriately sized for adults and 2 sized for immatures) showed signs of activity. On 7 closed sites, spot checks by a 3-person team revealed tortoise activity in only 4 burrows (2 appropriately sized for small adults and 2 sized for immatures). Many areas of seemingly adequate tortoise habitat contained only abandoned burrows. The site with the 3 larger active burrows had been previously closed to the public, but was opened for deer hunting in 1984. A local tortoise hunter noted that the burrows of the remaining tortoises on this particular site were deep and crooked. Interviews with Eglin employees revealed a possible explanation for the low tortoise numbers in closed areas: tortoises were apparently harvested in the past by bombing range personnel. Concern over tortoise decline on Eglin prompted the Air Force to prohibit tortoise harvest on the reservation in 1985. Surveys in other portions of extreme western Florida revealed scattered small tortoise colonies that were often associated with wildlife food plots, firelanes, fencerows, and other ruderal habitats. These findings substantiate earlier reports by Auffenberg and Franz (1982) regarding depletion of panhandle tortoise populations due to sustained heavy human exploitation.

Because they feel that tortoise numbers have declined in their area, many panhandle tortoise hunters now travel to southwest Georgia or the Florida peninsula to pull (remove with a long flexible rod) tortoises (Diemer 1986). A panhandle tortoise hunter arrested in the northern peninsula for exceeding the possession limit commented that tortoises were "about gone" in a 50 mile radius from his home due to human predation (J. Clements, pers. commun.). Another hunter mentioned that tortoise populations in the northern peninsula were already showing the adverse effects of this hunting trend (C. Scott, pers. commun.). Taylor (1982) reported that human predation appeared to be having a dramatic deleterious effect on gopher tortoise numbers in north-central Florida.

The number of tortoises obtained during a pulling trip varies with the soil and vegetation type, the season, the number of crooked burrows, the experience of the hunter, and the harvest history of the area. Estimates of pulling success provided by the hunters ranged from 3-60%, with crooked burrows being cited as the major problem. During 10 trips with 5 individual pullers, a range of 4-38% ($\bar{x}$=18%) was observed. This compares with earlier findings (20%) by Taylor (1982). During 5 field surveys with 1 puller at 4 different sites, success rates of 38% (sandhill), 21% (reclaimed mining site), 17% (pine plantation), 14% (same pine plantation), and 13% (coastal scrub/flatwoods) were observed. At the latter site, the relatively large number of tortoises that were touched or hooked

but then escaped (12 in addition to the 7 that were pulled) were attributable to crooked burrows and/or side pockets within the burrows. These side pockets (short shafts or indentations off the main burrow) have also been observed with a miniature TV camera used to survey burrow occupancy levels (D. Breininger, pers. commun.) and may represent tortoise response to the fluctuating water tables. The crooked burrows may be due to palmetto (*Serenoa repens*) roots and/or the hardpan layer in the flatwoods soils. Whatever the explanation, the result is that tortoises are very difficult to pull in these areas. In this case, the puller had been solicited to assist in a study; he acknowledged that many tortoise hunters might not readily associate the coastal palmetto scrub and flatwoods as tortoise habitat (being more accustomed to pulling on "blackjack ridges") and certainly would not find it desirable to venture into these thick, almost impenetrable areas (R. Stratton, pers. commun.). It may be that tortoise colonies in these vast palmetto-dominated habitats are less susceptible to human predation than colonies in sandhill or ruderal habitats.

Many hunters felt that they pulled slightly more female tortoises than male tortoises. Data gathered during pulling trips revealed slightly more males than females, but the ratio was not statistically different from 1:1 ($X^2=0.1$, $df=1$, $0.9>p>0.75$, $n=45$). Taylor (1982) also cited a 1:1 sex ratio based on his pulling trips in north-central Florida. Preliminary data from a gopher tortoise population model indicate that each adult female tortoise removed from the population represents a significant loss that is replaced very slowly (Abercrombie, pers. commun.). Landers and Garner (1981) discussed the law enforcement problems associated with implementing a male-only harvest.

The majority of hunters that were interviewed do not take small tortoises (<180 mm carapace length). However, regional differences in the size of harvested tortoises may exist. Field surveys and interviews indicated that panhandle hunters are beginning to take smaller tortoises due to the scarcity of larger animals. Although additional surveys with both panhandle and peninsula pullers would be necessary to substantiate a regional size difference, current harvest data provide some insight. For example, one hunter accompanied in the field mentioned that the tortoise (222 mm carapace length) he pulled was the "average fryer size" for his area (Eglin Air Force Base) (J. Hamilton, pers. commun.). The average carapace length of 5 harvested tortoises from extreme western Florida was 226 mm. Measurements taken from the shell pile of a northern peninsular hunter (who manually captures tortoises) revealed an average carapace length of 267 mm (n=15). Discarded tortoise shells found along roadsides in north-central Florida averaged 262 mm carapace length (n=12).

It is difficult to assess the current degree of illegal tortoise harvest and commercialization in Florida. FGFWFC records revealed 133 tortoise violation arrests in 31 counties from 1980 - May 1987. The majority of the arrests occurred in the central peninsula. Eight percent of the total arrests were for buying or selling tortoises; 32%, 28% and 24% were for possession during the closed season, unlawful possession, and exceeding the possession limit, respectively. Miscellaneous violatic accounted for the remaining 8% of the arrests. Fin ranged from \$13-250 ($\bar{x}$=\$75).

The questionnaire responses and interviews indicate that the buying and selling of tortoises occurs sporadically in certain Florida communities. Information regarding an ambitious puller's ability to make \$800-\$1000/month was provided by a wildlife officer (R. Jones, pers. commun.). Taylor (1982) noted that the economic gain by a hard working (though criminal) tortoise puller was impressive. Individual tortoises are still sold according to size, with prices generally ranging from \$3-7. In some areas, however, people will pay up to \$20 for a single large tortoise.

Natural Impacts on Tortoise Populations—Although generally less devastating than human-related impacts, other factors nevertheless affect gopher tortoise populations in Florida. Climatic variation, disease, parasites, and predation may subtly or greatly affect individuals or colonies. Catastrophic events may threaten the survival of some populations. Kushlan and Mazzotti (1984) discussed the possible effects of past hurricanes on the disjunct Cape Sable population at the tip of the Florida peninsula.

Little information exists regarding the effects of disease and parasites on gopher tortoise populations (Auffenberg and Iverson 1979). Tortoise die-offs have bee attributed to flesh fly (Sarcophagidae) infestations in southern Georgia (D. Speake, pers. commun.), northeastern Florida (H. Stahls, pers. commun.) and the Florida panhandle (T. Garrett, pers. commun.). Milstrey (1986) speculated on the relationship between tortoise densities and infestation levels by the gopher tortoise tick (*Amblyomma tuberculatum*).

Predation, particularly on eggs and juveniles (Alford 1980, Landers 1980), undoubtedly exacts the largest natural toll on gopher tortoise populations. Raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), grey foxes (*Urocyon cinereoargenteus*), and armadillos (*Dasypus novemcinctus*) have been cited as the major predators on tortoise eggs in Florida (Hallinan 1923, Douglass and Winegarner 1977). Avian predators on juvenile tortoises include red-tailed hawks (*Buteo jamaicensis*) and caracaras (*Polyborus plancus*) (Fitzpatrick and Woolfenden 1978, Layne 1987). Ophidian predators, such as the coachwhip (*Masticophis flagellum*) and the indigo snake (*Drymarchon corais*), have also been reported (Douglass and Winegarner 1977). Landers and Garner (1981) cited predation by bears (*Ursus americanus*) in Georgia, and remains of a juvenile tortoise were found in a bear scat in Florida (Maehr and DeFazio 1985). Additionally, scutes from 3 subadult tortoises were found in 3 alligator stomachs in north-central Florida (M. Delany, pers. commun.). The small size of these tortoises

makes it highly unlikely that the alligators merely ingested shells discarded by tortoise hunters.

Summary and Conclusions

The gopher tortoise's wide distribution in Florida belies the fact that many populations have substantially declined and are continuing to decline. Urbanization, agriculture, forestry practices, phosphate mining, fire exclusion, and human predation have contributed to this negative trend (Auffenberg and Franz 1982). Tortoise populations in coastal scrub and dunes are particularly vulnerable. Despite habitat preservation efforts by local and regional planning councils, the prognosis for remnant colonies on the southeast coast is not encouraging. Merritt Island National Wildlife Refuge, Cape Canaveral Air Force Station, and Jonathan Dickinson State Park currently contain the largest protected tortoise populations on Florida's east coast. In recent years, tortoise populations on the southwest coast, particularly in the Naples area, have been severely impacted by urbanization (D. Jansen, pers. commun.). Tortoises still occur on both privately-owned (e.g., Keewadin Island near Naples) and state or federally-owned barrier islands; Egmont Key National Wildlife Refuge contains a particularly dense gopher tortoise population (Logan 1981). The Gulf coast of the panhandle is also facing increased development pressures (Fernald 1981). Interior panhandle tortoise populations have been severely impacted by sustained heavy human predation, fire exclusion, and conversion of sandhill habitat to dense sand pine plantations (Diemer 1986). Panhandle hunters now travel to Georgia or the Florida peninsula to procure tortoises (Diemer 1986).

Yet in many areas of the peninsula, gopher tortoises are fairly common (or even locally abundant) and stable at the present time. Unfortunately, the urbanization predictions for Florida (Fernald 1981) do not bode well for continued tortoise population stability along major interior development corridors. This impending loss of habitat, coupled with the aforementioned shift in preferred hunting locations, will undoubtedly have a dramatic deleterious effect on peninsular tortoise populations. With the exception of federal and state lands, the tortoise's stronghold for the near future in peninsular Florida may be the expansive dry palmetto prairies and scrubby flatwoods on large private landholdings. The species' continued existence on these ranches would, of course, be contingent on landowner tolerance and benign (if not beneficial) land management practices. Landowners in both the panhandle and peninsula should be encouraged to burn and/or create openings that would benefit the tortoise as well as the more typically targeted game species.

To futher confound the scenario of a widely distributed, fairly common-uncommon, declining species facing ominous predictions of habitat destruction, the gopher tortoise also exhibits the lowest reproductive rate of any harvested species in the Southeast (Landers 1980). Female gopher tortoises reach sexual maturity at 10-20 years of age and produce a single annual clutch averaging 5-7 eggs (Iverson 1980; Landers et al. 1980, 1982; Diemer 1986). Extremely heavy predation on eggs and juveniles has been reported (Auffenberg and Iverson 1979, Alford 1980, Landers et al. 1980). Gopher tortoise decline, coupled with the species' low fecundity, necessitates further evaluation of tortoise harvest regulations in Florida. Taylor (1982) noted that one-time harvest is not necessarily the "death knell" for a colony; however, intensive sustained human predation (especially removal of female tortoises) could seriously deplete local populations (Landers 1980, Landers and Garner 1981, Taylor 1982), as evidenced by past overharvest in portions of the panhandle.

Diemer (1986) reviewed various management recommendations for *G. polyphemus* throughout the species' range. Prescribed burning, establishment of preserves, protection from overharvest, and public education are important conservation measures (Landers 1980). In Florida, unique problems require innovative management strategies. For example, the use of burning to ensure or maintain tortoise populations in sand pine scrub and/or urbanized areas (where smoke management is paramount) requires a special prescribed fire methodology; a combination of chopping and burning will probably be necessary on these sites (Richardson et al. 1986). Breininger et al. (1986) suggested incorporating both well-drained and poorly-drained sites in scrub and slash pine (*P. elliottii*) preserves. Management regimes for gopher tortoises should also consider other listed species, such as the threatened scrub jay (*Aphelocoma coerulescens*) (Breininger et al. 1986). Potential tortoise restocking sites should be identified throughout the state. Tortoises have already been relocated to reclaimed mining sites in northern and central Florida (Diemer 1984, Godley 1987). Several large areas of land that are currently public water supply wellfields may possibly serve as future tortoise restocking sites (J. Bays, pers. commun.). Prior to relocations, field surveys and determination of tortoise harvest history would be necessary to document past population depletion. Finally, increased protection at the legislative level is required for upland habitats in Florida; only then will gopher tortoises and the many species of wildlife that co-exist with them (Franz 1986) be afforded some degree of future security.

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Table 1. 1987 questionnaire responses regarding gopher tortoise utilization of 3 natural and 3 ruderal habitats in Florida.

Habitat Type	No. (n=217)[a]	%[b]
Sand pine-oak scrub	152	70
Sandhill	134	62
Old fields	101	47
Roadsides	93	43
Planted pines	86	40
Dry live oak hammock	58	27

[a]Number of respondents that answered the question.
[b]Percentages are not additive because respondents may have observed tortoises and/or burrows in more than one habitat type.

Table 2. 1987 questionnaire responses regarding gopher tortoise utilization of 2 natural and 3 ruderal habitats previously considered to be marginal for tortoises in Florida.

Habitat Type	No. (n=233)[a]	%[b]
Pine flatwoods	180	77
Dry prairies	117	50
Improved pastures	109	47
Clearcuts	90	39
Maintained orange groves	34	15

[a]Number of respondents that answered the question.
[b]Percentages are not additive because respondents may have observed tortoises and/or burrows in more than one habitat type.

Table 3. Comparison of 1979 and 1987 questionnaire responses regarding relative gopher tortoise abundance in Florida.[a]

Relative Abundance	1979 (n=152)[b] No.	%	1987 (n=240)[b] No.	%
Abundant	8	5	9	4
Fairly common	93	62	148	62
Uncommon	25	16	63	26
Rare	23	15	19	8
Not present	3	2	1	<1

[a]$X^2=11.33$, df =4, $0.025>p>0.01$.
[b]Number of respondents that answered the question.

Table 4. Comparison of 1979 and 1987 questionnaire responses regarding gopher tortoise population trends in Florida.[a]

Population Trend	1979 (n=142)[b] No.	%	1987 (n=225)[b] No.	%
Declining	77	54	135	60
Stable	64	45	86	38
Increasing	1	1	4	2

[a]$X^2=2.20$, df=2, $0.5>p>0.25$.
[b]Number of respondents that answered the question.

Table 5. Comparison of 1979 and 1987 questionnaire responses regarding regulation of gopher tortoise harvest in Florida.[a]

Opinion	1979 (n=101)[b] No.	%	1987 (n=151)[b] No.	%
Prohibit harvest	26	26	103	68
Increase restrictions on harvest	42	42	15	10
Current harvest regulations adequate	33	33	33	22

[a]$X^2=51.0$, df=2, $p<0.001$.
[b]Number of respondents that expressed on opinion regarding regulation of tortoise harvest.

Table 6. History of gopher tortoise regulations in Florida.

1972:	Ban on sale and export
1973:	Possession limit of 10
1975:	Listed as threatened species
1976:	Possession limit of 5
1978:	Ban on introduction of toxic substances into burrows
1979:	Listed as species of special concern
1980:	Closed season from April 1 to June 30
1982:	Ban on export revoked
1984:	Closed season from January 2 to June 30; Ban on bucket traps and snares; Gopher tortoise relocation policy statement issued
1985:	Closed season from January 2 to September 30; Possession limit of 2; Harvest prohibited in area south of a line designated by State Road 72 to Arcadia and eastward along State Road 70; Gopher tortoise interim relocation protocol issued; Gopher tortoise race guidelines issued
1986:	Harvest prohibited in 3 national forests; Use of paint to mark tortoise shells prohibited

* 1988 Harvest prohibited statewide.

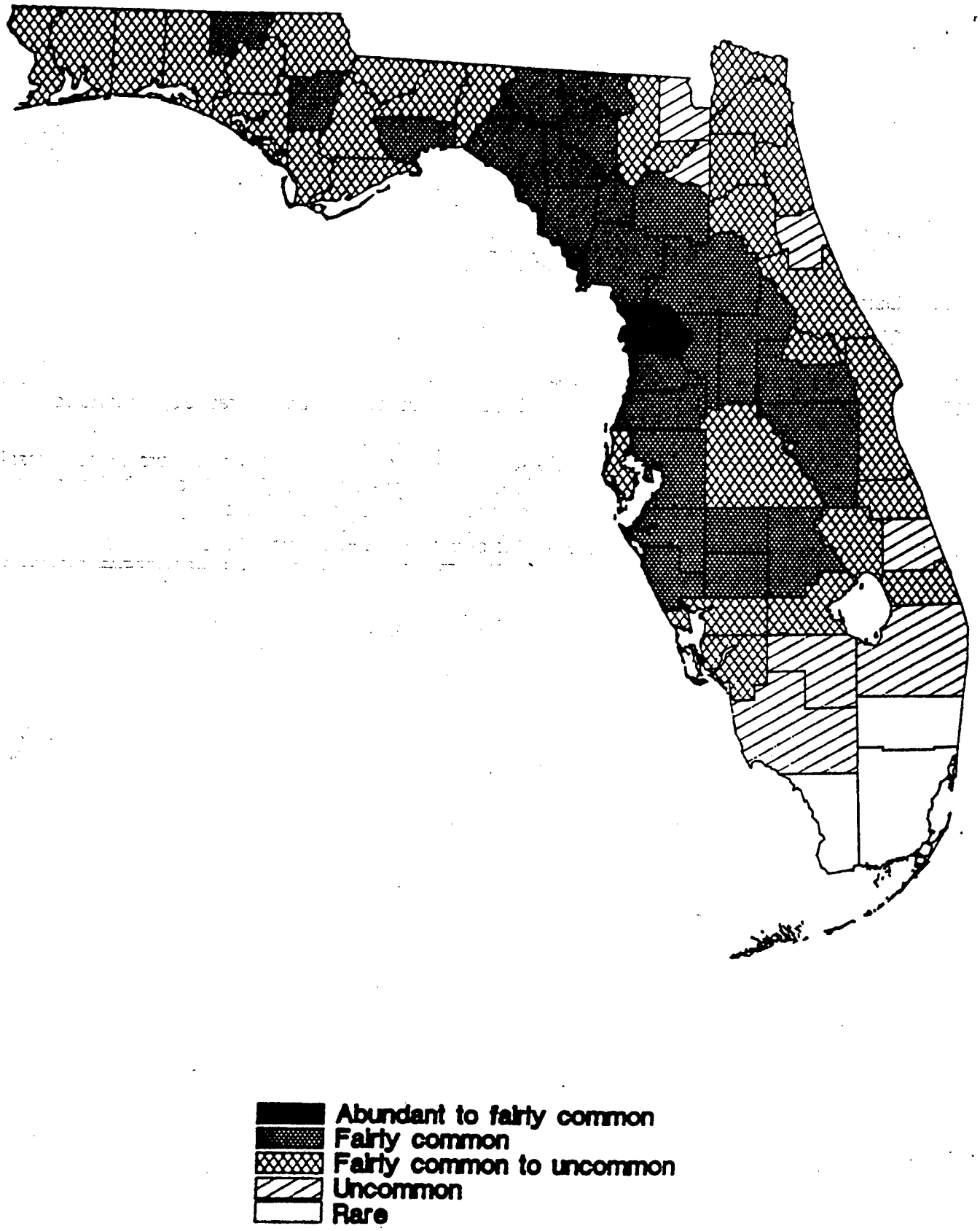


Figure 1. Relative gopher tortoise abundance in 67 Florida counties as determined by questionnaire responses.

Final Status Survey Report for the Panhandle Lily (Lilium iridollae Henry)

U.S. Fish and Wildlife Service Cooperative Agreement
No. 14-16-0004-89-961

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Introduction

This report presents the findings of a recent status survey for the panhandle lily, Lilium iridollae Henry, conducted by the Florida Natural Areas Inventory (FNAI) under contract to the U.S. Fish and Wildlife Service (USFWS). Additionally, because FNAI has an ongoing survey for rare plants at Eglin Air Force Base, we are able to augment the present survey with the results from Eglin generated during 1992. The final report on the status of L. iridollae is organized into four sections: 1) results of the de novo field surveys (includes Eglin data); 2) biological factors important to the distribution, reproductive biology, and survival of the species; 3) review of the known threats, and; 4) summary of the present status of the species with recovery action recommendations.

A previous status survey containing information on the known populations with site and habitat descriptions, a review of the taxonomy, technical botanical descriptions and other aspects relating to the status of this lily species was completed by Walter S. Judd in 1980 (U.S. Fish and Wildlife Service, 1980). The 1980 status survey noted a total of only one extant population, eight herbarium specimens, four extirpated sites, and four historic sites for L. iridollae, while it was not even possible to estimate the entire number of individuals still extant for the species. As presented below, the present status survey has tremendously expanded the known number of populations (and individuals) of this exceedingly rare and endangered lily.

A preliminary report to the USFWS in July, 1990, presented the results of a request for information on the biology and distribution of L. iridollae from all herbaria in the southeast with the potential to house specimens of this lily species. As well, the responses of botanists and other persons thought to be knowledgeable of the species were also included. In addition, an explanation of the methodology to be followed in the present status survey and a characterization of the habitat, including soil types, at known panhandle sites were included in the earlier report. Because of this previously submitted document, we will not reiterate those findings in the present report.

Results

Maps and Element Occurrence Records

De novo field surveys were conducted throughout the known range of L. iridollae in August 1990 and August 1991 (also on Eglin during 1992 - see below). In addition to large-scale participation by the FNAI staff, the Alabama Heritage Program and several other botanists were contracted to survey selected and/or reported localities of the species (see Appendix A for a list of these botanists). All known, reported, or historical sites were checked during the survey (where possible) and the resulting site information is provided on the accompanying Element Occurrence Records and maps.

All populations (with an exception for the 1992 Eglin data - see below), both extant and historical, for the panhandle lily are plotted on copies of USGS topographic quadrangle maps. The site specific information is organized into seven coded categories. These categories are represented by colored dots as follows:

Extant population - green
Presumed extirpated - dot with black X
Historical populations, pre-1960, not relocated - blue
Area surveyed 1990, L. iridollae not found - red
Area surveyed 1991 , L. iridollae not found - light brown
Previously extant occurrence, not found 1990 - yellow
Previously extant occurrence, not found 1991 - orange

Element Occurrence Records (EORs) corresponding to each site are attached to each copy of the topographic quadrangle map; the site code for the location is in the upper right corner. The results from the Eglin survey are provided only as EORs since the final report, and the precisely mapped localities of these populations, have not yet been submitted to Eglin personnel (complete results, however, will be available to USFWS in early 1993). The EORs contain all available information known about the population occurring at that site. A page explaining the EOR data fields is included as Appendix D. The EORs from the Alabama Heritage Program are slightly different in format but contain the same basic information. The maps together with the EORs are provided as Appendix E.

Summary of Results

Twenty six (26) populations of the panhandle lily were verified as extant in 1990 and 1991, tw of these in Alabama, the remainder in Florida. During the current survey, L. iridollae wa confirmed extant in a total of five (5) counties: Escambia, Okaloosa, Santa Rosa, and Walton counties in Florida; and Baldwin County in Alabama. This species was documented from 16 different topographic quadrangles during the 1990-1991 survey. The total extant range of this species covers an approximate area of 12,600 square miles. Thirteen (13) sites where the panhandle lily had previously been extant were also surveyed and L. iridollae was not found; all of these were on privately-owned land. The panhandle lily was reported from five other sites in 1986 and 1987, but we were not able to survey these sites in 1990-1991.

De novo searches that targeted potential habitat for the species were largely unsuccessful except for the Blackwater River State Forest (BWRSF) searches conducted by the FNAI staff. During the extensive FNAI field work in the BWRSF, 14 additional (i.e., new) populations were found. Additional work conducted by FNAI field botanist Richard Eilers on Eglin Air Force Base (AFB) during 1992 [not under current USFWS contract, but under separate Department of Defense contract] consisted of a rare plant survey of this extremely large, important natural resource-oriented AFB. During this investigation, nine (9) populations with ca. 74 individuals of the panhandle lily were located. A single, additional population with ca. 24 individuals was also discovered by FNAI staff scientists John Palis and Steve Orzell on a recent survey of

Garcon Point in Santa Rosa County, Florida. With the Eglin and Garcon Point data added, the total number of extant occurrences for this species is now 36, with an estimated number of individuals totalling 4,596. It should be noted, however, that ca. 3,500 of these individuals exist in a single population in Baldwin County, Alabama, that is immediately threatened with habitat destruction.

As noted above, the largest population of L. iridollae is located in Baldwin County, Alabama at the Splinter Hill Bog. It is estimated that 3,500 (potentially as many as 6,000 according to field assessments) individuals are found at this site (the estimated total includes grazed and small vegetative stems; the actual count was 2322 stems). A site survey summary for Splinter Bog is included as Appendix C. Population sizes in Florida ranged from a few individuals (sometimes one) to ca. 300; about half of these were in the range of 20-50 individuals and roughly the other half were reported with six or fewer individuals.

One description of the range for the panhandle lily (Kral 1983) includes the central Florida panhandle to as far east as Leon County. Although this may have been historically accurate, there are no verified reports or collections of L. iridollae known east of Walton County in the central panhandle. Kral (1983) may have derived the range of the species from material of potentially cultivated individuals of L. iridollae in the eastern panhandle. To our knowledge, however, the species does not extend naturally east of the Choctawhatchee River in Florida.

Within the survey area, weather conditions were near average during 1990. In the following year, 1991, late winter and spring rainfall was higher than average which created potentially favorable conditions for the appearance and flowering of L. iridollae. A related lily, L. superbum, for example, may not appear at sites that remain dry in the late spring, yet grows abundantly in subsequent wet years. There are similar observations reported for the panhandle lily. In support of this, the additional de novo searching conducted in the BWRSF, where 14 new populations were discovered during the 1991 search, may indicate that the more favorable weather conditions allowed more L. iridollae populations with stems and flowers to be visible. There was, however, generally little increase in the number of individuals observed at the known sites that were re-visited in 1991.

Soils

Soil associations found at Santa Rosa County sites where L. iridollae has been found are listed below, with most commonly associated soil given first, and with a brief description adopted from the Soil Survey of Santa Rosa County, Florida (U.S. Department of Agriculture, 1980). The description is followed by an example of a panhandle lily occurrence for this soil complex:

Bibb-Kinston-Johns complex are level soils, poorly drained and are stratified loamy or loamy. It occurs in swamps and on floodplains and stream terraces. These soils are usually extremely wet. Example: Occurrence #26.

Dorovan-Pamlico complex are nearly level, very poorly drained, organic soils that are underlain by sandy material. Soil types within the complex have a muck layer overtopping sand and are found in the southern part of Santa Rosa County. Example: Occurrence #3.

Lynchberg fine sandy loam is a somewhat poorly drained, nearly level soil occurring along narrow drainage ways, around depressions, and on low flats between small streams. The water table is at a depth of less than 12 inches for 1 to 3 months during the spring and winter in most years. Runoff is slow. Natural fertility is low. Example: Occurrence #23.

Rutledge loamy sand is a very poorly drained, nearly level soil, along small stream bottoms and ponded areas and on low upland flats. Slopes are less than 2 percent. Water table is at or near the surface for long periods. Example: Occurrence #14.

Soils at the sites within Escambia County have similar characteristics to those at the Santa Rosa County sites. They are classified by the Soil Conservation Service (U.S. Department of Agriculture, 1960) as poorly drained, mixed alluvial land. Groundwater is typically either perched for part of the year or subject to frequent overflow. In the latter case, the sites lie only a few inches above the water level of adjacent streams. Other sites characteristically have a 0-5% grade. These soils are primarily comprised of sandy peat with a high organic content and are sometimes mixed with loam. Most descriptions noted that the soil was sphagnous.

Habitat Characterization

Lilium iridollae occurs in freshwater wetland ecosystems of the Gulf Coastal Plain. The species is found in several different habitats within the complex of natural communities characterized as palustrine (i.e., freshwater wetlands dominated by plants adapted to anaerobic substrate conditions imposed by substrate saturation or inundation during 10% or more of the growing season - FNAI and Florida Department of Natural Resources, 1990) conditions that are typical of this landscape. Some characteristics in common between the natural communities where the panhandle lily is found are the sandy peat or loamy component of the soils, the site being saturated for at least part of the year, and filtered to full sun. The vegetation types of the localities supporting populations of L. iridollae are widely different and this observation may indicate that this species has always occurred in a variety of habitat types. This fact may also suggest that the species can persist, at least for a time, after successional changes in the vegetation and site conditions occur.

Natural communities where L. iridollae is found are baygalls, wet flatwoods, wet prairies, seepage slopes, floodplain forests, and bottomland forests (FNAI and Florida Department of Natural Resources, 1990). The brief descriptions of these communities that follow are composed from the EORs for the panhandle lily and therefore more accurately reflect the vegetational associates at these sites rather than for the community as a whole. Full descriptions of these communities taken from the above reference are included as Appendix B.

Baygalls

Lilium iridollae is most often found at the edges of baygalls in filtered light, while less commonly found in the interior. Canopy dominants at these sites are reported as Atlantic white cedar (Chamaecyparis thyoides), tulip popular (Liriodendron tulipifera), water oak (Quercus nigra), and southern red cedar (Juniperus virginiana). The understory and shrub layer are comprised of saplings of the canopy trees, and large gallberry (Ilex coriacea), titi (Cyrilla racemiflora), and black titi (Cliftonia monophylla). The latter two species are particularly common at the community edges and are considered invasive species that can form dense thickets in the absence of fire.

Floodplain\Bottomland Forests

As with the baygalls, panhandle lily is typically found at the edges of these communities, either along the stream corridor or on the outer edge in the ecotone between the more open pinelands. Lilium iridollae is also found in areas within the community where the canopy is sparse, or even open, but otherwise rarely in areas where the canopy is closed. Canopy dominants include swamp bay (Persea palustris), sweetbay (Magnolia virginiana), red maple (Acer rubrum), and Chamaecyparis thyoides, among others. Sweet pepper bush (Clethra alnifolia), Cyrilla racemiflora, Cliftonia monophylla, and swamp honeysuckle (Rhododendron viscosum var. serrulatum) are found in the understory\shrub layer with the titis being the most common. Other common associates are pig-potato (Oxypolis rigidior) and meadow beauty (Rhexia virginica).

Seepage Slopes

Many grasses, sedges and herbaceous species co-dominate seepage slopes. Wiregrass (Aristida stricta) is usually a dominant grass with other common genera including beak-rushes (Rhynchospora), yellow-eyed grasses (Xyris), and bog-buttons (Eriocaulon). The herbaceous ground flora has an exceptionally high species diversity. These communities are also referred to as hillside seepage bogs in the EORs. Herbaceous species that are characteristic of these systems and associates of L. iridollae are white-topped pitcher plant (Sarracenia leucophylla), trumpets (S. flava), bog-button (Lachnocaulon digynum), spoon-leaved sundew (Drosera intermedia), southern red lily (Lilium catesbaei), thread-leaved sundew (Drosera traceyi), water dropwort (Oxypolis filiformis), and common pipewort (Eriocaulon decangulare). Woody species such as St. John's wort (Hypericum nitidum), green brier (Smilax laurifolia), wax myrtle (Myrica cerifera), and blackberries (Rubus spp.), are found scattered on these gradual slopes where fire has been irregular or excluded.

Wet Prairies

According to historical descriptions in Mary Henry's original publication of L. iridollae (Henry, 1946), the largest populations of this species probably occurred in savannas or wet prairies. These open, herbaceous systems were once far more common in the Florida panhandle and adjacent areas. The floristic composition of this community type is similar to seepage slopes

but they are found on broad, expansive flat areas with poorly drained, often saturated, acidic soils. Most wet prairies have been either planted into pine or been invaded by woody shrubs and trees because of fire suppression. Although this natural community was apparently formerly more important as primary habitat for the panhandle lily, many of the wet prairies in this ar have been degraded and/or altered. It is notable that none of the extant sites for this species ar found in this community type.

Wet Flatwoods

As with other fire dependent communities in this region, most of the formerly expansive wet flatwoods have been degraded by alteration of natural fire cycles and pristine examples have been nearly eliminated through conversion to pine plantation and other agricultural practices. Slash pine (Pinus elliottii var. elliottii) is now the dominant canopy tree in many of these systems. Prior to extensive draining and other disruptions of these systems, L. iridollae may have occurred throughout wet flatwoods, or at least on wetter sites in this community. Extant populations associated with wet flatwoods are described strictly from the edges or transitional zones with wetlands having greater hydrological regimes such as baygalls, floodplain forest, and bottomland forests.

Public Lands - Status and Protection

With the inclusion of the 1992 FNAI rare plant survey data, 16 populations are confirmed extant on Eglin AFB and more could potentially be found with additional, intensive survey. The largest of all Florida populations is the Weaver Creek population on Eglin AFB. Natural fire regimes and patterns had for years been disrupted on Eglin to such an extent that much of the former habitat for the panhandle lily has been eliminated or degraded. As a resul encroachment of woody shrubs, the most invasive being black titi and titi, Cliftonia monophyll and Cyrilla racemiflora, respectively, is common in many types of wetlands on this federally owned and managed land. The Natural Resources Management Program at Eglin, however, is strongly committed to reversing this trend by restoring the natural fire regimes to appropriate habitats over much of the Base. One of the primary reasons that FNAI is conducting the rare plant survey for Eglin is so that resource managers will be better aware of the presence and precise locations of rare and sensitive plant species such as L. iridollae. Indeed, a new Natural Resources Management Plan, one that takes into account numerous important management considerations for both plant and animal species, has recently been completed. It is clear that the panhandle lily will begin to receive considerable, active management on its behalf under the new plan.

Prior to the FNAI rare plant survey of Eglin, access (because of national security reasons) to much of Eglin was difficult, if not impossible, for the typical botanist. Partially for this reason, the presence of the panhandle lily on Eglin was obviously overlooked by many because of lack of access to suitable habitat for the species. Even during a survey for the pine barrens tree frog circa 1982, however, which included Eglin AFB and was conducted by experienced field biologists, no new sites for the panhandle lily were reported. This was true despite the fact that

the researchers were aware of the significance of and potential for finding new populations of L. iridollae. Because of the vast size and natural community complexity of Eglin, it was not possible to survey all areas with potentially suitable habitat for L. iridollae even during the first year of the FNAI rare plant survey. During the second year of the survey (1993), however, it is likely that additional populations of this lily will be found, particularly more small populations located on the edges of the numerous baygall systems throughout the Base.

The Conecuh National Forest populations were not relocated. One population was last reported extant in 1982, but soon after discovery was eliminated by collectors (McGinty, 1983). Other reported populations in the Forest have not been relocated. It is herein suggested that these populations were vulnerable to grazing by livestock and have probably been extirpated. As with portions of Eglin AFB, the natural communities of Conecuh National Forest where panhandle lily was once found have been altered by fire suppression and timber management activities to such an extent that it is not likely the plant will be found (Marc Bailey, pers. comm. 1991 and D. McGinty, 1983).

A rare plant survey was conducted on Pensacola Naval Air Station and several of its associated satellite fields in 1988 (FNAI, 1988) but no panhandle lily populations were found.

Fourteen occurrences were found on Blackwater River State Forest (BWRSF). Most populations found on state forest lands are small, fifty individuals or fewer, with five of these having six or fewer plants. BWRSF has continued to burn most of the pinelands for brush control and panhandle lily has likely indirectly benefitted from this practice. Other fire management strategies and techniques do not benefit the growth of this lily, however, including fire suppression in wetlands and ecotones, burn schedules of five years and greater, and fire lane construction. FNAI is working with the managing agencies for these lands, Florida Department of Agriculture and Consumer Services, Department of Forestry, to develop appropriate fire regimes and other management strategies to protect the extant L. iridollae sites. BWRSF has also proposed that a known site for the panhandle lily be purchased through Florida's Conservation and Recreation Lands (CARL) Program and added to the State Forest. This tract has been approved for purchase but it is not known when or if the purchase will actually occur. The site is presently owned by E.F. Hutton, Inc.

A few plants were found in a wetland owned by the University of West Florida (EOR #28) but no specific protection measures are planned for this site nor has the University administration yet been contacted concerning this occurrence.

Biological Factors

Phenology and Pollination

Flowering has been reported as early as late July and continuing through early September. The peak period for flowering is usually around mid- to late-August. Annual hydrologic, weather conditions, and time since a given site was last burned appear to be some of the most important factors effecting flower production.

The percentage of the plants found in flower in extant populations was high, estimated to be 80% by field observers. This number is most probably high because vegetative plants are difficult to see, and therefore flowering individuals/populations are the ones most often observed.

A positive correlation between flower/seed production and plant size (larger size correlates with increased reproductive output) was made by Barrows (1989). Barrows suggests that plant size decreases in shaded, woody-dominated habitats. Barrows also surmised that because most plants had four or fewer flowers, even though eight flowers/plant are possible (Henry, 1946), that most plants are growing under sub-optimal conditions. There were no reports of individuals with more than three (commonly reported as only one or two) flowers during the 1990-91 field surveys.

Based primarily on floral morphology, coloration, position of anthers and stigma, etc., L. iridollae is presumed to be insect pollinated. Few observations of the pollination mechanism and/or potential pollinators, however, were made during the present survey. The only remark relating to the pollination biology of L. iridollae was the observation of hawk moth (family Sphingidae) visitation to the large, showy, and fragrant flowers of this species. The hawk moths were apparently gathering nectar from the base of the corolla tube and not necessarily facilitating pollination (Hilsenbeck, 1991, pers. observ.).

Seed Dispersal/Seedling Establishment

The seed capsule of the panhandle lily remains firm and green well into the fall (Burkhalter, 1990, pers. comm.) so seed dispersal probably occurs in the late fall or early winter. Indeed, this assumption was recently confirmed during early December of 1992 (Hilsenbeck, pers. observ.). As with most lilies, it is likely that the seeds fall within a few meters of the parent plant. Although there is no specific mechanism for dispersal away from the mother plant, except for the fact that most seeds exhibit a broad, flat "wing" along their outer margins (thus likely facilitating wind dispersal), seeds are probably also dispersed by water flowing through the wetland habitats of the species. Weather fronts typically move toward Florida from the north and west and often deposit heavy rainfall in the late autumn and winter months; the resulting surface water movement may be sufficient in some cases to disperse the newly fallen seeds to appropriate germination and seedling establishment sites.

Very few seedlings were located during the survey at the extant populations in either 1990 or 1991. Although Gunn and Bailey reported that seedlings were difficult to see in the field, seedlings were not found or were rare at the Florida sites even with intensive searching.

Population Ecology/Reproduction

Barrows (1989) and others have also associated decreases in population size of potentially successional bog species, such as the panhandle lily, with shaded, shrub-invaded habitats (Barrows, 1989; Henry, 1946; Folkerts, 1982).

Vegetative reproduction has not been observed in this species. It is therefore assumed that L. iridollae reproduces strictly through sexual means.

Threats

Habitat Destruction

Habitats for L. iridollae are sunny openings or edges of forested wetlands, in grass- and sedge-dominated seepage areas such as seepage slopes (bogs), wet prairies, and, most commonly, at the ecotonal edges between mesic flatwoods and adjacent wetlands (e.g., baygalls). There is a sharply decreasing number of undisturbed examples of any of these natural communities within the range of this lily species. This fact is particularly true of the open, herbaceous habitats that are maintained by frequent fire. The decline in habitat quality for most of the populations of this species is attributed to fire suppression which is common throughout this region of the southeastern United States. Intensive silvicultural and other agricultural operations, including crop production, grazing of domestic animals, development of pine plantations, and construction of holding ponds, have contributed to the elimination of the natural communities where L. iridollae is found. For example, the largest remaining population of L. iridollae in Escambia County, Florida was threatened and several plants destroyed by severe erosion and slash piling resulting from the clearcutting of the longleaf pine stand on the adjacent upland. Degradation of panhandle lily populations in several EORs is attributed to
erosion resulting from clearcutting of pine plantations. Overall, outright habitat destruction is the single most significant threat to the continued existence of L. iridollae.

Horticultural and Botanical Collection

A population of L. iridollae on Conecuh National Forest was reportedly removed by horticultural collectors (McGinty, 1983). This account lends credence to the view that collecting of this, and other horticulturally desirable native species, may be more common than currently believed. Other than the above account, however, there is little actual evidence of over-utilization of the species by collectors. Nevertheless, the panhandle lily is presently being offered for sale by a Florida nursery that has produced growing stock from tissue culture (R. McCartney, pers. comm.).

There is no evidence that botanical collection for scientific investigations is a significant threat to the species. Because most populations of this species are small, however, even the removal of a single flowering and/or fruiting individual could jeopardize the continuation of a given population.

Disease and Predation (Herbivory)

Reproductive output (flower, fruit, and seed production) can be significantly reduced by predation. Many of the field reports and literature accounts (including the EORs) mention damage primarily to the flowering tops, but also to the stems and leaves, due to various forms of herbivory. Barrows (1989) specifically mentions that the tettigoniid grasshoppers eat L. iridollae flowers. He also discusses other types of damage due to herbivory, such as stems severed at ground level and the presence of remnant piles of leaves and stems. Damage from grazing livestock and deer, as evidenced by the gnawed tops of plants, has been repeatedly observed. McGinty (1983) suggests that the succulent stems of L. iridollae are preferentially eaten by cattle. All of the sites where the species is currently extant are probably accessible to some type of grazing animal. At least one fungus is also reported as causing significant damage to the flowers (anthers) and pollen of L. iridollae (Barrows, 1989).

Regulatory Mechanisms

At least one population of L. iridollae is known to have been detrimentally impacted by the construction of a dam across the stream system where it occurs. The dam was reviewed and permitted for construction by the Florida Department of Environmental Regulation and the U.S. Army Corps of Engineers through the wetland protection review regulations. Information on the occurrence of this species was probably not available to these permitting agencies at the time of application review, however. In reviewing the rules and regulatory mechanisms developed for wetland resource protection, it is possible that populations of panhandle lily could benefit from the protection afforded to some wetlands (all forested wetlands), while other wetlands such as herbaceous-dominated wet prairies may not receive adequate protection. The various rules generally protect wetlands from outright destruction but many agricultural and silvicultural practices are still exempted and thus allowed. Many, if not most, of the wetlands damaging/degrading activities would appear to be highly detrimental to panhandle lily populations. As well, these rules do not regulate activities in upland areas adjacent to wetlands systems that may detrimentally impact panhandle lily populations through erosion, construction run-off, clearing, pesticide use, etc.

Populations in or near highway and power line right-of-ways, or similar situations, are endangered by pesticide application. Malcolm Pierson, Alabama Power Corporation, describes such a situation at a panhandle lily site in Alabama (Pierson, 1990). The federal Environmental Protection Agency is currently developing pesticide application regulations for the protection of endangered and otherwise sensitive species. If adopted, the regulations would be applied in areas within the distribution of federally endangered and threatened species.

Summary and Recommendations

General Assessment of Status

Although many more populations of L. iridollae have been discovered since the 1980 status survey was conducted, the species is nonetheless demonstrably rare within its very limited range. Fifteen populations that were previously extant were not relocated during the current survey thus unequivocally demonstrating a dramatic decline in population numbers. Many populations are reported as having fewer than six mature individuals and active threats to this species are described in nearly all reports of extant occurrences. These threats continue to contribute to the apparent decline of this species. Several populations do occur on public lands but even if protection agreements and management plans are developed/implemented for all of these populations, they may not collectively secure the existence of the species. The additional protection afforded under the Endangered Species Act is greatly needed for this exceedingly rare and declining species. Even though we have documented 36 extant populations of the panhandle lily, because of the substantiated decline of the species, the fact that it is threatened by habitat destruction at most sites where it is still extant, most known populations are small, and given that over three-quarters of the known individuals exist in a single, threatened population, we recommend that L. iridollae be listed as endangered by the USFWS.

Recommendations for Recovery Activities on Federal Lands

Eglin Air Force Base

Fire is presently being used to manage the forestry resources on the Eglin Air Force Base. With some expansions and changes in the burn management plans and schedules (as per the recently drafted Natural Resources Management Plan), fire could be used to restore the open aspect of the understories of the baygall, seepage slope, and floodplain swamp natural communities. It is likely that populations of panhandle lily, both known and yet to be discovered, could be recovered/augmented by such actions. The recovery and protection of L. iridollae on Eglin is particularly important because the Base is in the center of distribution for this species. The findings and recommendations stemming from the first year (1992) of the FNAI rare plant survey of Eglin are likely to be instrumental in protecting viable populations of the panhandle lily.

Conecuh National Forest

Gunn and Bailey, who surveyed these lands, suggest that the population might be recovered if active burn management is reintroduced to the mesic flatwood-seepage slope-baygall system where the panhandle lily was originally found. Another potentially major impact to the panhandle lily in the Conecuh is grazing by domestic livestock. An investigation of grazing impacts should be mandated if the panhandle lily is found extant within the Conecuh.

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LILIUM IRIDOLLAE
ELEMENT STEWARDSHIP ABSTRACT

ELEMENT CODE: PMLIL1A080
SCIENTIFIC NAME: *Lilium iridollae* M.G. Henry
COMMON NAME: Panhandle lily, Pot-of-gold lily, or Sandhills bog lily

STATUS
GLOBAL RANK: G1G2
STATE RANK: S1 (AL, NC), S1S2 (FL), unranked (SC)

FEDERAL GOVERNMENT AGENCY STATUS: The U.S. Fish and Wildlife Service has designated *Lilium iridollae* a Category ~~1 C~~ Candidate for Federal listing under the Endangered Species Act of 1973. The draft Status Survey Report for Panhandle Lily (*L. iridollae* Henry) was prepared in December 1992; it recommended *L. iridollae* for listing as Endangered (White, *et al.*, 1992).

NC STATE STATUS: State Candidate - "Species which are very rare in North Carolina, generally with 1-20 populations in the state, generally substantially reduced in numbers by habitat destruction (and sometimes also by direct exploitation or disease). These species are also either rare throughout their ranges (fewer than 100 populations total) or disjunct in North Carolina from a main range in a different part of the country or world. Also included are species which may have 20-50 populations in North Carolina but fewer than 50 populations rangewide. These are species which have the preponderance of their distribution in North Carolina and whose fate depends largely on their conservation here. Also included are many species known to have once occurred in North Carolina but with no known extant occurrences in the state (historical or extirpated species); if these species are relocated in the state, they are likely to be listed as Endangered or Threatened. If present land use trends continue, candidate species are likely to merit listing as Endangered or Threatened" (Weakley 1993a).

One site supporting *Lilium iridollae* has been registered in the NC Natural Areas Registry; it is at Weymouth Woods Sandhills Nature Preserve (state-owned) (NCNHP 1993).

OTHER STATE STATUSES: *Lilium iridollae* is listed as Endangered under the Preservation of Native Flora of Florida Act and defined as a species of plant native to the state that is in imminent danger of extinction within the state, the survival of which is unlikely if the cause of the decline in number of plants continues, and includes all species determined to be endangered or threatened pursuant to the Federal Endangered Species Act of 1973 as amended (FNAI 1992). It receives no further legal protection in Alabama (ANHS 1993). It is not being tracked in South Carolina (SCHT 1993).

TAXONOMY
Lilium iridollae was not described as new to science until 1946, when M.G. Henry (1946) summarized her findings and compared the new species to other known taxa of the southeastern United States. Her earliest specimens are dated 1940. Since that time *L. iridollae* has always been considered a rare plant, confined to southern Alabama and the panhandle of Florida. Once the salient features were made known to field botanists and other locations found, there has not been any question of the species' validity.

In the Carolinas, interest was sparked by J.H. Carter, III, who observed anomalous plants and collected specimens as early as 1974 in the Sandhills region of North Carolina. Radford, *et al.* (1968), make reference to what is probably *L. iridollae* in their account of *L. michauxii*, normally a plant of mesic uplands: "The plants in bogs tend to be more robust and resemble *L. superbum* more than the plants of upland habitats." Specimens at the University of North Carolina herbarium that closely resemble *L. iridollae* date back to 1927. Carter realized that his plant of Inner Coastal Plain Streamhead Pocosins and seepage slopes was certainly not *L. superbum*, known in North Carolina only from the montane region. It was not until the publication of Godfrey and Wooten (1979), with excellent descriptions and drawings, that Carter could entertain the

possibility that the Sandhills plant might be *L. iridollae*. However, reference specimens at herbaria were extremely rare (and often not complete) and the number of known sites in the Sandhills few, each consisting of less than 10 plants. The differences that existed between the published descriptions and the NC plants could not be satisfactorily resolved until more material became available. A.S. Weakley (1991) therefore tentatively assigned the plant the name "*Lilium* sp. 2."

During the late 1980s through mid-1991, Carter, Weakley, E. Hoffman, and a few others were able to survey portions of Fort Bragg, a U.S. Army facility of 100,000+ acres in the NC Sandhills. Several new occurrences were located and additional descriptions and photographs were obtained. In 1991-93 a detailed survey of Fort Bragg was undertaken by The Nature Conservancy and the North Carolina Natural Heritage Program, with the discovery of still more sites, both on and off post. It may be noted that during this survey several other Gulf Coast "endemics" were verified as disjunct populations: *Eriocaulon texense, Rhynchospora crinipes, R. macra, Xyris chapmanii,* and *X. scabrifolia.*

Subsequently, specimens of *L. iridollae* from the Gulf Coastal Plain have been examined and compared with Sandhills plants; they are indeed the same species, although they differ in minor ways, as follows:

(1) The Gulf Coast plant flowers tend to be yellow to orange, whereas the Carolina plants are orange to red, grading to yellow or orange basally. Flower color is a plastic character in *Lilium* and is expected to vary over the range of any species, especially over large distances (Skinner 1993). Sandhills plants apparently do not produce purely yellow tepal ground color, but occasional Gulf Coast plants are red-flowered (Henry 1946, Adams and Dress 1982), and most Gulf Coast plants are actually orange or orange-yellow, rather than yellow as implied by the literature (Anderson 1993, Kral 1993).

(2) Both Gulf Coast and Sandhills plants produce rhizomes, at the end(s) of which are additional bulb(s). It is likely that older plants (large plants with multiple flowers) produce them; small plants with single flowers do not, or seldom do so. Few specimens have preserved these rhizomes, so observed differences in thickness between northern and southern plants needs to be investigated further.

(3) Leaves are scabrulous along the margins and midrib below; this is more pronounced in southern plants.

(4) Northern plants tend to produce more whorls of leaves per plant and the length of the stem above the uppermost whorl (e.g., the peduncle) is shorter.

(5) Overwintering leaves produced by bulb(s) are briefly discussed by Henry (1946) and depicted by Henry and Godfrey and Wooten (1979). It is not known whether all or only some plants produce them; they have not yet been detected in a small sample of plants in the Carolinas. White, *et al.* (1992), do not mention them.

Whether these differences are significant at a taxonomic level needs additional research, including observations of individual plants over time and careful collecting of complete plants, crossing experiments, and electrophoretic and biochemical analyses.

GENERAL DESCRIPTION: The following description is based on field observations of *Lilium iridollae* by Sandhills Field Office staff (1991-93), augmented by literature. Panhandle lily is a tall (up to 2 meters) perennial lily with 1-5 nodding orange flowers that are yellow basally. Southern plants tend more often to produce yellow pigments in the flowers, so that some populations are largely yellow flowered. Uncommonly, plants have dark red flowers that are orange basally. Leaves on the middle part of the stem are whorled, those above and below mostly single; all leaves green above, a bit paler beneath, narrowly elliptic to oblanceolate. It typically occurs in small groups of one to five plants, inhabiting Streamhead Pocosins, Sandhill Seeps, and Gulf Coast Seepage Bogs and openings along streams--primarily in habitats that burn at least occasionally.

TECHNICAL DESCRIPTION: The following description is from Sorrie (1993a), with modifications from Godfrey and Wooten (1979) and Kral (1983). A member of the Lily Family (Liliaceae), *Lilium iridollae* is a perennial from a deep-set (10 cm into substrate), fleshy bulb. Bulb roundish (to ovoid), up to 2 cm in diameter (size varies presumably with age), covered with numerous thick, whitish, fleshy, ovate scales and

producing 1-2(more?) elongate, thick, fleshy, horizontal rhizomes. A new bulb develops at the end of each of these rhizomes, presumably as a means of vegetative reproduction. There is no evidence, as yet, of slender over-wintering "leaves" produced basally from bulb(s) of northern plants, as seen on some specimens of *L. iridollae* collected in Florida and Alabama.

Stem single, brownish-green, varying from almost straw-colored to chestnut brown on the same individual, green terminally. Stem erect to leaning somewhat (often partly supported by adjacent shrubs when heavy with multiple flowers), smooth, terete, normally 1-2 meters tall, 3-5 mm thick at midstem, up to 9 mm thick basally (size varies presumably with age). **Leaves** arranged mostly in (1-)2-6(-8) whorls, each whorl composed of 4-7 ascending leaves (more strongly ascending in upper whorls), above and below which are reduced, subappressed leaves disposed singly or in several whorls of 2-3 leaves each. Some plants produce mostly single leaves, with only one or two whorls. Leaves of the midstem whorls are narrowly elliptic to oblanceolate, on a given plant the longest and narrowest leaves are borne on the lower whorls, the shortest and broadest on the upper whorls. Uppermost stem leaves are shorter and broader, tending to be all oblanceolate or even obovate. Length/width ratio of lower whorl leaves range from 4.1-7.2; ratio of upper whorl leaves varies from 3.1-5.0. Leaf length ranges up to 9.6 cm on robust plants. Leaves taper gradually (lower leaves) to abruptly (upper) to an acute to short-acuminate tip. Color is medium to darkish green, paler beneath (this difference much more noticeable on pressed specimens than in the field), but never exhibiting the glaucescence beneath of *L. michauxii* with leaves markedly bicolored. Leaf margins densely beset with tiny, rounded to acute spicules which are just discernible with a 10X hand lens, but not imparting a rough feel to the finger; such spicules also more or less distributed along major veins beneath; spicule development more pronounced in southern plants.

Inflorescence with 1-5(-8) flowers (higher numbers presumably on older plants), each terminating a long peduncle with 1-2 leafy bracts. **Flowers** nodding; tepals merely spreading when first open, but soon recurving into a near-circular shape, thus projecting the style and stamens prominently. Tepals linear-lanceolate, 7.0-8.5 cm long, about 1.5 cm wide, orange on distal half (varying to yellow, reddish-orange, or dark red), changing to dull yellow (varying to pale orange or reddish orange) on basal half, there spotted with maroon or purple-brown dots. Most flowers also exhibit a green wedge of color basally on inside of tepals. Filaments long exsert (as a result of tepals recurving), slender, more-or-less connivent basally then spreading outward at about 45 degrees distally, whitish-green, terminated by versatile, somewhat curved, rich cinnamon or cinnamon-brown anthers 1.3-1.8 cm long. Style of similar length, also spreading distally, whitish-green; stigma 3-lobed, brown or cinnamon-brown. Pollen varies in tone from cinnamon to golden. Flowers weakly fragrant.

Fruit rapidly assuming an erect position following pollination (within 2-3 weeks of flower opening), a capsule 4 cm long, green, cylindrical with short taper basally and bluntly rounded apically with 6 elongate grooves evident exteriorly. Seeds ovoid-triangular, broadly winged, 6 mm wide and 8 mm long.

DIAGNOSTIC CHARACTERISTICS: In a recent paper on lilies of the eastern United States, Adams and Dress (1982) use the following combination of characters to separate *L. iridollae* from all others: (1) leaves rough or papillose on margins and veins below; (2) perianth with strongly recurved tepals (turk's-cap-shaped); (3) nectaries visible as a green star or triangle at interior base of flower; (4) anthers thin, 5-8 times as long as wide; and (5) flowers weakly fragrant. Other characters used by Adams and Dress in their key, such as leaf shape and flower color, do not hold up. — as far as NC stuff?

In the field, leaf shape is distinctly narrow-elliptic to slightly oblanceolate, but on pressed specimens most leaves dry to an oblanceolate shape, due to the leaf margins becoming partly revolute (SFO 1991-93). Over the full range of the species, flower color varies: plants of the Carolinas tend to have more orange and red floral pigment, while Gulf Coastal Plain plants tend towards yellow and orange. No mention is made by Adams and Dress of what is a unique character, at least among southeastern *Lilium*, the presence of rhizome(s) connecting the central bulb to peripheral bulb(s). Henry (1946) and Godfrey and Wooten (1979) point out this feature. However, the rarity of this species has meant that relatively few collections exist and that only a small percent of them are complete with underground parts. The presence of linear, overwintering leaves produced by the bulb(s) needs to be investigated further to determine whether it occurs rangewide.

Identification of *L. iridollae* in the field is straightforward. It is tall, with 1-5 nodding, weakly fragrant flowers varying from yellow to red, at least the middle leaves in whorls (those above and below alternate), leaves relatively short and narrowly elliptical, leaves rough along margins (use hand-lens), rhizome present, inhabits boggy to seasonally wet soils.

L. superbum can be recognized by its taller stature, much longer leaves that taper to a long point and that are smooth on margins, nearly all leaves in whorls, many more whorls present (5-20). *L. michauxii* is much shorter in stature, its leaves prominently oblanceolate to obovate and with a pale sheen or glaucescence below and barely or not roughened along margins, flowers very fragrant, inhabits upland mesic woods (seldom in wet habitats).

IDENTIFICATION: Searches are by far most efficient during flowering, late July to early September (inclusive dates 19 July to 5 September) in North Carolina (SFO 1991-93). Fruiting plants are surprisingly difficult to detect unless growing taller than or away from the often dense shrub associates. Fruiting capsules and stalks may remain erect and evident into the following spring. Vegetative plants, especially seedlings and immature plants, are difficult to detect at any time (SFO 1991-93).

DISTRIBUTION

Lilium iridollae, as currently understood, ranges discontinuously from southern Alabama and northwest Florida to North and South Carolina.

HISTORIC RANGE: Historic occurrences have not been relocated in the following states and counties (year last seen follows in parentheses): Covington (1982) and Escambia (n.d.) counties, Alabama; Nash (1949), Northampton (1958), and Richmond (1956) counties, North Carolina; and Chesterfield (1956) and Orangeburg (1957) counties, South Carolina (NCSC 1993, NCU 1993). No specimens were seen at the University of Georgia's herbarium in April 1993 (Sorrie 1993b), but it is expected that collections from Georgia will turn up at other herbaria.

CURRENT RANGE: *Lilium iridollae* is currently known from the following counties: Baldwin County, Alabama (White, *et al.,* 1992); Escambia, Okaloosa, Santa Rosa, and Walton counties, Florida (White, *et al.,* 1992); Cumberland, Harnett, Hoke, Lee, and Moore counties, North Carolina (NCNHP 1993); and Richland County, South Carolina (Weakley 1993b). Current population estimates are 3500 plants in a single population in Alabama, 1100 plants in 35 populations in Florida, 90 plants in 14 populations in North Carolina, and one population in South Carolina (Weakley 1993b).

INVENTORY

INVENTORY NEED: In 1990-92, a complete inventory was made in southern Alabama and in panhandle Florida (White, *et al.,* 1992); it is reasonable to believe that few current sites remain undetected there. Currently the greatest need for inventory is in Georgia and South Carolina, particularly in the Sandhills region of those states, as well as in southwestern Georgia. The SC population was found during the course of searches of impact areas for rare Lepidoptera (Weakley 1993b). Mown powerlines and gaslines that intersect streamheads are likely to harbor plants, as are well-burned Streamhead Pocosins, Baygalls, and Wet Flatwoods. It is surprising that no populations have been found west of Mobile, Alabama, especially in the rich hillside bogs in southeastern Mississippi. Yet, enough detailed fieldwork has been done there in the past ten years that it is unlikely that significant populations exist.

From 1991-93, a comprehensive inventory for rare plants was conducted at Fort Bragg and Camp MacKall military reservations, and 21 sites for *L. iridollae* were located on Fort Bragg (SFO 1991-93). An intensive survey on 25,000 acres of the Sandhills Game Land in Richmond and Scotland counties, NC, scheduled for 1994 may identify more occurrences.

OWNERSHIP SUMMARY: In North Carolina, *L. iridollae* occupies 21 sites on Fort Bragg Military Reservation (U.S. Army), one on Weymouth Woods Sandhills Nature Preserve (NC Dept. Parks and Recreation), one in a powerline right-of-way (Carolina Power & Light), and two on private land (NCNHP 1993). In South Carolina, the sole known occurrence is on Fort Jackson Military Reservation (U.S. Army).

In Alabama, the largest population by far (3500 plants) is on private land but is threatened by habitat destruction. *L. iridollae* was known from Conecuh National Forest in Covington and Escambia counties as recently as 1982 but was not relocated there in 1990-92 (White, *et al.*, 1992). However, due to the inconsistent appearance of individuals of this species at different times (SFO 1991-93), it is still likely to be found there. In Florida, 16 populations are confirmed extant on Eglin Air Force Base (U.S. Air Force), 14 on state-owned Blackwater River State Forest, and one on property owned by the University of West Florida (White, *et al.*, 1992).

HABITAT

In the Carolina Sandhills region, *Lilium iridollae* occurs in the shrub zone of Streamhead Pocosins and their ecotones and in Sandhill Seeps (Schafale and Weakley 1990). These are found at the headwaters of small streams in the Sandhills Region (innermost coastal plain; also known as "Fall-line Sandhills"), where clay content of soils forces water traveling through the sandy soil to the surface. In contrast, Sandhill Seeps are normally isolated from obvious stream systems. Soils are classified as Blaney (Arenic Hapludults), Candor (Arenic Paleudults), Gilead (Aquic Hapludults), Johnston (Cumulic Humaquepts), Torhunta and Lynn Haven (Typic Humaquepts and Typic Haplaquods), and Vaucluse (Typic Hapludults) (Hudson 1984, NCNHP 1993). Vegetation is dominated by Ericaceous and other shrubs, including *Clethra alnifolia, Cyrilla racemiflora, Fothergilla gardenii, Gaylussacia frondosa, Ilex glabra, I. laevigata, Lyonia lucida, L. ligustrina, Myrica heterophylla, Vaccinium corymbosum, Zenobia pulverulenta,* and others, with scattered small hardwoods, such as *Acer rubrum, Liriodendron tulipifera, Magnolia virginiana,* and *Nyssa biflora*, overtopped by *Pinus serotina. Chamaecyparis thyoides* and *Liquidambar styraciflua* may grow nearby. Herbs are sparse in fire-suppressed pocosins but diverse and locally dominant in well-burned pocosins (especially in their ecotones) and include members of *Andropogon, Aristida, Arundinaria, Calopogon, Carex, Chasmanthium, Eupatorium, Lycopodium, Osmunda, Panicum, Platanthera, Rhexia, Rhynchospora, Sarracenia, Sphagnum, Woodwardia, Xyris, Zigadenus, et al.*

Lilium iridollae occurs where shrubs and cane (*Arundinaria tecta*) form a dense cover from 0.7-1.5 meters high, as well as out into the ecotone where graminoids and low shrubs dominate, but all sites are subject to increasingly tall and dense shrub cover in the absence of fire (or cutting in powerlines). Because of its size and presumed longevity, the lily is apparently able to compete successfully among the shrubs but, like so many uncommon to rare species that occur in pocosin habitats, needs occasional disturbance to reduce shrub density and height (Kral 1983).

The following is taken from White, *et al.* (1992). In the Gulf Coastal Plain of Florida and Alabama, *L. iridollae* inhabits Baygalls, Wet Flatwoods, Seepage Slopes, and the edges of Bottomland Forests, typically in sandy peat or loamy soils which are saturated for at least part of the year and include soils classified as Bibb-Kinston-Johns complex, Dorovan-Pamlico complex, Lynchberg fine sandy loam, and Rutledge loamy sand (USDA 1980). The sites have open to full sun or filtered light. Gulf Coastal Plain Seepage Slopes are analogous to Streamhead Pocosins and Sandhill Seeps of the Carolinas (Schafale and Weakley 1990) and share many species in common. They occur where downslope seepage meets an impermeable layer (clay or rock) and is forced to the surface. Typical plants include *Pinus serotina, P. elliottii, P. palustris, Cyrilla racemiflora, Ilex coriacea, I. glabra, I. myrtifolia, Cliftonia monophylla, Lyonia ligustrina, Myrica heterophylla, Vaccinium corymbosum, Clethra alnifolia, Chamaecyparis thyoides, Liriodendron tulipifera,* plus many grasses, orchids, insectivorous plants, and other herbs. Soils are acidic, loamy sands with low nutrient availability. Many other rare plant species are associated with this community type, including *Dionaea muscipula, Lysimachia asperulifolia, Tofieldia glabra,* and *Xyris scabrifolia.* Fires with a frequency of about every five years limits shrub height and tree invasion.

Baygalls are forested, peat-filled seepage depressions often at the base of slopes. The canopy is tall, often dense, evergreen hardwoods dominated by *Magnolia virginiana, Persea palustris,* and *Gordonia lasianthus,* with an open understory of ferns and shrubs typical of Seepage Slopes. Soils are composed of acid peats. Fires occur much less frequently than in Seepage Slopes (perhaps every 50+ years) so that *Lilium iridollae* normally inhabits the margins of Baygalls in filtered light. There is no directly analogous community type in the Carolina Sandhills region, although Streamhead Pocosins may approach them in *Sphagnum* development.

Baygall-like communities, termed Bay Forests, occur in isolated Carolina bay depressions throughout the Middle Coastal Plain of the Carolinas, but to date no *L. iridollae* has been found in them.

Floodplain/Bottomland Forests occur in stream corridors and are subject to occasional (Bottomland) or frequent (Floodplain) flooding. They are characterized by a closed canopy of tall hardwoods, with an understory varying from densely shrubby to quite open. Dominants include *Acer rubrum, Quercus* spp., *Persea palustris, Magnolia virginiana,* and *Chamaecyparis thyoides.* Vines are often a common component. Soils are variable mixtures of clay and organic materials (Bottomland) or sand, organics, and alluvials (Floodplain). *L. iridollae* usually occurs at the margins of these habitats, in the ecotone between the more open pine/wiregrass uplands, or along the stream corridor itself.

White, *et al.* (1992), also include Wet Prairies as a habitat type based on descriptions in Henry (1946). However, Henry's habitat descriptions, although brief, refer to Seepage Slopes and borders of Bottomland Forests. Her use of the term "meadow" is imprecise and may connote a different plant community than intended. It is significant that none of the current sites for *L. iridollae* are found in Wet Prairies (White, *et al.,* 1992).

Wet Flatwoods are pine forests with relatively open canopies of *Pinus serotina* and *P. elliottii,* with either a thick shrubby understory and sparse ground cover or a sparse understory and dense ground cover. Typical shrubs are essentially the same as in Seepage Slopes and Baygalls. It is a high-hydroperiod community developed in flat, poorly drained terrain. Soils are acidic sands overlying organic hardpan or clay. Fire is an important component, naturally recurring every three to ten years. Extant lily populations associated with this community type occur in the edges or ecotones between other communities described above.

THREATS

Fire suppression over nearly all of the longleaf pine region during the twentieth century has rendered unsuitable many panhandle lily habitats. With proper management some may again be suitable, but lily plants will most likely have to be reintroduced, since *in situ* seeds may no longer be viable. Drainage of wetlands and conversion of vast acres to agricultural and silvicultural (pine plantation) sites has resulted in the loss of many suitable sites. Conversion of vast acres to pine plantations and to housing or industrial tracts has had a more permanent impact and most of these areas cannot be restored. On the plus side, increased development has provided some habitat in at least a few powerlines and gaslines; their importance needs to be assessed via extensive surveys. There is little doubt that the great majority of *L. iridollae* plants now are found on properties managed by prescribed burning, i.e., military bases, state forests and parks, private conservation lands, etc.

Grazing by deer in natural landscapes may be deleterious where their populations are not kept in check by hunting or natural predators. Kral (1983) states that "All lilies are highly palatable to both deer and cattle and are the first to go with any grazing pressure." Henry (1946) stated that "Cattle are permitted to graze 'at large,' and they roam freely, doing great damage as they are especially fond of the succulent stems and leaves of lilies. Hogs, too, which are very plentiful in some localities, are equally destructive, perhaps even more so, for they easily root up the delicate bulbs in the soft moist soil." Barrows (1989) also reports grazing by cattle, as well as predation by an unknown animal and herbivory by insects; the latter two may be natural events and not frequent enough to constitute a "threat."

In Conecuh National Forest of southern Alabama, a population was removed by horticultural collectors (White, *et al.,* 1992), but as far as is known, similar depredations elsewhere in the range have not been documented. *L. iridollae* is large and showy, so that collecting may be more common than currently believed, especially among those people desirous of possessing such a rare entity.

Construction of dams on streams where *L. iridollae* occurs has impacted at least one population in Florida, and the construction of farm and recreation ponds on dozens of streams has possibly impacted plants in the Carolina Sandhills. Populations in powerline rights-of-way are potentially threatened by herbicide and pesticide applications, but specific impacts on *L. iridollae* have not been studied.

BIOLOGY-ECOLOGY

Lilium iridollae is an apparent shade-intolerant ecotone species, which requires a regular fire regime or is otherwise susceptible to successional changes in vegetation. It is presumed that plants can persist for some time in overgrown, shrubby, fire-suppressed areas, but it is not known for how long. Over a long period of fire suppression, plants will surely lose vigor or be completely lost.

Based on field observations, the number of flowering plants within a population may be as high as 80% (White, *et al.*, 1992). However, this number is likely high due to the fact that seedlings and immature plants are more difficult to detect, while flowering individuals are the easiest. Barrows (1989) was able to determine a positive correlation between flower/seed production and plant size, finding that larger size increased reproductive output. Barrows suggested that plant size decreased in shaded, woody-dominated habitats. Although plants with as many as eight flowers are possible (Henry 1946), most plants are growing in sub-optimal conditions and thus produce only one or two, very seldom more than three, flowers per plant.

Vegetative reproduction has not been observed; therefore, it has been suggested by White, *et al.* (1992) that *L. iridollae* only reproduces sexually. However, the presence of fleshy, lateral bulbs strongly suggests that some asexual or vegetative reproduction may be possible; this phenomenon is need of study (SFO 1991-93).

PHENOLOGY: Flowering occurs from late July to early September with the peak period being mid- to late August (19 July to 5 September on Fort Bragg (SFO 1991-93)), and may be affected by weather and time since last burned (White, *et al.*, 1992). Flowers when first open are merely spreading to mildly recurved but soon recurve so that tepal tips touch each other or overlap. Fruits develop soon after tepals drop, enlarge during August and September and remain atop the dried stem through winter. In southern populations slender "overwintering leaves" are produced by the underground bulb(s). The timing of when these are produced (Henry says "autumnal"), their duration (Henry says "evergreen...often last for more than a year"), and their function is poorly known or not understood.

REPRODUCTION: Nothing is known about natural pollinators, but based on floral morphology, coloration, and position of anthers and stigma, it is presumed to be insect-pollinated. Moths and butterflies are suspected; hawk moths (Sphingidae) have been observed gathering nectar from the base of the corolla tube, though not necessarily facilitating pollination (White, *et al.*, 1992).

Seed capsules dehisce in late fall or early winter. Seeds are very small and light, as well as broad and flat, and so are likely wind-dispersed. However, seeds probably travel only a few meters from the parent plant. Seeds may also be dispersed by heavy rain runoff and water flowing through the wetland habitats of the species (White, *et al.*, 1992).

Underground bulb(s) are produced laterally at the ends of short rhizomes. It is unclear whether a given plant always produce a new bulb for the next year's stem growth. Limited sampling indicates that multiple bulbs are produced by larger, presumably older plants, especially ones that also produce multiple flowers. It is likely that such lateral bulbs do develop new plants. In wet soil habitats where fires often burn erratically, vegetative reproduction via bulbs may be a strategy for survival. However, such reproduction has not been verified. The requirements of germination need to be investigated in order to determine the proper conditions and timing of this event.

BIOLOGICAL RESEARCH NEEDS

The role of fire needs to be carefully researched to determine how it affects habitat suitability, germination, plant growth and size (including number of flowers), and how it affects production of lateral bulbs. In a study of 100 sexually reproductive plants in Florida, Barrows (1989) found that number of flowers per plant was positively correlated with other measurements of plant size, suggesting that occurrences with a high percentage of one-flowered plants are under stress. Only 11% of his study plants grew more than one flower, and none grew more than three flowers. However, low numbers of flowers per plant seems to be a universal phenomenon in *L. iridollae* (based on recent surveys in AL, FL, NC), and no one has determined what an average or mean number is for this species. It is possible that after many years of general fire suppression that all remaining occurrences of *L. iridollae* are stressed, but this hypothesis needs to be tested. In future

research, flower data need to be taken throughout the range of the species and compared with habitat "fitness" (including fire frequency or other management practices, shrub density, and height of woody vegetation).

Growth of seedlings and immature plants would be a fertile area of study, particularly as it relates to management practices. Similarly, a study of the growth of lateral bulbs and its probable relation to the production of new plants needs to be investigated and correlated with environmental parameters such as fire frequency, woody plant growth, etc.

Occurrences of *L. iridollae* usually contain small numbers of plants. It is unknown whether this is a normal result of its reproductive biology or the result of observing only stressed populations. Other research topics are suggested under the Reproduction section above.

BIOLOGICAL MONITORING

MONITORING NEEDS AND PROCEDURES: Individual plants and their specific locations need to be permanently marked and the plants monitored over time. Observations in the Sandhills of NC in 1991-93 indicate that individual plants are erratic in their appearance above ground. Their appearance needs to be compared with timing of most recent burn (or cutting/mowing in powerlines), as well as with age of plant and when it last flowered. These and other factors may be important in the reproductive biology of the species. Observations of the large population in Alabama (3500 plants) may shed some light on habitat preference, reproductive biology, and favorable management practices.

EXISTING MONITORING PROGRAMS: None.

BIOLOGICAL MANAGEMENT

MANAGEMENT RESEARCH NEEDS: Management research needs are dependent on first obtaining some hard data on the species' biology and autecology under controlled conditions of site management. Success of individual plants and of populations is likely to be directly linked to specific kinds of disturbances and these need to be quantified.

EXISTING RESEARCH PROGRAMS: None.

MANAGEMENT NEEDS AND PROCEDURES: Until specifics of research projects are gathered, managers and land stewards can return fire to the landscape, if this has not already been initiated. The number of occurrences of *L. iridollae* in Florida and North Carolina is in large part due to the prescribed burning programs conducted on U.S. Air Force, U.S. Army. and U.S. Forest Service lands. On Fort Bragg, NC, the program began in the late 1960s with winter, fuel-reduction burns every five years to suppress oaks and other hardwoods, followed in 1990 by growing-season burns in a three-year rotation (Crawford, *et al.*, 1993). The overall quality of the longleaf pine ecosystem on Fort Bragg, including Streamhead Pocosins and their ecotones, is a direct result of this burning program.

EXISTING MANAGEMENT PROGRAMS: Management programs specifically targeting *L. iridollae* are not known to exist.

STEWARDSHIP

RESTORATION/RECOVERY POTENTIAL: The potential for recovery of this species is unknown but presumed to be reasonably good, given the apparent success on Fort Bragg. The largest occurrences there are found in association with the frequently burned impact areas. Discoveries in areas on Fort Bragg where the ecosystem was fire-suppressed for many years until the initiation of a prescribed burning program in late 1960s demonstrates the ability of the species to survive such conditions and to re-emerge following reintroduction of fire to the system.

STEWARDSHIP SUMMARY: With the inclusion of *Lilium* sp. 2 into *L. iridollae*, thorough inventories to locate historic and unknown occurrences should be done on lands within this expanded range that have fire management programs. Biological research needs to be conducted on the sexual and asexual reproduction of this species, especially with respect to the effects of fire on reproduction. Biological monitoring and

management research programs also need to be developed and implemented to assess the effectiveness of existing management procedures. Protection against overcollection, mechanical damage, sedimentation, changes in soil hydrology, and shrub encroachment is imperative for habitat and species maintenance.

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NOTEWORTHY PLANTS FROM NORTH FLORIDA. VI

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ABSTRACT

The following appear to be first reports for the state of Florida: *Anredera baselloides*, *Chimaphila maculata*, *Scirpus subterminalis*, *Silene caroliniana*, and *Zigadenus leimanthoides*. Some additions to the Florida panhandle are documented also, and several significant range extensions, particularly for rare or endangered taxa within our area, are given.

RESUMEN

Las plantas siguientes parecen ser primeras citas para el estado de Florida: *Anredera baselloides*, *Chimaphila maculata*, *Scirpus subterminalis*, *Silene caroliniana* y *Zygadenus leimanthoides*. Se documentan también algunas adiciones para el extremo de Florida y se dan varias extensiones de área significativas, particularmente para plantas raras o en peligro dentro de este área.

Recent botanical discoveries in the western part of the state prompted this sixth installment of a series (Anderson 1984, 1986, 1988a, 1989, 1991) to update our knowledge of the flora of the Florida panhandle and Clewell's (1985) guide to the flora. The area of coverage is from the Suwannee River west to the Alabama state line.

New discoveries—i.e., taxa not listed by Clewell—and range extensions of selected rare or otherwise noteworthy taxa are given here. Only general locations are given for some of the rarer taxa; most Eglin Air Force Base localities are closed to the public, and the area is patrolled and protected by military and civilian personnel. Exotics that appear to be adventive or naturalized are also listed. Herbarium specimens are at FSU unless noted otherwise.

TAXA NEW TO THE AREA

Amaranthus palmeri Watson. Gadsden Co.: fallow field, Quincy, 3 Nov 1965, *R. K. Godfrey 67534* (FLAS, FSU), originally identified as *A. hybridus*; Jefferson Co.: frequent bordering pastures along Hwy 221 just N of Ashville, 19 Sep 1988, *L.C. Anderson 11833*; Leon Co.: roadside weed in Tallahassee, 12 Jul 1991, *L.C. Anderson 13469* (staminate plant), *13470* (pistillate plant); naturalized, new to Florida panhandle.

Anredera baselloides (H.B.K.) Baill. Leon Co.: locally common along

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railroad embankment, W of Cadiz Street in Tallahassee, 4 Aug 1993, *L.C. Anderson 14506*, 27 Oct 1993, *L.C. Anderson 14614*; naturalized, new to Florida. A tendency toward imperfect or functionally imperfect flowers exists in the genus (Bogle 1969). Our plants have bisexual flowers; the pollen appears fertile (as determined by microscopic examination of stained grains), but no fruits have been found. Another species, *A. leptostachya* (Moq.) Steenis occurs sporadically in peninsular Florida. Its flowers have three bifid styles and are subtended by separate, caducous bracteoles, whereas flowers of *A. baselloides* have single styles with three capitate stigmas and are subtended by connate, persistent bracteoles.

Belamcanda chinensis (L.) DC. Leon Co.: along fence at San Luis Ridge park, 1 Aug 1994, *L.C. Anderson 15168*; naturalized, new to Florida panhandle.

Blechnum serrulatum L.C. Richard. Bay Co.: large, local population in wet pine flatwoods in St. Andrews State Recreation Area near Grand Lagoon, 22 Jan 1995, *L. O'Kane s.n.*; naturalized (or native?), new to Florida panhandle.

Chimaphila maculata (L.) Pursh. Leon Co.: 15–20 stems seen in shade of magnolia-beech-oak woodland near Chaires, 27 Apr 1993, *L.C. Anderson 14185*; native, new to Florida.

Ficus pumila L. Leon Co.: Tallahassee, *R.K. Godfrey* ; Florida State University campus, Tallahassee, 12 Oct 1994, *L.C. Anderson 15306*; naturalized in Tallahassee for many years (apparently overlooked by Clewell).

Galactia elliottii Nutt. Taylor Co.: locally common in coarse sandy soil along Rte 361, ca. 10 air mi NW of Steinhatchee, 13 Jul 1992, *L.C. Anderson 13649*, native, new to Florida panhandle.

Lindera subcoriacea Wofford. Okaloosa Co.: shaded floodplain of Metts Creek, Eglin Air Force Base, 31 Jul 1992, *L.C. Anderson 13851*, 15 Jul 1993, *L.C. Anderson 14451*; native, new to Florida panhandle (possibly new to the state). Some collections from peninsular Florida have been tentatively identified as this species (McCartney et al. 1989), but B. Sorrie (pers. comm.) claims those plants represent *L. benzoin* (L.) Blume var. *pubescens* Palmer & Steyermark.

Melampodium divaricatum (Rich. in Pers.) DC. Leon Co.: Leon Sinks Geological Area in Apalachicola National Forest, 25 Oct 1993, *L.C. Anderson 15283*. A single plant of this Central American species was found (it is available through local nurseries for horticultural use and may become naturalized).

Monotropa hypopithys L. Okaloosa Co.: slopes of Silver Creek, E of Rte 85 on Eglin Air Force Base, 27 Jun 1994, *A. Schotz 1100*; Walton Co.: dried flowering stems infrequent along crest of steep head, Eglin Air Force Base, generally N of Choctaw Beach, 30 May 1994, *A. Schotz 1157*; new to

Florida panhandle. This endangered species (Coile 1993b) is known to occur in central peninsular Florida (Ward 1966).

Scirpus subterminalis Torr. Santa Rosa Co.: collected via canoe along edge of Big Coldwater Creek, T3N, R28W, Sec 13, 30 May 1994, *L. Chafin 2051*; frequent in coarse sand of shallow, shaded shoal, submersed in 10–15 cm water with *S. etuberculatus* (Steud.) Kuntze along bank of Big Coldwater Creek between Bass Brinks Creek and Wolfe Creek, ca. 7.5 air mi NNE of Milton, 1 Jul 1994, *L.C. Anderson 15053*; native, new to Florida.

Koyama (1962) concluded that *S. subterminalis* and *S. etuberculatus* were conspecific and made the combination *S. subterminalis* var. *cylindricus* (Torr.) Koyama for the latter. He reasoned that *S. torreyi* Olney should be merged with *S. subterminalis* and that *S. etuberculatus* was just a southern form of *S. torreyi* (hence all three belonged to one species), but Gleason and Cronquist (1991) treat all three as distinct species.

Apparently, *S. subterminalis* and *S. etuberculatus* do hybridize in South Carolina (A. Pittman, pers. comm.). He suggests the two morphologies (i.e., *S. subterminalis* with flaccid, terete submerged stems with inflorescences as single spikes and *S. etuberculatus* with rigid, triangular emergent stems with umbellate inflorescences) may be due to the respective plants growing at different levels in the water column. I found the two growing side by side on the same shallowly submerged shoal with no sign of intergradation; further, populations of typical *S. etuberculatus* are scattered across much of Florida, yet *S. subterminalis* has just now been found in the state—it should be more wide spread if it is indeed just an ecotypic variant. I consider the two as distinct species that may exhibit some hybridization in limited portions of their ranges.

Silene caroliniana Walt. Okaloosa Co.: infrequent at base of shaded N-facing bluff bordering Rocky Bayou, E of Niceville, 21 Jun 1994, *L.C. Anderson 15021*; native, new to Florida. This may be a relictual population persisting in a suitable niche in an otherwise inhospitable environment; a similar circumstance has been suggested for *S. virginica* L. (Anderson 1991; Kral 1966).

Solanum viarum Dunal. Leon Co.: wooded slope above Dog Lake, Apalachicola National Forest, 20 Oct 1994, *R.K. Godfrey 84074*; single plant seen and destroyed (naturalized?), first report for Florida panhandle. This noxious weed was recently found in southern Florida (Coile 1993a) and now infests considerable acreage there.

Sphagneticola trilobata (L.) Pruski. Leon Co.: roadside ditch, Tallahassee, 20 Jul 1994, *L.C. Anderson 15107*; naturalized, new to Florida panhandle. The species is widely cultivated and naturalized in peninsular Florida and around New Orleans; this new report represents the northern-most population known for the species.

This species was placed in *Wedelia* for many years. Strother (1991) said it should be in a separate genus, which he named *Complaya*, but Pruski (1995) noted the earliest available generic name is *Sphagneticola*.

Zigadenus leimanthoides A. Gray. Escambia Co.: along creek S of Nine Mile Rd, W of Pensacola, 27 May 1984, *J.R. Burkhalter 9390* (FLAS, FSU); Okaloosa Co.: shaded floodplain along Metts Creek, Eglin Air Force Base, 31 Jul 1992, *L.C. Anderson 13847*; shaded floodplain along Middle Creek, Eglin Air Force Base, 2 Jun 1994, *L.C. Anderson 14913*; sunny seepage slope under power line along Turkey Creek, Eglin Air Force Base, 9 Jun 1994, *L.C. Anderson 14944*; Walton Co.: northwest [part of county], 17 May 1938, *E.G. Hume s.n.* (FLAS); shaded bay-gall bordering seepage slope, Blount Mill Creek drainage, 29 Jul 1994, *L.C. Anderson 15140*; native, new to Florida.

The Burkhalter specimens are labeled *Z. densus* (Desr.) Fern., but that species is characterized as having racemose inflorescences as opposed to paniculate ones in *Z. leimanthoides*. Preece (1956) states the two species are closely related but distinct (he did not see the Hume specimen), whereas W. McDearman (pers. comm.) considers the two conspecific. The two species appear ecologically and morphologically distinct in the Florida panhandle. The taxonomic relationships are complicated further because the type specimens of *Z. leimanthoides* are relatively small plants from the mountains of North Carolina, whereas plants from the Florida coastal plain are very robust (they may represent a separate taxon).

ADDITIONAL RANGE EXTENSIONS

Asclepias viridula Chapm. Walton Co.: scattered in wet flatwoods at Alaqua Point, S of Rte 20, 1 Jul 1994, *A. Schotz 1104*; new to western panhandle (Wilhelm 1984, pers. comm.). This taxon is considered threatened in Florida (Coile 1993b).

Calycanthus floridus L. Walton Co.: in semi-shade of oak-sourwood-pine woodland along Rocky Creek, 6 mi NE of Niceville, 26 Apr 1994, *A. Schotz 1019*; new to western panhandle (Wilhelm 1984, pers. comm.). This species is considered endangered in Florida (Coile 1993b).

Coelorachis tuberculosa (Nash) Nash. Santa Rosa Co.: infrequent in depression marsh at Goose Ponds, Blackwater River State Forest, 11 Sep 1994, *J. Jensen s.n.*; new to western panhandle (Wilhelm 1984, pers. comm.).

Crataegus phaenopyrum (L. f.) Medic. Liberty Co.: swamp, Ochlockonee River, 4 May 1987, *H.G. Grant s.n.* (FLAS); Wakulla Co.: frequent on Ochlockonee River floodplain with *Nyssa ogechee*, *N. biflora*, *Liquidambar styraciflua*, and *Taxodium ascendens*, Apalachicola National Forest, T3S, R4W, Sec 18, 1 Jul 1993, *G. Anglin s.n.*, 12 Jul 1994, *L.C. Anderson 15067*; Walton Co.: *Nyssa ogeche* swamp, N side Sister River in

Piedmont jointgrass (better just call it Piedmont grass!) should be considered Sensitive.

Choctawhatchee River delta, 17 Oct 1988, *A.F. Clewell s.n.* (FLAS). The Wakulla County trees are 7–12 m tall, and the erect, leafless trunks (8–10 cm DBH) are armed with patches of thorns. This species is rare in Florida (Anderson 1986) and is listed as endangered (Coile 1993b). Coker and Totten (1934) reported this species (as *C. youngii* Sarg.) from Wakulla County; it has now been rediscovered for the county.

Cyperus hystricinus Fern. Okaloosa Co.: infrequent in dry sand of open hickory-pine woods at Rocky Bayou State Recreation Area, Niceville, 21 Jul 1994, *L.C. Anderson 15014*; this constitutes the second record for this species in the state. Carter (1988) reported the species from Walton County.

Eleocharis confervoides (Poir.) Tucker. Okaloosa Co.: common (vegetative) in Blue Spring, Eglin Air Force Base, 12 Mar 1994, *L.C. Anderson 14670*; Santa Rosa Co.: abundant (fruiting) in shallow waters of Atwell Pond on Eglin Air Force Base, 31 Jul 1992, *L.C. Anderson 13833*. This infrequently collected species was long assigned to the genus *Websteria*.

Liatris earlei (Greene) K. Schumann. Okaloosa Co.: open pine-oak woodland, Rocky Bayou State Recreation Area, 28 Jul 1994, *L.C. Anderson 15127*; infrequent in northern Florida, new to western panhandle (Wilhelm 1984, pers. comm.).

Linum westii Rogers. Okaloosa Co.: frequent in peaty sand along margin of small *Taxodium ascendens-Ilex myrtifolia* swamp on Eglin Air Force Base, N of Wynnehaven Beach, 14 Aug 1992, *L.C. Anderson 13911*. This is a significant extension westward for this endangered species (Coile 1993b).

Matelea alabamensis (Vail) Woodson. Walton Co.: locally common on wooded slopes above Piney Creek, N of Choctaw Beach, 17 Jul 1994, *A. Schotz 1125*. This species is endangered in Florida (Coile 1993b) and new to the western panhandle (Drapalik 1970; Wilhelm 1984, pers. comm).

Panicum nudicaule Vasey. Walton Co.: locally common on seepage slopes, Blount Mill Creek drainage, 28 Jul 1994, *L.C. Anderson 15120*, 29 Jul 1994, *L.C. Anderson 15142*. Clewell (1985) included this species in *Dichanthelium dichotomum* (L.) Gould [i.e., *P. dichotomum*], but the two are very distinct in morphology and habitat preference. This rare species (Hitchcock 1950, Lelong 1988) is considered a species of special concern by the Florida Natural Areas Inventory.

Pinguicula ionantha Godfrey. Wakulla Co.: frequent with *P. pumila* along upper edge of wet, roadside depression, N edge of St. Marks, 11 Mar 1986, *L.C. Anderson 9117*. This is a new county of record for this endangered species (Coile 1993b).

Rhexia parviflora Chapm. Santa Rosa Co.: outer edge of small gum pond in Blackwater River State Forest, ca. 7 air mi E of Munson, 21 Sep 1989, *S.L. Orzell & E.L. Bridges 12482*; locally abundant along edge of *Ilex myrtifolia* marsh at Goose Ponds, Blackwater River State Forest, 9 Jul 1994,

Small-flowered meadowbeauty
a sensitive species

J. Jensen s.n.; Walton Co.: edge of titi-gallberry depression at Alaqua Point, 1 Jul 1994, *A. Schotz 1103*; drainage ditch in pine flatwoods at Alaqua Point, 16 Jul 1994, *L.C. Anderson 15095*. These represent two new counties of record for this "rarest of the *Rhexia* species" (Bounds 1987) that is considered endangered in Florida (Coile 1993b).

Rhynchospora crinipes Gale. Okaloosa Co.: forming mats with *Sphagnum* along Malone Creek, 30 Jul 1992, *L.C. Anderson 13807*; infrequent (semi-floating) on shaded, wet bank of Metts Creek, Eglin Air Force Base, ca. 10 air mi W of Rte 85, 15 Jul 1993, *L.C. Anderson 14450*. These constitute an additional county of record in the Florida panhandle for this rare species (Anderson 1988b).

Rhynchospora leptocarpa (Chapm.) Small. Okaloosa Co.: frequent in wet peat near headwaters of Point Lookout Creek, Eglin Air Force Base, 23 Jul 1992, *L.C. Anderson 13746*; upper edge of tidal marsh on Rocky Bayou, 0.5 mi E of Niceville, 21 Jun 1994, *L.C. Anderson 14980*. This species is rarely collected in Florida.

Kral (pers. comm.) considers this species conspecific with the widespread *R. capitellata* (Michx.) Vahl. The latter is a more delicate plant with darker brown floral scales from higher elevations (piedmont and mountains), whereas the coastal plants of *R. leptocarpa* are more robust and frequently form tussocks with 30–40 culms which are gracefully arching to 12 dm long. The two geographical populations appear to be distinct in achene morphology (Blake 1918); this complex needs further study.

Ruellia pedunculata Torr. ex Gray ssp. pinetorum (Fern.) R.W. Long. Liberty Co.: frequent in seasonally wet depressions in pine woods, Apalachicola National Forest, 11 air mi SSW of Bristol, 26 Jun 1992, *L.C. Anderson 13660, 13675*. These represent the second county of record in the Florida panhandle for this infrequently encountered species.

Sideroxylon lycioides L. Santa Rosa Co.: floodplain swamp near E end of Grimes Lake, S of Yellow River, Eglin Air Force Base (ca. 1.95 mi E of Parkerville), 1 Aug 1994, *A. Schotz 1142*. This species, formerly known as *Bumelia* (see Pennington 1991 for evidence supporting transfer to *Sideroxylon*), is endangered in Florida (Coile 1993b); it is new to the western panhandle (Wilhelm 1984, pers. comm.).

ACKNOWLEDGMENTS

My field work was sponsored in part by the Florida Natural Areas Inventory (through a grant from the U. S. Department of Defense Legacy Program) and the Florida Division of Parks and Recreation. Al Schotz kindly provided specimens from his extensive, ongoing plant survey on Eglin Air Force Base, and Kent Perkins (FLAS) supplied pertinent herbarium data.

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BOOK REVIEW

ZOMLEFER, WENDY B. 1994. Guide to Flowering Plants Families. (ISBN 0-8078-2160-8, hbk.; ISBN 0-8078-4470-5, pbk.). The University of North Carolina Press, Chapel Hill and London. $55.00 (hbk); $27.50 (pbk). 430 pp., 165 text figures, 302 glossary figures, 22 tables, 2 appendices.

Rarely are the talents of a superb botanical illustrator and a qualified botanist combined in one person. Wendy Zomlefer is such a person, and her *Guide to Flowering Plant Families* is proof. Even a quick perusal of the illustrations shows them to be accurate, botanically significant, life-like, and crisp. The book is intended to be adopted as a laboratory manual or atlas of flowering plant families for a college/universities plant systematics or field botany course; although, it also makes a very nice reference for professionals and enthusiasts, as well.

Approximately 325 pages are devoted to 130 family treatments consisting of 1) full page plates illustrating whole plants, details, dissections, and even diagnostic anatomical features;. 2) a written diagnosis and important characters; 3) lists of important genera; 4) distribution; 5) economic members, 6) and commentaries on reproductive biology and phylogenetic problems and/or current studies.

The choice of taxa illustrated focuses on warm temperate and tropical U.S. representatives (a few cultivated ones also) to aid students in mentally generalizing from typical members of the family. Often, several taxa showing the range of variation are illustrated. Of special interest is the inclusion of tropical families usually left out of an introductory course but which are of major world wide importance, notably the Lauraceae, Sapotaceae, Sterculiaceae, Bombacaceae, Rhizophoraceae, Malpighiaceae, Rutaceae, Meliaceae, Sapindaceae, Combretaceae, Myrtaceae, Bignoniaceae, Palmae, Bromeliaceae, Zingiberaceae, and Marantaceae.

The book has several added bonuses for the student. First and foremost is an illustrated glossary showing structures of real species (cross referenced to the family plate), not some diagrammatic idealization. Secondly, in Appendix B is a complete chart comparing each family in term of size, distribution, vegetative habit, floral formula, fruit types, and any special diagnostic field characters. Also, there are introductory chapters on 1) illustration techniques and floral diagrams, and 2) cladistic concepts that are important in understanding the commentary. Because she has adopted Thorne's system (which she defends well), Cronquists' system is outlined in Appendix A as a cross reference.

In summary, this comprehensive atlas is up-to-date, well drawn, well planned, and user-friendly. It is highly recommended as a supplement to a text on systematic principles or as a general reference in every botanist's library.—*Roger W. Sanders.*

United States Air Force

Air Force Materiel Command

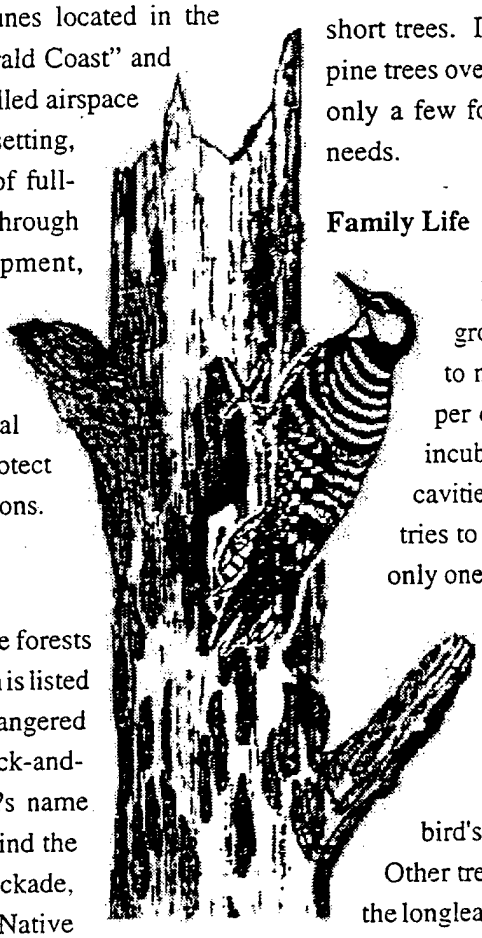
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The Red-Cockaded Woodpecker

Introduction

Eglin Air Force Base is the largest Air Force base in the free world, including 724 square miles of longleaf pine, mixed hardwoods, wetlands and coastal dunes located in the middle of Northwest Florida's "Emerald Coast" and about 130,000 square miles of controlled airspace overlying land and water. In this setting, Eglin conducts its primary mission of full-service air armament development through weapons system research, development, testing and evaluation; training; space operations; and base and range support. While fulfilling its mission, Eglin also manages its natural resources, acting as a steward to protect plants and animals for future generations.



At Home in the Longleaf Pines

Making its home in the longleaf pine forests is the red-cockaded woodpecker, which is listed by the federal government as an endangered species. This shy, 7-inch long, black-and-white bird is rarely seen. The bird?s name comes from the tiny red spot just behind the eyes of males. This spot looks like a cockade, an ornament worn on a hat as a badge. Native to the Southeastern United States, its numbers have been dwindling due largely to decreased habitat. Because more than 90 percent of the longleaf pine forests in the Southeast have been cut down, Eglin's stands of longleaf pine represent rare resource for this endangered bird.

The red-cockaded woodpecker is unique in that it is the only bird that makes its nest cavities in live, mature pines.

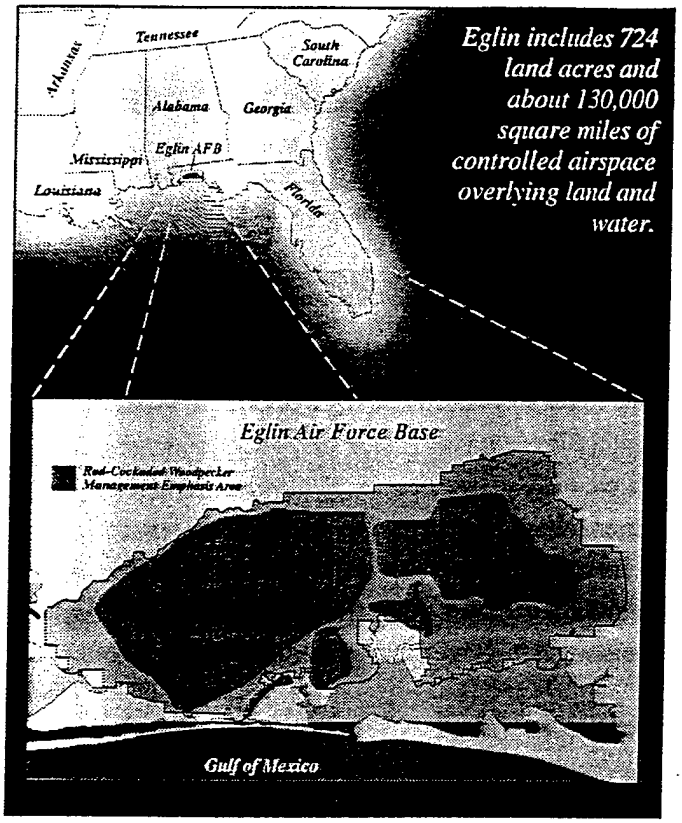
At Eglin, the bird typically chooses longleaf pines that are more than 90 years old. Only a small percentage of the trees at Eglin are this old. The bird also prefers trees that tower over low vegetation, such as wiregrass and a few short trees. It forages for insects nearby, usually in pine trees over 30 years old. Because of these habits, only a few forest areas are able to meet its habitat needs.

Family Life

Red-cockaded woodpeckers live in groups called clans. A clan consists of two to nine adult birds, with one breeding pair per clan. The other birds act as helpers to incubate the eggs, feed the young, make cavities and defend territory. Each clan member tries to have a cavity for roosting with usually only one bird per cavity. A group of cavity trees used and defended by a single clan is called a cluster.

The Problem: Lack of Habitat

Lack of suitable habitat is one of the bird's most serious problems, even at Eglin. Other trees have grown into its range and under the longleaf pines, limiting where the red-cockaded woodpecker can live and forage. In addition, many of the longleaf pine forests are broken up into areas too small for the bird. Natural resource managers at Eglin have identified five main areas of habitat, which vary in quality and cover approximately 260,000 acres. Two major areas with over 50 active clusters have been found at the base.



Habitat Protection through Forest Management

Forest management plays a key role in assisting the red-cockaded woodpecker. Five general actions can help:

- Retain existing cavity trees (for nest and roost sites)
- Provide trees for new cavities (a place for the chicks)
- Promote adequate foraging (plenty of insects)
- Control hardwoods within the cluster (maintain the habitat)
- Provide future cluster sites (a place for future generations)

To accomplish these goals, Eglin natural resource managers developed individual habitat prescriptions for each cluster site. The major need now is to control encroaching sand pines and hardwoods within these sites. This is being accomplished by a number of methods, including:

- Intentional burning (known as prescribed burning)
- Mechanical removal (cutting down unwanted hardwood trees)
- Limited herbicide application

In addition to improving habitat, these measures help improve present and future red-cockaded woodpecker nesting habitat. By providing the right conditions, the longleaf pine can slowly spread. Planting longleaf pine seedlings can help in some areas.

Natural resource managers are working to improve reproductive success of the bird by creating artificial cavities for nests and roosts, introducing females to solitary males, and monitoring the birds' status.

The Role of Fire

Planned burning is the most important tool at Eglin, allowing natural resource managers to return the longleaf pine forest habitat to its natural state. In the past, natural fires from lightning strikes were suppressed and put out. Natural resource managers now realize that natural fires removed encroaching species while helping the native species. For example, the longleaf pine survived because of its thick bark. Animals and birds escaped, many to return when ash from the fire fed the growth of new, low-lying plants. Natural fires also prevented the buildup of fuel in a forest, preventing intense fires that destroyed even hardy species. By using controlled fires now, natural resource managers can recreate the conditions necessary for the native forest and for the red-cockaded woodpeckers' continued survival.

An example of the forest's ability to renew itself was seen several years ago at Yellowstone National Park. Intense blazes caused concern for the environment and sparked fears that the forest might not regenerate. But just a few years later, biologists are reporting a remarkable rebirth. Controlled fires at Eglin will directly benefit not only the red-cockaded woodpecker, but also 16 to 18 threatened and endangered animals and at least 108 species of plants. By creating an overall healthier ecosystem, controlled fires at Eglin also give the military mission planners more flexibility; thus, man's work and nature's work can and do complement each other. In addition, burning the forest in a controlled fashion reduces the level of wildfire threat to Eglin and neighboring communities.

This fact sheet is one in a series designed to inform the public about ecosystem and resource management activities at Eglin Air Force Base.
For more information, contact Environmental Public Affairs Coordinator, AFDTC/PAV, (904) 882-4436, Ext. 321.
This fact sheet is also available on the World Wide Web via the Eglin Homepage at http://www.eglin.af.mil

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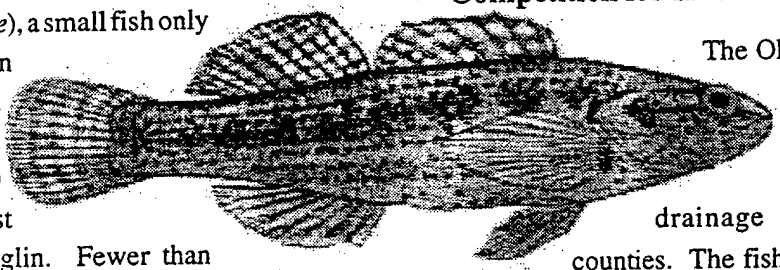
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The Okaloosa Darter

Introduction

Eglin Air Force Base is the largest air force base in the free world, including 724 square miles of land area and about 130,000 square miles of controlled airspace overlying land and water. In this setting, Eglin conducts its primary mission of full-service air armament development through weapons system research, development, testing and evaluation; training; space operations; and base and range support. While fulfilling its mission, Eglin also manages its natural resources, acting as a steward to protect plants and animals for future generations.

The streams at Eglin are home to the Okaloosa darter (*Etheostoma okaloosae*), a small fish only about 1 to 2 inches in length. The Okaloosa darter lives in a limited range of less than 250 miles of streams, almost all of which are at Eglin. Fewer than 10,000 Okaloosa darters are thought to exist, although the exact number is not known. Several stream sections that had darters just decades earlier no longer support this fish. A primary reason is alteration or loss of suitable habitat.



Because of its small range, limited numbers and population pressures, the Okaloosa darter is listed as endangered by the U.S. Fish and Wildlife Service. Eglin natural resource managers are cooperating with federal and state agencies to manage the recovery of the fish on base.

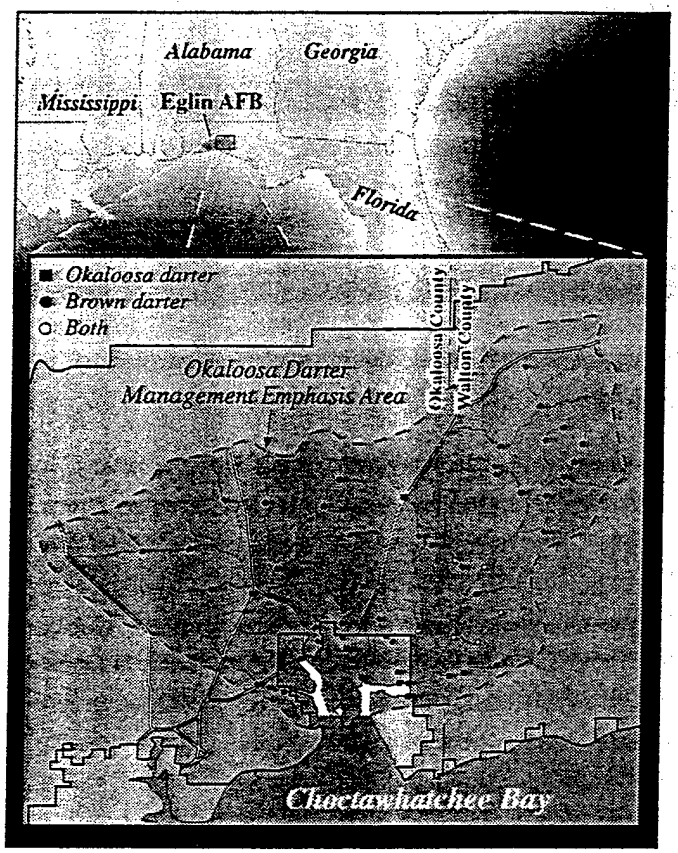
While little is known about the darter's development, biologists do know that the fish does not reproduce quickly. On average, only about 26 of its eggs are mature for spawning, and each of those is attached to submerged plants or woody debris, one or two at a time, following courtship.

Recently, the brown darter (*Etheostoma edwini*), an ecologically similar fish, was discovered in some stream sections that were formerly considered to have only Okaloosa darters. The brown darter has replaced the Okaloosa darter in some portions of the streams. Habitat loss or degradation has been associated with accumulations of silt in creekbeds, human and beaver interference with water flow, and. possibly, polluted runoff. The decline of the Okaloosa darter is significant as an indicator of habitat degradation.

Competition for Habitat

The Okaloosa darter is confined to six streams that flow into Boggy and Rocky Bayous of the Choctawhatchee Bay drainage in Okaloosa and Walton counties. The fish is found most often around plants, roots or woody debris along the margins of shallow, sandy streams 4- to 40-feet wide. These streams have predominantly clear, sand-filtered groundwater that is cooler in the summer and warmer in the winter than other surface waters. In contrast, the brown darter seems to thrive where runoff is a larger component of the streamflow. The brown darter also is capable of existing where little or no flow occurs. while the Okaloosa darter prefers flowing streams. Several stream sections have mixtures of the two darter species.

While the exact method or timing of brown darter colonization will probably never be known, brown darters are capable of replacing Okaloosa darters when stream



conditions change as they have in Swift Creek. So far, the brown darter has not established a home in the Boggy Bayou system.

Siltation

When land erodes and sediment runs off into streams, this process is known as *siltation*. Siltation is a serious problem for the Okaloosa darter and occurs at road crossings, sand and clay pits used to supply Eglin, and old railroad beds.

At some areas, several tons of sediment have been deposited into local streams. The Okaloosa darter is vulnerable to siltation and is rarely found where heavy siltation has occurred.

Siltation Reduction

Eglin is working with the U.S. Fish and Wildlife Service to help reduce siltation. Disturbed land sites are being planted with native vegetation to control erosion. The shapes of some of the sand and clay pits are also being changed to reduce the flow of soil into the creeks. On some of the more eroded pits, stairstep catch basins have been created to prevent sediment from moving downstream. Siltation at streams will be measured over the next several years to assess progress.

Studies also are underway to determine if silt is coming from other sources.

Okaloosa Darter Recovery Plan

Eglin has three main principles behind its Okaloosa darter recovery plan:

- determine biological characteristics and habitat requirements
- protect current populations and habitat
- increase population size and reestablish range

Improving the habitat by reducing siltation is one way to help meet these goals. Other efforts include limiting development of new roads and recreation areas that disturb habitat and reducing pollution from agricultural chemicals. Forest areas along some darter streams may be burned intentionally to increase the amount of sunlight reaching the stream bed. Additional sunlight will increase aquatic vegetation growth and improve habitat.

In addition to its work with the National Fish and Wildlife Service, Eglin is working with a variety of state and federal centers, including the Florida Game and Fresh Water Fish Commission and the Southeastern Biological Science Center of the National Biological Service. Research findings will help to identify the habitat requirements of the Okaloosa darter and ways to promote that habitat. Eglin has identified especially valuable habitat in its Okaloosa Darter Management Emphasis Area. Measures in this area will be designed to promote the long-term survival of the Okaloosa darter.



Okaloosa darter (actual size)

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EFFECTS OF FIRE REGIME AND HABITAT ON TREE DYNAMICS IN NORTH FLORIDA LONGLEAF PINE SAVANNAS[1]

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Abstract. Frequent, low intensity fire was an important component of the natural disturbance regime of presettlement savannas and woodlands in the southeastern USA dominated by longleaf pine (*Pinus palustris*), and prescribed burning is now a critical part of the management of these endangered habitats. Fire season, fire frequency, and fire intensity are three potentially important, though still little understood, components of both natural and managed fire regimes. In this long-term (8-yr) study, we experimentally (through the use of prescribed burning) tested for effects of fire season (eight different times throughout the year) and fire frequency (annual vs. biennial burning), on population dynamics (recruitment, growth, mortality, change in density, and change in basal area [the total basal area of all stems in a plot]) and species composition of trees in two quite different types of longleaf-pine-dominated habitats (north Florida sandhills and flatwoods). Limited fire temperature and intensity data were also collected during one year to examine the relationship between fire behavior (temperature and intensity) and tree mortality.

Contrary to prior hypotheses, our results showed few systematic or predictable effects of season or frequency of burning on dynamics of longleaf pine. Instead, variability in the population dynamics of this species appeared to be related largely to variation in fire behavior, regardless of the season of burning.

Consistent with prior hypotheses, we found that deciduous oak species (*Quercus laevis*, *Q. margaretta*, and *Q. incana*) were least vulnerable to dormant-season burning and most vulnerable to burning early in the growing season. This was shown particularly by seasonal trends in the effect of burning on oak mortality (both topkill and complete kill) and, to a lesser extent, on oak recruitment. Oak densities and basal areas also declined in the spring-burned plots, resulting in a shift away from oaks and towards increased dominance by longleaf pine. Detrimental effects of spring burning on oaks were partly explained by fire behavior, but there appeared also to be an important residual effect of burning season, particularly on complete kill.

Though longleaf pine population dynamics did not differ markedly as a result of burning season and frequency, we did find important differences in pine dynamics between the two habitats (i.e., sandhills and flatwoods). In general, populations of longleaf pines in the sandhills appeared to be density regulated, while flatwoods pine populations were declining regardless of the level of intraspecific competition. This suggests that long-term persistence of longleaf pine, and perhaps other fire-adapted species in frequently burned longleaf-pine-dominated communities, may be determined by complex interactions between habitat factors and fire regimes.

Key words: burning frequency; burning season; competition; fire regimes; flatwoods; habitat; North Florida; Pinus palustris; Quercus incana; Quercus laevis; *sandhills; species change.*

INTRODUCTION

Fire is an important ecological factor in many habitats worldwide (Kozlowski and Ahlgren 1974, Wright and Bailey 1982, Crawley 1986, Trabaud 1987, Johnson 1992). In these habitats the local fire regime (sensu Fox and Fox 1987, Malanson 1987) can strongly influence vegetation composition and dynamics (e.g., Gill et al. 1981 and papers therein, Keeley 1981, Trabaud and Lepart 1981, Krueger 1984, Hobbs and Gimmingham 1987, Bowman et al. 1988, Platt et al. 1988*a*, 1991, Collins and Gibson 1990, Fensham 1990, among many others). Aspects of the burning regime that may be important include fire frequency (e.g., Trapnell 1959, Rose-Innes 1972, Noble and Slatyer 1980, Hobbs 1984, Nieuwenhuis 1987, Fensham 1990), fire intensity (Moreno and Oechel 1991*a*, *b*), season of burning

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(Trapnell 1959, Trabaud and Lepart 1981, Le Maitre 1987, Malanson and Trabaud 1988, Platt et al. 1988*a*, Lonsdale and Braithwaite 1991, Swezy and Agee 1991), and regularity of burning (Keeley 1981, Malanson 1987, Rebertus et al., *in press*). In many areas, however, effects of different fire regimes remain poorly understood and, where important conservation or management issues are involved, controversial (e.g., Midgley 1989, Lonsdale and Braithwaite 1991, Robbins and Myers 1992, Johnson 1992).

The Coastal Plain of the southeastern United States is one area where the importance of fire as an ecological factor has long been recognized (Schwarz 1907, Harper 1911, 1962, Chapman 1932, Wells 1942, Garren 1943, Vogl 1973, Komarek 1974, Christensen 1981, Platt et al. 1988*b*, 1991, Platt and Schwartz 1990), but where much remains to be learned about effects of different fire regimes on vegetation (Christensen 1981, 1988). During presettlement and early settlement times, much of the landscape of this area was occupied by savannas (this term is used here to designate plant communities with an open, discontinuous tree canopy) and woodlands dominated by longleaf pine (*Pinus palustris*) (Bartram 1791, Baldwin 1811, Ruffin 1843, Schwarz 1907, Wahlenberg 1946, Frost et al. 1986, Silver 1990, Ware et al. 1993, Schwartz 1994, Harcombe et al., *in press*). Dominance of longleaf pine over other tree species is generally attributed to frequent natural burning (i.e., fire return intervals between 1 and 10 yr; see Chapman 1932, Garren 1943, Harper 1962, Komarek 1974, Christensen 1981, 1988, Frost et al. 1986, Bridges and Orzell 1989, Platt et al. 1991, Harcombe et al., *in press*, Rebertus et al., *in press*). However, except for complete fire suppression (see Heyward 1939, Streng and Harcombe 1982, Gilliam et al. 1993, Menges et al. 1993), little is known about effects of different fire return intervals on composition and dynamics of tree species in longleaf pine habitats (Rebertus et al., *in press*).

Another factor that may influence dynamics and composition of trees in upland habitats of the southeastern USA is season of burning. At least three reasons why this should be the case have been suggested. These are summarized below as three "hypotheses" for additional testing.

1) The "tree physiology hypothesis" postulates that seasonal variations in tree physiology and/or phenology are critically important in determining susceptibility of trees to fire (Wade and Johansen 1986*a*, *b*). This hypothesis also suggests that tree species vary in the timing of peak sensitivity to burning, so that fires at different seasons should produce different mixtures of trees. Partial support for the tree physiology hypothesis comes from several studies demonstrating that southeastern tree species do indeed differ in seasonal patterns of root carbohydrate storage and the capacity to refoliate following experimental defoliations (Hepting 1945, Woods et al. 1959, Weise et al. 1989; see also review in Robbins and Myers 1992). One general conclusion from these studies is that deciduous hardwoods should be most vulnerable to spring fires occurring shortly after leaf expansion; in contrast, pines and other evergreens are likely to be most susceptible to fires in late summer or autumn (Wade and Johansen 1986*a*, *b*, Wiese et al. 1989, Robbins and Myers 1992).

2) The "ambient temperature hypothesis" is based largely on a series of fire-behavior equations relating height of crown scorch (i.e., needle kill or bud kill) to fireline intensity, windspeed, and ambient air temperature (cf. Van Wagner 1973, Johnson 1992). According to these equations, height of scorch increases in a curvilinear fashion with increasing air temperature, assuming constant fireline intensity and wind speed (the reason is that if plant tissue is warmer to start with, a lesser increase is required to raise the temperature to a lethal level). Since air temperatures vary seasonally (i.e., from a minimum in midwinter to a maximum during the middle of the growing season), it might be expected that crown scorch, and related aspects of tree dynamics (e.g., mortality, growth), would also vary with season of burning (Robbins and Myers 1992).

3) The "tree physiology" and "ambient temperature" hypotheses may apply to virtually any tree species. However, the third hypothetical effect of season of burning on tree dynamics is unique to longleaf pine. This hypothesis, which we will term the "brown spot control hypothesis", is derived from several studies which appear to demonstrate a positive effect (i.e., increased growth or reduced mortality) of spring burning on juvenile longleaf pines (Bruce 1951, Maple 1977, Grelen 1983). Each of these authors suggested that this effect might be due to especially effective control of brown spot fungus (*Scirrhia acicola*) by spring burning (this fungus is known to infest juvenile longleafs).

Despite the above hypothetical relationships and a fairly large number of empirical studies (see reviews by Garren 1943, Wade and Johansen 1986*b*, Robbins and Myers 1992, Streng et al., *in press*), the effect of season of burning on dynamics and composition of southeastern trees is not well established. In part, this is due to design and analysis problems with at least some of the empirical studies (see Robbins and Myers 1992, Streng et al., *in press*). Perhaps the major reason for continued uncertainty, however, is that no previous study has included a complete set of seasonal burning treatments. Thus, it has been impossible to test statistically for seasonal trends in the effects of burning.

In this paper we present results from a long term (14 yr and still continuing) experimental study of the effects of different fire regimes on trees in north Florida longleaf pine savannas. [Data on understory plants have also been collected (see Platt et al. 1988*a*, 1991, Brewer and Platt 1994*a*, *b*, Streng et al., *in press*) but these will not be discussed here.] The study was designed in part to test for effects of habitat (sandhills vs. flatwoods) and frequency of burning (i.e., annual

TABLE 1. Surface fuel loadings (in kg/m²) in the two habitats during the study period. Data are based on eight 0.25-m² samples from each burn treatment plot (see Streng et al., *in press* for details on sample locations and collection dates). Data are presented separately for plots burned annually (A) and biennially (B) during 1984, due to differing times since last burn.

	Flatwoods					Sandhills				
		1984					1984			
	1983	A	B	1985	1988	1983	A	B	1985	1988
No. plots:	16	8	8	16	16	16	8	8	16	16
Time since fire (yr):	1	1	2	1	2	1	1	2	1	2
Fuel type										
Standing woody	.22	.16	.20	.18	.14	.04	.02	.04	.02	.04
Standing forb	.04	.03	.02	.05	.03	.03	.03	.02	.03	.03
Standing grass	.15	.13	.17	.11	.15	.19	.09	.13	.08	.12
Pine litter		.19*	.33*		.40		.44*	.76*		.62
Grass litter		...	...		.03		...	...		.04
Twigs + bark		...	...		.14		...	...		.19
Other litter		.11†	.26†		.11		.07†	.13†		.05
Grand total		.62	.98		1.00		.65	1.08		1.09

* Includes pine twigs and bark.
† Includes non-pine twigs, bark, and grass.

vs. bienniel burns), and we also collected some data on fire behavior effects (especially on tree mortality). However, the most useful feature of the experimental design was that it also included (and still does) a wide range of seasonal burning treatments. Thus, for the first time, we were able to rigorously evaluate prevailing hypotheses about effects of fire season on longleaf pine and associated tree species.

METHODS

Study area

The study was conducted in the Panacea Unit of the St. Marks National Wildlife Refuge, which is located in Wakulla County, Florida, ≈32 km south of Tallahassee. Established in 1931 to protect migrating waterfowl (Zontek 1966), the refuge also contains >7800 ha of upland habitats, most of it dominated by longleaf pine (Reinman 1989). The original timber was removed early in the present century, and most stands are now second growth (Reinman 1989). However, there is no history of soil disturbance, and the kinds and numbers of understory species are typical of those found in old growth longleaf pine savannas of the region (Platt et al. 1988*a*, 1991).

Little is known about fire history prior to establishment of the refuge, though it appears that open range burning (in late winter) was still common in the area in the late 1920s (as it is today on large tracts of private land) (Zontek 1966). After the government acquired the land, a policy of complete fire suppression was instituted, which lasted for most of the next decade (Zontek 1966). Controlled burning by refuge staff began in the early 1940s and a burning rotation of 4–6 yr was prescribed for most longleaf-pine-dominated habitats (Zontek 1966). In practice, this goal was seldom met, and actual fire return times averaged closer to 8 yr during most of the last five decades (Reinman 1989).

Sandhills.—Drier longleaf pine savannas (Subxeric Gulf Coastal Plain type of Peet and Allard, *in press*) are found in the St. Marks refuge on higher elevation sites (≈12 m above mean sea level), with deep, moderately to excessively drained, acid, sandy soils (Typic Quartzipsamments in the Ortega and Lakeland series) (Allen 1991). These soils are representative of the very xeric Entisols that are common on deep sand deposits throughout western Florida (Brown et al. 1990). In the refuge, the main canopy of these sandhill sites is dominated almost exclusively by longleaf pine. However, there is often a well developed midcanopy (usually ≤9 m in height) consisting of several species of xerophytic oaks. Turkey oak (*Quercus laevis*) is generally the most common species, but bluejack oak (*Q. incana*) and sand post oak (*Q. margaretta*) may also be locally abundant (nomenclature follows Clewell 1985, except as otherwise noted). Three other oak species, sand live oak (*Q. geminata*), myrtle oak (*Q. myrtifolia*), and upland laurel oak (*Q. hemisphaerica*) occur occasionally in dense patches. The ground cover is dominated by wiregrass (*Aristida beyrichiana*; Peet 1993) and grass-leaved goldenaster (*Pityopsis graminifolia*), though many other herbaceous plants and some small shrubs are also common (Platt et al. 1991 includes a species list and photograph of this habitat type; see also Christensen 1988, Myers 1990, and Peet and Allard, *in press* for more general descriptions of this type of community). Standing fuels reflect the dominant understory vegetation, and consist mostly of herbaceous plants (Glitzenstein et al. 1990, Streng et al., *in press*; see Table 1 for a summary of data for five years). Downed fuels consist mainly of pine needles (often partially burned by past fires) and twigs (Table 1). Due to the history of frequent

TABLE 2. Design of the field experiment within one habitat, indicating treatments (fires) applied over a pretreatment period (P) and four treatment cycles of 2 yr each (1981–1989). Each row in the data field represents one of the 16 plots located in each habitat; the dates in each row indicate years in which the plot was burned.*

Fire regime characteristic		Treatment cycle								
Season	Frequency	P	1		2		3		4	
Late November	Annual	1980	1981	1982	1983	1984	1985	–	1987	–
	Biennial	1980	1981	–	1983	–	1985	–	1987	–
Early January	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Late February	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Early April	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Late May	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Early July	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Late August	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Early October	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–

* Two plots were randomly assigned to each of eight seasons of burn. For each season of burn, plots originally were randomly assigned to either annual or biennial burns. Annual burns were eliminated after 1986; dashes mark the omitted burn years. Tree dynamics data were collected at the end of the third and fourth treatment cycles, just before plots were burned at the start of the fourth and fifth cycles, respectively.

burning, duff, as it is usually defined (see Johnson 1992), is virtually nonexistent in this and other longleaf-pine-dominated habitats (McKee 1982, Kalisz and Stone 1984, Brown et al. 1990).

Flatwoods.—Pine flatwoods vegetation occurs extensively throughout Florida on sites "characterized by low, flat topography, and relatively poorly drained acidic, sandy soil" (Abrahamson and Hartnett 1990). In the St. Marks Refuge, flatwoods vegetation (see Platt et al. 1991: Fig. 2 for a photograph) is found on lower elevation sites (1–2 m above mean sea level) where the water table is often within a few centimetres of the soil surface for much of the year. Soils typical of such sites are classified as Humaqueptic Psamments or Aquic Quartzipsamments, usually of the Scranton and Ridgewood series (Allen 1991). Except on scattered islands of slightly higher ground, the xerophytic oaks characteristic of sandhills are lacking from flatwoods. The ground cover is dominated by wiregrass, runner oaks (*Q. pumila* and *Q. minima*), gallberry holly (*Ilex glabra*), saw palmetto (*Serenoa repens*) and ericaceous shrubs (e.g., *Gaylussacia dumosa, G. frondosa,* and *Vaccinium myrsinites*). Scattered throughout are patches of slightly lower, even wetter, areas. Shrubs are much reduced in these hydric flatwoods (or "wet savannas"), which are dominated by wiregrass, other grasses (e.g., *Ctenium aromaticum, Sporobolus floridanus*) and sedges (*Rhynchospora* spp.)(see Wells and Shunk 1931, Means and Mohler 1979, Folkerts 1982, Walker and Peet 1983, Taggart 1990, Olson 1992, and Peet and Allard, *in press* for more thorough descriptions of these wet savanna habitats). Pond pine (*Pinus serotina*) or slash pine (*Pinus elliottii*) may also become prevalent in the hydric flatwoods and along intermittent streams that drain these habitats.

In comparison to the sandhills, fuels in the flatwoods are characterized by greater total live masses and a much greater proportion of live woody plants (Table 1). However, due to a sparser tree canopy and consequent reductions in pine needles and twigs, downed fuels are considerably less in this habitat (Table 1). Thus, total fuel loadings in the two habitats are roughly equivalent ($\approx$0.6 kg/m^2 after 1 yr without burning and 1 kg/m^2 after two fire-free yr, see Table 1).

Experimental design

The study was designed as a randomized-block experiment with three factors (Table 2). Habitat (either sandhills or flatwoods) was the blocking factor. Eight season-of-burn treatments included fires during the following 2-wk periods: (1) 15–30 November, (2) 1–14 January, (3) 15–28 February, (4) 1–14 April, (5) 15–31 May, (6) 1–14 July, (7) 15–31 August, and (8) 1–14 October. Frequency-of-burn treatments were either annual or biennial fires. An unburned control was not included in the experimental design because the effect of not burning is comparatively well established (see citations in *Introduction*); furthermore, the study was designed to compare effects of different burning regimes, not to contrast burning with the absence of burning (Platt et al. 1988*a*).

In 1980, all sandhills and flatwoods areas $\leq$2–5 ha in size in the Panacea Unit (see Reinman 1989) of the refuge were located using aerial photos. After exam-

ining each area in the field, 16 areas in each habitat were selected as sites for experimental burning treatments. Sites selected (henceforth referred to as plots) had similar densities of longleaf pine trees, oaks (in the sandhills), and wiregrass. Each combination of season and frequency of burning was randomly assigned to one plot in each habitat.

Before starting the experimental burning treatments, sandhills oaks were thinned to densities and size distributions similar to those found on the Wade Tract, an old-growth longleaf pine savanna in south Georgia (see Platt et al. 1988*b*). Thinning further standardized densities and size class distributions of these species. In addition, growth of herbaceous species and shrubs was stimulated, thus providing conditions more representative of presettlement vegetation in the area. After the oaks were thinned, all plots were subjected to a pretreatment burn in the winter of 1980 to reduce variation in the times since the last fire, and hence fire intensities, among plots. Cut oak stems and other debris from the thinning operation were burned in a few large piles within each plot to prevent any sort of general enhancement of fire intensity throughout the plot as a whole.

Experimental burning began in November of 1981, and all plots were burned for the first time (after pretreatment burns) over the following 12-mo period (Table 2). Both annual and biennial plots were burned during this first year. The following year (i.e., November 1982 through October 1983) only annual plots were burned. This and subsequent 2-yr periods including one complete set of all burning treatments will henceforth be referred to as a "treatment cycle" (see Table 2). In this paper we will consider data collected before and after the first three treatment cycles, as well as limited data collected after the fourth treatment cycle.

Annual burns tended to be patchy in some plots because of low rates of accumulation of dead vegetation and low flammability of the live vegetation (approximately 60% burned in most cases, according to field observations by M. Davis). Consequently, this treatment was eliminated from the experiment after the second treatment cycle; all plots were switched to a biennial burning schedule, providing replicate plots for analyses of season-of-burn effects (Table 2). Experimental burning has continued beyond the period of time reported here; seven treatment cycles had been completed as of mid-October 1994.

Experimental burns were standardized as much as possible, given our own time constraints and those of the refuge, which provided equipment and most of the field personnel to conduct the burns. Plots were generally burned within 2–3 d after a heavy rain, and exceptionally dry (i.e., relative humidity $< 30\%$) or windy (i.e., gusts > 5 m/s) conditions were avoided. In addition, the plots were nearly always burned using strip headfires, with the width of the strip increasing with the distance from the downwind side of the plot.

To minimize the costs to the refuge, all plots scheduled for burning during any given season (i.e., one or two plots in each habitat) were usually burned on the same day (exceptions occurred in a few cases when fires were postponed due to rain or extreme weather conditions). We recognize that this introduces a certain degree of lack of independence of experimental error (pseudoreplication; see Hurlbert 1984) wherein unique effects of particular fires (or environmental conditions at the time of burning) might be confounded with the seasonal burning treatments. Repeated fires over several years reduce the effects of any such pseudoreplication; in addition, we have employed analytical techniques designed to minimize such effects.

Fire behavior

Data on fire behavior were collected for six of the seasonal burning treatments during the fourth treatment cycle (i.e., fires from February through October 1988). At each of these fires, we measured temperatures, percent of plot area burned, and fuel consumption. These last data were then used to calculate two measures of fire intensity (heat released per unit area and fireline intensity; see Byram 1959, Wade 1986, Johnson 1992).

Field methods.—Fire temperatures were measured using Tempil (Big Three, South Plainfield, New Jersey) heat sensitive tablets. A series of 12 tablets was used, spanning a range of melting temperatures from 52°C to 804°C. Twenty sets of these tablets, each covered in aluminum foil, were placed in random locations prior to each fire. Tablets were collected and scored immediately following the fires (see Platt et al. 1991 for details). An analysis of these fire temperature data, presented in Platt et al. (1991) indicated significant effects of day of burning and proximity of nearby trees (i.e., areas with many large pines had higher fire temperatures), but no significant effect of season of burning.

Fuel consumed by the fires was estimated from four sets of paired (i.e., adjacent) 0.25-m^2 subplots. Unburned fuels (i.e., standing and downed material, including duff) were collected immediately prior to burning from one subplot in each pair. Following the burn, fuels not consumed by the fire were collected from the adjacent subplot. Fuel consumption (in kilograms per square metre) was then estimated as the average difference in mass per unit area between preburn and post-burn fuels for the four paired subplots.

One hundred permanent sample points are randomly located in each main treatment plot for the purpose of quantifying changes in understory vegetation (Platt et al. 1991, Streng et al., *in press*). Following experimental burns during the fourth treatment cycle, we checked each point in every plot to determine whether it (i.e., standing vegetation) had burned. The percentage of "burned points" was then used to estimate percentage of area burned in each plot as a whole.

Fire intensity calculations.—Heat released per unit area (in kilojoules per square metre) was calculated by

multiplying fuel consumption (see *Field methods*, above) by low heat of combustion (see Wade 1986, Johnson 1992). Low heat values used in these calculations were based on published values (Hough 1969, Hough and Albini 1978) for herbaceous live fuels, pine needles, and twigs, which together composed the bulk of our fuels (the range of low heat values for these three fuel types is 16 412–19 303 kJ/kg). A low heat value of 17 571 kJ/kg, close to the average value for live herbaceous fuel and pine needles, was used in the sandhill calculations. A slightly greater value (18 408 kJ/kg) was used for the flatwoods, because of the greater proportion of live woody fuel in this habitat. While these estimates may not be precisely correct, error due to this source is generally considered unimportant compared to other sources of variation in fire intensity data (Johnson 1992).

Neither rate of spread nor flame length were measured in the field, and we were therefore unable to calculate fireline intensity from field data alone. However, we did attempt to reconstruct rate of spread (in metres per second), and hence fireline intensity, from available climate data using Nelson and Adkins (1988: Eq. 14) (this equation, which calculates rate of spread from windspeed, fuel consumption, and flame residence time, has been found to work well in vegetation and fuels very similar to those in our study area). Wind data used in these calculations were average daily windspeeds, obtained from the nearest weather station in Tallahassee. The use of these data was justified by a high correlation ($r = 0.83$, $n = 8$, $P = 0.01$, for the eight burning dates in this treatment cycle) between the Tallahassee data and data from Apalachicola, the next closest weather station. Since the distance between Tallahassee and Apalachicola ($\approx$110 km) is much greater than that between Tallahassee and the St. Marks Refuge, it is likely that the correlation between Tallahassee windspeeds and windspeeds at the refuge was even higher than the observed correlation between the Tallahassee and Apalachicola data.

Flame residence time, the final variable in Nelson and Adkin's (1988) equation, was assumed to be 5 s in the sandhills and 7 s in the flatwoods (these values appeared reasonable, given data and examples in Nelson and Adkins 1988; again, a slightly greater value was used for the flatwoods because of the somewhat greater proportion of live woody fuels). After reconstructing rate of spread, fireline intensity (in kilowatts per metre) was calculated as the product of heat released per unit area and rate of fire spread (see Wade 1986, Johnson 1992).

Tree population censuses

Prior to the pretreatment burns in 1980 (but after thinning the oaks) all trees >2 cm dbh (diameter at breast height) in a centrally located 1-ha area in each burn plot were tagged with prenumbered aluminum tags, measured for dbh, identified to species, and mapped to the nearest 10 cm (see Platt et al. 1988*b* for a summary of mapping techniques used in this study as well). All stems joined above the ground were considered part of the same tree. If a tree had >1 stem, only the largest stem was tagged, though diameters were measured on all stems >2 cm dbh.

All plots were recensused for the first time in 1987–1988, immediately prior to burns that initiated the fourth treatment cycle. At this time, the former annual-burn plots had burned six times since the start of the study (including the pretreatment fires), while the original biennial-burn plots had burned four times (Table 2). During the recensus each tree was checked for mortality, and dbh was remeasured for all living stems. A tree was considered dead if it had no living branches above breast height. Dead trees were recorded as either topkilled (i.e., with sprouts or with living branches below breast height) or completely killed (i.e., no living sprouts or branches). Some small trees were entirely consumed in the fires and could not be relocated. Longleaf and slash pines that fell in this category were recorded as completely killed because these species do not sprout (at least as trees). Type of death could not, however, be determined for "missing" stems of sprouting species such as pond pine and hardwoods. In addition to checking for mortality and growth on previously tagged trees, we also identified, tagged, measured, and mapped all new recruits (i.e., trees that had grown to >2 cm dbh since the original census). A second recensus for mortality was conducted 2 yr later (prior to the burns that initiated the fifth treatment cycle).

Analyses: dynamics of longleaf pine and sandhills oaks

Of the various trees encountered in the censuses, only longleaf pine and oaks (the latter only in the sandhills) occurred abundantly in all plots (Appendices A, B). Tests for experimental effects on abundance and population dynamics were therefore limited to these two types of trees. All tree species were included in tests for experimental effects on changes in tree species composition. To obtain sufficiently large sample sizes (i.e., $n \geq 10$ trees for each of several size classes, see Appendix A) for analyses of oak dynamics, data were combined for the three most common species of deciduous oaks (*Q. laevis*, *Q. incana*, and *Q. margaretta*).

Pine dynamics.—Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were used to test for effects of habitat and the experimental treatments (season and frequency of burning) on longleaf pine population dynamics and changes in abundance. (Plot basal area was included as a covariate in all ANCOVAs to try to control for effects of competition). Several aspects of longleaf pine population dynamics were analyzed, including growth (defined as the average change in dbh between 1980 and 1987 for all living stems in a plot), recruitment, and percent mor-

tality (defined as the percentage of stems in a plot dying since the previous census). To test for effects of treatments on changes in longleaf pine abundance, we analyzed differences in plot basal area and density over the first three treatment cycles. Density and basal area of longleaf pine at the start of the experiment were subtracted from the same quantities determined in 1987 after 6 yr of experimental burning; these differences were then analyzed using ANOVA and ANCOVA. Prior to analysis, mortality and recruitment data were transformed to improve normality [i.e., percent mortality data were corrected for sample size differences and arcsine-transformed as recommended by Snedecor and Cochran (1981); recruit data (count-type data) were square root transformed (see Sokal and Rohlf 1982)]. ANCOVAs were tested for homogeneity of slopes (Snedecor and Cochran 1981) and, if the slopes differed significantly, the analysis was repeated for each level of a factor.

ANOVA and ANCOVA models varied somewhat depending on the date at which the data were collected and the type of data being analyzed. Data collected following the first six years of experimental burning (i.e., data on percent mortality, growth, recruitment, change in density and change in basal area collected during the first recensus in the summer of 1987) were analyzed using three-way ANOVAs and ANCOVAs. Habitat, frequency of burning, and season of burning were each considered fixed treatment effects in these analyses. Because the experimental design lacked true replication (i.e., plots within habitats treated identically) during the period encompassed by these data, the mean square associated with the three-way interaction was used as the error term for testing main effects and lower order interactions. Data on pine mortality collected after the fourth treatment cycle in 1989 were analyzed using two-way ANOVAs with replication, in which the within-cells variance was used as the estimate of experimental error. Because frequency of burning was no longer a factor in the experiment during this treatment cycle it was eliminated from subsequent analyses, and plots within habitats burned in the same season were treated as replicated experimental units regardless of whether they had previously been burned annually or biennially. Fire temperature and intensity measurements obtained during this treatment cycle were not included as additional covariates in the model, though this might seem like a reasonable approach. Fire behavior, like tree dynamics, is potentially dependent on the experimental burning treatments, and cannot, therefore, be considered as an independent effect in the model (S. L. Rathbun, *personal communication*). Instead, we simply tested for relationships between these variables and tree mortality using product–moment correlations.

Effects of burning often vary with tree size and small trees are usually more vulnerable than large ones (e.g., Abrahamson 1984, Rebertus et al. 1989, Guerin 1993). To determine whether differently sized trees in our study responded similarly to the experimental burning treatments, analyses of growth and mortality were repeated for each of several dbh-size classes. To maintain adequate sample sizes for the analyses ($n \geq 10$ trees, except in a few cases, see Appendices A, B), size classes were defined slightly differently for different variables and time periods. Mortality data collected after the first three treatment cycles were analyzed using four size classes: 2–4.9, 5–9.9, 10–19.9, and ≥20 cm dbh. Size class limits were more narrowly defined for smaller trees to make certain that we would not overlook effects of the experiment on these presumably most vulnerable individuals. After 6 yr of frequent burning, however, sample sizes for small trees were greatly reduced in some plots, and it was therefore necessary to combine the two smallest size classes when analyzing growth, as well as mortality data collected at the end of the fourth treatment cycle.

To take full advantage of the eight different seasonal burning treatments (spaced at roughly equal intervals), we used orthogonal polynomial contrasts to test for seasonal trends (see Snedecor and Cochran 1981, Rosenthal and Rosnow 1985). In these analyses, treatment means were arranged beginning with the January burns and ending with the November burns. Using this arrangement, the two lowest order contrasts (linear and quadratic) allowed us to test previously proposed hypotheses (see the *Introduction*) about effects of season of burning on dynamics of longleaf pine.

The ambient temperature hypothesis predicts that sensitivity of pines (and other trees) to fires should vary directly with ambient air temperatures. Given the climate in north Florida (Chen and Gerber 1990), this leads to the further prediction that vulnerability of trees to fires should increase from a minimum during the dormant season (when air temperatures are lowest) to a maximum during the middle of the growing season (i.e., June through September in north Florida), when air temperatures are highest. If this prediction is correct most response variables (i.e., the various aspects of longleaf pine demography monitored in this study) should follow either increasing (mortality) or decreasing (growth, recruitment, change in basal area, change in density) quadratic trends. (To simplify the terminology, an "increasing" quadratic trend in the context of this paper will be defined as a curve with a local minimum in the dormant season that rises to a peak during the middle of the growing season, and then declines again at the end of the growing season. In contrast, a "decreasing" quadratic trend will be defined as a curve that begins at a local maximum in the dormant season, decreases to a minimum in midsummer, and then increases once again at the end of the growing season.)

In contrast to the ambient temperature hypothesis, the alternative tree physiology hypothesis predicts that vulnerability of longleaf pine to fires should increase

TABLE 3. Mean fire behavior measurements for February–October burns in the fourth treatment cycle.

Burn season	Area burned (%)	Temperature (°C)	Fuel consumed (kg/m²)	Fuel consumed (%)
February	97.0	335.3	.4399	45.8
April	100.0	412.5	.6355	60.4
May	98.8	308.1	.4776	53.8
July	100.0	452.4	.8176	61.8
August	100.0	327.5	.4536	42.7
October	96.5	274.8	.5854	48.0

Burn season	Heat per area (kJ/m²)	Rate of fire spread (m/s)	Fireline intensity (kW/m)
February	7921	.1307	1025
April	11440	.1221	1390
May	8564	.2064	1816
July	14650	.1698	2629
August	8175	.1063	881
October	10510	.3358	3744

from a minimum in late winter to a maximum in early autumn. The precise shape of the predicted curve is not at all clear from the available information, but there should at least be a significant linear component (increasing for mortality, decreasing for growth and recruitment). Results of a recent study by Wiese et al. (1989) on two other pine species showed that artificial defoliation in October resulted in much higher mortality, and significantly less growth, than did the same treatment in January, April, or July, suggesting that there also might be a significant quadratic component (decreasing for mortality, increasing for other dependent variables).

The brown-spot control hypothesis predicts that juvenile pines, in particular, may benefit from spring burning (see Maple 1977, Grelen 1983). This effect, if it exists, should primarily influence recruitment, growth, and mortality, of small trees. Like the ambient temperature hypothesis, the brown-spot control hypothesis predicts significant quadratic trends for these three dependent variables. The difference between the two hypotheses is in the direction of the curves: the ambient temperature hypothesis predicts peak mortality and minimal growth and recruitment following spring and summer burning, while the brown-spot control hypothesis predicts just the opposite.

Some readers may be curious about why we used polynomial contrasts to analyze our data rather than other types of contrasts or paired comparisons. The answer, in part, pertains to the pseudoreplication problem mentioned earlier. Since all replicates of each seasonal burning treatment were burned on the same day, results of these burns do not represent independent determinations of the effect of a particular burning season, but rather reflect in large part conditions prevailing on the day of burning. The consequence of this is that the probability of falsely significant results is enhanced, especially if comparisons involve only a few of the possible seasonal burning treatments. This is especially likely during dry seasons (spring and fall), when burning under more hazardous conditions might tend to be avoided. For example, a significant contrast between October burning and April burning might result if the October plots were burned on a dry windy day and the April plots were burned on a calm humid day, though these conditions might not be generally representative of the prevailing conditions during those two months. Comparisons involving more than two burning seasons are less prone to this problem (i.e., because effects of individual burning days are averaged out), but there is still an enhanced possibility of Type II error (i.e., falsely accepting an untrue hypothesis). We chose to use polynomial contrasts to analyze our data in part because it seemed that this type of contrast would be least vulnerable to this sort of Type II error; that is, it seemed very unlikely that systematic seasonal patterns involving all eight burning dates could arise by chance, even if there might be some problem with pseudoreplication within particular burning seasons.

Sandhills oak dynamics.—Effects of season and frequency of burning on dynamics of sandhill oaks [i.e., on growth, mortality (topkill and complete kill), recruitment, change in basal area, and change in density, as defined previously] were tested using methods similar to those described above for pines. One minor difference was that because oak analyses (i.e., ANOVAs

TABLE 4. Product–moment correlations (r) among selected fire behavior variables and mortality of pines in different diameter (dbh) classes following experimental burns in the fourth treatment cycle. Results for total fuel consumed (not shown) are essentially identical to those for heat per area, since these variables are very highly correlated ($r = 0.99$).

	Fire temperature	Heat per area	% Fuel consumed	Fireline intensity	Pine mortality: 2–9.9 cm dbh	Pine mortality: 10–19.9 cm dbh
Heat per area	.47*					
Fuel consumed (%)	.59*	.76*				
Fireline intensity	−.04	.73*	.40*			
Pine mortality:						
2–9.9 cm dbh	.43*	.39*	.40*	.04		
10–19.9 cm dbh	.26	.48*	.23	.10	.18	
≥20 cm dbh	−.16	.21	−.07	.43*	.17	−.07

* Correlation significantly different from zero at $P < 0.05$.

TABLE 5. ANOVA (if the covariate is not significant) or ANCOVA (if the covariate is significant; $P < 0.05$) results of longleaf pine mortality for each of four diameter at breast height (dbh) size classes over the course of three prescribed-burn treatment cycles. Data were corrected for differences in sample size and arcsine transformed before analysis.

Source of variation	Diameter size class (cm dbh)															
	2–4.9				5–9.9				10–19.9				>20			
	df	ss	F	P	df	ss	F	P	df	ss	F	P	df	ss	F	P
Basal area in 1980	1	718.3	8.9	.03*												
Season of burning	7	933.7	1.7	NS	7	523.8	0.6	NS	7	180.5	0.4	NS	7	497.6	1.6	NS
Linear pattern	1	88.9	1.1	NS	1	35.4	0.3	NS	1	25.5	0.4	NS	1	44.3	1.0	NS
Quadratic pattern	1	1.6	<0.1	NS	1	86.5	0.7	NS	1	11.4	0.2	NS	1	<0.1	<0.1	NS
Frequency of burning	1	39.9	0.5	NS	1	166.8	1.3	NS	1	153.5	2.5	NS	1	17.9	0.4	NS
Habitat	1	1241.3	15.3	<.01*	1	82.0	0.6	NS	1	16.9	0.3	NS	1	13.2	0.3	NS
Season × Frequency	7	682.9	1.2	NS	7	546.8	0.6	NS	7	403.0	0.9	NS	7	276.7	0.9	NS
Season × Habitat	7	2215.4	3.9	NS	7	1929.1	3.9	NS	7	669.2	1.6	NS	7	578.9	1.9	NS
Frequency × Habitat	1	147.7	1.8	NS	1	<0.1	<0.1	NS	1	0.1	<0.1	NS	1	66.8	1.5	NS
Error (S × F × H)	6	486.5			7	929.3			7	427.7			7	308.6		

* $P < 0.05$.

and ANCOVAs) were limited to the sandhill plots, habitat was not included as a factor in these analyses. Other minor differences in analytical procedures were as follows: (1) Many oak recruits were observed to originate from stems cut at the start of the study. Thus, density of cut oak stems was included as an additional covariate in the ANCOVA of oak recruitment. (2) Since data on oak growth included observations from several different species, growth data for each species were converted to standard deviates before obtaining plot means; this prevented bias in favor of plots containing more stems of faster growing species. (3) Because the plots contained few oak trees ≥20 cm dbh, the two largest size classes (described above for pines) were combined for analyses of oak mortality data collected during the first recensus. Because of greatly reduced sample sizes in some plots, oak mortality data collected during the second recensus were not analyzed separately for different size classes.

As was done for pines, a priori orthogonal polynomial contrasts were used to test for trends in the effect of season of burning on oak dynamics. Two hypotheses were tested: (1) Negative effects of fire on oaks, as on pines, should be greatest following midsummer burns due to elevated ambient temperatures at this time of year (the ambient temperature hypothesis) and (2) oaks should be most vulnerable to fires in the spring, shortly after leaf expansion, when the trees are thought to be the most vulnerable physiologically (the tree physiology hypothesis). Both of these hypotheses predict significant quadratic contrasts ("increasing" for mortality, "decreasing" for growth, recruitment, and changes over time in basal area and density); they differ, however, in that the tree physiology hypothesis also predicts a significant negative linear trend (i.e., the combination of an increasing quadratic trend and a decreasing linear trend is a curve with the peak shifted somewhat to the left, that is, towards earlier burning dates).

Analyses: community-level changes

In addition to testing for effects of season and frequency of burning on population dynamics of oaks and pines, we also tested for effects of these factors on changes over time in tree species composition. This was accomplished by first converting the basal area and density data for each species into a synthetic "importance value" (IV, = relative basal area + relative density) and then ordinating the IVs using detrended correspondence analysis (DECORANA; see Ter Braak 1987 for a comprehensive discussion of ordination methods). Ordinations were run separately for each habitat due to a large difference in pretreatment species

TABLE 6. ANOVA or ANCOVA results of longleaf pine mortality for three size classes in the fourth prescribed-burn treatment cycle. Data were corrected for differences in sample size and arcsine transformed before analysis.

Source of variation	Diameter size class (cm dbh)											
	2–9.9				10–19.9				>19.9			
	df	ss	F	P	df	ss	F	P	df	ss	F	P
Basal area in 1987	1	184	6.29	.024*								
Season of burning	7	452	2.21	NS	7	116	.59	NS	7	298	3.38	.021*
Linear pattern	1	121	4.15	NS	1	<1	.02	NS	1	42	3.36	NS
Quadratic pattern	1	<1	.02	NS	1	16	.57	NS	1	56	4.47	.051*
Habitat	1	436	14.92	.002*	1	2	.07	NS	1	5	.42	NS
Season × Habitat	7	446	2.18	NS	7	107	.55	NS	7	83	.94	NS
Error (within cells)	15	439			16	444			16	202		

* $P < 0.05$.

TABLE 7. ANOVA or ANCOVA results of longleaf pine growth (measured as increments in diameter at breast height [dbh]) over the course of three treatment cycles. Because of significant habitat × covariate interactions, results are presented separately for sandhills (A) and flatwoods (B). Significant results ($P < 0.05$) are indicated with an asterisk.

		Diameter size class (cm dbh)								
		2–9.9			10–19.9			≥20		
Source of variation	df	ss	*F*	*P*	ss	*F*	*P*	ss	*F*	*P*
A) Sandhills										
1980 basal area	1	2.53		<.01*	2.39	15.8	<.01*	0.82	11.3	.02*
Season of burning	7	1.53	72.9	.02*	2.91	2.8	NS	1.27	2.5	NS
Linear pattern	1	<0.01	6.3	NS	0.29	1.9	NS	0.13	1.8	NS
Quadratic pattern	1	0.74	<0.1	<.01*	<0.01	<0.1	NS	0.19	2.6	NS
Frequency of burning	1	0.06	21.3	NS	0.13	0.9	NS	<0.01	<0.1	NS
Error (Season × Frequency)	6	0.21	1.7		0.91			0.44		
B) Flatwoods										
Season of burning	7	1.26	0.8	NS	2.55	1.1	NS	0.84	1.3	NS
Linear pattern	1	0.73	3.4	NS	0.90	2.7	NS	0.04	0.5	NS
Quadratic pattern	1	0.05	0.2	NS	0.03	0.1	NS	0.02	0.2	NS
Frequency of burning	1	0.16	0.8	NS	0.70	2.0	NS	0.61	6.8	.04*
Error (Season × Frequency)	7	1.52			2.38			0.63		

* $P < 0.05$.

composition. Each plot was entered twice in the ordination for its habitat, once using the pretreatment data and again using the recensus data. After ordinating the data in this way, the change in tree species composition for each plot was determined as the difference in ordination scores at the end of the first three treatment cycles (differences of this sort were calculated for each of the first three ordination axes). Finally, ANOVA and ANCOVA (including contrast analysis as described above) were used to test for effects of season and frequency of burning on species composition changes along each axis (see Bowman et al. 1988 and Wyant et al. 1991 for examples of similar analytical approaches).

RESULTS

Fire descriptions

Our fires (Table 3) were similar to other prescribed burns conducted in frequently burned pine savannas or flatwoods (e.g., Heyward 1938, Williamson and Black 1981, Nelson and Adkins 1988). In general, such fires are restricted to the ground surface and are characterized by low temperatures and intensities, and relatively rapid rates of spread (e.g., compare our results with Johnson 1992: Table 4.2). Like others (e.g., Albini 1976, Andrews and Rothermal 1982, Moreno 1989), we found that our various measures of fire behavior were not entirely independent. Fire temperature, which we measured at ground surface, was significantly correlated with fuel consumed, percent fuel consumed, and heat released per unit area (Table 4). These latter three variables were also highly correlated with fireline intensity, though the latter was not correlated with fire temperature (Table 4).

Despite our efforts to standardize burning conditions, we did detect some variability in both fire temperatures and intensities (Table 3). The data do indicate, however, that, following elimination of the annual burn treatments, almost all the area within a plot was burned during each fire (Table 3).

TABLE 8. ANCOVA results of recruitment of longleaf pine in the sandhills habitat over the course of three treatment cycles. Basal area is included as a covariate based on marginal significance.

Source of variation	df	ss	*F*	*P*
1980 basal area	1	12.7	4.3	.08
Season of burning	7	13.9	0.7	NS
Linear pattern	1	2.2	0.7	NS
Quadratic pattern	1	8.1	2.7	NS
Frequency of burning	1	4.4	1.5	NS
Error (Season × Frequency)	6	17.8		

* $P < 0.05$.

Dynamics of longleaf pine

Season of burn.—Previous hypotheses (ambient temperature, tree physiology, and brown-spot control hypotheses) regarding effects of season of burn on dynamics of longleaf pine were not well supported by results of this study. Omnibus *F* tests (i.e., tests of the general hypothesis that significant differences occurred among the means of the eight different season-of-burn treatments) were rarely significant (Tables 5–9), and quadratic and linear trends predicted by the three hypotheses did not materialize (Figs. 1–4). Results of these extensive tests, summarized in Table 10, reveal only two significant comparisons (out of >30 predictions). Thus, season of burning appeared not to influence most aspects of longleaf pine population dynamics.

Though most of the trends predicted by the three

TABLE 9. ANOVA results of changes in longleaf pine density and basal area over the course of three prescribed-burn treatment cycles.

Source of variation	df	Density			Basal area		
		SS	F	P	SS	F	P
Season of burning	7	1107	.76	NS	.90	.71	NS
Linear pattern	1	213	1.02	NS	<.01	<.01	NS
Quadratic pattern	1	7	.03	NS	.09	.49	NS
Frequency of burning	1	18	.09	NS	.16	.90	NS
Habitat	1	5832	28.00	.001*	6.33	34.50	.001*
Season × Frequency	7	5041	3.46	NS	.83	.65	NS
Season × Habitat	7	3514	2.41	NS	2.71	2.14	NS
Error (S × F × H)	7	1459			1.27		

* $P < 0.05$.

hypotheses were not significant (see previous paragraph), two predictions were supported by the data: (1) As predicted by the ambient temperature hypothesis, mortality of large (i.e., ≥20 cm dbh) trees during the fourth treatment cycle did indeed follow an increasing quadratic trend (Fig. 1G), and (2) growth of sandhill pines <10 cm dbh also followed an increasing quadratic trend (Fig. 2A), as predicted by the brown-spot control hypothesis. Upon close inspection, however, it was apparent that neither of these results provided strong support for either hypothesis.

Concerning the increasing quadratic trend in large-tree mortality during the fourth treatment cycle, notice first of all that during this treatment cycle (as in the previous three treatment cycles), mortality of trees in this size class was very low regardless of the season of burning (i.e., even at the highest point on the curve, average mortality was <1%; see Fig. 1G). Thus, despite its statistical significance, this trend was most likely insignificant biologically. Furthermore, this same pattern was not present in the mortality data for this size class collected over the first three treatment cycles (Fig. 1D). [In fact, there were no significant correlations between censuses for any size class in effects of burning season on mortality ($-0.56 < r < 0.47$, $n = 8$ burning seasons, $P > 0.05$)]. Therefore any quadratic relationship between season of burn and mortality of large longleaf would not appear to be a temporally consistent effect of growing-season burns.

A similar observation can be made for the other "confirmed" prediction, i.e., the significant quadratic trend in growth of sandhill pines <10 cm dbh. In this case, the trend was not consistent between habitats (i.e., flatwoods pines in the same size class showed no evidence of such a growth trend; Table 7, Fig. 2d), suggesting that any such trend, if it exists, is unique to the sandhills habitat. Furthermore, other predictions of the brown-spot control hypothesis (e.g., that minimal mortality of small trees should be associated with growing-season burning) were not confirmed for either habitat (Figs. 1a, e). Thus, the actual existence of a brown-spot control effect, even for the sandhills habitat, is doubtful.

Frequency of burn.—Frequency of burning, the other experimental factor, also appeared to have only a minor influence on longleaf pine demography. Effects of frequency of burn on pine mortality (Fig. 5) were not significant for any size class over the first three treatment cycles (Table 5). Likewise, there were no significant effects of burning frequency on growth of sandhill pines (Table 7A; Fig. 6, left), pine recruitment (Table 8; Fig. 7), or temporal changes in pine densities (Table 9; Fig. 8A) and basal areas (Table 9; Fig. 8B).

The only real effect of frequency of burn was on growth of pines in the flatwoods. For flatwood pines in each of the three size classes, growth was lower in biennially burned than in annually burned plots (Fig. 6D–F). This difference was significant for the largest dbh-size class (Table 7B).

Fire temperature and intensity.—Fire temperature and intensity data were collected (or, in the case of fireline intensity, reconstructed) for six burning dates (24 individual fires) during the fourth treatment cycle. For the period covered by these fires, pine mortality in each size class was significantly correlated with at least one measure of fire behavior (Table 4). Interestingly, however, the size classes differed in the particular fire behavior variables most highly correlated with mortality (Table 4). Mortality in the smallest (2–9.9 cm dbh) size class was most highly correlated with fire temperature, though the correlations with percent fuel consumed and heat per area were also statistically significant. Mortality in the next largest size class (10–19.9 cm dbh) was correlated with total fuel consumed and with heat released per unit area. Finally, mortality in the largest size class (≥20 cm dbh) was significantly correlated only with fireline intensity.

Habitat and competition.—Habitat (i.e., location of longleaf pines in sandhills vs. flatwoods), competition (i.e., stand basal area), and interactions between these two factors, strongly influenced most aspects of longleaf pine dynamics.

The most noticeable effect of competition was on mortality of small trees. In both sandhill and flatwoods habitats, and over both the first three treatment cycles and the fourth treatment cycle, increasing stand basal area was significantly positively associated with mortality of longleaf pine trees in the smallest size class

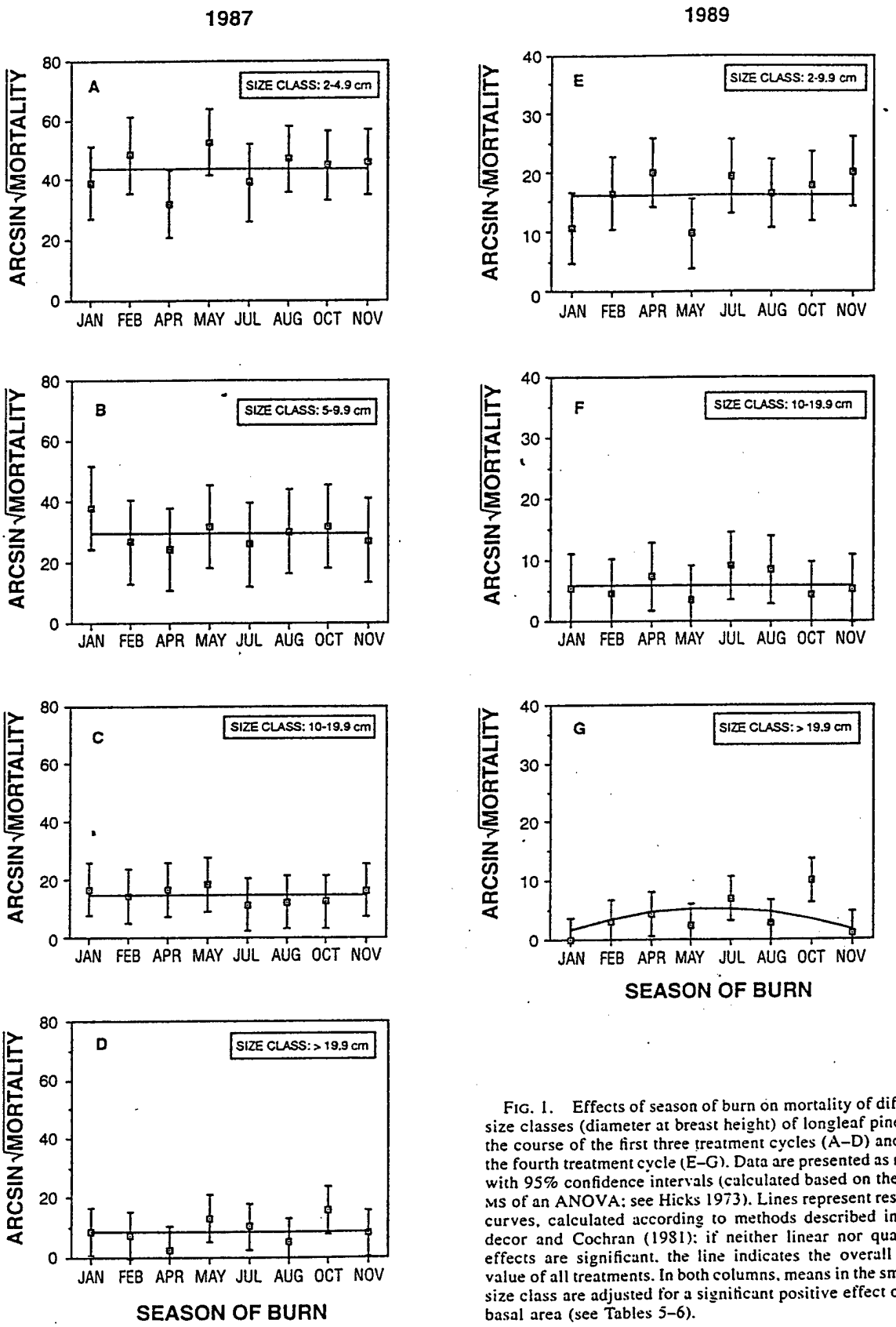


FIG. 1. Effects of season of burn on mortality of different size classes (diameter at breast height) of longleaf pine over the course of the first three treatment cycles (A–D) and over the fourth treatment cycle (E–G). Data are presented as means with 95% confidence intervals (calculated based on the error MS of an ANOVA; see Hicks 1973). Lines represent response curves, calculated according to methods described in Snedecor and Cochran (1981): if neither linear nor quadratic effects are significant, the line indicates the overall mean value of all treatments. In both columns, means in the smallest size class are adjusted for a significant positive effect of plot basal area (see Tables 5–6).

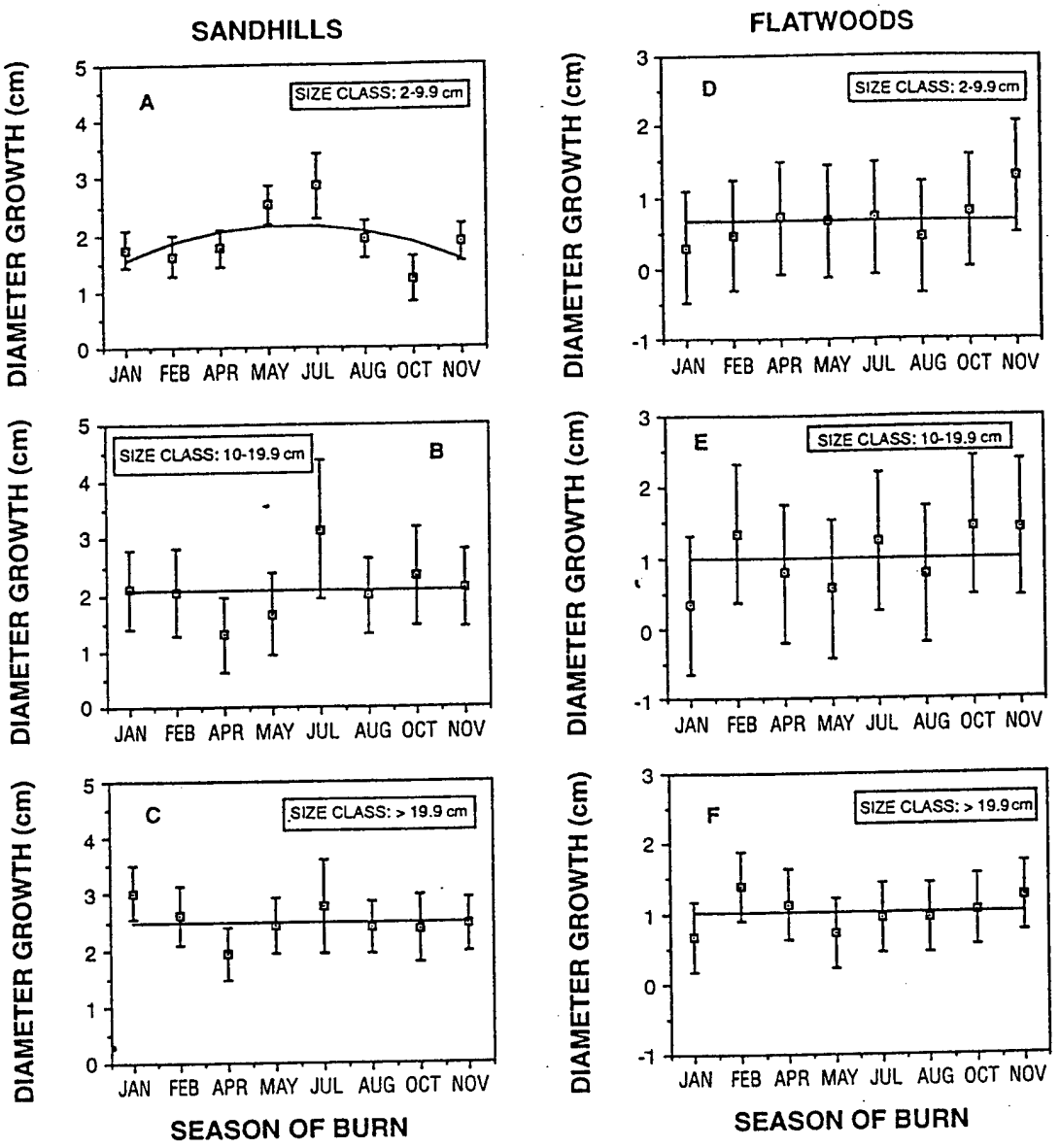


FIG. 2. Effects of season of burn on diameter growth of different size classes of longleaf pine in the sandhills (A–C) and flatwoods (D–F) over the course of the first three treatment cycles. Sandhills means are adjusted for a significant negative effect of plot basal area (see Table 7). Means, confidence limits, and curves are as described in Fig. 1 legend.

(r = 0.77 and 0.54 for the two between-census intervals; see Tables 5, 6 for degrees of freedom and F and P values). In the sandhills, increasing competition was also associated with significantly reduced diameter growth (of all size classes; see Table 7 and Fig. 9) and recruitment (Table 8, Fig. 10).

There were two important between-habitat differences in the demography of longleaf pine. First, rates of growth and recruitment were substantially lower in the flatwoods than in the sandhills (especially in plots with low basal areas; Figs. 9, 10). Second, rates of mortality in the smallest size classes, over both the first three treatment cycles (Fig. 11A) and the fourth treatment cycle (Fig. 11E), were significantly higher in flatwoods than in sandhills (Tables 5, 6). Low recruitment and high rates of small-tree mortality resulted in substantial declines in densities of longleaf pine in the flatwoods plots, while densities of sandhills pines remained essentially unchanged (Fig. 12A). Longleaf pine basal areas increased in both habitats, but the increase was much greater in the sandhills than in the flatwoods (Fig. 12B). Differences between habitats in both density changes and basal area changes were highly significant (Table 9). In general, longleaf pine populations in the sandhills appeared to be constant or increasing in density and to be influenced largely by intraspecific competition despite the regime of frequent burning. In contrast, flatwoods populations appeared in

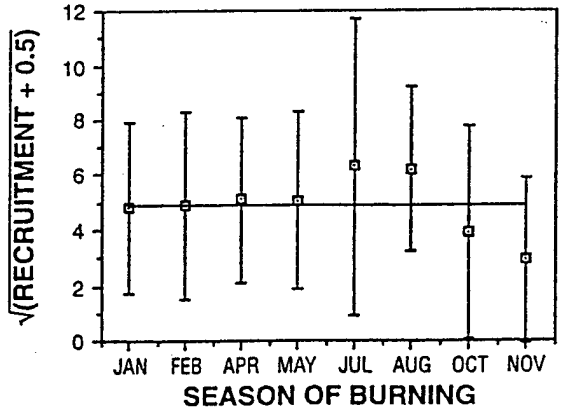


FIG. 3. Effects of season of burn on recruitment of longleaf pine (in stems/ha) into the smallest size class in the sandhills over the course of the first three treatment cycles. Seasonal means are adjusted for a marginally significant negative effect of plot basal area (see Table 8). Means, confidence limits, and curves are as described in Fig. 1 legend.

virtually all cases to be unstable and declining and to be much less affected by intraspecific competition.

Tree size.—Mortality and growth of longleaf pine were also influenced strongly by tree size. Mortality in both census periods declined noticeably with increases in tree size (Fig. 11) and larger trees usually grew faster than smaller ones (Fig. 9). In the sandhills, longleaf pine growth appeared to be strongly influenced by an interaction between tree size and level of competition: trees of all sizes grew at approximately equal rates in low-basal-area stands, but small trees grew more slowly than larger trees in stands with high basal areas (Fig. 9).

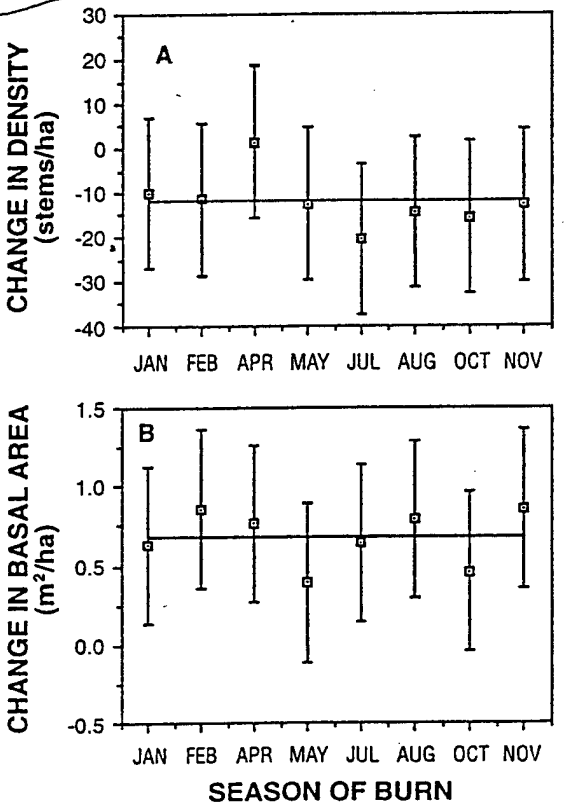


FIG. 4. Effects of season of burn on changes in density (A) and basal area (B) of longleaf pine over the course of the first three prescribed-burning treatment cycles. Means, confidence limits, and curves are as described in Fig. 1 legend.

Dynamics of sandhill oaks

Season of burn.—In contrast to the results presented above for longleaf pine, our data on oak population dynamics generally supported previous hypotheses (Tables 11–14, Figs. 13–16, summary in Table 15). Results on oak mortality in the sandhills habitat, in particular, strongly supported the tree physiology hypothesis. As predicted by this hypothesis, topkill (Figs. 13A–C, 14A) and complete kill (Figs. 13D–F, 14B) of sandhill oaks were highest in plots burned in April and May. Furthermore, increasing quadratic trends were observed for both dependent variables over both the first three treatment cycles and the fourth treatment cycle (Tables 11, 12; the single exception was for complete kill in the smallest size class during the first census interval). Although the linear component was not significant, residuals for the two spring-burning treatments were consistently above predicted means. Thus, the negative effect of burning early in the growing season on oak mortality appeared to be consistent over time, as well as among size classes.

Effects of season of burning on other aspects of the population dynamics of oaks in the sandhills were much less obvious. Oak growth, for example, was clearly not at all related to this factor (Fig. 15A, Table 13A). There was a significant overall effect (i.e., omnibus F test) of season of burning on oak recruitment (Table 13B), and mean oak recruitment in the spring-burned plots (April and May) was generally lower than in the other burning treatments (Fig. 15B). However, quadratic and linear effects were not significant (Table 13B), indicating that effects of burning season on oak recruitment did not vary predictably over the course of the year.

High rates of mortality and low rates of oak recruitment in spring-burned plots resulted in substantial declines in density and basal area of oaks in these plots over the first three treatment cycles (Fig. 16). These changes were reflected in significant quadratic and linear trends in the effect of season of burn on both of these variables (Table 14).

Frequency of burn.—Effects of frequency of burning on oak dynamics were limited largely to topkill and to resultant changes in density and basal area. Topkill of oaks (Fig. 17) in the smallest size class was significantly greater in biennially burned plots than in annually burned plots (Table 11), and a similar, but nonsignificant, tendency occurred for oaks in the next largest size class (Table 11). There was no discernible ef-

TABLE 10. Summary of tests of a-priori predictions of effects of season of burning on dynamics of longleaf pine, St. Marks National Wildlife Refuge, Florida. For details, see Tables 5–9 and Figs. 1–4.

Hypothesis	Response variable	Predicted trend	Result*
Ambient temperature	mortality	increasing quadratic	tc 1–3: sc 1–4 n tc 4: sc 1–2 n, sc 3 y
	growth	decreasing quadratic	tc 1–3: sc 1–3 n
	recruitment	decreasing quadratic	tc 1–3: n
	basal area change	decreasing quadratic	tc 1–3: n
	density change	decreasing quadratic	tc 1–3: n
Tree physiology	mortality	linear increase	tc 1–4: all sc n
		decreasing quadratic	tc 1–4: all sc n
	growth	linear decrease	tc 1–3: sc 1–3 n
		increasing quadratic	tc 1–3: sc 1 sh n†, fw n sc 2–3 n
	recruitment	linear decrease	tc 1–3: n
		increasing quadratic	tc 1–3: n
	basal area change	linear decrease	tc 1–3: n
		increasing quadratic	tc 1–3: n
	density change	linear decrease	tc 1–3: n
		increasing quadratic	tc 1–3: n
Brown spot control	mortality	decreasing quadratic	tc 1–3: sc 1 n tc 4: sc 1 n
	growth	increasing quadratic	tc 1–3: sc 1 sh y, fw n
	recruitment	increasing quadratic	tc 1–3: n

* Key to abbreviations: tc = treatment cycle (see *Methods: Experimental design*); n = predictions not confirmed (i.e., test results not statistically significant, or significant but with the wrong trend); y = prediction confirmed (test result significant, and trend as predicted); sc = size class (see *Analyses: Pine dynamics* for size class definitions during different time periods); sh = sandhill habitat; fw = flatwoods habitat (see *Methods: Study area* for habitat descriptions).

† Note that in the case of the tree physiology hypothesis, a significant quadratic trend is listed as a confirmed prediction only if it is coupled with the appropriate linear trend.

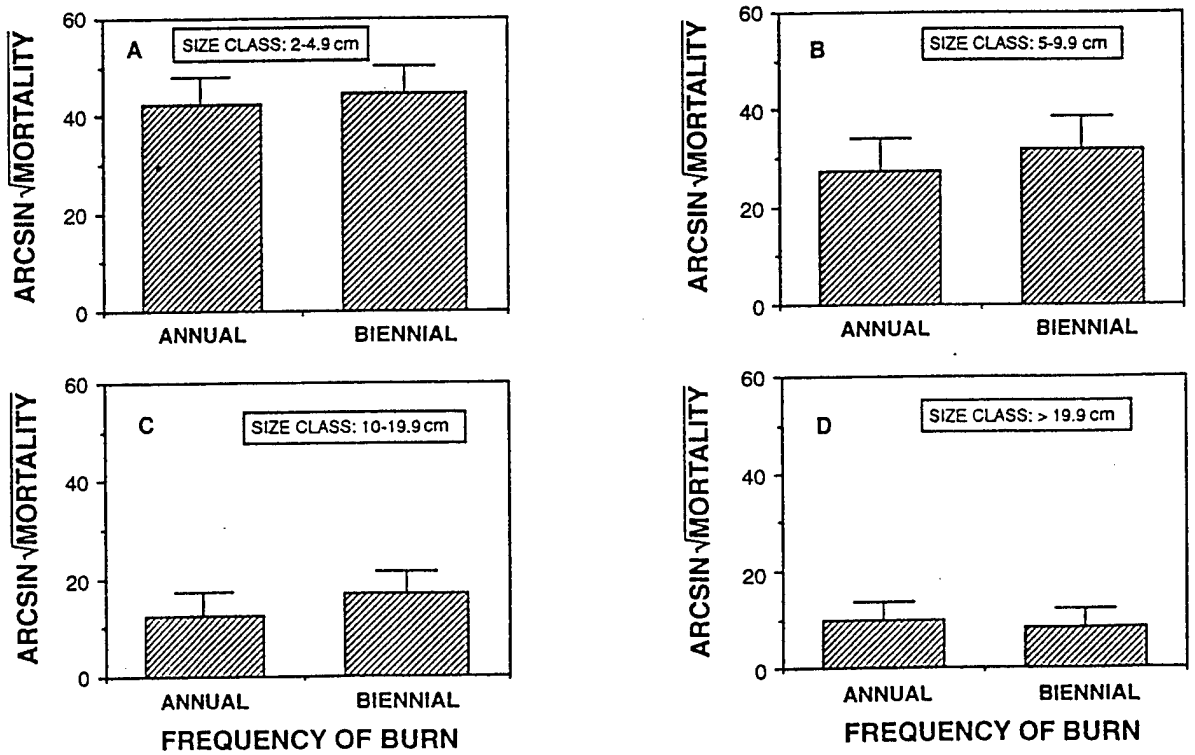


FIG. 5. Effect of frequency of burn on mortality of different size classes of longleaf pine over the course of the first three treatment cycles. Means in the smallest size class are adjusted for a significant positive effect of plot basal area (see Table 5). Means and confidence intervals are as described in Fig. 1 legend.

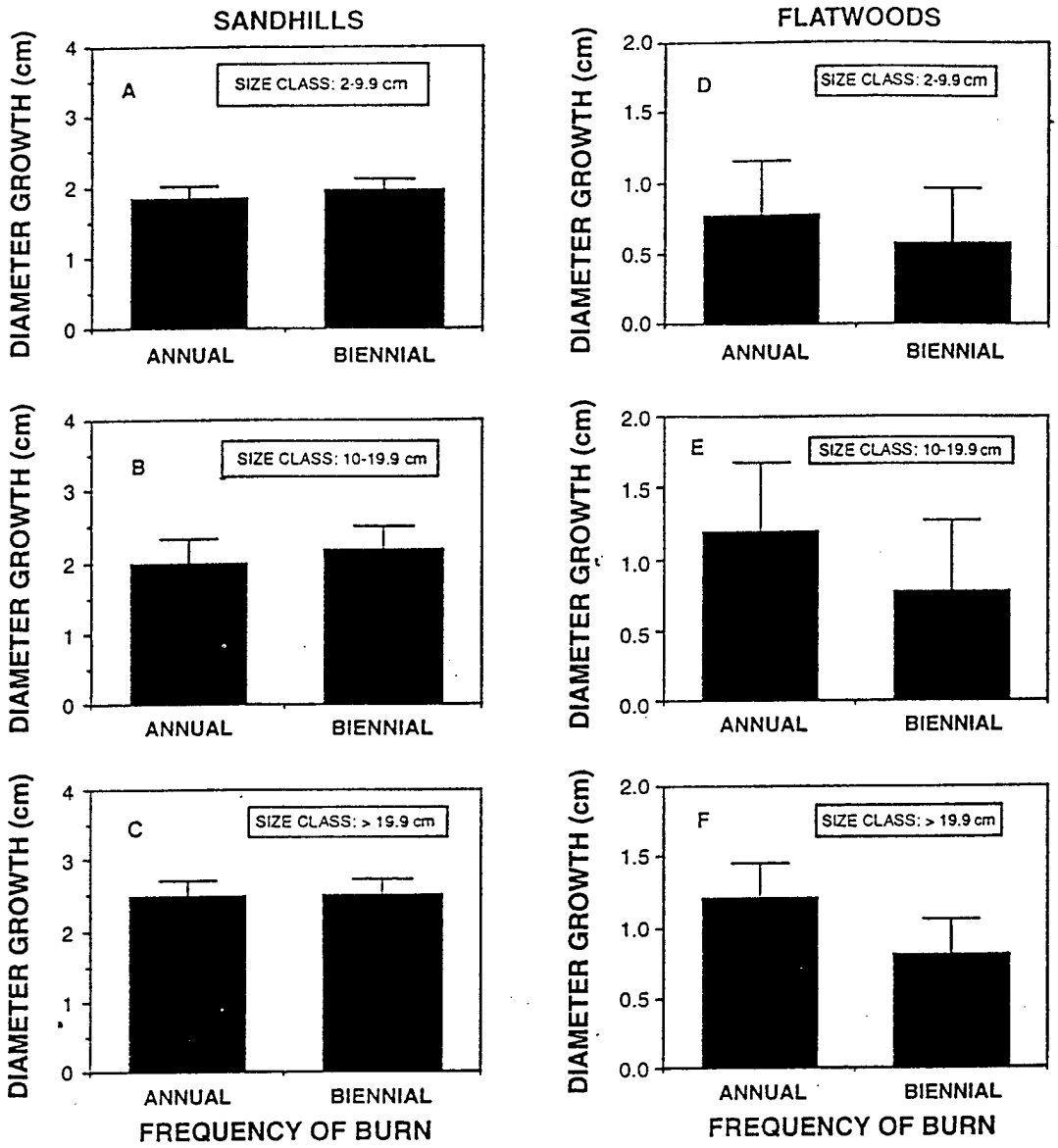


FIG. 6. Effect of frequency of burn on growth of different size classes of longleaf pine in the sandhills (A–C) and flatwoods (D–F) over the the course of the first three treatment cycles. Sandhills means are adjusted for a significant negative effect of plot basal area (see Table 7). Means and confidence intervals are as described in Fig. 1 legend.

fect of frequency of burning on topkill in the largest size class (Fig. 17C) or on complete kill in any size class (Fig. 17D–F). Frequency of burning also had no significant effects on growth or recruitment of oaks in the sandhills (Table 13). As a result of greater topkill among smaller size classes, the density of oaks (Fig. 18A) declined significantly (Table 14) in biennially burned plots (an average of >30 stems between 1980 and 1987), while only minor declines occurred in plots burned annually (<5 stems on average over the same time period). There was also a greater decline in oak basal area in the biennially burned plots than in the annually burned plots (Fig. 18B), although this difference was not statistically significant (Table 14).

Fire temperature and intensity.—Oak topkill during the fourth treatment cycle (i.e., February–October burns) was significantly correlated with both fire temperature ($r = 0.71$, $n = 12$ fires, $P < 0.01$, see also Fig. 19A) and percentage of fuel consumed ($r = 0.59$, $n = 12$ fires, $P < 0.05$). Correlations with other measures of fire intensity were not significant ($r < 0.23$, $n = 12$, $P > 0.05$). Correlations were also not significant ($r < 0.26$, $n = 12$, $P > 0.05$) between oak complete kill and any measure of fire behavior (e.g., Fig. 19B).

The relatively high correlation between oak topkill and fire temperature suggests that this latter variable may be responsible for much of the observed effect of burning season on topkill. This conclusion is supported

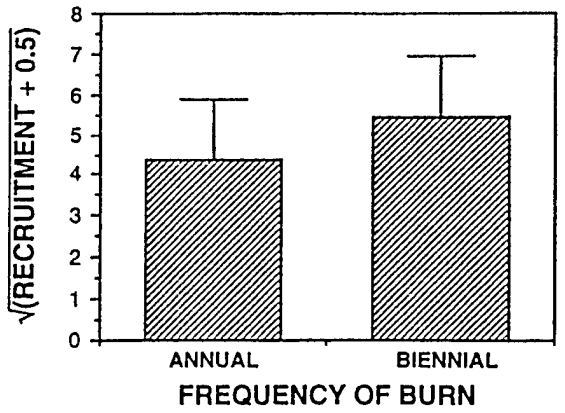


FIG. 7. Effect of frequency of burn on recruitment of longleaf pine (in stems/ha) into the smallest size class in the sandhills over the course of the first three treatment cycles. Seasonal means are adjusted for a marginally significant effect of plot basal area (see Table 8). Means and confidence intervals are as described in Fig. 1 legend.

by a graph of the data showing that even the spring-burned plots fall close to the linear regression of topkill on temperature (Fig. 19A). However, since three of the four spring-burned plots fall above this line, compared to only two of the eight plots burned at other seasons, there may still be some residual effect of spring burning.

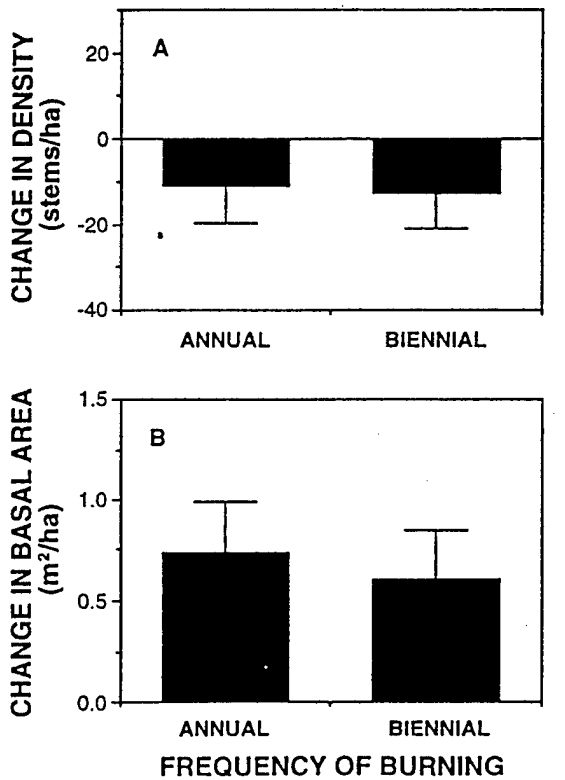


FIG. 8. Effect of frequency of burn on changes in density (A) and basal area (B) of longleaf pine over the course of the first three treatment cycles. Means and confidence intervals are as described in Fig. 1 legend.

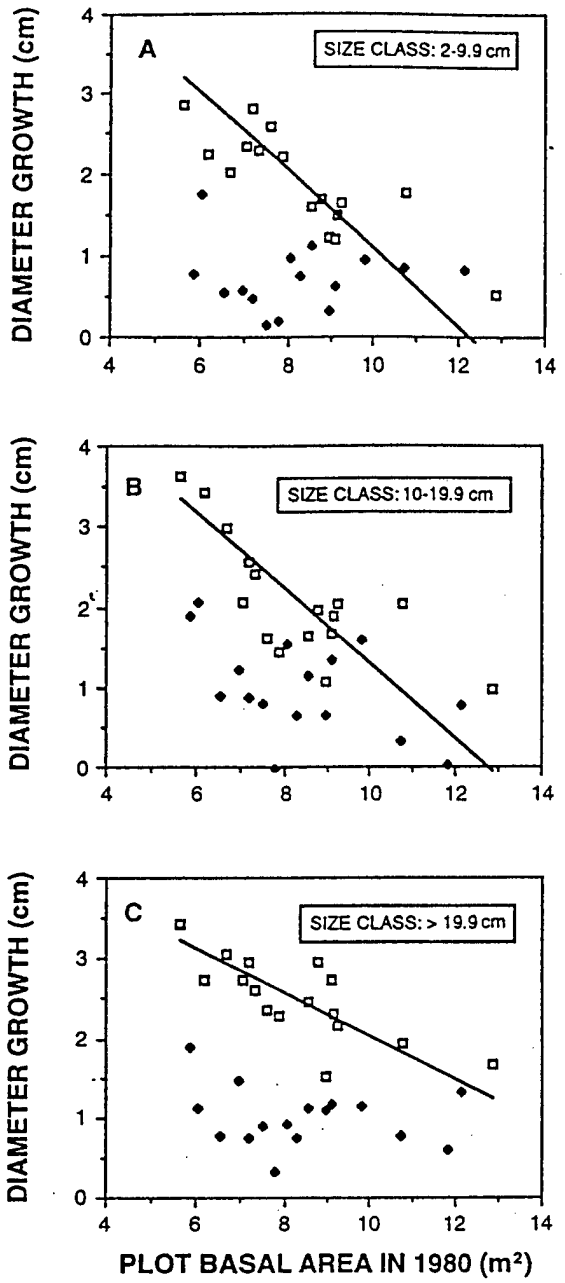


FIG. 9. Effect of plot basal area on diameter growth of longleaf pine in the sandhills (□) and flatwoods (♦) over the the course of the first three treatment cycles. Best fit regression lines for the sandhills were determined from ANCOVA (see Snedecor and Cochran 1981). Regressions for the flatwoods were not statistically significant and are not shown.

Competition.—In general, oaks appeared to be less susceptible than pines to effects of increasing competition. Whereas virtually all aspects of sandhill longleaf pine demography were significantly related to plot basal area, basal area did not significantly affect topkill, complete kill, or growth of the oaks ($F < 3.3$, df = 1, 6, $P > 0.05$). However, there were weak ($0.10 \leq r^2 \leq 0.21$), but significant (Table 13B, Table 14), negative

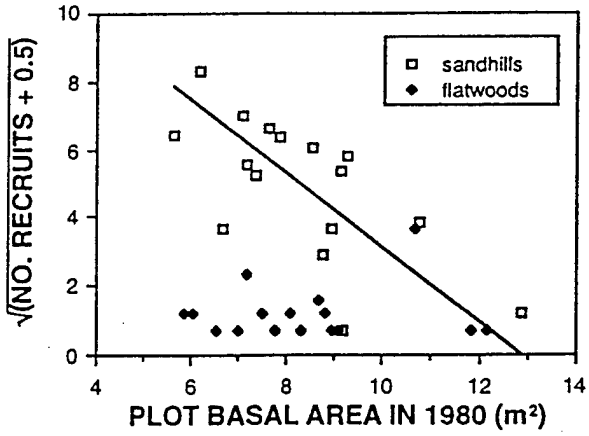


FIG. 10. Effect of plot basal area on recruitment of longleaf pine (in stems/ha) in sandhills (□) and flatwoods (◆) over the course of the first three treatment cycles. The best fit regression line for the sandhills was determined from ANCOVA (see Snedecor and Cochran 1981). The regression for the flatwoods was not statistically significant and is not shown.

effects of plot basal area on oak recruitment, and on changes over time in oak densities and basal areas.

Tree size.—Unlike pines, which became more resistant to fires as they increased in size, resistance of oaks to burning (or, at least, to the frequent burns in this study) did not increase with tree size (Fig. 17). In fact, because they were less likely to resprout and therefore more likely to be completey killed, larger oak trees, especially during the early growing season, were actually less resistant to fires than were smaller oak trees.

Changes in tree composition

Sandhills.—Plots of scores from the DECORANA ordination (Fig. 20) indicate several weak (i.e., eigenvalues range between 0.081 and 0.016 for the first three axes) gradients in composition of woody species in the sandhills. The first axis (Fig. 20A) represents a gradient from plots distinguished by higher relative abundances of three deciduous oak species (*Quercus margaretta, Q. laevis,* and *Q. incana*) and *P. palustris,* to plots with higher relative abundances of three common species of evergreen oaks (*Q. geminata, Q. hemisphaerica,* and *Q. myrtifolia*). In addition to differences in the relative abundances of deciduous and evergreen oaks, plots were also distinguished by differences in the relative abundances of two species of ericaceous shrubs (Fig. 20A). *Vaccinium arboreum* and *V. stamineum* each had high Axis-1 scores, and were thus associated more closely with evergreen than deciduous oaks.

A second, orthogonal, vegetation gradient was identified by Axis 2 of the ordination. In this case, the gradient extends from plots with greater relative abundances of *Pinus palustris, Q. margaretta,* and *Q. geminata* to plots where these species are somewhat less important relative to *Q. laevis, Q. incana,* and *Q. myrtifolia* (Fig. 20A). Relative abundances of the two *Vaccinium*s also change along this indirect gradient; both are associated with *Q. laevis, Q. incana* and *Q. myrtifolia* towards the lower end of the second axis (Fig. 20A).

The third ordination axis (Fig. 20B) illustrates a gradient from plots with high relative abundances of *Q. hemisphaerica, Q. laevis,* and to some extent *P. palustris* to plots where these species are less abundant and several other species of oaks (*Q. margaretta, Q. incana, Q. geminata, Q. falcata, Q. myrtifolia*) and the two species of *Vaccinium* are more abundant (Fig. 20B).

Vegetation gradients along the first (i.e., most important) ordination axis were unrelated to the experimental burning treatments. The average plot score along Axis 1 did not change significantly over time (i.e., a paired t test found no significant change between 1980 plot scores and 1987 plot scores: df = 1, 7; F = 0.50, $P > 0.05$) as would have been expected if the burning treatments were having an effect. Furthermore, neither season (Fig. 21A) nor frequency (Fig. 21D) of burn had significant effects on differences in individual plot scores over the first three treatment cycles (Table 16). Instead, site scores along Axis 1 appeared to be related mostly to a subtle difference in physical environments between two parts of the study area. Plots with low Axis 1 scores occurred relatively close to one another in compartment 11 of the refuge, while plots with high Axis-1 scores occurred farther away in compartment 7 (Fig. 20C).

Though the first axis of the ordination appeared unrelated to the experimental burning treatments, this was not true of the other two axes. Plot scores along the Axis 2 increased in a highly significant fashion between 1980 and 1987 (paired t test: df = 1, 7, F = 56.54, $P < 0.001$). Furthermore, these changes were significantly related to season of burning (Table 16). The effect of season of burning on vegetation change along this axis followed a quadratic trend with the greatest change observed after spring burning (Fig. 21B). Since this change was towards higher Axis-2 scores, it suggests that the effect of spring burning is to increase the abundances of longleaf pine, *Q. margaretta,* and *Q. geminata* relative to the abundances of *Q. incana, Q. laevis, Q. hemisphaerica, Q. myrtifolia,* and the two species of *Vaccinium.*

Increases in plot scores along the second axis occurred both for annually and biennially burned plots (Fig. 21E) and frequency of burn had no significant effects on plot scores along this axis (Table 16). However, changes in vegetation along the third ordination axis were significantly related to frequency (Fig. 21F), but not season (Fig. 21C), of burn (Table 16). Biennial burning resulted in a positive change along this ordination axis, indicating a shift toward higher relative abundances of longleaf pine, *Q. laevis,* and *Q. hemisphaerica,* and reduced relative abundances of *Q. incana, Q. margaretta, Q. geminata, Q. myrtifolia,* and

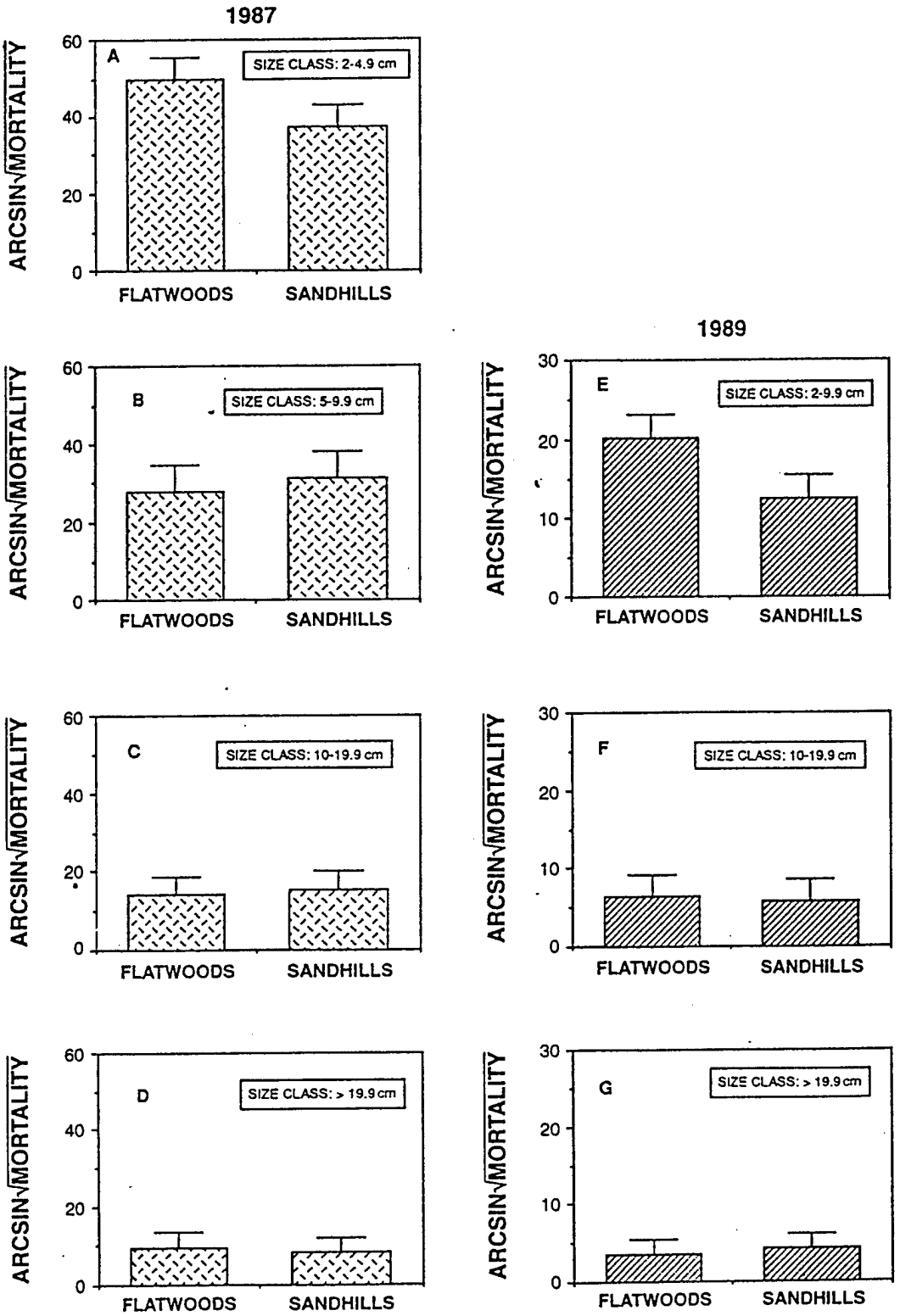


FIG. 11. Mortality of different size classes of longleaf pine in sandhills and flatwoods over the course of the first three treatment cycles (A–D) and over the fourth treatment cycle (E–G). Means in the smallest size class are adjusted for a significant positive effect of plot basal area (see Tables 5–6). Means and confidence intervals are as described in Fig. 1 legend.

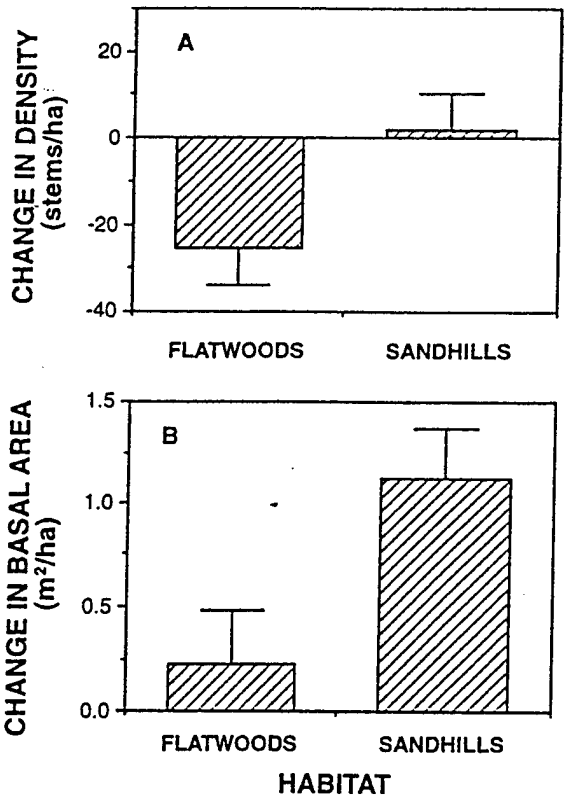


FIG. 12. Changes in density (A) and basal area (B) of longleaf pine in sandhills and flatwoods over the course of the first three treatment cycles. Means and confidence intervals are as described in Fig. 1 legend.

the species of *Vaccinium*. Annual burning resulted in reduced third axis scores, indicating changes in vegetation composition in the opposite direction.

Flatwoods.—The DECORANA ordination of the flatwoods tree data identified one comparatively strong vegetation gradient (eigenvalue = 0.34 for the first axis) and one weak but possibly meaningful gradient (eigenvalue = 0.06 for the second axis). Species separation along the remaining axes was so minor as to preclude meaningful interpretation (eigenvalues ≤0.01). Based on the plot of species scores (not shown, but available on request), the strong gradient was characterized as a transition from wet flatwoods codominated by slash or pond pine to dry flatwoods with longleaf the only pine present, along with a significant oak component. Tree species composition averaged across all plots did not change significantly along either of the first two axes during the first three treatment cycles ($F \leq 1.99$, df = 1, 7, $P > 0.05$). Neither season nor frequency of burn had significant effects on changes over time in individual plot scores (Table 17).

TABLE 12. ANOVA results of sandhill oak (*Quercus laevis, Q. incana, Q. margaretta*) topkill (A) and complete kill (B) in the fourth prescribed-burn treatment cycle. Data were corrected for sample size differences and arcsine transformed prior to analysis.

Source of variation	df	SS	*F*	*P*
A) Topkill				
Season of burning	7	2334	3.5	.05*
Linear pattern	1	163	1.7	NS
Quadratic pattern	1	1485	15.5	<.01*
Error (within cells)	8	769		
B) Complete kill				
Season of burning	7	1044	3.5	.05*
Linear pattern	1	137	3.2	NS
Quadratic pattern	1	389	9.0	.02*
Error (within cells)	8	346		

* $P < 0.05$.

DISCUSSION

Population dynamics of longleaf pine

Season of burn.—Results of our study did not support previous hypotheses regarding effects of seasonality of fire on population dynamics of southern pines.

TABLE 11. ANOVA results of sandhill oak (*Quercus laevis, Q. margaretta, Q. incana*) topkill (A) and complete kill (B) over the course of the first three prescribed-burn treatment cycles. Data were corrected for differences in sample size and arcsine transformed prior to analysis.

Source of variation	df	Diameter size class (cm dbh) 2–4.9 SS	*F*	*P*	5–9.9 SS	*F*	*P*	>9.9 SS	*F*	*P*
A) Topkill										
Season of burning	7	3553	12.2	<.01*	2553	3.8	.05*	3875	3.6	.06
Linear pattern	1	150	3.6	NS	171	1.8	NS	44	0.3	NS
Quadratic pattern	1	458	11.0	.01*	901	9.4	.02*	1729	11.3	.01*
Frequency of burning	1	326	7.8	.03*	399	4.2	NS	7	<0.1	NS
Error (S × F)	7	292			673			1070		
B) Complete kill										
Season of burning	7	1040	1.5	NS	2085	3.5	NS	3948	2.5	NS
Linear pattern	1	14	0.1	NS	14	0.2	NS	9	<0.1	NS
Quadratic pattern	1	477	4.7	NS	1273	15.0	<.01*	1669	7.4	.03*
Frequency of burning	1	8	0.1	NS	84	1.0	NS	19	0.1	NS
Error (S × F)	7	711			595			1590		

* $P < 0.05$.

TABLE 13. ANOVA and ANCOVA results of sandhill oak (*Quercus laevis, Q. incana, Q. margaretta*) growth (measured as increments in dbh) and recruitment over the course of three prescribed-burn treatment cycles.

Source of variation	df	ss	*F*	*P*
A) Growth				
Season of burning	7	1.72	.38	NS
Linear pattern	1	.43	2.21	NS
Quadratic pattern	1	.15	.78	NS
Frequency of burning	1	.01	.01	NS
Error (S × F)	7	1.36		
B) Recruitment				
1980 basal area	1	39.57	20.08	.004*
Season of burning	7	73.60	5.33	.029*
Linear pattern	1	9.47	4.81	NS
Quadratic pattern	1	0.05	0.03	NS
Frequency of burning	1	2.22	1.13	NS
Error (S × F)	6	11.83		

* $P < 0.05$.

All of these hypotheses (the "ambient temperature hypothesis," the "tree physiology hypothesis," and the "brown-spot control hypothesis") predict that fire effects will vary with the season of burn. No such effects were evident as clear, consistent trends for any size class of pines in either sandhill or flatwoods habitats.

We suggest three reasons why results of our study are not consistent with data and ideas used to develop these prior hypotheses. (1) Longleaf pine, widely acknowledged as the most fire resistant of the southern pines (see review of Landers 1991) may be particularly tolerant of fires regardless of when they occur (see also Ferguson 1955 and *Discussion: Fire behavior*). Longleaf pine, therefore, may be resistant to detrimental effects of late growing season burning or experimental defoliation documented for other southern pines (e.g., Ferguson 1961, Weise et al. 1989). (2) Though high ambient temperatures are sometimes mentioned as one possible cause for high levels of observed crown scorch (e.g., Cooper and Altobelli 1969, Villarubia and Chambers 1978), Van Wagner's (1973) theoretical relationship between ambient temperature and crown scorch has never been thoroughly validated. Van Wagner's (1973) own attempt at verification was unsuccessful, and he concluded that, at least within the range of temperatures included in his study, fireline intensity alone could account for most of the observed variation. Our results suggest that for longleaf pine as well, variation in fire behavior (temperature or intensity) may be much more important than ambient temperature or season of burning for predicting population dynamics. Considered within this context, isolated observations of elevated mortality or reduced growth following growing-season fires (e.g., Cary 1932, Boyer 1990) appear to be largely coincidental and do not constitute strong evidence for detrimental effects of growing season fires. Boyer's (1987) study, which documented slightly (but significantly) higher levels of longleaf pine mortality following summer burning (8.0% compared to 4.3% for burns conducted in winter and spring), continues to provide the only truly reliable evidence for the possible existence of an ambient-temperature effect on longleaf pine. It is important to note, however, that the negative effect of summer burning in this study was confined to only one of three summer burn treatments (i.e., the study was a factorial design with varying methods of supplemental understory control) suggesting that even in this case the effect of season of burning was probably rather minor compared to other influences on fire behavior. (3) Prior studies supporting the brown-spot control hypothesis were conducted mainly on "grass stage" seedlings, while our results were limited to stems ≥2 cm dbh. Thus, we cannot state unequivocally that this effect did not occur in our study; we can, however, conclude that even if there were some such effect it apparently had little impact on sapling recruitment or on the overall dynamics of longleaf pine populations.

Based on our evaluation of the literature (Streng et al., *in press*) and analyses of our data, we conclude that there is no *consistent* seasonal pattern to the vulnerability of longleaf pine to fire damage in frequently burned sandhill or flatwood habitats. We emphasize the word "consistent" because there may well be seasonal effects in any given year resulting from droughts, unusually hot or intense fires, or other exceptional conditions, but such effects are not likely to be constant from one year to the next. This conclusion helps to explain the widespread dominance of longleaf pine in original old growth savannas and woodlands of the southeastern Coastal Plain. Indeed, if longleaf pine were highly vulnerable to summer burning, as has been suggested, it could not have dominated vast areas of presettlement forest under a natural regime of frequent summer burning. There is also an important implication for habitat management: as long as fuel accumulations

TABLE 14. ANCOVA results of changes in density (A) and basal area (B) of sandhill oaks (*Quercus laevis, Q. incana, Q. margaretta*) over the course of three treatment cycles.

Source of variation	df	ss	*F*	*P*
A) Density				
Basal area in 1980	1	3140	14.1	.009*
Season of burning	7	21307	13.7	.003*
Linear pattern	1	4011	18.0	.005*
Quadratic pattern	1	1890	8.5	.027*
Frequency of burning	1	3144	14.1	.009*
Error (S × F)	6	1336		
B) Basal area				
Basal area in 1980	1	.094	18.6	.005*
Season of burning	7	.337	9.5	.007*
Linear pattern	1	.046	9.0	.024*
Quadratic pattern	1	.032	6.2	.047*
Frequency of burning	1	.008	1.5	NS
Error (S × F)	6	.031		

* $P < 0.05$.

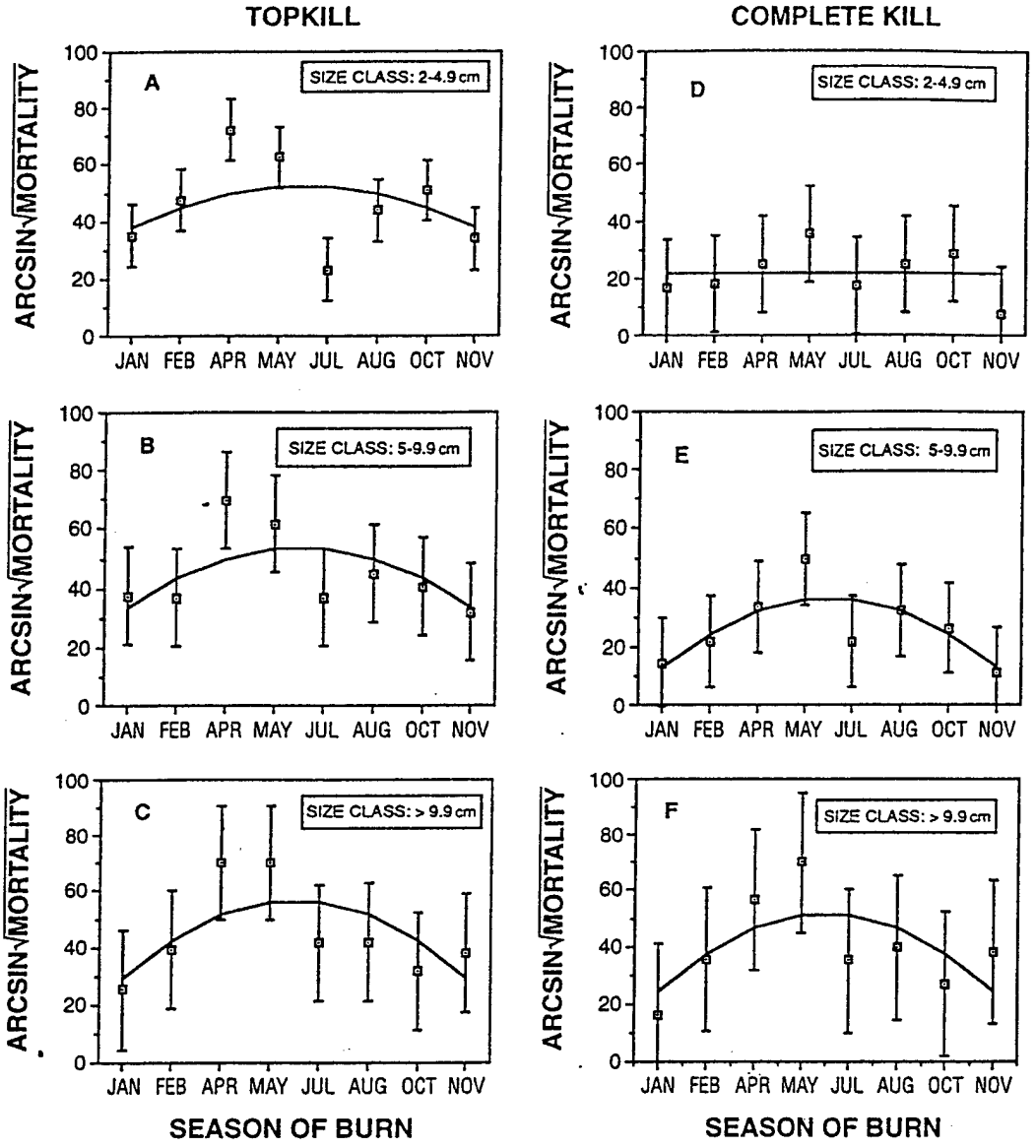


FIG. 13. Effect of season of burn on topkill (A–C) and complete kill (D–F) of oaks in sandhills over the course of the first three treatment cycles. Means, confidence intervals, and curves are as described in Fig. 1 legend.

are low and dangerous fire weather conditions are avoided (see also Bradshaw et al. 1983), prescribed (i.e., managed) burning can occur at any season without excessive risk to either canopy pines or new regeneration.

Frequency of burn.—Like season of burn, frequency of burn (i.e., the contrast between annual and biennial burning) had little impact on longleaf pine population dynamics. This suggests, as did our results on season of burning (see previous section) that longleaf pine is rather insensitive to minor fluctuations in the regime of frequent burning once characteristic of old growth forests in the region. One significant result was that growth of pines in the flatwoods, but not the sandhills, was significantly reduced by biennial burning (i.e., compared to the annually burned plots). This effect was most likely a result of greater fuel accumulations (see Table 1), and hence greater crown scorch (fire related defoliation), in the less frequently burned plots. [In woodlands/savannas of the Coastal Plain of the southeastern USA, there is ordinarily a strong relationship between accumulated fuel and fire temperatures/intensities (see e.g., Heyward 1938, Hare 1961, Williamson and Black 1981, and Platt et al. 1991).]

Fire behavior.—We have already noted that fire behavior may be a more important influence on population dynamics of longleaf pine than either season or frequency of burning. This finding is consistent with the results from a number of other studies which also emphasize the importance of fire intensity and related

variables (e.g., crown scorch) for predicting tree growth or mortality (Gruschow 1952, Cooper and Altobellis 1969, Van Wagner 1973, Villarubia and Chambers 1978, Greene 1987, Ryan and Reinhardt 1988). Our results do, however, demonstrate the extreme tolerance of longleaf pine, even to relatively intense surface fires. For example, Ryan and Reinhardt (1988), documented post-fire tree mortalities in the western USA ranging from 16% to 88%, depending on the species. Mortality rates for longleaf pine documented in the present study were considerably lower than this (except in the smallest size classes), even though burning techniques and the range of fireline intensities were comparable between the studies.

Another interesting feature of our results was the suggestion that effects of the different fire behavior variables might vary with tree size. The smallest trees appeared most vulnerable to high fire temperatures and other indicators of heat flux directly at the ground surface (e.g., percent fuel consumption, heat released per unit area). This may indicate that girdling (i.e., complete cambial death around the entire circumference of the stem), rather than crown scorch, may have been mostly responsible for killing these trees. Larger pine trees have thicker bark than smaller trees and are generally more resistent to girdling (Wade 1986, Wade and Johansen 1986*b*, Greene 1987). In our study, large longleaf pine trees appeared relatively insensitive to fire temperatures and other measures of heat flux near the ground surface. Instead, mortality of these trees was related mostly to fireline intensity. Since fireline intensity is generally correlated mostly with crown scorch or other canopy effects (Van Wagner 1973, Wade 1986, Ryan and Reinhardt 1988), it appears likely that high levels of crown scorch may have been responsible for killing the few large pine trees that died during our study.

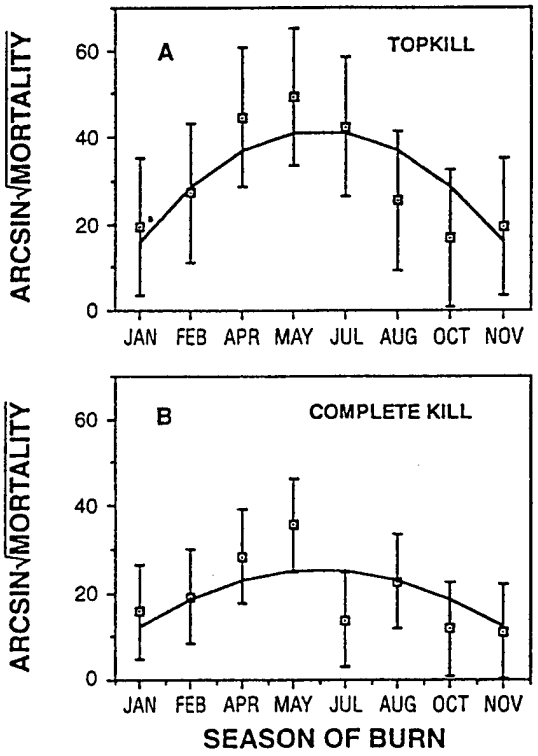


FIG. 14. Effect of season of burn on topkill (A) and complete kill (B) of oaks in sandhills over the fourth treatment cycle. Means, confidence intervals, and curves are as described in Fig. 1 legend.

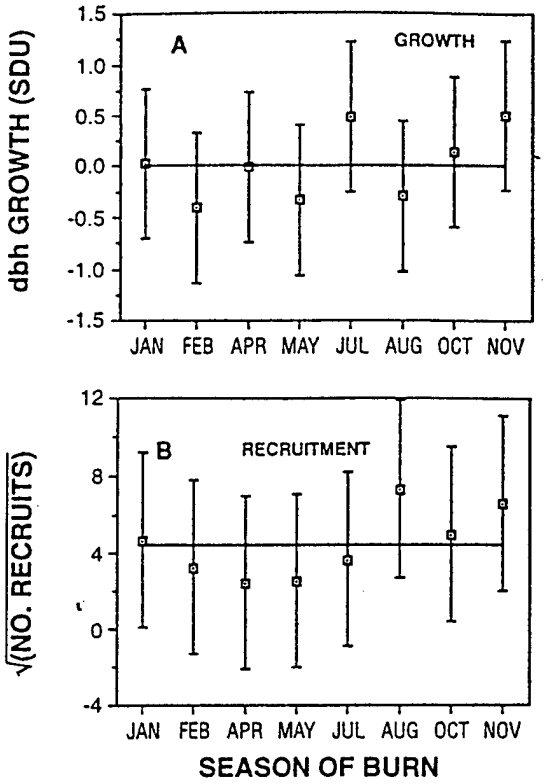


FIG. 15. Effect of season of burn on growth (A) and recruitment (B) of oaks in sandhills over the course of the first three treatment cycles. Data shown in (A) were derived by converting growth of each oak species to standard deviation units (SDUs) for that species and then averaging across species to obtain plot means (see *Analyses: Sandhills oak dynamics*). Means, confidence intervals, and curves are as described in Fig. 1 legend.

Habitat.—In addition to the above-mentioned differences between habitats in the effect of frequency of burning on pine growth, there were several other important differences between sandhill and flatwoods habitats in the population dynamics of longleaf pine. These differences, including less recruitment, as well as much higher mortality rates for small trees, consistently suggested that the flatwoods were a more stressful environment than the sandhills for longleaf pine. In fact, declining densities in all flatwoods plots suggest that the combination of a stressful environment and frequent fires could (if the experiment is continued),

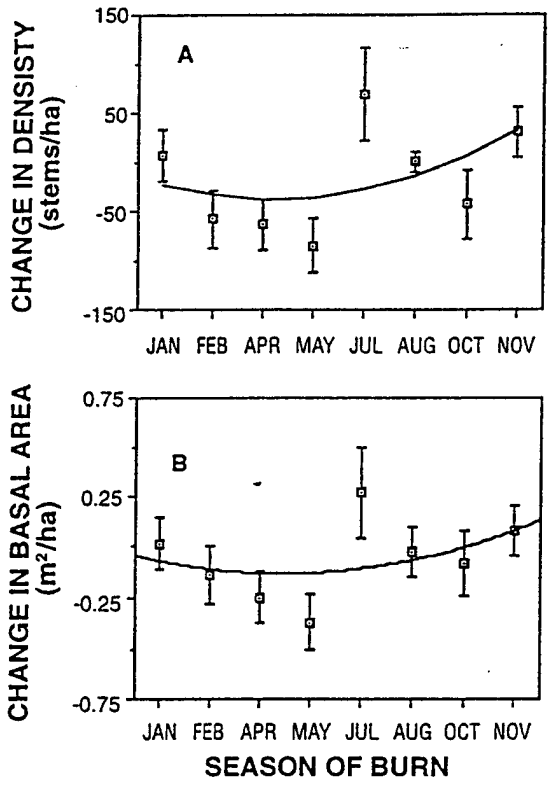


FIG. 16. Effect of season of burn on changes in density (A) and basal area (B) of oaks in sandhills over the course of the first three treatment cycles. Means, confidence intervals, and curves are as described in Fig. 1 legend.

eventually result in almost complete disappearance of longleaf pine from these plots.

It may be instructive to consider in more detail the reasons for declining longleaf pine populations in the flatwoods habitat. Prior studies (Wahlenberg 1946, Ferguson 1961, Maple 1975), and the results of our own study, emphasize that vulnerability of longleaf pine to fire generally declines with increasing size. An exception occurs during height growth (the transition between the grass and small sapling stages), when a secondary peak in post-fire mortality sometimes occurs (see Maple 1975, Rebertus et al., *in press*). Because we have shown (see also Bruce 1951) that juvenile growth rates, and in fact tree growth rates generally, are much lower in the flatwoods (presumably because of harsher environmental conditions, such as waterlogged soils, but possibly also because of more intense competition from groundcover vegetation) it follows that longleaf pines in the flatwoods spend more time in these vulnerable juvenile life stages than do longleaf pines in the sandhills. Juvenile longleaf pine in more stressful flatwoods (such as those that flood frequently) may even grow so slowly that, under a regime of frequent fire, they are unable to reach a fire-resistant size before being killed.

We suggest that this restriction on regeneration, produced by the interaction between juvenile life history attributes, burning regime, and environmental characteristics, may have produced very low densities of

TABLE 15. Summary of tests of a-priori predictions concerning effects of season of burning on dynamics of sandhill oaks (*Quercus laevis, Q. incana, Q. margaretta*), St. Marks National Wildlife Refuge, Florida. For details, see Tables 11–14 and Figs. 13–16.

Hypothesis	Response variable	Predicted trend	Result*
Ambient temperature	topkill	increasing quadratic	tc 1–3: sc 1–3 y tc 4: y
	complete kill	increasing quadratic	tc 1–3: sc 1 n, sc 2–3 y tc 4: y
	growth	decreasing quadratic	tc 1–3: n
	recruitment	decreasing quadratic	tc 1–3: n
	basal area change	decreasing quadratic	tc 1–3: y
	density change	decreasing quadratic	tc 1–3: y
Tree physiology	topkill	increasing quadratic	tc 1–3: sc 1–3 y tc 4: y
		decreasing linear	tc 1–3: sc 1–3 n tc 4: n
	complete kill	increasing quadratic	tc 1–3: sc 1 n, sc 2–3 y tc 4: y
		decreasing linear	tc 1–3: sc 1–3 n tc 4: n
	growth	decreasing quadratic	tc 1–3: n
		increasing linear	tc 1–3: n
	recruitment	decreasing quadratic	tc 1–3: n
		increasing linear	tc 1–3: n
	basal area change	decreasing quadratic	tc 1–3: y
		increasing linear	tc 1–3: y
	density change	decreasing quadratic	tc 1–3: y
		increasing linear	tc 1–3: y

* Key to abbreviations: tc = treatment cycle (see *Methods: Experimental design*); n = prediction not confirmed (i.e., test result not statistically significant, or significant but with the wrong trend); y = prediction confirmed (test result significant and trend as predicted); sc = size class (see *Analyses: Sandhills oak dynamics* for size class definitions during different time periods).

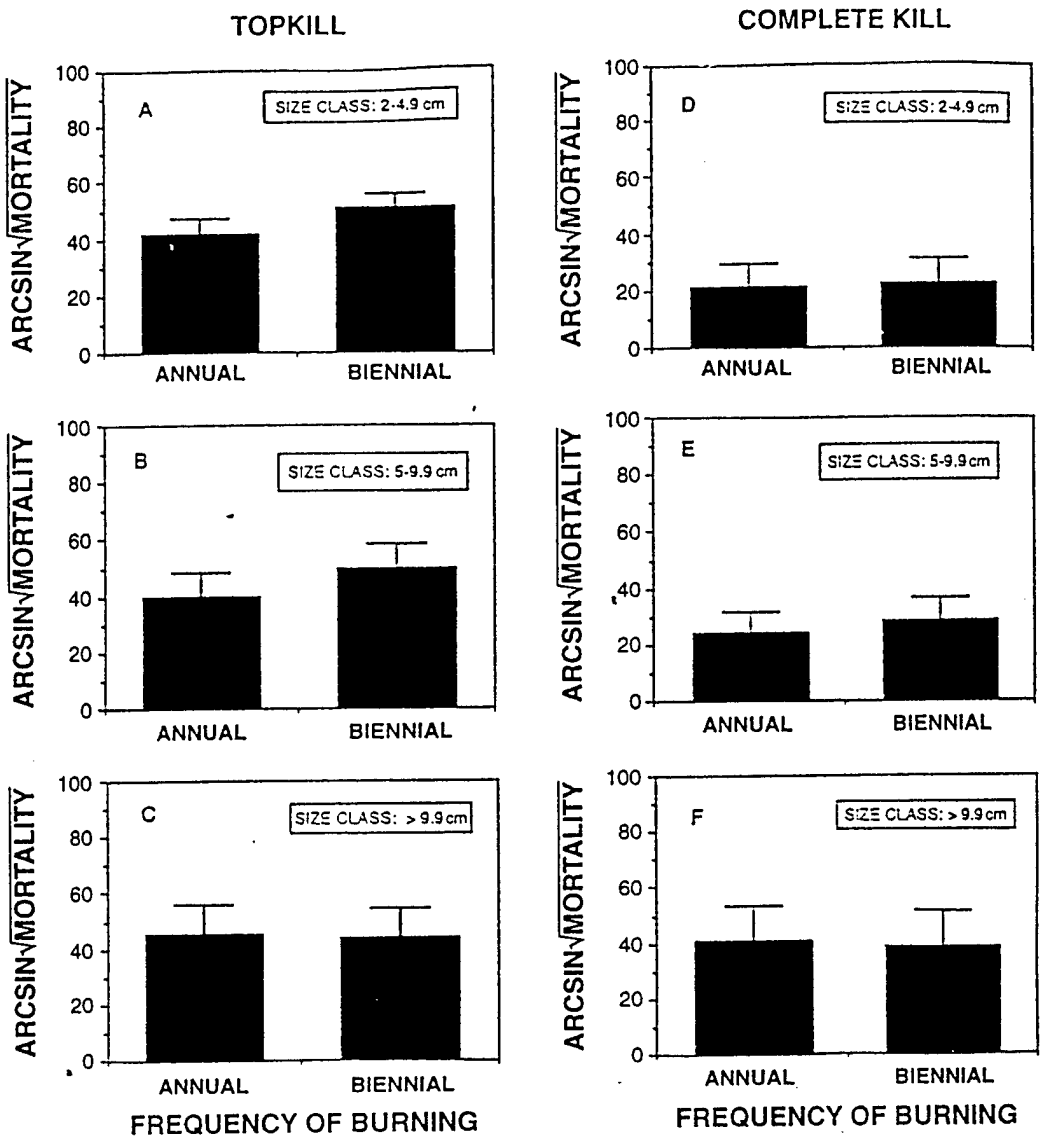


FIG. 17. Effects of frequency of burn on topkill (A–C) and complete kill (D–F) in three size classes of oaks in sandhills over the first three treatment cycles. Means and confidence intervals are as described in Fig. 1 legend.

longleaf pine in presettlement flatwoods. Variable fire frequencies that included periodic longer fire-free intervals probably enabled longleaf pine to invade and persist in flatwoods habitats. While others have emphasized the potential importance of interactions between disturbance regime and plant life history characteristics (e.g., Noble and Slatyer 1980, Keeley 1981, Keeley and Keeley 1988, Rebertus et al., *in press*), we note here that the local environment can strongly modify such interactions. [For a similar example of the interacting effects of environment and fire limiting the distribution of trees in a different habitat, see Barton (1993).]

In addition to the above theoretical considerations, our results on habitat related differences in dynamics of longleaf pine also have important practical implications. Of fundamental importance is the suggestion that techniques or practices developed for one habitat or environment may produce very different effects in another, even superficially rather similar, habitat. In the present case, it is quite clear that annual or biennial burning would maintain or even enhance longleaf pine populations in the sandhills, but would not accomplish the same objective in the flatwoods. Lower fire frequencies or, at the least, occasional extended fire-free intervals would be necessary for recruitment of longleaf pines in the flatwoods.

Competition.—Competition strongly influenced the population dynamics of longleaf pine (especially in the sandhills, where regeneration was not limited environmentally). This finding is consistent with results from the forestry literature (Wahlenberg 1946, Farrar, *in press*, and references therein) and with a recent model for the patch structure of old-growth longleaf pine for-

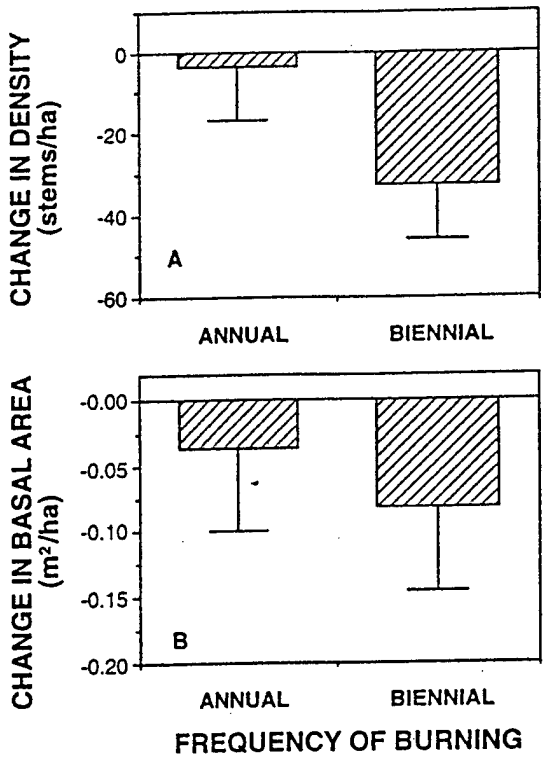


FIG. 18. Effects of frequency of burn on changes in density (A) and basal area (B) of oaks in sandhills over the first three treatment cycles. Means and confidence intervals are as described in Fig. 1 legend.

est developed for the Wade Tract, southeastern Georgia (see Platt and Rathbun, *in press*). When this model is applied to field data, significant effects of competition occur over distances up to 30 m from large trees. Moreover, as distances between neighbors decrease and the sizes of those neighbors increase, growth and survival of juveniles decreases markedly. Our current study demonstrates clearly that competition has much greater effects on pine dynamics (at least in the sandhills) than do seasonal and other minor differences in fire regimes. By comparison, the relative insensitivity of oaks to competition emphasizes the critical role of fire, especially during the spring, in limiting population sizes of these species.

Population dynamics of sandhill oaks

Though our results did not support previous hypotheses about effects of burning season on the population dynamics of longleaf pine, the results did tend to confirm the tree physiology hypothesis in the case of sandhill oaks. There was consistent evidence (especially from tree mortality patterns and consequent effects on basal areas and densities) that oaks were negatively affected by fires during the early growing season. This result supports findings of prior studies based on physiological data (Woods et al. 1959) and is consistent with other research demonstrating increased rates of hardwood topkill or complete kill after spring or summer burning (Hodgkins 1958 and references therein,

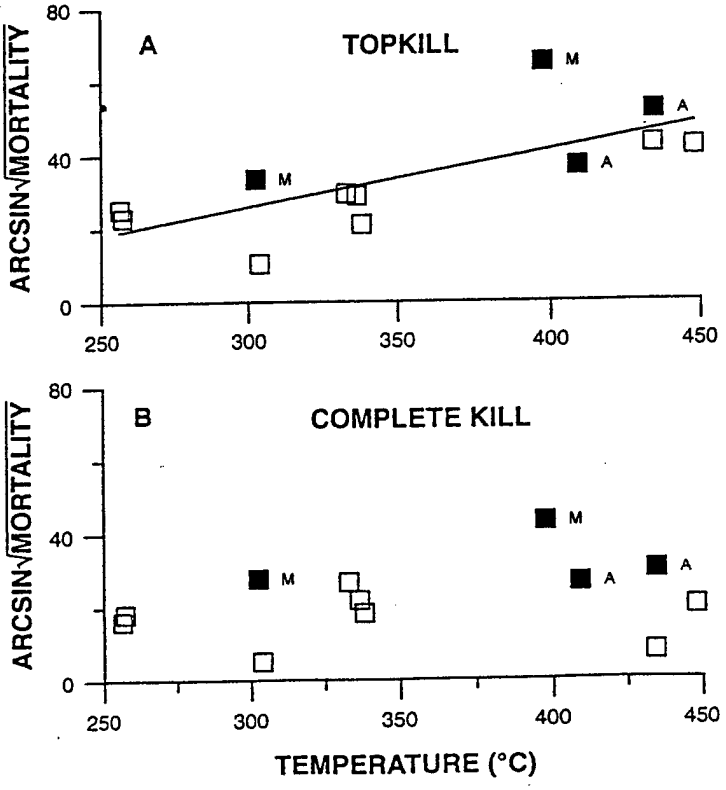


FIG. 19. Effects of fire temperatures on (A) topkill and (B) complete kill of oaks (*Q. laevis*, *Q. incana*, *Q. margaretta*) in the sandhills. ■ spring-burned plots (A=April, M=May); □ plots burned at other seasons. The correlation between temperature and complete kill was not significant ($P < 0.05$), so a line was not fitted to these data.

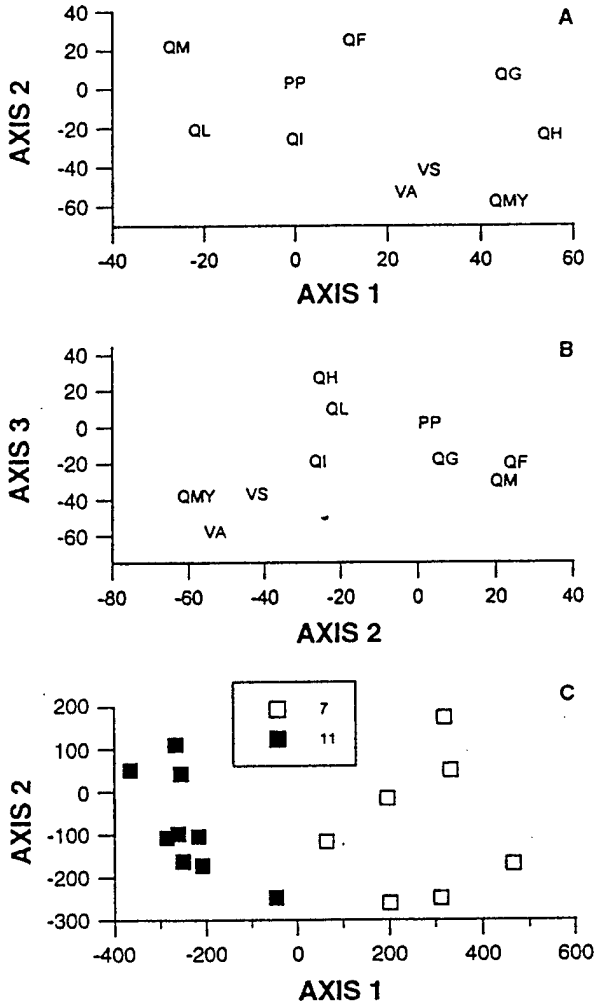


FIG. 20. DECORANA ordination results of woody species composition of sandhills. Species codes: PP=*Pinus palustris*, QF=*Quercus falcata*, QG=*Q. geminata*, QH=*Q. hemisphaerica*, QI=*Q. incana*, QL=*Q. laevis*, QM=*Q. margaretta*, QMY=*Q. myrtifolia*, VA=*Vaccinium arboreum*, VS=*V. stamineum*. In part C, plots located in compartments 7 and 11 of the St. Marks Wildlife Refuge are distinguished by □ and ■, respectively.

Ferguson 1961, Brender and Cooper 1968, Boyer 1990, 1993, Waldrop et al. 1992 and references therein).

The relatively strong correlation of oak topkill with fire temperature and intensity does implicate these variables as potentially important causes of the observed effect of season of burning on oak mortality. In north Florida, those environmental conditions that produce drier fuels and higher fire intensities are more likely to occur early in the growing season (Chen and Gerber 1990). However, the lack of fire behavior effects on oak complete kill suggests an important additional effect of tree physiology, particularly on the capacity of oaks to resprout after fires.

Community dynamics

Effects of seasonality of fire.—Results of the season-of-burn component of our long-term study have at least two important implications for understanding composition of longleaf pine savannas, at least as they existed prior to settlement. The first such implication concerns the role of spring fires in maintaining the dominance of longleaf pine over oaks. Presettlement fire regimes in the southeastern Coastal Plain probably were characterized by frequent spring fires, as suggested by evidence from lightning frequencies (Maier et al. 1979) and wildfire patterns (Komarek 1964, Robbins and Myers 1992). Our results showing sharp declines in densities of oaks in the sandhills following repeated spring burning thus strongly suggest that tree-sized oaks were a minor component (at best) of the vegetation in presettlement upland savannas. Longleaf pine would have comprised essentially monospecific stands of trees in any of these habitats where spring fires occurred frequently.

The second implication concerns the effect of temporal variability in seasonality of fire on maintenance of tree species diversity in longleaf pine savannas. Not all presettlement fires occurred in the spring. A significant proportion occurred later in the summer; data in Komarek (1964) suggest that any given area had a likelihood of burning in July and August about one-third as great as that in May and June. Occasional fires may also have occurred in the fall or winter as a result of rare thunderstorms or burning by Native Americans [Pyne 1982, e.g., Lawson 1709 (1967 edition):215]. Our results show clearly that oaks were much less susceptible to fires occurring outside of the early growing season. By reducing the frequency of fires to which oaks were susceptible, variability in fire season may have contributed to the persistence of oaks as trees in savannas dominated by longleaf pine (cf. Rebertus et al., *in press*).

Our finding of consistently lower sandhill oak mortality following non-spring fires also supports the hypothesis that a shift from growing- to dormant-season burning over the last several centuries (along with clear-cutting of large pines) has transformed many savannnas formerly dominated (in the canopy) almost entirely by longleaf pine into more or less closed woodlands or forests dominated largely by turkey and bluejack oaks (Means and Grow 1985, Myers 1990, Platt et al. 1991, Gilliam et al. 1993). This transformation has resulted in pronounced ecological changes, not only in the relative abundances of trees, but also in the diversity of understory herbs, which declines rapidly under an oak canopy (Lemon 1949, Vogl 1973, Streng 1979, Myers 1990).

Results of our study also suggest, however, that high oak densities may be rapidly reduced by frequent spring burning (if the ground cover is capable of carrying a fire). As few as three biennial fires in the spring greatly reduced the densities and basal areas of oaks in the sandhill plots. Such fires also enhanced flowering by a number of late-season flowering grasses and forbs (Platt et al. 1988*a*, 1991, Streng et al., *in press*). Fire-

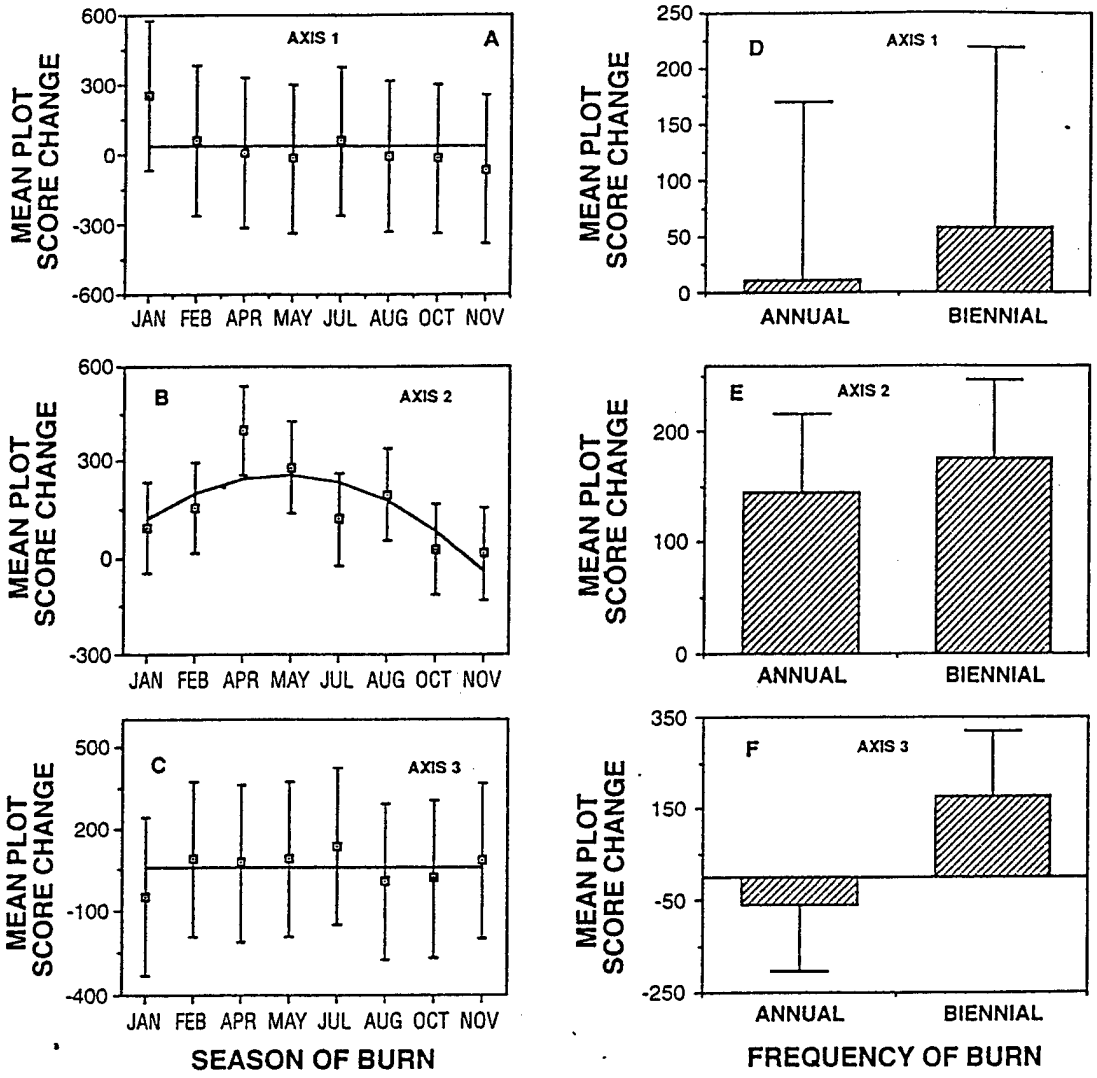


FIG. 21. Effects of season of burn (A–C) and frequency of burn (D–F) on changes in DECORANA ordination plot scores in the sandhills over the course of the first three treatment cycles. A,D: Axis 1; B,E: Axis 2; C,F: Axis 3. Means, confidence intervals, and curves are as described in Fig. 1.

stimulated flowering and/or reduced densities of mid-canopy oaks may also be responsible for recently observed increases in the abundance of the dominant forb, *Pityopsis graminifolia*, in the spring-burned sandhill plots (Brewer and Platt 1994*a*, *b*).

For the most part, ordination analyses indicated that spring burning significantly influenced tree species composition in the sandhills by increasing relative abundance of longleaf pine over oaks. However, one unexpected finding was the suggestion that sandhill oak species might differ in their tolerance to spring burning. In particular, it appeared that *Q. margaretta* and *Q. geminata* might be more tolerant of spring fires than other species of hardwoods. In the case of *Q. geminata*, this apparent resistance was most likely due not so much to greater fire tolerance per se, as it was to the tendency of this species to grow in dense clumps not often penetrated by fires (see Rebertus 1988, Guerin 1993). In contrast, high relative tolerance of *Q. margaretta* to fires in the spring may be a function of seasonal phenology. While *Q. laevis* and *Q. incana* leaf out in early spring and are therefore highly susceptible to both April and May burns, *Q. margaretta* often does not break dormancy until late April (J. S. Glitzenstein, *personal observation*). Consequently, this species may suffer less damage from early spring fires.

Effects of fire frequency and intensity.—Current theories suggest a rather straightforward relationship between fire frequency and tree species composition in upland habitats of the Southeastern Coastal Plain (Heyward 1939, Garren 1943, Komarek 1974, Veno 1976, Christensen 1981, Myers 1985, 1990, Myers and White 1987, Platt and Schwartz 1990, Platt et al. 1991, Rebertus et al., *in press*; however, see also Menges et al. 1993 for a somewhat more complex picture of long-term trends in the absence of fire). Highest fire fre-

TABLE 16. ANOVA results of changes in DECORANA ordination scores for the sandhill plots over the course of three prescribed-burning treatment cycles.

Source of variation	df	ss	F	P
	Axis 1			
Season of burning	7	133691	0.52	NS
Linear pattern	1	80198	2.17	NS
Quadratic pattern	1	16144	0.44	NS
Frequency of burning	1	8978	0.24	NS
Error (S × F)	7	58130		
	Axis 2			
Season of burning	7	235821	4.61	0.03*
Linear pattern	1	46295	6.33	0.04*
Quadratic pattern	1	97717	13.36	0.01*
Frequency of burning	1	3844	0.53	NS
Error (S × F)	7	51186		
	Axis 3			
Season of burning	7	48206	0.24	NS
Linear pattern	1	1857	0.06	NS
Quadratic pattern	1	11881	0.41	NS
Frequency of burning	1	228484	7.88	0.03*
Error (S × F)	7	203046		

quencies are predicted to favor longleaf pine over all other tree species; somewhat less frequent fires are predicted to favor mixtures of pines and the more fire tolerant hardwoods (e.g., sandhill oaks on dry sites); and complete fire suppression is predicted to produce a major shift in dominance toward fire intolerant, but more shade tolerant vegetation. While our comparisons of effects of annual and biennial burning did not test the complete range of fire frequencies that are covered by this hypothesis, they suggested that, at least toward the high end of the fire frequency spectrum, relationships between fire frequency and woody species dominance may be more complicated than previously hypothesized. Such complications appear to result from differences in fire intensities produced by variations in fuel loads at different fire frequencies.

In contradiction to the prevailing hypothesis, results of our ordination analyses indicated that increasing the fire return interval slightly at the high frequency end of the fire frequency gradient increased the abundance of pines relative to hardwoods. This is because oak trees in the sandhills experienced greater topkill, and hence greater declines in density, from biennial than from annual burns. In addition, mortality was lower for tree-sized pines than tree-sized oaks under regimes of biennial compared to annual fires. In southeastern pine forests, longer intervals between fires typically result in greater fuel accumulations (Table 1; Sackett 1975) and hotter and more intense fires (e.g., compare results of Heyward 1938, Hare 1961, and Williamson and Black 1981). Tree-sized pines are more tolerant of intense fires than are tree-sized hardwoods (Greene 1987; also our own *Results*). More intense fires associated with slightly less frequent burns thus favor pines over oaks by selectively eliminating the latter.

We note that increased abundances of pines relative to oaks resulting from increased fire return times (and hence more intense fires) are a result of increases in the topkill of oaks. Biennial burns did not result in increased complete kill of sandhill oaks relative to annual burns. As a result of their clonal nature, sandhill oaks might be considered more tolerant than pines of high intensity fires. The ability of oaks to remain as shrubs in the ground cover and grow into trees during long intervals free of growing-season fires was used to suggest mechanisms whereby clonal oaks could persist in a fire regime involving frequent fires, but variable return times (Rebertus et al., *in press*). We also note that hardwood sprouts are favored by the same burning regime that reduces densities of tree-sized individuals of these same species (Waldrop et al. 1992 and earlier papers, cited therein, describing the long-term burning study at the Santee Experimental Forest, near Charleston, South Carolina). Increased topkill and increased regeneration can only occur in stands characterized by fires erratic over space and/or time, where tree-sized hardwoods are able to become established in the first place (Rebertus et al., *in press*). Such patterns, characteristic of oaks in the sandhills, increase the difficulty of predicting changes in vegetation composition given complicated spatio-temporal variability in fire regimes (see also Noble and Slatyer 1980, Keeley 1981, Streng and Harcombe 1982, Rebertus et al., *in press*).

Relationships between pines and oaks.—Longleaf pines and sandhill oaks respond to the same aspects of the upland Southeastern Coastal Plain environment, but in different ways. Fires are essential for persistence of both longleaf pines and sandhill oaks, which tend to be replaced by less fire tolerant species of hardwoods if fire exclusion occurs. Very different attributes enhance survival of fires by pines and oaks, however

TABLE 17. ANOVA results of changes in DECORANA ordination scores for the flatwoods plots over the course of three prescribed-burning treatment cycles (between 1980 and 1987).

Source of variation	df	ss	F	P
	Axis 1			
Season of burning	7	97.8	0.38	NS
Linear pattern	1	0.3	0.01	NS
Quadratic pattern	1	3.4	0.10	NS
Frequency of burning	1	6.2	0.17	NS
Error (S × F)	7	253.8		
	Axis 2			
Season of burning	7	4947.8	0.93	NS
Linear pattern	1	289.7	0.38	NS
Quadratic pattern	1	407.4	0.54	NS
Frequency of burning	1	576.0	0.76	NS
Error (S × F)	7	5304.0		
	Axis 3			
Season of burning	7	1601.9	3.17	NS
Linear pattern	1	1.1	0.01	NS
Quadratic pattern	1	12.6	0.17	NS
Frequency of burning	1	10.6	0.15	NS
Error (S × F)	7	505.9		

(Rebertus et al., *in press*). In addition, there are strong suggestions of fire facilitation in pines (see Williamson and Black 1981, Platt et al. 1988*b*, 1991). Thus, the dynamics of tree populations in upland longleaf pine savannas might reflect interactions among trees that have a long evolutionary history involving frequent fire, but that are sensitive to different aspects of the environment.

Results of our study suggest, however, that stable mixtures of longleaf pines and sandhill oaks are unlikely. If fires occur frequently early in the growing season, the relative abundance of trees shifts rapidly toward longleaf pine, to the virtual exclusion of oaks. The oaks persist in the ground cover, however, as clonal shrubs, perhaps indefinitely (especially if there are spatial or temporal irregularities in the fire regimes). If fires occur frequently later in the growing season, the relative abundance shifts toward oaks. Although longleaf pine is not directly excluded, the formation of closed oak woodlands depresses longleaf recruitment and growth; the density of longleaf pine decreases very slowly (because the longevity of established longleaf is several hundred years; Platt et al. 1988*b*). Complete exclusion of longleaf pine from such a system, therefore, is probably not likely (see Williamson and Black 1981, Platt et al. 1991, Gilliam et al. 1993), given variability in fire regimes and other disturbances that might open space for regeneration of pines (e.g., hurricanes; see Platt and Rathbun, *in press*). Shifts over long periods of time ($\geqslant 10^6$ yr) in the seasonality of thunderstorms and accompanying lightning-initiated fires could result in shifts in relative abundances of pines and oaks in the southeastern U.S. such as those noted in palynological studies (see Watts 1980, Platt and Schwarz 1990). Predicted future changes in regional climate (e.g., drier summers, changes in the seasonal distribution of precipitation; see Smith and Tirpak 1990) are also likely to alter fire regimes (even under managed conditions), thus altering once again the balance between pines and oaks in upland habitats of the southeastern U.S.

Acknowledgments

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APPENDIX A

Stem densities of tree species in 1-ha sandhills plots in 1980, after thinning the oaks but before starting the experimental burning treatments. Plots are identified by season and frequency (A—annual, B—biennial) of burn. Size classes (SC) are as follows: (1) 2–4.9 cm dbh, (2) 5–9.9 cm dbh, (3) 10–19.9 cm dbh, (4) ≥20 cm dbh.

		Month of experimental burns															
		JAN		FEB		APR		MAY		JUL		AUG		OCT		NOV	
Species	SC	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Diospyros virginiana	(1)			1					3								
	(2)								1			1	1				
Ilex vomitoria	(1)	6						2									
	(2)	5															
Pinus palustris	(1)	12	15	90	50	8	9	33	72	11	10	48	43	10	61	25	7
	(2)	21	33	25	26	18	15	27	25	66	41	35	47	29	35	28	32
	(3)	44	53	36	38	29	38	43	54	40	35	51	43	33	48	53	26
	(4)	108	108	64	94	100	90	91	83	145	108	89	112	66	75	86	106
Quercus falcata	(1)									1							
	(2)			1			1			1				1			
	(3)						2										
	(4)													1			
Q. geminata	(1)	7	2	4		10	1	27		23	4		2	10			15
	(2)	8			3	2		5	1	13	1			8			6
	(3)						1	1						2			
	(4)	1															
Q. hemisphaerica	(1)	3	1	3	1					2	4						
	(2)	1												1			
	(3)																
	(4)	1			1												
Q. incana	(1)	10	20	17	29	15	23	30	26	3	36	24	12	8	9	19	12
	(2)	15	19	8	19	19	16	22	11	5	9	11	17	7	5	17	7
	(3)	2	4	1	3	6	3	3	2	7	4	1		5	3	1	6
	(4)	1	1			3	3		1	2			1		1	1	
Q. laevis	(1)		38	39	27	10	25	13	18	1	3	35	29	4	39	33	4
	(2)	1	16	20	16	3	17	5	16	1	2	23	14	1	26	17	3
	(3)	4	2	4	2		3	1	4			5	3		2	6	
	(4)		2	2	1		2		2	1	1	2	1		2	1	2
Q. margaretta	(1)		4	6	3		16	1	19	8	6	21		19	10		
	(2)		5	4			7	2	14		7	6	11		7	3	1
	(3)			1	1			1			2	1	4		3		
	(4)								1				1				
Q. myrtifolia	(1)	2				5											
	(2)					2											
Vaccinium arboreum	(1)	1			2	2	1	6			2					1	3
	(2)								1		2			1			
V. stamineum	(1)	4			2	2		16			6		1	2		1	1
	(2)								1	1							

APPENDIX B

Stem densities of tree species in 1-ha flatwoods plots in 1980, before the experimental burning treatments were begun. Plots are identified by season and frequency (A—annual, B—biennial) of burn. Size classes (SC) are as follows: (1) 2–4.9 cm dbh, (2) 5–9.9 cm dbh, (3) 10–19.9 cm dbh, (4) ≥20 cm dbh.

		Month of experimental burns															
		JAN		FEB		APR		MAY		JUL		AUG		OCT		NOV	
Species	SC	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Pinus elliottii	(1)	2	6	1	6	2		1	1	3						9	1
	(2)	7	6	2	11	5		8	1	4	1			5		5	
	(3)	14	2	1	2	3		43		11				17		6	1
	(4)	31	9	2	1			93	47				18	1	1		
P. palustris	(1)	6	4	52	26	9	25	3	8	36	17	48	23	29	14	6	14
	(2)	21	17	41	50	62	25	23	14	88	23	41	85	111	27	20	21
	(3)	18	47	41	134	134	37	33	52	102	20	49	155	91	15	71	13
	(4)	79	165	60	80	76	154	33	108	58	92	81	109	77	105	181	81
P. serotina	(1)		11				3										
	(2)		5	1			1										
	(3)		9				1										
	(4)		1	1													
P. taeda	(1)			3													
	(2)			2													
	(3)			1													
	(4)			1													
Quercus geminata	(1)				2					25							
	(2)		2							34							
	(3)									17							
	(4)				1					1							
Q. hemisphaerica	(1)						2										
Q. incana	(1)		2	15	41		1			12							
	(2)		2	6	4					8							
	(3)		3	2	1					1							
	(4)								2								
Q. laevis	(1)	1			1		1			47				2			
	(2)				1					35				5			
Q. margaretta	(1)				2					12							
	(2)		2		2												

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NATURAL DISTRIBUTION AND ABUNDANCE OF FOREST SPECIES AND COMMUNITIES IN NORTHERN FLORIDA[1]

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Abstract. Quantitative estimates of the distribution and abundance of trees in northern Florida prior to extensive land development are summarized from Public Land Survey (PLS) records. The PLS data on 127 653 trees at 48 831 sample locations, collected between 1822 and 1854 and tabulated from original field notes, are summarized here to examine the abundance and distribution of major tree species and plant associations. These results are compared to another early, quantified estimate of vegetation published in 1914. These two records of vegetation were compared within 20 vegetation zones in northern Florida. Both data sets describe the vegetation of northern Florida as strongly dominated by pine and similarly describe regions more heavily represented by upland hardwood or forested wetland trees. The data sets differ predominantly in that the PLS data indicate: (1) more pine; (2) less cypress, gum, and sweetgum than the early 20th-century survey; and (3) that, in contrast to major upland hardwood taxa, the representation of major taxa typical of pinelands and forested wetlands is only loosely correlated between data sets. The PLS records were used to map the distribution of species and community types across northern Florida. The PLS data support, and quantify, previously published accounts of the overwhelming dominance of pine in the presettlement vegetation of northern Florida. This abundance of pine refutes various hypotheses that mixed hardwood vegetation dominated upland habitats in northern Florida.

Key words: bearing tree; community composition; forest history; historical plant ecology; longleaf pine; mixed deciduous forest; northern Florida; presettlement; Public Land Survey; vegetation; wetland tree species distribution.

INTRODUCTION

Reconstructing the natural distributions of species and communities is helpful for understanding the natural history and ecology of our native plant communities. Knowledge of the composition and distribution of presettlement forest associations is also useful in guiding restoration and management of natural habitats. Further, information on predisturbance forest composition delineates long-term forest changes, both human induced and those caused by natural dynamic processes. This study estimates the presettlement abundance and distribution of trees in northern Florida using Public Land Survey (PLS) records. These records were first collected in northern Florida in 1822. The PLS records postdate localized Spanish settlement but predate the extensive habitat alteration associated with the widespread colonization of the region following Florida's accession into the United States. I compare the description of vegetation encapsulated in the PLS data to an early 20th-century measure of vegetation for the same region (Harper 1914). Harper's (1914) study provides the most exhaustive examination of local variation in the abundances of species by region within northern Florida. In addition, Harper's data are the earliest detailed account of the flora of northern Florida by a trained botanist. Finally, several authors have pointed out potential sources of error in PLS data as a result of surveyor bias (e.g., Bourdo 1956, Grimm 1984). Harper's work provides an opportunity to compare a quantitative sample of relatively undisturbed vegetation to PLS data over a large region.

The abundance and distribution of plant associations in northern Florida before European settlement are not well known. There is general agreement that the coastal plain vegetation of the southern states contained extensive stands of pine, particularly longleaf pine (*Pinus palustris*) (Harper 1914, Gano 1917, Braun 1950, Quarterman and Keever 1962, Glitzenstein et al. 1986, Platt et al. 1988), and that hardwoods replace these pine forests in the absence of fire (Long 1899, Harper 1914, Garren 1943, Braun 1950, Quarterman and Keever 1962, Glitzenstein et al. 1986). However, the degree of dominance of pine is not fully known. The lack of agreement on the degree of pine dominance stems from differing hypotheses regarding the origin of longleaf pine forests. The most notable of these hypotheses claims that extensive longleaf pine forests were a result of (1) abandonment of Native American agricultural fields (Quarterman and Keever 1962), (2) fires set by Native Americans (Braun 1950), or (3) natural lightning-strike fires (Chapman 1950, Komarek 1964, 1968). These three hypotheses are not mutually exclusive, and each of the three factors could have

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contributed to the abundance of pine. The first two hypotheses, however, predict a specific pattern, namely, a greater abundance of pineland near centers of Native American agriculture and a lower overall abundance of pine than is predicted by the third hypothesis.

Although it is generally believed that the vegetation of prehistoric northern Florida consisted of a mosaic of longleaf pine forests interspersed with hardwood forests (Harper 1914, Kurz 1944, Braun 1950, Blaisdell et al. 1974, Delcourt and Delcourt 1974, 1977), the relative abundance of these habitats is disputed. Braun (1950) and Quarterman and Keever (1962), who viewed fire as incidental and largely unnatural, present beech–magnolia forest as a moderately common climax vegetation of northern Florida. Other studies using historical data support this view of a relatively abundant hardwood forest (Delcourt and Delcourt 1977, Clewell 1986). Davis' (1967) map of the natural plant associations of Florida characterizes northern Florida as predominantly a mixed hardwood–pineland forest.

In contrast, early accounts of northern Florida depict a flora strongly dominated by pinelands (Bartram 1791, Williams 1827, 1837, Cabeza de Vaca and Garcilaso de la Vega, as cited in Small 1921*a*, *b*, and Andre Michaux, and Thomas Nuttall as cited in Harper 1948). Based on notes from his travels during the early 1800s, Williams (1827, 1837) estimated that longleaf pine occupied >90% of northern Florida.

The presettlement forest of northern Florida was, in itself, a landscape modified by humans. Native American settlement was extensive, with developed areas of agriculture in the Tallahassee region and in major river floodplains (Tebeau 1980). In addition, Native Americans used fire to manage pinelands (Pyne 1982). Despite these anthropogenic disturbances, an estimate of presettlement forest conditions provides the nearest measure of "natural" composition of forested vegetation in the region.

Postsettlement change in the forest landscape of northern Florida has been extensive. The Spanish, who ceded Florida to the United States in 1821, had occupied Florida since the late 1500s. While major Spanish settlements were restricted to the coastal communities of Saint Augustine and Pensacola, several missions were established in the Tallahassee region (Tebeau 1980). While missions in the central portion of the panhandle of Florida were numerous, it is thought that these missions were sparsely populated and did not disturb much additional land (Tebeau 1980).

Following cession to the U.S. and the opening of the land to settlement, it was common practice to burn pinelands to clear land and control hardwoods (Pyne 1982). Pyne estimated that 105% of the land area of Florida was burned in a single year during the early 1900s, an estimate that requires some land be burned more than once in a year. These frequent fires may have decreased the abundance, and altered the distribution, of upland hardwoods. The fire regime established by European settlers, however, might not have been much different than earlier fire regimes. Natural fire frequencies are thought to be between 1 and 3 yr in upland pine communities of northern Florida (Komarek 1964, 1968, Robbins and Myers 1992). Native Americans were thought to have augmented this natural fire regime over the past several hundreds, if not thousands, of years (Tebeau 1980).

Fire suppression has been widespread since the mid-20th century. Where fire is suppressed, hardwoods exclude pine regeneration and allow hardwoods to increase (Hubbell et al. 1956, Quarterman and Keever 1962, Blaisdell et al. 1974). A recent expansion of hardwoods may explain the current abundance of purportedly midsuccessional forest communities such as pine–oak–hickory. Alternatively, pine–oak–hickory assemblages may have been a natural component of presettlement forests.

I use the PLS bearing-tree data to examine five aspects of presettlement forest composition: (1) the abundance of major tree species, (2) the association of species into general community types, (3) the abundance of these associations, (4) the distributions of species and tree associations, and (5) the covariation between soil parent material and species and tree associations.

Both data sets presented in this study have merits as well as weaknesses. The strength of the PLS data set is that it is a systematically collected estimate of abundance, distribution, and species association prior to significant disturbance. The weaknesses of the PLS data are: (1) the taxonomy used by surveyors was not specific, (2) surveyors were often biased against small trees in their selection of bearing and witness trees (Grimm 1984), (3) surveyors may have been biased in the species of tree selected (Bourdo 1956), and (4) surveyors were not required to survey section corners in permanent standing water (Bourdo 1956). As a result, wetland tree species such as cypress were under-sampled.

The strength of Harper's data lies in the detailed and accurate taxonomy. Harper's study is weakened by three problems: (1) he used an unorthodox method of quantifying vegetation (see below), (2) he did not systematically cover the region, and (3) he surveyed Florida 90 yr after it was opened to settlement. Nonetheless, Harper's results, along with the PLS data, provide the best available reconstruction of presettlement vegetation for northern Florida.

Data

Public Land Survey data

I define northern Florida as that portion of the state north of Township 10 south (approximately at the latitude of Gainesville, 29°3′ N, Fig. 1A). I tallied all available Public Land Survey (PLS) data within this study region. Several large portions of the study area, however, have no PLS data (Fig. 1B). The largest of these regions is the Forbes Purchase in the central pan-

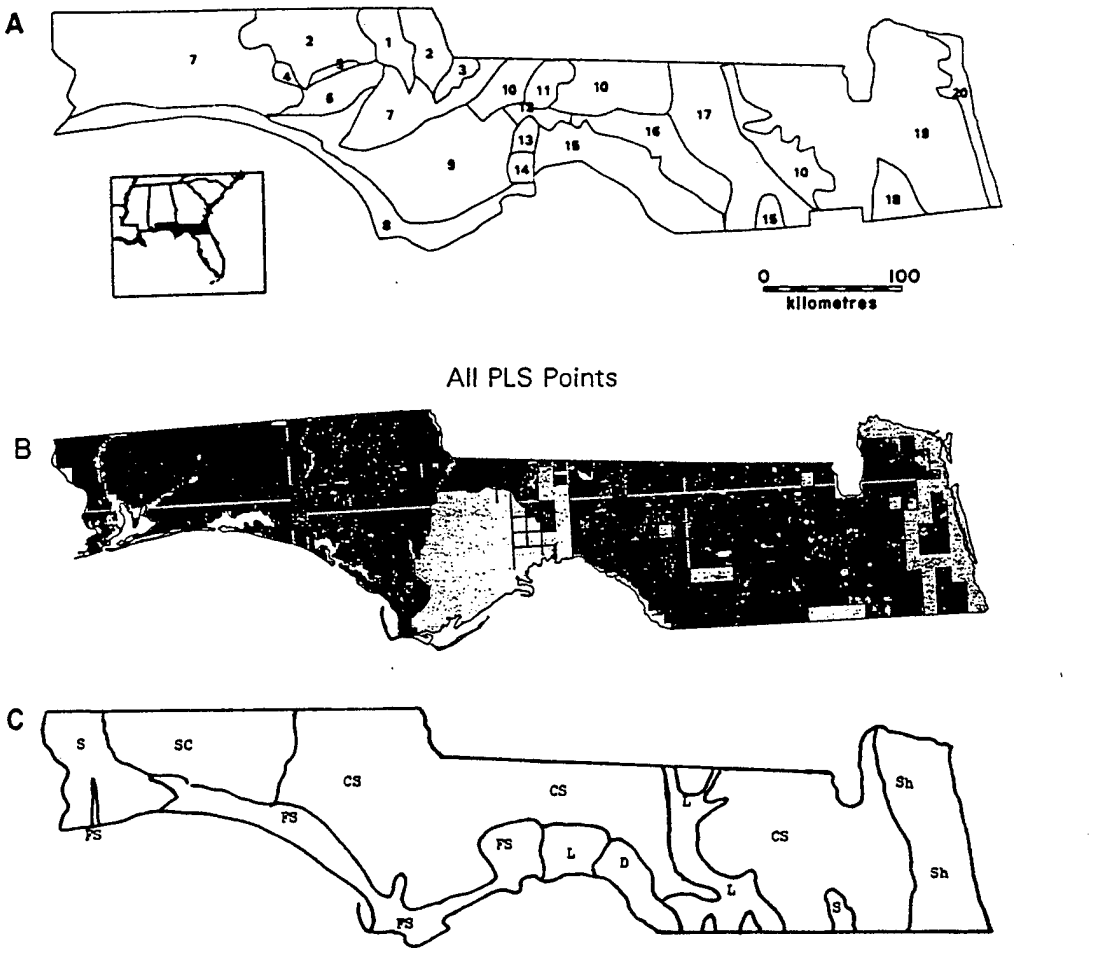


FIG. 1. Maps of northern Florida depicting the study region using Harper's (1914) division into 20 floristic regions: (A) delineation of vegetation regions: 1 = Marianna Redlands, 2 = West Florida Lime-Sink region, 3 = Apalachicola River Bluffs and Bottoms, 4 = Knox Hill Country, 5 = Holmes Valley, 6 = West Florida Lake region, 7 = West Florida Pine Hills region, 8 = West Florida Coast Strip, 9 = Apalachicola Flatwoods, 10 = Middle Florida Hammock Belt, 11 = Tallahassee Red Hills, 12 = Bellair Sand region, 13 = Wakulla Hammock Country, 14 = Panacea Country, 15 = Gulf Hammock Country, 16 = Middle Florida Flatwoods, 17 = Peninsular Lime-Sink region, 18 = Peninsular Lake region, 19 = East Florida Flatwoods, 20 = East Coast Strip; (B) the 48 831 sample points included in the Public Land Survey (PLS) data set; the large pale area in the center is the Forbes Purchase; and (C) the general distribution of soil parent material: S = gravel and sand, SC = sandy clay, FS = fine sand, CS = clayey sand, L = limestone, D = dolomite/limestone, Sh = shelly sand and clay.

handle of Florida. The Forbes Purchase land was surveyed privately and does not include vegetation data. I omitted other townships because they were surveyed after local settlement or because their PLS records are missing. Most of the 556 townships included in this study were surveyed between 1822 and 1834, but some portion of 101 townships was surveyed between 1847 and 1854. These later-surveyed areas were generally riverine or swampy areas deemed uninhabitable by earlier surveyors and unsettled when surveyed.

Townships are six miles by six miles ($\approx 10 \times 10$ km) and are divided into 36 1-mile^2 (2.6-km^2) sections. At each section corner four bearing trees were surveyed. Two additional bearing trees were sampled at the midpoints of each section line. Thus, a township has 36 section corners and 72 midsection line sites (counting only two of the four exterior lines from each township) at which a maximum of 288 trees may be sampled. I recorded the identity and location of all bearing trees at section corners and midsection line sites. This northern Florida PLS data set consists of 127 653 trees sampled at 48 831 locations (Fig. 1B).

Over 100 common names of bearing-tree designations were encountered in the PLS data. I use a list of 68 common types for analysis in this study (Table 1). An additional 35 species names were sampled <10 times and are reported simply as "unusual tree." Individual species designated by common tree names are from Harper (1914), Delcourt and Delcourt (1977), Clewell (1985), and Godfrey (1988).

Many of the common tree names used by surveyors lack specificity. For example, the term "oak" may refer

TABLE 1. Common names and abundances of all trees identified >10 times in the Public Land Survey (PLS) records for northern Florida. Each common name category includes all species likely to have been identified by that common name.

Common name	Scientific name(s)	Number of occurrences	% of sample	Plant association P	UH	W
	Gymnosperms					
Cedar	*Chamaecyparis thyoides, Juniperus silicola*	40	0.03	0	1	1
Cypress	*Taxodium ascendens, T. distichum*	3771	2.95	0	0	1
Juniper	*Juniperus silicola*	17	0.01	0	1	0
Pines						
Pine	*Pinus clausa, P. echinata, P. elliottii, P. glabra, P. palustris, P. serotina, P. taeda*	99 019	77.57	1	0	0
Longleaf, White Pine	*P. palustris*	137	0.11	1	0	0
Lightwood	*P. palustris*	186	0.15	1	0	0
Shortleaf Pine	*P. echinata*	19	0.01	1	1	0
Swamp Pine	*P. elliottii, P. serotina*	56	0.04	0	1	1
Spruce Pine, Spruce	*P. glabra*	82	0.06	0	1	1
	Angiosperms					
Ash	*Fraxinus americana, F. caroliniana, F. pauciflora, F. pennsylvanica, F. profunda*	569	0.45	0	0	1
Bays						
Bay	*Persea borbonia, P. palustris, Gordonia lasianthus, Magnolia virginiana, M. grandiflora*	5973	4.68	0	1	1
Magnolia	*Magnolia grandiflora*	444	0.35	0	1	0
Redbay	*Persea borbonia, P. palustris*	120	0.09	0	1	1
White Bay	*Magnolia virginiana*	76	0.06	0	0	1
Sweetbay	*Magnolia virginiana*	31	0.02	0	0	1
Baygall	cf. *Magnolia grandiflora*	20	0.02	0	1	0
Beech	*Fagus grandifolia*	327	0.26	0	1	0
Birch	*Betula nigra*	12	0.01	0	0	1
Cherry	*Prunus americana, P. angustifolia, P. caroliniana, P. serotina, P. umbellata*	20	0.02	0	1	0
Chinquapin	*Castanea ashei, C. floridana*	148	0.12	0	1	0
Cucumber Tree	*Magnolia cordata, M. pyramidata, M. ashei*	15	0.01	0	1	0
Dogwood, Swamp Dogwood	*Cornus alternifolia, C. florida, C. foemina*	539	0.42	0	1	1
Elm	*Ulmus alata, U. americana, U. rubra*	140	0.11	0	1	1
Gums						
Gum	*Nyssa aquatica, N. biflora, N. ogeche, N. sylvatica*	1526	1.20	0	0	1
Black Gum	*Nyssa biflora, N. sylvatica*	338	0.26	0	0	1
Tupelo Gum	*Nyssa aquatica, N. biflora, N. ogeche, N. sylvatica*	84	0.07	0	0	1
Hackberry	*Celtis laevigata*	24	0.02	0	1	0
Haw	*Cretaegus* spp.	42	0.03	1	1	1
Haw, Red	*Cretaegus spathulata*	16	0.01	1	1	1
Hickory	*Carya aquatica, C. cordiformis, C. floridana, C. glabra, C. ovalis, C. pallida, C. tomentosa*	853	0.67	0	1	0
Holly	*Ilex opaca*	309	0.24	0	1	0
Hornbeam	*Carpinus carolinianum*	110	0.09	0	1	0
Ironwood	*Ostrya virginiana*	151	0.12	0	1	0
Linden, Linn	*Tilia americana*	44	0.03	0	1	0
Locust	*Gleditsia triacanthos*	10	0.01	0	1	0
Maple	*Acer saccharum, A. rubrum, A. saccharinum*	349	0.27	0	1	1
Mulberry	*Morus alba, M. rubra*	10	0.01	0	1	0
Myrtle	*Myrica cerifera, M. inodora Ilex myrtifolia, Quercus myrtifolia*	147	0.12	0	1	1
Oaks						
Oak	*Quercus* spp. (25 species)	958	0.75	1	1	1
Black Oak	*Q. velutina*	451	0.35	0	1	0
Blackjack Oak	*Q. marilandica, Q. laevis*	3206	2.51	1	0	0
Laurel Oak	*Quercus hemisphaerica*	40	0.03	0	1	0
Live Oak	*Q. virginiana* (*Q. hemisphaerica, Q. geminata*)	427	0.33	1	1	0
Post Oak	*Q. stellata*	564	0.44	1	0	0
Red Oak	*Q. falcata, Q. laevis, Q. shumardii, Q. velutina*	1503	1.18	1	1	0
Spanish Oak	*Q. falcata*	15	0.01	0	1	0
Swamp Oak	*Q. prinus* (*Q. michauxii, Q. falcata*)	58	0.05	0	0	1
Water Oak	*Q. nigra*	864	0.68	0	0	1

Plant association values are used to determine community type (P = pineland, UH = upland hardwood, or FH = forested wetland) at each PLS bearing-tree site. See *Data: Public Land Survey data* for further explanation.

Common name	Scientific name(s)	Number of occurrences	% of sample	Plant association P	UH	W
White Oak	*Q. alba*	382	0.30	0	1	0
Willow Oak	*Q. phellos*	45	0.04	0	0	1
Cabbage Palm	*Sabal palmetto*	400	0.31	1	1	1
Palmetto	*Sabal palmetto*	72	0.06	1	1	1
Saw Palmetto	*Serenoa repens, Sabal palmetto*	36	0.03	1	1	1
Persimmon	*Diospyros virginiana*	70	0.05	0	1	0
Poplar	*Populus deltoides, P. heterophylla, Liriodendron tulipifera*	68	0.05	0	1	1
Privet	*Foresteria acuminata*	66	0.05	0	1	1
Sassafras	*Sassafras albidum*	49	0.04	0	1	0
Sourwood	*Oxydendrum arboreum*	220	0.17	0	1	0
Sumac	*Rhus copallina*	10	0.01	0	1	0
Sweetgum	*Liquidambar styraciflua*	278	0.22	0	1	1
Titi	*Cyrilla racemiflora, Cliftonia monophylla*	1747	1.37	0	0	1
Whortleberry	*Ilex* cf. *pauciflora*	31	0.02	0	1	1
Willow	*Salix caroliniana, S. floridana, S. nigra*	75	0.06	0	0	1
Yaupon	*Ilex vomitoria*	31	0.02	0	1	1
	Other trees					
Unusual tree		84	0.07	0	0	0
Other trees		113	0.09	0	0	0
Illegible		51	0.04	0	0	0
Dead		15	0.01	0	0	0
	Non-trees (not included in tree sum)					
No tree		707	0.55	0	0	0
Pit		29	0.02	0	0	0
Mound		132	0.10	0	0	0
Total trees		127 653	100			

to any of 25 species in northern Florida (Godfrey 1988). I limit my interpretation of the PLS bearing-tree data to taxonomic groups distinguished by common names. Given their abundance, common name usage presents a special problem with respect to the pines. There are seven species of pine in northern Florida (Table 2). Five of the pines may grow in monospecific stands (longleaf, shortleaf, slash, sand, and pond pine). Of these five pines, sand pine and pond pine are generally restricted to coastal areas and are relatively unimportant species at present. I make no assumption of the species of pine at individual sample locations. However, all historical accounts record longleaf pine as the overwhelmingly dominant pine of Florida (Williams 1827, Harper 1914, 1948, Small 1921*a*, *b*). Harper's analysis of vegetation highlights regions differing in the importance of the various pines, oaks, and other species that are insufficiently distinguished by the PLS data. I refer to Harper's (1914) regional descriptions for insight into the relative abundance of species within multispecific taxonomic designations.

Harper's (1914) data

Harper divided northern Florida into 20 floristic regions, of which three were further divided into subregions (Fig. 1A). Harper assessed the abundance of

TABLE 2. The pine species of northern Florida, and a brief description of the habitats (from Godfrey 1988).

Latin name (common name)	Habitat
Pinus clausa (sand pine)	Common near the Atlantic and Gulf coasts on sand ridges; associated with evergreen oaks.
Pinus echinata (shortleaf pine)	Invades fertile old fields and is found in mixed hardwood stands.
Pinus elliottii (slash pine)	Found in wet flatwoods, swamps along ponds, and coast.
Pinus glabra (spruce pine)	Found in mixed hardwoods, hammocks, and bottomland forests.
Pinus palustris (longleaf pine)	Occurs as dominant species in uplands, flatwoods, and sand ridges.
Pinus serotina (pond pine)	Found in poorly drained sites with marked fluctuations in water table.
Pinus taeda (loblolly pine)	Invades upland old fields and is found in mixed lowland hardwoods.

TABLE 3. Attributes of the vegetation within regions of northern Florida as delineated by Harper (1914). The number of trees and relative abundance are summarized for Public Land Survey (PLS) records (1822–1854) and Harper (1914). Percentage similarity and correlations compare the PLS and Harper's data sets within each region.

		Area† (km²)	Number of trees (PLS)	% Pine (PLS)	% Pine (Harper)
1.	Marianna Redlands	1140	3267	54.4	36.2
2.	West Florida Lime-Sink	4150	12 464	80.0	58.8
3.	Apalachicola Bluffs	130	1037	55.4	24.5
4.	Knox Hill Country	130	492	50.6	(1)‡
5.	Holmes Valley	65	510	67.7	(1)
6.	West Florida Lake	910	3104	78.3	(1)
7a.	West Florida Pine Hills, West	8290	22 511	79.2	63.0
7b.	West Florida Pine Hills, East	1940	6072	77.6	66.3
8.	West Florida Coast Strip	1040	3190	75.2	(1)
9.	Apalachicola Flatwoods	6730	6217	77.9	59.4
10w.	Middle Florida Hammock Belt, West	1140	1716	47.7	55.8
10c.	Middle Florida Hammock Belt, Central	2070	6227	57.1	54.5
10e.	Middle Florida Hammock Belt, East	1680	5012	88.0	54.5
11.	Tallahassee Red Hills	880	1067	51.5	39.4
12.	Bellair Sand	620	220	90.6	56.1
13.	Wakulla Hammock Country	390	220	67.3	36.4
14.	Panacea Country	150	32	50.0	(1)
15.	Gulf Hammock Country	3810	8326	64.5	62.9
16.	Middle Florida Flatwoods	2590	5508	75.3	(1)
17.	Peninsular Lime-Sink	5180	11 833	91.4	75.1
18.	Peninsular Lake	1290	2923	78.1	70.2
19.	East Florida Flatwoods	13 730	25 582	82.6	69.3
20.	East Coast Strip	470	123	48.0	(9)

* $P < .05$, ** $P < .01$.

† Areas originally given in square miles (1 km² = 0.3448299 mi²).

‡ Species ranks are presented in parentheses for the seven regions in which abundance values are not presented by Harper (1914).

species within regions using an unorthodox method that requires a detailed explanation. Harper's abundance values are based primarily on frequency, adjusted for local abundance. Traveling through each region by rail and on foot, Harper listed all species encountered with a designation of abundance (abundant, common, uncommon, or rare). At convenient stopping intervals, railway mile posts or streams, he would terminate one list and begin another. Subsequently, Harper tabulated the data from all lists within each region. Species were sorted by size and growth habit into three sub-lists (overstory trees, shrubs, herbs). Species noted as abundant received a score of three, common plants received a score of two, while species noted as rare were not counted at all. Harper then multiplied the figures for very common species (e.g., *Taxodium ascendens*) by two. For longleaf pine, which was exceedingly abundant, he multiplied the figures by four. Harper then arbitrarily adjusted these numbers when "the results are obviously inconsistent with the known facts."

Harper grouped species by physiognomy and weighted differences in size and growth habit of species. His methods are of interest to the current study only with respect to titi (*Cyrilla racemiflora* and *Cliftonia monophylla*). Harper divided the scores for small trees and shrubs (including titi) by a factor of 10. Hence, comparisons between Harper's estimates of the abundance of overstory and small trees are inappropriate. Finally, species scores were summed and transformed into percentage values.

Harper enumerates several potential sources of bias and error in his estimates of vegetation. First, logging was ongoing during his study and clustered around the travel routes he followed. Therefore, Harper stated that he underestimated the natural abundance of pine and cypress, the commonly harvested species prior to, and during, his survey. Second, uplands were preferentially selected for agricultural clearing. As a result, he underestimated the percentages of upland species found before European settlement.

Harper presented vegetation percentages for tree species within most (13) of the regions he described; data from 7 regions he described to be inadequate for estimating species percentages. For these seven regions, Harper opted to rank species in order of abundance (Table 3). In addition, Harper split two regions, the Middle Florida Hammock Belt and the West Florida Lime-Sink regions, into sub-zones with separate estimates of abundance. For comparison, I distinguish geographically distinct sub-zones in the PLS data.

Taxonomic differences between Harper's data set and the PLS data were minor. For tabulation, I changed archaic Latin names listed by Harper to currently accepted scientific nomenclature (e.g., *Quercus Catesbei* = *Q. laevis*, Godfrey 1988).

TABLE 3. Continued.

% Longleaf pine (Harper)	% Similarity in top 5 taxa	Correlations		No. of taxa exceeding 1% of trees		
		r^2	tau	PLS	Harper	Both
10.0	60	.19	.34*	15	20	14
46.0	80	.13	.50	6	7	5
6.0	20	.13	.19	13	17	9
(3)	60	...	...	15	...	...
(3)	100	...	...	8	...	...
(1)	80	...	...	5	...	...
51.0	80	.70**	.44	4	9	4
58.0	80	.74**	.83**	4	9	4
(1)	80	...	...	6	...	...
40.0	80	.60*	.76**	6	9	6
27.0	60	.10	.22	12	13	8
18.0	80	.50*	.60**	10	8	7
34.0	40	.36*	.50*	5	12	5
4.2	80	.15	.41	12	11	10
53.0	60	.17	.14	5	5	3
29.7	60	.14	.46*	7	16	7
(1)	60	...	...	5	...	...
44.1	80	.41*	.79**	10	12	10
(1)	80	...	...	7	...	...
73.8	40	.23	.20	2	5	2
52.0	60	.85**	81*	3	7	3
43.5	80	.37	.73	4	6	4
(−)	20	...	...	8	...	...

METHODS

Estimates of vegetation composition

To compare the two estimates of the relative abundance of trees within floristic regions, I transcribed Harper's map of regions onto a 1:500 000 base map of northern Florida. Although the quality of Harper's original map (Harper 1914) is rough, the accuracy of transcribing regions was aided by the fact that many regions are delineated by rivers and distinct topographical and geographical breaks. I digitized these regions using a Geographical Information System (ARC/INFO 1989). I then overlaid the coverage of Harper's regions (Fig. 1A) on the coverage of PLS (Public Land Survey) bearing-tree locations to tabulate PLS species abundances within Harper's regions.

Quantitative comparisons between data sets are available for the 16 geographical units for which Harper lists percentage estimates (Table 3). For these regions, I summed Harper's percentage values for species that are indistinguishable in the PLS data (e.g., all pines). I further limit my comparison to those taxa that are common, defined here as exceeding 1% within the region in either Harper's or the PLS data.

To assess the relationship between data sets for individual taxa I examined differences between the two estimates of abundance across regions using Wilcoxon signed-ranks tests (Conover 1980). These tests assess which taxa are not represented equally between the two data sets. I expect a nonsignificant result in regions where the data sets comparably measure a taxon.

The similarity between the PLS and Harper vegetation estimates within regions was summarized by three measures. First, a correlation of taxon percentages describes the relationship between the vegetation sampled within a region in the two studies. However, the extreme abundance of pine with respect to other taxa, different abundance measures, and measurement error weaken the expectation of a parametric relationship between data sets. For each region, I present a correlation of arcsine-transformed percentage data for all taxa exceeding 1% in either data set, excluding pine. Pine was excluded because it remained an outlier despite the data transformation; all regions exhibited positive significant correlations when pine was included.

Second, I used a nonparametric rank correlation between the data sets using Kendall's tau (τ; Conover 1980). A correlation of rank values is used because of the extreme absolute abundance of pine with respect to other taxa. A drawback of this method is that because most of the other taxa do not exceed 5%, ranks can vary substantially despite relatively small differences in abundance. Both of these aforementioned analyses are presented purely as a means to examine differences between vegetation estimates. As such, the P values are not presented in the context of hypothesis testing and are not corrected for family error rates.

Third, I compared the lists of the top five taxa cited

by each study within regions. A percentage matching of lists of the most abundant species provides a broad-scale comparison between the data sets. As such, the percentage match is presented to highlight regions that are described similarly between data sets.

Finally, I assessed whether inter-region vegetation differences are represented similarly by Harper and the PLS data. For each data set I examined patterns of similarity through a principal components analysis (PCA) of taxon percentages (Wilkinson 1990). The expectation is that graphical depictions of site scores should appear similar between Harper's and the PLS data. This comparison is complicated by the fact that Harper does not list numerical abundances for seven regions. I repeated the PCA on the PLS data with and without those regions where Harper does not list percentage abundance.

Plant association classification

I used the PLS sample of two (midsection line) or four (section corner) bearing trees to categorize the assemblage of trees at each sample location. The PLS data sample too few trees at individual sites to distinguish detailed associations. Therefore, I established a two-tiered classification system, beginning with three very broad plant associations: pineland, upland hardwood, and forested wetland.

To categorize individual sites I assigned each common tree name a score toward one, or more, of the three general associations, based on its modern habitat affinities (Clewell 1985, Godfrey 1988; Table 1). Trees with unambiguous common names and clear community affinities (e.g., beech [*Fagus grandifolia*]) were assigned a score for the appropriate association (e.g., upland hardwood). Trees with ambiguous common names where all possible species have the same habitat affinity (e.g., cypress [*Taxodium ascendens* and *T. distichum*]) were also assigned a discrete designation (e.g., forested wetland). Trees with unambiguous common names and wide habitat affinities (e.g., hackberry [*Celtis laevigata*]) were assigned scores in each appropriate association (e.g., upland hardwood and forested wetland). Trees with ambiguous common name whose species range across habitats (e.g., oak = *Quercus* spp.) contributed equally to all associations (pineland, upland hardwood, and forested wetland). For each sample location (a section corner or section line midpoint), I designated an association by the sum score for the PLS sampled bearing trees. This initial classification successfully identified associations for 91% of sample corners, leaving 4332 sample locations with ambiguous designations (Table 4). Several additional categories were created for samples that did not unambiguously fit one of the three basic associations (Table 4).

I further classified plant associations at PLS sample sites based on species composition. For instance, the pineland association (38 583 sites) was subdivided into sample locations containing only pine (34 888 sites), a mixture of pine and oaks (2957 sites), and a mixed pineland association (738 sites) (Table 4). Owing to the few trees sampled at individual data points, I created numerous categories of ambiguous assemblages of trees for which I could not discern among the three basic plant associations. For instance, the mixed upland–wetland hardwood assemblage includes sites that had equal wetland and upland hardwood scores (1421 sites); these sites probably include mostly hydric hammock and floodplain sites. Table 1 contains community weightings for the 64 tree names sampled and examples of all assemblage categories.

Soil parent material

The most abundant species and the three general associations were tested for affinity with soil parent material using the Environmental Geology Series maps (Fig. 1C; Knapp 1978*a*, *b*, Schmidt 1978*a*, *b*, 1979, Scott 1978, 1979). These maps provide a general soil parent type for each section corner. I used separate chi-square tests for nonrandom association of each species, and community, with the major soil types.

Results and Discussion

Individual species

Pines.—The PLS (Public Land Survey) sample indicates that the pines are the overwhelming dominant tree taxa of northern Florida, representing 77.6% (99 019 trees) of all trees sampled (Table 1). Pine was most often found in association with itself, being exclusively sampled at 71.4% of bearing-tree sites (Table 4). The PLS data include four unique common names for pines. Longleaf pine (*Pinus palustris*) was the most frequently encountered designation; however, 99.6% of the pines sampled are recorded simply as "pine" (Table 1).

Harper lists a pine as the most abundant species in 19 of 20 regions; longleaf pine is the most abundant pine in 14 of these regions (Table 3). The 14 regions where longleaf is the dominant pine constitute >95% of the area of northern Florida. Where longleaf is the dominant pine and Harper provides quantitative estimates, longleaf constituted an average of 72.1 ± 18.1% (mean ± 1 SE) of all pines and 46% of all species. The next most frequent pines listed by Harper are slash (*P. elliottii*) and loblolly (*P. taeda*), which averaged 6.1% and 5.9% across regions, respectively. The six largest regions from which Harper presents species percentages constitute over two-thirds of the area of northern Florida (Table 3). Longleaf pine within these six regions averaged 54%, compared to 9.8% for slash pine and 2.2% for loblolly pine. Thus, pine was clearly the dominant genus and longleaf the dominant pine for northern Florida prior to settlement.

A Wilcoxon signed-ranks test indicates an underrepresentation of pine by Harper with respect to the PLS sample (Fig. 2A, Table 5). This pattern can be

TABLE 4. Frequencies of 20 categories of plant associations described by the Public Land Survey data from northern Florida. Primary community types, defined as per species weightings, are listed in Table 1, as are likely species equivalents for the common names. Second-level categorizations are based on frequently encountered assemblages of species.

Community type	Number of sites	% of total
1) Pineland	38 583	79.01
Pine only	34 888	71.45
Pine and oak	2957	6.06
Pineland association	738	1.51
2) Upland Hardwood	1929	3.95
Xeric hardwoods	381	0.78
Mesic hardwoods	1548	3.17
3) Forested Wetland	3987	8.16
Bay swamps	1346	2.76
Cypress swamps	783	1.60
Titi swamps	517	1.06
Gum swamps	208	0.43
Wetland mix	1133	2.32
4) Unresolved associations	4332	8.87
Pine/upland hardwoods	532	1.09
Pine/titi	138	0.28
Pine/cypress	695	1.42
Pine/bay	26	0.05
Pine/mixed wetlands	61	0.12
Pine/gum	3	0.01
Palm	102	0.21
Pine/palm	97	0.20
Palm/mix	118	0.24
Upland/wetland mix	1421	2.91
Undifferentiated	640	1.31
No trees	748	1.53
Total no. sites	48 831	100.00

attributed to two factors. First, Harper undersampled pine. As Harper states "A great deal of long-leaf [sic] pine . . . has been removed by lumbermen, so that these trees are relatively less abundant now than they were originally." In addition, PLS surveyors probably oversampled pine by preferentially selecting them as bearing trees over the associated small oaks found in pineland habitats. Thus, the PLS and Harper's estimates of pinelands probably bound reasonable estimates of the true presettlement abundance of pine.

Major hardwoods.—The most abundant of upland species after pine are oaks, representing 6.7% of sampled trees (8513 trees, Table 1). There are 25 species of oak listed as occurring in northern Florida (Godfrey 1988). Twelve specific designations of oak were recorded in the PLS data. For the most part these oak names designate either a single species or a suite of species common to similar habitats (Table 1). For instance, water oak (*Quercus nigra*, 864 trees), occurs in wetlands and hydric hammocks, while white oak (*Q. alba*, 382 trees) is predominantly found in mesic upland hardwood forests.

Two of the six most common specific oaks sampled (blackjack oak, 3206 trees; and post oak, 564 trees) are pineland associates. Blackjack oak (*Q. laevis, Q. marilandica*) is underrepresented in the PLS data compared to Harper's estimate of abundance, and its representation among regions is not correlated between the two data sets (Fig. 2B, Table 5). This result is expected; the small stature of blackjack oak would discourage its use as a bearing tree by surveyors.

Red oak (1503 trees) may indicate any of four species: *Q. falcata, Q. shumardii,* and possibly, though probably not commonly, *Q. velutina* and *Q. laevis.* While some of these species are not commonly referred to as red oak, it would have been consistent with the taxonomic precision of surveyors to include all oaks with pointed leaves under this designation. The representation of red oak between the two data sets is comparable (Table 5); however, this reflects a mixture of species, all of which may be misrepresented (Fig. 2B). The five regions in which red oak percentages are higher in the PLS than in Harper's data are the regions with the lowest abundance of pine (as sampled by the PLS). It is probable that the majority of red oak designated by surveyors in regions with low pine abundance (1031 of 1503 occurrences) represents species characteristic of upland hardwood forests (e.g., *Q. falcata, Q. rubra,* or *Q. velutina*).

Red oak sampled in association with pine may rep-

TABLE 5. Comparative representation of major tree taxa in the Public Land Survey's (PLS) and Harper's assessments of northern Florida vegetation. Kendall's tau (τ) is a nonparametric regression method used to test for a significant relationship between data sets, while the paired Wilcoxon's signed-ranks test was used to assess whether representation significantly differed from expected (P values not adjusted for family error rates).

Taxon	n	Kendall's τ	Paired signed-ranks test
A) Taxa underrepresented by Harper with respect to the PLS data			
Bay	15	.73**	−2.67***
Black oak	14	.04	−2.49**
Hickory	15	.60***	−2.95***
Pine	17	.36*	−3.43***
White oak	16	.09	−1.85*
B) Taxa overrepresented by Harper with respect to the PLS data			
Blackjack oak	14	.06	2.35**
Cypress	17	.37**	3.48***
Gum	16	.36*	2.53**
Live oak	15	.39**	2.44**
Magnolia	15	.44**	3.29***
Maple	9	.15	2.66***
C) Taxa with no difference in representation between data sets			
Ash	16	.41**	−0.60
Bay	15	.39**	−0.36
Beech	15	.72***	0.24
Dogwood	15	.76***	1.60
Holly	15	.67***	1.22
Oaks	16	.29	−0.10
Red oak	11	.52**	−0.80
Post oak	16	.39**	−0.85
Water oak	16	.29	1.06
Sourwood	15	.24	−1.36

* $P < .10$, ** $P < .05$, *** $P < .01$.

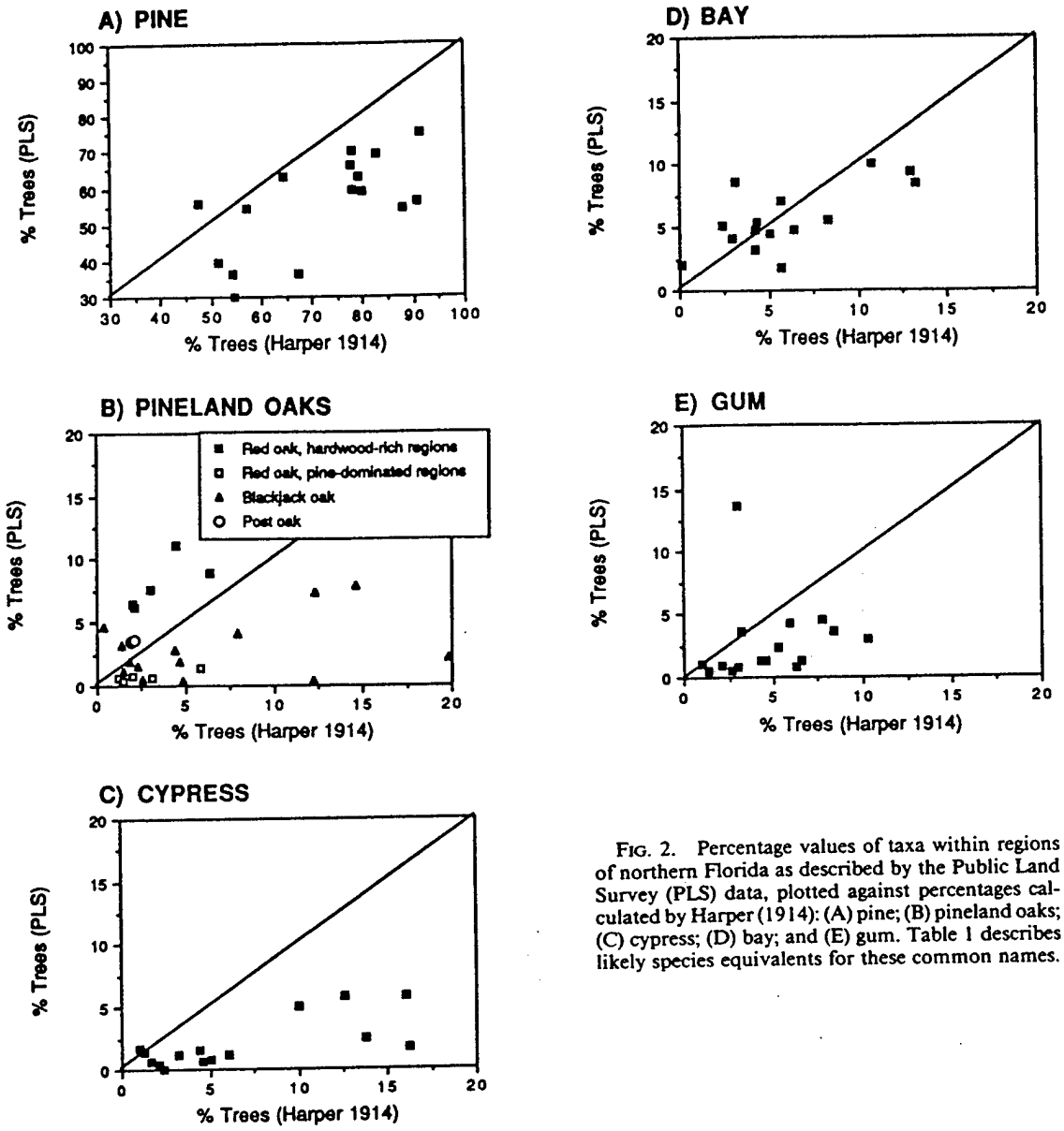


FIG. 2. Percentage values of taxa within regions of northern Florida as described by the Public Land Survey (PLS) data, plotted against percentages calculated by Harper (1914): (A) pine; (B) pineland oaks; (C) cypress; (D) bay; and (E) gum. Table 1 describes likely species equivalents for these common names.

resent: (1) a common pineland associate (*Q. laevis*) in an upland pine forest; (2) a pine characteristic of hardwood forests (*P. glabra*) in a hardwood forest that contains red oaks; or (3) a mixture of southern red oak (*Q. falcata*) with longleaf pine. This third possibility would be supported by frequent pine–oak–hickory communities (see *Species associations: Upland hardwood*, below). As a result of the potential confusion between species, I designated red oak to weight community classification equally toward pineland and upland hardwood communities.

Another two oaks (black oak, 451 trees; white oak, 382 trees) are primarily upland mesic hardwood species. Live oak (427 trees) may refer to *Q. virginiana*, *Q. geminata*, or possibly *Q. hemisphaerica*. While *Q. virginiana* and *Q. hemisphaerica* are primarily found in hardwood hammocks, *Q. geminata* may be found in xeric uplands in association with hardwoods or pine. Of all sites that contain live oak, 36% were categorized as pineland and 26% as upland hardwood based on other trees sampled, while 15% contained only live oak trees. These latter sites were classified in a xeric hardwood category (Table 4), by convention. Finally, the name "oak" is applied to an additional 958 trees (Table 1). Oaks, when not allowed to contribute toward classification of mixed-species sites, are distributed fairly evenly among the three basic community types (44% pineland, 33% upland hardwood, 23% forested wetland). One third of the locations containing oak contained only oak. By convention, these sites are classified in a xeric hardwood category (Table 4).

Of the major wetland species, cypress (*Taxodium*

ascendens and *T. distichum*, 3771 trees) and titi (*Cyrilla racemiflora* and *Cliftonia monophylla*, 1747 trees) are exclusively wetland species. The PLS routinely records a lower abundance of cypress than does Harper (Fig. 2C, Table 5). This pattern becomes problematic in determining the true abundance of cypress prior to settlement. Cypress often grows in standing water, beyond the realm of the surveyor's purview. Harper claimed he undersampled cypress in 1914 because of logging. Thus, cypress was probably undersampled by both studies, with Harper's estimates probably being closer to the true abundance. Determining the relative representation of titi between the data sets is problematic for two reasons. Harper treats titi as a small shrub and calculates percentage values differently (see *Introduction: Harper's (1914) data*, above). In addition, titi is abundant within only a few regions, providing a small sample for comparison.

Bay (5973 trees) may refer to any of five species in three genera (*Gordonia lasianthus, Magnolia grandiflora, M. virginiana, Persea borbonia*, and *P. palustris*). Of these species, Harper lists either *M. virginiana*, a wetland species, or *M. grandiflora*, an upland species, as more abundant than the other three species in all regions. Of these less common bays, only *Persea borbonia* is not strictly a wetland tree, being more typical of upland sites (Godfrey 1988). *Magnolia grandiflora* is likely to have been designated in the PLS as either bay or magnolia. A comparison between the data sets indicates that this taxon is underrepresented in the PLS when restricting the definition to magnolia (Table 5). Combining taxonomic categories of all five species of bay results in a uniform representation between the two data sets (Fig. 2D, Table 5). Accordingly, bearing trees of specific types of bay weighted the classification of the assemblage to the appropriate category, while the more generic term "bay" weighted the classification equally toward wetland and upland hardwood communities (Table 1). Sites that contained only bay trees were, by convention, classified as forested wetland.

Gum, black gum, and tupelo gum (*Nyssa* spp., 1948 trees) are predominantly wetland species. Sweetgum (*Liquidambar styraciflua*, 278 trees) appears to also have been recorded as "gum" in the PLS data. The frequency of sweetgum within regions is uniformly lower in the PLS data than is reported by Harper (Fig. 2E, Table 5). This discrepancy probably represents an increase in sweetgum in disturbed forests by the early 20th century. Sweetgum thrives in various situations, although it is not usually found in dry sites or on poor soils. One true gum, *Nyssa sylvatica* var. *sylvatica*, is usually found in well-drained rich soils. Unlike the other gums, however, *N. sylvatica* var. *sylvatica* and *L. styraciflua* rarely form single-species stands in upland sites (Godfrey 1988). I designated sites that sampled gum exclusively (0.9% of sites) as wetlands.

To estimate the relative abundances of species classified as "gum" by surveyors, I examined the relative abundance of *L. styraciflua, N. sylvatica* var. *sylvatica*, and all other *Nyssa*. Harper lists *Nyssa sylvatica* var. *sylvatica* as the least abundant of the gums in all regions. He cites *Liquidambar styraciflua* as more abundant than *Nyssa* spp. in regions dominated by hardwoods and areas more extensively settled (Table 4). This may be a result of the weedy nature of *L. styraciflua* and its ability to invade disturbed areas. When gum was excluded from contributing to the community classification of PLS sites, 83% of survey locations where gum was sampled in association with other species are classified as forested wetlands. This result supports the contention that Harper's data reflect a dramatic increase in *L. styraciflua* between the presettlement period and 1914. With these results, I designated "gum" as a wetland type, allowing *N. sylvatica* var. *sylvatica* and *L. styraciflua* in mesic sites to be misclassified.

The hickories (*Carya aquatica, C. cordiformis, C. floridana, C. glabra, C. ovalis, C. pallida*, and *C. tomentosa*) were recorded 853 times (0.66%, Table 1) in the PLS, never exceeding 10% of bearing trees in any one region. Nonetheless, hickory was overrepresented in the PLS with respect to Harper's results (Table 5).

Most hickories are upland species. Among the hickories, only *C. aquatica* is found in floodplain habitats. In no region does Harper designate *C. aquatica* as more abundant than the upland hickories. In fact, *C. aquatica* is only mentioned in two regions: the Apalachicola River Bluffs and Bottoms, where it is uncommon (0.1%), and the West Florida Lime-Sink region, where it is as uncommon as upland hickories (0.15%). The PLS data record 2.79% and 1.02% hickory in these two regions, respectively.

The remaining six species of hickory are all found in mesic-to-dry hardwood forests. *Carya ovalis* and *C. pallida* are rare and local to a small portion of the study area, while *Carya cordiformis* is a species of more northerly distribution and enters the study area only in the central panhandle of Florida along river courses (Godfrey 1988). Of hickories recorded at mixed-species locations, 73% were in association with oaks and other upland hardwoods. A total of 22% of bearing-tree locations that contained hickory recorded only hickory. These sites were classified into the xeric hardwood category.

Hickory, along with red oak in hardwood-rich regions, highlights a problem with discerning species abundances using the PLS data. Both hickory and red oak (in certain regions) are overrepresented in the PLS data with respect to Harper's estimates (Table 5). In contrast, the PLS data underestimate the abundance of small trees typical of mesic upland forests, such as ironwood and hornbeam. This pattern probably reflects the nonrandom selection of bearing-tree species by PLS surveyors rather than changes in the abundance of these species between sample dates.

The remaining major hardwood taxa are a diverse group of primarily rich mesic hardwood species, in-

cluding dogwood (*Cornus florida, C. foemina,* and *C. alternifolia,* 539 trees), maple (*Acer rubrum, A. saccharum,* and *A. saccharinum,* 349 trees [*A. negundo* is morphologically distinct and not included in this designation]), beech (*Fagus grandifolia,* 327 trees), holly (*Ilex opaca,* 309 trees), and sourwood (*Oxydendrum arboreum,* 220 trees) (Table 1). Of these taxa, maple was underrepresented by the PLS with respect to Harper (Table 5), possibly because maples are frequently small trees that may have been overlooked by PLS surveyors. The relative rarity of beech in the PLS, and its equitable sampling compared to Harper, is remarkable because its smooth bark is easily blazed and makes beech prone to oversampling by surveyors (Bourdo 1956). While beech is often cited as a codominant in mesic hardwood forests of the southeast, this species is patchy in distribution within the study area as it reaches its southern range limit there.

Among the primarily mesic hardwood taxa, the maples and dogwoods are each represented by a single wetland species (*A. saccharinum* and *C. foemina,* respectively). These genera are listed with upland hardwoods because the majority of mixed-species bearing-tree sites are associated with upland rather than wetland species (76% and 83%, respectively). Both maple and dogwood were occasionally recorded in single-species sites (43 and 76 sites, respectively). Harper lists dogwood exclusively as *Cornus florida.* Sites in which dogwood and maple are the only taxa recorded are counted as mesic upland sites, by convention.

Four species of ash (*Fraxinus caroliniana, F. pauciflora, F. pennsylvanica,* and *F. profunda,* 569 trees) are found in floodplain and river swamps. A fifth ash, *F. americana,* is an upland species. Mixed-species sites that included ash were dominated by other forested wetland species in 79% of cases. Harper lists wetland ash species as more abundant than the upland ash (*F. americana*) in all but the Apalachicola region.

Species associations

Pineland.—Pineland samples are separated into three categories: (1) pine only (71.45% of all sites), (2) a mixture of pine and oak (6.06%), and (3) pineland oaks (1.51%, blackjack or post oak) (Table 4). This is a somewhat conservative measure of total pineland habitats because some proportion of bearing-tree locations that recorded pine with other species may also represent primarily pineland habitat (e.g., pine–palm).

Pineland sites, while distributed throughout northern Florida, were less abundant in several regions (Fig. 3A). First, pinelands were less abundant along the floodplains of major rivers across the panhandle. Second, pinelands were less abundant in the several relatively small regions delineated by Harper (1914), namely Knox Hill, Holmes Valley, Marianna Redlands, Apalachicola River Bluffs and Bottoms, Tallahassee Red Hills, Gulf Hammock, and the Middle Florida Hammock Belt (Fig. 1A).

The Marianna Redlands have relatively rich calcareous soils (Schmidt 1979) that support a diverse hardwood forest (Platt and Schwartz 1990). The Tallahassee Red Hills region and Middle Florida Hammock Belt (western and central sections) contained extensive Native American agriculture (Clewell 1986) as well as Spanish missions (Tebeau 1980). By the beginning of the 19th century, agriculture had changed the landscape considerably to where it appears to have been dominated by xeric hardwoods (Clewell 1986). The Gulf Hammock region is underlain by limestone and dolomite (Knapp 1978*a*, Schmidt 1979) and was dominated by palm flatwoods and hardwood swamps.

Upland hardwood.—Upland hardwood sites are clustered in the Marianna Redlands, Tallahassee Red Hills, Apalachicola River Bluffs and Bottoms (see also Delcourt and Delcourt 1977) and near the Choctawhatchee River in the Knox Hill and Holmes Valley regions (Fig. 3B). Mesic upland hardwood assemblages (3.2%) contained the highest number of non-rare species (defined as a taxa with >50 occurrences). Problematic assemblages of mesic hardwood trees and species associated with other community types were frequent. A mixed pineland–upland hardwood classification describes 1.1% of PLS sample points. The majority of these sites were probably sampled from a hardwood community that contained pines other than longleaf (e.g., spruce pine). Those corners that contain both mesic and wetland hardwoods are classified into the mixed upland–wetland category (2.9%) along with corners that sample a diverse mixture of primarily wetland species.

Bearing-tree sample sites containing a mixture of oak and hickory, all oak, or all hickory were classified into a xeric upland assemblage (381 sites, Table 4). To assess the abundance of longleaf pine–oak–hickory assemblage, I tabulated corners that sampled exclusively: (1) pine, oak, and hickory (97 sites), (2) pine and hickory (16 sites), (3) oak and hickory (95 sites), (4) pine and oak (1855 sites), and (5) hickory (189 sites). All oaks with the exception of exclusively pineland oaks (blackjack and post oak) are included in this tabulation (Table 4). The combination of pine, oak, and hickory occurred on only 0.61% of four-tree PLS sample points. This figure is considerably less than the frequency with which pine was found with other mesic hardwood species (1.09% of sites, Table 4), indicating that these occurrences may be entirely explained by the presence of spruce pine (*P. glabra*) within oak–hickory assemblages.

This 0.61% figure underestimates the true amount of pine–oak–hickory assemblages. If pine, oak, and hickory were equally abundant and randomly distributed at a given location, the probability that a surveyor would sample a pine, an oak, and a hickory in noting four trees is 0.44 (the probability of choosing each of three equally abundant objects given four selections). If (1) surveyors were biased in the trees they selected,

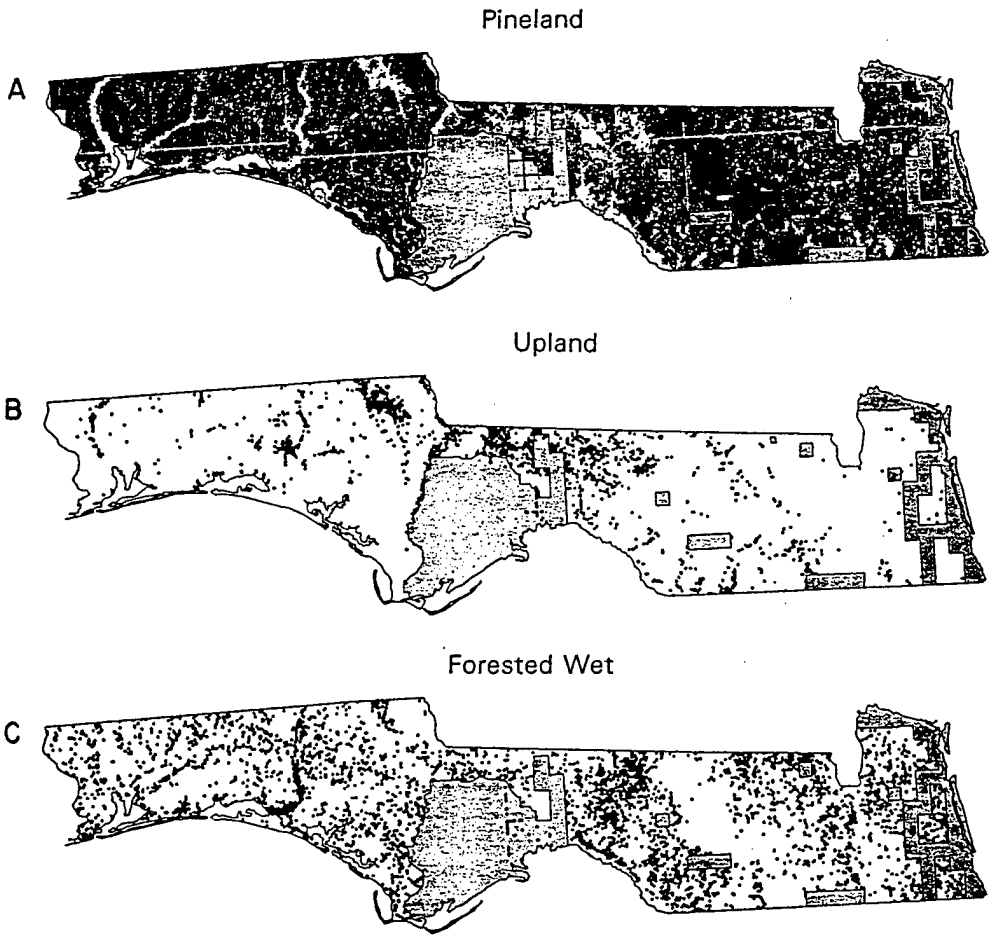


FIG. 3. The distribution of major plant associations in northern Florida as described by the Public Land Survey: (A) pinelands; (B) upland hardwoods; (C) forested wetlands. Black shading indicates the presence of a particular plant association, while white indicates its absence; grey shading indicates regions where data are lacking.

(2) the species differed in abundance, or (3) the species were not randomly distributed, then the probability that all three species would be sampled would be reduced.

While surveyor bias cannot be ruled out in undersampling this community type, we do have some evidence to suggest that it probably does not explain the paucity of pine–oak–hickory assemblages. Over two-thirds of bearing-tree sites that included pineland oaks (blackjack oak and post oak) were recorded in combination with pine. Neither of these oaks becomes large trees, indicating that surveyors would use these oaks as bearing trees within pineland communities, suggesting that surveyors would also use oaks and hickories in a mixed pine–oak–hickory assemblage.

A combination of pine, oak, and hickory may be sampled from: (1) a mixed hardwood forest that includes pines other than longleaf, (2) a transition zone between upland pinelands and oak–hickory hardwood forest, (3) a mid-successional community between hardwoods and longleaf pine, or (4) a stable longleaf pine–oak–hickory assemblage. The rarity of oak–hickory (0.2%) and pine–hickory (0.03%) assemblages supports the observation that, whatever the occurrences represent, pine–oak–hickory was very uncommon prior to settlement.

As mentioned above, the co-occurrence of red oak with pine may represent a mixture of *Q. falcata* with longleaf pine in an upland community. This would support the importance of pine–oak–hickory forest. Bearing-tree sites that sample a mixture of red oak with pine vary between 0 and 6.1% of all sites within regions; however, red oak–pine mixed samples exceed 1% only in regions where pine abundance is relatively low (Marianna Redlands, Apalachicola Bluffs, Knox Hill Country, Holmes Valley, Middle Florida Hammock Belt, Tallahassee Red Hills, and Wakulla Hammock Country). This pattern suggests that much of the red oak–pine mixtures represent pine within hardwood assemblages rather than red oaks in a longleaf pine assemblage.

Forested wetland.—Various types of forested wetlands are scattered throughout the region (Fig. 3C). These assemblages of species primarily found in for-

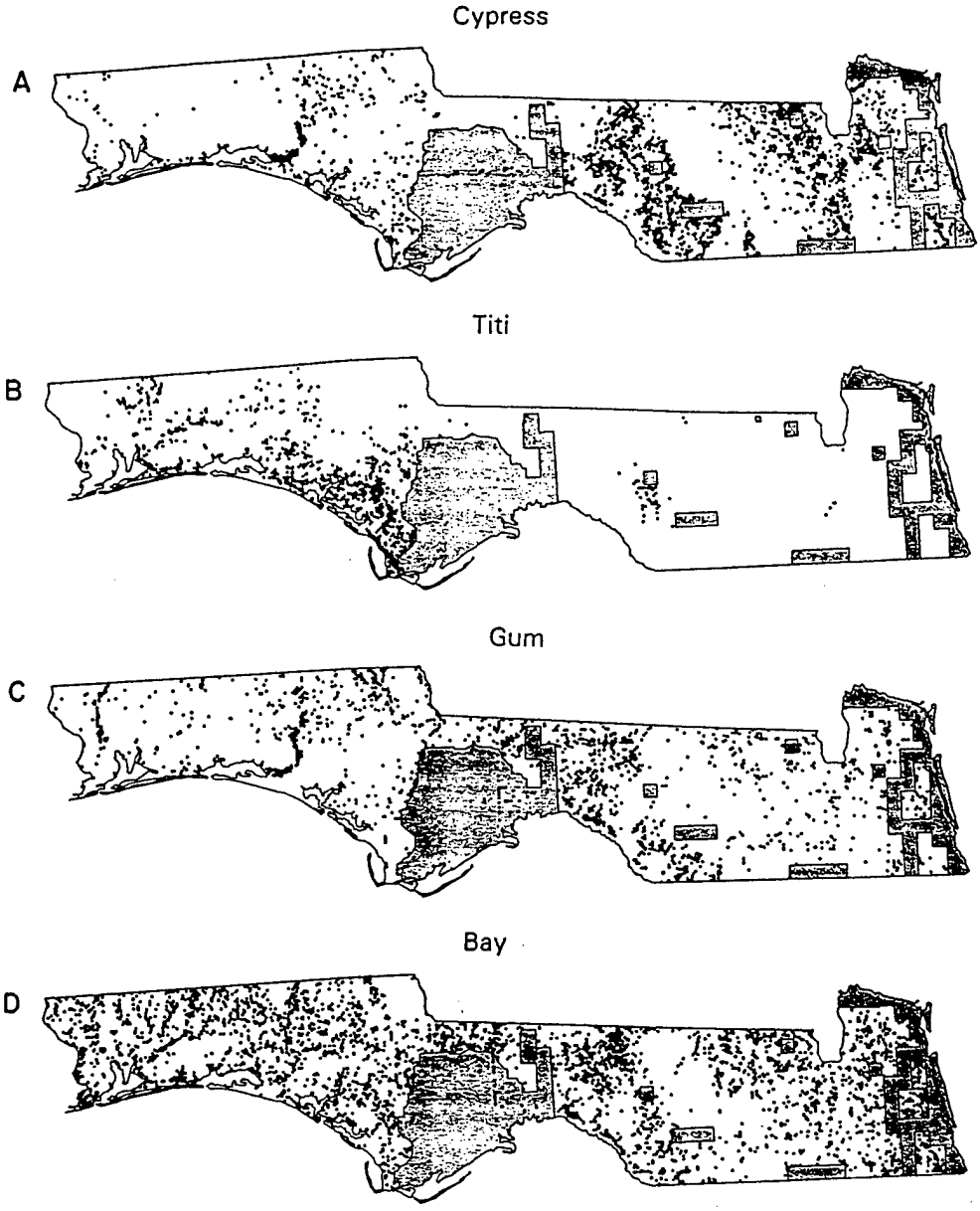


FIG. 4. The distribution of observations of major forested wetland taxa in northern Florida as described by the Public Land Survey: (A) cypress; (B) titi; (C) gum; and (D) bay. (Table 1 gives likely species equivalents for these common names.) Black shading indicates the presence of a particular plant association, while white indicates its absence; grey shading indicates regions where data are lacking.

ested wetlands can be divided into several categories. The major wetland species (bay, gum, titi, and cypress) are tabulated by single-species samples as well as in association with pine (Table 4). These pine–wetland associations (1.9%) could represent either ecotonal sites between wetlands and pineland or mixtures of lowland pines within a wetland community. Mixtures of wetland dominants such as cypress and bay, cypress and gum, and cypress and titi were grouped into the mixed upland–wetland type (2.9%). The mixed upland–wetland category also included mixed-species corners that were dominated by ambiguous wetland–mesic hardwood species (e.g., bay, dogwood, maple).

Of the major wetland species, cypress and titi were found to be distributed in a markedly nonrandom pattern. Cypress is found along major waterways and along the Gulf Coast, but most (63.1%) trees were found in the eastern portion of the study area where Cypress constituted 6.0% of all PLS trees sampled in the Gulf Hammock, Middle Florida Flatwoods, and East Florida Flatwoods regions (Fig. 4A). In contrast, most titi (63.5% of all recorded) were found in the West Florida

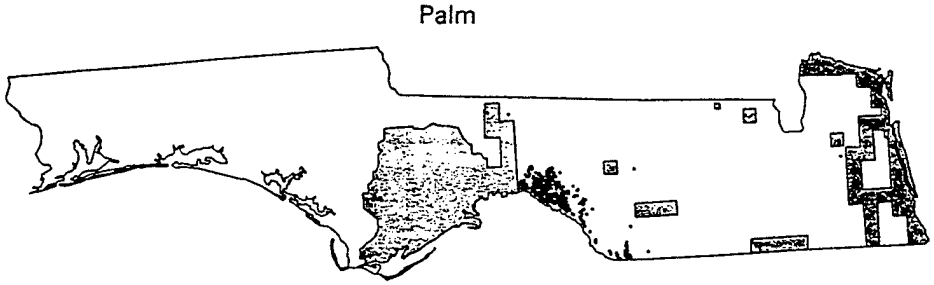


FIG. 5. The distribution of observations of palm in northern Florida as described by the Public Land Survey. Black shading indicates the presence of a particular plant association, while white indicates its absence; grey shading indicates regions where data are lacking.

Coast Strip, Apalachicola Flatwoods and eastern portion of the West Florida Pine hills regions where it comprised 7.2% of trees sampled in those regions (Fig. 4B). In contrast, gum (Fig. 4C) and bay (Fig. 4D) appear scattered throughout northern Florida, perhaps as a result of the broad taxonomic spread encompassed by this common name designation.

Palm.—Cabbage palm (*Sabal palmetto*) was sampled 508 times (0.39% of PLS trees) at 317 sites. Palm is primarily associated with other palm (102 sites), pine (97 sites), or oak (39 sites) (Table 4). Sites with palms are restricted to limestone/dolomite soils in the Gulf Hammock Region (Fig. 5).

Regional vegetation

For each region in which Harper presents quantitative data, I present a comparison of the abundance of all taxa that exceed 1% in either data set (Table 3). Both data sets rank pine as the most abundant taxa in all but one region (Table 3). Six of 17 regions demonstrated significant ($P \leq .05$) correlations of both percentage values (arcsine-transformed data, excluding pine as an outlier) and species ranks (using Kendall's τ) between the PLS and Harper's data sets (Table 3). There does not appear to be a pattern among regions demonstrating significant correlations between data sets with respect to the abundance of pine (Table 3). Finally, the data sets compare favorably in the overlap among the top five taxa by region (Table 3).

Principal components analysis (PCA, Wilkinson 1990) of vegetation samples within these 17 regions was used to further discern whether the PLS and Harper data sets described regional vegetation similarly. Owing to established differences in percentage data, PCA was run separately on each data set to discern whether the pattern of regions was depicted similarly. The first two principal components explained $\approx 50\%$ of the variance in both data sets (51.7% for Harper's data, 48.6% for PLS data). Plotting regional scores for the first two axes results in a fairly good comparison between the two data sets in depicting regions of similar nature (Fig. 6). In particular, the PLS data and Harper's survey compare favorably in distinguishing those regions with higher representation of hardwoods (Marianna Redlands, Apalachicola River Bluffs and Bottoms, Tallahassee Red Hills, and the Middle Florida Hammock Belt) and the region showing strong representation of palm (Gulf Hammock). Further, regions where Harper lists longleaf pine as the most abundant species and where the PLS data record pine as >65% of all bearing trees are clustered on the first two principal axes from both studies (Table 3, Fig. 6).

Two major differences between the data sets are highlighted by the PCA of vegetation values for Harper's regions. First, the Wakulla Hammock region (Table 3:13) is described by the PCA of Harper's data to be distinct from either hardwood-rich regions or pine-dominated regions, while the PLS data classified the region with pine-dominated regions. This discrepancy is likely to be a result of the small PLS sample for the region (220 trees); the majority of the Wakulla Hammock region falls within the Forbes Purchase and was not sampled by the PLS. The second difference is that the eastern portion of the Middle Florida Hammock Belt is described by Harper as similar to other hardwood-rich regions, while the PLS data place this region with pine-dominated regions. It is not clear whether this difference reflects temporal changes in vegetation with settlement or sampling differences.

Soil parent material.—Both species and communities were tested for nonrandom association with soil parent material as defined by the Environmental Geology Series (Knapp 1978*a*, *b*, Schmidt 1978*a*, *b*, 1979, Scott 1978, 1979). Section corners and midpoints were classified to one of the 10 soil parent material categories found within the study area (Table 6, Fig. 1C). I eliminated all PLS bearing-tree sites where I could not resolve discrepancies between adjacent soil parent material category. Three categories (peat, dolomite, and shell beds) are very rare and were eliminated from the test for vegetation affinity. The remaining seven soil parent material categories were tested against the seven most abundant species and the three basic community types.

In each case I found a significant nonrandom association of species and communities with soil parent material (Table 6). Pine was negatively associated with limestone/dolomite and fine sand, and positively with

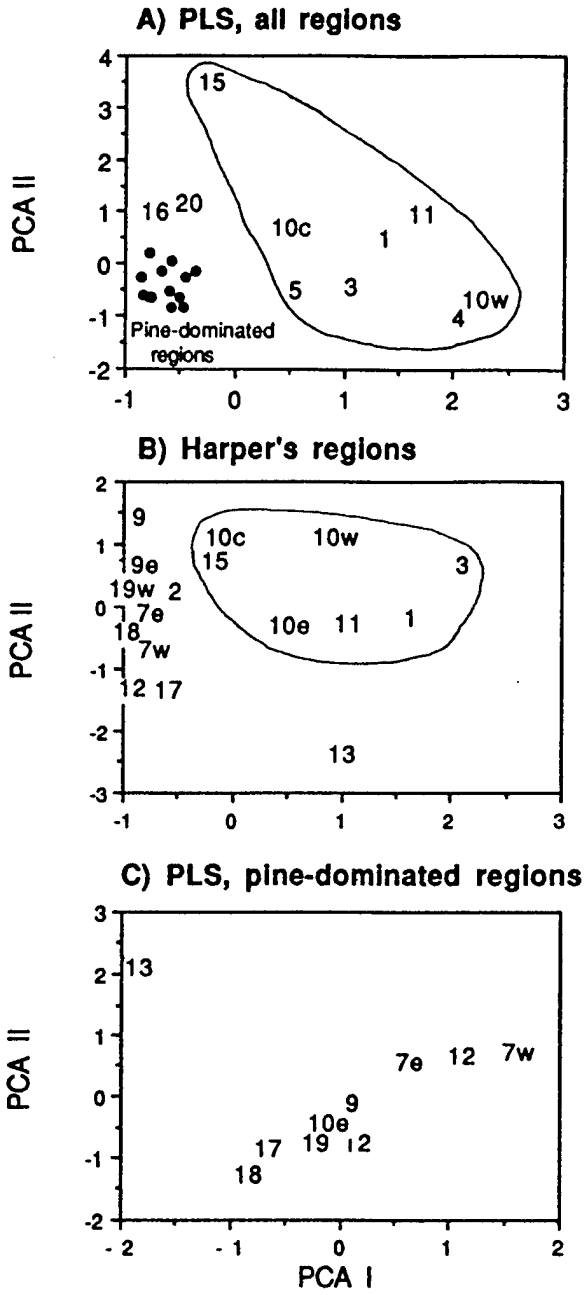


FIG. 6. Principal Components Analysis (PCA) site scores of vegetation regions of northern Florida. Regions are plotted by number (see Fig. 1 and Table 3 for region definitions and code number identification). (A) All regions using the Public Land Survey (PLS) data ; (B) all 16 regions for which Harper (1914) presents quantitative data; (C) the 14 pine-dominated regions using the PLS data. All taxa that exceed 1% of all trees sampled in at least two regions were used for the PCA on both PLS data (25 taxa) and Harper's data (34 species). Circled samples include the regions rich in hardwood forests, as described by both data sets; these are highlighted to illustrate similarities in the ordination between data sets.

limestone and gravel and sand. The most common oaks (blackjack and red oak) also show a negative association with limestone/dolomite but are distinct from one another with respect to most other soil categories (Table 6). Upland hardwoods have negative associations with gravel and sand and with shelly sand and clay, with a positive association with clayey sand and limestone. Forested wetland was associated with five of the seven common soil types. The strongest associations are with limestone/dolomite (positive), fine sand (positive), and gravel and sand (negative). Titi and bay contributed most to the positive association of wetlands with fine sand, while cypress and gum contribute to the association with limestone/dolomite.

CONCLUSIONS

Historical accounts cite longleaf pine as abundant in presettlement north Florida (Bartram 1791, Williams 1827, 1837). Harper (1914) considered pineland to be the dominant vegetation type in northern Florida even in the early 20th century. Previous vegetation reconstructions using the same Public Land Survey (PLS) data of small portions of this study area have indicated pineland to be less dominant. Delcourt and Delcourt (1977) summarized survey data from four townships along the Apalachicola River and found that hardwood forests were more abundant in presettlement times than they are today. Likewise, Clewell (1986) used PLS data to describe vegetation in a region north of Tallahassee and found a mixture of pine, oak, and hickory dominated the region (although few individual sites contained a mixture of pine with oak and hickory). Clewell attributes this abundance of oak and hickory to the abandonment of agriculture by Miccusukee Indians. Extensive agricultural fields in this region were abandoned after 1704 (Clewell 1986). Notably, this is also the only inland region significantly settled by the Spanish through missions (Tebeau 1980). The PLS appears to have sampled this region at a time of successional recovery from old field. Alternatively, the presence of the pine–hardwood mixtures in this region may be a result of local edaphic conditions. Davis (1967) presents a map of presettlement vegetation for Florida that depicts north Florida as being predominantly a mixed pine–hardwood region.

The PLS data presented here support the regional abundance of hardwoods in the study areas of Clewell (1986) and Delcourt and Delcourt (1977) but show that results from these areas do not pertain to the majority of northern Florida. This study supports the historical reports (e.g., Bartram 1791) and early quantitative measures of community abundance (Williams 1827, Harper 1914) in finding pineland as the heavily dominant community type in northern Florida. This work is also supported by paleoecological studies from the region, which show a dominance of pine in the region over the past 7000 yr (Watts 1971, Delcourt 1980, Watts and Stuiver 1980, Watts et al. 1992).

TABLE 6. Chi-square tests of the association† of the major presettlement community types and species in north Florida with the seven major soil parent material types. Each vegetation category is treated separately.

Species association Species	Soil parent material type‡							
	Fine sand	Clayey sand	Sandy clay	Shelly sand and clay	Gravel and sand	Limestone	Limestone and dolomite	Chi-square
Pineland	−	0	0	0	++	0	−−−	256.8***
Pine	−−	0	0	0	+	+	−−	115.0***
Blackjack oak	+	−−	+++	−	+++	−−	−−	1190.8***
Red oak	−	++	0	−	−	0	−	237.8***
Upland hardwood	0	+	0	−	−−	+	0	123.4***
Forested wetland	++	0	0	+	−−	−	++	626.1***
Cypress	0	+	−−	0	−	0	+++	349.2***
Gum	+	−	−	0	−	0	+++	380.7***
Bay	++	0	+	++	−−	−−	+	272.4***
Titi	+++	−	+	−	0	−−	−	567.0***

*** $P < .001$ (df = 6, critical $\chi^2_{.001} = 22.5$).

† Symbols represent magnitude and direction of the association between soil type and species. This relationship is expressed in proportion to the individual cell contribution to the test-wise chi-square. −, +: Chi-square deviation is more than half of the critical $\chi^2_{.001}$ (i.e., >11.3); −−, ++: Chi-square deviation more than twice the critical $\chi^2_{.001}$ (>45.0); −−−, +++: Chi-square deviation more than five times the critical $\chi^2_{.001}$ (>112.5); 0: χ^2 contribution is small, indicating no association.

‡ Excludes three rare soil types (peat, dolomite, shell beds).

It is interesting to note that the historical descriptions of forest composition and structure, often dismissed because they are anecdotal, were quite accurate in northern Florida. It was later ecological studies, perhaps influenced by Clementsian views of plant communities and succession, that seem to have obfuscated the importance of pine in the vegetation of northern Florida.

Florida contains the second largest acreage of corporate tree farms for pulp production, virtually all of which is in northern Florida (Fernald 1981). The vast majority of the original longleaf forest has been converted to pine plantations for pulp production or other uses. Thus, fragmentation of natural communities has been extensive. However, the relative amount of habitat fragmentation has been much greater for those remaining pineland (particularly longleaf pine) patches than for the naturally fragmented patches of wetland and hardwood forests.

Those regions with greater abundance of hardwoods are associated with: (1) river basins such as the Apalachicola River Bluffs and Bottoms region (as studied by Delcourt and Delcourt 1977); (2) abandoned Native American agricultural fields such as in the Tallahassee Red Hills (as studied by Clewell 1986); (3) regions with unusual soil types such as the limestone-rich Marianna Redlands or the palm-rich limestone/dolomite-dominated Gulf Hammock region, or (4) extensive coastal lands and wetlands.

The rarity of mid-successional communities such as pine–oak–hickory and the association of most upland hardwood communities with areas of richer soils or wetlands suggest that the distribution of small pockets of hardwood habitat was relatively stable. In contrast, paleoecological data show that the matrix of upland vegetation has fluctuated between dominance of pine and oak over intervals of several thousands of years through 33 000 yr BP (Watts et al. 1992). This interpretation of stable hardwood communities in fire-protected areas runs counter to the hypothesis that the abundance of pine was, in part, a result of the abandonment of Native American agricultural fields (Quarterman and Keever 1962). Under Quarterman and Keever's hypothesis, we would expect more sample locations with trees indicative of transitional assemblages between pineland and upland hardwood forest. Further, north of Tallahassee, the single region where we have a record of agriculture abandonment, pine is less common than average—exactly the opposite of what this hypothesis predicts.

This study reaffirms Harper's observations on the general locations of forests dominated by wetland and hardwood species. This study differs somewhat in that Harper lists higher abundances of non-pineland species than does the PLS data. However, the PLS data is both earlier and more systematically collected. Both studies confirm the modern observation that mesic hardwood and wetland associations contain most of the woody species of northern Florida.

The PLS data go beyond the species abundances presented by Harper (1914) to demonstrate that mesic hardwood and wetland communities were clustered by soil type and were contagiously distributed (Schwartz 1990). These data demonstrate that most populations of hardwood species in northern Florida were relatively small, fragmented, and patchy in distribution. The species-rich upland hardwood forests of northern Florida have long been noted for the high frequency of endemics (Harper 1948, Hubbell et al. 1956, Neill 1957, James 1961). A suite of persistent hardwood forest refugia, isolated within a matrix of pine and protected from fire, could allow the persistence of isolated populations.

Isolation during periods of pine dominance, along with long-term fluctuations in the composition of the surrounding matrix (Watts et al. 1992), may have facilitated speciation events and given rise to the large numbers of sparse endemic species found in northern Florida at the present time.

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Seasonal Effects of Prescribed Burning In Florida: *A Review*

Louise E. Robbins and Ronald L. Myers

The Nature Conservancy
Fire Management and Research Program
Tallahassee, Florida

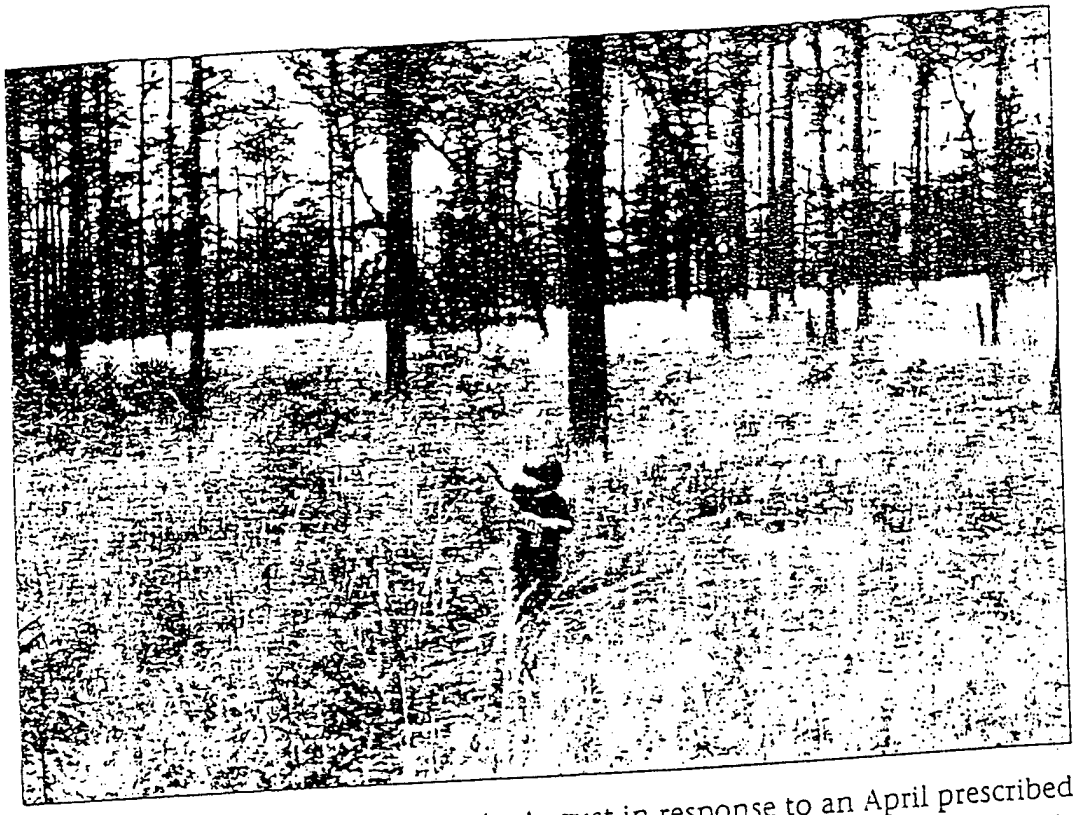
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Wiregrass and forbs flowering in August in response to an April prescribed burn, Janet Butterfield Brooks Preserve, Hernando County, FL. This preserve is managed by The Nature Conservancy to maintain an example of the upland longleaf pine-wiregrass ecosystem. A varied burn regime is applied to this site. The burn schedule is determined by the procedure outlined in Appendix II of this report.

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INTRODUCTION

Prescribed burning should be completed before the start of the spring fire season, about March 1 (Bickford and Newcomb 1947, p. 21).

During the past several decades, prescribed burning has become an accepted management practice for southeastern pine woods. In the 1940s, when foresters first started using prescribed fire, they viewed it not as a natural part of the ecosystem being reinstated after years of suppression, but as a tool that could produce desired results; without it hardwoods would eventually replace the commercially valuable pines. As the above quote illustrates, prescribed fire was clearly distinguished from natural fire. In particular, foresters drew a sharp line between the preferred season for prescribed burning (winter) and the "natural" fire season (after March 1).

Over the past 30 years this sharp division has dulled somewhat. Foresters in the Southeast found that growing-season fires were better at controlling the hardwoods land managers were continually battling and began conducting some burns during the spring and summer, while still primarily following the traditional winter-burning schedule. Range scientists found that late spring and summer fires promoted flowering of native grasses, and as early as 1943 suggested possible changes in burning of range lands (Biswell and Lemon 1943). Environmentalists began pressing for reinstatement of a natural fire regime in Florida's national and state parks and forests. In 1977 the Florida Park Service instituted a policy of burning only during the "lightning season," and the U.S. Forest Service's recent vegetation management plan for the Coastal Plain/Piedmont states that "growing season burns will be allowed to maintain certain fire-dependent ecosystems" (U.S. Forest Service 1989b, p. 6).

In response to these changes, critics charged that summer fires kill pine trees, destroy bird nests and wildlife habitat, and are more difficult to control. Unfortunately, a lack of well-designed studies concerning many aspects of burning at different seasons has induced proponents of both viewpoints to bolster their arguments with unsupported assertions.

The goal of this report is to attempt to separate fact from fiction. First we review the history of fire in Florida. We delineate the lightning fire season, discuss the effect of burning by Native Americans, and outline the changes in fire regime after European settlement. In the following sections we summarize data concerning the effect of different seasonal fire regimes on soils, flora, and

fauna. The final two sections include an outline of how to plan burn schedules to meet particular objectives and practical guidelines for conducting prescribed burns at different seasons.

Our intention is not to recommend a preferred season for prescribed burning. Rather, we present information regarding the effects of burning at different seasons so that managers can make their own decisions about how to achieve specific goals. These decisions will still be far from straightforward. We have not provided cookbook-style guidelines for several reasons. First, nothing is known about the effect of fire season on a number of species or communities, and the data we do have are, in many cases, incomplete or unreliable. We hope this report will spur researchers to fill some of these gaps. Second, seasons are broad time periods encompassing a range of weather conditions and phenological stages of plants and animals; fires occurring at different times within these seasons will have different effects. Third, season is only one of many factors determining how fires affect flora and fauna; others include amount of fuel and its moisture content; weather conditions before, during, and after the fire, and ignition pattern. Factors such as these may accentuate, diminish, or interact with seasonal effects. We hope this report will remind managers that fires are complex and often unpredictable; season of burn is rarely the sole determinant of the effect of a fire.

Before continuing we should define what we mean by season. "Winter," "dormant season," and "cold season" are often used synonymously, as are "summer," "growing season," "warm season," and "lightning season." We prefer the terms "growing season" and "dormant season" because they are the most biologically meaningful. The growing season in most of Florida extends from approximately mid-March through early September. South Florida seasons are more appropriately divided into wet season (mid-May to October) and dry season (November to mid-May). Another term we use is "wildfire season." This term refers to the time of year when wildfires (originated either by lightning or by humans) have consistently burned the greatest amount of acreage in Florida. For most of the state this period roughly corresponds to early growing season (March, April, May, and June).

FIRE HISTORY

Before European Settlement

Discussions of when to conduct prescribed burns often center on when fires have historically occurred. Many biologists and others interested in managing natural areas believe that native species should respond best to a fire regime that mimics the frequency and season of "natural," pre-settlement fires. When did these fires occur? The answer depends on one's definition of "natural." Some use the term strictly for lightning fires, while others include anthropogenic fires.

Lightning fires have probably been occurring for millions of years, while Native American Indians have inhabited Florida for approximately 12,000 years (Milanich and Fairbanks 1980). Lightning fires have undoubtedly been the primary selective force favoring the evolution of fire-adapted traits in the plants and animals of the Southeast, but one cannot dismiss the possible effect of Indian fires. Extensive, consistent burning by Indians in a pattern different from that of lightning fires could constitute a strong selective force, and examples exist of plants evolving local genetic adaptations in periods on the order of a few hundred years (see Hamrick 1982). Even if the Indians' burning practices did not genetically alter native species these practices could, however, have altered aspects of the landscape such as the relative proportion of pyrogenic and nonpyrogenic vegetation. Thus, land managers interested in restoring conditions present in Florida at the time of European discovery may want to know how extensive Indian fires were and when they occurred. In the following sections we discuss evidence concerning the seasonal distribution of fires ignited by lightning and by Native Americans.

Lightning

> *...on the nine and twentieth of August a lightning from heaven fell within halfe a league of our Fort, more worthy I beleeve to be wondered at, and to bee put in writing, then all the strange signes which have bene seene in times past, and whereof the histories have never written. For although the medowes were at that season all greene, and half covered over with water, neverthelesse the lightning in one instant consumed above five hundred acres therewith, and burned with the ardent heate thereof all the foules which tooke their pastime in the medowes, which thing continued for three dayes space...* (de Laudonniere 1587; near Fort Caroline, Florida, p. 31).

De Laudonniere's awe at Florida's violent weather was shared by other early explorers. One of the earliest, Alvar Nunez Cabeca de Vaca (who pre-dated De Soto by 11 years), observed while approaching the region near present-day Tallahassee, "many of the standing trees were riven from top to bottom by bolts of lightning which fall in that country of frequent storms and tempests" (Nunez Cabeca de Vaca 1542, p. 33).

It is no wonder that these explorers were impressed. Florida has the greatest number of thunderstorm days per year in the United States (U.S. Dept. of Agriculture 1941). (A thunderstorm day is defined as a day in which thunder is heard at a recording station.) This number varies from 70 in northeast, extreme southern, and western Florida to over 90 in the interior of the peninsula south of Lake Okeechobee (Jordan 1984).

As any Floridian knows, thunderstorm activity is not constant throughout the year; more thunderstorms occur in the summer, when sea breezes breed afternoon convective storms (Chen and Gerber 1990). The mean number of thunderstorm days per month (averaged over the entire state) increases from 6.6 days in May to 12 in June, 17 in July, and 16 in August, decreasing to 10 in September (Davis and Sakamoto 1976). The number of thunderstorm days during the peak months of July and August varies from a minimum of 13 to 15 per month in Key West, Jacksonville, and Apalachicola to a maximum of 21 to 23 in central Florida (Jordan 1984, Davis and Sakamoto 1976). The percentage of the annual total occurring during the winter varies from five percent in South Florida to 15 percent in western Florida (Jordan 1984), with an average of one to two thunderstorm days per month (Chen and Gerber 1990).

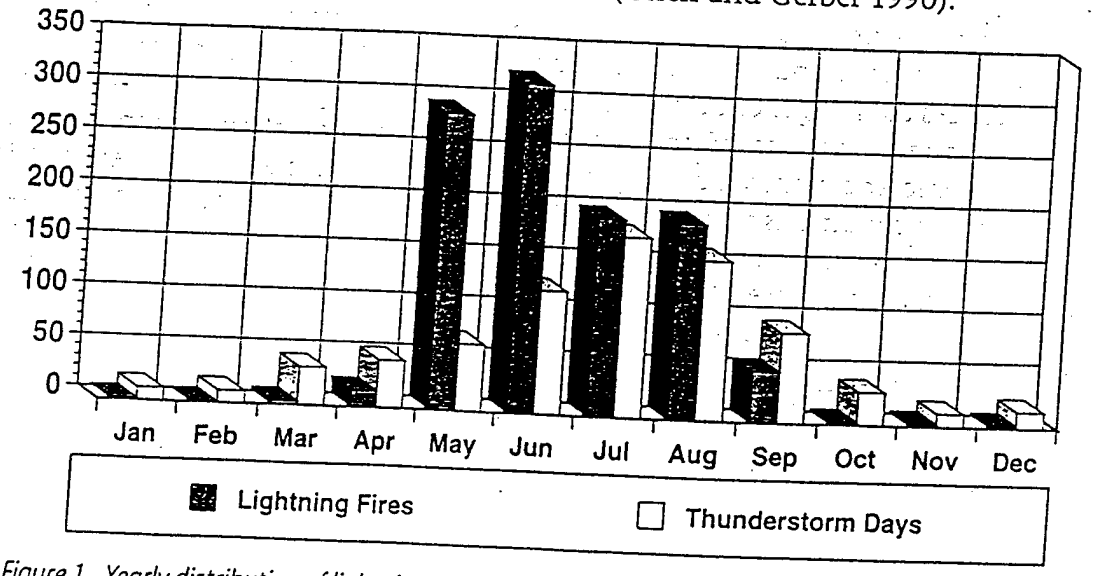


Figure 1. Yearly distribution of lightning fires and thunderstorm days in Florida. Numbers indicate totals for 1962 and 1963 combined. Lightning fires peak in May and June, while thunderstorm occurrence is greatest in July and August. From Komarek (1964).

Geographical and seasonal distributions of thunderstorms do not necessarily parallel corresponding distributions of lightning fires. Lightning fires in Florida are most common in May and June, despite the fact that more thunderstorms occur in July and August (Figure 1) (Komarek 1964). We discuss the reason for this discrepancy below. Data compiled from the National Forests in Florida (Figure 2), all of which are in northern Florida, and from the Everglades in South Florida (Figure 3) show the same general trend with a few variations. Before discussing these figures we should point out that these data

must be interpreted cautiously for several reasons. First, because we have not statistically analyzed these data, we can make only very general comparisons among months, fire source, and location; 20- to 30-year averages obscure a great deal of annual variation. Second, data on acreage burned show only the number of acres burned before the fire was suppressed, not the acreage that would have burned under natural conditions. Third, only fires that were observed are recorded. Many small lightning fires, particularly during the peak lightning period, may go unnoticed or unreported if they do not create a fire-control problem. Finally, winter prescribed burns and man-made barriers such as roads and canals may reduce the acreage available for lightning fires to burn.

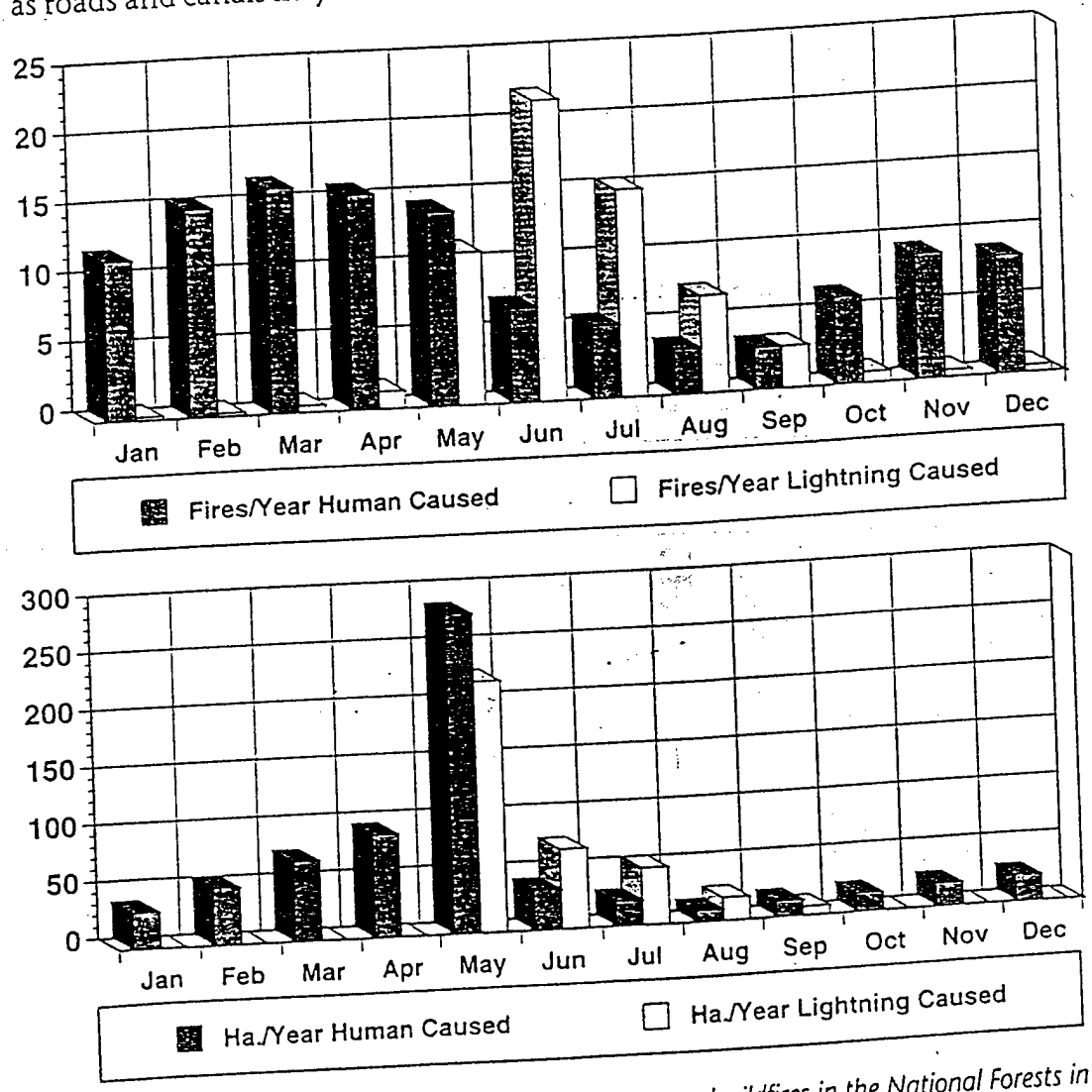


Figure 2. Yearly distribution of lightning- and human-caused wildfires in the National Forests in Florida, 1968-1987 (compiled from USDA Forest Service fire records). Human-caused wildfires occur throughout the year, but a greater number are ignited during the dormant season. Lightning fires occur year-round, but the vast majority occur during the growing season. In either case, the important statistic is not occurrence but rather area burned. Regardless of ignition source, the greatest area burned occurs in May—the height of the spring drought.

Nevertheless, some patterns are evident. In the national forests the number of fires appears to be greatest in June and July, with almost all lightning fires occurring between May and September (Figure 2). The area burned per fire is highest in May and diminishes through the rest of the summer. This large peak in May is caused primarily by a several-thousand-acre fire that occurred in 1977. Large fires are probably typical occurrences in May because of dry conditions, but the data presented here are insufficient to confirm this trend.

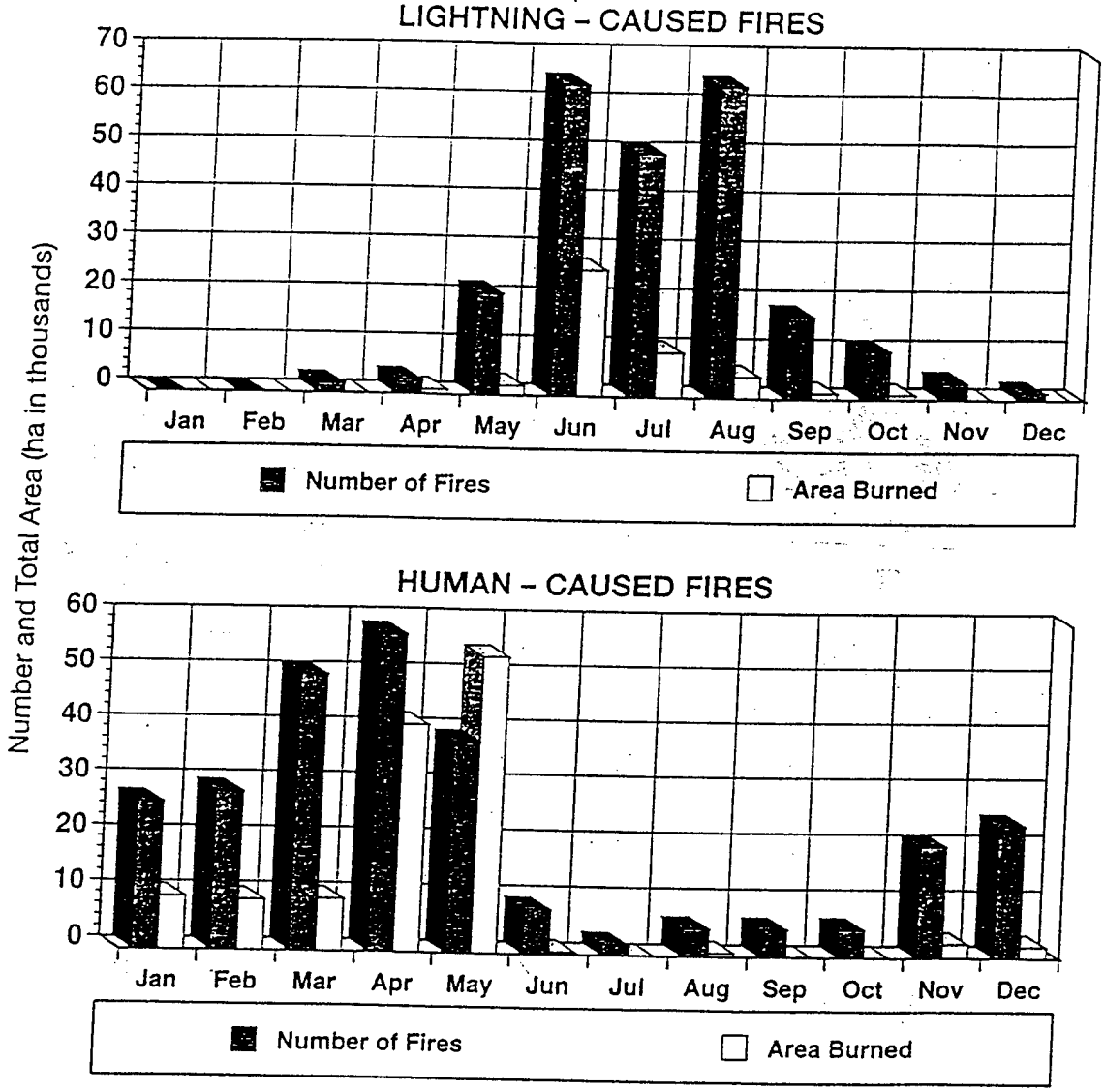


Figure 3. Yearly distribution of lightning- and human-caused fires in Everglades National Park, 1948-1981. The number of ignitions and area burned exhibit the same seasonal pattern as in Figure 2. From Snyder et al. (1990).

Data for South Florida from 1948 to 1981 show similar patterns, although the area burned appears to peak in June and decrease through September (Figure 3). Human-caused fires peak in May. J. R. Snyder (Big Cypress National Preserve, pers. comm.) speculated that many of these May fires were actually

caused by lightning rather than humans. Those responsible for classifying fires early in the recording period may have assumed that May fires were human caused because many people are still out in the backcountry at that time and the summer thunderstorm season is just beginning.

As we have seen, the peak number of lightning fires occurs about a month earlier than the peak number of thunderstorm days. Similarly, acreage burned by lightning fires does not strictly parallel the distribution of numbers of fires;

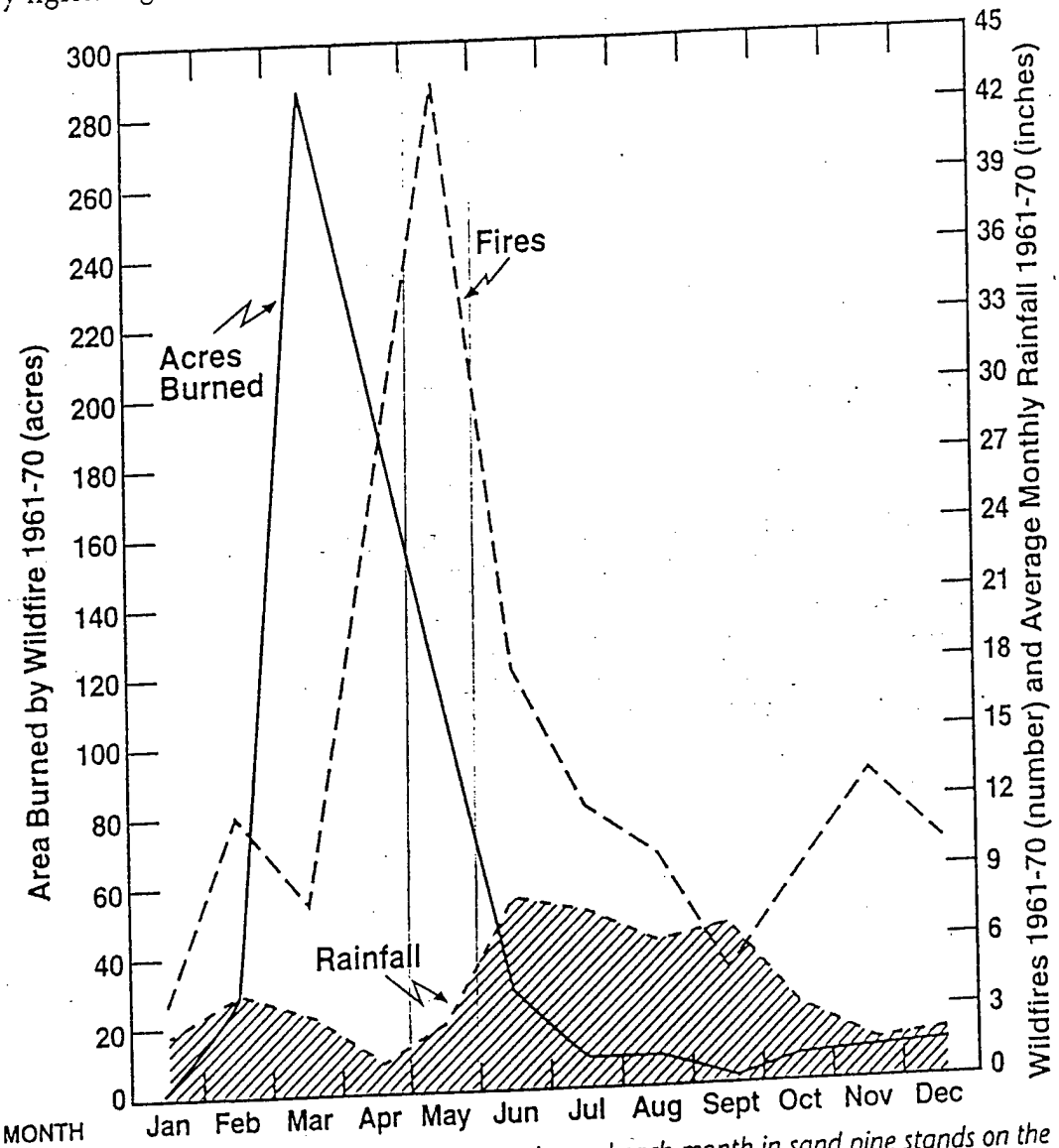


Figure 4. Total number of wildfires and acreage burned each month in sand pine stands on the Ocala National Forest and average monthly rainfall at Orlando, Florida, from 1961 through 1970. The early growing season peaks in acreage burned and number of fires coincide with both limited rainfall and a period of high flammability of sand pine needles. From Hough (1973).

area per fire is greater earlier in the summer. What is responsible for these discrepancies? The most obvious explanation is rainfall. Fuel moisture is one factor determining both whether a lightning strike ignites a fire and how large

the fire gets (Pyne 1984). Lightning strikes in Florida may tend to ignite and burn large areas early in the lightning season because surface fuels have not yet become moisture laden by daily rainstorms. In northern Florida, April and May are usually the driest months because they fall between a winter rainfall peak and a higher peak in summer (Jordan 1984). The winter rainfall peak gradually diminishes toward the south, giving South Florida a wet season/dry season climate, with almost all the rain falling between May and October (Jordan 1984).

Another factor that may affect the seasonal distribution of fire is the moisture content of live vegetation. The moisture content in needles and leaves of sand pine and some other species is lowest in spring, possibly contributing to the large number of fires and acreage burned at that time (Figure 4) (Hough 1973).

Other seasonally-varying factors may influence the occurrence of lightning fires. For example, trees are reported to be better conductors during the growing season when the moisture content inside the tree is high (Viemeister 1961); whether or not this higher conductivity increases the chance of lightning strikes and ignitions is not known. Lightning itself is variable, some types of strokes apparently being more likely to start fires than others (Viemeister 1961, Fuquay et al. 1967). This variation could have a seasonal pattern, though we know of no research on the subject.

In summary, thunderstorms in Florida occur primarily from May to September and peak in midsummer. Lightning fires occur during the same time period, but tend to peak about a month earlier. The pattern of area burned is similar to that of numbers of fires, but tends to be skewed even more toward the early growing season, with a late spring/early summer peak. Lightning fires are uncommon, but do occur, from November to March.

What evidence is there that the seasonal pattern of lightning fires we see today is similar to what existed in the past? We do know, from charcoal found in ancient lake sediments, that fires have occurred in North Florida for at least 25,000 years and in South-central Florida for at least 50,000 years (Watts and Hansen 1988; these are the earliest dates for which cores have been obtained). Watts and Hansen (1988) speculate, based on charcoal density, that fires were common from about 50,000 to 20,000 years ago, decreased in frequency, and then became more frequent about 12,000 years ago. We can guess that larger areas burned before roads, cities, agricultural fields, and fire plows impeded the spread of fires. And, although we do not know the details of the weather patterns, we do know that 18,000 years ago summers were warm, winters were cool, and the temperature of the ocean was not much different than it is today (Watts and Hansen 1988). These conditions probably generated summer thunderstorms just as they do now. Thus it appears that summer fires have been affecting Florida's vegetation for many thousands of years.

Indians

I feel, however, that the Indian who lived on the "natural livestock," ranging from grasshoppers to bison, probably did use summer fires (Komarek 1965, p. 195).

Archaeologists tell us that the Indians probably burned the woods at every opportunity.... It is logical to assume that most of this burning was done in the wintertime after the first frost (Perkins 1971, p. 60).

It is doubtful that [indigenous peoples] practiced winter burning because the slow response of vegetation during the non-growing season would have meant longer distances to travel for game (Dye 1985, p. 7).

Because logic can lead to different conclusions about the Indians' use of fire, we would like to review some of the historical evidence regarding Indian burning practices. Before doing so, however, we briefly address the question of how many Indians lived in Florida at the time of European contact. If, as some have suggested, there were so few that they could have had little impact on the environment, then the question of how and when they used fire becomes moot.

A major difficulty in estimating the original size of aboriginal populations is that by the time Europeans began counting them, the Indians had been decimated by diseases brought from abroad. There had been a long-standing assumption that Florida's aboriginal population was very low (approximately 10,000), and estimates at this level have continued until very recently [see Hann (1988) for a discussion of aboriginal population estimates]. Assuming a substantial population decline due to various European diseases, Dobyns (1983) estimated a total population of 700,000 to over 900,000 for three northern Florida tribes, the Timucua, Calusa, and Apalachee. Dobyns' methods and assumptions have been questioned, however, and these numbers are probably too high (Hann 1988). Milanich and Fairbanks (1980) estimate the native population of Florida at the time of European contact to be at least 100,000, with approximately 25,000 Apalachee in the northwest (see also Hann 1988) and 40,000 Timucua in the northeast. They also conclude, based on the limited number of artifacts from the very early period, that the population was quite small from 12,000 B.C. to 6,500 B.C. (Many settlements may have been in areas that are now underwater, however.)

Were indigenous peoples too few to have significantly altered the Florida landscape with their burning practices? We don't know, but to put the question in perspective, the population of the Territory of Florida in 1830 was only 34,730 (Fernald 1981). It grew to 140,000 by 1860 and reached 500,000 by 1900. Thus, during the 1800s when woodsburning was pervasive throughout the South [see Pyne (1982) and the next section], the populace doing the burning was not much different in number from the pre-Columbian population.

Florida Indians comprised several tribes scattered throughout the state. [See Hudson (1976), Larson (1980), Milanich and Fairbanks (1980), and Hann (1988) for more information on their distribution and culture.] Those in the

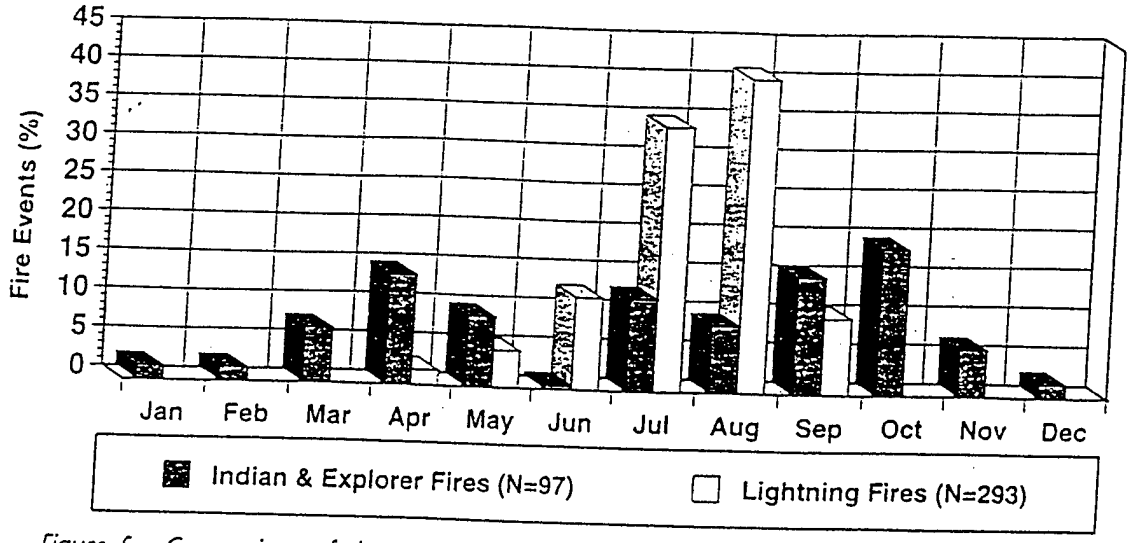


Figure 5. Comparison of the monthly distribution of recent lightning fires to historical fire accounts, northern Great Plains. Note that seasonal distribution of anthropogenic fires does not coincide with that of lightning fires. From Higgins (1986b).

north and around Lake Okeechobee cultivated maize, squash, and other crops, while coastal tribes in South Florida were primarily hunter-gatherers. We will never know for sure what impact they had, but it seems reasonable to conclude that, given their numbers, distribution, and activities, Florida Indians, like other aboriginal peoples, had a significant effect on their environment.

In his review of the use of fire by Australian aborigines and the Indians of northern and western North America, Henry Lewis (1982, p. 45) concluded that "one of the most important general features of aboriginal applications of fire is that they differed significantly from natural fires in terms of seasonality, frequency, intensity, and selectivity." He argues that aboriginal peoples used fire to manipulate their environment, often by creating habitats that would not have existed, or would not have been as common, under natural conditions. Altering the season in which fires occurred was one of their most powerful tools. For example, in northern Alberta, lightning fires are most common from midsummer to early autumn, but most Indian fires were set in early spring (Lewis 1982, p. 49). Higgins' (1986b, p. 8) summary of burning by northern Great Plains Indians also showed that "[they] did not pattern their use of fire with the seasonal patterns of lightning fires" (Figure 5).

Did Florida Indians follow this same pattern of burning outside the natural fire season? Unfortunately, we cannot conduct personal interviews as Lewis did in Alberta or put together several hundred eye witness accounts as did Higgins. The Indian tribes that existed at the time of European contact are now extinct (having been annihilated by disease and warfare), and we have relatively few accounts of Indian life before disruption by European settlement. The data we have, summarized below, suggest that Florida Indians did burn outside the lightning season, but we do not know how widespread these fires were or what effect they had on the environment.

Southeastern Indians used fire to clear fields for cultivation, to drive game, and as a means of communication (de Laudonniere 1587, Lawson 1714, Swanton 1946). Rene de Laudonniere, commander of the French troops at Fort Caroline (near the mouth of the St. John's River) observed that the Indians let their maize fields lie fallow for 6 months; then in March, before sowing, "they set the weedes on fire, which grewe up the 6 moneths, and burne them all (de Laudonniere 1587, p. 455). A century later, Coreal reported that Florida Indians burned off the brush twice a year, in March and July, before planting (Braudel 1817).

A second common use of fire was for signalling. When de Laudonniere and his crew discovered an extensive lightning fire, they first thought it had been set by the Indians: "wee thought that they had discovered some shippes in the Sea, and that according to their custome they had kindled many fires here and there, to signifie that their Countrey was inhabited" (de Laudonniere 1587, p. 7). D'Iberville, who explored along the Gulf Coast and the Mississippi River around 1700, described a similar fire. In late February, he saw two columns of smoke in a place where he had planned a rendezvous with the chief of the Bayogoula Indians. When he got to the rendezvous point he found it deserted and "the columns of smoke came from fires sweeping through the woods." Later the chief told him that "they had made some columns of smoke, which we had seen, to notify us that they had set out from there during the morning" (d'Iberville 1698-1702, pp. 48-49). These accounts suggest that signal fires may often have been widespread, and it is likely that they were used all year round. Northern Great Plains Indians also ignited large fires for signalling—not the campfire-size "smoke signals" of cowboy and Indian movies (see Higgins 1986b). We do not know whether signal fires were used away from the coast or before the arrival of Europeans.

In New England, the central Atlantic states, and western North America, Indians used broadcast fire to drive game and to improve forage to attract game animals (Lawson 1714, Day 1953, Lewis 1982, Pyne 1982, Higgins 1986b). John Smith (1607, p. 444), for example, described the "fire surround" method in Virginia.

> *...at their hunting in the desarts they are commonly two or three hundred together. Having found the Deere, they environ them with many fires, and betwixt the fires they place themselves... The Deere being thus feared by the fires and their voices, they chace them so long within that circle, that many times they kill six, eight, ten, or fifteene at a hunting.*

Nunez Cabeza de Vaca (1542, p. 106) describes a similar hunt somewhere in Louisiana or East Texas, which had the added benefit of driving off mosquitoes.

> *The Indians of the interior have a different method [of ridding themselves of mosquitoes]...which is to go with brands in the hand firing the plains and forests within their reach, that the mosquitos may fly away, and at the same time to drive out lizards and other like things from the earth for them to eat. They are accustomed also to kill deer by encircling them with fires. The*

> *pasturage is taken from the cattle [bison] by burning, that necessity may drive them to seek it in places where it is desired they should go.*

It seems reasonable to assume that Indians in Florida used fire for the same purposes. Early Spanish and French accounts do not mention the intentional use of broadcast fire, although several eighteenth century accounts do (see next section). Larson (1980) concludes from this discrepancy that fire drives were not widely used in the southeastern coastal plain until the trade in deerskin hides increased hunting pressure. We did find one early account of Indians burning prairies "for the buffalo hunt" in January near Choctawhatchee Bay (d'Iberville 1698-1702, p. 29), but the history of buffalo in Florida is not well known. An extinct bison species, *Bison antiquus*, may have overlapped briefly with humans (see Robertson 1974, Clausen et al. 1979). The first Spanish explorers observed modern bison (*Bison bison*) in Florida, but Rostlund (1960) maintains that the animals had only recently entered the South, lured there by Indian burning. Robertson (1974) disputes this contention because two bison bone-fragments from north and central Florida have been dated to an earlier time (one to 800-1200 A.D.). We do not have enough evidence to estimate the size of the bison population or the probability that Indians used fire to manage it.

One study suggests that Indian burning did alter the distribution of different vegetation types. Kalisz et al. (1986) studied the longleaf pine islands that occur within the scrub vegetation of Ocala National Forest. They noted that lightning strikes are probably not frequent enough to maintain these pockets of fire-dependent vegetation within the less flammable scrub (a statement disputed by some), that the islands have been larger in the past, and that all of them show evidence of having been inhabited during the St. Johns Period (from 2,500 years ago to European contact) and earlier. Only one prehistoric site was found in the scrub area. From these observations they conclude that frequent Indian burning must have been responsible for maintaining the longleaf pine vegetation.

In summary, we have some, but hardly overwhelming, evidence that Florida Indians burned extensively in the prehistorical period. If they did so, at least some and possibly most of these fires occurred outside the lightning season. Accounts from later periods and from other areas frequently mention burning in fall or winter; most hunting probably took place then, particularly by agricultural tribes (see Swanton 1946); and, as noted above, many aboriginal peoples alter natural burning regimes. Were these fires extensive enough both spatially and temporally that native species adapted to them? We simply do not know enough to be able to answer this question. We can guess, however, that even if human ignitions were more common in fall and winter, the largest acreage probably burned during the drought period early in the growing season (see previous sections).

We should point out that the reason we find the evidence of widespread burning by native Florida Indians to be less convincing than do some other

authors is that we have used information from only the earliest accounts. A quote from William Bartram's *Travels* is often used to illustrate Indian burning practices (see, e.g. Wade 1983, Kalisz et al. 1986): "the deserts are set on fire...almost every day throughout the year, in some part or other, by the Indians, for the purpose of rousing the game, as also by the lightning" (Bartram 1791, p. 139). Bartram, however, is referring to the Seminole Indians, and he made his observations 250 years after Europeans first settled Florida. The Seminoles, an amalgam primarily of Creek Indians, along with some other tribes and a few escaped slaves, immigrated into Florida in the mid-1700s, and their use of fire was not necessarily the same as that of the original Florida Indian tribes. They belong to the next chapter of Florida's fire history.

After European Settlement

Florida's history from its discovery in 1513 to the time it became a United States territory in 1821 is a confusing succession of occupation by Spain and Great Britain, reoccupation by Spain, disappearance of native Indians, immigration of the Seminoles, and intermittent skirmishes among all these groups. Amid these upheavals European and Indian settlers farmed, raised cattle, and hunted. Accounts from the 17th and 18th centuries in Florida and neighboring states show that settlers used fire in almost all of these activities.

During this period Seminole Indians appear to have burned extensively. Thirty years before Bartram, Stork (1769) commented on the Indians' use of fire in Florida: "the hunting parties of the Creek Indians, who are dispersed through the whole province, continually set the grass on fire, for the conveniency of hunting...." In North Carolina, Lawson (1714) observed Indians burning cane swamps in January to drive out bear, deer, and turkeys. DeBrahm, in his report of a survey of the Southeast from 1751-1771 (De Vorsey 1971, p. 80), noted that in South Carolina, "the burning of the Grass and Underwoods in the Forrests is an ancient Custom of the Indians" practiced "to alure the Deers upon the new Grass" and to make enemy tracks more visible.

Early settlers, however, burned primarily to improve forage for cattle (see Vignoles 1823, Greene 1935, Pyne 1982). In the early 1900s most of this burning was done in late winter, to "green up" the early spring growth of grasses (Otto 1986). In previous centuries, however, burning in other seasons may have been more common. In 1775, for example, Romans remarked that in the pine barrens, where cattle would eat the tough wiregrass (the predominant groundcover) only when it was freshly sprouted, "the woods are frequently fired, and at different seasons, in order to have a succession of young grass" (Romans 1775, p. 11).

Human-ignited fires became so common that 105 percent of Florida supposedly burned in one year in the early 1900s, a result of semiannual range fires (Pyne 1982). The annual fire cycle was clearly outlined by Eldredge in 1911 (quoted in Pyne 1982, p. 151):

> *The turpentine operator burns his woods and all other neighboring woods during the winter months, generally in December, January, or February. The cattlemen set fire during March, April, and May to such areas as the turpentine operator has left unburned. During the summer there are almost daily severe thunderstorms, and many forest fires are set by lightning. In the dry fall months hunters set fire to such "rough" places as may harbor game. It is only by chance that any area of unenclosed land escapes burning at least once in two years.*

This quote illustrates the sharp distinction made between the human-caused fire season and the lightning fire season. People burned outside the lightning season partly in an attempt to transform fire (which was inevitable in some form or other in the Southeast) from an uncontrollable and unpredictable force of nature to one controlled by man. In 1910, E. P. Powell, a transplanted Yankee, quoted a "simple-hearted neighbor" as saying that burning is necessary because "if the grass is not burned away annually lightning may strike somewhere, and the accumulated vegetation will make a furious blaze." Powell was not convinced, replying sarcastically that "lightning sometimes strikes a Northern church or school house, a thing which could not occur if we had the forethought to burn them ourselves annually" (Powell 1910, p. 218). For southerners, gaining control over fire was equivalent to shifting the fire season from summer to winter.

Recent fire history has been outlined many times; there is no need to repeat it in detail here (e.g. Pyne 1982, Croker 1987). In brief, annual burning combined with clearcutting virgin timber eliminated pine regeneration and prompted the attempt to suppress all fires. The impossibility of this task and undesirability of the results (hardwood encroachment, reduced quail populations, extensive wildfires) eventually led to the institution of prescribed fire. As described earlier, prescribed fires were set in the winter; lightning fires occurred in the summer. Now we are entering a new phase, considering whether to relinquish some of our hard-won control over fire by returning to a more natural fire regime. In the next three sections we explore how soils, plants, and animals are affected by fires occurring at different seasons.

EFFECTS ON SOILS

> *The literature on fire is a bit like the holy scripture; by careful selection of results, one can "prove," for example, that fire increases, decreases, or has no effect on nutrient availability, or that fires result in considerable or negligible loss of nutrient capital from ecosystems. Whereas some of this apparent conflict in results is attributable to variations in methodology,...many of the variations in observed results reflect the actual range of potential fire effects (Christensen 1987, p. 2).*

Prescribed burning affects soils by altering their physical, chemical, and biological characteristics. Whether these changes are construed as beneficial, detrimental, or of little consequence depends on specific burn objectives and long-term management goals. Burning releases nutrients tied up in slowly decomposing organic detritus. These nutrients in turn raise the surface soil pH and alter the environment for soil microorganisms (McKee 1982). The mobilized nutrients are either taken up by plants and soil microorganisms or exported from the ecosystem by volatilization, leaching, and surface runoff.

It is fairly well documented that fire intensity and frequency directly affect soil properties, particularly those having to do with nutrient cycling and loss (Wells et al. 1979). Few effects, however, have been attributed directly to the season when burning takes place. Nevertheless, the simple fact that plant growth and the environmental factors that limit it (namely nutrients, soil moisture, and soil temperature) vary seasonally suggests that the time of year when burning is done would have demonstrable and varied effects on soils. One would expect nutrient mobilization and loss to be influenced by the phenological stage of the dominant plant species and by the rapidity of vegetation recovery, both of which vary seasonally.

Nutrients

There are two opposing arguments regarding the effect of season of burn on soil nutrients. One maintains that leaching losses would be greatest from sites burned in the fall and early winter because dormant vegetation cannot efficiently take up released nutrients. Losses would be lowest during the early part of the growing season when plants are physiologically active and are accumulating nutrients in new growth. The opposing view is that during the growing season nutrients are concentrated in aerial plant parts (i.e. twigs, leaves, flowers, and fruits) and thus would be lost by volatilization when these parts are consumed in the fire. In the winter, on the other hand, a large proportion of the nutrients are sequestered in underground plant parts and would be unaffected by the burning of surface and aerial fuels.

Unfortunately, there is little empirical evidence to support or refute either view. In North Carolina longleaf pine savannas Schneider (1988) showed that post-fire plant production was greater following late-winter fires (March 13) than following midsummer (July 9) and late-fall burns (December 5). Gilliam

and Christensen (1986) found a similar pattern of production in South Carolina flatwoods. Both studies suggest that seasonal variation in nutrient losses may be responsible for the differences in ecosystem productivity. Schneider (1988) did detect a significant increase in soil phosphorus following the late-winter burn compared with summer and fall burns, but he found no significant differences in nutrient leaching losses related to season of burn. There may be a number of explanations for the higher phosphorus concentrations in the soil following the late-winter burn. The differences may be more related to variability of factors affecting fire behavior and fuel consumption than to some specific seasonal influence.

Schneider's detection of greater phosphorus concentrations in soils following late-winter burning contrasts with the results of two other studies. Owensby and Wyrill (1973) in a Kansas prairie and Wells (1971) at the Santee Experimental Plots in South Carolina found no significant differences in soil phosphorus related to season of burn. The methods employed in these studies, however, were so markedly different that comparisons may be meaningless.

Nitrogen is frequently cited as the nutrient most subject to fire-induced losses because it is readily volatilized in the combustion process. Studies that have measured soil nitrogen at various sites throughout the Southeast Coastal Plain have failed to show that prescribed burning (at any season) adversely affects ecosystem nitrogen capital (McKee 1982). Apparently, fire-stimulated nitrogen fixation by soil microorganisms and symbiotic bacteria associated with legumes and other plants replaces any nitrogen lost during burning. Neither the short-term study of Schneider (1988) nor the results of 20 years of burning with different fire regimes in South Carolina (Wells 1971)

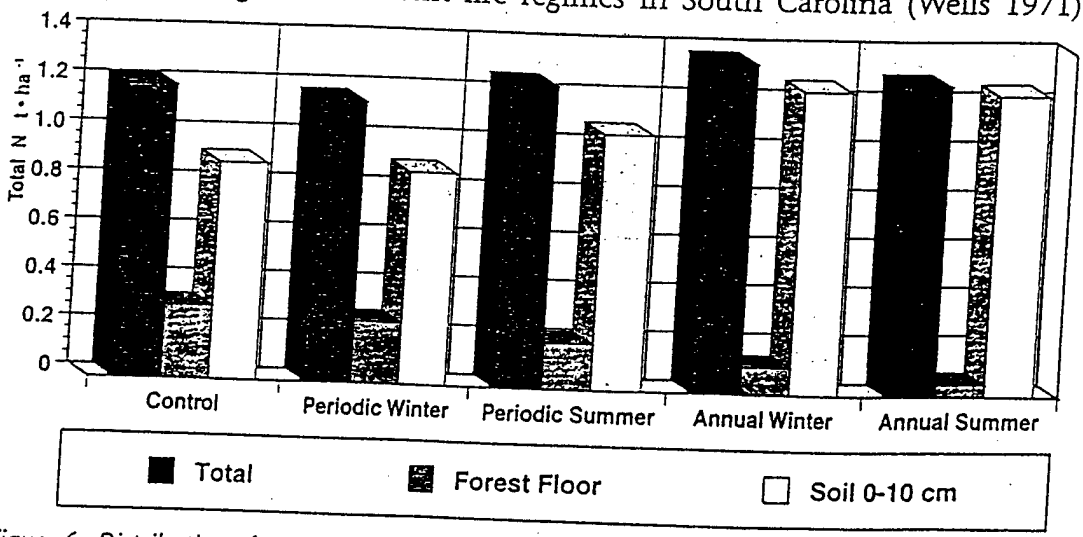


Figure 6. Distribution of nitrogen in the soil and the forest litter on the Santee Fire Plots in South Carolina following 20 years of varying fire regimes. Note that the distribution of nitrogen varied considerably with fire regime, but total nitrogen (forest litter and soil pools combined) was unaffected by burning regardless of burn frequency or season. From Christensen (1987), redrawn from Wells (1971).

showed that season of burn affects the combined nitrogen pool of forest floor and soil (Figure 6).

Runoff and Erosion

In addition to fire-induced changes in nutrient status, removal of cover by burning may alter rates of erosion and runoff. However, nearly all of Florida and much of the Southeast Coastal Plain lack appreciable topographic relief, and most of the soils are porous sands, so fire-related nutrient and soil losses from Coastal Plain ecosystems associated with surface runoff are generally negligible.

A single experimental study has addressed the relationship between sediment production and season of burn. Dobrowolski et al. (1987), using spray-nozzle rainfall simulators, looked at sediment production from long-term burn plots on the Palustris Experimental Forest in central Louisiana. Because vegetation regrew more quickly, spring (May 3) and summer (July 1) burning exposed mineral soil to direct raindrop impact for shorter periods than did winter (March 1) burning. Sediment output was highest from the winter-burned treatment. The output from the summer-burned treatment was appreciably lower than from either winter- or spring-burned plots, but the difference was due in part to a patchy summer burn that initially exposed less mineral soil than did the winter or spring treatments. In all treatments the period of increased sediment production was short-lived, with background levels returning by the end of the treatment-year growing season.

Conclusion

Christensen (1987) pointed out that species in the Southeast Coastal Plain's oligotrophic/pyrogenic ecosystems may have developed traits enabling them to efficiently retain and utilize fire-released nutrients. The inability to detect an effect of season of burn on ecosystem nutrient status may simply be a function of the endemically low nutrient levels of these fire-maintained systems coupled with the efficiency of the biota in capturing any fire-caused increase in nutrient availability. Clearly, the definitive study on the seasonal interaction of fire and nutrients remains to be done.

EFFECTS ON PLANTS

The effect of fire on plants can depend on the timing of the fire relative to the plant's seasonal phenology. Fire season influences the abundance and morphology of many plant species. Some species bloom only when burned during a certain season; others resprout if burned in one season but are killed if burned in another. These effects, in turn, influence the insects, birds, and other animals that use plants for food, cover, and nesting. In this section we review studies that have investigated the effects of fires at different seasons. We concentrate on Florida's primary fire-dependent communities — pine uplands (high pine, sandhill, clayhill) and flatwoods, which consist of a pine overstory, an understory of deciduous oaks (in the uplands), saw-palmetto (in the flatwoods), a variety of evergreen and deciduous shrubs, and a groundcover of grasses and forbs. We discuss each of these three strata separately. The groundcover section includes data from some other communities such as seepage slopes (also known as savannas, herb bogs, and wet prairies) and South Florida marshlands. Fire also influences other Florida ecosystems — for example sand pine scrub and swamps — but no one has done the long-term studies needed to investigate seasonal fire effects in systems such as these that burn infrequently.

Before continuing we would like to mention some of the difficulties in interpreting the data from these studies. First, some early studies referred only to season without specifying the month during which fires occurred. Second, some studies look at the results of only one year of burning, which may reflect unusual conditions during that year rather than general seasonal effects. Even long-term studies are subject to the vagaries of weather and fire behavior. If data are collected only at the end of a long-term study it is impossible to tell if seasonal differences represent consistent, cumulative effects or simply a single unusual occurrence (e.g. a particularly intense fire in one plot). Third, the effect of season alone is very difficult to separate from other factors with which it is correlated. Season may often be confounded with environmental variables such as air temperature, humidity, fuel moisture, and wind speed, all of which can affect fire behavior. Finally, many of the experimental studies are not scientifically sound; experimental design is often poor, and statistical analysis may be lacking, improperly done, or not presented fully enough to be evaluated. We have tried to point out the most blatant errors and omissions, but do not have the space to thoroughly critique each paper. We cite several poorly done studies because, if nothing else, they provide anecdotal evidence. However, we caution readers not only to approach these papers with a critical eye, but to be suspicious, in general, when a single short-term study is cited as proof that a particular fire regime produces a particular effect.

Pines

Many people are reluctant to burn during the growing season because they fear that the likelihood of damaging or killing pines — both seedling and

mature trees — is greater at this time. In land managed primarily, or even partly, for timber production, this can be a very important consideration. Before discussing the basis and evidence for this contention, we briefly review the different ways in which fire can damage pines. Our treatment of this subject is drawn from review articles by Ryan (1982) and Wade and Johansen (1986).

Fire Damage to Pines

Fire damages plants by raising the temperature of tissues to a lethal level, killing the cells. The temperature that kills plant tissues after about one minute of exposure, 140°F (60°C), is usually considered to be the lethal temperature, although lower temperatures can be lethal if sustained over a longer period of time.

Heat can damage a tree's roots, bole, or crown, reducing its growth rate or killing it. Root damage usually affects only surface roots because soil insulates deeper roots. Root damage is difficult to detect and, according to Wade (1987), its importance may often be underestimated. Bole damage occurs when cambium in the trunk is killed; if it is killed all the way around the trunk the tree will die (although pitch, shortleaf, and pond pine occasionally resprout). Once southern pines reach a diameter of two to three inches, however, girdling of the bole is almost always accompanied by lethal crown damage (Wade and Johansen 1986). Crown damage has two components: crown scorch and bud mortality. Crown scorch occurs when tissue in the needles reaches the lethal temperature and the needles die. Because they are larger and are protected by foliage, buds can withstand temperatures higher than those that kill needles. Foliage is killed at 140°F (60°C) but does not ignite until it reaches about 400°F (204°C); thus, charred or consumed foliage usually indicates that enough heat has been applied to kill branch cambium and buds (see Wade 1985).

Relation between Fire Damage and Season of Fire

General Principles

Are any of the above three types of damage more likely to occur during the growing season? We briefly discuss this question in reference to root and bole damage and then address seasonal aspects of crown damage. Roots may be vulnerable at several different times. Fine roots grow rapidly in spring and die off later in the summer; timing of fire in relation to this activity may be important (D. Wade, U.S. Forest Service, pers. comm.), but the topic has not been investigated. Roots growing in duff around the base of a tree may be vulnerable when fuel moisture is low (often during the dormant season) and the duff is dry enough to burn (Ryan 1982; D. Wade, pers. comm.). The extent of bole damage is determined by fire temperature, residence time, and bark thickness (Wade 1987; also see Ryan 1982). Residence time, or fire duration, depends on the amount and size of fuel (Ryan 1982) and combustion rate (D. Wade, pers. comm.). None of these factors, nor flame temperature, would be expected to vary considerably with season, although low relative humidity in

the winter could increase residence time as well as the size of available fuel (D. Wade, pers. comm.).

Crowns are often considered more vulnerable to damage during the growing season than during the dormant season. We first explore the basis for this belief and then review empirical data on pine growth and mortality following fires at different seasons. The first reason growing-season fires are thought to be more harmful is because fire behavior theory predicts that the height at which a tree is scorched depends on air temperature. Byram (1958) pointed out that the amount of heat required to raise plant tissue to the lethal temperature depends on the initial temperature of the tissue. Therefore, he suggested, scorch height should increase as initial vegetation temperature increases. He presented a graph of initial vegetation temperature versus scorch height that included both a theoretical curve and a set of points that roughly followed the curve; these points were said to "represent observed height of scorch for experimental fires." No details were given about the location of these fires, what species was involved, or whether other variables such as fireline intensity (defined as the heat per unit acre released by an advancing flame) differed among the fires. Van Wagner (1973) presented a more complete theory, developing an equation that expressed the scorch height as a function of fireline intensity, wind speed, and ambient air temperature. According to the equation, scorch height on a 95°F day would be 1.8 times as high as on a 60°F day (see graph in Albini 1976, p. 64), given equal fire intensity and wind speed. Although there is little empirical evidence to support Van Wagner's theoretical relationship between scorch height and temperature, it is commonly used to predict scorch height from prescribed fires (e.g. Albini 1976).

Van Wagner did test the equation with data from 13 fires in Ontario, but because these fires occurred over a small range of wind speeds and temperatures, the only relationship that could be verified was between height of crown scorch and fire intensity. Van Wagner (1973, p. 377) stated, "the main conclusion to be drawn from the present work is that the lethal scorch height varies with the 2/3 power of line-fire intensity...if air temperature or wind differ markedly from average, then their additional effects may be tentatively estimated from the theory presented" (our emphasis). Van Wagner's equation is based on data from northern tree species and has not been tested on other species or locations. Wade (1983) points out that it has not been validated in southern pines and seems to overpredict scorch height in slash pine.

In addition to causing greater crown scorch because of higher air temperatures, growing-season fires are thought to increase the other component of crown damage—bud mortality—because of plant tissue's supposedly greater sensitivity to heat during the growing season (see Hare 1961). Some experimental work supports the contention that lethal temperature differs with season, but none of these studies has investigated southern pines or indeed any plant species from the southeastern U.S. One study found that the lethal temperature of several tree and grass species from Arizona varied up to 10°C through the

year, with highest lethal temperatures in the winter (Jameson 1961). Times of low heat-resistance differed between the two years of the study. In the first year they were lowest in late spring, with a second low point in September; the second year the lowest point occurred in early summer. The author suggested that low heat-resistance corresponded to periods of hot, dry weather. It is not clear how these results would apply to Florida's climate. Lower heat-resistance during the growing season could be explained in part by greater susceptibility to heat of actively growing cells (Alexandrov 1964, Kayll 1968). Structural changes could also increase vulnerability. Buds are not as well insulated early in the growing season when they elongate beyond protective needles and bud scales (Wade and Johansen 1986). Finally, cold-hardening in the fall (Alexandrov 1964) or below-freezing temperatures (Byram 1948) may increase heat resistance during the winter.

We need more studies of seasonal changes in heat resistance in southern pines. We also need information on the effects of actual fires; seasonal differences are important only if they are substantial enough to influence the amount of damage caused by fires occurring at different seasons.

Empirical Data

In this section we review data from the Southeast on growth and mortality of pines burned in different seasons. The theories presented above suggest that southern pines should be more vulnerable to crown damage during the growing season. Seasonal differences in vulnerability may be irrelevant, however, if these differences are slight or of minor importance compared to other variables. Increased vulnerability might reach a critical level only under extreme conditions such as high-intensity fires or when trees are young. Evaluation of these studies is difficult, not only because of problems of design and analysis, but because it is usually not possible to tell whether differences in growth and survival reflect seasonal differences in extent of crown damage or differences in recovery following damage. Nonetheless they give some indication of what can be expected under different fire regimes.

Pine Growth

Crown scorch can retard the growth of pines, although mild scorch may increase growth (see references in Wade and Johansen 1986). Three studies of mature southern pines showed no difference in growth among plots burned at different times of the year, while two others revealed some differences but no consistent seasonal pattern. Grass-stage longleaf pines, however, appear to grow better following growing-season rather than dormant-season burns.

Of the three studies that found no effect of season of burn on growth of mature pines, only one was designed specifically to look at this question. Boyer (1987) subjected longleaf pine in Alabama to biennial winter, spring, and summer fires for ten years; trees were 14 years old at the beginning of the study. Four measures of pine growth revealed an apparent reduction in growth in the burned plots when compared to the unburned plots, but, to the author's

surprise, season had no effect. Hughes (1975) found no effect of season of burn after six years of biennial prescribed burns in a plantation of South Florida slash pine that was 13 years old at the beginning of the study. Plots were burned in October, November, January, March, and May. The author concluded, "the burning season may be extended to include May and November...without harm to trees." Unfortunately, this result was reported without any data, so its reliability cannot be verified. A 41-year study in South Carolina showed no difference in growth of loblolly pine among five treatments: annual or periodic burning in winter (December) or summer (early June), or unburned (Waldrop et al. 1987). The authors pointed out, however, that this lack of difference could be explained by the fact that the pines were approximately 40 years old at the beginning of the study.

Two studies have found an effect of season of burn on pine growth, but no general patterns emerge. Grelen (1983a) set up plots in a four-year-old slash pine plantation in Louisiana and found that, after eight years, height and diameter growth were lowest in annually burned March plots and approximately equivalent in annually burned May plots, biennially and triennially burned March and May plots, and unburned plots. A study done in 80-year-old second-growth longleaf pine forests in St. Marks National Wildlife Refuge near Tallahassee, Florida, is one of the few to investigate burn treatments throughout the year. Plots set up in 1980 in longleaf pine sandhills and flatwoods have been burned annually or biennially at eight different times of year—fall: early October and late November, winter: early January and late February, spring: early April and late May, summer: early July and late August (Glitzenstein et al. 1990, Platt et al. 1988). After eight years, growth of longleaf pine in the sandhills was lowest in spring-burned plots among 10-20 cm (4-8 in) dbh trees, while flatwoods longleaf pines tended to grow fastest in fall-burned plots (Glitzenstein et al. 1990). The reason for the differences in growth are difficult to evaluate without information on type and extent of fire damage.

There appears to be good evidence that early- or mid-growing-season fires benefit young longleaf pines. Grelen (1983b) showed that after seven years, grass-stage seedlings burned annually or biennially in May were, on average, over twice as tall as those burned annually or biennially in March. Three years into the study more seedlings had begun height growth in the May plots than in the March plots. Among seedlings that had begun height growth at the beginning of the study, growth was greater in annually burned May plots than in any of the other plots. Bruce (1951) had previously reported similar results in Mississippi. He compared height of 11-year-old longleaf pines burned at ages four and nine in January and February to that of pines burned in July and August; trees subjected to severe summer burns grew taller than those subjected to severe winter burns. Maple (1977) also found that a single May burn stimulated height growth of grass-stage longleaf pines in Alabama. Grelen (1983b) proposed several reasons to explain his results: new grass growth in May may produce a cooler fire; longleaf buds are better protected in May than in March by elongating needles (buds are exposed several times during the

growing season and the exact time varies with location [D. Wade, U.S. Forest Service pers. comm.]); competition from woody plants may be reduced; and brown-spot disease appears to be better controlled by May burns. (Brown-spot is a fungus that infects and often kills grass-stage longleaf pines.) Both Grelen (1983b) and Bruce (1951) found that grass-stage seedlings burned during the growing season had a lower rate of brown-spot infection. This benefit was one of the factors that prompted the Wakulla District of the Apalachicola National Forest to begin conducting more prescribed burns during the growing season (L. Ford, U.S. Forest Service, pers. comm.).

Pine Mortality

Studies of the effect of fire season on pine mortality, like those on pine growth, show a variety of findings. Conflicting results are sometimes difficult to reconcile because so many variables differ among the studies (month of burn, geographical location, pine species, age of trees, amount of accumulated fuel, etc.). We review these studies and then consider some factors that may explain the different results.

Several studies indicate higher mortality following growing-season burns. Boyer (1987), in the same study described above, reported slightly higher mortality from summer prescribed burns than from winter or spring burns (8% vs. 4.3%). This higher mortality is puzzling, particularly since Boyer (1987) stated that crown scorch following the burns was too light to cause damage and fire intensities were actually lower, on average, during summer fires than during spring or winter fires (Boyer 1985). It turns out, however, that the increased mortality was restricted to one of three summer-burn treatments (especially 2 of 3 plots within this treatment) and that some of the initial burns caused considerable crown scorch—up to 50 percent scorch was considered negligible by those recording damage (D. Wade, U.S. Forest Service, pers. comm.). Perhaps one particularly intense fire caused the increased mortality. Alternatively, trees in summer plots may have been stressed by being burned twice (January and July) during the first year of the study (W. Platt, Louisiana State University, pers. comm.; see burn schedule in Boyer 1985).

A paper that is often cited as evidence that summer fires are detrimental is that of Ferguson (1955, p. 107) who reported, from a survey of severely burned stands (probably from wildfires) in Texas, that "summer fires were twice as lethal to shortleaf and loblolly pines as winter fires." Survival was lower after summer fires even among trees with equivalent crown and bole damage, but needle scorch and needle consumption were not separated. In addition, as the author pointed out, these data are from only one year. Some experimental work has shown similar results. Ferguson (1961) did an experimental study in loblolly and shortleaf pine stands in east Texas, burning different replicated plots in four seasons for three consecutive years. He reported twice the mortality in plots burned in late summer (late August to mid-September) than in those burned in December, February and March, or late April to mid-May. Bruce (1951) found that an August fire killed twice as many 9-year-old longleaf

pines as did a January fire. Grelen (1975) also reported, with no substantiating data, higher mortality in July-burned plots than in March- or May-burned plots after 12 years of burning in a young (Seven years old at the beginning of the study) longleaf pine plantation.

In contrast, two studies found that growing-season fires did not increase mortality rates. In the St. Marks study described above, results differed in the two habitats. Longleaf pines in the sandhills had the highest mortality rate in fall-burned plots and the lowest rate in winter-burned plots, while the trend in the flatwoods was reversed, with lowest mortality in fall-burned plots and highest mortality in winter-burned plots; mortality in spring- and summer-burned plots was intermediate (these trends were significant for only some size classes). Glitzenstein et al. (1990) suggest that these habitat differences may reflect variation in other stresses; dry periods in the fall may stress sandhill pines, while wet periods in summer and winter may stress flatwoods pines. In a longleaf pine seedling experiment Grelen (1983b) found that grass-stage seedlings in annually burned May plots had higher survival rates than did those in biennial May plots, annual and biennial March plots, or unburned plots. In seedlings that had begun height growth, however, frequency appeared to be more important than season; survival in annual May and March plots was equally good and was higher than in either of the biennial plots.

One factor that may explain some of the discrepancies among these studies is the amount of fuel accumulation. In Ferguson's (1961) study showing greater summer mortality, more than ten years had gone by without a fire. Hare (1961, p. 13) cites papers by Cary (1932) and Hodgkins (1958) as evidence that "greater damage results from summer than from winter fires," but both of these also referred to fires occurring after years of fuel accumulation. It has become standard practice to conduct a winter burn before switching to summer burning. For example, in describing the setup of his season-of-burn study Grano (1970, p. 2) stated, "a heavy accumulation of ground fuel makes initial summer burns in pine stands hazardous. Thus, it was decided to have a winter fire initially to minimize the risk, and summer fires thereafter." The fires in this study produced little mortality in any season. It is possible that heavy fuel accumulations increase fuel consumption, and thus fire intensity, enough that air temperature and degree of heat susceptibility then come into play as important factors.

A second important factor to consider is during what part of the growing season the fires occur. Of the studies cited above that mention month of burn, detrimental results generally occurred following burns from July through early September, while neutral or beneficial results followed May or June burns. [It would be interesting to know if the lethal summer fires in Ferguson's (1955) survey occurred late in the summer.] Fire managers at the Wakulla District of the Apalachicola National Forest also observed this seasonal effect saying that September burns "killed the hell" out of knee-height longleaf pines, but burning until about July 1 was safe as long as fuel loads were low. Rangers at Ocala National Forest have made similar observations; they noted that longleaf

saplings were most vulnerable to late August fires. Data from the St. Marks sandhills pines, showing higher mortality rates after fall burning, appear to be consistent with this pattern, but the low mortality rate following fall burning in the flatwoods suggests the pattern does not hold in all habitats.

These data mesh well with some observations and experiments by Wade and Johansen that suggest southern pines are more likely to die following crown scorch late in the growing season than early (although we do not know the extent of crown scorch that occurred in most of the studies cited above). Wade and Johansen (1986, 1987) pointed out that, unlike northern pines, which have preformed buds and cannot survive complete defoliation after the spring flush is completed, southern pines are multinodal, forming new buds and producing additional needles three or four times during the growing season. Thus, southern pines can refoliate after being defoliated during the growing season, but the later the defoliation, the fewer new flushes of needles they can produce. If defoliated after the last flush has occurred in late summer, they will not refoliate until the next spring. In addition, conifers may be less able to recover from injury in the fall because of low carbohydrate reserves. Hepting (1945) found that carbohydrate reserves in shortleaf pine roots were lowest in the fall and highest in the spring.

A recent study confirms that defoliation in the fall is detrimental to slash and loblolly pine. Weise et al. (1989) subjected 4-year-old pines to five defoliation levels (0 to 100 percent; needles were manually removed) at four times of year (January, April, July, or October). The experiment was replicated in two locations for each species (loblolly in Georgia and South Carolina, slash in Georgia and Florida). Mortality occurred only among trees completely defoliated in October. Ninety-three percent of the loblolly pine in this treatment died, as did 40 percent of the slash pine in one of the two locations. Defoliation levels of 66 percent or more reduced diameter and height growth rates for one growing season, but the amount of growth loss did not differ with season of defoliation (excluding the 100 percent defoliation in October). Because all trees completely defoliated in January, April, or July survived, the authors suggested that mortality of pines following fires at these times of year is probably due to bud damage rather than just needle loss.

Summary

1) All other things being equal, the higher the air temperature the higher the lethal temperature zone will extend above a fire.

2) The lethal temperature may be lower during the growing season than during the dormant season.

3) Factors 1 and 2 may come into play only when fire intensity is high (e.g. from heavy fuel accumulation) or in young trees.

4) Effect of season of burn on pine growth is unclear, but growth of grass-

stage longleaf pines appears to be enhanced by early growing-season burns.

5) Mortality is usually greater following late growing-season fires than early growing-season fires.

6) Low-intensity prescribed fires in mature pine stands could probably be conducted in any month of the year without injuring the pine overstory. The higher the intensity of the fire and the younger the trees, the more risky growing-season fires become. Even then, this risk is generally slight early in the growing season, becoming more severe late in the growing season. This pattern may vary in different habitats and among species.

Understory Vegetation

While most land managers try not to damage the pine overstory when they conduct prescribed burns, they often have the opposite goal with respect to understory hardwoods and shrubs. Foresters battle the oaks, titi, gallberry, and other shrubs that impede harvesting and replanting, increase the damage caused by wildfires, and compete with pines for resources. Cattle ranchers try to eliminate saw-palmetto and other shrubs that replace the more palatable grasses and forbs. Managers attempting to restore or preserve natural areas try to recreate the open "park-like" aspect, free of understory clutter, that existed before the era of fire suppression. Wildlife biologists generally agree that most animals that inhabit uplands benefit from a healthy groundcover of grasses and forbs, but they stress the need to retain some understory vegetation to provide cover, habitat diversity, and food (particularly berries and acorns).

Many organizations, including the U.S. Forest Service, The Nature Conservancy, and the Florida State Park Service, have begun using growing-season burns as one method of reducing the abundance and dominance of understory species. This change in management was prompted in part by the results of some studies comparing the effect of dormant- vs. growing-season burns on understory vegetation. In this section we summarize those studies and discuss some hypotheses that have been advanced to explain the results.

Effect of Season of Burn on Understory Vegetation

Like southern pines, the understory species of Florida's pinelands such as turkey and bluejack oak, sweetgum, wax myrtle, gallberry, titi, and saw-palmetto are well adapted to fire; their adaptive mechanism, however, is quite different. The above-ground parts of these species are not as well protected as are those of pines, and the entire stem is often killed by fire (with the exception of saw-palmetto). Unlike most pines, however, many understory species can resprout from dormant buds.

Evidence from several studies done in different parts of the Southeast strongly suggests that growing-season fires affect most understory species differently than do dormant-season fires. One of the most comprehensive of

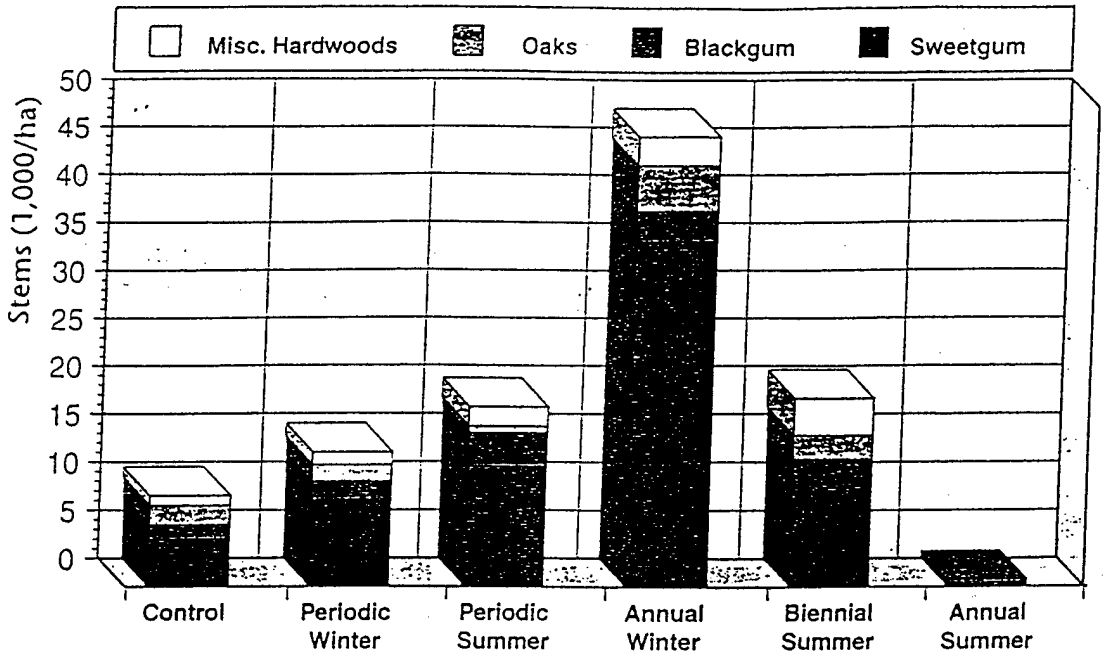


Figure 7. Number of understory hardwoods less than 2.5 cm (1 in.) dbh after 30 years of prescribed burning, Santee Fire Plots, South Carolina. Note that annual winter fires significantly altered the structure of vegetation on the plots by allowing the proliferation of hardwood stems. Annual summer burns were most effective in reducing the number of hardwoods. From Waldrop et al. (1987).

these studies was set up by the U.S. Forest Service's Southeastern Experiment Station in 1946 and is still continuing. Treatment plots (known as the Santee Fire Plots) were established in a 40-year-old loblolly pine plantation in Berkeley and Georgetown counties, South Carolina. Treatments included periodic burning in winter (December) or summer (June), annual burning in winter or summer, and no burning. A biennial summer burn treatment was added in 1951. The periodic treatments were applied at three- to seven-year intervals; burns were conducted when understory hardwoods reached a certain size. Data on the effects of these fires on hardwoods have been presented by Chaiken (1952), Lotti et al. (1960), Langdon (1981), and Waldrop et al. (1987); the latter two give Langdon's data on results after the 30th year of the study.

After 30 years, dramatic differences existed among the treatments. All burn plots except annual summer burn plots had a greater density of small hardwood stems [<2.5 cm (1 in) dbh] than did the unburned plots; this effect is the result of resprouting by topkilled plants. The number of stems in the annual summer burn plots was much lower than in the other plots, however, because most of the roots had been completely killed (Figure 7). By the eighth year almost 100 percent of the sweetgum and wax myrtle had been killed (Figure 8). Oaks were eliminated and blackgum severely reduced after about 20 annual burns. Annual summer burning also reduced shrub density, leaving only a few stems of blueberry and sumac in these plots. Biennial summer burns appeared

to be less effective than annual summer burns at completely killing root systems (Figure 8).

Five biennial burns killed 44 percent of the wax myrtle and 21 percent of the oaks, whereas mortality after an equal number of annual burns was, respectively, 95 percent and 48 percent. After 13 biennial summer burns (26 years), fewer than 50 percent of the oaks had been killed. Survival of root stocks in the periodic burning treatments appears not to have been determined, but

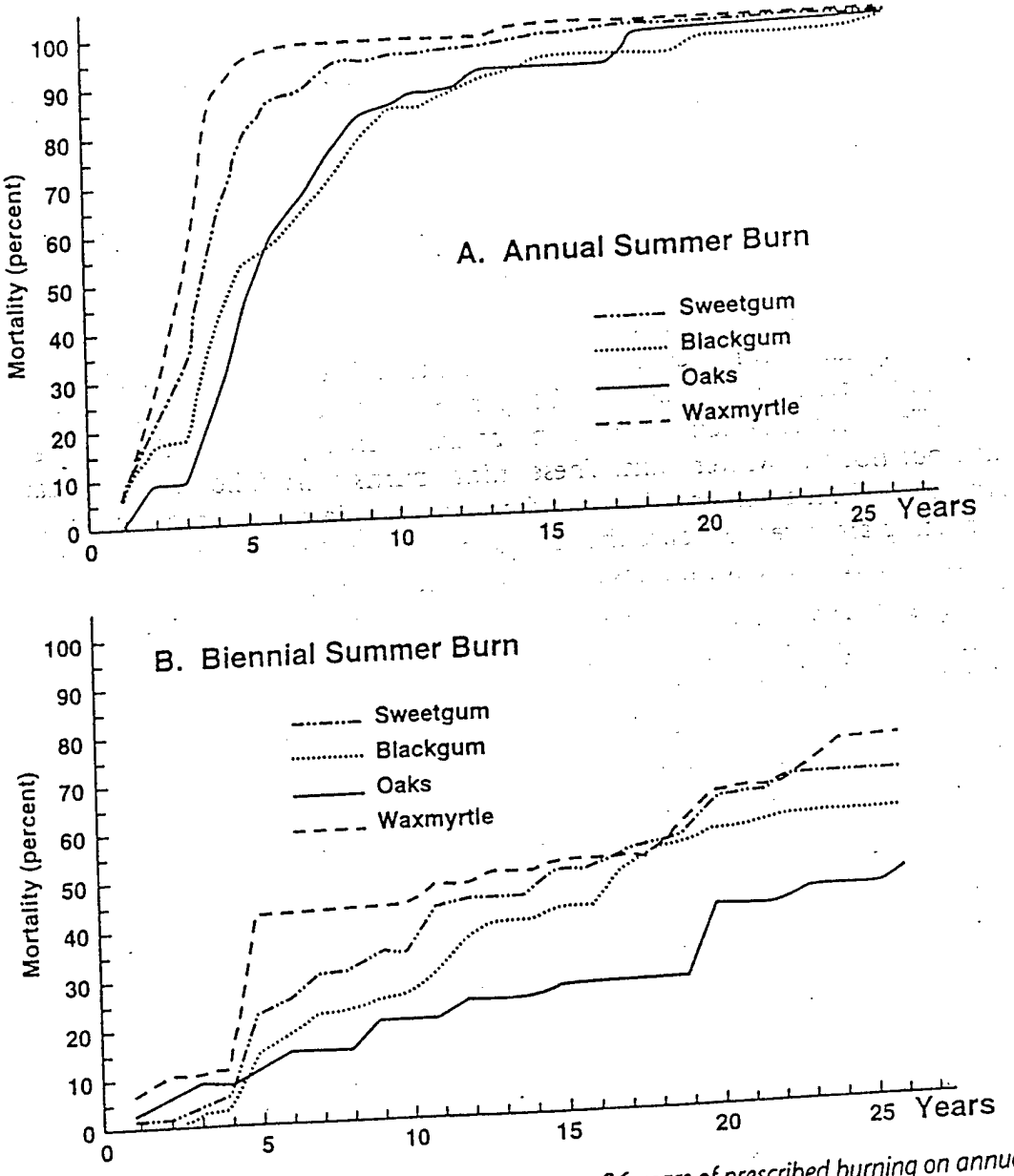


Figure 8. Cumulative mortality of hardwood roots over 26 years of prescribed burning on annual and biennial summer burn plots, Santee Fire Plots, South Carolina. Note that annual summer burns were considerably more effective in killing hardwood rootstocks. From Waldrop et al. (1987).

data in Waldrop et al. (1987) indicate approximately equal numbers of stems in the periodic winter and summer plots. Percent crown coverage of larger hardwoods [>1.5 m (5 ft) tall] was lower in summer plots than in the corresponding winter plots. Waldrop et al. (1987) point out that trees over 5 cm (2 in) dbh usually succumbed as a result of "hotspots" (locally intense flare-ups), and that hotspots were more common during summer fires (this comment was not quantified). A few trees over 15 cm (6 in) dbh were topkilled during summer burns, but none succumbed during winter burns. Interpretation of some of these data is hindered by a lack of statistical analysis. If analyses were done, they were not presented in the published reports.

Studies in other parts of the Southeast have revealed similar seasonal effects. The eight-year St. Marks, Florida study (see p. 31) showed that topkill of oaks was higher following spring fires than following fall, winter, or summer fires (Glitzenstein et al. 1990). Rates of complete kill were unaffected by season (although there was a trend toward lower resprouting following growing-season fires), but the authors suggested that because the rate of resprouting decreased with tree size and topkill was greater after spring burns, spring fires might kill more large oaks than would fires in other seasons. In a loblolly pine plantation near Macon, Georgia, summer fires topkilled more small hardwoods than did winter fires (Brender and Cooper 1968; the date of the burns is not given). Trees in the 6-inch (15 cm) dbh size class were topkilled by the summer burn, but not the winter burn. These initial burns were followed by repeat burns at different seasons, but no data on complete kill or on vigor of resprouting are given. Because the results are from only one year of burning, they could reflect chance factors rather than seasonal effects.

Ferguson (1961) also compared topkill after single fires in different seasons, but this experiment, conducted in a loblolly-shortleaf pine stand in East Texas, was replicated over three different years as well as in different plots. Ferguson found that winter burns (December) topkilled fewer sweetgum, post and southern red oak than did burns in late winter (mid-February to early March), spring (late April to late May) or late summer (late August to early September). Season of burn did not affect the percentage of sweetgum stems completely killed, but more oaks were completely killed by spring and summer fires (10 percent) than by winter or late winter fires (2 percent). Sprouts from topkilled stems were larger, taller, and more numerous after winter and late summer burns than after late winter or spring burns. The different results for sweetgum and oaks suggest that season of burn does not affect all hardwoods similarly.

Grano (1970) tested the efficacy of growing-season burns for hardwood control by following an initial winter burn with 13 years of annual or biennial summer burning (no date given) in a loblolly-shortleaf pine plantation in Arkansas. The number of stems completely killed increased with each burn; 85 percent of all hardwoods less than 3.5 inches (9 cm) diameter at 6 inches (15 cm) above the ground had been killed after 12 annual summer burns, while 60 percent had been killed after 7 biennial burns. This study, in contrast to the one

in South Carolina, found that equal numbers of annual or biennial burns produced about the same degree of complete kill.

Boyer (1990) documented hardwood mortality from spring and summer burns in longleaf pine stands in southwestern Alabama. Although topkill was high following initial summer burns and follow-up summer burns two years later resulted in high mortality, especially among bottomland hardwood species, no comparable winter burns were conducted to ascertain if summer burns were more effective. Boyer's spring burn treatments were designed to test whether phenological stage of the hardwoods influenced the degree of damage and mortality. Burns were conducted as soon as possible after bud break beginning, bud break complete, and full leaf. The results were variable, and inconclusive, and the effect of fire intensity could not be separated from differences in fire intensity.

Growing-season burns also appear to hinder gallberry's resprouting ability (Hughes and Knox 1964). Replicated plots near Alapaha, Georgia were burned annually in January, April, June, August, or October. After 3 years, number of stems per square foot was lower than pre-burn levels in the April and June plots, higher in January and October plots, and about the same in August plots. Foliage cover was reduced in June, August, and October plots. Lack of statistical analysis makes interpretation of these results difficult.

In contrast to the previous data, a study in South Florida (Everglades National Park) showed no effect of season of burn on hardwood recovery (Snyder 1986). This study was conducted in South Florida slash pine forests with an understory of tropical evergreen hardwoods. Two plots in each of two sites were burned, one during the wet season (August at site 1, September at site 2) and one during the dry season (January at site 1, March at site 2). At one site hardwood recovery (biomass of sprouts divided by original biomass) was greater following the wet-season burn than the dry-season burn, while the outcome at the other site was the reverse. Snyder hypothesized these results reflected the effect of temperature during the fire; higher temperatures occurred in the plots with the lower recovery rates. Because fire characteristics may have obscured seasonal effects, Snyder is conducting a second study to assess biomass recovery after stems have been cut back to ground level. Three native species (wax myrtle, myrsine, and rough velvet-seed) and two exotic species (Brazilian pepper and melaleuca) have been treated once every month for a year. Preliminary results show less sprouting after cutting from June to August, suggesting that, given equal fire intensities, sprouting might be reduced by wet-season fires (J. R. Snyder, Big Cypress National Preserve, pers. comm.).

Despite some problems with experimental design and data analysis, the studies described above allow one to tentatively conclude that, in contrast to dormant-season burns, growing-season burns 1) topkill a higher percentage of stems; 2) topkill larger stems; 3) reduce the amount and vigor of resprouting; and 4) increase the percentage of individuals completely killed, particularly after frequent burns.

We still lack data on how these effects vary within the growing season and with respect to different species. Early growing-season fires are often thought to be more detrimental to hardwoods, but only one study (Glitzenstein et al. 1990) supports this view; almost all other studies include a single growing-season treatment, and can thus shed no light on within-growing-season differences. Anecdotal evidence suggests that late growing-season burns may be particularly detrimental to some understory species if the tender sprouts produced after the fire are killed by frost (B. Mueller, Tall Timbers Research Station, pers. comm.; S. Vander Kloet, Acadia University, Canada, pers. comm.), but no published data have documented this effect. We do not know much about how season and frequency interact. The South Carolina study seemed to indicate that periodic growing-season burns did not reduce the abundance of understory hardwoods any more than did periodic dormant-season burns, but the data were not very clear. Also, it is important to remember that season is only one of several factors that determine how fire affects vegetation. Variation in amount of fuel, fuel moisture, wind speed, etc., may obscure or accentuate seasonal differences.

Explanations for Seasonal Patterns

The two main factors that differ between dormant- and growing-season burns are the weather (particularly temperature) and the physiological state of the vegetation. Both may explain why growing-season burns are more effective at knocking back understory species. As we discussed in the section on fire damage to pines, scorch height increases with increasing ambient air temperature, and plant tissue may be more susceptible to heat injury during the growing season. Because understory trees and shrubs are short-statured and have relatively unprotected buds, scorch height and variation in heat susceptibility may play much more important roles than they do in mature pines; they may be responsible for the greater rates of topkill achieved by growing-season fires.

An additional factor has been proposed to explain whether or how much a stem resprouts after it is topkilled. Ferguson (1957, p. 427) stated that "the ability of a stem to sprout is a function of its physiological condition rather than the character of its injury," and the physiological condition that is often considered crucial is the amount of carbohydrate reserves in the root or rhizome. Sprouting should be least vigorous when carbohydrate reserves are lowest. Waldrop et al. (1987, p. 7) used this theory to explain why frequent growing-season fires completely killed many stems in the Santee Fire Plots: "topkill early in the growing season halts carbohydrate production when carbohydrate reserves normally in the root system are at their lowest levels. When summer burns are repeated annually, carbohydrate reserves are eventually depleted and root systems die." Other studies, however, suggest that repeated burning, even at the most vulnerable time, will probably not eradicate some hardy species [e.g. saw-palmetto (Hough 1968) and gallberry (Hughes and Knox 1964)].

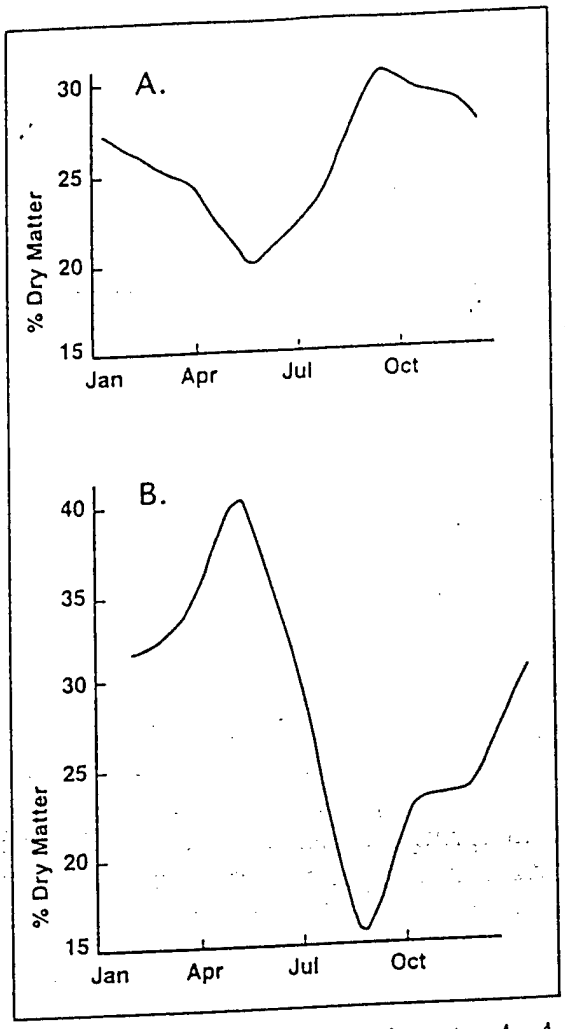


Figure 9. Hydrocarbon reserves in roots. A. A deciduous species, European chestnut (Castanea sativa). From Sablon (1904). B. An evergreen species, holly oak (Quercus ilex). From Sablon (1906). Note: for the deciduous species carbohydrate reserves are lowest in the spring, while the reserves of the evergreen species are lowest in the early fall.

If carbohydrate reserves influence the degree of sprouting, then knowledge of how these reserves vary seasonally could help predict how different species would respond to fires in different seasons. Some data suggest that seasonal patterns differ between deciduous and evergreen species. An early study done in France showed that starch reserves in roots of several deciduous species decreased rapidly to a minimum in spring, when new leaves were forming. Reserves increased through the summer, reaching a maximum at the time of leaf drop in the fall (Figure 9a) (Sablon 1904). Evergreen species, in contrast, had maximum root starch reserves in early spring. Levels dropped during the spring and summer, reaching a minimum in mid- to late summer and then increasing throughout fall and winter (Figure 9b) (Sablon 1906). Sablon explained that carbohydrates accumulate over the winter in evergreen species because cold temperatures reduce respiration more than they reduce photosynthesis (thus this effect may be more pronounced in North Florida than in South Florida).

Later studies from the United States have generally confirmed these patterns. Preston and Phillips (1911) measured starch reserves in the roots of one evergreen and eight deciduous tree species in Michigan from October to June and found that they diminished in April and May, near the start of spring leafing out (because the study did not continue through the summer, possible differences between the evergreen and deciduous species were not detected). Woods et al. (1959) found that two deciduous oaks, turkey oak and bluejack oak, in Northwest Florida had lowest carbohydrate reserves in late April or early May, when leaves were almost fully expanded. Starch reserves in roots of an evergreen tree, shortleaf pine, are lowest in the fall and highest in the spring (Hepting 1945), reserves in rhizomes of an evergreen shrub, gallberry, are lowest in August (Hughes and Knox 1964), and saw-

palmetto rhizomes also follow this pattern (Hough 1968). We do not know of any studies of semideciduous species such as live oak, laurel oak, and Chapman's oak that lose their leaves for a few weeks in late winter.

The hypothesis that low carbohydrate reserves should limit sprouting ability is supported by data on oak resprouting in Arkansas. This experiment involved girdling oaks at two-week to one-month intervals throughout the year (Grano 1955). Southern red oaks showed greatest mortality and least sprouting following April to June girdling, while post oaks showed greatest mortality following May to July girdling, and least sprouting following May girdling.

One study of evergreen shrubs supports the idea that evergreens are most vulnerable in the fall. Kramer and Wetmore (1943), working in North Carolina, found that a variety of broad-leaved evergreen shrub species fared poorly, most dying, when defoliated in October, in contrast to the minor effect of April defoliation.

Wenger (1953) disputed the carbohydrate theory, based on results from a study of sweetgum sprouting in South Carolina. He found that sweetgum stems cut every two weeks during the growing season resprouted the least in May (when the first leaves had reached full size), but a second minimum occurred in late summer. This pattern did not mirror the pattern of carbohydrate reserves in the roots, which were lowest in the spring but increased steadily all summer. Wenger proposed that sprouting vigor may depend more on hormone levels, photoperiod, and other factors than on carbohydrate reserves. Auxin, which inhibits sprouting of lateral buds, is produced by growing buds in the spring; high levels of this hormone in the uncut stem could inhibit sprouting. The late season minimum, on the other hand, might reflect the general slowing down of growth late in the growing season, prompted by decreasing day length. A study on stump sprouting by pin oak supports Wenger's theory. Vogt and Cox (1970) found that variation in carbohydrate reserves did not affect number, height, or weight of sprouts produced after decapitation. They hypothesized that sprouting vigor might be influenced by hormones such as gibberellins and cytokinins.

More studies of the seasonal effects of fire on sprouting, as well as physiological investigations, are needed to determine the mechanism of seasonal patterns and to confirm differences in seasonal vulnerability between evergreen and deciduous species.

Herbaceous Vegetation

Many of Florida's pinelands are essentially prairies with trees scattered through them; they are remarkably diverse underfoot. The groundcover includes a variety of grasses, forbs, and other herbs, with wiregrass usually the dominant species on undisturbed sites. Nearly treeless wet savannas and seepage areas, once covering extensive areas of North Florida, harbor numerous herbaceous species including pitcher plants and sundews. In South Florida,

treeless marshes and prairies cover thousands of acres. Those charged with managing such areas may have different goals concerning the groundcover — maximizing forage for cattle, increasing the abundance of a particular rare species, maintaining high species diversity — but they share the common problem of needing to know what effect different fire regimes have on the vegetation. Deciding when to burn is made difficult by our ignorance of what results we can expect. In this section we review what is known, or suspected, about how burning at different seasons affects herbaceous vegetation.

The major questions asked concerning the effect of season of burn on herbaceous vegetation are: 1) How does it affect overall production? 2) How does it affect the abundance of particular species or groups of species — and do changes in abundance reflect altered growth or mortality rates? 3) How does it affect flowering and seed production? and 4) How does it affect vegetation that is important to animals as food or shelter? We will discuss the last topic in the section on wildlife.

Overall Production

The question of overall production is primarily of interest to those trying to maximize forage for cattle or other grazing animals; it probably has little ecological significance, although very low production might indicate low nutrient levels. Overall production is usually expressed as biomass per area and may include all species or just grasses and other forage species. One difficulty with assessing production is deciding when to measure it. The usual method is to measure at the end of the growing season, or sometimes several times during the growing season. If some burn treatments occur during the growing season, though, measuring growth becomes more difficult. Should biomass measurements include just the amount of regrowth after the burn, or post-burn biomass plus pre-burn biomass, or biomass at the end of the next year's growing season? No one method is better—what to measure depends on what question is being asked—but comparisons among studies using different methods can be extremely misleading.

Studies in the Southeast and Midwest have revealed some general relationships between season of burn and overall production.

1) Post-burn biomass may be greater following early growing-season burns than dormant-season burns. Towne and Owensby (1984) found higher herbage production in a Kansas prairie following late-spring burns (May) than following burns in December, March, or April, and overall production in a North Carolina pine-wiregrass savannah was higher following late dormant-season burns than early dormant-season burns (this difference was significant in only one of two years; Schneider 1988).

2) As burns occur later in the growing season, post-burn biomass diminishes (Grelen and Epps 1967, Lewis and Harshbarger 1976, Grelen 1978). This result is hardly surprising, since vegetation burned later in

the growing season does not have as much time to regrow before it is harvested (usually in October).

3) If pre-burn and post-burn biomass are added together, some growing-season treatments appear to increase total production. Grelen and Epps (1967) found that mid-growing-season burns (July) in Louisiana pine-bluestem range produced more total herbaceous material than did March or May burns. Lewis and Harshbarger (1976) surveyed herbaceous vegetation in the Santee Fire Plots in South Carolina (see p. 36). They did not collect pre-burn biomass, but speculated that, although post-burn yields were highest in annual winter burn plots, biennial June burning treatments probably produced the greatest total forage (see graph of estimated yields in Lewis et al. 1982).

4) Differences in yield may not last much beyond the year of burning. Grelen (1975) found no difference in yield the first year following 12 years of biennial burning in March, May, and July in Louisiana, and in South Florida, Hughes (1975) found no difference two years after three or four biennial burn treatments in October, November, January, March, and May. An exception to this pattern, where yield in March-burned plots 1 year after the last fire was greater than in May-burned plots (Grelen 1983a), may have been caused by differential growth of the slash pine overstory.

5) Vegetation regrows more quickly during the growing season than during the dormant season. Hughes (1975) measured yield one month, two months, and two years following burning on treeless saw-palmetto/wiregrass range in South Florida. One- and two-month post-burn yields were highest following May burns and lowest following November and January burns. Vegetation also regrew faster after growing-season burns than after dormant-season burns in the St. Marks plots in North Florida (W. Platt, Louisiana State University, pers. comm.).

Relative Abundance of Species

Fire occurring at different seasons can shift the relative abundance (i.e. biomass) of different species or groups of species. This phenomenon is well documented for the prairies of the Midwest and the Great Plains, where dormant-season burns tend to favor C_4 grasses (grasses that thrive in warm, dry conditions) while mid- to late-growing-season burns favor C_3, or cool-season, grasses (Towne and Owensby 1984, Steuter 1987, Ewing and Engle 1988 and references therein). Other plant groups may also be affected. Towne and Owensby (1984) found that, after 56 years of annual burning in a Kansas tallgrass prairie, May burns increased grass production and decreased forb production relative to burns in December, March, or April. May burns also produced the lowest relative abundance of sedges (measured as percent composition). In a Missouri glade (grasses interspersed with post

oak, red cedar, and mixed hardwoods) August burns increased forb production relative to burns in March, April or June (Lewis et al. 1965). Yield was measured the year following the burns. Grass production did not differ among treatments.

Few data are available from the Southeast. Lewis and Harshbarger's (1976, p. 13) report on herbaceous vegetation in the Santee Fire Plots in South Carolina states that "grasses were dominant on the annual summer and biennial summer plots, while low-growing shrubs were dominant on the periodic summer and on the winter-burned plots." This statement is illustrated by a figure in Waldrop et al. (1987) (Figure 10), but without statistical analysis it is impossible to tell whether the apparent differences among treatments are due to differences in fire regime or to random factors. Schneider's (1988) study of a pine-wiregrass savanna in North Carolina showed that grasses accounted for a greater proportion of total production after February-March and July burns than after November-December burns, while shrubs showed the opposite trend, being favored by fall burns. These conclusions are based on only one (July) or two years of data (February-March and November-December). The eight-year St. Marks study in North Florida showed no difference in biomass of major plant groups (woody plants, forbs, C_3 grasses, C_4 grasses, and wiregrass) among plots burned in winter, spring, summer, and fall (Platt et al. 1989).

Explanations for seasonal effects include that of Anderson et al. (1970), who speculated that fires occurring when individuals of a species are actively growing will be more injurious (i.e. result in less production) than fires occurring when the plants are dormant or just beginning growth—thus the reduction of C_4 grasses when fires occur during their mid-summer growth period. Levels of carbohydrates in roots and rhizomes have also been invoked as determining regrowth capability of herbaceous plants (this explanation might be equivalent to the former, if reserves are depleted during periods of active growth). We know of few studies that have measured carbohydrate reserves. Woods et al. (1959) found lowest levels in wiregrass roots in mid-July, with highest levels from January through March, but there are no data yet on regrowth of wiregrass burnt at different times of year.

Some species may be particularly vulnerable at specific times of year. Sawgrass in the Everglades, for example, can be devastated by intense burns during the dry season (Hofstetter 1974). These fires burn down into the peat, killing sawgrass rhizomes. Sawgrass can also be killed if it is flooded before it is able to regrow after a fire (Hofstetter 1974).

Flowering and Seed Production

Numerous studies have shown that season of burn can influence flowering characteristics of many grasses and forbs. These include number of flowers, proportion of plants flowering, and date and duration of flowering.

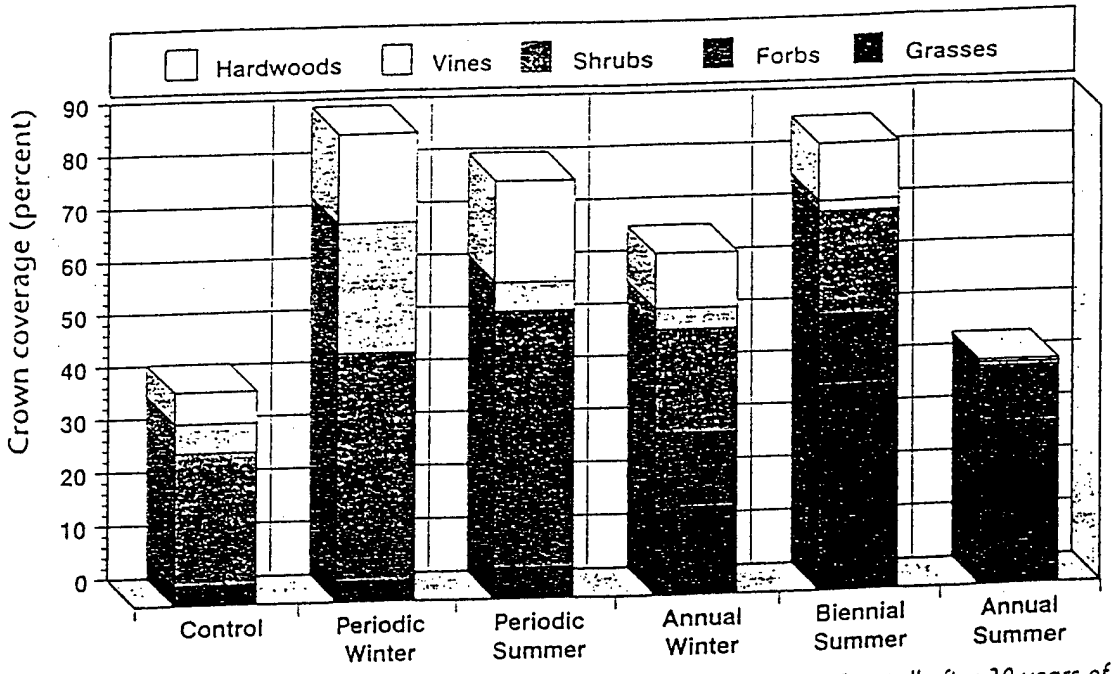


Figure 10. Percent crown coverage of all understory plants less than 1.5 m tall after 30 years of prescribed burning, Santee Fire Plots, South Carolina. Annual and biennial summer fires produced the greatest percentages of grass cover. Annual summer fires precluded shrubs. Annual winter fires also appear to have favored grasses and forbs. Less frequent winter fires have led to the dominance of shrubs. From Waldrop et al. (1987).

Wiregrass is the classic example of a species whose flowering response is influenced by season. For many years it was thought that wiregrass rarely flowered or produced viable seeds. Eventually, however, people began to notice wiregrass flowering after summer wildfires. In 1964 Clifford Lewis reported that wiregrass on South Florida range flowered profusely when burned in May, compared to little or no response following October, November, January, or March fires. Parrott (1967) confirmed this observation, adding that a July wildfire also stimulated flowering. Since then many have observed wiregrass in Florida flowering after fires occurring between April and August (e.g. Platt et al. 1989). In North Carolina, by contrast, Parrot found that fires anywhere from November to August stimulated flowering. The difference between Florida and North Carolina may provide a clue as to what stimulates wiregrass to flower. Perhaps the presence of bare soil (which could be sensed through elevated soil temperature) sometime during the growing season is the necessary stimulus. Mild Florida winters allow some plant growth to occur, so that bare ground exposed by a winter fire is covered by early spring. In North Carolina, however, bare ground might still be exposed in the spring, mimicking conditions following a spring fire and stimulating flowering (this theory could also explain why wiregrass in disturbed areas sometimes flowers even without being burned).

Although May burns prompted profuse flowering, Parrot (1967) claimed that the flowers were imperfect and would not produce seeds; he stated that a

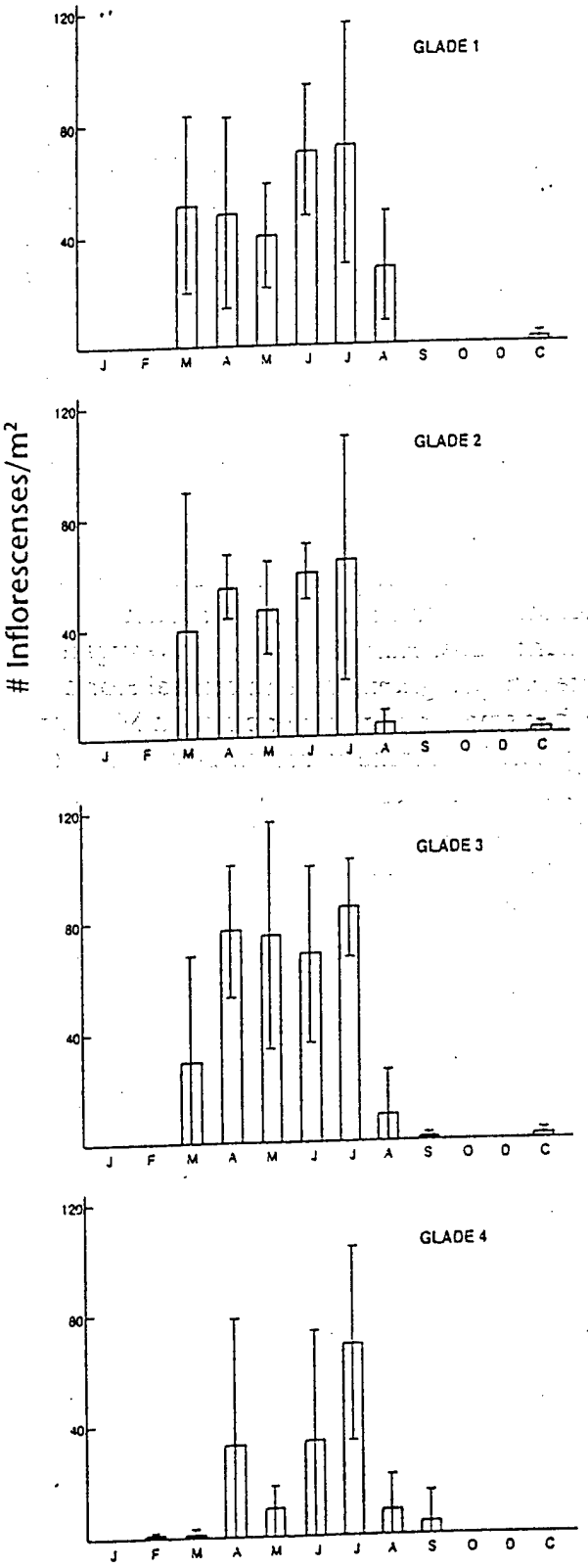


Figure 11. Flowering response of cutthroat grass (Panicum abscissum) at four sites in central Florida following burns in different months. Burns occurring March-July stimulated massive flowering responses. Sites burned in the dormant season and unburned sites (C) exhibited limited flowering. Myers and Boettcher (unpublished data).

July wildfire and an experimental September defoliation were the only treatments that produced perfect flowers. In a pilot study done by The Nature Conservancy's Fire Management and Research Program, however, seeds from May-burned wiregrass in northern and central Florida did germinate (Seamon et al. 1989). Seed production in wiregrass is a topic that needs much more study.

Other native grasses appear to respond favorably to growing-season fires, although there are some exceptions. In 1943 Biswell and Lemon published a brief note reporting that late spring or early summer fires stimulated seed stalk production by six southeastern forage grasses (the species were not identified). More recently, Myers and Boettcher (1987) have found that cutthroat grass, a threatened central Florida endemic, flowers abundantly when burned between mid-April and mid-August, but rarely flowers if burned at other times (Figure 11). In the St. Marks plots in North Florida, little bluestem and other bluestem grasses (as well as wiregrass) showed a similar pattern, flowering much more following growing-season burns than dormant-season burns (Platt et al. 1989). Burning season did not affect flowering of three other grass species (thin paspalum, *Dicanthelium aciculare*, and *D. ovale*), while dormant-season fires enhanced flowering of the sedge *Scleria ciliata*.

Growing-season fires also appear to favor flowering of many native forbs. Snyder and Ward (1987) burned plots in South Florida marl prairies (also known as muhly prairies after the dominant species *Muhlenbergia filipes*) at different times of year, spaced at four- to seven-week intervals. Their preliminary results show the greatest increase in flowering (compared to unburned plots) following fires from February to June (late dry season to early wet season). In the St. Marks study growing-season burns (April to August) produced more flowering stems than did dormant-season burns, but did not increase the total number of species flowering. A survey of seven common fall-flowering species showed that four flowered more following growing-season burns (blazing star, two species of golden aster, and pencil flower), two were unaffected (Florida elephant's foot and a third golden aster species), and one flowered more following dormant-season burns (pinweed) (Platt et al. 1989). These results are for the growing season following the burn; flowering response the second year is not yet known.

Platt et al. (1988) note that the increase in number of flowering stems following growing-season burns at St. Marks appeared to be due to an increase in the number of ramets (separate stems of the same individual), and was most pronounced among composites. In contrast to dormant-season burns, growing-season burns kill the apical meristem, resulting in the production of multiple stems from previously dormant buds. Hartnett (1987) investigated this response in the sandhill composite *Pityopsis graminifolia* in central Florida. He found that plants produced more, but smaller, ramets per clone in May- or June-burned plots than in unburned plots. In summary, growing-season fires can increase flowering either by stimulating more plants to flower (e.g. wiregrass and cutthroat grass), or by increasing the number of flowering stems per individual (e.g. composites). While most species respond best to growing-season fires, a few flower more following dormant-season fires.

Growing-season burns can also delay flowering. Platt et al. (1988) documented a delay in peak fall flowering, particularly following July and August fires; as a result, synchronization of flowering among different species increased. Snyder and Ward (1987) reported that season of burn shifted the flowering date of some species but not others. Date of seed production by several *Panicum* species in South Florida appeared to be affected by season of burn, according to Hughes (1975). He observed that plants burned in October produced seeds in April, whereas those burned in January, March, and May produced seeds in May, June, and July, respectively. Flowering of some species may be delayed for a year after a growing-season burn. Pitcher plants and some true orchids, for example, rarely reflower; thus a fire occurring at any time from bud formation to seed dissemination will destroy seed production for that year (S. Hermann, Tall Timbers Research Station, pers. comm.). Loss of a single year's seed production would probably not harm populations of these long-lived species as long as it did not occur too frequently; in addition, fire may enhance flowering the following year (S. Hermann, pers. comm.).

Changes in a species' flowering and fruiting phenology could potentially affect its population biology. Dates of seed production could be shifted toward, or away from, periods beneficial to seed dispersal and/or germination; likewise, flowering might be made to coincide more or less with the availability of pollinators.

Changes in flowering time may also influence hybridization rates. It has been suggested that frequent winter burning of savannas may alter the flowering phenology of pitcher plants so that blooming periods among different species overlap more than they would under a regime of growing-season burns. This overlap may increase cross-pollination and lead to increased hybridization (S. Hermann, Tall Timbers Research Station, pers. comm.).

Platt et al. (1988) uncovered an interesting effect of fire season, a change in flowering duration. In fact, this effect was more pronounced than was that of increased flowering. Relative to dormant-season burns, growing-season burns decreased flowering duration within species. That is, all individuals of a species tended to flower at about the same time. Shortest durations followed July burns. Platt et al. (1988) suggest that increased synchronization of flowering could increase pollination levels and/or outcrossing rates. At the same time, however, a greater number of ramets per clone could increase the rate of self-pollination, and greater flower density could reduce outcrossing levels if pollinators moved shorter distances (e.g. Palmer et al. 1988, Redmond et al. 1989).

The increased response of many native species to growing-season burns suggests that these species are adapted to a regime of lightning-season fires. This overall trend, however, includes species that respond best at different times during the growing season, as well as some that respond best to dormant-season fires. As an example from a different part of the world, Taylor (1977) reported preliminary data showing that seeds of a rare species endemic to South Africa's Cape of Good Hope Reserve are killed by a fungus unless the plant is burnt in the winter, not the natural fire season. He suggests that this requirement may explain why the species is so rare.

EFFECTS ON ANIMALS

> *Nothing, for instance, can be more destructive to ground nesting game birds than summer fires which destroy nests and young, together with growing food supply and cover, and all conservationists should combine against them (Stoddard 1935, p. 347).*

> *Summer fires...occur not only during the...reproductive stages of grasses and forbs but also of the animal inhabitants. These animals have had to evolve under such conditions, too, so that natural selection over a long period of time has "fitted" them to survive under a summer, lightning-caused fire regime (Komarek 1965, p. 195).*

Good data concerning the effect of fire season on animals are understandably slim. Animals are much more difficult to study than are plants, and long-term effects take considerable time and effort to detect. Until such data are acquired, discussions of the effect of season of burn must remain primarily in the realm of speculation. Native species may be adapted to a summer fire regime, as Komarek suggested, but it does not necessarily follow that growing-season fires will produce optimum conditions for every species. Also, because prescribed fires are unnatural in other ways, restoring the natural season is not equivalent to restoring the fire regime under which these species evolved.

Fire affects animals in many ways, any of which could vary with season (see Bendell 1974, Lyon et al. 1978 for reviews of fire effects on fauna). Fire effects are generally divided into direct — mortality caused by the fire — and indirect — alteration of habitat, both short-term and long-term, including availability of cover, nesting sites, and food. We first discuss in general how some of these factors might be expected to vary following dormant-season or growing-season burns. We then discuss seasonal effects specific to particular species or groups of species.

How Fire Affects Animals

Direct Effects

Fire-caused mortality is by far the most frequently voiced objection to growing-season burns. Recommendations of when to conduct prescribed burns invariably warn against burning when birds are nesting or young of other species are present. For example, a review of prescribed burning on national wildlife refuges (Czuhai 1981, p. 38) states:

> *Most Refuges burn during the months of December, January and February. Other Refuges select October through March but all select the winter months when nesting activity is minimal. Summer burning has been done experimentally, and if it is needed to accomplish a wildlife objective, it will be done after the nesting season.*

Similarly, the U.S. Forest Service's plan for vegetation management in the Southern Region states that, although growing-season fires are allowed, "gen-

erally, understory burns are not scheduled during nesting season to avoid disrupting reproductive activities" (U.S. Forest Service 1989b, p. A-7). Fire season can certainly affect the incidence of fire-caused mortality in many animals, but the effect must vary among species depending on where and when they breed and how readily they renest. Many species breed at times other than spring and summer, particularly in South Florida.

Indirect Effects

Indirect effects come about through alteration of habitat. Not only are they difficult to study, but they are often surprisingly at variance with what might be predicted from knowledge of direct effects. Protecting the lives of individual animals, for example, may harm the population as a whole if it leads to elimination of the species' habitat. In the Southeast we have found that we must use fire, a seemingly destructive force, to maintain the habitat for many plants and animals. At the same time, we have tried to minimize fire's destructiveness by applying it during the dormant season. Has this practice diminished the quality of the environment for native species? Would growing-season burns improve the habitat enough to outweigh increased direct mortality?

Burning at different times of year affects wildlife habitat by influencing vegetation structure and composition and affecting food availability. A summary of vegetation effects as they might relate to wildlife habitat follows.

Short-term effects on vegetation:

1) Prescribed fires conducted in rainy, humid weather during the growing season may be patchier than those occurring during drier weather (dormant season or early growing season).

2) Vegetation regrows more quickly following growing-season burns.

3) Growing-season burns promote increased flowering of some herbaceous species, but flowering and fruiting may be delayed, particularly by mid to late growing-season fires. Flowering and fruiting of some species may be delayed for a year.

Long-term effects on vegetation:

1) Growing-season burns favor herbaceous over woody vegetation; the more frequent the fires, the more pronounced the effect.

2) Early growing-season fires are the most detrimental to understory deciduous hardwoods. Evergreen species may be most affected by late growing-season fires.

Effect of Season of Burn on Different Animals

Invertebrates

Direct Effects

Insects and other invertebrates are most vulnerable to fire during life stages that occur within surface litter or in plant stems or leaves. Stages occurring in the soil, as well as mobile adults, are much less vulnerable. Force (1981), for example, found a number of nonflying arthropods in soil samples taken three months after a November fire in California chaparral. Because migration from unburned areas could not have occurred so quickly, he speculated that these animals had been in diapause in the ground at the time of the fire. Protected areas above ground may also harbor survivors; after a prairie fire, Rice (1932) found live insects in the center of a burned clump of grass and under unburned debris. Metz and Farrier (1971) sampled mesofauna (mites, collembolans, and small insects) before and immediately after an August fire in South Carolina and found 45 percent as many individuals in the mineral soil after the fire as before, while 13 percent of those in the surface litter survived. The time of greatest vulnerability will vary among species depending on their life histories. Some species may be less vulnerable during the dormant season because they are in a resistant stage; others may be less vulnerable during the growing season because they are more mobile and can escape the fire (see Ahlgren 1974 and Lyon et al. 1978 for reviews of the overall effect of fire on invertebrates).

Short-term Indirect Effects

Although the abundance of insects and other invertebrates decreases immediately after a fire, it usually increases again as vegetation starts to grow and both surviving individuals and migrants from surrounding unburned areas recolonize the burned site (Rice 1932, Force 1981). Recolonization would obviously occur more quickly following small and/or patchy burns than following large and/or complete burns. For several weeks or months following recolonization, the abundance of some insect groups may be higher in burned than in unburned areas (Cancelado and Yonke 1970, Y. Gillon 1971, Nagel 1973). Herbivorous insects may be attracted to the fresh young growth, which is generally more palatable than older plant tissue.

How does season of burn affect recolonization by invertebrates? We have very little data that bear on this question. Because vegetation regrows more quickly following growing-season burns, one would expect recolonization to occur more rapidly. Warmer temperatures might also increase growth rates. D. Gillon (1971) presented anecdotal evidence that hemipterans recolonized an African savanna more quickly following a wet-season (April) fire than dry-season (January) fires and suggested that this was due both to quicker vegetation regrowth and to the life cycle of the insects, which were in reproductive, adult stages in April. The identity and relative abundance of recolonizing species must surely be influenced by season of burn, but we know of no studies that have investigated this point.

The effect of fire season on flowering phenology may affect food availability for migrating insects. Some preliminary data from coastal Northwest Florida showed that July burns delayed flowering of many composites, including *Liatris provincialis* (a State endangered species) and some goldenrod species. Because of this delay, flowering of these species was synchronized with the arrival of migrating monarch and Gulf fritillary butterflies in late fall, a time when few other food sources are available (S. Hermann, Tall Timbers Research Station, pers. comm.).

Long-term Indirect Effects

Vegetation structure and composition undoubtedly affect abundance and diversity of invertebrates. Thus one might expect that two sites managed with different seasonal fire regimes might have very different invertebrate faunas. Long-term seasonal burning studies such as those at the Palustris Experiment Station in Louisiana, the Santee Fire Plots in South Carolina, and the St. Marks, Florida fire plots would provide excellent opportunities for investigating this question. Metz and Farrier (1971) did investigate soil mesofauna in the Santee plots, but they sampled only winter-burned plots for long-term effects (samples from a summer-burned plot did not represent long-term effects, being taken 24 hours after the fire).

Panzer's (1988) review of the effect of fire on insects inhabiting Midwestern prairie remnants provides some information on the effect of fire season. He found very little evidence that long-term burning had detrimental effects, even on species thought to be particularly vulnerable to fire at a certain time of year (e.g. butterflies, which are present as vulnerable caterpillars and eggs during spring and fall when most prairie burns are conducted). He recommended, however, leaving some unburned areas and burning with head rather than back fires (the former elevate temperatures for a shorter period of time), particularly if rare species are present.

Vertebrates

Amphibians and Reptiles

We do not know much about the effect of fire season on amphibians and reptiles. It has been suggested that these groups might be more susceptible to direct mortality from fire during cold weather because they move slowly then (Means 1988). Winter-breeding amphibians may also be particularly vulnerable to dormant-season fires, but one of these, the flatwoods salamander, does not appear to have suffered from a regime of winter burning (Means and Campbell 1981). Species that are inactive in protected burrows during the winter may be less vulnerable to fire during the dormant season. Direct fire effects are probably of minimal importance relative to indirect effects (Means and Campbell 1981), but we have too little information to be able to generalize about the indirect effects of different fire regimes on these groups.

One of the few reptiles about which we have some information is the gopher tortoise, a species of special concern in Florida. Concern over declining

gopher tortoise numbers has prompted much discussion of how to keep the species from disappearing as Florida continues to develop. This species occupies most of the upland fire-prone habitats in the state, and to protect it we must properly manage its habitat. Some evidence suggests that proper management may include burning during the growing season.

Gopher tortoise densities are higher in open areas with herbaceous groundcover than in brushy, shaded sites; the former have patches of bare ground needed for nest excavation and also provide abundant herbaceous vegetation for feeding (Cox et al. 1987). This type of habitat, as we have seen, is promoted by growing-season fires. In addition, Cox et al. (1987) suggest that growing-season fires might increase the amount of food available in late summer when food quality is declining and would provide good conditions for new hatchlings, which emerge in late summer and early fall. These latter effects are short-term and would be important only in the year of the burn.

Florida Game and Fresh Water Fish Commission biologists are currently conducting a study in Ocala National Forest that compares gopher tortoise densities in July-burned plots to those burned in February (O'Meara 1987). After the first year there were significantly more burrows in the July-burned plots, but because pre-burn data were not collected this result could merely reflect preexisting differences in density. A second set of plots will be censused both before and after burning at different seasons.

Birds

Songbirds

Fire may have a direct effect on songbirds (passerines) if nests with eggs or nestlings in them are destroyed. Ground-nesting birds (see Quail and Turkey section) or those that nest in shrubs would be more vulnerable than those nesting higher in the canopy (assuming surface, not crown fires). Fire just before nesting season could also destroy nest sites. The long-term effect of nest destruction on a particular species would depend on the percentage of nests destroyed, the rate of renesting, and how frequently burns during the nesting season were conducted. Long-term effects will be very difficult to predict without more data.

Indirect fire effects are probably much more important than direct effects in determining species composition and abundances in a particular area. Because growing-season burns tend to reduce the density of understory vegetation, frequent growing-season burns would tend to favor birds that prefer open woodlands and grasslands. Dormant-season burns, on the other hand, would tend to favor species that prefer shrubbier habitats with more understory hardwoods. Dickson (1981) lists some of the species associated with these different habitat types in southern forests, and Jackson (1988) discusses the native bird species of southeastern pine forests.

One species that is of concern to a number of land management agencies is the Florida scrub jay. The Florida scrub jay is a subspecies of the scrub jay that

is widespread throughout the western U.S.; the Florida population is endemic to the oak scrub of central Florida (see Woolfenden and Fitzpatrick 1984). The jay is of interest not only because of its unusual system of cooperative breeding, where young birds help their parents rear the next year's brood, but because its restricted range is threatened by development and loss of habitat. It is a federally and state-listed threatened species. The jays require low-statured shrub vegetation (Woolfenden and Fitzpatrick 1984), a type that either develops in the course of post-burn regrowth of sand pine scrub or is maintained in oak scrub by fires occurring at intervals of one to several decades. If scrub jay habitat is maintained with prescribed fire, is there a preferred season for burning? Researchers at Archbold Biological Station, where most of the scrub jay work has been done, caution that a fire occurring during peak nesting season (usually May) could produce a long-lasting reduction in the population if it killed a large number of nestlings (R. Curry, Archbold Biological Station, pers. comm.). The effect would continue in subsequent years because an entire generation of young birds would not be available to help at the nest. Renesting following nest destruction does occur, but probably only if part of a pair's territory remained unburned. While periodic population declines probably occurred frequently in the past as a result of spring wildfires, the effect would not have been as serious as it would be now that the species is broken into small, scattered populations.

Red-cockaded Woodpecker

Red-cockaded woodpeckers, once widespread throughout the Southeast, have been dwindling in number along with their preferred habitat—mature stands of southern pine species. The woodpecker was designated an endangered species in 1970, and federal agencies are consequently required to protect colonies occurring on their land. This requirement has prompted some research into the species' habitat preferences, as well as exploration of how to best manage areas containing colonies.

Red-cockaded woodpeckers appear to prefer nesting in open pine stands with few or no hardwoods in the understory (Van Balen and Doerr 1978, Locke et al. 1983 and references therein). Growing-season burns would seem to be an appropriate management tool for creating or maintaining this type of habitat, but concern about disturbing nestlings might make managers hesitate to burn at that time. Baker (1971) notes that in North Florida nesting occurs from late April through June and occasionally early July.

Stamps et al. (1983) conducted two spring burns (late May and early June) in red-cockaded woodpecker colonies in North Carolina and did not observe any detrimental effects on nestlings. Cavity trees, which are usually covered with flammable resin, were raked around before the burn, and backfires were set around the trees before the rest of the area was burned. Temperature readings taken in two nests during one of the fires reached a maximum of 35°C (95°F), which the authors did not consider dangerously high. Adult birds did not feed their young while people were working around the nest trees, but

again, the authors did not consider this disruption to be serious. Nine birds ultimately fledged from the four nests that contained nestlings at the time of the fires. A fifth nest that contained three eggs failed, but according to the authors that is the usual fate of such late nests. One cavity tree was ignited and died the following year. Cavity trees may be more susceptible to ignition in the spring when resin is more abundant, but winter fires have also ignited and killed cavity trees (Conner and Locke 1979).

Stamps et al. (1983, p. 80) concluded that colony sites could be safely burned while the birds are nesting, but recommended the following precautions: "(1) burn early in the day while ambient temperatures are relatively low; (2) burn only in sites with light fuel accumulations; (3) remove woody vegetation from around cavity trees; (4) back-fire 10m to the windward side of cavity trees before allowing head fires to approach; and (5) burn in colony sites only after nests have been identified."

Quail and Turkey

April and May prescribed fires should be avoided when managing for turkey because this is their peak nesting season (Wade 1983, p. 213).

[Summer] fire will destroy nests, eggs, and young of the various birds that may be residing in the area... Rarely would I recommend such a fire (Rosene 1969, p. 315).

Special consideration should be given to wildlife since prescribed burns could be very harmful to nesting birds or young wildlife (Lewis et al. 1982, p. 24).

Warnings of the damage spring and summer fires can do to ground-nesting birds abound in the literature. While the short-term effect of growing-season fires may indeed be destructive, no one really knows what the long-term effect would be on quail, turkey, and other ground-nesting birds. There is probably no simple answer; the effect certainly depends on fire frequency and coverage and may also depend on geographical location, habitat type, and weather conditions at the time of the burn. Until direct evidence is available, we will have to make inferences from indirect evidence. In this section we attempt to determine what effect burning at different seasons would have on nesting and reproduction, food, and cover.

Nesting

In North Florida, quail may nest anytime from April to October, with peak nest initiation occurring from mid-May through early July (Simpson 1972; data are from SW Georgia) and peak hatching usually occurring in late July (Landers and Mueller 1986). Quail in South Florida may start nesting as early as late January, although hatching usually peaks in mid-June (Campbell 1988). The nesting season of the wild turkey is slightly earlier and more compressed. In the Red Hills region of North Florida, turkeys may begin laying in mid-March with a peak onset of incubation in mid- to late-April, and a peak hatch in mid- to late-May (Sisson et al. 1990). In Central and South Florida, turkeys lay from

early March to early June (with an early-April peak), incubate from early April to early June (mid-April peak), and hatch from late April to early July (late May peak) (Williams and Austin 1988).

The effect of burning during the nesting period will depend on how many nests are destroyed, how many birds renest, the size and percent cover of the burns, and how frequently such burns occur. We do not know of any studies in the Southeast that have compared nesting success of areas burned during the nesting period with those not burned or burned at other times (merely recording the number of nests destroyed by fire is not sufficient for determining fire-caused nest failure because some of these nests might have failed later for other reasons). In North Dakota, Kruse and Piehl (1986) found that 31 percent of active ground-nesting bird nests were destroyed by May and June fires (averaged over two years). Of those nests that survived, some were in areas where the vegetation did not burn, while approximately an equal number were in the burned area (that is, vegetation on at least one side of the nest had burned). Higgins (1986a) compared the effect of spring and fall burns in North Dakota and found that nesting success, averaged over four years following the burns, was 13 percent in spring-burned plots and 23 percent in fall-burned plots. This result reflects much reduced success in spring-burned plots the year of the fire (all nests active at the time of the fire were destroyed) combined with inferior nesting conditions in subsequent years (vegetation growth was greater in fall-burned plots than in spring-burned plots). Similar studies in the Southeast would give us some idea of how destructive fire is to quail and turkey nests. In the meantime, we can merely say that burning during nesting season will most likely destroy some nests, and that patchier burns will probably destroy fewer nests than complete burns.

The long-term effect of nest destruction on ground-nesting bird populations will depend, in part, on the rate of renesting. Quail nests often fail, and a hen may renest two or three times a summer (Stoddard 1931, Landers and Mueller 1986). Nest destruction by fire might not have a major effect on overall nesting success for the year if nesting sites were available after the fire and if environmental conditions were suitable for renesting. If a fire occurs early in the growing season, vegetation can regrow enough to provide nesting sites later in the summer (see Simpson 1972). Mid-growing-season fires might reduce overall nest success if no unburned cover remained.

Turkeys are considered by many wildlife biologists and land managers to be much more vulnerable to fire because they do not readily renest. Recent research from Florida suggests that renesting may be more common than was thought, though still much less frequent than in quail. Williams and Austin (1988) collected data on renesting rates of turkeys in central and southern Florida and found that 57 percent of 30 hens whose nests were disrupted during the laying period renested, while 28 percent of 98 hens disrupted during the incubation period renested. None renested after 18 or more days of incubation. Burns late in the incubation period, from late-April to early-June,

thus would appear to be the most detrimental to turkeys, and if conducted at frequent intervals might keep turkey populations low. May and June burns conducted at several-year intervals or alternated with burns at other times of the year would have less impact than frequent growing-season burns.

Food

Particular burning regimes are often recommended or criticized because of the effect they are supposed to have on the preferred food of quail and turkey (similar arguments are advanced for other game animals). There are two major difficulties with such arguments. First, increasing or decreasing the amount of available food will not affect the population unless food is a limiting factor, something which is hardly ever known (and very difficult to determine). Second, consumption of a certain food does not necessarily indicate that the species requires that type of food: "animals may show a selection or preference for certain foods, but preference may not mean need so that correlations between foods that are simply preferred and the welfare of wildlife may be trivial" (Bendell 1974, p. 96).

Keeping these difficulties in mind, we can nevertheless draw some general conclusions about quail and turkey foods and how they may be affected by burning at different seasons. Both quail and turkey take food from on or near the ground and eat a variety of plant material, especially seeds, berries, and acorns, as well as insects. Legume seeds are an important quail food (Stoddard 1931, Landers and Johnson 1976, Landers and Mueller 1986), and insects have been found to be particularly important during the first weeks of life for both quail chicks (Hurst 1972) and turkey poults (Williams and Austin 1988).

Different fire regimes would effect different components of this diet. Growing-season burns increase flowering of some herbs, although this has not yet been demonstrated for species with high food value for vertebrates. After early growing-season burns, new green growth and associated insects are available for young chicks and poults. Some researchers have become interested in using growing season burns to increase insect numbers and improve brood habitat. Landers and Mueller (1986) suggest that late spring burning in small openings might play a role in making good brood habitat for quail. Sisson (1991) however, found no statistical difference in the number of insects available to turkey broods following a winter and an early growing-season burn.

Growing-season burns may also have detrimental effects on some quail and turkey foods, although these negative aspects have been somewhat exaggerated in the past. Warnings of possible (but unproven) detrimental effects were initially stated by well-known authorities and are unquestioningly repeated in the literature. H. L. Stoddard, in his quail "bible," *The Bobwhite Quail: Its Habits, Preservation, and Increase*, stated that spring and summer fires reduce the overall food supply and destroy annual legumes (Stoddard 1931, p. 406; p. 413). A more recent book on quail management noted that April fires kill young plants

and newly hatched insects (Rosene 1969, p. 296). Other authors have echoed these warnings and added that spring and summer fires delay fruiting of some food plants (Hughes 1975), destroy seeds that may be important quail food (Moore 1957, Landers 1981), and reduce insect populations (Hurst 1972, Landers 1981). Many of these statements have some truth to them but others are misleading. The discussion below attempts to give perspective to these statements.

As a rule, growing-season burns do not reduce the total annual supply of herbaceous vegetation (see Groundcover section). Any fire temporarily reduces the food supply, but this reduction would actually persist longer following dormant-season than growing-season burns. Would a reduction in food be most serious during the nesting season when animals are less mobile? There are no data on this subject, but the problem could be minimized by burning either before or after peak incubation and hatching times and by making sure burns are patchy. In fire regimes other than annual burning, detrimental effects would be short-term, occurring only in the year of the burn.

What about destruction or delayed production of seeds? Several studies have shown that flowering and fruiting are more prolific following growing-season burns than dormant-season burns (see Groundcover section), and perennials will resprout and flower even after late growing-season fires (Platt et al. 1988); thus any loss of seeds should be made up for later in the season. A delay in fruit production could be critical if other food sources were not available. Whether or not delayed fruiting results in overall food scarcity could be determined by studying food habits of birds in areas burned in different seasons. Similar experiments are needed to determine whether destruction of recently sprouted annual legumes by growing-season fires would lead to a food shortage.

A few studies have been done on the effect of burn season on legumes and other quail foods, and none has shown that growing-season burns reduce the amount of available food; some of these data, however, are not very reliable. In an analysis of data from the long-term Santee plots in South Carolina, Lewis and Harshbarger (1976) found that *Lespedeza* had the greatest coverage on annually burned winter plots, but partridge pea coverage was greatest on biennial summer plots. A study done in the Missouri Ozarks (Lewis et al. 1965) found that overall legume production, as well as that of the "preferred" legumes *Lespedeza* and *Desmodium*, was not significantly different in plots burned in March, April, June, or August. The study included only one year of burning, thus minimizing the generality of the results. Another one-year study in Georgia (Cushwa et al. 1966) found no difference in the number of legumes present in summer- or winter-burned plots (one year after burning), while a similar study in South Carolina (Cushwa et al. 1970a) found legume numbers in plots burned in April or May were not different from those in plots burned in July or August. The latter study found more legume seeds on the summer-burned plot than the spring-burned plot. Moore (1957) found that August burns in Alabama produced "greater coverage of quail food plants" than

January burns. Despite the problems with these studies, they certainly do not suggest any detrimental effect of growing-season fires on legumes. A three-year study is currently underway at Tall Timbers Research Station to investigate the effects of late-summer fires on legumes.

One legitimate concern is that growing-season fires reduce availability of berries and acorns. Frequent growing-season burns tend to reduce the occurrence of mast-bearing species; in addition, a fire early in the growing season when shrubs are flowering may eliminate fruit production for that year. On the other hand, fruit production of runner oak and some blueberry and huckleberry species is said to be stimulated by late growing-season burns (see Black Bear section).

In summary, although growing-season fires may reduce the availability of some types of quail and turkey foods, they may enhance other types; the overall effect of different fire regimes is not known, and will depend on habitat type and fire frequency.

Cover

Do growing-season burns reduce the cover that ground-nesting birds depend on for concealing their nests and hiding from predators? All fires temporarily reduce cover, and the timing of that reduction could be important. A fire coming before or during nesting season could eliminate sites for nesting or renesting. Simpson (1972) states that quail, at least, do not like to nest in very recently burned areas. April, May, and June are often dry months in Florida, and fires during this time tend to burn very completely, killing hardwood stems and significantly limiting woody cover and nest sites. Fires during the dormant season, on the other hand, remove cover at a time when it grows back slowly, possibly exposing birds to increased predation by raptors (Mueller 1989). As far as cover is concerned, late growing season might be the best time to burn. The detrimental effects of burns at other times of year could be reduced by conducting patchy burns—special efforts may be required to ensure patchiness.

What about long-term changes in vegetation structure? Consistent use of growing-season burns would tend to reduce the number of understory hardwoods and brushy thickets; the amount of heterogeneity remaining in the site would depend on many factors, including timing and frequency of burns, burning technique used, and environmental heterogeneity within the site. Again, long-term studies are needed to determine how changes in cover would affect bird populations.

Conclusion

Based on current knowledge, we cannot conclude that there is clearly a best time to burn for maintaining natural population levels of ground-nesting birds. In northern Florida and South Georgia, game bird populations on private shooting reserves have been successfully managed for decades using late dormant-season (primarily March) burns, as well as other habitat management

techniques. The vegetation is predominantly old-field pinelands and hardwoods interspersed with wooded drainages, draws, and swamp thickets. The burns are typically patchy, and vegetation begins to regrow within a few weeks followed by nesting of quail a month or two later. The goal on these reserves is to maintain artificially high "shootable" populations.

On many public lands in Florida, management objectives are not nearly so directed, and management practices frequently fail to maintain shootable populations; season of burn would probably have little effect on game bird populations in these areas unless other management practices were also instituted (B. Mueller, Tallahassee, FL, pers. comm.).

Both growing-season and dormant-season regimes have advantages and disadvantages, and some wildlife biologists suggest that growing-season burns can benefit game birds if the burns are well planned and properly implemented (Sharpe and Curtis 1988; N. Eichholz, Florida Game and Fresh Water Fish Commission, pers. comm.). Managers considering burning during the growing season can lessen possible negative impacts by reducing the size of burn units, by making sure burns are patchy, and by varying the time of year at which they occur.

Mammals

White-tailed Deer

Fire is generally thought to cause little direct mortality to large animals such as deer (Bendell 1974, Lyon et al. 1978). Some authors, however, have expressed concern that spring fires might harm young fawns (e.g. Springer 1977). For the first couple of weeks after birth fawns are mostly sedentary, staying hidden except when their mothers return to nurse them, but they are able to run by the time they are a few days old (Marchinton and Hirth 1984). It seems likely that all but the youngest fawns could escape most fires, although fawns separated permanently from their mothers would probably not survive. Because white-tailed deer have a long breeding season in Florida, few vulnerable fawns would be present at any one time.

Discussion of the effect of fire on deer usually concentrates on indirect effects, particularly on plant species or types of plants that are thought to be important deer foods. Deer eat a wide variety of plant foods, including grasses and forbs, browse (twigs and leaves of woody plants), hard mast (acorns and other nuts), soft mast (berries and fruits), and mushrooms (Verme and Ullrey 1984). Different seasonal burning regimes would promote different components of this diet—growing-season fires would tend to promote the herbaceous component while dormant-season fires would promote browse production by stimulating woody plants to sprout. Because browse is often considered to be the more important component, prescribed burning recommendations for managing deer habitat usually recommend dormant-season burning (Lewis and Harshbarger 1976, Wade and Lunsford 1989).

Some wildlife biologists question the importance of browse relative to herbaceous vegetation, particularly in the South. Verme and Ullrey (1984, p. 112) believe that white-tailed deer can be considered true grazers, "probably turning to browse when herbaceous forage is unavailable" (see also Harlow 1984). Cushwa et al. (1970b) found that deer in the Southeast ate twigs only in the spring, when they were succulent (although leaves of evergreen shrubs were eaten in the winter). Stransky and Harlow (1981, p. 135) reviewed several studies showing that "forbs and grasses constitute a large portion of the diet of deer in some seasons."

Realization of the importance of herbaceous vegetation to deer has prompted some wildlife biologists to suggest possible benefits of growing-season fires. Landers (1987), for example, suggests that growing-season burns in small patches might provide succulent new growth for fawns and pregnant does, and Stransky and Harlow (1981) point out that infrequent summer burning increases the abundance and kinds of herbaceous vegetation. Nevertheless, browse (mostly in the form of evergreen leaves) and mast may be important food sources for deer in the winter when herbaceous vegetation is not available, particularly in North Florida (see Harlow 1961 for list of winter foods for Florida deer).

Would frequent summer burning eliminate all browse plants, as Stransky and Harlow (1981) contend? If "frequent" is taken to mean "annual," then this statement may be true. Twenty years of annual summer burning at the Santee Fire Plots in South Carolina did eliminate most woody plants (Lewis and Harshbarger 1976, Waldrop et al. 1987). Sixteen years of biennial summer burning reduced but did not eliminate them, and periodic summer burning resulted in the same woody plant crown cover as did periodic winter burning. Thus growing-season burns conducted at several-year intervals or alternated with dormant-season burns should not destroy deer habitat, and might enhance it by increasing the density of grasses and forbs.

Black Bear

Discussion of when to burn to maintain good black bear habitat has centered on the issue of mast production by blueberries and runner oak (a low-statured shrub oak). Anecdotal information has apparently been circulating for some time that summer burns promote fruit production of these species. A 1979 report on managing bear habitat in the Southeast recommended "in certain coastal pine types, burn in summer to stimulate runner oak" (Southeast Working Group 1979, p. 238), and a recent article on deer management stated "both runner oak and low-bush blueberries produce much more mast...when burned during July or August" (Oldenburg 1987, p. 28). Maehr and Brady (1982) studied the fall food habits of black bear in Florida and found that their diet consisted primarily of saw-palmetto berries. The authors proposed that this diet reflected necessity rather than choice. Bears, they argued, would rather eat more palatable and nutritious runner oak acorns and blueberries, but winter burning (primarily associated with timber management) encourages saw-palmetto at the

expense of these species. However, there does seem to be a difference of opinion on the nutritional value of saw-palmetto berries to bears (J. Landers, J.W. Jones Ecological Research Center, pers. comm.). Furthermore the data of Maehr and Brady (1982) may have been collected late in the fall when blueberries and acorns were no longer available to bear and the results have little to do with burn history.

There do not appear to be any data to substantiate the theory that July or August burns increase blueberry and acorn yields. Williams (1977a, b) stated that summer fires increase both runner oak and dwarf live oak acorn production, but did not provide any documentation. The only study we know of is an unpublished report from Osceola National Forest (Anonymous 1979). This study provided preliminary evidence showing that fruit yield of dwarf live oak, dwarf blueberry, and huckleberry was higher in August-burned plots than in unburned plots, but no comparison was made to plots burned at other times of year. Fruit yield of dwarf live oak and dwarf blueberry was high the year following the burn, declining in subsequent years. Peak huckleberry fruit yield occurred three years after the burn.

Better data may soon be available from the season of burn study going on at St. Marks National Wildlife Refuge. Both shrub oaks are found in these plots, which are burned at eight different times of year, as are two blueberry species (Platt et al. 1988). Although we have too little information to recommend summer burns for improving bear habitat, we do not believe there is any evidence to support the opposite view: "[summer burning] could deprive bears and many other wildlife species of a wide variety of...foods. Therefore, winter burns are preferred" (Hamilton 1981, p. 130).

BURN OBJECTIVES AND GOALS

> *If the objective of management is to maintain all the species present, it is imperative that the prescribed burning seasons should be strictly defined to exclude ecologically unfavorable seasons. Prescribed burning events can then be defined by the opportunity of suitable weather conditions in the ecologically favourable season... Fires during these seasons, however, have the potential to be uncontrollable and fire managers must be provided with guidelines for the safe limits under which prescribed burns may be conducted during these seasons (Bell et al. 1987, p. 142).*

Land managers may use prescribed fire for numerous reasons including one or more of the following:

1) fuel reduction
2) site preparation for seeding or planting
3) enhancement of wildlife habitat
4) control of undesired vegetation
5) range forage improvement
6) forest pathogen control
7) improved access
8) improved appearance
9) biotic community restoration and maintenance
10) enhancement of rare or endangered species

The above quote illustrates how a particular management objective may determine when burns are conducted. Choice of burn season is just one of many decisions that must be made in developing a burn program around one or more of the purposes listed here. All aspects of a planned burn regime — season, frequency, intensity, pattern, burn size, and fire type — should be directed toward stated management goals for the burn unit, site, or landscape under consideration. Each burn within the defined regime should also have specified objectives. It is important to recognize that a particular burn or burn regime can be termed beneficial or detrimental only in relation to a particular management aim (for example, killing all hardwoods at a site might be considered beneficial if the objective was to produce pine timber, but detrimental if the objective was to improve wildlife habitat).

Where management goals are narrow or short-term (e.g. maximizing fiber production in a commercial pine plantation or next year's harvest of quail on a gamebird reserve), the decision of when (and how) to burn may be well-established; large bodies of experience and research usually point to appropriate burn "windows." Choice of season, in these cases, may also be influenced by tradition and convenience.

As an example of management for a well-defined goal, the objective for a burn unit may be to maximize timber production on a sustained-yield basis. The most appropriate burn regime might be a series of winter burns, each with the objective of reducing fuels to a specified level to minimize the danger of damaging wildfires. One of these burns might also specify a desired scorch height with the objective of controlling a disease agent. The final burn of the rotation would be a post-harvest growing-season burn to control invading hardwoods and to remove debris prior to replanting. If the unit happened to have multiple goals (e.g. maintaining game habitat in addition to timber production), a goal of maximizing one resource may not be reasonable. Multiple goals generally require more complicated prescribed fire regimes.

The relatively recent appearance of the last two items on the list of reasons for prescribed burning — the restoration and maintenance of biotic communities and perpetuation of endangered species — has stimulated interest in prescribing "natural fire season" burns, and, in certain instances, letting naturally ignited fires run their course. The assumption has been that fires occurring during the natural fire season are the most ecologically favorable for perpetuating fire-dependent species and maintaining fire-type communities. In Florida such burns are often termed "ecological burning." The present trend in ecological burning is focusing on the lightning-fire season (May and June) rather than the broader wildfire season (March-June). The effects of natural fires occurring outside of these peak seasons have generally been considered ecologically unimportant and are frequently ignored by advocates of lightning-season burns.

Although managers of wilderness areas and nature preserves are guided by philosophies of "naturalness," they frequently face conflicting management goals. For example, maintaining a high degree of habitat diversity within a preserve may preclude recreating an historic landscape, and vice versa. Imitating natural ecosystem processes may result in local or global extinctions of certain species, while maintaining an endangered species' habitat often creates a static ecosystem structure. A lightning-season burn regime may be the most effective for achieving some wildland management goals while being far too narrow for others. If the goal is to maintain the local and regional diversity of a community, a better approach would be to establish a more varied schedule that would include burns at all times of year, but favoring the wildfire season (see Appendix II for an example of an approach to scheduling burns in upland longleaf pine communities).

For example, strict adherence to peak lightning-season fires would favor species able to respond positively to burns in May and June, but might eliminate species whose phenologies were not in sync with such a narrow burning period. As an example, the studies at St. Marks in North Florida have found that two common fall-fruiting perennial herbs, pinweed and nutrush, exhibit increased flowering following dormant-season fires (Platt et al. 1989). Apparently, these two species are unable to recover rapidly enough after

growing-season fires to flower in the fall. Unknown, however, are the flowering responses of these two species the second (or later) year after a burn.

How should one determine the appropriate fire regime for a natural area? Once the general management direction or philosophy for a natural area has been established, the importance of the seasonal aspect of the fire regime needs to be evaluated relative to other components. Some of the issues that should be considered are presented below.

1) What is the natural response of the target ecosystem(s) to the fire regimes to which it may be exposed?

2) What are the fire and land-use histories of the site? What environmental and cultural factors produced the present site conditions?

3) What are the life histories of the species of concern (endangered, keystone, dominant, indicator)? How do they respond to different fire regimes?

4) What are the community dynamics and how do community structures vary under different fire regimes?

5) What components or processes of the ecosystem are missing or irreversibly altered (e.g. lack of intercommunity connections, species extirpations or extinctions, exotic species introductions)?

6) How important is the seasonal component of fire to each of the above? Can other facets of the fire regime be manipulated to achieve the same result?

7) Can a reasonable facsimile of the natural fire regime be created? What compromises need to be made for safety and public relations, or because of conflicting uses?

8) Once each of the above questions has been addressed and researched, refine your management goals by deciding if you will be maintaining present, restoring past, or creating new conditions on the site. Integrate your conclusions to develop a conceptual model of what your target ecosystem will "look like." Then outline steps to achieve your goal.

Managers of multiple-use areas face some of the most difficult fire management decisions, because the timing and application of burns must be juggled to satisfy the various and often conflicting goals of consumptive and nonconsumptive users. Multiple-use areas by definition have multiple goals. They must supply the raw material for a wood products industry, provide forage to support cattle, maintain game populations for hunters, present an aesthetically pleasing landscape to the recreationist, and ensure the survival of rare and endangered species and natural biotic communities for research, education, and genetic preservation.

Innovation, knowledge, and experience are required to develop management procedures and techniques to handle all of the demands placed on public lands. The fact that public lands harbor some of the last remaining examples of intact natural ecosystems and are refugia for rare species presents a problem to the public land manager. How can traditional forest and land-use practices be modified to ensure the long-term maintenance and survival of these natural vestiges? Modifying traditional burning practices is only one of many considerations. Fortunately, Florida's public land management agencies (both state and federal) have taken the lead in the Southeast in recognizing the importance of protecting these areas.

As critical as various interest groups are of the management of public lands in Florida (see Noss 1987, 1989; U.S. Forest Service 1989a), the managers of Everglades National Park, the Florida State Park Service, the National Forests in Florida, and the state forests and reserves are considerably ahead of their counterparts in most other states and regions in recognizing the ecological benefits of burning under various fire regimes. Each of these agencies is developing the techniques and expertise needed to conduct burns outside the traditional winter season.

Regardless of approach, focus, or concern, the ecologic and economic goals of fire management are always compromised by fire control and smoke management considerations. They are further tempered by the public's perception of the role of fire in our environment. We all recognize the hazards and liabilities associated with prescribed burning. As the quote that heads this section points out, burning in nontraditional periods may be more difficult and will require additional guidelines, as well as more experienced burners and restrictions on who is qualified to conduct prescribed burns (this problem is not unique to Florida; in fact, the quote refers to Australia). In the next section we suggest some guidelines for conducting prescribed burns during nontraditional periods.

PRACTICAL CONSIDERATIONS OF SEASONAL BURNING

> *During the winter burning season, winds [in Florida] with a westerly component are more persistent than those with an easterly component. In early autumn, northeasterly winds are most persistent, while November is a transitional month between the early autumn and winter regimes. The other months are much less consistent, and in many areas favorable winds are so rare that burning may be impractical in the warmer months (Krueger and Pachence 1961, p. 6).*

> *...burning operations start with the west or northwest winds and continue as the high pressure area passes through and the winds shift to the north in a clockwise direction. Generally, northerly winds are constant and reliable. When they shift to the east, stop burning. Easterly winds are unreliable (Dixon 1966).*

The generally accepted guidelines for prescribed burning in the Southeast have evolved over the past few decades in response to an expanding number of burn objectives. This evolution is reflected in the U.S. Forest Service's periodically updated *Guide for Prescribed Fire in Southern Forests* (Dixon 1966; Mobley et al. 1978; Wade and Lunsford 1989). However, because they were designed primarily to meet the hazard reduction and site preparation needs of the forest industry (Sackett 1975), and secondarily for game habitat maintenance, burn guidelines have long focused on cool winter-season fires.

Prescribed burners have become accustomed to, and are familiar with, dormant-season prescriptions. These emphasize winter burns "conducted 1 to 3 days after the passage of a cold front which has brought ½ to 1 inch of rain and is followed by a cold airmass" (Mobley et al. 1978). Until recently, burns at other times of the year were recommended only for hardwood control and for site preparation for natural seed fall. Predictability of burning conditions following winter-season cold fronts was the primary impetus behind the development of these guidelines. Winds accompanying the leading edge of a cold air mass are predictably out of the northern quarter, they are steady, temperatures and humidities are low, the moisture contents of fine fuels are low, but moisture contents of heavier fuels, soil and duff are high. These are ideal conditions to meet most silviculturally based objectives. They also minimize direct effects on some wildlife species. They do not, however, imitate natural ecosystem processes (Boerner et al. 1988), and may be ineffective in the long-term maintenance of the habitats of many species.

A preferred "boiler plate" prescription for winter burns is 1) northerly winds, 2) midflame windspeed 2-10 mph, 3) relative humidity 30-50 percent, 4) temperature 20-50°F, 5) fine fuel moisture 7-20 percent, and 6) neutral to moderately unstable atmosphere (Wade and Lunsford 1989). During the growing season few of the above parameters lie within these acceptable ranges; thus burns conducted outside of traditional burn windows have been consid-

ered risky. Warm-season winds are not only light and variable but are also subject to sudden changes in speed and direction with the advent of afternoon convectional storms. Growing-season burns are also perceived to be more intense than winter burns. This higher intensity, coupled with light winds and elevated temperatures, may increase the risk of damage to timber stands.

Nevertheless, proponents of growing-season burning maintain that most of the problems ascribed to summer fires stem from lack of experience on the part of many managers with developing and using nontraditional prescriptions, coupled with a lack of appreciation for the benefits resulting from a variable burn season. A winter-burn/summer-burn controversy has arisen around the opposing views that summer burns are ecologically the most desirable vs. summer burns are imprudent, if not reckless.

One source of confusion lies in defining the summer or growing season as it relates to fire behavior, fire effects, and fire control problems. We have seen that fire effects vary considerably both with season and within a season. Likewise, fire behavior during the growing season changes with predictable weather patterns and burning conditions.

The growing season in Florida can be divided into the dry months (spring drought) and the wet months (summer convectional storms). The timing and severity of these periods vary from year to year and geographically within the state. The transition period from one to the other represents the height of the lightning-fire season. Prescribed burns during the spring drought exhibit behavior very different from burns conducted during the wet summer months. This point is frequently missed in the summer vs. winter burn debate. Huge, ecologically significant fires certainly occurred in the past during severe spring droughts. Today, however, because wildfire conditions are at their extreme during these periods, prescribed burning is advocated only in situations where burn units are well-designed and long-term ecological objectives are paramount. On the other hand, during normal years, there are usually periods during the spring drought when burns can be safely conducted. Winds may be variable but, because of minimum convectional activity, the probability of sudden downdrafts and significant windshifts is low. Fire intensity, scorch, and spotting potential can be minimized by 1) managing the fuels (heavy fuels can be reduced by an initial dormant-season burn), 2) proper design and adequate preparation of burn units to allow for unanticipated windshifts, and 3) understanding and utilizing the principles of fire behavior prediction when developing an appropriate prescription.

The transition period from dry season to wet season (usually May or June) is favored by advocates of lightning-season burns because, from an evolutionary perspective, fires during this period probably had the greatest influence on the development of fire-dependent traits. This period does present special fire control problems and precautions need to be taken. The spring drought that precedes the onset of the lightning season increases available fuels by drying

heavier fuels and exposing combustible litter and soils. Because of the heavy fuel loads and low fuel moisture contents, fire intensities can be severe if not preceded by fuel reduction burns. Care must be taken to prevent muck and peat fires if these are deemed undesirable for ecological reasons or because of air quality concerns. The fire manager must also be aware of possible erratic weather that may occur with afternoon thunderstorms. Wind shifts of 180° can be expected as thunderstorms pass nearby. High-velocity downdrafts or microbursts from dissipating thunderstorms can cause short-term extreme fire behavior. For example, on June 8, 1981, at Merritt Island National Wildlife Refuge, a microburst occurring during a wildfire resulted in the death of two firefighters (Haines 1988). Similar incidents could occur unexpectedly on prescribed burns during the lightning season. Potential problems can be minimized by 1) burning small units that can be completed in a short period of time (i.e. complete the burn before afternoon storms develop), 2) using firing techniques that speed burnout (e.g. aerial ignition), 3) designing burn units to accommodate shifting winds, and 4) avoiding burns on days when thunderstorm probability is high.

In contrast to the spring drought, the summer wet season is characterized by higher relative humidities and high fuel moisture contents. Larger fuels and duff are unlikely to burn; fine fuel moisture contents may be below the moisture of extinction only during the afternoon. Available fuels are limited primarily to live volatile vegetation (e.g. wiregrass, saw-palmetto, sawgrass, gallberry) and pine needle litter. Less flammable vegetation can frequently be used as effective fire breaks. Spotting potential and control problems are generally minimal. Unexpected changes in wind speed and direction are the primary concerns. Other problems result from high relative humidities and fine fuel moisture, which limit the use and effectiveness of backing fires and narrow the daily burn window. Fires must be started later in the day and end sooner relative to other times of the year. This not only dictates smaller burn units but also necessitates the use of heading fires to speed burnout. The tendency to use heading fires during the summer may be one of the reasons why fires during this season are considered more intense than winter burns.

Summer (wet season) burning is often ruled out as an option because of the following.

1) Frequent afternoon thunderstorms make it more difficult to predict a good burning day and be confident that good burning conditions will last until the burn is completed.

2) The spatial distribution of summer rainfall cannot be predicted so the site has to be checked the day of the burn to make sure the area was not rained on the day before.

3) High air temperatures and lack of steady winds to dissipate heat increase the likelihood of crown damage, a consideration if timber production is one of the site objectives.

The primary reason for conducting growing-season burns is that certain objectives can be achieved that are not possible with dormant-season burns. Agencies and organizations that have incorporated growing-season burns into their fire management programs also find that 1) burns during the wet part of the growing season have low spotting (and thus escape) potential when compared to winter or spring burns because of higher humidities and fuel moistures and because vegetation is green; 2) because of the features listed above, line construction needs and personnel requirements are frequently reduced; 3) in some instances, burn units situated in smoke sensitive areas can be safely burned using the light winds and convective lifting associated with summer atmospheric conditions; and 4) the burn season is extended allowing more burns to be completed in a year (see Lotti et al. 1960).

In summary, there are recognized problems associated with conducting burns during the growing season, but it is also clear that many desirable fire effects can be achieved by burning within this period. The problems associated with growing-season burns can be overcome by careful planning, using appropriately trained personnel, gaining experience in fire behavior prediction and fuels management, and, most importantly, explicitly defining burn objectives and fire management goals. In fields of management where growing-season burns are considered appropriate, it would behoove fire managers to become familiar with their benefits and to gain experience in conducting burns without the predictable weather conditions that follow winter cold fronts. Resistance to growing-season burning usually comes from managers unversed in ecological fire effects and unskilled in the art and science of fire behavior prediction. The use of fire behavior prediction models instead of traditional guidelines indicates that many fuel types can be burned safely under weather conditions currently considered unsatisfactory by many managers. Furthermore, there are many more days available for burning than are recommended under existing guidelines (Madden 1987). In certain situations, tradition-bound managers may unknowingly be affecting the resources under their stewardship in adverse ways. One only has to remember that less than fifty years ago complete fire exclusion was the standard fire management guideline!

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APPENDIX I

Scientific names of plants and animals mentioned in the text.

PLANTS

Blackgum
Nyssa sylvatica

Blazing star
Liatris spp.

Blueberry
Vaccinium spp.

Bluestem grasses
Andropogon spp.

Brazilian pepper
Schinus terebinthifolius

Cutthroat grass
Panicum abscissum

Dwarf blueberry
Vaccinium myrsinites

Florida elephant's foot
Elephantopus elatus

Goldenrod
Solidago spp.

Gallberry
Ilex glabra

Golden aster
Pityopsis spp.

Huckleberry
Gaylussacia sp.

Little bluestem
Schizachyrium scoparium

Melaleuca
Melaleuca quinquenervia

Myrsine
Myrsine guianensis

Nutrush
Scleria ciliata

Oaks
Quercus spp.

- Bluejack
  Q. incana
- Chapman's
  Q. chapmanii
- Dwarf live
  Q. minima
- Laurel
  Q. hemisphaerica
- Live
  Q. virginiana
- Pin
  Q. palustris
- Post
  Q. stellata
- Runner
  Q. pumila
- Southern Red
  Q. falcata
- Turkey
  Q. laevis

Partridge pea
Cassia fasciculata

Pencil flower
Stylosanthes biflora

Pines
Pinus spp.

- Loblolly
  P. taeda
- Longleaf
  P. palustris
- Pitch
  P. rigida
- Pond
  P. serotina
- Shortleaf
  P. echinata
- Slash
  P. elliottii
- South Florida Slash
  P. elliottii var. densa

Pinweed
Lechea sessiliflora

Pitcher plants
Sarracenia spp.

Red cedar
Juniperus virginiana

Rough velvet-seed
Guettarda scabra

Sawgrass
Cladium jamaicense

Saw-palmetto
Serenoa repens

Sundews
Drosera spp.

Sweetgum
Liquidambar styraciflua

Thin paspalum
Paspalum setaceae

Titi
Cliftonia monophylla

Cyrilla racemiflora

Cyrilla racemiflora var. parvifolia

Wax myrtle
Myrica cerifera

Wiregrass
Aristida stricta

ANIMALS

Florida black bear
Ursus americanus floridanus

Bobwhite
Colinus virginianus

Northern mourning dove
Zenaida macroura

Flatwoods salamander
Ambystoma cingulatum

Florida scrub jay
Aphelocoma coerulescens coerulescens

Gopher tortoise
Gopherus polyphemus

Gulf fritillary butterfly
Dione vanillae

Monarch butterfly
Danaus plexippus

Red-cockaded woodpecker
Picoides borealis

Turkey
Meleagris gallopavo

White-tailed deer
Odocoileus virginianus

APPENDIX II

Burn Schedule for Upland Longleaf Pine-Wiregrass Community

Attached are three tables that can be used to assist you in determining fire schedules for upland longleaf pine/wiregrass communities. A number of assumptions were used to develop the tables and certain conditions should be met before you use them. The purpose of the tables is to enable managers to easily develop burning schedules that mimic the variability found in nature, and thus avoid artificially uniform schedules.

Assumptions and conditions

1) The fire return interval in the longleaf pine-wiregrass community is 1-10 years.

2) Mesic sites burn more frequently than xeric sites. (The reverse may be true if the xeric site supports relatively dense longleaf pine.)

3) The site in question is in a maintenance phase. No restoration is needed and there are no specific conservation goals besides community maintenance.

4) Fires naturally occurred year-round but more fires were ignited and they covered greater area in the spring and summer due to normal drought conditions coupled with the onset of the lightning season.

5) The unit for which you are developing a schedule was recently burned.

Why the table was developed

1) To introduce variability in season, frequency, and pattern of burn in order to avoid rigid fire schedules that tend to favor a single suite of species.

2) To insure that occasionally there is an eight- to 10-year rest period that may be needed for seedling establishment.

How the table was developed

Ten years was assumed to be the maximum fire return interval. Numbers between 1 and 10 were generated randomly, but certain numbers were weighted depending on site moisture class. For mesic sites, lower numbers (shorter intervals) have twice the probability of being generated on the table. For intermediate sites the low to middle numbers are favored, while for xeric sites the higher numbers are favored.

Season of burn was weighted so that the spring and summer seasons are twice as likely to appear as are fall or winter.

How to use the tables

1) Determine if your site falls into the "mesic," "intermediate," or "xeric" category.

CATEGORY	MODEL
Mesic	Wade Tract
Intermediate	J. Butterfield Brooks Preserve
Xeric	Tiger Creek Preserve

2) To determine the first fire return interval for your schedule, randomly select a point on the table. You can do this by dropping a pencil on the table or by putting it on the wall and throwing a dart at it. The value closest to your point indicates the number of years until the next burn and the season when it is to take place.

3) There are two ways to develop a schedule for subsequent burns for any given unit:

   a) following each burn select another random point—this will be the time of the next burn, or

   b) once you select your first value, proceed vertically down that column to develop a long-term schedule of burns.

4) Keep in mind that the schedule generated is only a guide. You define what constitutes a season. You decide when to burn during that season. You decide when there are other management issues and objectives that need to be addressed which will cause you to deviate from the generated schedule.

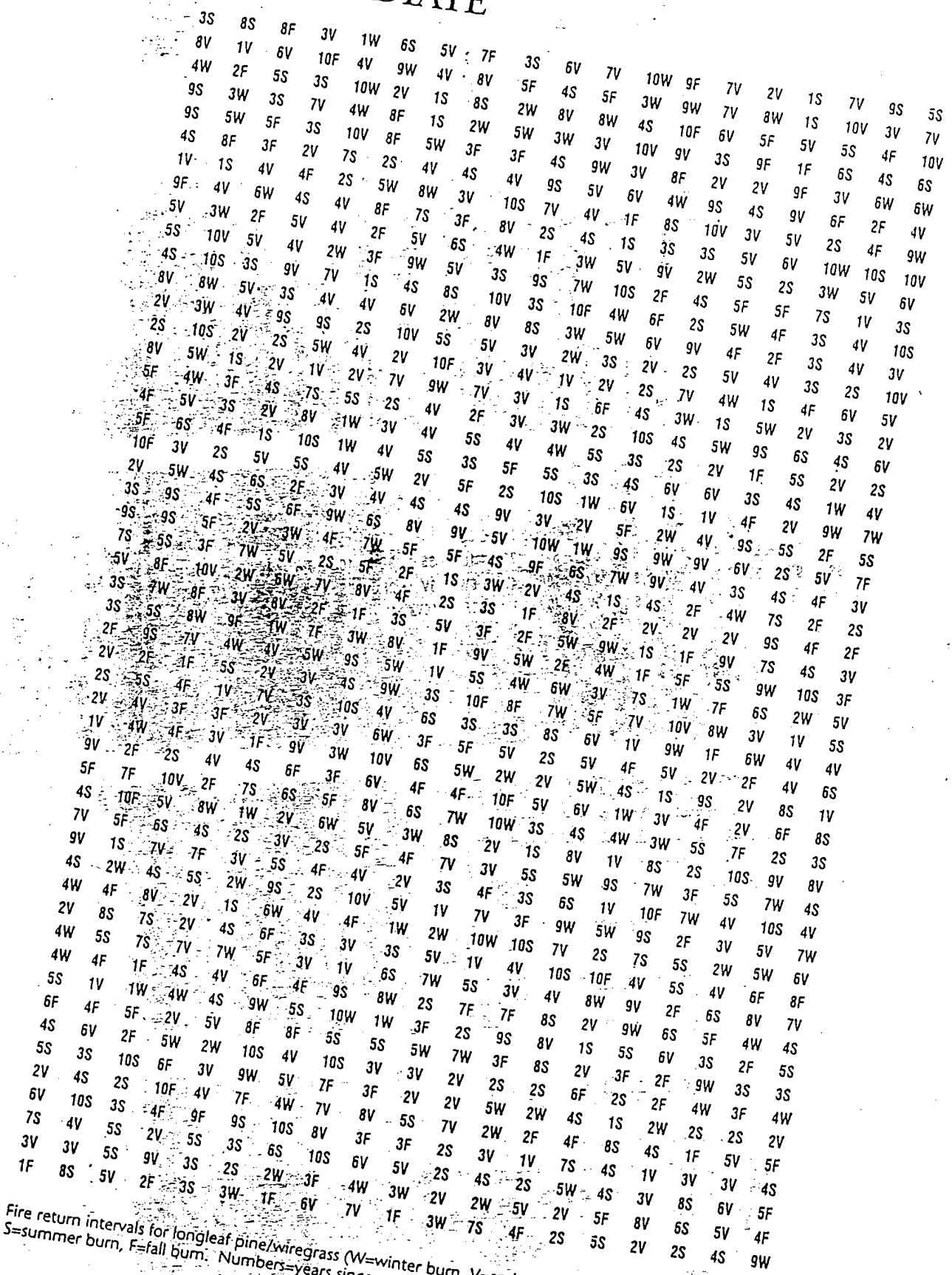
Good luck!

MESIC

3F	3V	9S	7V	4F	2S	4F	9S	3V	2V	6S	3F	2S	1W	8S	2F	1S	3S	8W
8V	2W	8S	5V	6F	9F	1V	1S	8S	4W	7V	2V	2F	10S	2V	1V	9S	1V	4S
3S	3S	9S	6V	3F	8W	4F	7F	4F	7S	4W	7V	6F	6S	4W	9S	2W	1S	9V
2F	6S	8F	9W	4S	8W	9W	1W	5V	2S	8F	5F	8V	9S	10V	10S	6S	3V	3S
2V	4S	2F	4S	1S	1S	8V	10V	4F	1W	1S	10F	9V	4V	2W	3S	9S	1V	4V
4V	9W	3V	1S	7V	1V	3F	2V	6S	6S	4S	9S	3S	1V	1F	4F	1V	8W	4V
3V	8S	8S	2F	6F	7F	3W	10S	9S	2V	4S	2F	4S	1V	9F	2V	3S	10S	4S
4S	2F	7V	4V	7S	4V	2V	4V	1V	9S	2W	1V	6W	8F	6W	3F	4S	7F	4F
9S	9S	4F	10S	2W	10W	10V	3V	2S	1S	10S	6V	3V	4V	1V	5W	10S	2S	2W
4S	1V	3V	1V	9S	2S	4W	4S	5F	3S	4F	6V	5W	2S	4F	2V	1V	9F	10V
3V	3V	10V	2W	2S	3S	2V	5F	2S	1V	2S	2V	6V	1W	4W	5V	2V	10W	3S
2S	9S	10S	2V	5V	8V	4F	9V	3W	6S	1F	1S	4F	2V	8W	5V	7W	2V	7W
4S	5V	1V	3F	8W	1V	7V	9S	2S	1F	3V	3S	4S	5V	2S	1V	4S	5S	1F
7V	6F	2S	4S	1S	8V	2V	7F	4V	1W	6F	1V	4F	2S	8S	1W	4V	2V	5F
6S	1V	10F	1V	7W	7F	6S	4V	2V	9V	2V	2S	5V	4S	10W	4V	2F	4W	4S
8F	6S	6S	1S	3S	9V	9S	2V	4F	1W	4S	2S	4F	8V	5S	1S	7S	2V	10V
1W	2S	1S	10V	10W	1V	7V	2S	10V	7F	2W	4S	2V	10V	1V	2V	9V	1F	1F
10V	6V	10W	3F	4S	4S	1S	3S	1V	3V	5V	8V	3V	6W	4S	1S	3S	3V	4V
1W	3S	10F	10V	3V	5S	5S	7W	10S	10S	4S	3V	3S	2S	3W	1V	7F	5W	10S
10S	8W	7S	6F	6V	2S	3W	6V	1S	1V	4W	8V	3W	7W	6V	3W	3S	9S	10S
4V	3W	8V	6S	7V	3V	2V	4S	3F	10V	3V	3S	5V	4W	2S	1V	3V	1W	1F
3S	2F	1W	5V	5V	4W	3S	3V	9W	10W	2S	8V	4V	2S	1S	2F	7S	3S	7S
1S	3W	9V	2V	2W	3S	1S	4F	4F	2S	3V	7S	5W	10S	1V	3V	2S	7F	1V
10V	4F	3V	3V	3F	6W	4S	2V	6V	3F	3F	8V	1S	1F	2S	4V	10V	10S	5S
2S	1S	4F	2S	10W	4V	1W	9V	8S	5S	10V	1S	2V	2F	1W	4S	10V	9W	4S
4F	7F	5S	4F	1W	10V	1W	3W	9S	2V	7F	4S	10W	2V	1S	3W	9W	7S	10W
4V	2V	2F	6W	4F	4S	5V	9F	10S	3W	7V	9S	7V	10V	8V	3S	4V	6S	3V
8S	7V	9V	7V	8F	5S	7V	7V	5W	7V	1W	9V	4W	6S	5V	2S	9V	2S	5W
9S	4S	5W	3V	1S	2V	4S	9S	8S	4V	1W	7S	6S	2S	3S	2V	8S	1S	4W
3W	3S	2W	4S	1S	4W	2S	10F	8S	10V	5V	3W	9V	4V	4W	2V	6S	1S	6S
3S	4S	9V	10S	9V	2V	8S	4S	8V	6W	9W	5V	3S	5W	5S	3F	8V	2V	9V
3S	4F	4S	1S	1S	9S	4S	7F	2S	8W	4S	1V	10S	9S	1S	3W	2F	2V	10W
6S	4V	1S	1S	3W	8F	4F	3V	1F	4S	7S	4W	2S	9S	7W	3F	5S	2V	7F
8S	9V	1W	10S	3S	1S	3V	9F	1F	5F	2W	2W	5V	6S	4V	2V	5W	9S	4S
4S	3W	10V	9W	6W	3W	2S	9S	8V	9V	8F	10F	2F	1S	1V	5W	7S	8V	2W
4V	4V	5V	7W	1V	1S	5S	9S	6V	3V	7V	1V	3S	9W	9V	6S	6W	8W	1S
2V	5F	1S	4S	10V	10F	2S	2V	5V	4F	3S	8W	5F	1S	10F	1V	10S	10V	1S
4V	7S	9W	5S	6V	7V	8W	8V	3S	8S	8S	2F	4S	2V	2W	4F	3W	1W	5V
1F	3S	6V	4W	1V	2S	2W	3S	3S	7F	5V	3S	4V	7S	2V	2F	9V	5W	2F
3V	4V	4F	4V	5S	6F	3V	3F	3W	7W	9S	1V	4V	3S	4S	6F	8S	6W	7V
9S	4W	1F	2V	10W	2V	2F	2V	2S	3S	1W	7V	3S	2F	4W	4V	2V	4W	9W
1V	8S	2V	7V	1W	4S	2V	7V	9V	7V	4W	6S	3S	3V	8F	7F	7S	3W	7S
2S	2F	3S	2S	2S	3V	1S	6S	1V	2S	9S	1F	1W	1S	7W	4F	9S	3V	10S
2V	10V	1F	3F	8S	5S	9W	3S	3S	1S	8F	4S	4W	3S	1W	7S	1V	5V	10V
2W	7W	9V	4V	1S	4S	3S	7S	2W	10W	1F	4F	4S	2W	3F	3V	3F	7F	6S
3F	4S	4W	1V	4W	1V	10S	9F	3V	3W	6V	10S	4V	2V	8W	4V	4F	7V	2S
8V	9S	2V	6V	3W	3V	4V	1S	4V	6W	10W	4F	3V	4S	3V	2F	1S	1V	7F
1F	3F	2S	5V	4S	3W	1V	5V	2V	7V	7V	2S	7F	1S	4S	2V	10V	2S	2S
1W	2V	1S	2S	10S	5V	1W	2W	4V	4V	4F	4S	2F	8V	5V	1S	2V	3V	2W
5S	8S	9F	3V	8V	2V	5F	2V	1V	5V	1V	3F	6W	10S	10W	2V	5V	4S	1V

Fire return intervals for longleaf pine/wiregrass (W=winter burn, V=spring burn, S=summer burn, F=fall burn. Numbers=years since previous burn.)

INTERMEDIATE



Fire return intervals for longleaf pine/wiregrass (W=winter burn, V=spring burn, S=summer burn, F=fall burn. Numbers=years since previous burn.)

XERIC

7S 3W 8S 9F 8W 4S 9S 6F 8S 5W 6W 8V 8W 9V 7F 7F 9V 7W 5V
6F 9W 9S 2V 6S 10S 8V 7V 4W 6S 7V 5S 2S 7S 7V 1W 4S 9V 10V
3S 8F 8S 10S 2S 7V 5W 5S 8S 3S 10F 4S 10S 3V 7S 9W 8S 8S 4V
9V 10V 2S 3V 8S 9V 6S 1W 2F 9S 10S 4V 8S 8S 9S 2S 10V 7V 10S
9V 7S 2S 6W 8V 7F 6F 8S 2S 10F 9V 6F 7W 9F 8V 10F 5F 5W 6S
7F 6S 8W 9S 5S 3W 2V 2S 9F 1S 8W 8V 7S 7V 9S 8W 4V 7S 6S
7V 7S 5F 1V 8V 4S 9S 6S 6W 10S 2W 7F 8V 8V 7V 3V 3W 7S 7V
9W 4S 1S 8V 7V 7V 5S 4V 1F 8V 2S 1S 3S 5S 2V 8F 10V 10S 7V
7W 5W 2S 7V 7W 8W 3V 8S 6F 6V 9F 5W 7W 4S 3V 5S 10W 1V 10V
10W 8S 10V 6V 3F 8V 2W 6F 8S 2S 10V 3V 3V 6W 7V 1V 9F 8F 10F
8S 10S 8F 6S 2V 3V 6F 6F 1S 7W 8S 10V 8F 9S 9V 10W 8S 7F 4V
7S 3S 3V 4S 8W 4V 9S 10S 10S 8F 10W 10F 3V 9W 3V 8S 7S 1V 5S
8W 4F 4S 8S 9S 10S 8V 6S 10V 6V 5W 1V 5S 8S 1S 6V 3W 10W 5S
2W 7S 2W 8V 9S 7S 6S 9F 7V 8W 8W 8F 10V 2S 1V 9S 1V 4V 5F
10S 7V 1S 5V 3F 3V 1F 7F 1V 10S 4W 6F 7S 9W 1V 7V 3S 8V 3V
7V 5F 10V 8W 10S 9S 5S 6W 10V 6V 6F 1W 7V 1S 2S 8W 8S 8S 9V
10S 9S 8W 6V 8F 10F 1W 3S 1S 5V 8V 9F 10S 9V 4S 10V 9S 6V 6W
10S 9V 6W 8V 10S 2W 5V 1S 7S 6S 1S 8V 8S 7S 2V 8S 10S 7W 8W
4V 4V 1V 9S 1S 4F 2W 3F 9V 1S 3S 2S 4S 4W 10V 8V 9S 9V 7F
4W 4S 10F 10F 4S 2V 2W 10S 5S 1S 9S 2S 7F 5V 6S 3W 7F 1V 10S
9F 6S 10F 7V 8V 2V 10F 5V 8V 9V 8V 7S 4F 7W 8S 1V 7V 7V 7F
10V 8F 7V 8S 3V 9V 10S 8W 7V 8W 4F 2W 9F 8V 7F 7F 7F 7F 9S
1S 3S 5V 8W 9F 9V 9W 2S 2S 2S 2W 7V 10S 7S 5V 7W 8S 8S 10V
5W 3V 9W 4V 8S 6S 3S 5W 7S 10V 5F 3S 10S 7W 10F 7V 8W 9S 8W
8S 9S 5V 7F 3V 8S 1V 10F 4V 6W 3V 2F 9S 10W 7W 5S 9S 8S 5V
10S 7S 5S 9W 4V 6V 5V 4S 1S 6F 10V 4S 9W 6V 7V 7S 6S 4S 5W
3S 9S 8S 7S 9W 5V 1V 6V 9F 1S 2S 8W 10F 6F 4F 9W 1V 8W 9F
10S 9F 9W 7S 5S 1V 4V 7F 9V 8V 3S 8F 5S 9S 8V 8S 1V 8V 3S
9S 10W 9W 10V 3F 10W 7S 7V 10S 10V 6V 6S 3V 3S 9S 9V 4V 8S 3W
8S 4S 3V 1W 10W 6V 9F 10V 10V 7S 8S 3S 3F 6S 8S 9F 7S 10V 6S
7V 5S 7V 10W 9W 1S 4F 3V 4W 3F 10F 8W 4S 8F 2V 8S 6V 2F 10S
3F 8V 4V 7S 5V 5V 7F 8V 1W 10S 7W 10F 7V 5V 1V 9V 9S 9S 8V
2F 3V 10S 7V 9S 8S 2V 10V 8S 4F 10W 7S 8S 7S 7S 8V 10S 9S 7V
9S 1V 8S 3F 1F 9W 3S 7V 10W 10W 9S 9F 10W 10F 8F 5F 7S 3W 3V
8F 7W 8S 9V 10S 4S 5S 1F 7V 8F 1V 5W 8V 8W 5V 9S 8S 9V 1V
7V 3F 4S 6V 1V 5S 10S 2V 6V 7S 8V 4S 10V 10F 2V 3S 8W 10S 7V
10F 2V 9W 4V 2F 9S 10V 7F 9V 7V 5W 10S 3S 8V 9F 5S 3S 5S 3W
3F 8F 1S 8V 4V 3V 4W 8S 10F 9V 2S 4V 9F 7W 10W 5S 3S 4W 9W
4V 10S 1F 7W 10V 8S 4F 10F 3V 4V 5F 1F 7S 8S 5S 7V 7V 5S 5F
4F 4V 3V 3S 7W 1V 10V 8S 7S 1S 8V 9W 9W 8W 7W 10V 7W 10S 7V
9V 7F 4S 6F 2S 5S 7S 8V 8F 10S 7W 8S 9F 2V 4W 1S 5S 10W 3V
3W 3F 9W 3V 6V 2W 3W 9V 10W 1F 9F 7F 9S 6F 7V 5S 10W 8V 8F
7S 5W 9V 4V 9F 1S 3S 4V 10V 8S 9S 2F 1V 6V 10F 7V 8W 4S 4S
10S 9F 9S 5V 4S 4F 4S 9F 10W 7V 3S 9S 9V 10S 7V 10S 8V 2S 4F
6S 8F 10V 10V 3V 5V 8S 10S 9F 9W 5F 8S 8V 2V 10V 7S 4V 1F 7S
7S 6S 3S 10S 6W 8S 9V 5F 4W 1S 9V 7S 7F 8V 1W 10F 1W 6V 8V
8S 2V 3V 4W 9V 8F 4S 10S 10V 8W 10S 2S 2V 4F 1S 6V 7V 7S 9V
10F 9V 1S 3V 8S 10V 7W 10W 4F 4F 10V 6F 1F 3F 1V 10V 9V 8S 7S
10S 7S 3V 1S 7S 7V 9V 10F 4V 8W 4W 8V 4S 3W 9S 7V 9S 7S 1V
7S 3S 10S 8V 9V 8W 1W 4V 10S 5W 1F 5S 9W 10S 10S 9S 9S 8W 3F

Fire return intervals for longleaf pine/wiregrass (W=winter burn, V=spring burn, S=summer burn, F=fall burn. Numbers=years since previous burn.)

Prescribed Fire and Wildlife in Southern Forests

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GENE W. WOOD

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KEYNOTE ADDRESS

HISTORY OF PRESCRIBED FIRE AND CONTROLLED BURNING IN WILDLIFE MANAGEMENT IN THE SOUTH

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The use of fire in wildlife management has occupied me both professionally and as an avocation for nearly half a century. During that period, I have been fortunate to be able to study fire ecology and fire management, not only in the southern United States, but in North and Central America generally as well as in Africa, Australia, Asia and Europe. I have personally ignited fires experimentally as well as for management practices every year since 1934 when I became associated with H.L. Stoddard and the Cooperative Quail Study Association at Thomasville, Georgia.

Previous to that time, my attitude toward fire in any shape or form was like those of most people. I was trained as an ecologist at the University of Chicago and was the mammalogist of the Chicago Academy of Sciences for 8 years. From 1931 to 1934, my brother and I (Komarek and Komarek 1938) conducted mammal and bird studies in the Great Smoky Mountains National Park. There are many references in my field diaries primarily in regard to ground fires in the Smoky Mountains and nearby regions. The following is a typical example which shows my attitude at that time:

> "It seems as if all the mountains are on fire - everywhere we went it was continuously smoky and more woods on fire. In twenty miles we saw over fifteen forest fires - all of good size - no wonder this place hasn't much forest - they never fight a forest fire unless house or barn are in danger. No wonder that mammals are scarce." (Nov. 17, 1933. This was in the region where Georgia, Alabama and Tennessee meet.)

First, I was apparently oblivious to the fact that it was the lumbermen that had devastated the forest. Second, I did not realize that the mountaineer lived by his livestock as much as by his crops. And third, I was ignorant of how to trap small mammals on recently or periodically burned lands.

As a youth I acted in the capacity of a summer junior ranger in the Cook County Forest Preserves around Chicago, Ill. I fought fire with all the diligence and fervor of a fire-fighter! I did not realize then that in doing so the very prairie wildflowers and birds we were supposed to protect were being eliminated.

The use of fire for the management of game animals is certainly an ancient practice and was used by Indians and early settlers in this country. The usage of the term "controlled burning" has been prevalent in quail management in the Southeast for well over 75 years on perhaps a million acres of privately owned hunting plantations. Stoddard (1925) used the term in his first report of the Cooperative Quail Study Association and certainly it has been used, even in preference to prescribed burning, since that time by private game managers.

Terms such as "light burning", "broadcast burning", "under-burning", "ground fires", etc., have been used for many years by foresters and game managers. Such early chiefs of the U.S. Division of Forestry, the predecessor of the Forest Service, as Pinchot (1898), Graves (1899), and many others used these terms for the reduction of fuel to prevent catastrophic fires. In recent years the phrase "under-burning" is being used by foresters more and more to denote the burning of the surface layer of grass, forbs and shrubs primarily to control hardwood invasion in forests.

It is virtually impossible to separate the effects of fire for forestry practices from wildlife management. After long periods of fire exclusion, catastrophic conflagrations can occur that may drastically reduce certain wildlife populations. Conversely, light or ground fires, even though conducted for such forest practices as fuel or hazard reduction, are beneficial for many kinds of wildlife.

The usage of the terms "fire by prescription" or "prescribed burning" are quite recent, since about 1944, and were originally used for purely forest management practices. In more recent years both terms appear to be used and I will do so interchangeably because the "history" of the use of fire dictates that I do so.

In the Southeast, the emphasis on the ecological effects of prescribed fire has been on quail, turkey and deer, but, until recently, little attention has been given songbirds, desirable plants, etc. Thus, of necessity my comments will have to be primarily on the history of burning as it relates to quail, turkey and deer. Fortunately, however, the Bobwhite is an excellent *index species* for the broad pine belt with a grass and forb understory that originally covered most of the South. I will discuss this evolution of burning for wildlife management under 10 broad categories:

1. Indian Period,
2. European Settlement,
3. Hunting Plantations,
4. Dixie Crusaders,
5. Cooperative Quail Study,
6. Cooperative Quail Study Association,
7. Greenwood Plantation,
8. Tall Timbers Research Station,
9. Fire Ecology Conferences, and
10. Progress of Prescribed Fire Use in Wildlife Management.

THE INDIAN PERIOD

The American Indians, except the Cherokee, did not have a written language so their use of fire in managing the wildlife upon which they depended for food, clothing and, in some cases, shelter had to be passed down from one generation to another by parent to child. Unfortunately, in the early pioneer days those few writers who wrote down their observations only recorded the most obvious and, in most cases, the most unusual events that they witnessed. These people came from several different cultures where the knowledge of the use of fire had long been forgotten. Perhaps more importantly, they were city folk and to them the Indians were uncultured and uncivilized savages from whom they thought they could learn nothing. Thus, records of how and why the Indians properly used fire are meager. One of the clearest items of interest is contained in the original treaty made in the settlement of New Amsterdam (New York) on October 4, 1965 and has this statement:

> "Indians are not to set fires to the grass before the month of March without consent of the town." (Taylor 1923)

A large portion of Long Island was a grassland that was later well studied by a long series of botanists. All agreed that this prairie (or "downs") was very similar to the typical grassland understory of the pine forests of the deep South and the prairies of the Midwest. Catlin (1926) also remarked that the Indians burned in Missouri presumably for improving conditions for game and not just for driving it. He gave an excellent description of how he and his associate hunted ahead of such a fire and painted a picture of such a prairie fire.

That aborigines were capable of developing sophisticated techniques in fire management can be verified in Africa today. In 1968, while traveling a "track" on the western side of Murchison Falls in Uganda, we noted a series of small burned out areas, about 1 to 2 acres in size, in the midst of 6 to 7 foot tall dry grassland. These had been burned out without the use of any fireline. They had apparently set these fires late in the afternoon and with knowledge that certain kinds of grasses would burn while others would not. After the burning, snares had been set to catch animals of small size, such as antelope. We were told that even elephants had been snared at times. Snares were even set in the ash shortly after burning, because animals would congregate on such ash for minerals. These areas, particularly when they "green-up", attract large numbers of animals before the Park itself has been burned off (Komarek 1969, 1972).

We had also observed this utilization of areas covered with new ash at Tall Timbers Research Station. In 1966, a graduate student working at Tall Timbers on bryophytes and their possible fire relationships wanted an acre burned in an Andropogon grassland. He asked me to warn all the staff so no one would even walk across the ash and disturb it. The tract was burned late in the afternoon in July. Early the next morning I happened to pass by and noted that the ash covering had been practically destroyed. My first reaction was that someone had literally played on the area. Closer examination showed that deer had congregated on it and ruined it for this study completely.

From 1954 to 1968 I was engaged in research on hybrid corn. During this period I visited Arizona and other western states 2 or 3 times a year. Because of my experimental corn studies on the Hopi and Zuni Indian reservations, I became a friend of the people. I found that some of the older people still retained a knowledge of proper burning and witnessed this on both reservations. However, this was against the policy of the Bureau of Indian Affairs and had to be done

quietly and on a small scale. One time on the Hopi reservation, tumble weed (Russian thistle *Salsola kali*) had banked up around a barbed wire fence in one of my experimental corn fields. The Indians I was with decided to burn it in spite of dry weather and a strong wind. I remonstrated with them by pointing out that it would get away on the grassland surrounding the area. They assured me that it would not and said, "You shall see." The dry tumble weed went off like a flash but did not spread away from the area.

Another time on the Zuni reservation, I was with an Indian who had been assisting me in the field work and I spotted small burned areas well scattered over the mesa top. When I remarked about this, he pointed out that he did it only under certain conditions because he did not want the fire to spread from what he wanted burned. He said he needed to do this for his sheep but the government was strongly against it. He had burned small areas all over the mesa top without the benefit of firelines. He pointed out that if he burned too much at any one time, his sheep would not have enough food to maintain themselves until the burned areas greened-up. He had a very good understanding of the fire ecology of the grasses, forbs and bushes and of the requirements of his sheep.

I consider all the above burning as "controlled burning", for at all times these fires were under control. It should be evident that if the whole region was burned off at any one time the native people would suffer for lack of food for their livestock.

Thus, the American Indians were the first people in North America that practiced what we now call "prescribed burning" or "controlled burning" for game management. Their use of fire certainly fits the terminology of the Society of American Foresters. The big difference, of course, is that foresters think primarily of trees, whereas the Indian thought in terms of food, such as game and other items of importance to him and his culture (Komarek 1965, 1981a, 1981b).

EUROPEAN SETTLEMENT

The early settlers of the Southeast certainly learned from the Indians some of their age-old burning techniques as it applied to game management. The gun and the game that it produced furnished much of the animal protein available to these early farmers. However, like the Indian they did not write of their day-to-day chores. Their livelihood was considerably enhanced, however, by the introduction of domestic livestock, particularly cattle. When the early Spaniards introduced cattle to the deep South they were already familiar with the use of fire for livestock production. Regular burning is still practiced today in some of the areas from which they came. Most of these early conquistadores came from a small area in Spain adjacent to Portugal, and later most of those that followed came from the lower section of the Iberian Peninsula. The first European settlers that came along the eastern seaboard or down the Appalachian Mountains came into a region where fire was already being used by the Indians and by the Spaniards. Now, let me put at rest the commonly accepted tale that the early forest agencies spread throughout the country that these people, Indians, Spaniards and early settlers, were careless with the use of fire (Komarek 1977).

As a boy, Stoddard lived in south-central Florida from 1893 to 1900 and worked with the cattlemen of that period. In 1962 he wrote:

> "In my opinion the much maligned pioneer cattlemen of Florida 'flatwoods' and elsewhere in the piney woods of the southeastern coastal plain, had many valid reasons for burning off the dead grasses, pine needles and other forest debris in the vast forest that covered much of the terrain surrounding them ...."

Of the region where Stoddard lived as a boy, he wrote that the cattlemen

> "..... had used fire liberally for generations, and had no doubt in my mind as to its necessity and effectiveness in accomplishing certain things of importance to them ..... Florida, it must be remembered was ..... the nation's first cattle industry. The cattleman believed, with reason, that the woods had best be kept open and ground cover short ..... so that most of the upland terrain would produce a maximum of the most palatable grasses, legumes, and other herbaceous vegetation for their grazing livestock.
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> "The forefathers of these cattlemen had come in from the North Carolina mountains long before the nineties. ..... As they rode the ranges, they set fires at intervals when conditions were right for light burning, from early fall to late spring. They knew from the way cattle gravitated to the fresh burns that the tender grass would make them grow and fatten." (Stoddard 1962)

HUNTING PLANTATIONS

The eastern seaboard was settled by Europeans, some of whom were used to hunting on large estates in Europe, and who continued such formalized

shooting here. Apparently this development took place quite early for there are scattered references to such estates on Long Island and Staten Island, N. Y. in the 1900's. By late 1875 these were quite common (Henry L. Beadel, pers. comm.). The initial development of these estates may have been as waterfowl shooting preserves, but upland game, such as quail, heath hen, upland plover, etc., were also hunted. There is an early French shooting wagon on display at the Arcadia National Park Museum that is quite similar to those that were used in south Georgia in the 1920's and early 1930's, except the latter had a wire crate fastened on the back to hold English pointers and setters.

This development spread southward along the seaboard as far as Florida and became an adjunct to the early agricultural plantations. Then later, starting about the late-1800's and early-1900's, these were turned into hunting estates with winter residences of considerable size for the owners and their many guests. One of the earliest of these in the Georgetown area of South Carolina was Hobcaw Barony, purchased by Bernard Baruch, a native South Carolinian, who had made a fortune on the New York Stock Exchange.

> "In 1905 he had put together all of the plantations (agricultural) at the foot of Waccamaw Neck, recreating what he called the Hobcaw Barony. His 17,000 acres were, however, more extensive than the original barony. He eventually built a spacious new dwelling in the white-columned manner." (Rogers 1970)

Thomasville, Ga. developed into a winter health resort with the advent of the railroad from Savanna, Ga. in 1861, and was, in fact, the "Miami" of that period. It had 5 large wooden hotels with "modern conveniences," and about 300 bedrooms each. It even had a grand opera house. Hunting of the Bobwhite became one of the fashionable recreational sports; first on leased lands from surrounding farmers, and then on land later acquired in fee simple as on the eastern seaboard. These eventually developed into hunting plantations with their own individual winter residences. By 1915 there were about 200,000 or more acres in this region that were hunted over for Bobwhite, using English pointers or setters. In 1916 the Georgia and Florida Field Trail Club was organized because there was so much interest in the hunting dogs and quail hunting (Humphrey and Krech 1948, Chubb *et al.* 1967).

The subdivision of the extensive agricultural areas of the old plantations into small fields, developed through subsistence farming and the invasion by pine trees and grassland vegetation provided excellent habitat for quail. Hunting remained satisfactory as long as the small farms, interlaced with piney woods, fallow fields, broomsedge and plum thickets, existed and annual burning continued. However, by 1920 forest agencies, led by the U.S. Forest Service, had started an intensive campaign to stop all burning. Many of the plantation owners were well educated and were active in conservation and game problems. They were convinced that fire was destructive and stopped burning. Thus by 1923 the quail population had diminished to such an extent that a meeting was held in New York by the owners to find out why their quail hunting had become so poor (Komarek 1973, 1975). The outcome of that meeting was the formation of the Cooperative Quail Study Investigation and H.L. Stoddard was chosen to head the work under the auspices of the U.S. Biological Survey. Within the first year he had sized up one of the primary problems of the poor hunting based on his background of quail habits learned as a boy and their dependence upon regular burning (Stoddard 1925). He recommended that they go back to regular burning. Some of the owners were not quite sure about this. Typical of the northerner's regard for fire is the following by H.L. Beadel, owner of Tall Timbers Plantation, which is now Tall Timbers Research Station. He had first started coming to the region as a young student in 1894. He said:

> "Nothing in its aspect suggested to us that the land had ever been burned off. So our ingrained northern notions about fire suffered a shock when one day towards the end of the quail season - in late February - we saw the whole country on fire, which within a few minutes left the ground black and bare except for scattered clumps of bushes. The country looked to us irretrievably ruined, and the quail doomed, until our trusty Charley informed us that this burning took place regularly every spring as far back as his grandpapa could remember. Thus our alarm somewhat abated when a few calmer squints through the smoke showed all the trees still standing, and we even found that we could walk behind the flames without scorching our boots. Later we realized that what had burned was merely a year's accumulation of litter, or 'duff', and that the soil had taken no harm .... And when we were assured by our local friends that the country would look the same by the following winter as it had when we first saw it, and that they took the practice so much for granted that it had not occurred to them to mention it to us, we were comforted. Nevertheless, the practice left in us a feeling of repugnance that lasted a long time." (Beadel 1962)

His statement that everyone took the practice so much for granted, and that it had not occurred to others to mention it to him, is typical of the problem the investigator finds when searching through the literature of the Southeast to find out more about the early burning pattern. It was such a commonplace custom that nobody seems to have written about it very much, except scattered Northerners or people from Europe who were totally unfamiliar with burning.

Although he was one of the original contributors to the Cooperative Quail Study Investigation, Mr. Beadel still was not convinced, so he did a few small burning experiments on his own:

> "So the frequency of burning experiments consisted simply in excluding fire from selected plots for terms of one, two or three or more consecutive years. Three years of exclusion were enough to convince me that the old-time settlers knew very well, in fact better than some of us do now, what they were about when they burned yearly." (Beadel 1962)

The Investigation started at a rather critical time in forestry in the South. The magnificent forests of the Southeast were destroyed, not by fire, but by "cut-out and get-out" timbering operations and clearing the land for farming. These early timber operators cut only the best logs out of the best trees and the rest were left to rot and burn. Many of the original timber stands were relatively even-aged virgin longleaf pine. The clearcutting operations left the land covered with highly flammable logs, branches, needles, and so forth, and this was more flammable fuel per acre than nature could have ever produced on a large area. This lumbering did not interfere at the moment with range operations and range burning continued. The annual and regular burning, of course, kept reproduction of pine trees to a low level, especially in the areas where the forests were clearcut and very few seed trees were left. We must not forget that this was range country, and as long as the original forest stood, the regular burning occurred without much material damage. However, because of the devastation of the forest by lumbering followed by high accumulations of slash and only inadequate seed stock, fire was quickly termed "the red scourge" of the South.

I came into Georgia and Florida in 1933 and, then, in 1934, worked with hunting plantations in South Carolina, Alabama and Mississippi and saw the last of these destructive forest operations in some regions. Curiously enough, the improper lumbering activities were hardly recorded; fire was always blamed for the devastation.

The forest and conservation agencies and organizations took the lead and embarked "on a crusade to convert the country to conservation" and "the men in green" acquired "an introverted, militant corporate spirit" (Schiff 1962). A former chief of the Forest Service wrote in later years that the Service "was born in controversy and baptized with the holy water of reform" (Greely 1951). Unfortunately, however, because of its highly emotional appeal, fire was singled out to be extinguished by this "holy water."

About this time, the Clarke-McNary Act, sponsored by the American Forestry Association and the U.S. Forest Service, provided for federal matching funds for the development of state forest agencies in the South. These were definitely ear-marked for fire fighting, not for fire prevention. Bonninghausen (1962) pointed out that:

> ".... in order to carry out the cooperative fire control agreements, which the Florida Forest Service entered into with private landowners at that time, it was necessary to stipulate the exclusion of fire, or funds would not be made available, and the Florida Forest Service would be subject to criticism."

Thus southern silviculture in practice became largely fire control. Along with the stimulus of federal funds came the philosophy that all that was necessary for the splendid forest to return was to "prevent fire, exclude hogs, leave ample seed trees, and nature herself would restore longleaf to its primeval state."

THE DIXIE CRUSADERS - SOUTHERN FORESTRY EDUCATIONAL PROJECT

The stage had been set. The South was then subjected to, what was termed by the American Forestry Association and the participating southern state forest services (Florida, Georgia and Mississippi), a "crusade." This was the Southern Forestry Educational Project (1927-1930) which was essentially an evangelical mission with all the furor of such conviction.

> "Teams of young men (were sent) into the south called 'Dixie Crusaders' who spearheaded the assault on southern customs (on woods, range, game and agricultural burning) as their truck caravans rolled through the piney woods broadcasting 'with all the drama of the day' .... the crusaders traversed 300,000 miles, disseminating two million pieces of literature along the way. More than 5,200 motion picture programs and lectures were presented to three million people, one

half of them children, with the USDA film 'Trees of Righteousness,' enjoying the most universal appeal. By 1923 the woods burner, sought out in his own lair, had been made to know the way of his transgression. 'A great tide of indignation', the association asseverated, was 'sweeping out over the piney woods' mobilizing sentiment against the woods burner." (Schiff 1962).

The following statements were taken verbatim from a pamphlet of the Southern Forestry Educational Project (circa 1930):

"Fire destroys the natural breeding places of birds and animals, ... Game experts say that fires often kill more game than the hunters .... until fire is kept out of places where they live and care for their young, birds and animals will be fewer and fewer .... Shelter is essential to most wild game and bird life. Forest fires burn up this shelter, destroy nests, eggs, young quail and turkey, besides many beneficial insectivorous birds .... Game birds, animals and fish thrive in regions of unburned forest growth. .... So long as fire is kept out of the woods the community of trees and plants and animals have a chance to take care of themselves."

Stoddard (1925, 1931) had already published reports on his findings that control burning must be used in the region if quail were to be plentiful. In fact, it was the prohibition of burning on the surrounding game plantations in Thomasville, Ga. and Tallahassee, Fla. region and the consequent decrease in quail that created his study. It is interesting to note that Stoddard's research was conducted near Thomasville but the "evangelism" by the American Forestry Association was so strong that the Thomasville Chamber of Commerce provided office space and secretarial assistance to the headquarters of the Dixie Crusaders. Stoddard's efforts along with studies by men in the Southern Forest Experiment Station and S.W. Green in animal husbandry in Mississippi were so devastating with their scientific evidence that the Dixie Crusaders finally were cancelled.

THE COOPERATIVE QUAIL STUDY INVESTIGATION

The Investigation began on March 17, 1924 and lasted until the publication of Stoddard's book "The Bobwhite Quail, Its Habits, Preservation and Increase" in 1931. Mr. Stoddard had considerable difficulty in having his fire chapter cleared by the U.S. Forest Service. At that time the Forest Service had the editorial right to delete any references to the possible benefits of burning. Although the Investigation was privately financed, the direction of it had been turned over to the U.S. Biological Survey and this government agency had to yield to the Forest Service. Stoddard (1962) wrote:

".... I had first outlined the fire chapter in 1928 and 1929, for I had anticipated we were going to run into publication difficulties of a serious nature (with the U.S. Forest Service). Manuscripts originating in one bureau had to 'go through channels' and be approved by others concerned before publication. .... I rewrote the fire chapter five times in the attempt to get it cleared. Finally seeing no other course to pursue, I passed the word where I knew it would spread to the effect that the fire chapter, already sadly 'watered down', would have to be cleared for publication or else I would resign and write a book on the subject that would *not be a compromise*."

Thus, Stoddard had to live with a watered down chapter. When the recent reprinted edition (published in 1978) was authorized, I was asked to write a preface. In that preface I tried to point out that Stoddard had to live with a watered down chapter for many years, and that if he had been alive to rewrite the "Bobwhite Quail" he certainly would have changed that chapter considerably. I had included the statement that I have just quoted above in the preface but that was deleted by editorial censorship! Only a statement was made to the effect that fire was a controversial subject in place of the above quotations of Stoddard's own words. It is curious to me that this attitude still remains today in some circles, for the deletion of that quotation was the only editorial correction made in my preface (Komarek 1978).

Stoddard, however, was able to retain the following statement in his book. He mentioned that fire and burning

".... present a complex problem, one that would require years of careful research on the part of the personnel of a well equipped experiment station to work out. Such research is greatly needed, and should be carried on, *for fire may well be the most important single factor in determining what animal and vegetable life will thrive in many years.*" (Stoddard 1931) (italics Komarek)

COOPERATIVE QUAIL STUDY ASSOCIATION

At the conclusion of the Investigation, Stoddard had made such an impression on the plantation owners and, particularly, on Col. L.S. Thompson, whose property of 1,000 acres in Grady County, Ga. had been used as an experiment station for the Investigation, that it was given outright to him. Col. Thompson said he never wanted Stoddard to leave this part of the country.

Henry L. Beadel, being a retired architect and familiar to consulting work, realized that the value of the Investigation would not have accomplished its purpose unless a service organization followed. Thus, on May 1, 1931 the Cooperative Quail Study Assciation was organized with Mr. Beadel as Secretary-Treasurer, representing the owners, and Mr. Stoddard as Director. In the initial prospectus for the Association is the following chapter:

> "A. Burning or controlled fire. The use of properly controlled fire is considered absolutely essential in the maintenance of most southeastern lands for quail and quail shooting. It is realized, however, that fire may do great damage as well as great good, the difference depending largely upon the degree of severity of the fire, when, where, and under what conditions used, and so forth." (Beadel *et al.* 1962)

This organization was a consulting service with its office and research base at Sherwood Plantation. As a mammalian ecologist I had been making studies on the ecology of small mammals, first in what is now the Great Smoky Mountains National Park, and throughout the southern part of the United States, as well. Because of this background and Stoddard's concern about the cotton rat as a potential predator of the Bobwhite quail, I was fortunate to join him on July 1, 1934. We quickly found that the proper use of fire along with agricultural techniques could certainly lessen the cotton rat problem until it became no problem at all.

By 1936 the membership in the Association had increased to such an extent that we estimated in a report that we were recommending the use of fire on over 400,000 acres of owned land and 70,000 acres of leased land from South Carolina to Stuttgart, Arkansas.

During this period there was considerable controversy in regard to the use of controlled burning on leased land. It had been the custom for a good many years in many areas to own a plantation and lease additional land for quail hunting. However, it was always with the proviso that the land be controlled burned. When the forest agencies began to point out the value of timber, the owners of the leased land were in a quandry. If they protected their land and let the pine trees seed in heavily, then they would lose their lease and would get no income from that land for at least 20 or 30 years. However, by leasing their hunting right, they would get sufficient funds, in most cases, to pay their annual taxes on the land. Thus, in many areas, and I speak from knowledge, not from rumor, owners of leased land would cooperate with the State Foresters, but then claim that their land had been burned by wildfire. In fairness to the Alabama State Foresters of that early period this may have been one of the reasons of my threatened arrest for burning Guerryton Plantation.

The Quail Study Association was an excellent opportunity to test Stoddard's ideas originally developed in the Investigation. Thus, we had the opportunity to use fire and study the effects of burning, as well as other management techniques, over a large area representing a large variety of soils and other conditions throughout the Coastal Plain of the Southeast. As one example, Mr. Robert Carrier of the Carrier Lumber Company wondered about expanding his hunting acreage from the pine covered hills adjacent to the delta lowland of the Mississippi River where the original hardwood had been cut. After controlled burning, we were amazed at the response of desirable grasses and legumes on this soil. They grew thicker and heavier than we had seen anywhere else.

As consultants we had little time to do research on other properties except on Sherwood Plantation and then, shortly thereafter, on our property, Birdsong Plantation purchased in 1938. The Quail Study Association published annual reports and other leaflets in very limited editions, primarily for our own membership. These were all republished in 1961, but are now out of print.

In the late 1930's game management was beginning to attract attention throughout the Nation. During the life of the Quail Study Association the number of visitors grew tremendously. These were members of the forest and agricultural experiment stations, the U.S. Forest Service, various state forest services, cooperative wildlife units, U.S. Biological Survey, Soil Conservation Service, and many universities from the east to the west coasts. The Cooperative Quail Study Association was disbanded in 1943 because of the war. Mr. Stoddard became a consulting forester and was involved in cutting timber for the war effort. I became involved in agricultural work for the War Foods Administration in increasing rice and peanut production.

Although the Cooperative Quail Study Association had been disbanded, Beadel, Stoddard, I and others met regularly at my wife's nature and bird window. This became a meeting ground on Sunday mornings for all of us, along with a constant stream of visitors.

THE GREENWOOD PLANTATION PROJECT

It is rare that scientists have the opportunity to test and evaluate the findings of ecological investigation and management activities. This is particularly true of fire management activities on small areas. Stoddard and I carried on a considerable amount of this type of work on our own land and under our own auspices and control, but we had long felt the need of taking a large block of land and actually developing all of its potential for a combination of quail hunting, agriculture and forestry with proper fire management as a principle tool.

In 1945 the opportunity presented itself when I was asked to take over the management of Greenwood Plantation with my brother Roy as my assistant. Stoddard became our consultant on both timber and game production. The emphasis on the 18,000 acre plantation was to be on quail management and the ecosystem of which it was a part. This included forest and agricultural resources as well as other wildlife. Basically the management practices had 3 primary objectives, all of which Stoddard had discussed in "The Bobwhite Quail":

1. The proper use of controlled burning in the development and increase of the necessary plant and animal foods and of the habitat in which quail thrive.

The proper use of controlled burning was to be expanded so as to improve the habitat of the Bobwhite, as well as to improve the hunting conditions for the hunter and his bird dogs, as well as to make the hunting experience more aesthetically pleasing.

2. The rebuilding of farm fields worn out by improper farm practices by the use of proper agricultural practices, as well as the use of controlled burning in changing farm crop residues into "natural fertilizers."

Stoddard had recognized that land of poor fertility could not produce abundant crops of quail. We dramatically increased the fertility of the 2,000 acres of farmland by using cover crops, rotations, and proper fertilization of the corn crop, as well as burning. In cooperation with the Georgia and Florida agricultural experiment stations and the U.S. Department of Agriculture we developed hybrid seed corn for the deep South (Komarek 1972, 1976b, 1978).

3. The proper management of the timberlands by methods which were first proposed in several of the annual reports and other publications of the Cooperative Quail Study Association.

Stoddard had pointed out that by opening up timber stands, sufficient light could then reach the ground and encourage larger crops of plants that produced seeds eaten by quail.

The goal of our original management program was to provide each pair of hunters with 18 covey rises per day, but for the last 10 years the actual find of coveys has been an average of over 30.

TALL TIMBERS RESEARCH STATION

Throughout the 1930's, 40's, and even into the 50's, public pressure was being brought to bear to curtail controlled burning. The Smoky Bear Program (begun in 1944) followed the Dixie Crusaders and all burning was condemned by propagandistic agencies. Literature by the millions of copies was being distributed annually. News media were actively engaged, and through constant repetition an age-old practice was publically condemned. Even the definition of a "forest fire" in standard dictionaries was and is considered a "wildfire in the forest."

This barrage continued after the publication of "The Bobwhite" and the principle that all fires were evil was expounded, not only by foresters, but by conservationists and wildlife management people. Heyward and Barnette (1934) had shown that ground fires in the South were not destructive to the soil, and Prof. H.H. Chapman, Yale Forestry School, and active in the Society of American Foresters, had long since pointed out that fire was necessary for the welfare of the longleaf pine forest. On January 30, 1935 he convened a symposium on fires in the South which brought out facts that fire was an excellent management tool not only for the longleaf pine but for range and wildlife management. It was also pointed out that controlled burning could be a very excellent method to keep down devastating forest fires.

Although there were some signs of change beginning to develop in administrative and propaganda circles, we were being constantly put on the defensive even though we had always explicitly pointed out that we were 100% against *wildfires*. In fact, these attitudes were being promulgated not only to the general public but to schools, and yes, even universities. Universities, except Yale, simply ignored the fact that fire might even be an ecological factor of considerable importance. If fact, the prevalent attitudes were not only beginning to affect our livelihood as wildlife consultants, but at one time it appeared that such burning would be virtually stopped by bureaucratic regulations and possibly legal restrictions. However, I wish to make very clear that the state foresters, particularly in Georgia, Florida, Alabama and South Carolina, gave us little interference, except in some very rare instances, and even tactfully condoned the practice when they could without loss of funds.

Thus, we began to talk among ourselves that an institution, somewhat along the lines Stoddard had first outlined in "The Bobwhite Quail" would have to be developed or the pine woods and

grassland ecosystems that stretched from Virginia to east Texas in the Coastal Plain would be in jeopardy and might even cease to exist.

In 1956 Mr. Henry L. Beadel suggested that we go ahead and start an ecological experiment station where experiments for both research and management could be conducted. In 1958 the Tall Timbers Research Station was chartered as a non-profit, educational and scientific research foundation. Upon Mr. Beadel's death he left the nearly 3,000 acres of Tall Timbers Plantation to the Foundation, and in his will is the following clause, charging the Foundation with the development of a "fire type" nature preserve:

> "By 'fire type' there is meant the maintenance, by controlled burning, of pine forest in an open and park-like condition, with herbaceous vegetation, and although it is conceded that young pine forests must be thinned from time to time, it is also contemplated that mature and over-mature pines will not ordinarily be cut therefrom on such preserve, but instead that mature pines will be allowed to die naturally and left standing for woodpeckers and other wildlife, for ecological study and the study of the uses of dead and dying trees as food producers for wildlife, or as furnishing homes for wildlife."

The Station was also charged by the Foundation's charter:

> ".... to manage and conduct ecological research," to conduct ".... demonstrations of educational work," and "..... to publish and distribute to the public generally any knowledge or information acquired as a result of such research, experiments, and studies ...." (Komarek 1977)

FIRE ECOLOGY CONFERENCES

The Tall Timbers Research Station has as one of its primary interests the ecology of fire and use of fire in land management and in conservation generally. The Fire Ecology Conferences which it has sponsored have promoted a better understanding of the use of fire and of its many ramifications in nature. Fifteen Fire Ecology Conferences have been held. Their speakers and the consequent Proceedings have brought international recognition to the Station. Scientists and investigators in many diverse fields (forestry, wildlife, agriculture, botany, zoology, geography, anthropology, etc.) have reported on their studies and ideas. The speakers (more than 400) have come from all parts of the world (22 countries) and have represented government agencies, private industry, and publicly and privately financed research institutions. There is no doubt that these meetings have done much to stimulate research in fire ecology (words that were joined together for the first conference and are now universally recognized) and the use and management of fire.

The 14th Conference was held jointly with the Intermountain Fire Research Council at Missoula, Montana. The Council consists of federal, state and other foresters. The first paper presented was entitled "From Fire Control To Fire Management: A Major Policy Change in the Forest Service." Since the purpose of these conferences was to stimulate interest and research in this vital field, the Station has largely accomplished its original objectives.

PROGRESS ON THE USE OF PRESCRIBED FIRE FOR WILDLIFE MANAGEMENT

In the last 2 decades, prescribed or controlled burning has moved ahead with considerable speed, particularly in the last decade. The change among the foresters was hastened by Wahlenberg's books on the silvicultural aspects of the longleaf (1946) and loblolly pine (1960) which helped to signal a change of direction in the Forest Service. The research by the Southern and Southeastern Forest Experiment Stations was beginning to bear fruit and administrative support as well. Range experiment stations were organized in the 1940's in several southern states by joint efforts of the Forest Service and State Agricultural Experiment Stations which showed by comprehensive studies the ecological relationshps of fire on many grasses and forbs of the Southeast as well as the other aspects of fire on the environment. The development of the Forest Service Fire Laboratory at Macon, Ga. also hastened the conversion from total fire exclusion to prescribed burning.

This change in attitude or direction in the use of fire, primarily for silvicultural purposes had its impact on the use of controlled burning in wildlife management (Komarek 1971). In the past decade or more, public attitudes have changed and commercial timber companies now advertise that prescribed burning "sweeps the forest" of flammable debris. Likewise the number of articles, both popular and scientific, on the benefits of fire in wildlife management and conservation have greatly increased and public support for such burning has changed very much.

I wish to point out, however, that as far as the use of controlled burning for wildlife management is concerned, private hunting preserves have led the way and that this effort has been supported entirely by private funds. This was inspite of heavy pressure by federal, state, and other public agencies discouraging the practice. The hunting preserves of the Southeast have consistently been burning between 750,000 and 900,000 acres for well over 50 years. Nearly half of this

amount has been in south Georgia, southeast Alabama, and north Florida. Table 1 shows the average acreage control burned by different categories for the Southeast (Komarek 1981b).

It is fitting that the first symposium devoted entirely to the use of fire in wildlife management is being sponsored by an institution that emerged, one might say, out of an old established hunting plantation, the Hobcaw Barony. Tall Timbers Research Station has a similar history having once been known as Tall Timbers Plantation. Both institutions have worked closely with federal agencies such as the Forest Service, and its several forest experiment stations, with state forestry, and agricultural agencies and with public educational and conservation organizations, as well as with private interests.

CONCLUSIONS

A historian has the unique advantage of looking backwards in time, reviewing the present, and, to some extent forecasting the future on the basis of past events. As I review my own active participation over the past 50 years on the use of fire for game and other wildlife practices, I cannot help but wonder "Why did it take so long?" Are there lessons from which we can learn, particularly in regard to all land and environmental management practices and policies?

Certainly the young men in the Dixie Crusaders, as well as those of the Smokey Bear Program, were sincere and meant well. They were fired by enthusiasm and a fervor that can best be regarded as evangelism in many respects. As Schiff (1962), who was a professor of public administration, pointed out, problems arise when research is dominated either by administration or by the propaganda of other organizations, all of whom may also, in all sincerity, think their's is the only way.

When I was a young man I wanted to be a ranger. Why? Because a ranger fought fires. There is something about fighting a fire that does affect one, young or old. An old-time friend in the Forest Service got excited during a panel discussion years ago, got up from his chair, raised his arm with a clenched fist and said, "Fire does something to me!" I could not help but rise and say, "Just like a missionary that sees a heathen in the bush!" And yet man would indeed be a poor creature if he did not develop convictions and even fight for them.

From purely a game management viewpoint there are, however, some lessons to learn. Stoddard published "The Bobwhite Quail" in 1931 and received the Brewster Medal from the American Ornithologists Union, their highest honor. Although these scientists quoted him extensively on the habits of the Bobwhite, they simply ignored his references and ideas on fire as an ecological factor. For example, in the standard bible of many ornithologists of that period, and still used avidly by both scientists and birdwatchers, is the section on the Bobwhite quail in Bent's "Life Histories of North American Gallinaceous Birds" (1933). Stoddard is quoted profusely but there is not a single mention of fire as an ecological factor!

We all develop blind spots in our thinking and writing, but it is difficult for me to realize that Aldo Leopold ignored controlled burning as a management tool for game in his book "Game Management." He quoted avidly from Stoddard's "The Bobwhite Quail." He visited Sherwood Plantation and the area where Stoddard made his studies, yet he could not face the facts. Leopold's book is still considered a major text in wildlife management courses. In an excellent study of Leopold and his ideas, Flader (1974) pointed out:

> "It is ironic that the very features of the southwestern landscape that were most attractive to Leopold - the grasscovered pinyon-juniper foothills, the open sunlit stand of ponderosa pine, the 'infinity of bays and cover, points and strings, peninsulas and parks,' the endless vistas - in short, the very openness and diversity of the country, were even then trending toward a monotony of brush and pine too impenetrable for a man to move about in freely, too dense to support the variety of grass, herbs, and browse required for diverse and abundant wildlife, and too thick even for proper growth and health of the trees themselves. Leopold as ecologist observed the beginnings of this process; as forester he rejoiced in new thickets of sapling pine and the spread of juniper into formerly treeless meadows; as game conservationist he thrilled to the sight of whitetails fattening on the abundant new growth of brush on the foothills; but he did not, *could not, imagine the extent to which this process would be carried under the regime of grazing and exclusion of fire.*" (Flader 1974) (italics Komarek)

How far these blind spots can lead us is clear in the following event that occurred while I was Chairman of the Georgia Game and Fish Commission. I had assisted in the formation of this body under a constitutional amendment "to take politics out of the Commission." When the Pittman-Robertson Act was passed I encouraged the Commission to put as much money as we could into land purchase for future public hunting grounds. We purchased 2,000 acres of land in excellent condition for both quail and wild turkey, and in fact had a very good population of both. It had been a preserve and was surrounded

Table 1. Extent of prescribed fire utilization in the U.S. Forest Service - Southern Region (Annual average 1977-80 in acres).

	Fuel & Hazard	Site Prep.	Natural Regen.	Game & Wildl.	Desire Plants	Brush Mgmt.	Range Mgmt.	Disease Control	Other	Total
National Forests	201,788	20,769	6,396	115,087	22,679	53,008	53,640	4,614	35,901	524,882
National Parks	2,335	--	--	--	2,406	--	--	--	2,459	7,200
National Wildlife Refuges	9,375	525	5,250	30,156	335	1,086	--	273	4,311	51,311
Bureau Land Management	--	--	--	--	--	--	--	--	--	--
Bureau Indian Affairs	--	--	--	--	--	--	--	--	--	--
Military Lands*	93,543	412	2,325	11,228	--	950	14,170	1,800	--	124,428
State Forests	67,795	38,111	8,089	39,668	--	3,250	553	3,561	6,300	167,277
State Game Commissions	87	1,524	652	199,466	1,417	550	--	--	--	203,696
Game Plantations (est.)	100,000	--	--	600,000	100,000	100,000	--	--	--	900,000
Pulp & Timber Companies (est.)	354,715	155,933	2,043	4,085	--	11,020	625	--	--	528,421
Other Private Lands	211,255	19,740	20,000	--	--	35,751	200,000	--	--	586,746
Conserv. Agencies, Airports, etc.	--	--	--	--	--	--	--	--	--	--
Totals	1,040,902	237,014	44,705	999,690	137,837	205,615	368,988	10,248	48,971	3,093,961

*incomplete

(Komarek 1981b)

by other larger hunting lands. The owners of the plantations surrounding the property were members of the Cooperative Quail Study Association. I received a certain amount of condemnation from the owners, but pointed out to them that the State needed to have a demonstration area in that region. Shortly after we purchased the property we were told that we could not control burn, in spite of the fact that it had been burned annually for many years. I was told by the U.S. Fish and Wildlife Service regional office that we would have to have a "research study" over a period of years. I fought to be allowed to continue with this management procedure that had been going on for years, but the Service would not budge. We were supposed to create another quail study within 60 miles of Stoddard's original study! A year after I left the Commission (I served 7 years) the area was sold because they could not use fire in its management!

In these 3 examples we have 3 different methods that occurred as they relate to fire: (1) by scientists who simply ignored the ecology of fire, (2) by a trained forester, who then wrote on management and for all practical purposes ignored fire as a management tool, and (3) the stopping of controlled burning by administrative decree under the guise that more "research" was needed.

These are historical facts that "educated" the public and educational institutions. These errors of judgment cannot be recalled. Today the use of prescribed fire by forest, wildlife, park agencies and conservation organizations is expanding very rapidly so that in a few years such use of fire will be routine. Let me point out, however, that hunting plantations continued control burning throughout this long period of 80 or more years. Why! Because their policies were not controlled by state or federal agencies. They were concerned with relatively small acreages (as compared to national forests, parks, refuges, etc.) and because they were managed by local people. However, when danger threatened the sport of quail hunting, these individuals banded together, in cooperation with the federal government, and organized the Cooperative Quail Study Investigation, *a research project*. Following that, occurred the development of the Cooperative Quail Study Association which was primarily a *management service*. Then the Greenwood project was started to study the *control and management* of a large acreage. Then when the threat of the elimination of a primary management practice, controlled burning, occurred, the development of the *Tall Timbers Research Station*, a wholly independent research organization but one that worked very closely with federal and state agencies, and conservation organization. Thus, for over 50 years, quail management, along with its entire ecosystem has primarily, until recently, depended upon private enterprise working closely with other agencies and these plantations spear-headed the use of fire for game management.

Now to the future. The use of fire not only for game management but for many other purposes is expanding rapidly. Even as I write this, a Florida National Forest is being prescribed burned by aerial ignition - a helitorch - primarily for forestry purposes but secondarily for wildlife and range. Thus, it appears to me that we should look hard upon other management practices of field and forest so that they do not again get locked up in administrative detail and control by "blind-spot" scientists, and the influence of modern propaganda news media. We must be certain that management and research views, particularly by the public, is not developed by Madison Avenue.

Today we seem to operate as isolated groups, representing commercial forestry, public foresters, environmentalists, wildlife management or conservation. I am concerned that entirely too much emphasis has been put on trees and on purely forestry practices in such public properties as wildlife refuges, recreation lands and wilderness areas. Can privately endowed *independent* organizations aid in assisting with development of more closely cooperative programs and more efficiently direct the energy wasted in adversary actions? Can the Belle W. Baruch Forest Science Institute, with major emphasis on forestry, and Tall Timbers Research Station, whose major concern is ecological habitat management, join forces to benefit wildlife in its broadest sense? On behalf of the Directors of the Tall Timbers Research Station, I offer our efforts to the Belle W. Baruch Forest Science Institute for greater cooperative effort on our part in such a venture.

Time has shown that privately endowed *independent* organizations are necessary so as to act as a balance between government, conservation groups, and large private industrial holdings. All of these should, and must, cooperate, but from my personal experience it appears that an outside source becomes necessary, somewhat like the arbitration panels between labor and industry. This is no reflection on the above mentioned groups but human nature is such that we always have our "own axe to grind." The past has shown that by purely propaganda methods, not only the public, but scientists, universities, and organizations were drastically imprinted with fallacious material. The answer seems, at least to me, to be that we need more independent research and management institutions, and the bringing together of all these various groups in meetings such as this symposium.

Thank you for the opportunity to review nearly 50 years of active participation in the use of controlled burning and burning by prescription and I hope that my comments may prove of value for the future of conservation management.

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Prescribed Burning for Managing Wildlife in Southeastern Pine Forests

J. Larry Landers

Abstract.--Reports involving today's wildfires or prescribed burns often fail to recognize fire's primal influence on wild animals. There is much ecological evidence that recurring fires have been a long-standing, evolutionary agent of habitat change to which native species are adapted in the Southeast. Wildlife mortality from flames or smoke is generally insignificant in southern forests. Many upland, resident species thrive in herb-shrub stages that occur in post-fire succession beneath pine (Pinus spp.) canopies, and these species diminish when hardwood overstories begin to overshade lower plant strata. Wildlife species characteristic of complete hardwood overstories should be maintained on true hardwood sites where fire rarely penetrated naturally. Brushy patches, inclusions of deciduous subcanopies, and groups of large living and dead hardwoods add diversity to open pine forests with grassy-forb groundstories. Interspersion could be enhanced in the short term by spot burning under moist conditions together with protection of selected parcels, but on many sites a hotter fire is needed periodically to refurbish the open pine community. Research is needed to determine the proportion at which habitat components should be placed together to support different wildlife assemblages. Long-term studies of the effects of fire or its exclusion on forest communities would also help land managers choose appropriate burning schedules to reach wildlife objectives.

INTRODUCTION

Ecologists have long recognized that lightning-set fires must have been a recurring force in original forests of the Southeast for at least 8000 years (Harper 1911, Heyward 1939). Thus, there are many examples that show resident wildlife species to be adapted to fire, if not dependent upon it. During most of that period American Indians apparently set fires to drive game as well as to meet other objectives. Natural fire regimes were further altered by settlers--through range burning with livestock grazing, extensive farming, and lumbering--and by subsequent eras of fire protection and modern land uses.

By the time research-based wildlife management emerged in this country (early 1920s) there were no virgin tracts left in the Southeast remote or large enough to experience lightning-set fire at its natural frequency. The historical relationships between fire, natural plant communities, and wildlife niches are essentially unknown. Thus, wildlife management is primarily involved with on-the-ground judgment guided by observations, and the use of prescribed burning to influence wild animal populations is still very much an art.

This report summarizes the effects of fire on selected wildlife species and fire's relation to habitat management in southeastern pine forests.

I appreciate the helpful comments on this manuscript by James G. Dickson, Lowell K. Halls, A. Sydney Johnson, Roy Komarek, Brad S. Mueller, and Dan W. Speake.

DIRECT EFFECTS OF FIRE

Some behavioral reactions of vertebrate animals to burning have been summarized in a report pertaining mostly to wildfire (Lyon et al. 1978). It has been commonly observed that less mobile species, such as small rodents, are most likely to panic while larger animals usually move calmly during a fire. White-tailed deer

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(Odocoileus virginianus) are known to congregate on burned-over range and lick the ash residue, apparently to obtain minerals. Upland game birds, raptors and many smaller birds often are attracted to fire or to the smoking landscape as foraging sites.

Deaths of wild animals are seldom attributed to fire in the Southeast. Apparently, birds rarely succumb to fires (Bendell 1974). Means and Campbell (1981) noted deaths of several glass lizards (Ophisaurus spp.) and several diamondback rattlesnakes (Crotalus adamanteus) in mid-ecdysis (preshedding stage) at the time of prescribed burning, but they went on to say that very few herps are thus killed in southeastern forests. Similarly, review papers edited by Wood (1981) listed no fire-induced mortality of tree squirrels, furbearers, or black bears (Ursus americanus). Hill (1981) reviewed mortalities of rabbits in northern and western habitats caused by wildfires or intense summer burns, but he did not list specific incidents involving southeastern forests. However, after a fast-moving experimental fire through a South Florida prairie, Taylor (1981) recovered carcasses of five marsh rabbits (Sylvilagus palustris) on a 20-ha. plot; some degree of susceptibility of this species was noted previously by Komarek (1969). The more widespread cottontail (S. floridanus) seems to easily escape flames, as do most of the smaller mammals which inhabit upland sites. The ability of small mammals to go underground or to emigrate apparently accounts for the scant evidence of mortality from heat or suffocating smoke (Taylor 1981).

In a review by Stransky and Harlow (1981) no records of deer death by fire were noted. But recently, Osborne et al. (1986) documented numerous deer deaths in a North Carolina pocosin after a wildfire had moved through during a dry period; carcasses were typically found in smoldering hollows within the peat soils. Deer mortality to this extent has not been reported in other southeastern habitat types and most likely did not occur under natural fire regimes.

Indications are that fast-moving burns in habitats of the less mobile species would likely be involved when death results. When mortality does occur, it is usually negligible at the population level (Lyon et al. 1978). A proper evaluation should include the effective loss to the population in relation to losses that would have occurred through other causes had the burn not taken place (cf. Cringham 1958). Most undesirable direct effects can be overcome by choosing proper times, places, and methods for prescribed burning.

INDIRECT INFLUENCE OF FIRE

Fire makes its most important impact on wildlife through habitat alteration. There are many variables involving vegetation types, soil properties, topography, animal niches, and characteristics of individual fires that would require species-by-species accounts for thorough discussion. Such detailed analyses are beyond the scope of this report. Therefore, general conclusions of several publications are presented here to form overviews of wildlife groups.

Reptiles and Amphibians

Habitats of herps span the entire moisture gradient from xeric to aquatic. Certain very dry forest types in the southeastern Coastal Plain are inhabited by species which travel in loose sand (sand-swimmers) or live just above sandy substrates. This group depends upon sites open at ground level, particularly those associated with patches of turkey oak (Quercus laevis) within longleaf pine (Pinus palustris)-wiregrass (Aristida stricta) communities or young sand pine (P. clausa) stands (Campbell and Christman 1982). Because sand ridges must have periodic fire to keep dense hardwoods from dominating the landscape (Bozeman 1971), reptiles keyed to these open habitats are considered likewise dependent. Another sand ridge reptile, the gopher tortoise (Gopherus polyphemus), burrows and nests in sunlit sites and thrives on herbaceous plants that are dependent on frequent fire; several other rare or threatened herps and many common species utilizing tortoise burrows are indirectly benefited by fire (Landers and Speake 1980).

Mesic forests support a less site-specific herpetofauna. For example, Means and Campbell (1981) captured 38 species in a study conducted in northern Florida red hills. Three amphibian and 1 reptile species were predominantly in annually burned pine forests, and 3 amphibians were predominantly in hardwood hammock; the rest were not clearly site specific. These authors also summarized results from a summer burn in longleaf pine flatwoods and from a winter burn in slash pine (Pinus elliottii) flatwoods. The overall trap take reached a new high one month post burning on the longleaf site, and the herp species dependent on surface cover did not show a population decline after the burn; 26 species were active throughout the burned area. In the slash pine study there was no noticeable decline in trap take of any species following winter burning.

Very little information is available regarding the more aquatic herps. Those which thrive in or adjacent to sizable water bodies are probably affected very little by fire. The American alligator (Alligator mississippiensis) and associated marsh animals benefit from occasional burning of shoreline vegetation (Lyon et al. 1978). Species which inhabit small bogs, such as the pine barrens treefrog (Hyla andersoni), depend on fires to prevent woody plants from dominating their sites (Means and Moler 1979).

Much more research is needed to clarify relationships between fire and herp species. However, existing data indicate that prescribed burning benefits most species native to southern pine forests (Means and Campbell 1981).

Birds

Fire is one of the most important factors determining the abundance of forest birds. Avian food resources are strongly affected by burning. Total seed production peaks the first growing season after fire and quickly decreases thereafter (Buckner and Landers 1979). Fleshy fruits are severely reduced the first year after a fire except in cases where the more fire-tolerant species such as dogwood (Cornus florida) or beautyberry (Callicarpa americana) are present. These plants may actually produce more fruits at this time. In open pine flatwoods, fruits of most shrubs peak three to five years thereafter (Johnson and Landers 1978). Understory burning may induce longer-term reduction of most soft mast species on certain upland pine-hardwood sites (Lay 1956).

The litter-dwelling forms of invertebrates eaten by birds are reduced by ground fires in the short term; herbivorous insects quickly increase with the regrowth of succulent plants; and certain species of flies and beetles are drawn to the smoke and heat, or later, to damaged trees (Dickson 1981). These changes may affect reproductive success because arthropods supply critical nutrients for breeding birds.

The physical makeup of bird habitat is also of great importance. Structurally complex areas generally support a greater diversity of birds than uniform habitats, so fire can strongly influence the composition of avian assemblages through its effects on vegetation.

Nongame Forest Birds.--Only general discussions are available on most resident birds in the Southeast. Conner (1981) drew several pertinent conclusions regarding cavity users. He pointed out that woodpeckers and secondary cavity users will decline where fire eliminates snags. Similarly, the ignition of pine gum associated with red-cockaded woodpecker (Picoides borealis) cavities can reduce nest sites which are a very limited resource in most of today's forests. Certain foods of woodpeckers can dwindle when fire reduces litter-dwelling insects, deciduous foliage supporting caterpillars, and the availability of acorns and other important fruits. Conner (1981) also listed some potential benefits: new snags are often created by burns, especially in old-growth forests; low, open understories characteristic of burned areas are essential to red-cockaded woodpeckers; production of certain fruits eaten after the breeding season can increase with prescribed burning; many bird species are drawn to residual foods in burned-over areas; and fire provides open feeding grounds where birds capture ants, grasshoppers and spiders. The complexity of the potential negative vs. positive effects on cavity-users points out the need for research on maintaining needed diversity through careful burning techniques.

In a review of songbirds, Dickson (1981) indicated that burning favors the species closely tied to pine stands or early successional vegetation; it selects against those dependent on deciduous canopy foliage, midstory trees, or litter accumulation; and "edge species" may depend on a habitat interface such as occurs at the edge of burns or around hardwood islands within open pine forests.

The fertility of pine sites may have a pronounced influence on bird habitat development. Studies in slash pine stands show that winter burning has little overall effect, apparently because resident birds resume site faithfulness immediately afterwards (Emlen 1970) and because subsequent midstory recovery is too slow to markedly effect bird diversity, at least during 5-year burn intervals (Johnson and Landers 1982). Since warm-season fires formerly entered these poor soil habitats every few years (Wharton 1978) and these fires inhibit hardwoods and shrubs much more than winter burns, it is probable that deciduous canopy birds were originally restricted to wet hardwood drains rather than being common residents of pine stands. This deduction might also apply to the infertile, dry soils of the Coastal Plain where summer fires thoroughly inhibited hardwoods. On the other hand, the mesic clay regions (parts of the Coastal Plain and Piedmont) probably experienced natural fires less frequently and responded quickly after a burn. Bush birds and midstory leaf-gleaners would most likely increase with the rapid post-fire succession. They were probably ephemeral in richer pine forests as well as regular residents of hardwood flats.

Diversity and abundance of birds would be enhanced in areas with a mixture of grasslands and multilayered hardwoods interspersed in open pine forests. These diverse conditions can be achieved by applying fires that result in patchy vegetation (spot burning under moist conditions, etc.) and by sparing selected hardwood areas from fire.

Upland Game Birds.--Habitat requirements of upland game birds have been thoroughly studied but there are still many gaps in knowledge of fire effects. Mourning doves (Zenaida macroura) commonly forage on fresh burns (Stoddard 1963a). Such bare areas are particularly important where doves do not have access to the kinds of seeds produced by mechanical soil disturbance. It might be deduced that, before man's influence, the mourning dove had to be a follower of fresh burns because it generally does not scratch in litter for seeds, nor does it alight in dense vegetation when feeding. The tendency for doves to nest in small trees or occasionally in lower plant strata also indicates that periodic fire may have been beneficial in providing early successional stages

Gallinaceous game birds are affected by fire in several ways. Parasites that infect this bird group are reduced by burning (Stoddard 1931, Metz and Farrier 1971, Ahlgren 1974, Bendell 1974, Jacobson and Hurst 1979). In pine forests, bobwhite (Colinus virginianus) and wild turkey (Meleagris gallopavo) brood habitat consists primarily of recently burned herbaceous vegetatio (Stoddard 1931, Exum 1985).

Cool weather foods of quail and turkey that increase the first year after burning include legumes and certain other large-seeded herbs. Many shrubs and midstory trees will increase fruit production if burned occasionally. Because acorn production declines in many areas with frequent burning, protection of oak patches has been recommended in habitat management of both quail (McRae et al. 1979) and turkey (Hurst 1981).

Annual winter burning over most of a management area is essential to maintaining huntable populations of quail in pine forests (Stoddard 1931, Speake 1966). Although responses of turkey populations are less clear, studies of important requirements (plant food diversity, insect production, brood-rearing sites, etc.) indicate that occasional burning is necessary to keep pine-dominated forests from becoming choked with brush (Hurst 1981). Recommendations for habitat maintenance range from burning turkey brood areas at least every other year (Exum 1985) to a general interval of once every three years (Stoddard 1963b). Burning before the nesting season is often recommended, with small, scattered areas burned each year throughout winter for regular production of greenery (Stoddard 1963b) and others every 2-4 years to insure some fruit production (Speake et al. 1975).

Ruffed grouse (Bonasa umbellus) select herbaceous habitats for brood rearing (Harris 1981). One of the major winter forages (Kalmia latifolia) of grouse in the Southeast has been shown to increase in crude protein and phosphorus with burning (Thackston et al. 1982). This game bird is considered a fire climax species, or at least one that benefits from recurring fires (Sharp 1970).

Birds of Prey.--Predatory birds are indirectly affected through fire's influence on nesting sites and food supplies. Red-tailed hawks (Buteo jamaicensis) have been recorded feeding on grasshoppers fleeing from fires. Kestrels (Falco sparverius) and many other hawks and owls also are attracted to burns in search of prey (Stoddard 1963a, Komarek 1969).

An important factor in the ecology of most predatory birds is the population level of prey species. Most hawks and owls depend on the cotton rat (Sigmodon hispidus) and cottontail rabbit and other major prey species (herps, large insects, etc.) that are affected by any disturbance that changes the balance between understory cover and forage. Since regular burning keeps habitat in a suitable condition for the more common mammals but temporarily exposes them when cover is ignited, and since thickets retard the efficiency of predators, it is probable that fire benefits avian predators through availability of food (see Mammal section). The maintenance of prey populations for golden eagles (Aquila chrysaetos) is an objective of burning mountain balds in the Southeast.

Cooper's and sharp-shinned hawks (Accipiter cooperii and A. striatus) seem to key in on quail and the larger or more colorful passerines. These "blue darter" hawks are primary predators of such birds that are abundant in fire-maintained game lands in the Deep South.

Because hawks nest mainly in living hardwoods and the more widespread owl species nest in tree cavities, fire has the potential to adversely affect reproduction if it is intense enough to destroy nest trees. Light winter burning probably does no substantial harm.

The burrowing owl (Athene cunicularia) inhabits sand hills in southern Florida. Periodic fire is important in keeping the substrate open for burrowing, as well as maintaining early successional stages for the herp-mammal food base on which this owl depends.

Mammals

A variety of mammals inhabit each stage of understory and subcanopy development in southern pine forests. No single species satisfies all of its seasonal needs in any one uniform stage. Rather, their dietary and structural requirements are partially in opposition because of competition for sunlight within a stratum and progressive dominance of taller strata over shorter ones. Therefore, some degree of habitat patchiness is essential to all mammal species; the acceptable scale of this patchiness is related to the home range size of the species under consideration.

Small mammals.--Of the 44 species of small mammals in the southeastern states, only 16 had been mentioned in research reports when Taylor (1981) reviewed the literature regarding fire effects. He concluded that the fulvous harvest mouse (Reithrodontomys fulvescens) and cotton mouse (Peromyscus gossypinus) showed a consistent population increase following fire; the cotton rat, eastern harvest mouse (R. humulis), and round-tailed muskrat (Neofiber alleni) showed population decreases; the old-field mouse (P. polionotus) and Florida mouse (P. floridanus) showed no measurable change; and nine other species were listed under "response unknown."

The problem with deciphering small mammal responses is related to the very short duration of most studies. The previous evaluation was heavily influenced by data from ten studies conducted from 4 to 28 months; one investigation (Layne 1974) was conducted over a three-year period and another (Baker unpubl.) had run for seven years at the time of Taylor's (1981) review. The complete impact of forest burning is difficult to assess because (1) erratic annual population changes can occur independent of habitat conditions, (2) several years are required for significant changes in seral stages, (3) populations can be depressed immediately by a given burn, but increased in the long run, and (4) when regular burning is stopped, populations can increase immediately but become depressed in the long run.

The best available information comes from Baker's (unpublished) study which was conducted in a park-like loblolly (Pinus taeda)-shortleaf pine

(P. echinata) stand that had been winter-burned annually for decades. Burning ceased in March 1967, and plant succession was allowed to proceed unhindered. A live trap census was begun immediately after the last fire, continued for 12 consecutive years, and initiated again in 1986.

Many least shrews (Cryptotis parva), several eastern harvest mice, and a few cotton mice, short-tailed shrews (Blarina brevicauda), and golden mice (Ochrotomys nuttalli) were recorded on the fresh burn. During the first and second years post-burn, herbivores and granivores became dominant [cotton rats, cotton mice, eastern harvest mice, and house mice (Mus musculus)]. Growth of woody cover mixed in with abundant herbs was an important factor in this increase. Shrews (insectivores) apparently declined during this period, then became rare or absent for the next six years.

The early brush stage (years three and four) also supported abundant cotton rats and cotton mice, but eastern harvest mice and house mice did not persist beyond this stage; the more omnivorous and arboreal golden mouse began a marked increase. Golden mice increased further during the next two growing seasons and remained common for at least six years thereafter. Species more fully dependent on groundstory vegetation gradually declined during this period, but the eastern flying squirrel (Glaucomys volans) became quite abundant after the ninth growing season. The short-tailed shrew reappeared during years 8 through 11 after fire exclusion, probably as a result of optimal litter structure and arthropod abundance.

Nineteen years after fire was excluded (1986), a few golden mice and many flying squirrels were captured, and gray squirrels (Sciurus carolinensis) were often seen (all arboreal species). To date, it appears that the terrestrial species and even the semiarboreal golden mouse depend on early post-fire successional stages in this forest. Whereas Baker's data might apply only to certain pine forests, it serves here to illustrate a basic premise: the majority of small mammals thrive in early- to midsuccessional habitats which are maintained (if not created) by fire, or by some other disturbance that has a similar effect on vegetation. The relationship between sunlight intensity, lower-level vegetation, and small mammal species should be investigated in other forest types to more fully assess the role of fire.

Tree Squirrels.--Burning can have a major impact on tree squirrels. Kirkpatrick and Mosby (1981) pointed out that fire significantly degrades habitat of squirrels when it is employed effectively to maintain pure pine stands. In such cases the most serious negative factor was thought to be the damage to den trees, developing hardwood saplings, and mature mast producers. In contrast, they felt that low-intensity ground fire might have no adverse effects in squirrel woods other than the destruction of acorns in the duff.

Fire may have a positive influence on squirrel habitat in some situations. For example, it is generally accepted that squirrel population levels depend to a large degree on the supply of acorns; low-growing oak species in the Coastal Plain are dependent on periodic fire for maintenance and for acorn production (Williams 1977). Furthermore, squirrels require certain nutrients that are insufficient in acorns (protein, key minerals). For a balanced diet they also feed on mushrooms (which often increase with burning) or fruits and seeds such as dogwood drupes (a species maintained by fire in many forests).

Population data are very scarce for any squirrel species in pine-dominated forests. Least is known about the ecology of southern flying squirrels. In Baker's study (op. cit.) this secretive species was not captured frequently in a post-fire study plot until about the tenth year when water oaks (Quercus nigra) and other hardwood saplings formed a tall midstory. However, in this same pine forest (Tall Timbers Research Station) flying squirrels are very abundant, even though most of the landscape has been winter-burned annually for over a century. W. Baker (pers. comm.) documented 20 to 30 flying squirrels denning together during winter in a nest box erected in open pine woods. Habitat quality is enhanced by mature live oaks (Quercus virginiana) spaced throughout the annually burned property. Also very abundant in this forest are gray squirrels and fox squirrels (Sciurus niger).

In frequently burned pine-dominated forests, gray squirrels primarily inhabit drains, wet depressions, and upland hardwood islands which get their start where fire misses areas for a few successive years. These hardwood islands develop less frequently on flat terrain than clay hill terrain. For example, on quail plantations in the Red Hills region of southwest Georgia and northern Florida, the spread of hardwoods is a constant problem where old field loblolly and shortleaf pines predominate. Hardwood encroachment advances as lightning strikes and pine beetles gradually kill the large pines while annual winter fires tend to repress pine regeneration. Fire quickly becomes less effective at controlling hardwoods as pine needle cast decreases. Since practically all pine forests on well-drained clay sites, whether in the Coastal Plain or Piedmont, are old-field communities, it is probable that squirrels will be provided for where winter prescribed burning is the sole tool for controlling hardwoods in such forests. Because gray squirrels feed to a large degree on pine seeds, habitat quality could be more stable with parcels of mixed pine-hardwood than in pure hardwood forests where fluctuating oak mast is the only mainstay. However, in Coastal Plain forests where wiregrass is still abundant in the understory, repeated fires suppress hardwoods so thoroughly that gray squirrels are uncommon.

Fire has probably been a determining factor in the niche separation between gray and fox squirrels in the Coastal Plain. Even though both

exist in mixed pine-oak forests and feed heavily on acorns, the more competitive gray squirrel dominates locally where the overlap of oak crowns allows tree-to-tree travel through the canopy. The much smaller body size of grays may also have advantage in contending with low ebbs in acorn supplies.

It has been reported that fox squirrels are more abundant where patches of oaks comprise less than 30% of pine-hardwood stands (Hilliard 1979). From long-term studies in longleaf pine forests, Weigl et al. (1983) theorized that southern fox squirrels evolved into the largest sciurid in North America (1 kg or larger) through the advantage of traveling long distances to find longleaf pine cone concentrations and the greater ability to handle and tear apart these large cones. This theory together with the fact that fox squirrels are quite clumsy when trying to travel in canopies, and spend a great deal of time foraging for acorns as well as bulbs, seeds, etc. on the ground, would indicate they do best in fire-type pine forests with scattered hardwood inclusions. A lush, grassy groundstory maintained by fire is important as protective cover from predators (Hilliard 1979). The gradual disappearance of this mixture of habitat components has led to a serious population decline of fox squirrels throughout the South.

Rabbits.--The subject of prescribed fire and rabbits in southern forests was reviewed by Hill (1981). He stated, "Most wildlife researchers believe that any planned fire that reduces plant succession to an earlier stage will generally be beneficial to rabbits." The immediate adverse effects of cover reduction are thought to be overridden by improved forage quality and quantity for two or more growing seasons after burning. Hill (1981) also concluded that burn cycles longer than two-year intervals would be less beneficial, but that "any fire is believed better than fire exclusion."

There are important implications that burning helps reduce the parasite burden on rabbits (Hill 1971; Van Rensburg 1971). By combining the findings that rabbit litter size depends on the nutritional quality of forage (Hill 1972) with the numerous data that show light burning increases high-protein herbs (legumes, grasses, etc.) eaten by rabbits, the potential becomes clear for a positive reproductive response to fire. However, since rabbits also feed on certain shrubs and vines (especially during winter) and require thickets for escaping from their many predatory enemies, it would seem that a clean annual burn would be far less ideal than mosaic burning that would leave sizable patches of woody plants. It is also possible that burning a number of scattered parcels periodically during the colder months might provide greenery that would help overcome food shortages. To maintain habitat diversity, Hill (1981) suggested alternating the burning on adjacent plots during a given year.

Furbearers.--There are eight medium-sized mammals classified as fur bearers that live in southern forests. All are highly mobile, terrestrial species--foxes (Urocyon cinereoargenteus and Vulpes fulva), bobcat (Lynx rufus), raccoon (Procyon lotor), skunks (Spilogale putorius and Mephitis mephitis), opossum (Didelphis marsupialis), and coyote (Canis latrans). There are apparently no references indicate any direct effect of fire on these mammals, but indirect effects on foods and ot resources can be quite important (Hon 1981).

The welfare of major predators--foxes, bobcat, and coyote--depends to a great degree on accessibility to smaller mammals. The benefits of fire in maintaining early successional habitats for these prey species was discussed in previous sections. It is also probable that predator efficiency is improved by ground fires (open substrates for quieter stalking and easier capture of prey, concentrating effect on prey in patches missed by fire, etc.). If improved efficiency is a significant advantage, it may be that burning annually provides better stalking grounds than biennial or longer intervals that actually yield the most total prey. This factor might account for a dense bobcat population recorded on a quail plantation where winter burning was conducted annually (Miller and Speake 1978). Furthermore, it has been suggested that, under natural conditions, frequent fires worked together with predators in keeping small mammals in normal population bounds (Komarek 1939).

While terrestrial furbearers all eat smaller mammals to some extent, other food items are important to various degrees. Insects are primary or secondary food items. Litter dwellers (certain ground beetles, etc.) are often displaced by herbivorous insects (grasshoppers, etc.) after fire; the latter insect group typically constitutes the bulk of insect components of furbearer diets.

Fruits are important in diets of the more omnivorous species (foxes, coyotes, raccoons, and opossums). Of the major fruit species, acorns, persimmons (Diospyros virginianus), plums and cherries (Prunus spp.), and grapes (Vitis spp.) can be severely reduced by fire in the short run. However, these woody species require openings for establishment, so edges of burns in pine forests may be common regeneration sites for many of these plants. Important berry producers such as blackberry (Rubus spp.), blueberry (Vaccinium spp.) and gallberry (Ilex glabra) produce the most fruit a few years after fire pruning. Fire at three-year intervals would optimize fruit production in open slash pine forests (Johnson and Landers 1978).

Hon (1981) inferred that burning on a three-year rotation should create desirable furbearer habitat in the southeastern pine region. He also noted that certain fire-sensitive fruit producers should be protected for longer periods. To these suggestions might be added that some upland areas be burned more frequently to maintain grasshoppers, etc. and low vegetation where predators could more efficiently catch prey.

Black Bear.--Black bears ranged throughout the southern pine belt before the build-up of human population centers. Occupied range south of the mountain regions is now restricted to large, relatively inaccessible forests in the Lower Coastal Plain.

Hamilton (1981) synthesized information concerning fire effects based primarily on his bear research in North Carolina and the investigations of other researchers in Florida. He pointed out that periodic winter burning is propitious for production of fruits [dwarf oak, saw palmetto (Serenoa repens), etc.] and tender shoots which comprise the bulk of the diet, but advised against summer burning because it can deprive bears of a wide variety of foods. For pocosins, Hamilton (op. cit.) suggested that periodic burning (every three to seven years) be restricted to zones between pine-scrub oak sand ridges and Carolina bays or hardwood swamps. Because broad-scale burning temporarily reduces food supplies over large areas and pushes bears into unfamiliar territory where they are quite vulnerable, he recommended burning numerous, small areas throughout bear habitat to create a maze of post-fire stages, and to burn pine-hardwood habitats on a 5-10 year rotation. This recommended frequency might have to be modified depending on soil fertility of a given management area. Planning for juxtaposition of various successional stages seems as appropriate for managing habitat for black bears as it does for the mid-sized omnivores discussed in the previous section. In pocosin country it is critical to schedule prescribed burns when peat soils are saturated to guard against subsurface fire. However, the benefits of careful burning are evident when compared to the destructive nature of wildfires which occasionally ravage through "protected" pocosins.

White-tailed deer.--Most information regarding the effects of fire on deer pertains to habitat influences. Stransky and Harlow (1981) pointed out that burning typically causes several changes: 1) an increase in certain essential nutrients (protein and phosphorus which are generally limiting in the Southeast) and Palatability of forage during the first growing season or longer; 2) initial reduction of leafy biomass, followed by effective increases until browse grows beyond a deer's reach (above 1.5 m after about three years); and 3) an initial decrease in fruit yields of most shrubs, followed by increases in the next three to five years in some forests or longer-term decreases in others. The overall higher plane of nutrition resulting from fire can improve antler development in bucks and the condition of fawns (Beasom and Springer 1981).

Negative effects commonly noted by biologists are the reduction of acorns and a temporary dislodging of deer from their home ranges after large-scale fires. Regular burning favors herbs over woody browse plants, more so by warm-season than by winter burns. Some of the highly preferred forage plants are woody vines which are notably pruned back by fire and may be virtually eliminated by repeated burning of areas with dense deer populations. Therefore, the burning interval and percentage of an area burned each year are major considerations in deer range management.

Since browse plants generally surpass their prime by the fifth growing season after sprouting, deer range might approach optimum condition with a five-year cycle scheduled to burn about 20% per year in small parcels. The conflicting requirements of low browse vs. hard mast supplies would suggest that delineating browse production areas apart from major oak stands would benefit deer. Research on the optimum size and shape of burning units would help refine management schemes. Studies are also needed on effects of small, warm-season burns to see if the resulting succulent growth might better meet the nutritional needs of pregnant does and young fawns.

CONCLUSIONS

The complexity of the foregoing summaries show that any generalization about "how fire affects wildlife" would be tenuous at best. Not only is each wildlife species affected differently, each forest type and local habitat situation reacts differently to a given fire. Cumulative information must be interpreted cautiously.

Even though fire is generally an insignificant direct cause of wildlife mortality, it indirectly influences the abundance and species composition of pine forest wildlife through regulation of lesser vegetation. Most residents are early- or midsuccessional species. Habitation in preclimax stages of today actually reflects a primal dependence on fire--the prevailing disturbance force for thousands of years.

Prescribed burning is perhaps the most under-utilized but valuable tool available to wildlife managers. A critical evaluation of burning is needed before its usefulness can be fully realized in even a single-species plan. If the habitat is decadent then fire may provide benefits quickly, but if the habitat is already in prime condition, fire may set back the targeted species, at least in the short term.

Goal-setting is essential in management with fire. An objective of general wildlife diversity is self-conflicting. But because most species require at least some habitat patchiness, this goal might be approached by blending spot burning with parcels spared from fire for various lengths of time, depending on site fertility and vegetation type. Research is needed for developing recommendations for patch size to accommodate different species. In all cases, the quality of pine sites should be taken into consideration because the richer the site, the greater the probability that increasing numbers of hardwoods will reach fire-resistant size and outstrip the control of low-intensity fires.

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The opportunity for "natural community stewardship" in southern pine forests has been foregone for several decades. Attempts to duplicate what anyone might visualize as truly natural should be accompanied by plant ecology research involving variable summer fires together with documentation of resulting gains and losses of wildlife. The trade-offs in choosing one goal over another must be evaluated more closely as managers try to provide for wildlife on dwindling forest lands in the future. The easiest goal--featuring deciduous canopy species--can be reached in pine forests after many years of benign neglect unless a wildfire occurs. The wisdom of taking that course should be closely scrutinized by all decision makers involved in conservation. A better approach for accommodating such species would be to manage for hardwood stands on true hardwood sites.

Management with fire will always require on-the-ground judgment and a thorough knowledge of the requirements of targeted wildlife. Long-term studies of fire-community relationships are needed to help land managers choose the proper burning schemes to reach their objectives.

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Small mammal response to pine-grassland restoration for red-cockaded woodpeckers

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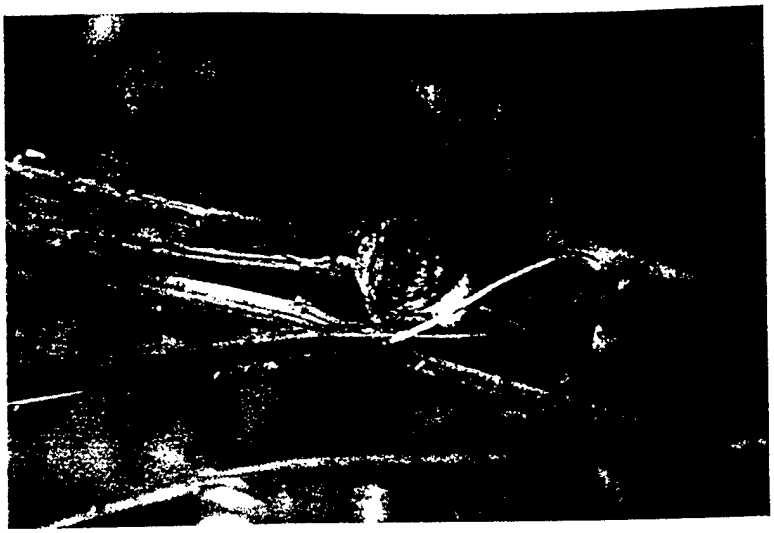
Abstract The U.S. Forest Service plans to restore >40,000 ha of the fire-dependent shortleaf pine (*Pinus echinata*)-grassland community on the Ouachita National Forest and potentially >780,000 ha of the pine-grassland community throughout the Southeast to benefit the endangered red-cockaded woodpecker (*Picoides borealis*). Concern has arisen over impacts of large-scale conversion of closed-canopy forests to open pine-grassland woodlands. We evaluated how an ecosystem approach to habitat improvement for the red-cockaded woodpecker affected small mammals. During 2 winters we compared small mammal occurrence and abundance in untreated pine-hardwood stands to stands following wildlife stand improvement (WSI; midstory removal), and with WSI-treated stands in the first, second, and third dormant seasons following prescribed fire. Total abundance of small mammals was highest in WSI stands and was a more direct response to WSI (change in stand structure) than to fire. Increased species richness and diversity in the second year of this study was strongly related to both WSI and fire. No species was adversely affected by WSI or by fire. Rather, WSI and fire-reduced midstory, increased dead debris in the understory, promoted herbaceous production, and increased woody sprouting. Total community abundance, richness, and diversity were lowest in untreated stands. White-footed mice (*Peromyscus* spp.; primarily white-footed mouse [*P. leucopus*]) were the dominant species, accounting for 68% of the 611 individuals collected. Restoration efforts may be particularly beneficial to generalist species such as *P. leucopus* as well as to more specialized species, such as golden mouse (*Ochrotomys nuttalli*) and fulvous harvest mouse (*Reithrodontomys fulvescens*) that historically may have depended upon pine-grassland habitats. Restoration of pine-grassland communities may enhance small mammal communities by reestablishing a landscape element that was present during presettlement times.

Key words Arkansas, fire ecology, Ouachita Mountains, *Picoides borealis*, pine-bluestem, prescribed fire, red-cockaded woodpecker, small mammals, wildlife stand improvement

Historic evidence suggests that fire-maintained, shortleaf pine (*Pinus echinata*)-grassland communities were characteristic of the presettlement Ouachita Mountain region (Foti and Glenn 1991, Masters et al. 1995) and that open-woodland or pine-grassland habitats were once prevalent across the southeastern United States. (Christensen 1981, Buckner 1989, Waldrop et al. 1992). The endangered red-cockaded woodpecker (*Picoides borealis*) is an endemic species of southern pine-grassland forests.

Management of red-cockaded woodpeckers has been approached on an ecosystem basis since 1990 in the Ouachita National Forest. Use of wildlife stand improvement (WSI; midstory removal) and prescribed fire was broadened to restore shortleaf pine-grassland communities. Midstory removal is fol-

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Fulvous harvest mouse in restored shortleaf pine-bluestem stand, Ouachita National Forest, Arkansas.

lowed by dormant-season, prescribed burning every 3 years (U.S. Dep. Agric. 1985). Although vegetation and structural changes resulting from WSI improve the quality of forest stands for red-cockaded woodpeckers, controversy has arisen over the effects of this management technique on nontarget species (Brennan 1991, Brennan et al. 1995, Masters et al. 1996).

Alterations of the forest ecosystem that result in modification of primary production, primarily herbaceous forage, or vegetation structure (cover) may alter habitat suitability for small mammal species. Vegetation structure and composition of stands treated with WSI and fire differ markedly from untreated stands (Wilson et al. 1995, Masters et al. 1996). The impacts of fire on herbivorous small mammals have been well established (Cook 1959, Ahlgren 1966, Krefting and Ahlgren 1974). Small mammals are responsive to slight microhabitat changes in the forest floor (Dueser and Shugart 1978). Little is known about small mammal community responses to silvicultural practices incorporating both fire and midstory vegetation removal.

We tested the hypothesis that small mammal populations and communities would respond following habitat changes (i.e., pine-grassland restoration) according to their respective habitat requirements. We expected increased relative abundance, species richness, and diversity following WSI and fire. We compared relative abundance, species richness, and diversity of small mammals in untreated closed-canopy pine-hardwood stands and treated stands, following WSI and prescribed fire.



Historic photo (circa 1924) entitled "Forest Interior" of shortleaf pine-bluestem ecosystem on the Ouachita National Forest. Photo was taken north of the Jessieville-Umphers Ranger District on Powell Mountain Trail in what was then Arkansas National Forest. Photo courtesy of U.S. Forest Service.

Study area

The study area was in the west-central Ouachita Mountains on the Poteau, Mena, and Cold Springs Ranger Districts of the Ouachita National Forest, Arkansas. The area is mountainous, with east-west trending ridges and valleys with forests composed of second-growth, mixed pine-hardwood stands. Shortleaf pine dominates south-facing slopes and hardwoods dominate north-facing slopes (Foti and Glenn 1991). Study sites were 14-45 ha pine-grassland restoration stands with active woodpecker clusters or evidence of past woodpecker occupation (Neal and Montague 1991). These stands were used to monitor breeding birds and forage response to WSI and prescribed fire (Wilson et al. 1995; Masters et al. 1996).

Methods

Experimental design

Our study design was completely randomized with 3 replications of 5 treatments in 2 years. Treatments were:

1. Control (n = 3);
2. WSI, no burn (WSI-NB; n = 3);
3. WSI, following first growing season postburn (WSI-B1; n = 3);
4. WSI, following second growing season postburn (WSI-B2; n = 3); and

5. WSI, following third growing season postburn (WSI-B3; $n = 3$).

In 1992, we randomly chose 15 stands to sample from a total of 61 treated stands. In 1993, all WSI-NB and WSI-B3 stands were burned in early spring and, therefore, became WSI-B1 stands; WSI-B1 became WSI-B2; and WSI-B2 became WSI-B3. Controls remained the same, and we added 3 randomly selected WSI-NB stands and randomly dropped 3 WSI-B1 stands for 15 stands sampled in 1993.

Small mammal survey

We used livetraps and mark-recapture methods to survey small mammals during winter in 1992 and 1993 (27 Dec–4 Jan; similar to Tappe et al. 1994). We located 80 trap stations at 15-m intervals along 3–8 randomly located transect lines (depending on stand configuration) within each stand. Transect lines were perpendicular to the contour and ≥50 m from stand boundaries to avoid ecotone effects. Trapping effort and design were identical on all stands, and all sampling was conducted in 7 consecutive-day periods.

We used Sherman livetraps (7.6 x 8.9 x 22.9 cm) baited with whole oats and with cotton batting for bedding material. Traps were located within 2 m of each trap station and checked daily between 0800 and 1200. We had 560 trap nights of activity per stand per year. Captured animals were identified to species, sexed, aged (adult or juvenile), designated a capture status (new capture or recapture), marked (toe-clipped), assigned a trap location, and released at capture site. All sprung traps were recorded, and total trap nights of effort available was determined after correcting for sprung traps (1/2 of all sprung traps were subtracted from 560 each day to determine total trap nights of activity).

Vegetation sampling

We characterized woody species composition and forest structure in each stand in 24, 5-m-radius plots in May–June of each year. Woody stems were counted and tallied in 0.5 to 1.4-m and >1.4-m height classes. Woody stems >1.4 m were categorized in 8 diameter classes. We sampled the vertical vegetation profile at 9 points in each plot with a 10-m pole divided into 1-m increments. We also collected information on basal area and canopy cover at plot centers. These data and further description of methods were reported by Wilson (1994), Wilson et al. (1995), and Masters et al. (1996).

We sampled herbaceous and woody standing crop <1.4 m in July and August each year in 30, 1- x 1-m plots on randomized transects. After clipping, each sample was hand sorted into 7 forage categories and bagged for ovendrying. These data and methods were reported by Masters et al. (1996).

Data analysis

Relative abundance was calculated as the number of new captures per 100 trap nights of effort (Nelson and Clark 1973). Additionally, estimated sex and age ratios were calculated for each species. Community structure was assessed by calculating total abundance (N = number of individual animals caught), species richness (S = number of species caught), and diversity (H'; Shannon and Weaver 1949). Similarity indices were calculated for 1992 and 1993 separately, using relative abundance estimates as described by Horn (1966); results were presented using single-linkage cluster analysis (Krebs 1989).

We tested differences in relative abundance (population and community level) among treatment stands by year with Kruskal-Wallis nonparametric tests. We used orthogonal contrasts to further differentiate treatment effects between control, WSI, and burned and unburned stands. We used the stand (treatment) Type III mean square as the error term (SAS Inst. Inc. 1985). We used the Least Significant Difference (LSD) test to separate mean ranks at $\alpha = 0.05$ (Conover and Iman 1981). We used a large population effect (F-ratio = 4.0) to determine power ($1 - \beta$). Power (the probability of a Type II error) was 0.21 (*Critical* $F = 3.5$; 4, 10 df).

We used Pearson product-moment correlations to examine relationships between population and community parameters and vegetation attributes of forest stands. We used $\alpha = 0.10$ because of the inherent variability of both data sets.

Results

Small mammal abundance

Small mammal abundance differed between years, with only 58% as many animals captured in 1993 as in 1992 (Table 1). In addition to actual declines of small mammals, weather conditions may have contributed to observed capture differences between years. Temperature conditions were mild during 1992 (12 days in Dec ≤0°C) and colder with some snowfall in 1993 (20 days in Dec ≤0°C).

Over the 2-year study period, white-footed mice (*Peromyscus* spp., predominantly white-footed mouse [*P. leucopus*]) were the most abundant species in small mammal communities. They accounted for 68% of the 611 individuals collected (Table 1). Fulvous harvest mouse (*Reithrodontomys fulvescens*) and southern short-tailed shrew (*Blarina carolinen-*

Table 1. Total new captures of small mammals in mixed pine–hardwood stands treated with wildlife stand improvement (WSI) and fire on Ouachita National Forest, Arkansas, during winter, 1992 and 1993.

	Treatment[a]															
	Control			WSI-NB			WSI-B1			WSI-B2			WSI-B3			Grand Total
Species	1992	1993	Total	1992	1993	Total	1992	1993	Total	1992	1993	Total	1992	1993	Total	
Peromyscus spp.[b]	22	11	33	75	60	135	74	33	107	38	33	71	38	34	72	418
Reithrodontomys fulvescens	0	0	0	14	1	15	14	31	45	3	2	5	7	6	13	78
Blarina carolinensis	6	4	10	11	0	11	14	2	16	13	2	15	13	2	15	67
Neotoma floridana	2	0	2	7	0	7	2	2	4	5	0	5	0	0	0	18
Sigmodon hispidus	0	0	0	0	1	1	3	1	4	0	0	0	0	0	0	5
Ochrotomys nuttalli[c]	5	0	5	5	0	5	1	0	1	9	0	9	2	0	2	22
Microtus pinetorum[c]	0	0	0	1	0	1	0	0	0	0	0	0	2	0	2	3
Total individuals	35	15	50	113	62	175	108	69	177	68	37	105	62	42	104	611
Total species	4	2	4	6	3	7	6	5	6	5	3	5	5	3	5	7
Total trap nights	1,622	1,638	3,260	1,520	1,632	3,152	1,589	1,628	3,217	1,535	1,637	3,172	1,589	1,640	3,229	16,030
Trap success (%)	2.16	0.92	1.53	7.43	3.80	5.55	6.80	4.24	5.50	4.43	2.26	3.31	3.90	2.56	3.22	3.81

[a] Control = no treatment; WSI-NB = midstory removal and no burning of downed trees; WSI-B1 = midstory removal, late-winter prescribed burn, following first growing season after fire; WSI-B2 = midstory removal, late-winter prescribed burn, following second growing season after fire; WSI-B3 = midstory removal, late-winter prescribed burn, following third growing season after fire.

[b] *Peromyscus* species include *P. gossypinus, P. leucopus,* and *P. maniculatus.*

[c] Captured in 1992 only.

[d] Percent trap success for new captures only.

sis) were equally abundant, with pine vole (*Microtus pinetorum*) and hispid cotton rat (*Sigmodon hispidus*) occurring infrequently (Table 1 and 2).

In winter 1992, new captures totaled 386 over 7,855 trap nights on the 15 study areas for a relative abundance of 4.9 animals per 100 trap nights (Table 1). We collected 7 small mammal species across all study areas in 1992. These included 1 insectivore, *Blarina carolinensis* and 6 cricetid rodents; *P. leucopus*, eastern woodrat (*Neotoma floridana*), golden mouse (*Ochrotomys nuttalli*), *M. pinetorum*, *R. fulvescens*, and *S. hispidus*.

Peromyscus spp. comprised the largest numbers of small mammals with 247 individuals captured (Table 1). *Peromyscus* spp. increased (orthogonal contrast; $P = 0.022$) as a direct result of WSI (Table 2). At least 3 cotton mice (*P. gossypinus*) were collected in 1992, but most captures were recorded as *P. leucopus* because of difficulty in distinguishing the 2 species. *Blarina carolinensis* was also relatively abundant in all stands (Table 1).

We captured 225 new animals in winter 1993, after 8,175 trap nights, for a relative abundance of 2.8 animals per 100 trap nights (Table 1). In 1993, we collected only 5 of the 7 species captured in 1992; we did not capture *O. nuttalli* or *M. pinetorum*. In 1993, after technicians were trained with study skins we identified *Peromyscus* to species. *Peromyscus leucopus* (most abundant), *P. gossypinus*, and 2 deer mice (*P. maniculatus*) were captured (Table 2).

Relative abundance of all species except *R. fulvescens* declined from 1992 levels, especially the least common members of small mammal communities. *Peromyscus leucopus* and *R. fulvescens* accounted for 206 of the 225 new captures in winter 1993 (Table 1). *Peromyscus gossypinus* was found only in burned stands (orthogonal contrast; $P = 0.039$), and *P. leucopus* showed a tendency to increase in the WSI stands over control stands (Table 2). When combined, *Peromyscus* spp. were more abundant (orthogonal contrast; $P \leq 0.031$) for both years in WSI stands than in unthinned control stands (Table 2). *Reithrodontomys fulvescens* showed a direct increase in response to WSI (orthogonal contrast; $P = 0.036$) and a further increase to fire (orthogonal contrast; $P = 0.016$) in the second year (Table 2).

Relative abundance of the total small mammal community was 2- to 4-fold greater on WSI treatments compared to controls in both years (orthogonal contrast; $P \leq 0.016$). The total small mammal community had a tendency to be more abundant in burned versus unburned stands (Table 2). Differences in total community abundance among WSI treatments were not as apparent, but appeared to decline slightly each succeeding year postburn. No differences in total community abundance were observed between unburned WSI stands and WSI-B1 stands (Table 2).

Species richness and diversity

A major difference between control stands and WSI-treated stands was the complete absence of *R. fulvescens* from controls and predominance of this species in WSI-treated stands. Neither *M. pinetorum* nor *S. hispidus* were captured in control stands. More species were captured in WSI stands than control stands. However, species richness and diversity differed only in the second year as a response to WSI (orthogonal contrast; $P = 0.009$ and $P = 0.016$ respectively) and a direct response to fire (orthogonal contrast; $P = 0.029$ and $P = 0.029$, respectively; Table 2). More species were captured from WSI-NB and WSI-B1 stands than other stand treatments.

Similarity of community composition

In winter 1992, similarity indices indicated that community structure of untreated controls was most similar to WSI stands following the second growing season postburn (97.5% similar; Fig. 1A). Other WSI stands were more similar (96.2% similar) to one another than to control stands. The WSI small mammal communities (WSI-NB, WSI-B1, WSI-B3) were 92.9% similar to control and WSI-B2 communities. This resulted from low *Peromyscus* spp. and *R. fulvescens*, while having high numbers of *O. nuttalli* (Fig. 1A).

We found that all burned WSI treatments clustered together in winter 1993 (Fig. 1B). Among burned WSI treatments, stands following the second and third growing season postburn were 98.2% similar in community structure; stands following the first growing season postburn were 84.3% similar to these. Of the WSI treatments, the unburned (WSI-NB) stands were 83.9% similar to controls in community structure. These 2 nonburned treatments were only 78.8% similar to burned stands because of a lack of *P. gossypinus* and few *R. fulvescens*.

Correlation with stand structure

Following WSI treatment, stands were characterized by open midstories with dense ground cover of slash, shrubs, vines, grasses, and forbs (Masters et al. 1996). Burning of WSI stands reduced the understory woody component and resulted in increased forb and grass production. In the second and third growing seasons following fire in WSI stands, the woody shrub component became an increasingly dominant element of the understory, with sustained herbaceous

Table 2. Small mammal population and community response (animals/100 trap nights) to wildlife stand improvement (WSI) and fire on Ouachita National Forest, Arkansas, during winter, 1992 and 1993.[a]

Community level, parameter	Yr	Treatment[b]					$P > F$		
		Control	WSI-NB	WSI-B1	WSI-B2	WSI-B3		Contrasts[c]	
		$\bar{x}$ (SE)	$\bar{x}$ (SE)	$\bar{x}$ (SE)	$\bar{x}$ (SE)	$\bar{x}$ (SE)	Treatment	C vs. WSI	NB vs. B
Species									
Peromyscus gossypinus	1993	0.0 (0.0)	0.0 (0.0)	0.4 (0.1)	0.3 (0.3)	0.4 (0.4)	0.175	0.176	0.039
Peromyscus leucopus	1993	0.7 (0.3)	3.7 (1.9)	1.6 (0.4)	1.7 (0.4)	1.7 (0.5)	0.390	0.066	0.420
Peromyscus maniculatus	1993	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)	0.579	0.497	0.276
Peromyscus spp.[d]	1992	1.4 (0.6)b	4.9 (0.8)a	4.8 (0.6)a	2.4 (0.7)b	2.4 (0.3)b	0.020	0.022	1.000
	1993	0.7 (0.3)	3.7 (1.9)	2.0 (0.3)	2.0 (0.1)	2.1 (0.8)	0.237	0.031	0.228
Reithrodontomys fulvescens	1992	0.0 (0.0)	0.9 (0.3)	0.9 (0.9)	0.2 (0.2)	0.4 (0.4)	0.305	0.153	0.683
	1993	0.0 (0.0)b	0.1 (0.1)b	1.9 (0.5)a	0.1 (0.1)b	0.4 (0.3)b	0.017	0.036	0.016
Ochrotomys nuttalli	1992	0.3 (0.3)	0.3 (0.2)	0.1 (0.1)	0.6 (0.6)	0.1 (0.1)	0.898	1.000	0.495
	1993	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.000	0.000	0.000
Blarina carolinensis	1992	0.4 (0.2)	0.7 (0.2)	0.9 (0.6)	0.8 (0.4)	0.8 (0.4)	0.748	0.212	0.598
	1993	0.2 (0.2)	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.406	0.193	0.712
Neotoma floridana	1992	0.1 (0.1)	0.5 (0.3)	0.1 (0.1)	0.3 (0.1)	0.0 (0.0)	0.212	0.683	0.393
	1993	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.452	0.628	0.433
Microtus pinetorum	1992	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.579	0.497	0.852
	1993	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.000	0.000	0.000
Sigmodon hispidus	1992	0.0 (0.0)	0.0 (0.0)	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	0.452	0.628	0.433
	1993	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.579	0.497	0.852
Community									
Total community abundance	1992	2.2 (0.7)c	7.4 (0.4)a	7.1 (1.3)ab	4.3 (1.1)bc	3.9 (0.7)c	0.007	0.006	1.000
	1993	0.9 (0.4)	3.9 (1.9)	4.2 (0.2)	2.3 (0.2)	2.6 (0.7)	0.069	0.016	0.082
Mean species richness	1992	2.7 (0.3)	4.7 (0.9)	3.3 (0.9)	3.7 (0.7)	3.0 (0.6)	0.447	0.247	0.715
	1993	1.3 (0.3)c	1.7 (0.3)bc	4.3 (0.3)a	2.7 (0.7)ab	3.0 (0.6)ab	0.009	0.009	0.001
Mean species diversity (H')	1992	1.1 (0.1)	1.5 (0.3)	0.9 (0.5)	1.4 (0.3)	1.1 (0.4)	0.837	0.751	0.717
	1993	0.3 (0.3)b	0.3 (0.3)b	1.6 (0.1)a	0.9 (0.3)ab	1.1 (0.3)a	0.017	0.029	0.003

[a] Column means within rows followed by the same letter or without letters were not significantly different at the 0.05 level (LSD).

[b] Control = no treatment; WSI-NB = midstory removal and no burning of downed trees; WSI-B1 = midstory removal, late-winter prescribed burn, following first growing season after fire; WSI-B2 = midstory removal, late-winter prescribed burn, following second growing season after fire; WSI-B3 = midstory removal, late-winter prescribed burn, following third growing season after fire.

[c] Specific orthogonal contrasts: C = control, WSI = midstory removal, NB = nonburned stands, B = stands burned within previous 3 years.

[d] *Peromyscus* species include *P. gossypinus, P. leucopus,* and *P. maniculatus.*

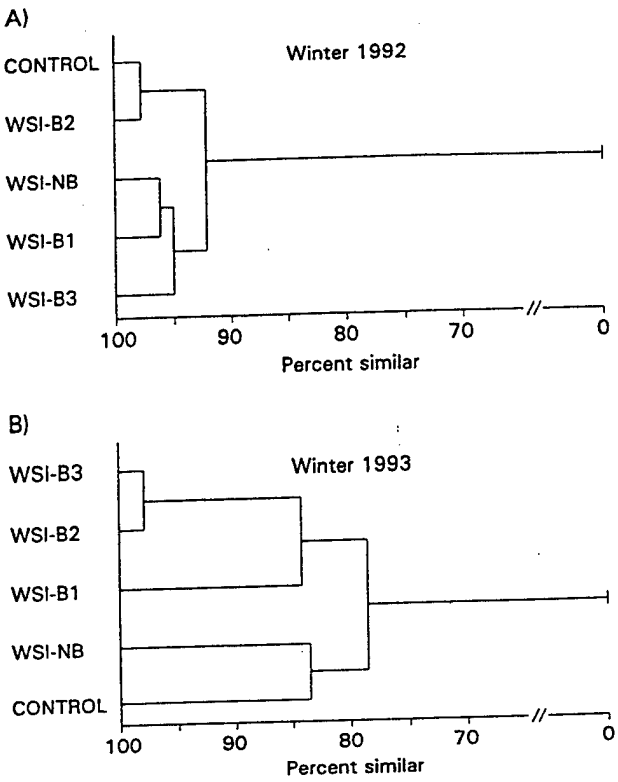


Fig. 1. Horn's similarity indices for comparisons of small mammal community structural attributes among wildlife stand improvement (WSI)-treated and control stands in the Ouachita National Forest, winter 1992 (A) and winter 1993 (B), using single-linkage cluster analysis. Control = no treatment; WSI-NB = midstory removal and no burning of downed trees; WSI-B1 = midstory removal, late-winter prescribed burn, following first growing season after fire; WSI-B2 = midstory removal, late-winter prescribed burn, following second growing season after fire; WSI-B3 = midstory removal, late-winter prescribed burn, following third growing season after fire.

forage production (Masters et al. 1996). All WSI stands had lower hardwood and conifer basal area than controls (Masters et al. 1996, Wilson et al. 1995). Dead, woody debris on the forest floor (excellent cover for small mammals) was consistently greater on WSI treatments than on controls (Wilson 1994).

Correlation analysis provided clues as to why WSI altered some aspects of the small mammal community. Relative abundance of *Peromyscus* spp. and total small mammal abundance was positively related with the presence of dead, woody debris and woody structure on or near the forest floor (Table 3). Relative abundance of *Peromyscus* spp. and total small mammal abundance showed a negative relationship with larger amounts of woody vegetation in the lower to upper midstory and overstory. Species richness and diversity were positively related with the occurrence of woody vegetation (primarily hardwoods) in the 0- to 1-m height profile. These observations were supported by positive correlations of total small mammal abundance, species richness, and diversity with increased total standing crop in the understory and negative correlations with total basal area (Table 3). *Ochrotomys nuttalli* and *R. fulvescens* were the only species showing a significant positive correlation with herbaceous forage production. *Reithrodontomys fulvescens* abundance, total relative abundance, species diversity, and species richness were also negatively related to increased presence of overstory (Table 3).

Discussion

Small mammal communities are the most important mammalian component of forest ecosystems for consumption of primary production and secondary production (Batzli and Pitelka 1970, Grant and French 1980, Gessaman and MacMahon 1984, Rose and Birney 1985) and their impact on forest regeneration (Stephenson et al. 1963, Everett et al. 1978). The small mammal associations (relative abundance and species composition) we observed on all treatment stands were similar to those described previously for similar habitat types (Atkeson and Johnson 1979, McComb and Noble 1980, Huntly and Inouye 1987, Tappe et al. 1994).

Relative abundance of small mammals on our study sites tended to be slightly higher (especially for *P. leucopus* and *B. carolinensis*) than those reported by other investigators in similar pine forests (McComb and Noble 1980, Scheibe 1985). However, our species and community results for control stands were nearly identical in concurrent years to control stands in a study on silvicultural practices elsewhere in the Ouachita Mountains, i.e., low abundance, richness, and diversity (Tappe et al. 1994). We found relative abundances considerably higher in WSI stands than in unmodified forest stands surveyed by other investigators.

Our results suggest that WSI treatments benefit small mammal communities by increasing richness and abundance. Such benefits include: increased sunlight penetration to the forest floor, reduction of forest floor litter, and resprouting of hardwoods which (1) increase dead debris in the understory, and (2) increase herbaceous forage and woody stem production in the 1- to 2-m height stratum. The result is a more structurally diverse understory that provides improved cover and forage resources to a variety of small mammals.

The most prevalent small mammal was *P. leucopus*, a habitat generalist (Ormiston 1984, Adler and Wilson 1987). Our observations concur with other studies showing a positive relationship between low (0–2 m), dead woody vertical structure and total

Table 3. Significant ($P \leq 0.10$) correlation coefficients of small mammal occurrence (animals/100 trap nights) to forest conditions and standing-crop estimates (kg/ha) by forage category on Ouachita National Forest, Arkansas, during winter 1992 and 1993. Details of vegetation sampling can be found in Wilson (1994), Wilson et. al. (1995), and Masters et al. (1996).

Variable	*Peromyscus* spp.	*Reithrodontomys fulvescens*	*Ochrotomys nuttalli*	Total abundance	Species diversity	Species richness
Conifer BA (m2/ha)		–0.49**		–0.44**		–0.37*
Hardwood BA (m2/ha)						
Total BA (m2/ha)	–0.39*	–0.53**		–0.54**	–0.36*	–0.47**
% canopy cover	–0.39*	–0.33		–0.43**		
Woody stem density > 1.4 m ht						
1.1–2.5 cm dbh	–0.45**			–0.43**		
2.6–8.0 cm dbh	–0.46**			–0.47**		
8.1–15.0 cm dbh	–0.47**			–0.48**		
Total stems	–0.47**			–0.39*		
Woody vertical structure						
0–1 m ht						
Hardwood		0.30		0.39*	0.30	0.39*
Dead	0.44*			0.39*		
Total	0.47**	0.40*		0.52*		0.38*
1–2 m ht						
Hardwood	–0.40*		0.35			
Dead	0.40*			0.35		
Total	–0.30		0.31			
2–3 m ht						
Hardwood	–0.47**	–0.33		–0.49**		–0.30
Dead						
Total	–0.44*			–0.45**		
Forage class						
Woody		0.33	0.44*	0.43*	0.43*	0.50**
Forb		0.50**				
Grass		0.38*	0.55**	0.37*	0.33	0.44**
Legume			0.43*		0.43*	0.35
Total standing crop		0.43*	0.46**	0.42*	0.45**	0.49**

* $P \leq 0.05$
** $P \leq 0.01$

structure at 0–1 m and abundance of *P. leucopus*. M'Closkey (1975) reported increased densities of this species were highly correlated with foliage-height diversity, a measure of the relative complexity of vegetation in the <2-m height stratum or the herb–shrub layer. Huntly and Inouye (1987) made similar observations for overall small mammal community structure. They found that *P. leucopus* responded positively to increased variability (i.e., standard deviation in vegetation standing crop) in vegetation. Additionally, Huntly and Inouye (1987) observed that overall abundance or density, species richness, and diversity of small mammals in the community were positively correlated with vegetation standing crop.

In a recent Missouri study, Root et al. (1990) observed positive increases in density of *P. leucopus* in oak–hickory forests, following clearcutting. *Ochrotomys nuttalli* also selects habitats according to overstory and shrub characteristics (Packard and Garner 1964). In contrast to the more abundant *Peromyscus* species, *O. nuttalli* which occurred less frequently in our captures, is a microhabitat specialist. Dueser and Shugart (1978) reported *O. nuttalli* occurred at sites with primarily evergreen canopy, and high woody and herbaceous foliage density. This may explain the positive correlation we found between abundance of this species and estimates of standing crop.

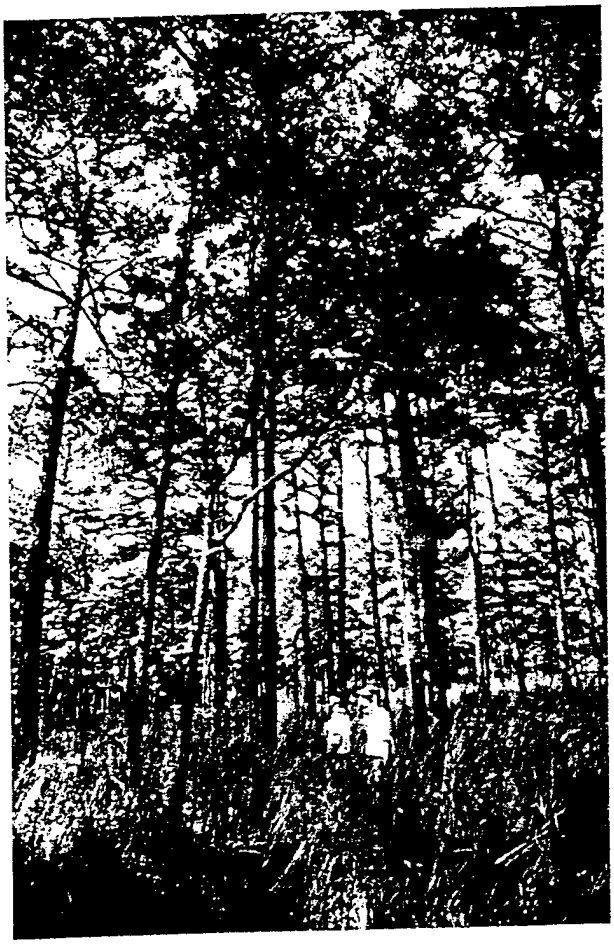
Occurrence of *R. fulvescens* and *S. hispidus* on WSI treatments, but not on controls, probably reflects increased herbaceous-forage production in response to midstory removal. Both of these species are dependent on adequate monocot communities within their habitats (McMurry 1989, McMurry et al. 1994, Clark et al. 1996). In particular, *R. fulvescens* prefers a complex of rank vegetation composed of grasses, interspersed with forbs, and woody shrubs (Clark et al. 1996), similar to our WSI stands, albeit with overstory. We predict that further opening of the forest canopy in WSI-treated stands will promote additional herbaceous vegetation production, which should result in additional increases in *S. hispidus* and *R. fulvescens* populations.

The impact of prescribed fire on small mammal communities was not easily discernable in 1992, but appeared to result in distinct community structure changes in 1993, as indicated by similarity indices and orthogonal contrasts. Small mammal communities tended to be structurally more diverse in species richness and abundance on burned WSI treatments, particularly in the second year, when relative abundance was lower. Fire reduces the litter column and increases understory herbaceous production (Masters et al. 1996).

Management implications

Until recently, the impacts of management for endangered species on wildlife other than game species were not considered of great importance (Brennan 1991, Brennan et al. 1995, Masters et al. 1996). However, other species comprise a large portion of the overall biotic community of forested ecosystems. Our neglect of other species is often responsible for many of the conflicts between wildlife-habitat needs and timber-management objectives (Silovsky and Pinto 1974). The same is true of single-species management efforts. Species endangerment may be indicative of larger community-level problems (Wilson et al. 1995). It is important to consider the community as a whole in order to select management programs that will achieve desired objectives.

Our research provides forest ecologists with valuable information on the impacts of management for an endangered species, at the ecosystem level, considering the other vertebrate components of the forest ecosystem. Pine-grassland habitat restoration will enhance overall vertebrate diversity, as indicated by our small mammals studies, breeding bird surveys (Wilson et al. 1995), and forage production studies for white-tailed deer (*Odocoileus virginianus*; Masters et al. 1996). Restoration will most likely result in greater representation of typical, grassland, rodent species such as *R. fulvescens* and *S. hispidus*, and continued maintenance of woodland species such as *P. leucopus*. Increased standing crop in the understory will support a greater abundance of small mammals as well. Results from this study provide the first investigation of composition and structure of small mammal communities, following pine-grassland restoration, in the southeastern United States.



Late summer in restored shortleaf pine-bluestem stand, Ouachita Mountains, Oklahoma.

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Associate Editor: Brennan



Season-of-Fire Studies at Tall Timbers: A Unifying Research Theme

Scientists at Tall Timbers are studying the effects of seasonal applications of prescribed fire on populations of plants and animals.

During the past decade, land managers throughout the Southeastern Coastal Plain have started to use prescribed fire during the time of year (April through August) that lightning strikes most frequently ignited fires. The rationale behind the use of prescribed fire during the lightning season is that it mimics a natural ecosystem process that shaped the Coastal Plain landscape over an evolutionary time scale. During the past century, most applications of prescribed fire occurred during January, February or March. This is the time of the year that most quail plantations burn (see Figure) and it is when most state and federal land management agencies have typically applied prescribed fires.

Use of dormant-season (January-March) fire will always have a significant place in the annual cycle of management events on quail plantations and on public lands. However, lightning season fire can be a powerful and economical land management tool for reducing or controlling hardwoods. Some plants, such as wiregrass, and other native vegetation in the understory of longleaf pine forests, must be burned during the lightning season for these plants to flower and make viable seeds.

Land managers need to understand how different seasonal applications of prescribed fire (for example dormant versus lightning season fires) influence populations of plants, insects and vertebrates. Research that documents the trade-offs between dormant and lightning season fire is extremely limited. For example, in their review of the scientific literature on seasonal effects of prescribed fire in Florida, Robbins and Myers (1992:5) stated: "...a lack of well-designed studies concerning many aspects of burning at different seasons has induced proponents of both viewpoints to bolster their arguments with unsupported assertions."



Scientists at Tall Timbers have been conducting a number of studies on the effects of seasonal applications of prescribed fire. These studies are designed to assess how applying fire during dormant and lightning seasons influences populations of plants, insects and vertebrates.

Seasonal Fire Effects on Plants

Research Scientists Jeff Glitzenstein and Donna Streng, in collaboration with Bill Platt of Louisiana State University, have been studying the effects of fire regime on tree dynamics in longleaf pine savannas on the St. Marks National Wildlife Refuge for the past 8 years. Their results (Glitzenstein et al. 1995:441) "...showed few systematic or predictable effects of

season or frequency of burning on dynamics of longleaf pine." However, oak densities "declined on the spring-burned plots, resulting in a shift away from oaks and towards increased dominance by longleaf pine." The work conducted by Glitzenstein et al. at St. Marks is one of the longest-running field experiments to assess seasonal fire effects on plants in the Southeast.

Plant Ecology Research Scientist Sharon Hermann has been collecting baseline data on seasonal affects of fire on bird census plots at the Apalachicola National Forest and Sandhills Region of North Carolina. It is too early in the project to make conclusive statements about all types of vegetation response, however there are some observations that have important implications for Red Hills land management. The baseline data indicate that lightning season fires are the most effective tool for hardwood control and encouraging a grassy understory in the sandy soils of Florida's Apalachicola National Forest and the Sandhills of North Carolina.

This may also prove to be true on land in the Red Hills but early data suggests that soil type and frequency of fire could be significant factors. This land tends to have soils that are high in nutrients and moisture when compared to sandier areas. Although overall patterns of vegetation response to burning should be similar across the Southeast, the exact periodicity of prescribed fire required to meet a management objective may be different from region to region. Tall Timbers hopes to study these regional variations in the future.

Seasonal Fire Effects on Insects

Insect Communities

Milton Lara Pavon of Florida A&M University recently completed a Master of Science thesis on effects of seasonal burns on arthropod communities in longleaf pine forests (Pavon 1995). He found that season of burn had no effect on the abundance of flies (Diptrera) and plant hoppers (Homoptera). Bees, wasps and ants (Hymenoptera) were most abundant on sites burned during winter. Beetles (Coleoptera) were most abundant on the lightning season burned plots. In general, Pavon's results suggested that arthropod communities are not negatively affected by summer (lightning season) burning.



Research technician collecting insects.

Insects Needed by Bobwhite Quail

In addition to the work by Pavon, the game bird research staff at Tall Timbers has been extensively involved in assessing the effects of seasonal burning on bobwhite quail brood habitat. Breeding bobwhite hens, and newly-hatched quail need abundant populations of insects to meet their nutritional requirements. In general, game bird researchers found that winter burning produced, on average, more insects than summer burning. However, the amounts and kinds of insects produced by the different fire applications compliments each other. Winter burn plots produced more grasshoppers, caterpillars and spiders, whereas summer burn plots produced more beetles and ants. Therefore, with respect to quail brood habitat management, our preliminary conclusion is that a limited amount of light-



The game bird research staff at Tall Timbers has been assessing the effects of seasonal burning on bobwhite quail brood habitat.



ning season burning compliments more extensive use of dormant season fires for quail habitat management. Also, in the context of quail management, we found that dormant season fires produced more broomsedge near the ground (good for nesting) and more partridge pea (good for both insects and seeds). However, winter fires also produced more oak stems near the ground, indicating the potential for hardwood encroachment problems.

Seasonal Fire Effects on Birds



Bobwhite Quail

Many wildlife managers are reluctant to use lightning season fire for hardwood control because they are afraid of burning up nests of quail and other ground-nesting birds. Conventional wisdom holds that applications of fire during the lightning season will dramatically reduce the number of quail available for hunting during the fall. We tested this idea at two plantations in the Red Hills and found little difference in quail abundance on plots that were burned during March or May. Our results showed that, at least from a short-term perspective, a limited amount of lightning season fire can be applied for hardwood control without negatively impacting abundant and huntable bobwhite populations.

Land managers need to know which plants and animals will benefit from or be harmed by burning at different times of the year.

Song Birds

Two studies to determine the season of fire effects of songbirds are being conducted by research staff at Tall Timbers. On the Apalachicola National Forest south of Tallahassee, Ornithology Research Scientist Todd Engstrom, with research technician Doug McNair, have been conducting bird surveys on plots burned during January and other plots burned during June. Their preliminary results show that relatively few nesting birds were affected by lightning season fires, probably as a result of the long (March - July) breeding season in Florida.

In the Sandhills region of North Carolina, Carol Hardy, Ph.D. candidate, in association with Wes Burger, Research Scientist at Mississippi State University and Tall Timbers Research Associate, are conducting a field study that parallels the project at Apalachicola National Forest. So far, they have found that Bachman's sparrows and summer tanagers are most abundant on sites burned during the lightning season. Their preliminary results indicate that song bird species which tend to be most abundant on lightning season burned plots are regionally or nationally declining species of special concern, whereas species that were less common on lightning season plots are, at the landscape scale, relatively common and widely distributed.

A Unifying Research Topic

Understanding how different seasonal applications of prescribed fire influence populations of plants, insects and terrestrial vertebrates is a unifying research theme at Tall Timbers Research Station. Information generated from these investigations is directly useful for land managers who want to know which plants and animals will benefit from or be harmed by burning at different times of the year.

Results from the studies described above show that applications of lightning season fire can be a useful land management tool for controlling hardwoods, and that different combinations of dormant and lightning-season fire are useful for

effort. Reducing nest predators is simply one more technique in the tool box of the effective bobwhite manager!

We assume that the bobwhite population increase we observed is either from increased nesting success, increased brood survival, or perhaps some combination of both. Future work with radio-tagged quail on trapped and untrapped shooting courses will be required to unravel this mystery.

Clearly, the results of the past two years of trapping nest predators in an experimental context at Foshalee have shown that we are meeting a key part of our research mission by **increasing the production of wild quail.**

We know of no other current bobwhite management research project that has resulted in a 150% population increase.

MAY FIRE RESULTS SHOW HARDWOOD CONTROL AND MORE BIRDS!

At May's Pond Plantation, the past two years of comparing hunting success on a shooting course burned in March and one burned in May have been quite surprising. The answer to our initial research question **"Can you burn in May for hardwood control and not hurt the birds?"** is YES! During 1994 and 1995, the shooting course burned during May produced better hunting success than a comparable course burned during February (See Figure 4).

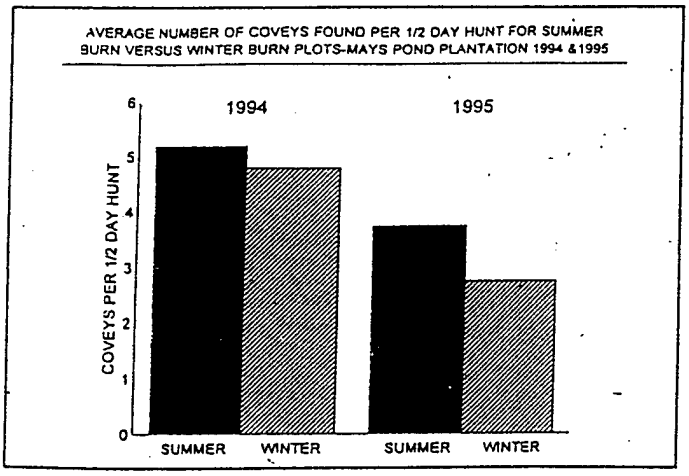


Figure 4. Average number of bobwhite coveys found per half-day hunt during 1994-95 and 1995-96 shooting seasons at May's Pond Plantation, Jefferson County, Florida on a shooting course burned during winter (February) and summer (May). Note the greater number of coveys found on the May-burned course.

Insects available for quail during the breeding season were also more abundant on the course burned du May (see Figure 5).

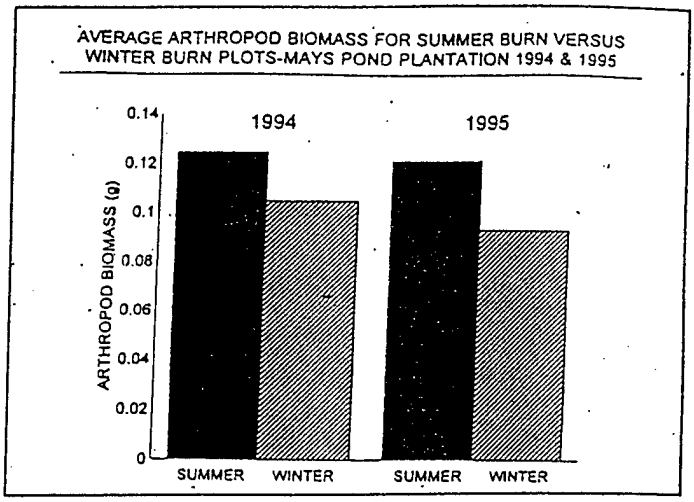


Figure 5. Abundance of arthropods available to breeding bobwhite adults and chicks on a shooting course burned during winter (February) and summer (May) at May's Pond Plantation, Jefferson County, Florida. Note the greater arthropod abundance on the May-burned course.

These results are highly significant for quail mana because of the huge cost savings that can be realized by using fire as opposed to mechanical equipment for hardwood control. All quail managers are locked in a war to control ever-encroaching hardwoods. Using lightning-season fire to control hardwoods is one way to **work with the system, rather than against it.**

DISKING INSTEAD OF FEED PATCH PLANTING RESULTS IN 70% COST SAVINGS WITHOUT LOSS OF QUAIL!

During the past two years, results from our disking versus feed patch experiments have shown that it is possible to switch from planting feed patches to using simple disking or harrowing, and not cause a decrease in the quality of quail hunting. Bobwhite hunting success between the disked only and comparable feed patch courses **varied widely, with no consistent pattern** at both May's Pond and Millpond-Sedgwick during the past two years (See Figure 6 and 7).

The Wild Turkey

Biology and Management

Edited by James G. Dickson

Southern Forest Experiment Station

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Chapter 14

HABITAT REQUIREMENTS

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BACKGROUND

Restoration of the wild turkey is a foremost success story in wildlife management. The achievement is a sterling example of the value of coordinating wildlife research and management.

Success of the management programs can be attributed to the exceptional adaptability of this species. Also critical to the success, however, have been not only the accelerating research into the habitat requirements of this species in the past 2 decades but also the rapid transfer of this knowledge to wildlife managers.

Unusual circumstances shaped the original ideas of biologists about the habitat requirements of the wild turkey. Research began in earnest in the 1940s, when turkey populations remained only in areas of extensive timberland. These areas supported turkeys because topography made them inaccessible and kept legal and illegal hunting to a minimum. Inaccessibility also made logging and agriculture difficult, so these areas remained forested.

As a result, biologists began to associate the wild turkey with big timber. A minimum of 10,000 hectares (25,000 acres) of mature forest land was a common criterion for evaluating turkey habitat. Shaw (1959:100) concisely summarized opinions on habitat requirements at the first wild turkey symposium: "A wild turkey needs one thing for sure, lots of timberland and not much human disturbance."

Three significant advances brought about a major reassessment of this conventional wisdom during the 1960s and 1970s.

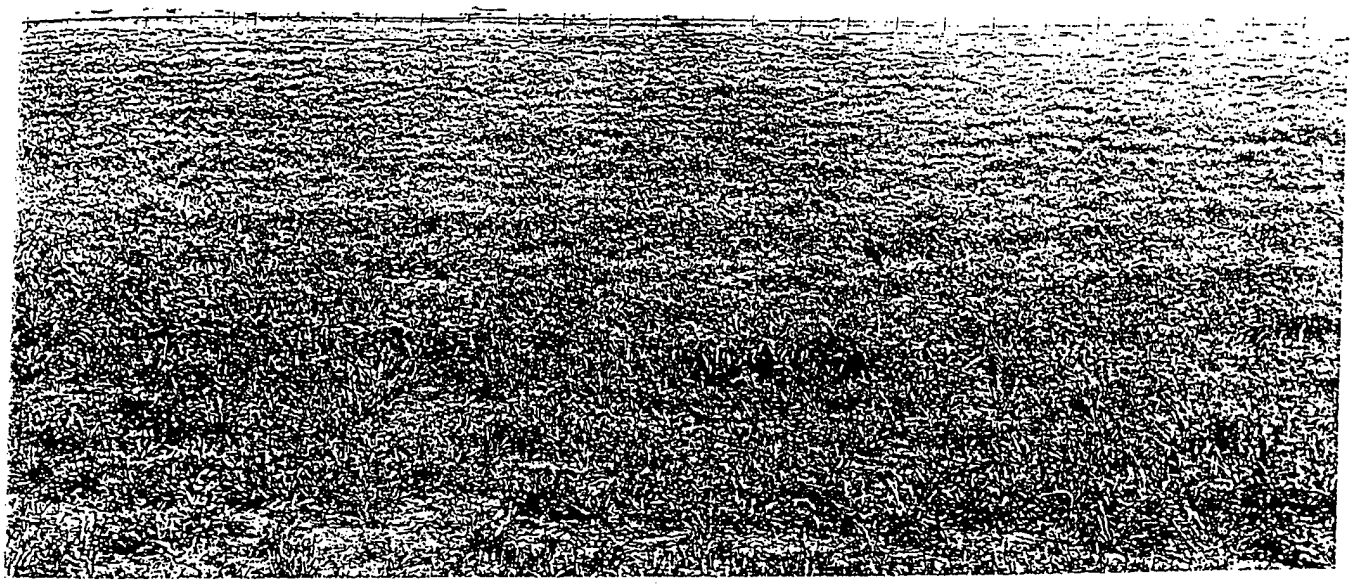
First, development of cannon- and rocket-netting techniques for livetrapping in the 1950s had resulted in successful transplants of wild turkeys into areas from which they had been eliminated. These transplants were so much more successful than those of game-farm stock that conservation agencies generally abandoned game-farm propagation in favor of livetrapping programs.

Second, vastly improved law enforcement and increased public interest in seeing turkeys resulted in a reduced illegal kill and allowed these transplanted populations to grow. In many areas, populations grew exponentially, doubling every year in the first 5 to 10 years.

By the late 1960s, transplant programs and population growth filled what was then considered good range, and wildlife managers began experimenting with transplants in other areas. Populations took hold in Washington and Oregon, well beyond historic distribution of the wild turkey. Perhaps more important, turkey numbers began to grow in agricultural areas where forest cover was extremely limited. These areas previously had been considered unsuitable for wild turkeys.

Third, the expansion into unconventional habitats prompted an explosion of research during the 1970s. Biologists were keen to understand habitat characteristics critical for the wild turkey. Coincident with the transplant programs, technological advances in radiotelemetry allowed biologists to investigate habitat requirements in much greater detail. Regional comparisons of turkey populations with broadly defined landscape patterns were complemented by behavioral studies of turkeys and their use of narrowly defined habitat types.

In the 1980s, biologists began to synthesize the findings of this research into a modern approach to assessing habitat quality. With the passage of the National Environmental Policy Act in 1969 came the need for objective, quantitative evaluations of habitat condition. Biologists borrowed techniques developed in computer science, engineering, and sociological and medical research to construct mathematically based habitat evaluation models.



Extensive cleared land is not suitable wild turkey habitat. *Photo by J. McConnell, USDA Soil Conservation Service.*

Because of the wealth of information available on the wild turkey, it was among the first species to receive this kind of attention.

This chapter provides a summary of what we have learned about the habitat requirements of the wild turkey in the past 2 decades. From the extensive data base, I have attempted to draw the patterns that constitute common denominators across the range of this species, from Florida to Oregon. For the layman, I hope this chapter will provide insight that will enrich the experience of seeing the wild turkey. For the scientist, it will provide some hypotheses to stimulate thinking.

GENERAL REQUIREMENTS

Directly or indirectly, moisture seems to be key to determining the ability of the wild turkey to survive and reproduce. Distribution of the species in the South and East is bounded by the coastal wetlands. The wild turkey is largely cursorial (ground dwelling and ground feeding) and is not well adapted to marsh environments. In the North, distribution is limited by persistent deep snow (more than 25 centimeters, 10 inches), which restricts movement and feeding ability. In the West, dry conditions that limit access to water and food (and preclude the development of trees suitable for roosting) set limits to the wild turkey's distribution.

More specifically, suitable habitat includes 2 key ingredients. Regardless of the nature of the environments or subspecies, turkeys must have a combination of trees and grasses. Trees provide food, daytime resting and escape cover, and—most important—nighttime roost sites. Grasses provide food for adults and are especially important to poults as environment in which they can efficiently forage for insects. The annual home range of wild turkeys varies from 150 to 550 hectares (370 to 1,360 acres) (Brown 1980) and contains a mixture of these cover types.

How much woodland and grassland is optimal? The proportional distribution of vegetation cover types has been central to reassessing the habitat requirements of the wild turkey. Early research suggested that ideal habitats were composed of woodlands with grassy openings,



The nesting hen (look for the eye) is usually well concealed by low vegetation. *Photo by W. Healy, U.S. Forest Service.*

and quantitative estimates of 5 to 10 percent in grass are common (e.g., Hillestad and Speake 1970, Bailey 1973, Dellinger 1973, Donohoe and McKibben 1973, Holbrook 1973, Dickson et al. 1978).

Experiences in west Texas and the upper Midwest during the 1970s and 1980s cast new light. With the extension of rural electrification into west Texas and the development of concrete livestock watering ponds, turkeys colonized the region (Kothmann and Litton 1975). In the upper Midwest, studies in Minnesota began to show that extensive forest cover was not necessary for turkeys. Townships with as little as 15 percent forest cover were supporting viable populations (Hecklau et al. 1982). In Iowa, the potential of many counties was reevaluated several times as trap-and-transfer efforts succeeded in areas of increasingly limited forest cover. By 1980, Iowa had populations averaging 8 to 12 birds per square kilometer (21 to 31 per square mile) in areas where stands of timber more than 400 hectares (1,000 acres) are rare (Little 1980).

These findings do not seem to reflect recent adaptations by the species. In fact, a rereading of accounts by early explorers suggests that high densities of wild turkeys lived in the coastal plains of the South and in the tall-grass prairies of the Midwest. Common to these areas are trees and grass in plant communities influenced by fire. Both the coastal plains from Texas to Georgia and tall-grass prairie regions of Iowa, Missouri, Illinois, and Indiana were in constant transition from grassland to savanna to forest, depending on what the fires did. When fires burned frequently, grass predominated; when they burned less frequently, trees invaded the areas.

These are highly productive environments for turkeys, providing a rich diversity of food resources. Also in these environments, the species is easily exploited by man. Wild turkey populations were rapidly eliminated after the introduction of firearms. It is easy to understand why biologists more than a century later would not think open environments suitable habitat for the wild turkey.

Today, because of the wild turkey's protection from overexploitation, the full range of habitat tolerance is open to exploration. The wild turkey, once viewed as a wilderness species, adapts well to a wide diversity of environments. The next habitat factor tested will likely be density of human population. Reports of turkeys in sub-



Fairly dense, low vegetation is appropriate brood habitat. Young poults forage on the invertebrates and plant parts found here. *Photo by L. Williams.*

urban areas are increasing. Possibly turkeys will respond to suburban environments as did ring-necked pheasants, Canada geese, white-tailed deer, and raccoons, becoming abundant in some locales.

BREEDING AND NESTING HABITAT

What is ideal nest habitat for the wild turkey? The key elements have long eluded biologists. Wild turkeys are known to nest in areas as dissimilar as mature oak forests and alfalfa hayfields. Nests are frequently found at the base of trees and in logging slash, shrub cover, and herbaceous vegetation. But in the 1980s as a result of radiotelemetry studies, researchers began to recognize a pattern.

The characteristic common to habitat immediately surrounding the nest of the wild turkey is lateral cover. Lateral cover obscures horizontal vision. Many studies, from Alabama to Oregon, describe forest stands in which turkey nests were found in areas having an open overstory and well-developed understory. Turkeys often nest in small openings in the forest, or along forest roads and edges between forest and open field. Nests occur in power-line rights-of-way (ROWs) through forests, and in fields of herbaceous vegetation close to forests. All these nesting habitats are environments with well-developed vegetation 1 meter (1.1 yards) above the ground.

This pattern is consistent across the wild turkey's range. For example, in Alabama, 37 percent of nests were found in utility rights-of-way, even though such habitat was only 0.6 percent of the area. Wild turkeys nested in

ROWs only when average vegetation height exceeded 25 centimeters (10 inches). Overall, 73 percent of the nests in the study area occurred in habitats with well-developed herbaceous and shrub vegetation (Everett 1982).

In Minnesota, nest sites occurred in parklike forest areas with an average of 40 percent canopy closure, 0.9 woody stems per square meter (0.8 per square yard), and 20 to 30 percent cover by forbs, or in open fields near forest edges (Lazarus and Porter 1985).

In Oregon, nest habitat had high shrub density and visual obstruction at 0.5 meters (0.5 yards). Most nests were found in Douglas fir that had been selectively cut or thinned to less than 50 percent of the original stocking. Slash and shrubs provided lateral cover (Lutz and Crawford 1987b).

The occurrence of a well-developed overhead cover—a canopy layer at 0.5 to 3.0 meters (0.5 to 3.4 yards)—at the nest is a less-prominent pattern. Studies in Georgia (Hon et al. 1978), Oklahoma (Logan 1973), and New Mexico (Goerndt 1983) all report immediate overhead canopies of from 50 to 90 percent cover associated with many nests. Minnesota studies showed that 80 percent of successfully hatching nests were associated with overhead cover, but only 25 percent of the unsuccessful nests had overhead cover (Lazarus and Porter 1985). A tree or other guard object adjacent to the nest is widely reported, but this factor has not been evaluated quantitatively.

Another pattern that may be emerging is a preference for sites described as mesic (having moderate soil moisture). Minnesota and New Mexico studies have demonstrated that turkeys choose mesic slopes most frequently for nesting (Jones 1981, Goerndt 1983, Lazarus and Porter 1985), although they sometimes use xeric (dry) sites with good vegetation cover. Whether the mesic condition provides an important microclimate for the female and eggs, or is simply correlated with greater development of vegetation in the 0 to 1.0 meter (0 to 1.1 yards) stratum, needs examination.

Finally, Lazarus and Porter (1985) suggest that wild turkeys may select nest sites partly because of proximity to brood cover. The data show that females establishing nests early in the spring tend to place them in woodland areas distant from brood cover. But nests established later in the season are closer to brood cover (Figure 1).

Woodland sites provide denser lateral cover early in the spring. But as lateral cover develops with growth of herbaceous vegetation in the fields, females nesting later (or renesting) selected open-field sites. These open fields are subsequently used for rearing broods. Theoretically, broods hatching closer to suitable brood-rearing habitat would have higher probabilities of survival (Figure 2). This hypothesis has yet to be tested elsewhere.

BROOD-REARING HABITAT

During the first eight weeks after the hatch, there are 3 essential ingredients for brood habitat.

First, poults need an environment that produces insects and in which they can efficiently forage.

Second, they need habitat that permits frequent foraging throughout the day.

Third, poults need an area that provides enough cover to hide them but allows the adult female unobstructed vision for protection from predation.

All these ingredients must occur within a relatively small area. Weekly home ranges average less than 30 hectares (75 acres), and total summer home ranges are about 100 hectares (250 acres) (Speake et al. 1975, Porter 1980).

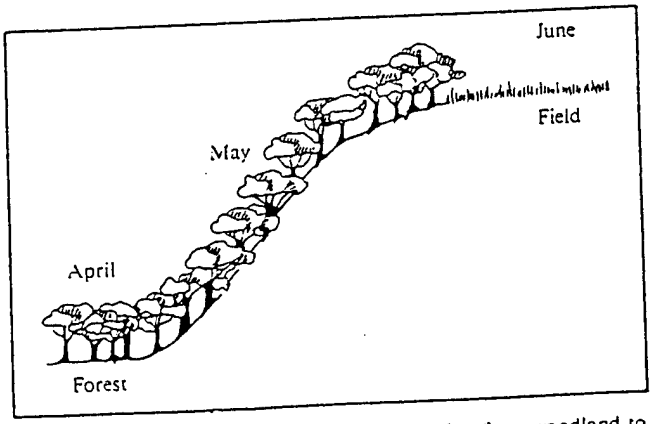


Figure 1. Turkeys in Minnesota show a progression from woodland to open field for nest sites, with early nests occurring in woodlands and late nests or renests occurring in open field (Lazarus and Porter 1985).

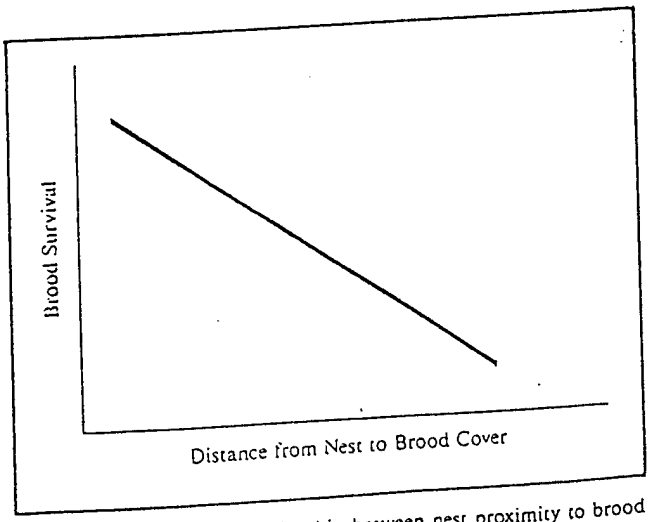


Figure 2. Hypothesized relationship between nest proximity to brood cover and poult survival.





Photo by E. Kurzejeski, Missouri Department of Conservation.

Grassy openings are important for year-round habitat suitability. Insects and other foods are abundant there, and these openings are used for strutting areas.

Patterns in the wild turkey's brood habitat are the most consistent of any habitat relationship. The key to brood habitat is herbaceous vegetation interspersed with forest. Here are some examples:

Ideal turkey brood habitat in Pennsylvania consists of forested sites with grassy understories, or savannas adjacent to mature forest (Hayden 1979a).

Adult females with broods using old fields in Alabama have the highest poult survival rate (Metzler and Speake 1985).

In Texas, broods use riparian woodlands and savannas (Baker 1979).

Broods less than 4 weeks old in South Dakota use south-facing woodlands with a 50 percent canopy closure and grass- or forb-dominated understory (McCabe and Flake 1985).

Brood habitat in New Mexico is described as grassy openings in mixed conifer forests, meadows, and aspen glens (Schemnitz et al. 1979).

In Minnesota, broods spend the first week in forest vegetation and make increasing use of fields beginning the second week. Peak use occurs during the seventh week, when broods spend as much as 60 percent of the daytime in open fields (Porter 1980). Ideal habitat in Minnesota is characterized by a field-to-forest ratio of 4 to 1.

Herbaceous vegetation is key because it provides an ideal foraging environment for young poults. Hurst and Poe (1985) estimate that turkey poults require 9 to 12 grams (0.3 to 0.4 ounces) of spiders and insects each day to meet protein requirements for growth. Insect abun-



Summer brood roost. Wild turkeys prefer certain tree and stand characteristics for roosting. *Photo by L. Williams.*

dance is greater in open fields than in forest habitats, particularly when the fields are not mowed (Hurst 1978, Hurst and Owen 1980). Foraging efficiency of poults is highest in areas with standing crops of grass cover of 600 to 3,000 kilograms per hectare (530 to 2,700 pounds per acre) and is lower in all forest types except those of the very best sites (Healy 1978, 1981). Heavier vegetation supports more insects, but poults have difficulty moving through it.

The height of vegetation is another key feature. Porter (1980) observed extensive use of alfalfa fields by broods and hypothesized that these fields provided excellent protection from predators. The vegetation is 30 to 70 centimeters (12 to 28 inches) tall, allowing adult females to see predators at long distances and also allowing poults to hide. Exum (1985) and Songer (1987), working in different plant communities, reached the same conclusion: Vegetation height is one of the most important features.

Nevertheless, turkey broods are seldom found far from tree cover. Trees may be important for 2 reasons.

First, microclimate is critical to heat regulation in young poults. Healy and Nenno (1985) report that cold, wet conditions when poults are 12 to 15 days old are an important factor in poult deaths. At this age, the poults have consumed the energy reserves of the yolk sac and are becoming too large for the hen to efficiently brood. Trees provide shade from heat and shelter from rain.

Second, trees provide escape cover once poults can fly (10 to 12 days after hatching). Broods will venture away from trees, and I have observed adult females with poults more than 5 weeks old in hayfields farther than 300 meters (330 yards) from the nearest tree cover but adjacent to corn approximately 1.5 meters (5 feet) tall. Upon being disturbed, the broods immediately retreated into the corn. This example may serve to support the following basic hypothesis: Thermal and predator cover are all that are necessary.

The emerging pattern for brood habitat is that of a parklike environment. Investigations in Alabama, Georgia, West Virginia, Mississippi, Michigan, Minnesota, Texas, Arizona, Utah, and Oregon all describe brood habitat as consisting of complete ground cover of forbs and grasses with average heights of approximately 50 centimeters (20 inches), and 10 to 50 percent overhead or nearby tree cover. This pattern fits the description of a savanna and suggests a hypothesis: Savannas constitute the best habitat condition for broods.

Under natural conditions, most savannas are a product of fire. The value of fire in maintaining brood cover is receiving increasing attention. Highest mortality for turkeys occurs during early brood rearing, and any increase in insect abundance could lead to survival of more poults. The underlying relationship may be that increased insect abundance reduces the need to move about (which is energetically expensive) or promotes more rapid growth (larger poults are less prone to hypothermia), or both. Pattee (1977) demonstrated that an increase in available protein, phosphorus, and calcium can significantly increase the production and survival of young to late summer.

Fire promotes production of food resources. It increases the amount and vigor of seed-producing grasses and forbs. It does likewise for legumes important to adults and to young in late summer (Buckner and Landers 1979). Fire also increases total animal food available during the first 3 years after burning (Hurst 1978).

Fire can enhance the structural characteristics of vegetation. In the Southeast, for instance, succession in the understory of pine forests moves through a grass-and-herb stage to perennial herbs and shrubs and finally to trees. Prescribed burning in pine forest reduces mat-

forming perennial herbs and woody plants (Buckner and Landers 1979). This strategy can produce a vegetative environment that is optimal for poults because it allows easy movement and increases food resources.

Disturbances and variable habitat conditions are common throughout the range of the wild turkey. It's reasonable to hypothesize that the wild turkey is adapted to taking advantage of periodic, highly favorable reproductive conditions. Fires, like mild winters in the North and wet winters in the Southwest, provide conditions conducive to maximum reproduction. Such events are episodic and unpredictable.

Studies in environments as dissimilar as West Virginia, Texas, and Minnesota show that unfavorable conditions can adversely affect nesting success and poult survival without hurting adult survivorship (Beasom 1973, Porter et al. 1983, and Healy and Nenno 1985).

The wild turkey lives long (adults frequently survive more than 6 years) and has a high innate capacity for reproduction. When conditions are favorable, more than 90 percent of females nest, producing an average of 5 females per female in the population. When 40 percent of young survive to breeding age (higher rates are common in good years), the finite rate of growth is more than 2.0 (i.e., the breeding population more than doubles in a single year) (Pattee 1977, Porter 1978).

FALL AND WINTER HABITAT

Wild turkeys seek 2 key habitat ingredients for the fall and winter: food and roosting cover. During the fall, food is critical to continued growth of young and the building of fat deposits by young and adults. For most of the winter, at least in northern latitudes, growth is halted and turkeys are on a sustaining or declining energy supply. Food is critical. But, in many regions, protection from adverse weather is equally important.

Vegetation used by turkeys during fall and winter is highly varied. In southern latitudes where snow does not persist for weeks, hardwood stands containing a diversity of tree species—interspersed with softwoods and field edges—are important. Turkeys increase their use of forested cover during the fall and winter and decrease their use of open areas. This pattern is prevalent from Virginia to Texas (e.g., Speake et al. 1975, Kennamer et al. 1980a, Campo 1983, Holbrook 1984).

Mast (pine seeds, acorns, and other fruits) is the principal food during fall and winter. Habitat value increases with the proportion of mast-producing species in the forest and their degree of maturity. Forest types, ranked according to acorn yields (highest to lowest) in Virginia are mixed oak, oak-pine, cove hardwood, and mixed pine (Forsythe 1978). Green vegetation is also an important food, however (Kennamer et al. 1980b), so there's a need for forested areas to be interspersed with herbaceous growth.



Spring seeps provide foraging areas in northern habitat when snow covers the ground. *Photo by G. Eckert.*

In areas where snow exceeding 15 centimeters (6 inches) covers the ground for 2 to 16 weeks, the wild turkey needs additional habitat resources. In the mountainous environments of the Northeast and West, spring seeps are an important source of food (Healy 1981, Goerndt et al. 1985). The seeps provide invertebrates, mast, and green vegetation. Because such water does not



Excellent wild turkey habitat usually is well watered. *Photo by G. Smith.*



Photo by U.S. Forest Service.



Photo by J. Dickson, U.S. Forest Service.

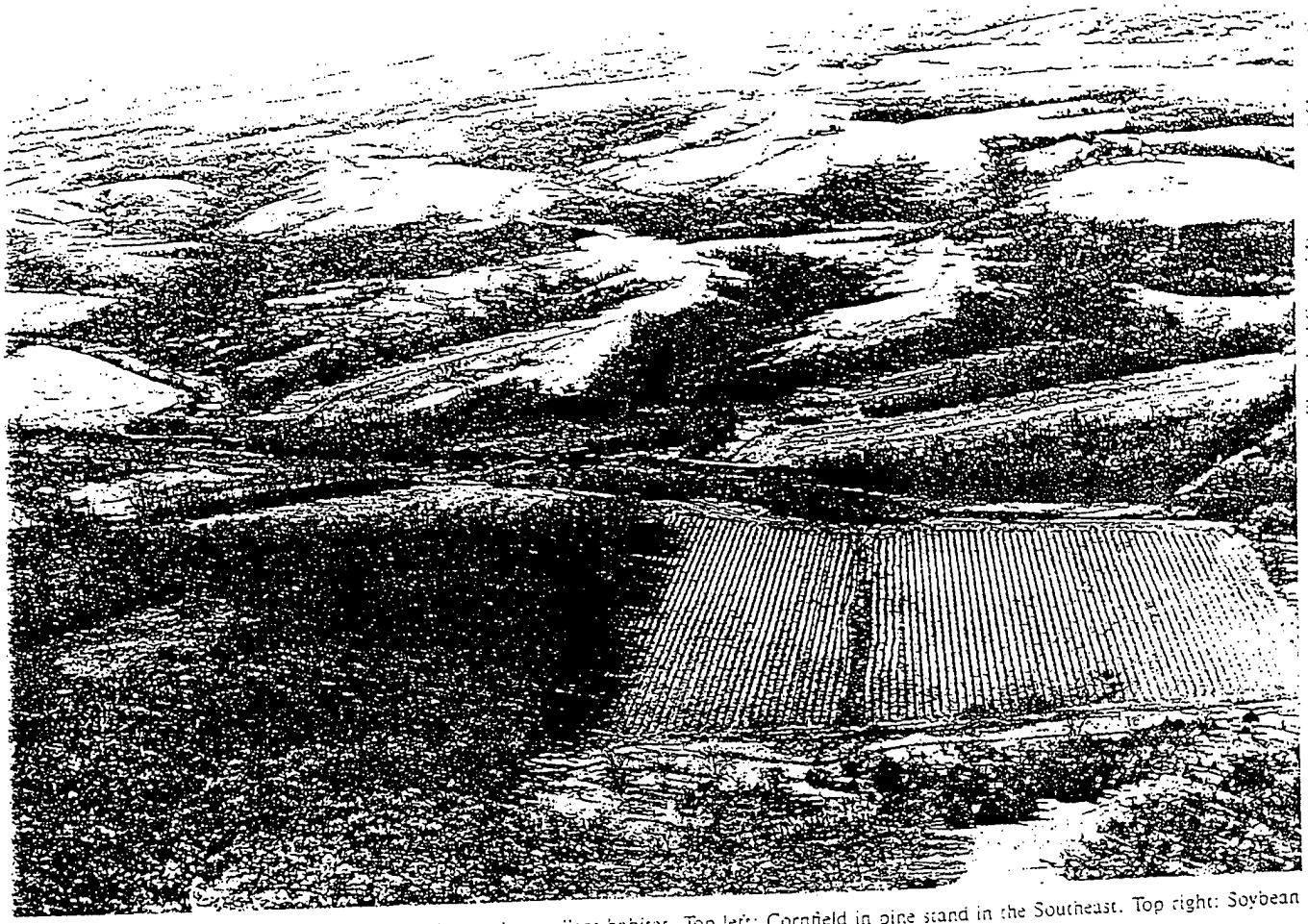


Photo by Missouri Department of Conservation.

Small agricultural crops interspersed with woodlots make excellent habitat. Top left: Cornfield in pine stand in the Southeast. Top right: Soybean stubble with adjacent riparian zone in Kansas. Above: Field-forest mixture in Missouri.

freeze, it provides a microenvironment that allows foraging throughout the winter. Optimal conditions occur on south-facing areas with less than 20 percent gradient and where seeps are spread out, covering more than 15 square meters (18 square yards).

Where agriculture is prominent, a mix of cropland and forest cover seems to be highly suitable habitat. In the North, turkeys make extensive use of corn (Porter et al. 1980, Crim 1981, Clark 1985, Kulowiec and Haufler 1985, Kurzejeski and Lewis 1985). Corn, compared with

acorns, is higher in protein, lower in fats, and similar in carbohydrates (Crim 1981). Turkeys can feed on corn while it is standing, when it's on the ground after picking, and when it's residual in manure spread from dairy-farm operations. My own observations suggest standing corn is superior because the structure of the rows provides protection from avian predators such as golden eagles.

In the South, chufa is an important resource. The plant produces tubers that are easily scratched out by turkeys, particularly when chufa is grown on sandy soils. Both in the North and South, optimal fall and winter conditions may be a 1 to 1 mix of forest cover and agricultural land (Little 1980).

Historically, turkey populations along the northern and southern edges of their range have fluctuated with food resources. Acorns and beechnuts constitute an irregular and unpredictable food resource. Studies in very diverse environments show that adverse food conditions can hurt not only winter survival but also reproduction (Beasom and Pattee 1980, Porter et al. 1980, 1983).

In Minnesota, deep snows restrict movements and prevent turkeys from exploiting widely dispersed food resources. Because corn is a much more reliable and concentrated food resource, agriculture in northern regions may be the foundation for these turkey populations.

In Texas, adequate rainfall is critical to vegetation growth that supplies nutrients (protein, phosphorus, and calcium) essential for reproduction (Pattee and Beasom 1979).

Experiments with free-ranging turkeys show that supplementing natural foods with crops and artificial feed can reduce winter deaths and can enhance reproduction. This knowledge has led to a series of management programs to offset the periodic severe winter. Fields of standing corn, shrub plantings, and spring-seep management seem to be far more effective than feeding stations (Porter et al. 1980, Crim 1981, Healy 1981, Clark 1985, Kulowiec and Haufler 1985, Kurzejeski and Lewis 1985).

The difficulty with feeding stations is that they tend to be supplied only in severe winters. Turkeys often fail to find these feeding stations. When they do, the feeding stations concentrate birds and this density increases risk of predation and spread of disease. The key is to provide consistent food resources (all winter, every winter), spread over relatively large areas (1 to 3 hectares, 2.5 to 7.5 acres).

The second characteristic critical to winter habitat is roosting cover. Roost habitat is necessary throughout the year. In general, characteristics of roost sites do not seem to be highly specific. Perhaps the best evidence to support this belief comes from the use of artificial structures (power poles and lines) in Texas (Kothmann and Litton 1975). The essential feature is a horizontal spreading structure 10 to 30 meters (30 to 100 feet) above the ground.

An additional feature, however, physiography, may be important to roost sites in regions where winter temperatures are frequently below freezing. Winter roosts tend to be in areas protected from prevailing winds. Reports from Pennsylvania, Minnesota, Arizona, New Mexico, and Colorado indicate that roosts tend to occur on northeasterly slopes (Hoffman 1968, Boeker and Scott 1969, Tzilkowski 1971, Porter 1978, Goerndt 1983). Turkeys roost most frequently on the upper third of the slope (Mackey 1972, Goerndt 1983, Porter unpublished data). This location in ravines and small river valleys may provide an advantage in maintaining body temperature. Such a site protects turkeys from prevailing winds and allows them to be above the cold-air drainage. Where conifers are available on these slopes, turkeys use them, further reducing the energy required to maintain body temperature.

SUMMARY

That the wild turkey is a highly adaptive species has become increasingly clear over the past 2 decades. Individual subspecies have adapted to regional environments, and the specific conditions that contribute to habitat suitability vary from region to region. Still, there are general patterns in the data that suggest fundamental habitat requirements common across the range of the species. These patterns reflect our best scientific evidence to date. An important direction for future research will be the close examination of these emerging patterns. A synthesis of our current knowledge of the wild turkey suggests 7 hypotheses that warrant examination.

1. The key to nesting habitat is lateral cover and cover types with well-developed herbaceous or woody vegetation at 0 to 1.0 meter (0 to 3 feet) above the ground.
2. Moisture conditions at mesic sites provide an important microclimatic characteristic for nests.
3. Close proximity to brood cover is an important criterion in selection of nest sites by female wild turkeys.
4. The keys to brood cover are food and thermal cover, and savannas are the best brood-rearing environment.
5. Ideal brood-raising conditions are episodic and unpredictable. The wild turkey is an opportunistic breeder, adapted to widely fluctuating environmental conditions.

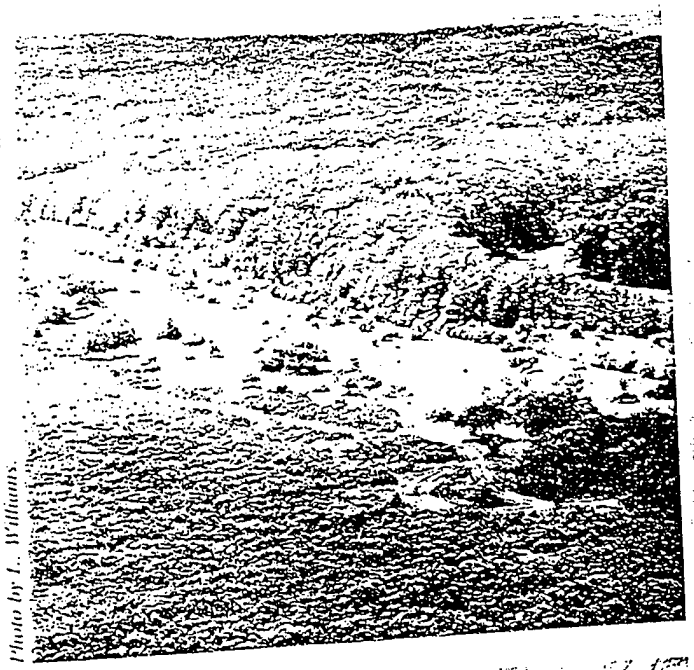


Photo by L. Williams.

Photo by G. Wurz, Pennsylvania Game Commission.





Photo by R. Williams, USDA Soil Conservation Service.



Photo by J. McConnell, USDA Soil Conservation Service.



Photo by J. Dickson, U.S. Forest Service.



Photo by J. Dickson, U.S. Forest Service.

Many different vegetation types make appropriate wild turkey habitat. Opposite page, clockwise from top left: Florida turkey cypress-oak scrub habitat; Eastern wild turkey oak habitat in Pennsylvania; Eastern wild turkey mature pine habitat in the southern Coastal Plains; Eastern wild turkey bottomland hardwood habitat; clockwise from above: Rio Grande turkey oak-juniper savanna habitat in the Rolling Plains of Texas; Merriam's turkey ponderosa pine habitat in the Black Hills, South Dakota; Gould's turkey oak-savanna habitat in Chihuahua, Mexico.

6. Roost trees on northeast-facing slopes and that allow turkeys to roost above cold-air drainage are important in regions of cold winter weather.
7. This species is not restricted to wilderness environments, and even suburban environments provide suitable habitat.

Finally, the hypothesis that the wild turkey has evolved in a widely fluctuating environmental condition has important implications to habitat management. In assessing habitat suitability, biologists tend to focus on deficiencies. However, a critical characteristic may not be consistently deficient. But when the deficiency occurs, the result may be such a decline in turkey abundance that the population cannot recover in a single normal breeding season. Prudent management may require annual effort and investment for conditions that occur only once or twice a decade. Good examples of this strategy are the technique of leaving corn standing through the winter as an alternative during years of poor mast production, the development of shrub planting, and spring-seep management.



Photo by J. Dickson, U.S. Forest Service.

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HOW CAN WE REVERSE THE NORTHERN BOBWHITE POPULATION DECLINE?

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Northern bobwhite (*Colinus virginianus*) populations have been declining at an alarming rate during the past 3 decades. Every broad-scale population index of bobwhites indicates a significant downward trend. Trends from Christmas Bird Count (CBC) data (Fig. 1, Table 1) and Breeding Bird Survey (BBS) data (Droege and Sauer 1990) indicate that bobwhite populations have undergone significant declines in 77% of the states within their geographic range. Especially troubling is the fact that the most precipitous declines in bobwhite populations have occurred in the southern region of the United States (Fig. 1B, Table 1). The slope from the regression analysis of the southeastern region CBC data (Fig. 1B) is steeper than the slope from the midwest and northern region data pooled ($P < 0.05$, 2-sample F-test; Fig. 1C). This is quite unexpected because the southern U.S. is the center of the bobwhite's geographic range (Rosene 1969, Gutiérrez et al. 1983) and has historically been associated with good quail habitat management and abundant quail populations.

If the current population trend continues, we are likely to lose bobwhite hunting opportunities across the majority of this quail's geographic range by the year 2000. Projections using regression analyses of data from Fig. 1 indicate that the CBC index (number of quail detected per hour of observer effort) for the bobwhite will effectively be 0 by the year 2005. The irony of this projection is nearly unfathomable because effective habitat management techniques for bobwhites have been known for over half a century (Stoddard 1931). Nevertheless, until a broad-scale, well-coordinated effort in education, management, and research is made by the agriculture, forestry, and wildlife communities, bobwhite populations most likely will continue to decline and the tradition of hunting wild bobwhite coveys will largely be a thing of the past. Therefore, my purpose in this paper is to outline a research and management manifesto for the northern bobwhite in the 1990's. My objectives are to (1) describe the probable causes for the northern bobwhite population decline, (2) outline the research agenda that will be required to solve northern bobwhite habitat management problems, and (3) describe some strategies that extension services and private interest groups can use to educate the public about bobwhite habitat and population management techniques.

WHY THE DECLINE?

There are several probable reasons why the bobwhite is declining over a broad portion of its geographic range. Clean-farming practices and silvicultural systems that maximize basal area are 2 of the most likely causes of habitat loss and subsequent decline in bobwhite populations. Since the end of World War II, farming practices have been completely revolutionized (O'Connor and Shrubb 1986). Nearly all agricultural methods have been mechanized, and chemical control of pests (both arthropod and plant) is now the rule rather than the exception. Field sizes have been increased by an order of magnitude to accommodate the new equipment and methods (O'Connor and Shrubb 1986). In the southern U.S., sociological events such as the collapse of the tenant farming system and the national trend toward a service-based economy (Beale 1982, Bradshaw and Blakely 1982, Henry et al. 1986, Winter 1988) have eliminated tens of thousands of small farms that once provided ideal bobwhite habitat. For example, in Mississippi, the number

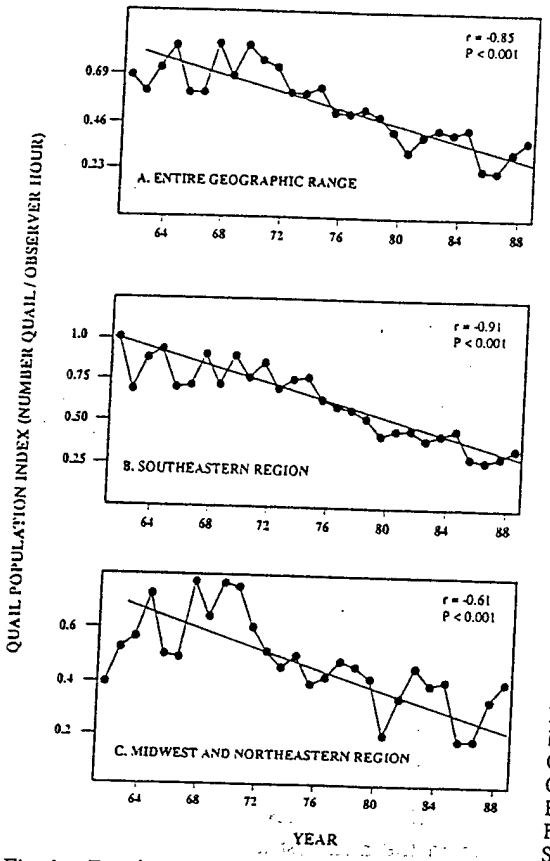


Fig. 1. Trends of northern bobwhite populations in the United States, 1961–1988, based on Christmas Bird Count data published in *American Birds*. Statistics based on simple linear regression analyses of standardized counts (numbers of quail detected divided by person-hours of observer effort) using year as the predictor variable. A. Entire geographic range in the United States. B. Southeastern region of the geographic range (AL, AR, DE, FL, GA, KY, LA, MD, MS, MO, NC, SC, TN, TX, VA, WV). C. Midwest and northeastern region of the geographic range (CO, CT, IL, IN, IA, KS, MA, MI, NE, NJ, NY, OH, OK, PA, RI).

Table 1. Statewide trends of northern bobwhite populations in the United States, 1961–1988, based on Christmas Bird Count data published in *American Birds*. Statistics based on simple linear regression analyses of standardized counts (numbers of quail detected divided by person-hours of observer effort) and year.

State	r	b[a]	P[b]
Alabama	−0.45	−0.012	0.010
Arkansas	−0.46	−0.010	0.010
Colorado	−0.19	−0.005	0.330
Connecticut	−0.53	−0.001	0.003
Delaware	−0.56	−0.020	0.002
Florida	−0.89	−0.024	<0.001
Georgia	−0.87	−0.044	<0.001
Illinois	−0.59	−0.022	<0.001
Indiana	−0.58	−0.022	0.001
Iowa	−0.03	−0.001	0.870
Kansas	−0.21	−0.021	0.290
Kentucky	−0.45	−0.011	0.010
Louisiana	−0.60	−0.016	<0.001
Maryland	−0.86	−0.050	<0.001
Massachusetts	−0.54	−0.021	0.002
Michigan	−0.73	−0.011	<0.001
Mississippi	−0.75	−0.016	<0.001
Missouri	−0.15	−0.007	0.420
Nebraska	0.03	0.001	0.850
New Jersey	−0.77	−0.013	<0.001
New York	−0.52	−0.006	0.001
North Carolina	−0.86	−0.034	<0.001
Ohio	−0.85	−0.029	<0.001
Oklahoma	−0.16	−0.011	0.420
Pennsylvania	−0.83	−0.013	<0.001
Rhode Island	−0.71	−0.016	<0.001
South Carolina	−0.77	−0.044	<0.001
Tennessee	−0.46	−0.009	0.010
Texas	0.03	0.001	0.870
Virginia	−0.89	−0.041	<0.001
West Virginia	−0.59	−0.036	0.001

[a] Slope of the line fitted by simple linear least-squares regression.
[b] Probability that correlation coefficient (*r*) is different from 0.

of farms decreased from 291,092 in 1942 to 42,415 in 1982. Concomitantly, farm size in Mississippi increased from 22 ha in 1942 to 118 ha in 1982 (Mississippi State Board of Development 1944, Bouchillion 1989). These broad-scale changes in land use have eliminated hundreds of thousands of kilometers of weedy fence rows and millions of ha of small fields that once provided prime nesting and brood-rearing habitat for the bobwhite across its geographic range (Klimstra 1982).

Many marginal areas in the southern U.S. that once were farmed for crops have been abandoned for agriculture or converted to pine plantations. In abandoned locations, 5–10 years of undisturbed plant succession renders the habitat unsuitable for quail (Stoddard 1931, Rosene 1969). In pine plantations, the silvicultural systems used in these areas typically provide little in the way of adequate bobwhite habitat. After tree harvest, quail invade the

clear-cuttings for 2–5 years, but then are subsequently eliminated from these areas when the tree canopy closes. Canopy closure shields the ground from sunlight, and key quail food plants are no longer produced. High basal area and dense stocking rates of trees are maintained throughout the rotation so that wood and fiber production can be maximized. Unfortunately, these practices serve to minimize quail production in wildland habitats (Rosene 1969).

Compared to the past, controlled burning today plays a greatly-reduced role in the management schemes of both agriculture and forestry. Controlled burning is one of the most effective and cost-efficient management tools for enhancing the quality of bobwhite habitat (Stoddard 1931, Rosene 1969, Landers and Mueller 1989). Burning stimulates the growth of important bobwhite food plants. Burned areas provide a significantly greater biomass of available insects for broods than unburned areas (Hurst 1972). For burning to be used effectively, however, areas must be burned every 1–2 years. The burns must leave a patchwork mosaic of unburned areas within the block that is burned so that nesting and escape cover will be available. A burn that eliminates the nesting and escape cover components of the habitat actually does more harm than good (Stoddard 1931, Rosene 1969). Thus, incorrect burning can be as bad as not burning at all. Although there is some evidence that growing-season burns can enhance quail habitat in certain situations, extensive, overly-hot burns at the wrong time of the year can severely depress the suitability of the habitat for wild bobwhites (Stoddard 1931). Today, many areas (especially federal public lands) are burned every 5–7 years, if at all. This has little beneficial effect on quail populations, especially when it is done in dense pine stands where canopy closure approaches 100%. This kind of burning results in a sterile understory with a ground cover of pine needles and mineral soil that provides nothing in the way of bobwhite habitat requirements. Furthermore, it is becoming increasingly difficult to obtain the necessary permits required for prescribed burning. Agencies are reluctant to issue permits even under ideal conditions because of complaints from the public about smoke (Maynard 1990).

Regardless of the particular agriculture or forestry practices responsible for the bobwhite decline, all available evidence points to 1 main reason why we have far fewer bobwhites today than we did 30 years ago. Current land use practices do not provide habitat for the bobwhite, whereas bobwhite habitat was a by-product of land use 30 years ago (Klimstra 1982). Nevertheless, many people commonly consider coyotes (*Canis latrans*) and fire ants (*Solenopsis invicta*) the primary causes of low northern bobwhite numbers. Excellent experimental work by Johnson (1961) established that fire ants have no influence on quail production. A field study of 1,072 bobwhite nests by Simpson (1976) implicated fire ants in the loss of only 1 nest. At Circle Bar Ranch, in Marion County, Mississippi, bobwhite density is 2 birds per ha, and the density of active fire ant mounds is 200 per ha (Brennan, unpubl. data.). Still, the fire ant myth persists, and must be eliminated through education.

Another persistent belief is that the coyote is responsible for the bobwhite population decline. In the southern U.S., the coyote has undergone a range expansion and now occupies many regions that were once the domain of the nearly extinct red wolf (*Canis rufus*). However, there is no conclusive evidence that coyotes are a significant bobwhite predator. In the western U.S., where coyotes are common, Leopold (1977:142) listed them as an unimportant predator on California quail (*Callipepla californica*). Evidence also shows that bobwhites compose only a minor (1–2%) part of the coyote's diet (Korschgen 1957, Gipson 1974, Hoerath 1990). There is no doubt that predation, in general, is an important ecological process that affects all quail populations. The widespread deterioration of bobwhite

habitat may have resulted in increased mortality from predation due to lack of escape cover, lack of suitable brood habitat, or both. Still, people must understand that quail have evolved in the presence of a wide variety of predators. They need to realize that when the habitat needs of a quail population are met, the population can be productive enough to sustain losses to predation and still withstand hunting if managed correctly (Stoddard 1931, Rosene 1969). Bobwhite populations typically endure tremendous annual losses, in many cases up to 80% per year (Stoddard 1931, Rosene 1969, Dimmick 1975, Klimstra and Roseberry 1975, Roseberry and Klimstra 1984). Thus, although the role predators have played in the bobwhite decline is unknown, the decline still apparently results from a lack of suitable habitat, which, in turn, is a direct function of land use (Klimstra 1982).

MANIFESTO FOR A COORDINATED RESEARCH AND MANAGEMENT AGENDA

Effective habitat management programs must be conducted on a broad geographic scale if the bobwhite decline is to be reversed. When the correct habitat components are developed and maintained, bobwhite populations usually respond favorably. I have seen a parcel of private land in southern Mississippi that supported <1 quail per 50 ha 5 years ago. Today, this same area, with good quail habitat management, supports a population of approximately 2 bobwhites per ha (Brennan, unpubl. data). Nevertheless, tales of frustration abound from people who have tried the traditional quail habitat management techniques of Stoddard (1931) and Rosene (1969) and have met with failure. We need to reassess some of the management formulae that have been historically used as a "prescription for plenty" (Rosene 1969:224). The contemporary world of agriculture and forestry is vastly different from the one that existed when Stoddard did his seminal work. However, by no means should we abandon the classic works by Stoddard and Rosene and start over. In fact, a large part of the problem is that too few people have read and are familiar with the concepts outlined by Stoddard (1931) and Rosene (1969), especially with respect to burning and disking as management tools for the bobwhite. We must, however, conduct research to reassess the traditional bobwhite habitat management techniques and determine the methods that are best suited for bobwhite management in the modern world. For example, chemical control of agricultural pests did not exist when Stoddard worked on bobwhites during the late 1920's. The silvicultural systems commonly in use today were only in their infancy prior to World War II. These 2 facts have a significant bearing on the contemporary management opportunities for the bobwhite.

Pesticides

While it has long been established that agricultural chemicals have a deleterious effect on bobwhite populations (Rosene 1959, Rosene et al. 1961), there is still a pressing need for research on the interactions between agricultural chemicals and the productivity of bobwhite populations. Agricultural chemicals are a fact of life. However, we need to understand how to minimize the direct and indirect effects of pesticides on quail populations.

Although the organophosphate pesticides that are in wide use today do not persist and accumulate like organochlorine compounds, many organophosphate compounds have highly toxic, direct effects on birds for short periods after application due to inhibition of acetylcholinesterase enzyme activity in brain tissue (Ludke et al. 1975, Hudson et al. 1984). Although there are no data that directly link use of organophosphate compounds with the decline in bobwhite populations, organophosphates have been implicated as a possible bobwhite mortality factor (White et al. 1990) and

as a factor in several die-offs of sage grouse (*Centrocercus urophasianus*; Blus et al. 1989). Thus, because of the direct toxic effects that organophosphate pesticides can have on game birds, it is essential to establish the size and extent of pesticide fallout bands on the perimeter of agricultural fields. For example, if a fallout band ranges in size from 0.5 to 1 km around the perimeter of a cotton (*Gossypium* sp.) field, then bobwhite habitat management efforts within these areas will be a waste of time and money, and will need to be conducted outside of this sphere of contamination.

The indirect effects of pesticides on quail populations are poorly understood, at best. Agricultural chemicals also indirectly affect game bird populations by suppressing arthropod populations that are key food resources. Potts (1986) established that the indirect effects of using herbicides to control weeds in cereal fields was a key factor limiting brood production of the gray partridge (*Perdix perdix*). Weeds provide food and feeding substrates for phytophagous insects that are essential to the growth and development of partridge chicks. Production of partridge broods was increased significantly, with a crop yield loss of only 4%, when a 6-m margin on the field edge was kept free of herbicides (Potts 1986, Hudson and Rands 1988).

Releases of Pen-raised Quail

Although it is well-established that releases of pen-raised quail do not serve to increase populations (see Roseberry et al. 1987, and references therein), we know little about ecological interactions between released pen-raised and wild bobwhites. This was painfully evident at a recent workshop on this topic sponsored by Tall Timbers Research Station and the Southeast Cooperative Wildlife Disease Study (16–17 Aug 1990; Landers et al. 1991). We must determine if there is a link between releases of pen-raised quail and outbreaks of disease such as avian pox in wild bobwhite populations. This is a difficult hypothesis to test because it is hard to determine whether an outbreak of pox, or other disease, in a wild population resulted from contact with released quail, or was a natural epizootic. Still, technological tools are available to test the hypothesis that pen-raised quail vector pox to wild bobwhites. DNA "finger-prints" of pox virus, or other pathogens, in released and wild birds can be compared to determine if pen-raised quail are the source of the pox virus in wild populations within a release area. This kind of investigation should be particularly fruitful in places where population declines have occurred in the absence of major changes in land use, such as Fort Bragg, North Carolina (P. Doerr, North Carolina State Univ., Durham, pers. commun.).

We also need to determine the effects on general habitat use and movement patterns of wild bobwhites when pen-raised quail are released. Releasing several thousand pen-raised quail in the midst of a wild bobwhite population can possibly modify daily movements, habitat use patterns, and the social structure of the wild bobwhite population. It would be very informative to set up controlled, replicated experiments using radio-tagged wild quail, and to examine their movements and habitat use patterns before and after pen-raised quail are released.

Another aspect of the pen-raised quail issue is predation. Many people have speculated that releasing large numbers of pen-raised bobwhites serves to attract predators to an area, causing both a functional and numerical response (Solomon 1949, Holling 1959, Taylor 1984), with possible carryover effects on wild bobwhites. Data that support or refute this notion unfortunately do not exist. Establishing a raptor and mammalian predator monitoring program on areas with and without released quail would be a major contribution toward providing information on the dynamics of predation on released groups of pen-raised bobwhites.

In my opinion, however, one of the most pernicious problems of the pen-raised quail issue centers on economics and education. Economics comes into play because every dollar spent on producing pen-raised quail for release is a dollar that won't be put toward habitat management for wild bobwhite populations. The education issue is significant because releasing pen-raised bobwhites reinforces a quick fix, instant gratification mentality. Releasing pen-raised quail allows people to develop and reinforce an attitude that precludes the patient, methodical, year-round work required to manage habitat for wild quail.

There is also a double standard in policies that govern the releases of pen-raised game birds. In Mississippi, for example, translocation is commonly used as a management strategy for population restoration of wild turkeys (*Meleagris gallopavo*) but not bobwhites. Release of pen-raised turkeys is not allowed in many states because a link in disease transfer was established between wild and pen-raised turkeys (Schorger 1966). However, shooting preserves that use released pen-raised bobwhites exist in every state within the quail's geographic range.

The disease link between pen-raised and wild turkeys, coupled with knowledge of the heritability of wildness in turkeys (Leopold 1944) formed the basis of a widespread policy that effectively eliminated releases of pen-raised turkeys. Translocation of wild turkeys into areas of suitable habitat then became the standard management policy for turkey population restoration. With bobwhites, however, most agencies strictly forbid trapping and translocation of wild quail as a population management technique. The rationale here is that if habitat is managed correctly, wild bobwhites will be recruited into this new habitat from surrounding areas, much like a source-sink phenomenon (Wiens and Rotenberry 1981). Furthermore, because home ranges are small and dispersal distances are relatively short, the time and effort expended to trap and transfer wild quail generally benefits far fewer people than a similar effort with turkeys would. There are, however, many situations where people have attempted habitat management for several years, and still have had no response by bobwhites. These kinds of situations present an excellent opportunity to test the suitability of the habitat with translocated wild bobwhites. Without translocation as a management tool, landowners who have had no luck with habitat management are forced into the use of pen-raised birds as their only legal means of getting bobwhites on their property.

The Woodpecker Connection

The red-cockaded woodpecker (*Picoides borealis*) has been the center of a forest management controversy in the southeastern U.S. for the past 20 years. Many people resent the large amount of money spent on managing habitat for this nongame, endangered species. Yet, there is a distinct possibility that red-cockaded woodpecker habitat management has a positive impact on northern bobwhite populations. Anecdotal reports of red-cockaded woodpecker habitat management being "good for bobwhites" abound, but data on this topic are scarce. During the initial phase of planning my bobwhite research program, I placed 4 km of line transects in red-cockaded woodpecker colonies, and 4.5 km in similar-aged (≥50 yr), but "unmanaged" (i.e., the stands have not been burned or thinned for at least 10 years) pine (*Pinus* spp.) stands on the Noxubee National Wildlife Refuge in east-central Mississippi. After walking these transects 7 times over 9 months, it was clear that there were significantly more ($P < 0.05$, Wilcoxon sign test) bobwhites in the woodpecker colonies than in the similar-aged, but unmanaged, old-growth pine stands (Table 2). Many of the techniques used for managing red-cockaded woodpecker habitat (1–3 year burning frequency, elimination of the hardwood midstory, reduction of tree basal area) have been used in bobwhite

Table 2. Numbers of northern bobwhites detected on transects in mature (≥50 yr) pine stands at Noxubee National Wildlife Refuge, Noxubee, Oktibbeha, and Winston counties, Mississippi, July 1990–March 1991.

Stand type	Transect length surveyed (km)[a]	Number of quail/km[b]	Basal area[c]	
			$\bar{x}$	Range
Red-cockaded woodpecker colony	28.0	1.07	14.2	10.2–20.4
Unmanaged	31.5	0.30	24.4	20.4–30.7

[a] Seven replicates were used in each stand type. Individual replicate transect lengths were 4.0 km in colonies and 4.5 km in unmanaged stands.
[b] Number quail detected per km of transect significantly greater in colonies than in unmanaged stands ($P < 0.05$, Wilcoxon sign test).
[c] Basal area (m^2/ha) estimates significantly lower in colonies than in unmanaged stands ($P < 0.001$, Mann-Whitney *U*-test) based on 14 sample points per stand type.

habitat management for years (Stoddard 1931, Rosene 1969). This kind of comparative study needs to be replicated on larger scales and in different habitat types with different red-cockaded woodpecker habitat management regimes to assess the magnitude of the response of bobwhites to red-cockaded woodpecker habitat management. Dead woody material resulting from removal of the hardwood midstory may play an important role in providing escape cover and hence protection from predators during the nesting season. Conversely, disposal of slash "off site" may result in poor quality nesting habitat and low subsequent recruitment into the breeding population. Experimentation using paired comparisons between colonies and similar-aged, but unmanaged stands is the easiest and most efficient way to test such hypotheses, especially if quail population densities are estimated with line transect models (Brennan and Block 1986, Guthery 1988). If there is a general, positive response of bobwhite populations to red-cockaded woodpecker habitat management, then the public relations potential of this phenomenon could be enormous. Linking red-cockaded woodpecker and bobwhite habitat management in wildland systems may prove to be an especially symbiotic relationship, that, if publicized correctly, could go a long way toward selling red-cockaded woodpecker (and other endangered species) management to the public. Hunting bobwhites in red-cockaded woodpecker stands apparently does not disrupt colonies or clans. At Noxubee National Wildlife Refuge, there is no evidence of red-cockaded woodpecker colony abandonment as a result of quail hunting (D. Richardson, U.S. Fish and Wildlife Service, Brooksville, Miss., pers. commun.). The apparent link between red-cockaded woodpecker and bobwhite habitat management in mature pine forest systems can, and should, be used to demonstrate the value of adaptive, integrated habitat management for terrestrial vertebrates in forest ecosystems.

Assessing Effects of Hunting

We have, at best, only a poor understanding of how hunting influences bobwhite populations, especially on public lands where pressure and demand are intense (Vance and Ellis 1972). Conventional wisdom, and many published studies, imply that hunting mortality in bobwhites is compensatory rather than additive (Errington and Hamerstrom 1935, Baumgartner 1944, Leopold 1945, Parmalee 1953, Marsden and Baskett 1958). However, it must be pointed out that the bobwhite populations studied by these people were either stable or increasing when data were collected. Furthermore, these studies were conducted in situations when agricultural and forestry land use practices were far different from those currently in use. Today, the situation of different land use practices and declining bobwhite populations indicates a need to reassess the role of

hunting on bobwhite populations. The bobwhite population decline may be because recruitment of juveniles into the breeding population is insufficient to offset adult mortality. Thus, mortality from hunting may be additive rather than compensatory. This kind of situation is likely on public lands where quail hunting pressure is often intense (Vance and Ellis 1972). Special efforts need to be made to regulate quail hunting access and harvest on public lands. Few public land management agencies assess fall population levels of bobwhites and use this information to regulate bag limits. Clearly, there is a pressing need to conduct experiments that would simulate open and closed hunting seasons on bobwhites. The experimental design (sequence of paired comparisons of open and closed seasons) outlined by Anderson et al. (1987) for testing the additive versus compensatory hypothesis with waterfowl is particularly appropriate for testing this hypothesis using bobwhite populations. Other approaches might involve keeping particular areas closed for consecutive years and comparing population parameters (age and sex ratios, general productivity, recruitment into breeding populations) between hunted and unhunted areas.

Need for Experimentation

In general, most wildlife professionals rarely conduct experiments that provide a basis for scientific management (Romesburg 1981, Macnab 1983). Granted, it is difficult or impossible to conduct rigorous experiments on the habitat relationships of wide-ranging raptors or large carnivorous mammals. Nevertheless, because of its general habitat ecology and behavior, the bobwhite lends itself to experimentation that can be used as a scientific basis for management. Bobwhite home ranges are typically small (<10 ha), and day-to-day movements are seldom >1 km (Roseberry and Klimstra 1984). Thus, if designed in an experimental context, different configurations of habitat components could be evaluated with respect to their influence on bobwhite population productivity.

Extension and Education

I perceive a critical need to educate the public about habitat management techniques to enhance bobwhite populations. Far too many people continue to blame "those coyotes and hawks" as the primary reasons why bobwhite numbers have dwindled. The concept that habitat structure plays a key role in predation has not been effectively communicated to the public. Despite this, private interest groups, such as Quail Unlimited, have tremendous potential to play a key role in reversing the bobwhite decline. Probably the most promising development on this front involves demonstration areas. Rather than spread limited resources for equipment, labor, seed, and fertilizer thinly across a broad area such as an entire county, a better strategy would be to acquire several hundred to ≥1,000 ha and manage the area for quail. People could align management actions with the seasonal habitat needs of the bobwhite, and monitor the progress of the population response by doing call counts during spring, brood counts during summer, and covey counts during early fall. Funds could be raised by selling chances for hunts on the demonstration area. Of course, harvest would need to be tailored to the abundance of bobwhites during a particular year.

The value of a demonstration area lies in the fact that it provides a concrete example of how habitat should be managed for bobwhites. People who participate in managing and monitoring the demonstration area should subsequently be inclined to use these techniques on their own property. Furthermore, I believe that when a group manages a demonstration area cooperatively, the benefits from this type of activity will far outweigh simple distribution

of seed and fertilizer for food plots, especially when lack of food may not even be a factor limiting bobwhite populations.

Special interest groups, such as Quail Unlimited, have a tremendous opportunity and obligation to educate the public about quail management. Good things for quail can happen when private, special interest groups work cooperatively with researchers, biologists, and extension wildlife specialists.

In the land-grant university system, extension is the key to getting information from the researcher to the public. Continuing education programs are essential for keeping agency personnel and biologists abreast of research developments. Private interest groups can provide assistance in reaching a target group who should be interested in attending a 1-day short-course that outlines specific management techniques and reports on progress from ongoing research. Providing short-courses in management and research in different parts of a state is essential for informing the public about bobwhite research and management.

Along with extension, university wildlife departments, and forestry departments with wildlife programs, should provide coursework and expertise to educate resource managers about the management techniques for enhancing bobwhite populations. Very few college-level wildlife programs offer an upper division course in the management and population ecology of upland game birds. Adding such a course, if one is not already part of the curriculum, should be a priority when curricula are evaluated.

Conservation Reserve Program: A Lost Opportunity?

The Conservation Reserve Program (CRP) has a tremendous potential to benefit bobwhite populations. Unfortunately, this potential is far from being realized in many places because administrators often require landowners to mow fields enrolled in the CRP during June and July, the peak of the bobwhite nesting season (Hays and Farmer 1990). Many bobwhite nests and broods are destroyed by midsummer mowing and cutting for hay (Stoddard 1931). Enhancing wildlife habitat has been a major selling point of the CRP legislation, yet, the basic fundamental relationship between summer mowing and the destruction of nests and broods is often not considered because administrators are either not aware, or do not care about the impact midsummer mowing has on ground-nesting birds. Despite positive reports from Missouri about bobwhite response to the early successional (1–5 yr) period of habitat change after fields are enrolled in CRP (Burger et al. 1990, Howell 1991), widespread use of tall fescue (*Festuca arundinacea* cv. K-31) for permanent cover plantings, and lack of flexibility for allowing landowners to use strip-disking as a quail habitat enhancement technique, continue to limit the potential of the CRP for bobwhites. Furthermore, in the southeastern U.S., conversion of fallow cropland to extensive, densely-stocked pine plantations has the potential to further decimate bobwhite populations on a broad geographic scale (Stauffer et al. 1990).

Some aspects of the CRP, such as reduced use of pesticides, have the potential to benefit bobwhite populations. Thus, we have an unprecedented opportunity to manage bobwhite habitat over broad areas while the confounding effects of agricultural chemicals are minimized. However, periodic disturbances, such as fire and disking, are required to maintain mosaics of small (2–10 ha) early successional (1–5 yr) patches of vegetation that bobwhites require (Landers and Mueller 1989). Fire and strip-disking employed judiciously as bobwhite habitat management techniques should be used in the CRP context, and are far superior to mowing as tools for enhancing bobwhite habitat. Strip-disking can be applied along contours and terraces, or used as fire breaks on relatively small proportions (10–25% annually) of fields. This would maintain the fields in her-

baceous cover, enhance the habitat for bobwhites, and meet CRP goals of holding top soil. Administrators in the county offices that oversee CRP contracts need to consider the northern bobwhite management opportunities that can be coordinated with this program, and allow landowners who want to enhance habitat for quail the flexibility to tailor specific management techniques to individual situations.

What Does the Future Hold?

Clearly, the fate of the northern bobwhite hangs in the balance of how we farm our land and manage our forests. Emerging trends in both agriculture and forestry offer opportunities for enhancing quail habitat over broad areas. A strategic North American Quail Management Plan is being developed and will be published in the proceedings of the 3rd National Quail Symposium, to be held during July 1992. This plan will serve to set priorities and coordinate quail research and management by federal and state resource management agencies, and private interest groups. However, whether the agriculture and forestry communities will embrace quail habitat management in the context of low-input, sustainable agriculture, or multiple use forest management and stewardship remains to be seen. Unless wildlife professionals and the general public make sound and effective quail management a priority within the agricultural and forestry arenas, the northern bobwhite will likely join company with other North American galliforms such as the masked bobwhite (*C. v. ridgwayi*) and lesser prairie chicken (*Tympanuchus pallidicinctus*) that have been driven to the brink of extinction by changing land use patterns.

SUMMARY

Northern bobwhite populations have undergone a severe decline during the past 3 decades. The decline is apparently related to changes in land use that have eliminated large areas of bobwhite habitat. Because the bobwhite is no longer a by-product of land-use practices in agriculture and forestry, broad-scale management programs will be required to maintain huntable populations. Although the bobwhite is one of the most studied game birds in the world (there are nearly 2,800 titles cited by Scott [1985]), there are still fundamental questions that need to be addressed with respect to pesticides, predators, releases of pen-raised quail, the relationship with habitat management of red-cockaded woodpecker colonies, and the effects of hunting. Controlled experimentation, usually in the form of paired comparisons, can be used to great advantage for evaluating all of the above questions.

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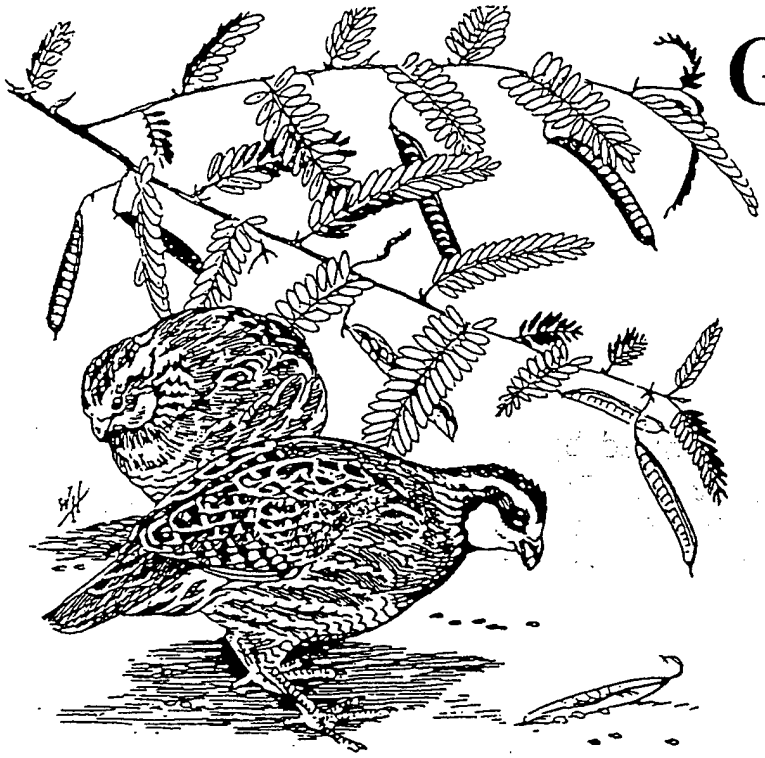
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PROCEEDINGS

TALL TIMBERS GAME BIRD SEMINAR 1995



TALL TIMBERS RESEARCH STATION

TALLAHASSEE, FLORIDA

WHY SHOOTING PLANTATIONS SHOULD CONSIDER SOME USE OF LIGHTNING SEASON FIRE

James A. Stevenson, Department of Environmental Protection, 3900 Commonwealth Blvd., Mail Station 45, Tallahassee, Florida 32399

My first visit to Tall Timbers Research Station was twenty-five years ago, soon after the Florida Park Service transferred me to Tallahassee to serve as Chief Biologist. At that time, the Florida State Park System had never used prescribed fire. In fact, we considered fire to be an enemy. Smokey Bear's propaganda had been so effective that when a fire occurred in a state park, we would risk life and limb to put it out. Upon arriving at the Tall Timbers office, I introduced myself to the Director, Ed Komarek. On the issue of prescribed burning, Ed was a dedicated preacher and a persistent salesman. He took me on a tour of the fire plots and, that afternoon, convinced me that we should be burning in Florida's state parks. I returned to the office and started selling the concept to the Park Service senior management. Within a couple of months, we conducted our first burn in a Florida State Park and Ed's wife, Betty, was the fire boss on the burn. Today, we burn 140,000 acres in 66 state parks.

You've heard about lightning season fires during the past few years. You may have heard the terms growing season fires, warm season fires, spring burns, summer burns; it's all the same. These are just different terms that land managers are using to label fires during that time of year. I use the term "lightning season" fire for reasons that will become clear later in the presentation.

Anyone attending a Game Bird Seminar in the Southeastern Coastal Plain is interested in managing quail and turkey lands for the purpose of producing healthy populations of these game birds at the lowest cost. As you know, invasive hardwoods, such as laurel oaks, water oaks, and sweetgum degrade pineland habitat, and increase management costs.

Let's step back to the turn-of-the-century to observe the conditions and appearance of the landscape in south Georgia and north Florida. I have collected old photographs of the pinelands and grasslands of this region from family albums, state archives, university libraries and research reports to learn what this land looked like when natural and human-caused fires were frequent. Photographs taken near Moultrie, Georgia in 1904; (Figure 1) Pensacola,

Presented at Tall Timbers Spring Game Bird Seminar, Tall Timbers Research Station, 10-11 April 1995.



Figure 1. Old-growth Longleaf Pine forest near Moultrie, Georgia, 1904.

Florida in 1907; and Sumter County, Georgia in 1904 illustrate the same conditions of the pinelands. We note large, widely spaced longleaf pines, no hardwoods or shrubs, and a carpet of wiregrass, ferns, and other herbaceous plants. These photographs match the written documentation, from the 1600's through the early 1800's, that I've collected that describe the appearance of this part of the Coastal Plain. These are the conditions that a lot of federal, state and private landowners would like their lands to be in today.

Now let's move ahead from the turn-of-the-century to Wekiwa Springs State Park in Orange County, near Orlando. In 1977, we conducted the first Florida Park Service Ranger Academy at this park for the purpose of training new park rangers. It was the month of May. We wanted to teach them about prescribed burning, however, since prescribed burning was only conducted during the winter, we were very concerned that serious damage would be caused by burning in May. We finally decided that it was important to teach those new rangers how to burn and that we would risk damaging a few acres and proceed with the burn. The turkey oaks were so dense that the wiregrass had been suppressed; therefore, the fire was of low intensity because of the poor fuels. I photographed the site the day after the burn to record the conditions (Figure 2). Within a couple months, we were surprised to see the dense flowering stalks of the wiregrass which we had never before observed.

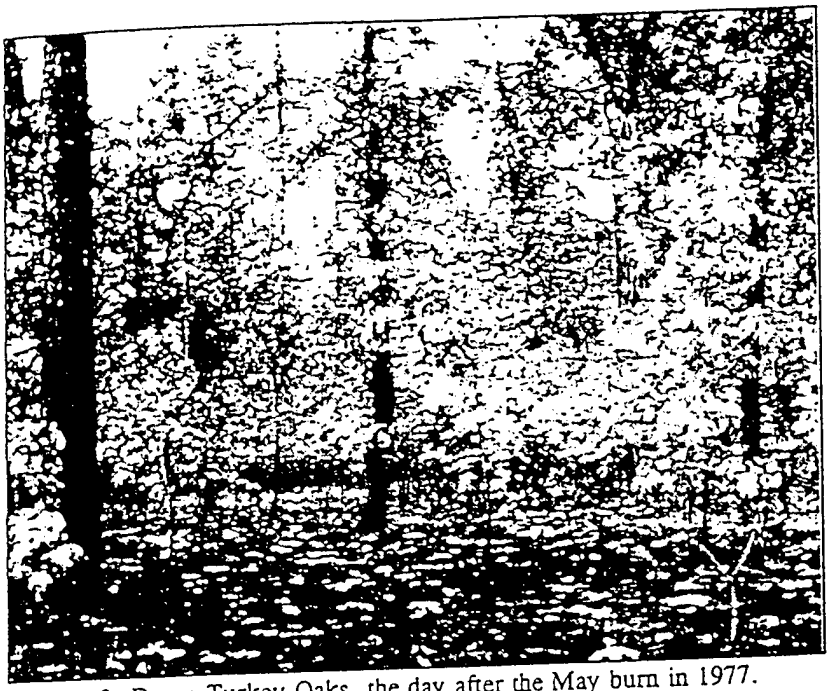


Figure 2. Dense Turkey Oaks, the day after the May burn in 1977.

We burned the tract two more times in May, at three year intervals, totalling three burns over a period of six years during May. When we compare the before and after photographs it is clear that the tract was restored to a condition that matches the turn-of-the-century photographs (Figure 3). We had achieved effective hardwood control for the cost of three prescribed burns.



Figure 3. Condition of the area in Figure 2., six years later, after three May burns.

Our land management objective, in the state park system, is to restore the land to its original biological diversity, to the extent possible. We believe the pinelands and grasslands will be essentially restored when the condition of these habitats is similar to the conditions depicted in the historic photographs. Due to the results of the burns at Wekiwa Springs, we began studying the relationship of lightning and the "natural" fire season. We learned that the highest number of thunderstorm days in the continental United States occurs in southwest Florida and all of Florida and south Georgia receive more lightning strikes than any other location in the United States. A Division of Forestry computer-generated map of Florida, during a two hour period on August 8, 1990, shows hundreds of lightning strikes, each being an opportunity for lightning to ignite a natural fire (Figure 4). That's the way mother nature ignited fires for hundreds of thousands of years.

We obtained the dates of all lightning caused fires that were recorded in Florida, during a six year period, from the Florida Division of Forestry. The data indicates that lightning fires begin in April, peak in June, begin decreasing in July as the humidity increases, and phase-out in September (Figure 5). Based on this data, and the results of the lightning season burns at Wekiwa Springs, we changed our prescribed fire program in 1982, from the winter (dormant) season to the lightning season. The lightning season differs somewhat from the growing season, in that, the growing season begins before the lightning season and ends after the lightning season. Some winter burning is occasionally conducted in order to reduce heavy fuels before we switch to lightning season burning on recently acquired park lands. We seldom burn in late August or September because of the stress that can be caused to pines late in the growing season.

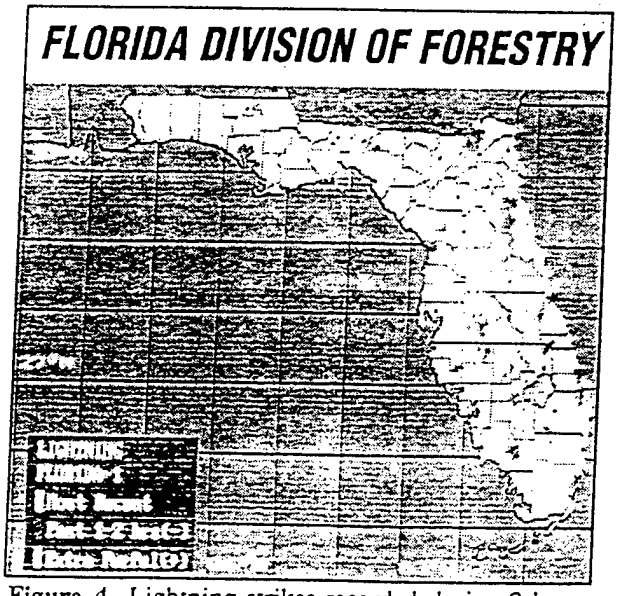
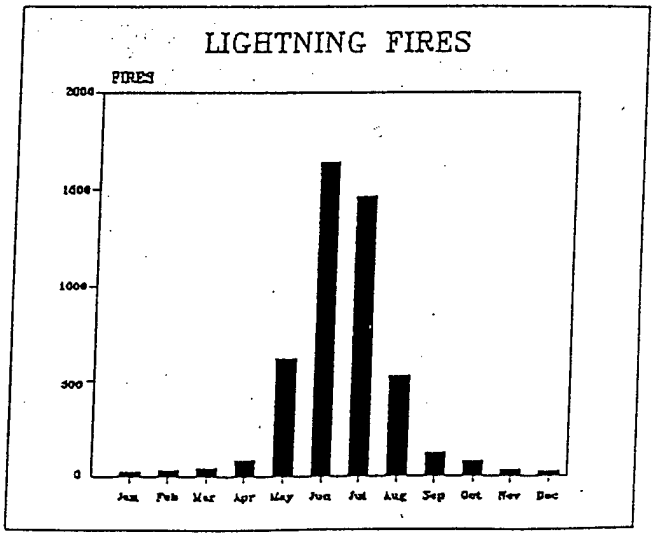


Figure 4. Lightning strikes recorded during 2-hour period 8 August 1990.



Department of Environmental Protection

Figure 5. Lightning fires recorded 1981-1986 indicate the lightning-fire season.

How did the practice of winter burning begin? Naval stores was a very big forest industry in the Southeastern Coastal Plain in the late 1800's and the early 1900's. The pine woods were burned annually to keep the woods open for the turpentine workers and as a safeguard against wildfires. The burning was conducted during the winter since the sap was not flowing and the catfaces were less likely to catch fire. Perhaps this was the origin of the practice of winter burning.

We have many before and after photographic sequences that very effectively illustrate the rapid progress we have made in suppressing hardwoods and restoring native ground cover on the state parks through the use of lightning season fires.

However, what are the effects of lightning season fires on wildlife? We have numerous field observations and research results that demonstrate that wildlife of the pinelands and grasslands of the Coastal Plain are adapted to and thrive under a lightning season fire regime.

For example, the park manager at Ichetucknee Springs State Park near Gainesville, observed turkey hens and poults feeding in an open longleaf pine savannah that had been burned in late April. They were eating wiregrass seeds by stripping them from the stalks with their beaks. Wiregrass seeds are produced by lightning season fires.

Game and Fresh Water Fish Commission research conducted in Osceola National Forest demonstrated that runner oak and blueberry production is significantly greater the first year after a lightning season fire than the production after a winter burn (Stafford, 1983). Walter Sedgwick has reported that in the quail season following a lightning season burn in 1994, on Mill Pond Plantation, they brought in more quail in one morning off the lightning season burn tract than they had at any time in the previous forty years, on any part of Mill Pond Plantation.

When we switched to lightning season burning, some wildlife specialists believed we would destroy the wildlife cover and mast trees. Again, the written documentation and early photographs of hunters posing with their game demonstrated that game was plentiful when this region was more of a grassland, a savannah, than a dense pine forest.

Others were concerned that we would destroy bird nests and their young by burning during the spring. We investigated that issue by determining where all of the species that inhabit the pinelands place their nests; in the canopy, in cavities, in the shrub layer, or on the ground. We determined that thirty-eight percent of the birds in the pinelands nest high in the canopy well above the heat and flames. Thirty-seven percent nest in woodpecker cavities where they are safe. Two percent are shrub nesters and twenty-three percent nest on the ground. Therefore, twenty-five percent are vulnerable to fires. An analysis of bird nesting behavior indicated that some of these species begin and finish nesting before the lightning-fire season begins. Some species have two or more broods per year so the loss of a brood is not significant for the annual production of the pair. Other species

renest if their nest is lost. The birds of the pinelands and grasslands have been living with lightning season fires for hundreds of thousands of years and are very well-adapted to living with this natural process. For instance, ninety-one percent of bald eagle nests in Florida are in large, old pine trees. The principle target of lightning is large, old pine trees. Why would any bird put its entire reproduction on a lightning rod? Bald eagles begin building or repairing their nests after the lightning season, in September and October. They begin laying eggs in December, and their young are fledged and out of the nest by late April and early May, just as the lightning season begins. The eagle is in sync with the lightning season.

Let's consider some ground nesters. The chuck-wills-widow is known to nest on a bed of live oak leaves. Those of you that are experienced burners know that it is nearly impossible to burn a layer of live oak leaves. This species is able to select nest sites on the ground that are unable or unlikely to burn. The nighthawk, a species related to the chuck-wills-widow, is another ground nester. This species selects nest sites that have been recently burned. Is there a safer location for a nest than a site that has recently burned? Is it no coincidence that nighthawk chicks are speckled black and gray, the color of charcoal and mineral soil? As we study each species that inhabits fire-dependent habitats, we find each is well-adapted to lightning season fires.

What about the turkey? Wouldn't you think that a game bird as smart as a turkey is just as well-adapted to successfully nest on the ground, during the natural fire season, as are other birds? Research conducted at Pebble Hill Plantation in 1993 indicated that the turkey's preferred nest sites are open canopy sites composed of 1-4 year old oaks and sweetgums (Peoples, 1992). You know how difficult it is to burn sites like that during the lightning season; therefore, the turkey also selects nest sites that are not likely to burn.

I have always heard that the turkey is a forest-dependent species and that its principle food is acorns. According to Lovett Williams, author of "The Book on the Wild Turkey," 30% of the turkey's habitat should be open. In the state parks, where turkeys are not hunted, we commonly see them feeding in open grasslands. Perhaps they are dependent on forests primarily for escape cover. Turkeys need grasslands. The number one food for poults, according to Lovett Williams, is insects. The number one food for all other ages of turkeys is grass, and grass seeds. What about the diet of the turkey in the fall, when the acorns are on the ground? Lovett found that fifty-one percent of the diet of the wild turkey in the fall is composed of grasses. Fourteen percent is insects, and only twelve percent is acorns (Williams, 1981). Lightning season fires maintain grasslands, and enhance the production of grass, grass seeds and insects.

By studying a species of bird, we can learn more about managing land. For example research conducted on the Cape Sable Sparrow, demonstrated that the population of singing males steadily increased on a burned marsh during the first, second and third years after the burn

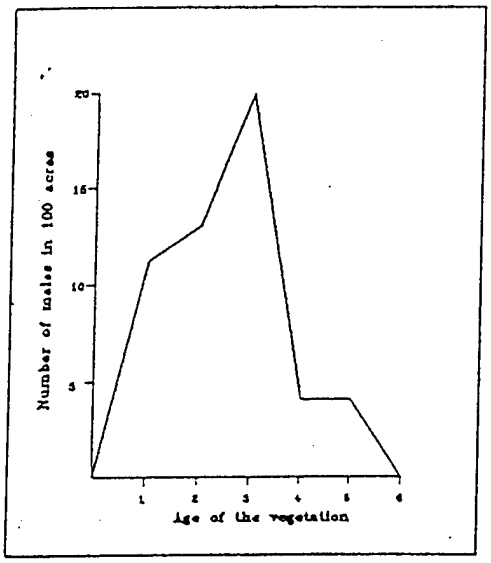


Figure 6. Observed density of male Cape Sable Sparrows in relation to age of the vegetation after a fire (Werner and Woolfenden, 1993).

to a peak number of twenty birds. After the third year the population began declining and by the sixth year, after the fire, there are no singing males remaining on the tract (Figure 6). This suggests that the Cape Sable Sparrow is a good indicator of the health of its marsh habitat and demonstrates that the ideal fire frequency is a three-year interval.

What is the ideal fire frequency for quail - one, two or three years ? Are we burning on a one to two year interval because that's what it takes to keep the hardwoods under control or because that's the best frequency for quail? If we are managing old field lands with serious hardwood problems, then a one to two year frequency is needed. However, if the land has not been plowed and the native ground cover is still intact, then hardwoods are not likely to be a problem and a three-year interval may be adequate.

Why would anybody want to study Red-cockaded Woodpeckers when there are so many other important things to study? Dr. Lenny Brennan, Tall Timbers' Director of Research has written a paper that demonstrates that management that is good for Red-cockaded Woodpeckers is also good for quail. (Brennan and Fuller, 1993)

Does a manager of a quail plantation need to understand hawk migration? There is a lot of burning conducted on the quail plantations during February and March. When do the hawks come back across the Gulf of Mexico and pass through this area? The hawks come back across the Gulf of Mexico and pass through this area during February and March. I like hawks and really enjoy seeing them but I don't believe we should provide them free handouts. I think a hawk should have to work for a living. When there is no cover for quail, because we have just burned it off at the time that the hawks are passing through, then we are out of sync with the natural system. Whereas, if we burn in mid-April (the beginning of the lightning season), the migrating hawks will have flown north and we will have rapid growth of the ground cover after the burn.

Why would we want to study lightning season fires? Because quail and turkey have evolved with lightning season fires for hundreds of thousands of years. They are adapted to them. The better we understand these fires, the better we will understand game bird management in the Southeastern Coastal Plain.

Let's return to hardwood control. In the state parks, we often stated that, "In order to restore the pinelands we're going to eliminate the turkey oaks." However, as time passed we learned that turkey oaks belong in the pinelands. We have determined that we only need to reduce the density and change the structure of most of them from trees to shrubs. Again, the early photographs illustrate that turkey oaks were commonly only knee high because of the frequent fires and they produce acorn mast at that height. Lightning season fires will very quickly and effectively reduce turkey oaks from tree structure to the shrub level where they will continue to provide ecological benefits without shading the wiregrass and other herbaceous growth. This can be observed on the Wade Tract, and other well-managed pinelands that still have intact native ground cover.

All oaks are not created equal. The turkey oak, the post oak, and the red oak belong in these pinelands, and are easily managed with fire. But, there are other "invasive" oaks that we must now control because of the way we've altered the land. We can easily control all of the oaks if we have the superior fuels that mother nature has provided. Let's use an analogy. If you want to be successful in bagging a turkey, will you use a 12 gauge, a 410, or a B-B gun? You will likely choose a 12 gauge. In controlling hardwoods, the 12 gauge fuel in these pinelands is the longleaf pine needle. Wiregrass is equivalent to the 16 gauge. The combination of the 12 gauge and the 16 gauge fuels provide the most effective fire power, the killing power, needed to control unwanted hardwoods.

If the lands you are managing have been cleared and plowed and have succeeded back to forest, they are called "old field lands." The wiregrass is gone, having been replaced by broomsedge and briars, and the pines are probably loblolly rather than longleaf. The excellent natural fuels are no longer present; therefore, water oak, laurel oak, and sweetgum have easily invaded. The weedy, inferior fuels on old field lands are inadequate for the effective elimination of these invasive hardwoods.

Since lightning season fires are so effective for controlling hardwoods, the Tall Timbers staff is experimenting with lightning season burning to determine the conditions under which it can be used most effectively to control hardwoods on old field lands. To date, they have learned they must have low humidity and two to three years of fuel available. Burning in late April and May, before the rainy season begins, is necessary because of the poor quality fuels. They will continue to fine tune these procedures and will be sharing findings with land managers as they are developed.

Virtually all of the state and federal land managing agencies in Florida are experimenting with, and converting to, lightning season burning including the National Forest Service and the Florida Division of Forestry.

The research being conducted here at Tall Timbers is discovering the missing pieces of the land management puzzle. All land managers can participate in this process by carefully observing and recording the results of your management and sharing the

information with others. Sensitive stewardship of the land requires us to be open to new ideas and willing to try new methods in order to leave the land in better condition than we found it.

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THE BENEFITS OF WIREGRASS ON SHOOTING PLANTATIONS

J. Larry Landers[1]

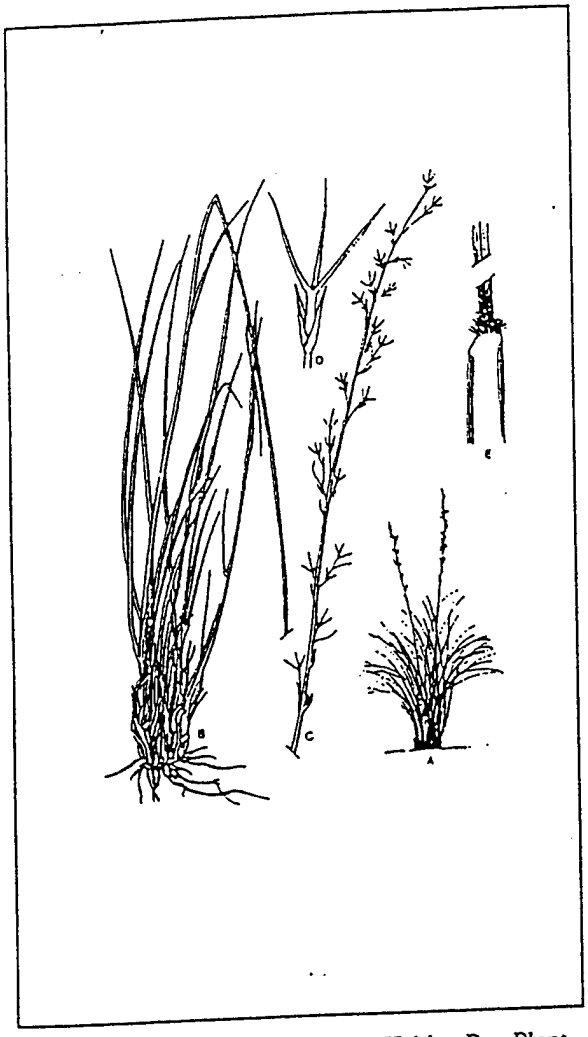


Figure 1. *Aristida stricta*. A = Habit. B= Plant. C = Inflorescence. D = Floret, showing awns. E = Base of upper surface of leaf blade, showing rolled bade and hairs.

Nat. Areas J., Vol. 9(4), 1989

Wiregrass is a "keystone" species of central importance to the longleaf pine community. This grass added to longleaf pine straw comprises the primary fuel base for frequent fire. At least 141 rare plant species, literally hundreds of other plants, and many wildlife species are closely associated with wiregrass.

When burned, this extremely flammable grass reduces woody brush much better than any other type of ground cover vegetation. Management of lands without wiregrass must include much more use of machinery (mowing, disking) and manpower to control brush.

Wiregrass is ideal for nesting cover of quail and many other ground-nesting birds.

Wiregrass is ideal concealment cover from predators.

Wiregrass encourages quail coveys to "freeze-hide" rather than run when bird dogs approach, thus improving hunting success.

Wiregrass seed are eaten by turkey, particularly the young of the year.

Wiregrass produces beautiful scenic, pine parkland vistas and is a significant part of the natural heritage of the Red Hills.

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Hall, D.W. 1989. Is it wiregrass? Nat. Areas Journal. Vol.9(4) 219-222.

[1]Larry Landers, now deceased, was Station Director at Tall Timbers for many years. Larry was one who knew of the benefits provided by wiregrass as a fuel for fire and cover for wildlife.

THE NEW BOBWHITE RESEARCH INITIATIVE AT TALL TIMBERS: FIRST YEAR PROGRESS REPORT

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INTRODUCTION

The past year was a busy and productive one for bobwhite management research at Tall Timbers. Four new bobwhite research projects were initiated by the game bird management research personnel at Tall Timbers. These projects have been designed to help land managers and plantation owners understand:

- Long-term bobwhite population trends in the Red Hills, and
- How bobwhite habitat management can be made better and more cost-effective.

Each project has been designed to build on the firm foundation of bobwhite natural history built by Herbert Stoddard. Stoddard posed a number of important questions about factors that influence bobwhite populations. Many of these questions remain unanswered. Our job at Tall Timbers is to find answers to these important questions through research and experimentation. Our purpose in the new initiative is to answer four key bobwhite management questions:

- What has happened to bobwhites in the Red Hills area during the past 50-80 years?
- Will trapping nest predators such as raccoons and opossums improve the quality of quail shooting?
- Is it possible to use fire during late spring or summer for hardwood control and not hurt the birds?
- Do we really have to plant food plots for bobwhite habitat management, or can we just disk patches?

Our goal with game bird management research at Tall Timbers is to provide reliable knowledge that can be used to produce high-quality bobwhite hunting without incurring excessive costs.

What Happened to Our Bobwhites? The Red Hills Game Book Project

A wise man once said, You need to know where you have been before you can

Presented at Tall Timbers Spring Game Bird Seminar, Tall Timbers Research Station, 10-11 April 1995.

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figure out where you are going. With bobwhites in the Red Hills, we have numerous outstanding opportunities to see where we have been and examine how bobwhite populations, and the resultant quality of hunting, have ebbed and flowed over the years. These opportunities stem from the fact that a number of families have kept long-term records of their quail hunting success in plantation game books. During the past year, we have taken information from several plantation game books around the Red Hills and in the Coastal Plain, and plotted the average numbers of coveys found per hunting period. The results and trends have been very interesting.

For example, long-term data from the Red Hills indicate that population trends in this region have been very different from what bobwhites have experienced at the broader scale in the Southeastern Coastal Plain.

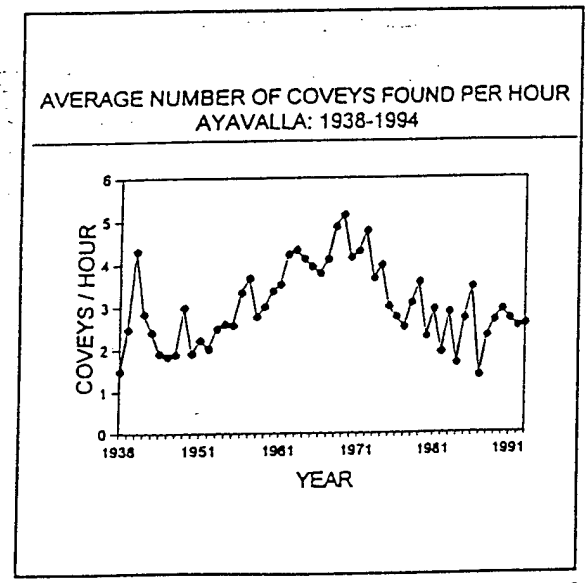


Figure 1. Long-term trends in average number of bobwhite coveys per hour flushed on a Red Hills plantation, 1938-1994.

Numerous factors have been attributed as the reasons for the bobwhite decline in the Southeast. These factors range from expanding coyote and fire ant populations to global warming to the population recoveries of turkeys and white-tailed deer. However, data from the Red Hills show that when high-quality habitat management is practiced, abundant, stable populations of bobwhites can be maintained, or even increased, at a time when the birds are declining at a regional or continental scale. Information from the Red Hills game books shows the importance of habitat management and the fact that there is no substitute for good habitat management when it comes to producing wild quail for shooting.

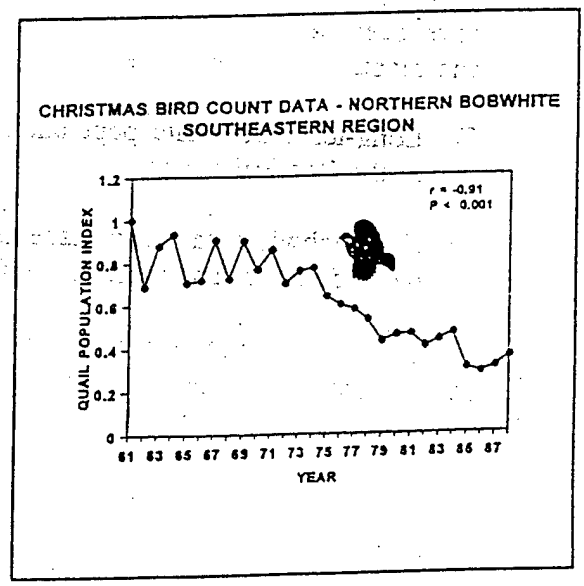


Figure 2. Bobwhite population trends in the Southeast, based on Audubon Society Christmas Bird Count data.



Will Trapping Nest Predators Improve Bobwhite Shooting?

The breeding season is a dangerous time of the year to be a bobwhite. During the time of year (late September through April) when bobwhites are in coveys, survival data from radio-marked birds at Tall Timbers indicates that mortality is about 25%.

That means if 100 birds are radio-marked on 1 September, about 75 of them will still be alive on 1 April. However, during the bobwhite breeding season (from April through September), the picture changes, and mortality is about 70%. That is, for every 100 adults in the population at the beginning of the breeding season, only about 30 will be alive at the end of the breeding season.

Bobwhite hens, especially, are susceptible to predators while they sit on nests and incubate eggs. The primary bobwhite nest predators are raccoons and opossums, two animals with populations that are at an all-time high because few people are interested in trapping anymore.

Our goal in the nest predator trapping experiment is to take a 500 acre shooting course and remove mammals that can disrupt bobwhite nests (mostly raccoons and opossums). We want to see if reducing nest predators results in increased bobwhite production and ultimately improved hunting in the fall.

During the first year of the study, we removed raccoons, opossums and armadillos from a 500 acre shooting course. During the year before predator removal, hunters averaged 0.3 birds per acre hunted, after one season of predator removal, hunters averaged 0.68 birds per acre hunted (Figure 3) indicating that nest predator reduction may be a viable bobwhite habitat management technique. However, several more years will be required before this result is confirmed or refuted.

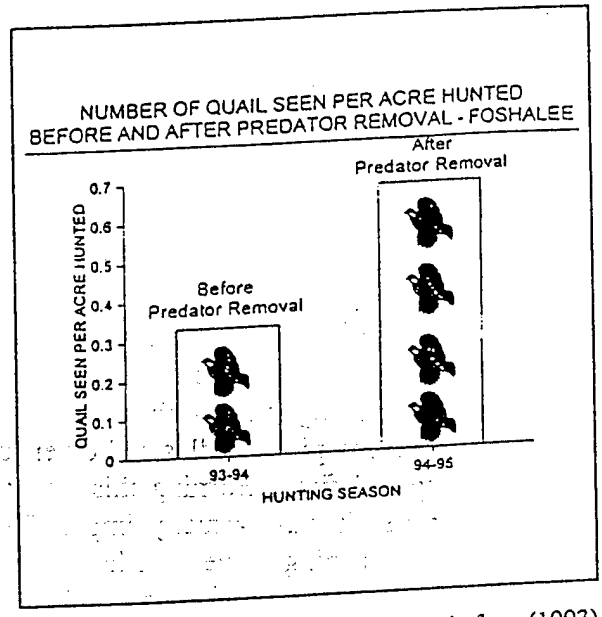


Figure 3. Bobwhite hunting success before (1993) and after (1994) nest predator reduction at Foshalee Plantation.

Can We Burn During April or May for Hardwood Control and Not Hurt the Birds?

Any plantation owner or manager knows that hardwood control is expensive. As time goes on, hardwood control, especially using mowing and chopping, will get even more expensive. Fire can be a cost-effective method of hardwood control, but relatively cool fires during February and

March (when plantations do most of their burning) may not be fully effective at killing hardwoods or controlling their encroachment. Hot fires during late spring or early summer may be useful from time to time to get problem hardwood areas back under control.

However, people are reluctant to use fire for hardwood control during late spring or summer for fear of burning up nesting bobwhites and ruining the quality of shooting on a particular hunting course. However, burning later may be able to keep more cover on the ground to provide protection from hawks.

Years ago, before the drip-torch came on the scene, people burned the piney woods by setting fire with matches and raking burning pine needles and other fuel along to spread fire. Burning this way took a long time. It was virtually impossible to get all the burning done in March; it often took until April or even early May to get the burning done. Without a drip-torch, it was impossible to burn several thousand acres in two weeks time like it is today.

So what's the point? The point is that we really do not know if fire can be used for hardwood control during April or May without hurting the birds. In the past, people burned late because they had to burn late. But, what about the birds?

We designed a set of experiments to compare how burning during February and March compared to burning during April and May. We set out to test the effects of these two different applications of fire on: 1) insect abundance during the nesting and brood-rearing season, and 2) bobwhite hunting success during the following fall and winter.



The Importance of Insect Foods for Bobwhites

Insect foods have been overlooked as important bobwhite foods. Most of what we know about the diet of bobwhites comes from samples of birds killed by hunters during fall and winter. While this information is interesting, it does not tell us what the birds need to eat when they are breeding. As it turns out, both growing bobwhite chicks and laying hens need PROTEIN, and lots of it (see Figure 4). While some plants, especially legumes such as vetch, partridge pea, etc., contain protein, animal foods, especially insects, are crucial for bobwhites. Production of young birds is essential for good fall hunting because 70-80% of birds bagged were hatched during the same year.

For many years, people knew it was important to burn for bobwhites. Stoddard established this nearly 70 years ago. However, it was not until the early 1970's that George Hurst from Mississippi State University showed that recently-burned areas contained more insects that are eaten by bobwhites, both in quantity and quality, than adjacent unburned areas. This was an important step in understanding the dynamics between burning and bobwhites.

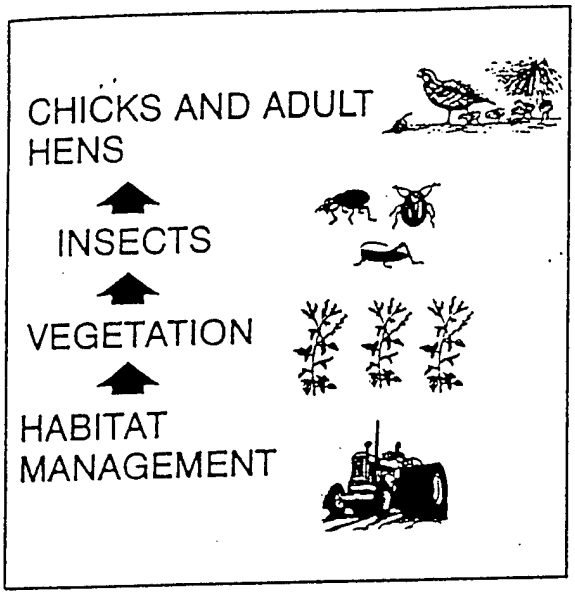


Figure 4. The bobwhite food chain in relation to habitat management.

The next step in the research process is to understand how burning at different times of the year influences insect populations (and hence brood habitat quality) for bobwhites.

During the past year, we found that there were significant differences in insect abundance on our winter versus summer burn plots. At Mays Pond, summer-burned plots exhibited a major increase in insect numbers during the middle of the summer, at the time when bobwhites need bugs the most (Figure 5).

At Mill Pond-Sedgwick, winter burn plots contained the most insects throughout the brood-rearing period (Figure 6). The important point is that both summer and winter burning produced abundant insect food resources for quail. From a management perspective, it would probably be a good idea to do both summer and winter burning.

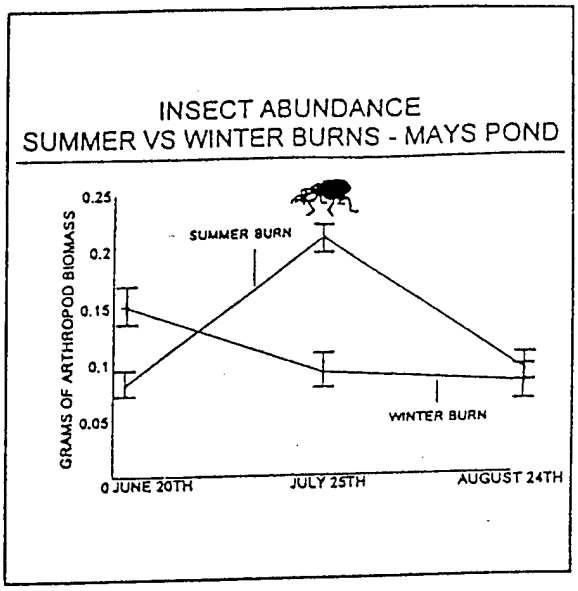


Figure 5. Insect abundance during the bobwhite breeding season at Mays Pond Plantation on summer versus winter burned shooting courses.

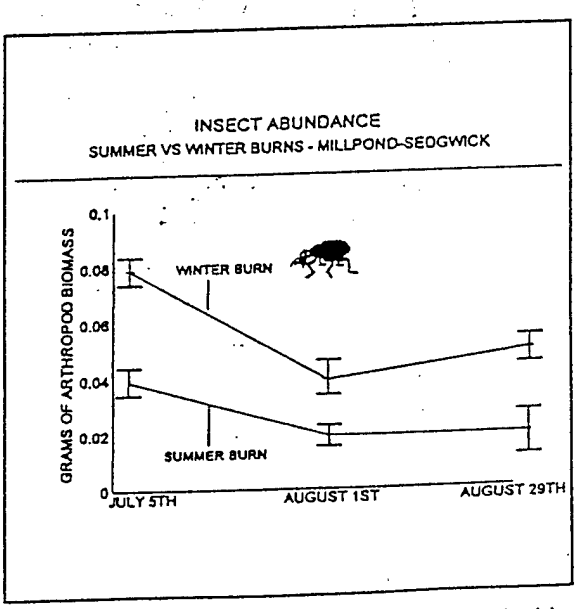


Figure 6. Insect abundance during the bobwhite breeding season at Mill Pond-Sedgwick Plantation on summer versus winter burned shooting courses.

Hunting success, as measured in coveys found per half-day hunt, did not differ greatly between the winter and summer burn plots at Mays Pond or Mill Pond-Sedgwick (Figures 7 and 8). This supports the management theory that some use of summer fire for hardwood control will not necessarily destroy bobwhite hunting on a particular shooting course.

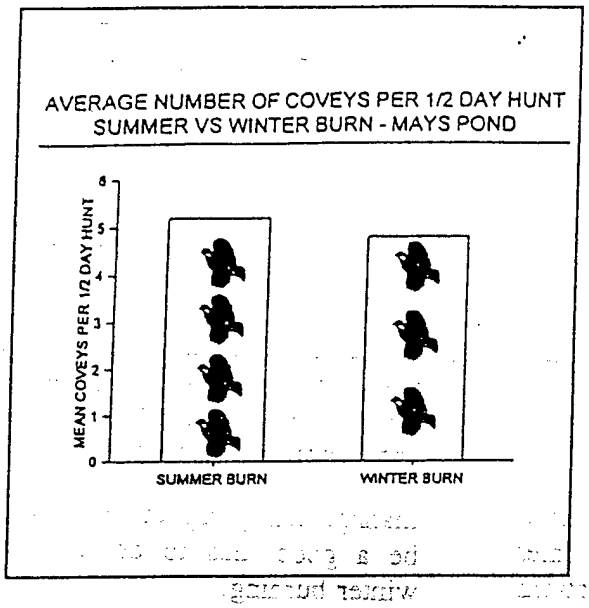


Figure 7. Bobwhite hunting success at Mays Pond Plantation on summer versus winter burned shooting courses, 1994-1995 hunting season.

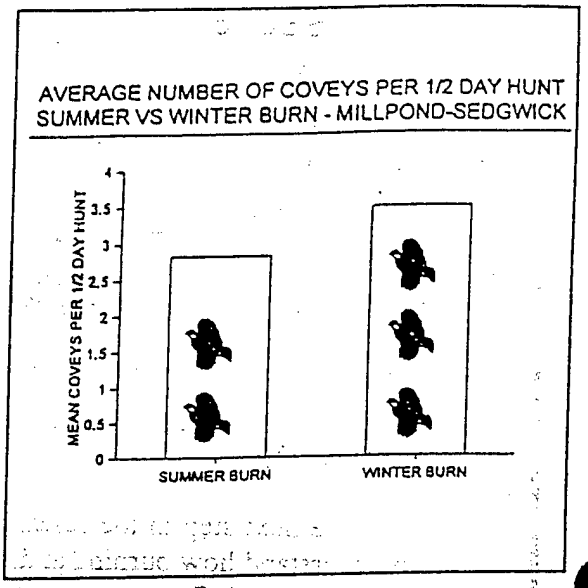


Figure 8. Bobwhite hunting success at Mill Pond-Sedgwick Plantation on summer versus winter burned shooting courses, 1994-1995 hunting season.

Do We Need to Plant Food Plots to Have Good Bobwhite Shooting?

More than 60 years ago, Herbert Stoddard was skeptical about the costs versus benefits of food plots or "quail feed patches" as he called them. In his classic bobwhite book Stoddard wrote, *"...there is little doubt that methods such as strip-disking are more practical for Southeastern quail preserves than artificial plantings."*

Landowners could realize huge economic savings if they only disked strips instead of planted feed patches. The costs for feed patches can be tremendous. Not only is seedbed preparation more tedious and costly for planting feed patches, but additional costs of seed, fertilizer and weed control can also be very expensive. Such expenses are worth it if they are essential to good bobwhite production and good hunting. However, until we started our study last year, nobody had made an effort to test Mr. Stoddard's idea about the effectiveness of feed patches as a bobwhite management technique.

Our purpose with this project was to compare feed patches versus simple disking to test: 1) how these two management techniques influenced insect abundance for brood habitat quality, and 2) how these two management techniques influenced bobwhite hunting success during the subsequent fall and winter.

During 1994, we found that there were large differences in insect abundance in feed patches at both Mays Pond (Figure 9) and Mill Pond-Sedgwick (Figure 10). At Mays Pond, feed patches provided a pulse of insects early in the season and trailed off, whereas at Mill Pond-Sedgwick, the feed patches produced a large pulse of insects during the middle of the brood-rearing season. In all cases though, it appeared that both disking and food plots provided adequate insect food resources.

Hunting success, as measured in coveys found per half-day hunt, did not significantly differ between the disked and feed patch plots at Mays Pond or Mill Pond-Sedgwick (Figures 11 and 12). Curiously, the increased abundance of insects provided by the feed patches did not improve hunting on either area.

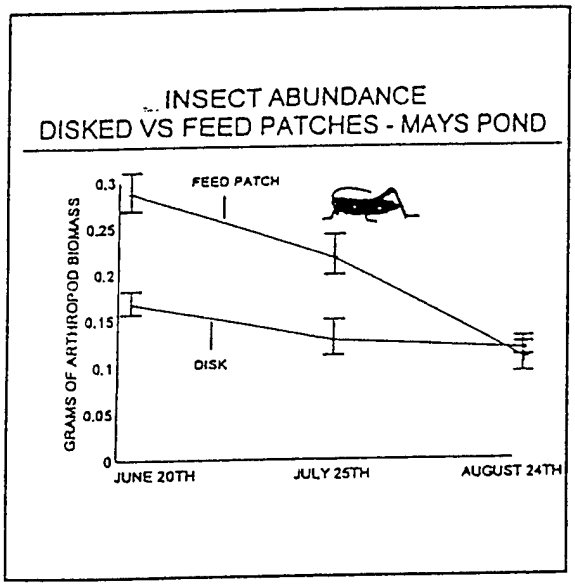


Figure 9. Insect abundance during the bobwhite breeding season at Mays Pond Plantation on feed patch versus strip-disked shooting courses.

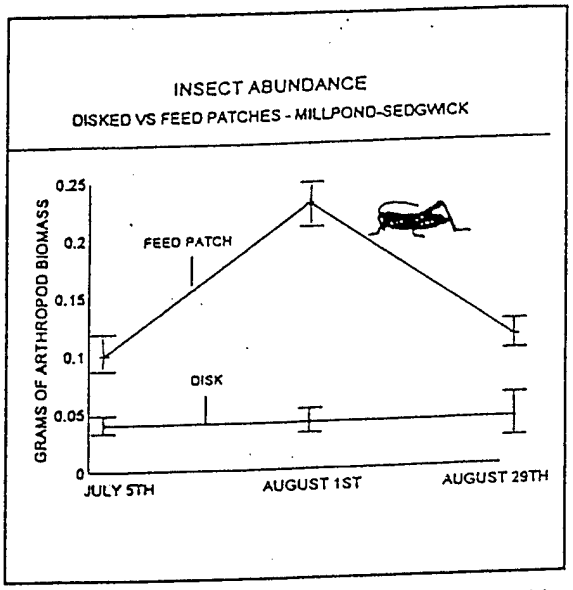


Figure 10. Insect abundance during the bobwhite breeding season at Mill Pond-Sedgwick Plantation on feed patch versus strip-disked shooting courses.

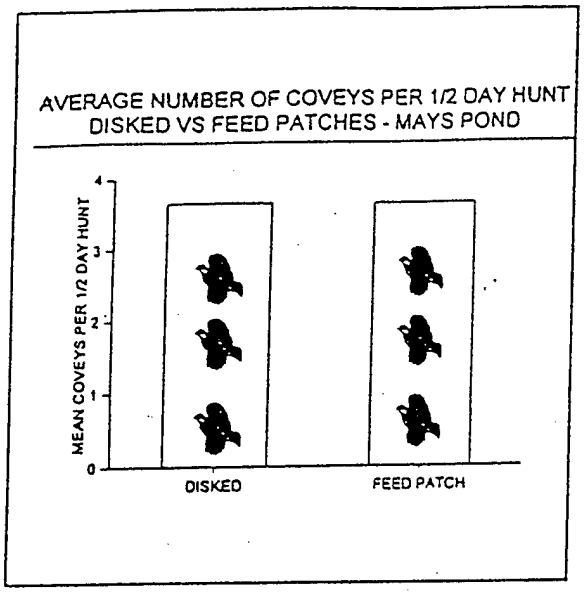


Figure 11. Bobwhite hunting success at Mays Pond Plantation on feed patch versus strip-disked shooting courses, 1994-1995 hunting season.

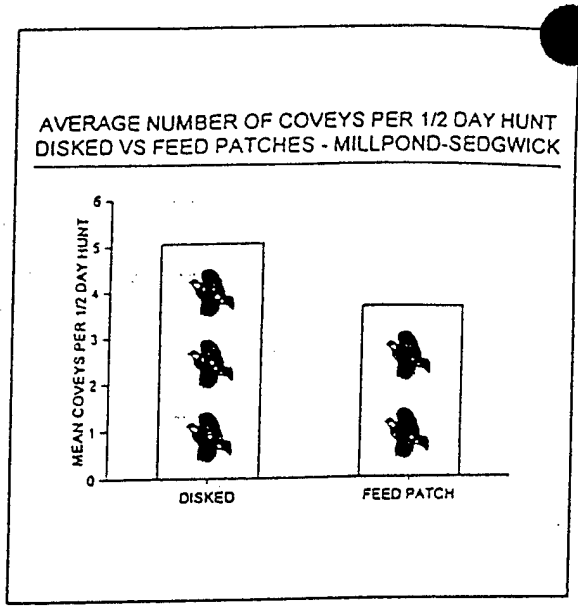


Figure 12. Bobwhite hunting success at Mill Pond-Sedgwick Plantation on feed patch versus strip-disked shooting courses, 1994-1995 hunting season.

BOBWHITE QUAIL MANAGEMENT RESEARCH AT SEDGWICK LAND COMPANY

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INTRODUCTION

This paper will feature an update of recent bobwhite management research activities at Sedgwick Land Company. During the past two years, we have been conducting several projects on this property, which is the eastern third of the original Mill Pond Plantation, located just south of Thomasville, Georgia.

Our Tenth Annual Fall Field Day was held at Sedgwick Land Company during November 1995. The program was hosted by the Sedgwick Family, and Walter Sedgwick, Chairman of the Tall Timbers Board of Trustees. Our bobwhite management research conducted there during the past two years was a featured part of the program. This article was written to give both fall field day participants, and our membership, an overview of the research conducted on this property during the past two years.

We decided to conduct a series of bobwhite habitat experiments at Sedgwick Land Company for two main reasons. First, this property contains extensive stands of high-quality longleaf pine forests. Second, the owners and managers have kept careful records of both bobwhite and pine saw timber harvests for the past 35 years. This interested us because we want to examine relationships between quail and forest management.

In this report, we will discuss three projects from Sedgwick Land Company:

1) Relationships between bobwhite abundance, timber harvest and timber production;

2) Response of quail foods produced by vegetation and insects in relation to planting feed patches versus simple disking and harrowing;

3) Response of quail foods produced by vegetation and insects in relation to burning during March versus burning during May.

Bobwhite Abundance, Timber Harvest, and Timber Production

Game book data maintained by the Sedgwick family over the years indicate that bobwhite numbers on Sedgwick Land Company - Mill Pond have remained stable

Presented at Tall Timbers Game Bird Management Field Day Seminar, Sedgwick Land Company-Mill Pond, 13 November 1995.

since at least 1961. Although numbers of quail (based on average number of coveys found per hour of hunting each year) fluctuated widely, and underwent a decline during the mid 1970's (something that happened throughout the South, though nobody knows why), the TREND for quail numbers at Sedgwick Land Company has been stable. There are essentially the same number of quail available for hunting during 1994 as there were during 1961 (see Figure 1).

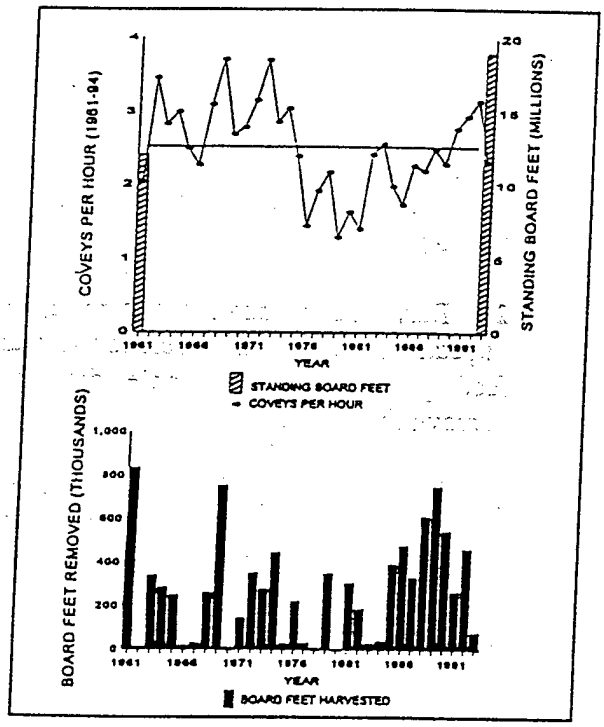


Figure 1. Relationships between timber and quail at Sedgwick Land Company 1961-1994. Shaded bars indicate amount of standing timber in 1961 and 1994. Black bars indicate amount of board feet harvested during different years. Black circles indicate the average number of bobwhite coveys seen per hour hunted during each hunting season from 1961-1994. Horizontal line on top graph illustrates stable population trend from 1961-1994.

One of the unique aspects of the data from Sedgwick Land Company is that the landowners also know the amount of standing timber that was present during 1961, the amount that is present today, and the amount that was cut each year during this period.

From 1961 until 1994, the amount of standing timber on Sedgwick Land Company increased from 12 million board feet to 19 million board feet (see Figure 1). During this same period, more than 10 million board feet of timber were harvested from this property (see Figure 1). Quail numbers remained stable. The amount of standing timber increased, and in the meantime substantial economic returns were generated from harvesting pine saw timber and other forest products. Since 1994, 1.8 million board feet have been harvested at Sedgwick Land Company. Talk about being able to have your cake and eat it too!

Data from quail shooting, tree harvest, and timber stands at Sedgwick Land Company show how land can be managed to produce an economic return, yet at the same time sustain and protect important ecological resources. The Sedgwick Land Company property is unique not just in light of the numbers of quail and amount of timber produced, but also because other resources on this property have been protected over the years. This property has supported some of the most abundant populations of Red-cockaded Woodpeckers in the world. Extensive areas of wiregrass and intact native ground cover are found throughout the property.

We think that information on relationships between quail and timber at Sedgwick Land Company shows that there are significant and viable alternatives to the standard industrial forest management model of clear-cut and replant when a landowner wants to grow timber, and sustain other resources. By maintaining a continuously standing forest of trees, the owners, their consulting forester (Mr. Leon Neel), and a land manager (Mr. Roger Croft) have perpetuated a working landscape that generates economic returns, produces game populations, and protects endangered species. Besides all this, the forest looks good, too!

Season of Fire: Can Lightning Season Fire Be Used and Not Hurt the Birds?

One of the age-old questions in bobwhite management is, "When is the best time to burn?" Over the years, quail managers have gravitated toward burning during late February or early March. This is because old field vegetation is dead and dry and burns easily after a long winter. It is also a pleasant time of year to burn because the weather is cool. Most bobwhites are still in coveys, and it will be a while before they start nesting.

However, persistent use of cool winter fire may result in hardwood encroachment over time. Also, concentrating all of the burning during March may expose the birds to undue predation pressure because this is when many raptors (hawks and owls) resume their northward migration. Perhaps some limited use of prescribed fire during the lightning season (when most fires historically were ignited by natural means) might be a useful tool for a manager who wants to control hardwoods economically and diversify their management schedules?

During the past two summers, we measured plants and bugs that were associated with cool winter fires and hot, summer ones on two shooting courses at Sedgwick Land Company.

Overall, we found that winter fire produced more broomsedge near ground level (good for nesting) and partridge pea (good for seeds and bugs) than summer fire (see Figure 2). However, winter fires also produced more oak stems (not good, especially since most were 10 inches or higher above the ground), indicating a possible encroaching hardwood problem (see Figure 2).

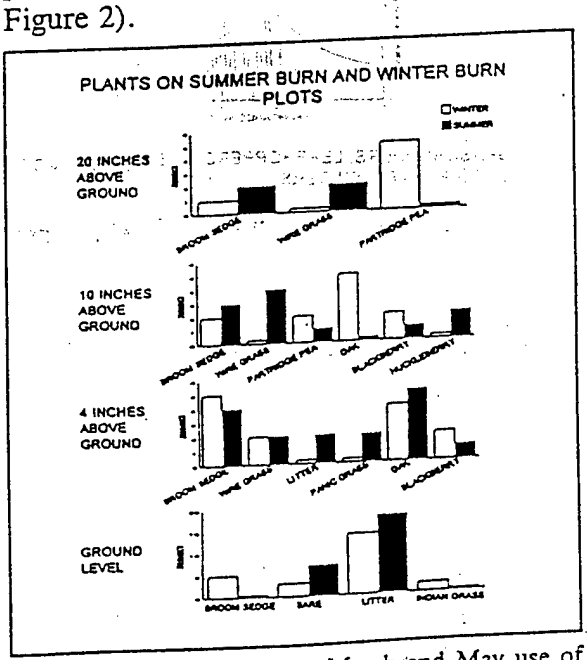


Figure 2. Plant response to March and May use of prescribed fire at Sedgwick Land Company. Open bars show amounts of plants detected on plots burned during March. Solid bars show amounts of plants detected on plots burned during May.

With respect to bugs, winter fires produced more bugs than summer fires (see Figure 3). However, it is important to note that the overall diversity and abundance of bugs on the winter fire courses was complimented by bugs on the summer fire plots (see Figure 3).

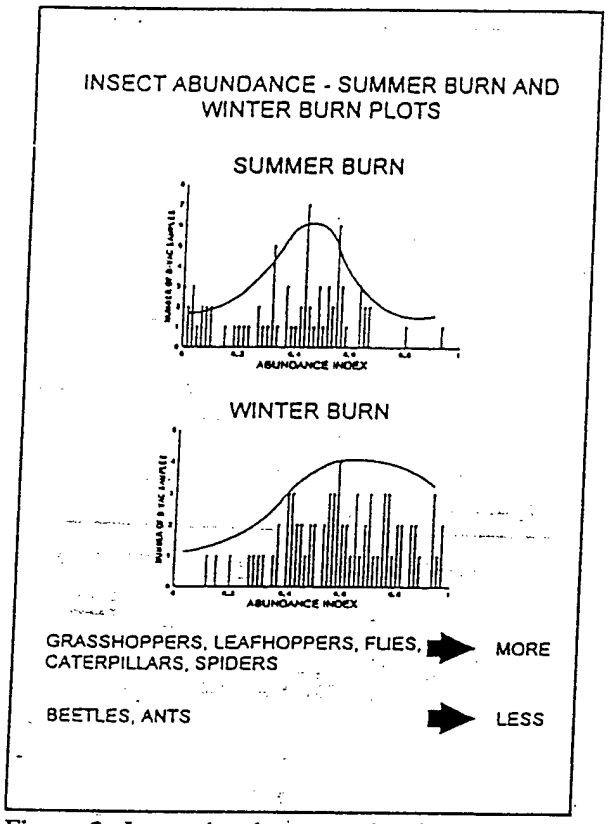


Figure 3. Insect abundance on plots burned during March and May on Sedgwick Land Company. Top graph shows insect abundance on plots burned during May. Bottom graph shows insect abundance on plots burned during March.

Therefore, our preliminary conclusion is that a limited amount of lightning season (May) fires, compliments more extensive use of winter (February-March) burning for bobwhite habitat management. A limited amount of lightning season burning reduces hardwoods, and adds to the plant and insect diversity which produce food resources for the birds.

Should You Disk and Disk Alone, or is it Better to Plant Again?

Like fire, the disturbances from mechanical means such as disking and planting are essential for producing wild bobwhites for hunting. However, for some reason, people insist that it is better to plant small-scale agricultural patches rather than simply disturb the soil by disking and let native weeds volunteer. Years ago, Stoddard was skeptical about the value of feed patches for bobwhites relative to disking or simple mechanical soil disturbance. However, the critical experiments to settle this question have not been conducted. That is, until we began our fieldwork at Sedgwick Land Company two years ago.

Our objective was to compare plants and bugs on shooting courses managed by disking and shooting courses with planted feed patches. We wanted to see if there were significant differences in the amounts and kinds of food produced for the birds, and if whether these differences (if any) translated into differences in the numbers of birds available for hunting.

Overall, we found that disked patches produced more partridge pea, broomsedge, blackberry, and pine regeneration than feed patches (Figure 4). Feed patches, produced (of course), more Egyptian wheat, and overall, more bugs, than disked patches (see Figure 5).

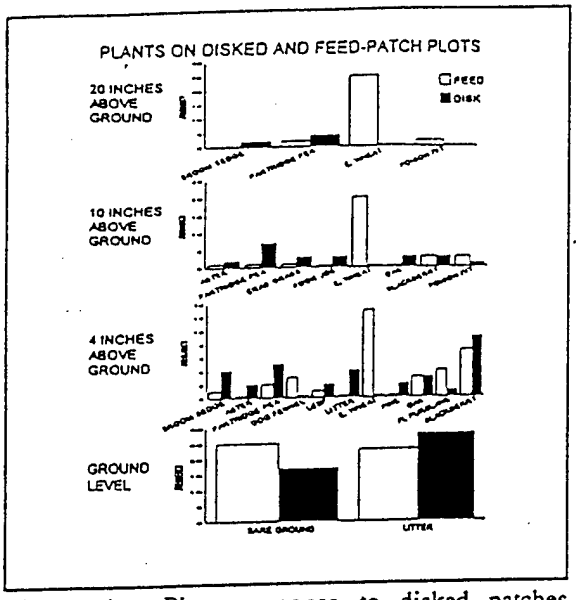


Figure 4. Plant response to disked patches compared to planted feed patches at Sedgwick Land Company. Open bars show amounts of plants in disked plots. Solid bars show amounts of plants detected in feed-patch plots.

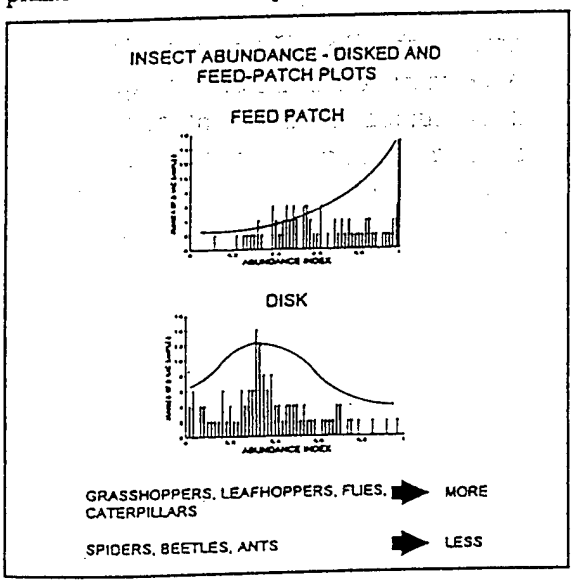


Figure 5. Insect abundance on disked patches compared to planted feed patches on Sedgwick Land Company. Top graph shows insect abundance on feed patch plots. Bottom graph shows insect abundance on disked patches.

However, our preliminary conclusions, like those from the season of fire comparisons, were that even though feed patches produced more bugs, disking patches, as a management technique, compliments small patch planting. When combined, feed patches and disking produce a more diverse array of foods that can be eaten by the birds than either type of management alone.

The implications of our Disk and Feed Patch experiments at Sedgwick Land Company are that landowners could probably reduce the number of feed patches that they plant (perhaps by as much as 50%), if they compliment the remaining feed-patch plantings by disking small patches and strips throughout the property. Significant economic savings could be realized by using disking to compliment a more limited program of feed patch planting. We plan to continue the disking and feed patch experiments for several more years so that we can determine if disking can serve as a complete replacement for feed patches.

An Important Note About Intact, Native Ground Cover

Our disking and feed patch experiments at Sedgwick Land Company were conducted on areas dominated mostly by old field vegetation that contained only sparse patches of intact native ground cover. This was intentional. Extensive areas of intact, native ground cover do not contain a bank of seed resources for plants like beggar lice, partridge pea, ragweed, etc., that are common in old field environments. Thus,

in areas of intact, native ground cover, it will not be realistic to expect weedy plants to volunteer after disking because seeds of these plants do not exist in sufficient numbers in the soil. In areas of intact, native ground cover, managers who want to plant feed patches for the birds should consider using patches for multiple years to minimize disturbance and fragmentation, and perhaps catch longleaf seeds during years when cone crops are abundant, and therefore create natural regeneration patches. New patches should only be created if and when existing patches become dominated by longleaf regeneration. Intact, native ground cover is a precious and declining resource. Extensive disking and mechanical disturbance ruins intact, native ground cover not only from the standpoint of the plants, such as wiregrass, but also for the quail who need wiregrass for nesting, and the other plants for food production.

General Land Management At Sedgwick Land Company: Game Book Data Revisited

One final point about bobwhite habitat management at Sedgwick Land Company is that management across the 3,000 acres of this property has been, over the years, conducted in a consistent manner. Data from the Game Books support this contention. This is because when quail numbers are averaged on a per course basis, the average number of bobwhite coveys seen per hour has been surprisingly consistent over the years (see Figure 6).

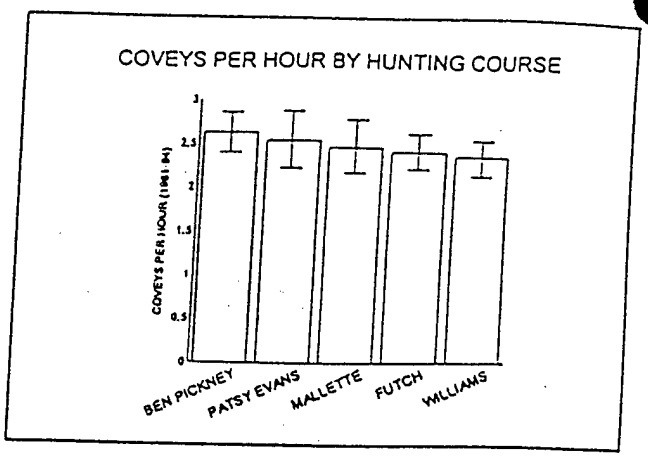


Figure 6. Average number of coveys seen per hour hunted at Sedgwick Land Company on five different shooting courses, from 1961-1994. Thin bars at the top of thick bars indicate upper and lower limits of variation each year. Thick bars indicate average number of coveys seen and shot into per hour hunted, averaged over each year from 1961-1994.

These data are extremely interesting because many land managers and owners around the Red Hills, and elsewhere, see wide variation in number of quail seen per hour hunted on different courses. Game book data from other areas show that on some properties, coveys seen per hour hunted are, on some courses, 2-3 times greater than on others. This is clearly not the case at Sedgwick Land Company. The consistent number of birds seen per hour hunted on the courses with data from 1961-1994 point to the fact that forest practices and general land management have been conducted in a consistent, and excellent manner throughout this property. The annual cycle of land management events at Sedgwick Land Company is outlined in Table 1.

SPEAKING CONSERVATIVELY

by Henry Chappell

The Bobwhite Quail Today

Scott Cox swept the antenna slowly across the Packsaddle Research Area's snow-draped prairie and adjusted his receiver. After a few seconds, he stopped the antenna; the receiver chirped steadily and upland Game Biologist Steve DeMaso, Scott Perry and I followed him toward a radio-tagged covey of bobwhites.

A hundred yards into the pasture he stopped and adjusted his receiver again. "They're running," he said. DeMaso's dogs Ella and Angie swung around in front of us and picked up the birds. I readied my camera. Cox stopped and pointed with his antenna toward a half-acre shin oak motte.

Twenty yards from the motte, the dogs began catwalking, and just as they came to a stop the birds spurted out the opposite side, sailed 200 yards, set their wings and banked out of sight behind a low hill. The dogs bustled excitedly in the shin oak. DeMaso shrugged and whistled them out and we headed toward the scattered covey. Cox's receiver chirped. "I've got 'em," he said.

Radio Technology

Biologists divide quail research history into two eras: BT and AT—Before Telemetry and After Telemetry. Prior the early 1980s, before radio technology reached the point where quail could be safely fitted with radio collars, researchers relied primarily on bands, tags, dyes, hunter surveys and plain old leg work to track quail movement.

Legendary Texas biologist A.S. Jackson literally camped out with bobwhite coveys for days at a time to track their movements. As unsophisticated as these techniques seem by today's standards, they were effective—researchers were right far more often than not. Imagine what Herb Stoddard could have done with today's technology.

After the ground-breaking successes at the Tall Timbers Research Station in the mid 1980s, telemetry came into wide use and biologists were able to look at the bobwhite's life with striking clarity. Long held beliefs were suddenly cast aside while many of the suspicions held by biologists and experienced hunters were confirmed. But some of the findings were shocking.

Bobwhite quail are homebodies, we're told. Every hunter knows that. Yet the latest evidence suggests that we might be mistaken.

Big-Going Bobwhites

Biologists have the sometimes maddening habit of couching their statements. "Our data suggests that..." or "based on the evidence, it's conceivable that..." I like pat answers, but the experts couch their remarks with good reason.

Bobwhite quail are homebodies, we're told. Outside of the spring breakup and the fall shuffle they live out their lives within a square mile or so. Every hunter knows that. We've heard it and read it time and again. Yet the latest evidence suggests that we might be mistaken.

In October 1991 biologists with the Oklahoma Department of Wildlife Conservation began a study on the Packsaddle Research Area in western Oklahoma to learn the effects of supplemental feeding of wild bobwhites. Quail were trapped and three to four birds per covey were fitted with radio collars. Predictably, the researchers found that feeders are of little benefit to wild bobwhites, although by concentrating the birds they sometimes make things easier for predators and lazy hunters. The surprise came when birds began to disappear, radio and all. At first the researchers assumed the radios had malfunctioned or had been destroyed or carried away by predators.

To make sure, they made concentric searches around the perimeter of the research area, hoping to pick up signals, but they found nothing. The following spring, they flew over the countryside in an airplane and found their birds.

"In the spring of 1992 we found the first bird seven miles from the research area," said Scott Cox. "That surprised us. Then we found another bird about 10 miles away. That fall we found one 35 miles away and several had moved about half that distance.

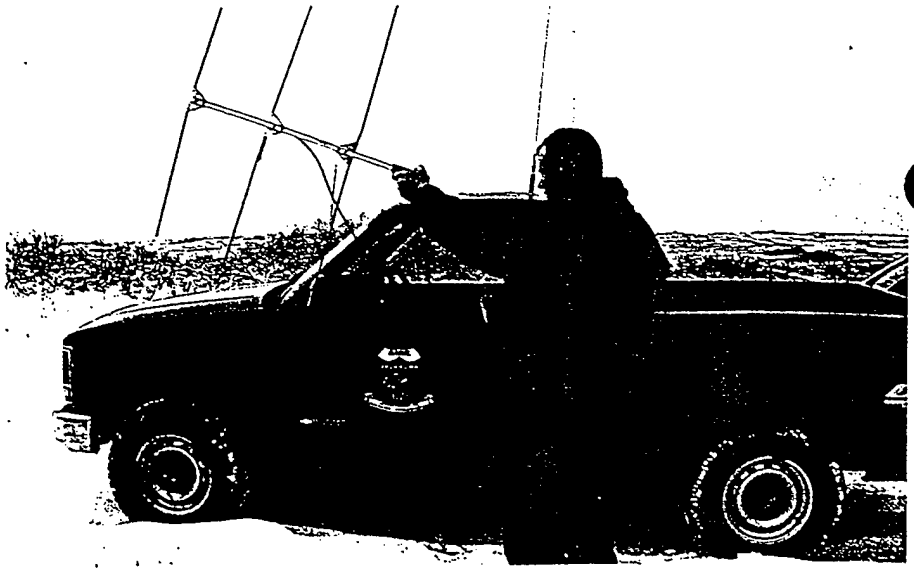
"They moved in all directions but most moved north to northeast. And we have no idea why. In most cases, they moved to habitat that was no better than the habitat they left and in some cases they moved into inferior habitat. Movements of a mile per day were typical."

Then there was the legendary Bird 908 that moved six miles in one day, another four miles the next, then fell into a back-and-forth pattern of six miles forward one day and six miles back the next. "We were sure that radio was in a coyote's stomach," said Cox. "But we got permission from the landowner and I walked out there and flushed the bird—a single male."

I find the idea of migratory quail intriguing, but Steve DeMaso, in the true tradition of cautious wildlife



Lightweight radio collars allow biologists to track bobwhite movements without adding significantly to mortality.



Wildlife Technician Scott Perry gets a bearing on a covey at Oklahoma's Packsadle Research Area.

experts, brings me back to earth. "We're not sure that this behavior is typical across the bobwhite's range. There may be something unique about this area that causes our birds to move around so much." But just think...little columns of bobwhites marching forth to fill up every available acre of habitat...Okay, I suppose further study is called for.

Evasive Maneuvers

In *The Old Man and the Boy*, Robert Ruark told us (through the Old Man) that the bobwhite is a gentleman and must be approached gentleman to gentleman. I agree completely, but standards change.

Don Dietz is a wildlife biologist with Temple Inland Forest Products. "Since I started tracking radio-tagged bobwhites, I'm surprised anyone ever kills a quail," he said. Dietz oversaw an ambitious study, funded by Temple Inland, to develop quail management techniques for the East Texas Pineywoods. Through habitat improvement and introduction of wild transplanted birds, Dietz and his associates increased the quail density on several thousand acres of pine forest from next to nothing to nearly a bird per acre. Throughout the study, radio telemetry was used to track mortality and movement.

"Time and again, I've had radio-collared birds run ahead of the dogs and me, and as often as not, they double back and end up right back where I initially picked them up. They never stop for me or the dog. Here in East Texas, we love our close-working dogs, but we've had the best luck using a close worker along with a big runner wearing a beeper collar. The big runner will be the one to catch and pin the running coveys. Then the close worker handles the singles.

"We've also been very surprised at the number of birds in three- to six-year old pine plantations, but these plantations are basically unhuntable. We've actually lost transmitters in them because we couldn't get the birds to flush."

Probably the most extensive use of radio telemetry to date is being made under the Albany Quail Management Project, a huge study funded by quail plantations in south Georgia and northern Florida and overseen by Auburn University's Department of Zoology and Wildlife Science. "We've put radios on nearly 2,000 bobwhites," said Project Coordinator Clay Sisson. Although the project is aimed at nearly all facets of quail management, Sisson and his associates just completed a five-year study on the effects of hunting parties on bobwhite behavior on the Nilo and Pineland Plantations in southern Georgia.

According to Sisson, hunters and their dogs found only about half of the coveys along their hunting routes. Most of the coverys that were missed simply sat tight and allowed





Wildlife managers have long known how to produce wild bobwhites. Continuing research not only adds to the body of knowledge but enriches the sport of quail hunting as well. *Photo by Brad Carter.*

the dogs and hunters to pass. Sisson said that entire hunting parties, dogs, horses, mule-drawn wagons and all, often passed within a few yards of coveys without knowing it.

About a third of the missed coveys simply ran away from approaching dogs and hunters or ran away from dogs on point before hunters could dismount or climb down from the wagons and walk past the dogs. Not surprisingly, running birds were the primary reason for false points. Many of the coveys ran a hundred yards, and one covey ran 500 yards before flushing wild. Also, coveys showed an uncanny ability to screw themselves into the ground.

In some instances tight-sitting coveys were located and pointed by dogs, but amazingly the hunters were unable to flush them. Thirteen percent of the missed coveys flushed wild. About half of these were pointed but flushed prematurely while the others flushed as the party approached and were never detected. Both running and wild flushing were more pronounced late in the season.

What do birds do after they flush? "Most of the time birds fly much further than you think they do," said Steve DeMasso. "Often you think they're going down, then they set their wings and peel one way or another after they've flown behind or below some type of cover or land feature. Then they'll either run again or screw themselves into the ground cover.

"Lots of times we'll see them go down and start tracking them with the antenna and they'll flush again before we get within 60 yards of them. Or we'll watch an 18-bird covey go down and we'll go right at them and only get one or two birds up. They're survivors. They definitely know how to avoid detection."

...entire hunting parties, dogs, horses, mule-drawn wagons and all, often passed within a few yards of coveys without knowing it.

The Need for Speed

Wildlife managers know from hard-earned experience that stocked, pen-raised quail provide an easy meal for resident predators. Yet biologists with the Texas Parks and Wildlife Department feel that game farm quail may prove valuable in the battle to save one of our endangered species.

"The Attwater's prairie chicken is on the brink of extinction," said retired Small Game Program Leader Don Wilson. "We're looking at both wild and pen-reared quail hoping that some of the things we learn can be used in developing techniques for the protection and propagation of prairie chickens.

"Prairie chickens have now been produced in captivity at Fossil Rim Wildlife Center, Texas A&M, and the Houston Zoo—that had been a big stumbling block. The second part of the problem is to produce birds that can survive and reproduce in the wild."

Using a radar gun, Wilson found that wild quail flew an average of about 28 mph while pen-raised birds averaged around 19 mph. First generation captive birds—captive quail with trapped wild parents—averaged about 20 mph. But speeds varied drastically, even among wild birds. Birds flushed at night typically flew faster than those flushed during daylight hours, and the researchers were very surprised at the low speeds they measured in the heavy South Texas brush. "I think quail fly as fast as they need to to get away," said Wilson. "We clocked a bird at 36 mph that was being pursued at night by a horned owl."

Experienced quail hunters won't be surprised to learn that the fastest quail are those flushed in front of bird dogs. On a North Texas quail hunt, Wilson clocked a bobwhite at 47 mph. "Hunting pressure makes a dif-



Wildlife technicians band and radio tag an Oklahoma bobwhite.

Except as noted, photos by the author.

ference," said Wilson. "We took readings on birds in South Texas after they had been hunted for about 100 days. A lot of those birds clocked in the 40s and we rarely saw one of them land."

The differences go beyond speed. After being released and flushed, the wild birds flew an average of nearly 70 yards. Pen-reared birds, on the other hand, flew an average of only 30 yards, and first generation captive birds flew an average of about 35 yards. The researchers also noticed that when a covey of wild birds was released one bird at a time, all subsequent birds took the exact same flight path as the first bird. The pen-raised birds typically flew in random directions.

"We were certain that the wild birds were keying on the sound of the wing beats so they could land close together out in the brush and regroup without an assembly call," Wilson said. To test their theory, the researchers put a covey of trapped wild birds in the cab of a pickup, rolled the windows up and turned the radio on, then released one quail at a time. Sure enough, nearly every bird took a different direction.

Survival in the wild often comes down to a fraction of a second. Wilson summed it up well: "If I'm part of a bunch of birds heading for cover and they're going 28 and I'm going 20, I'm going to be the one that gets eaten."

The Future

"The quail chicks are the missing link in our research," said Steve DeMaso. From hatching to six weeks of age when we first put a radio on them, we really don't know what's going on. You've got a hen with a brood and suddenly the chicks are gone. What happened? All we can do is guess because we really don't know."

That'll be changing soon. Late last spring, DeMaso and his associates with the Oklahoma Department of Wildlife Conservation began testing tiny state-of-the art radios that can be worn by chicks only five days old. As soon as researchers are sure that the tiny radios aren't causing excessive mortality, a full-fledged quail chick study will begin.

Through the study of radio-tagged adult hens, Packsadle researchers have already documented double brooding and, more interestingly, polygamy. Oklahoma biologists coined the term "gypsy hen" to describe hens that leave their clutches with males then pair up and nest again with another male.

All of the researchers felt that more emphasis should be placed on chick survival. "Nesting and brood-rearing form the bottleneck in quail management," said Don Dietz. "Food plots are important in the Southeast, but not for the reason most people plant them. Adult quail just don't eat that much of the planted seed. We've found that the best reason to plant food plots is for their ability to produce insects for young chicks. Our telemetry studies showed that within a day of hatching, the hens took their broods directly to the nearest food plot—obviously for the insects."

Sisson added, "Most hunters worry about survival of adult birds, but a coon eating a nest full of eggs is a lot more significant than a Cooper's hawk killing an adult bobwhite in January."

Of course the research never ends. In addition to the chick telemetry study, the Oklahoma researchers plan to study the effect of hunting on bobwhite movements, while Sisson and his associates are working to determine the effects of weather on quail behavior and pointing dogs' ability to find them. Quail hunters should note that much of the current research is being paid for by Quail Unlimited chapters, bird dog clubs and other private conservation groups.

Biologists know how to raise wild quail. According to Sisson, hunters on the Pineland and Nilo plantations often moved 40 or more coveys per day during the 1996-97 season. So why should we spend time and money studying polygamous hens and chick feeding habits? Inevitably it comes down to attitude.

Are bobwhites merely targets, a source of food and recreation, or do they matter for their own sake? Watch a serious quail hunter's reaction to the bobwhite's springtime proclamation and you'll get your answer. Robert Ruark's Old Man was right about at least one thing. Associating with gentlemen can't hurt you. ❑

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Quail & Habitat Forest Management

WHAT ARE THE OPPORTUNITIES?

by W. Keith Moser
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Tallahassee, Florida

illustrated by
Nicole G. Sherriff

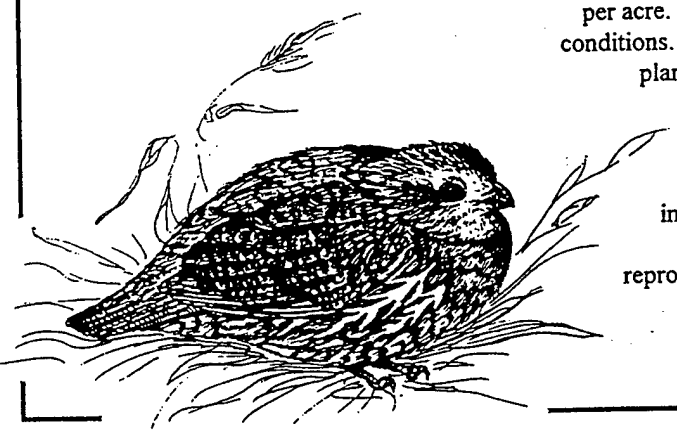
Herbert L. Stoddard once defined the management of bobwhite quail as "creating a surplus to be harvested by the gun." As with many of Stoddard's ideas on managing bobwhites, he was right then and now. However, the challenge for today's forest managers who want to produce huntable quail populations is determining how quail management fits into modern silvicultural systems with current economic pressures.

Gone are the days (1890-1920) when crude agriculture mixed with native forest ground cover to produce quail in abundance. The patchwork of field and mature forest provided the right habitat to create remarkable quail populations. While quail are no longer an automatic byproduct of current land management, proper habitat management can still produce abundant quail for the hunter. Maintenance of high quail densities is expensive; however, moderate quail numbers are more economical. The goal of this paper is to provide the landowner with the necessary information to develop strategies for quail and timber management on their lands.

BIOLOGY

Life History

Quail are relatively sedentary with small home ranges (10-50 acres) in areas of good habitat. In poor habitat, home ranges greater than several hundred acres have been documented. If given the proper habitat, densities can reach greater than one quail per acre. As many as three quail per acre have been documented in ideal habitat conditions. Densities around two quail per acre have been maintained on shooting plantations in Florida since the 1920s, demonstrating that intensive habitat management still works today as it did in Mr. Stoddard's era.



Bobwhite quail populations suffer high annual mortality rates. Research has documented annual mortality rates as high as 95 percent in heavily hunted populations; however, 65-80 percent mortality is more the norm. To offset high annual mortality, quail have an impressive reproductive potential. Quail breed from April to September and hatch nests from May until October. Hens lay about one egg per day with a typical clutch consisting of 12-15 eggs. Clutch size declines, however, as the season progresses. By September clutch sizes from five to 10 eggs are

common. Quail are vigorous renesters and under some circumstances may produce three or more nests in a single season. A hen may produce multiple clutches, sequentially, with the same or different mates. As many as 30 percent of nests in a given year may be incubated by males, while the hen is producing another nest. In the past, it was thought that males only incubated nests if the hen was killed by a predator. The message here is that quail are adapted to be highly productive given the right weather and habitat conditions. A single hen has been found to produce more than 50 chicks in a single year. Given their high mortality rate, managing habitat for nesting and brood rearing is paramount to producing huntable surpluses of quail. While quail use a long breeding season to produce a successful clutch, maintaining quality nesting and brooding habitat throughout the nesting season is important because weather conditions can greatly affect the timing and success of nesting.

Once hatched, quail chicks forage vigorously on arthropods, mostly insects. A 3-day-old chick consumes 2-3 grams of insects each day and by 10 days of age is eating as much as 6 grams of insects per day. That translates into hundreds of insects per day. Energy and protein provided by insects drive growth and feather development which are critical to chick survival. Studies of game birds similar to quail have linked arthropod abundance to the survival of chicks and to shootable surpluses available in the fall. Therefore, it is critical that management of lands to produce a huntable surplus of birds provides adequate insect-rich brood habitat.

Habitat

Northern bobwhite use early successional (i.e., weedy) habitats across a variety of landscapes in the South. Shootable populations can be produced in agricultural, forested and mixed landscapes. This section will outline the important characteristics of five key components of quail habitat: nesting, brooding, loafing, escape and feeding cover. To maximize quail numbers, each of these should be present within each 20-30 acres of your managed areas—however, less will do if lower numbers will suffice.

Nesting Habitat

Having adequate quantities of quality nesting habitat is vital to producing quail. Quail usually locate nests in residual vegetation from the previous growing season. This type of vegetation is found in areas not burned or disked for two years. Patches of sparse broomsedge or other warm-season grasses offer excellent cover for nesting. Quail will avoid nesting in areas where the ground is covered with thick vegetation. Preferably, patches of nesting habitat should be two to 10 acres. Small patches of nesting cover make nests more vulnerable to predators. Also, plan to locate nesting cover on upland sites, away from lowlands that harbor many nest predators. Preferably, nesting habitat should cover 15-30 percent the landscape.

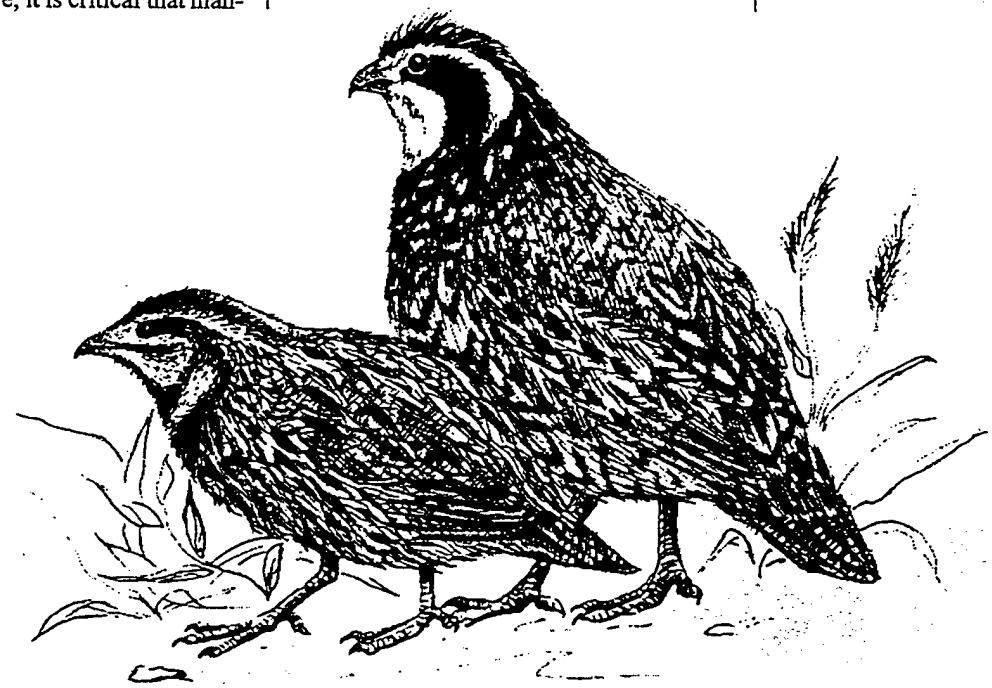
Brood habitat

Quail chicks require a diet rich in insects. They also need cover from predators and loafing areas for escape from mid-day heat. Brood habitat is provided by a low (20-60 inch) canopy created by herbaceous vegetation that maintains a relatively open nature underneath. Areas with bare ground exposed (20-60 percent) are selected by chicks. For instance, ragweed or partridge pea create an excellent ground cover for broods and produce excellent insect populations. As with nesting cover, thick ground cover is avoided by broods. Brood habitat does not need to be large—one to five acres will suffice—but it should be well-dispersed and near nesting cover.

Loafing cover

Quail with broods and fall/winter coveys often have loafing areas for resting, dusting and eluding the mid-day sun in summer. Quail chicks quickly become uncomfortable when exposed to the mid-day su Broods often use shaded areas beneath t perennial vegetation, such as pokeberry, with bare ground underneath. In the winter, coveys use woody thickets, impenetrable to avian predators, for loafing cover.

continued on page 58



continued from Quail Management *page 57*

Escape Cover

In open woodlands or agricultural areas, significant amounts of thicket are often necessary to localize coveys throughout the hunting season. Too much cover, such as large 4- to 8-year-old pine plantations, can reduce hunting opportunity. Providing well-dispersed patches of cover 15-50 yards wide increases the suitability of an area for quail and improves hunting success. Destroying too many thickets is a sure way to reduce the number of coveys on a property, especially during late winter.

Feeding Habitat

Though an opportunistic seed-eater, the quail's diet varies by season, sex and age. Table 1 shows the breakdown of food sources, by volume, taken from a sample of crops. In fall/winter, seeds of legumes, cultivated grains, tree mast and other seeds are important. Spring and summer, greens and insects are important for hens producing eggs. Consider that a single clutch of eggs weighs about as much as the hen—of which she may produce several. Later summer and early fall, grass seeds and fruits are taken. As mentioned earlier, insects are the primary diet item for quail chicks.

Quail prefer to forage directly from the ground and up to 12 inches above the ground. They are weak scratchers; therefore, maintaining areas of understory vegetation with ample bare ground exposed underneath is a critical aspect of feeding habitat. Planting food patches can help to localize coveys of quail for improved hunting. While no research in the South has demonstrated a quail population increase due to supplemental feeding or food patches, food patches are used heavily by quail in habitats with poor mast and low food resources in the winter. Table 2 provides some suggestions for planting food patches. If you are interested in planting prescriptions, contact your state wildlife agency, extension specialist or Quail Unlimited.

Quail Management Strategies

Habitat Management Tools

Quail require areas that have been disturbed within the past one to three years. Disking and prescribed burning are common techniques for producing the proper groundstory conditions for all components of quail habitat. It is, however, the frequency and distribution of disturbance that "make or break" each component of quail habitat. To provide the proper groundcover environment, aggressively thin your stands. Remove hardwoods not directly related to mast production and reduce the stocking of your pines.

Disking

Strip disking through open woodlands and abandoned agricultural fields was developed by Stoddard in the 1920s as a method to produce brood and feeding habitat for quail. Disking in November through January can create excellent brood habitat the following summer, depending on soil fertility. Recent research at Tall Timbers found that broods selected these areas over areas that were disked in the spring. In the fall and winter, areas disked the previous fall are used by quail as feeding habitat. Disking can be incorporated into habitat management by disking fire lanes, feed patches, skid lanes, landing areas, open woodland patches and fallow agricultural fields. Disking up to 30 percent of an area each year is not extreme, but it is expensive. Given a choice between spending money on planting food patches or disking more acreage, the latter has a better chance of increasing quail populations.

If a landowner plans to use food plots on a widespread basis, he needs to make proper

Table 1. Food habits of bobwhites collected on Tall Timbers Research Station. (Numerals in the body of the table are percent volume of crop contents. Numerals in parentheses indicate the number of birds in each monthly sample).

Food Item	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
	(20)	(10)	(10)	(10)	(10)	(10)	(16)	(19)	(20)	(20)	(20)	(20)
Pine seeds, small acorns	81	84	67	20	2							
Legume seeds	13	3	20	21	4	3	5	10	1	6	8	1
Greenery	1	1	2	31	4				1			
Insects	1	1	1	9	20	24	37	19	22	25	5	2
Soft Mast (berries, etc.)			1		9	61	29	23	18	14	1	
Grass seeds					20	1		29	45	1		
Misc. seeds	4	11	11	19	41	11	29	19	13	20	5	6

Source: Landers and Mueller 1992

management of the deer herd part of the overall quail management plan.

Prescribed Burning

Prescribed fire is the best tool, ecologically and economically, for maintaining quail habitat because it:

- makes food easier to find after the litter is removed;
- reduces populations of ectoparasites, such as ticks;
- promotes important seed-producing plants, such as legumes;
- improves the structure of the groundstory for quail;
- releases minerals and ash tied up in vegetation - a net fertilizer effect;
- reduces hardwood encroachment; and
- increases palatability and nutrition of green shoots.

Burning or disking in a forest with high canopy cover will accomplish little. Also, burning infrequently, say every three to five years, will accomplish little for quail management.

On sites without significant native ground cover, prescribed burning can be practiced from the end of hunting season at least until late April to early May. Sites with species that sprout soon after the first warm spell, such as the annual lespedezas, are better burned during this time. On sites with significant amounts of wiregrass or other native ground cover, the vegetation is generally adapted to lightning-season burns. Burns during April, May and June will increase the likelihood of successful reproduction of these native species. These burns will also reduce the encroachment of hardwood tree species that eventually increase canopy closure and reduce the amount of light reaching the forest floor. Preliminary studies indicate that limited "growing season" fires do not negatively impact quail populations.

The objective in prescribed burning is to control the fire so that growing space is increased for seed- and insect-producing plants while leaving necessary amounts of escape, loafing and nesting cover and food. The best results are obtained from a mosaic pattern with 50-75 percent of the site burned with the remainder in scattered patches. This diverse condition could be achieved through night burning or during the day after a rain has stopped. Another alternative is to burn about one-third of the area in 10- to 40-acre units each year, covering the entire property over three years. Using this methodology, the nature of the fire is not as critical to the "mosaic," but can be designed to cover each unit well, thereby providing some quail and forestry benefits. The landowner should understand that vegeta[illegible] types, weather patterns and governm[illegible] regulations are the ultimate constraints o[illegible] the timing and location of a burn. The intensity of the fire and the uniformity of the fuel influence the variability of the post-burn site. Where fuels are uniform and lend themselves to high-intensity fires, mechanical fire lines or "ring-arounds" can provide nesting, food or cover sites.

If a landowner wishes to use prescribed fire on his property, he should consult with experienced land managers or forest consultants about the necessary equipment, required permits and smoke management techniques. Here in the South, landowners and managers face increasing numbers of new residents who have neither the connection with the land and its products nor a fair understanding of fire. Prescribed fire practitioners must recognize that the right to burn can be taken away by a public mistrustful of unprofessional conduct.

Forest Management and Quail

Most professional foresters will tell you that forest management activities must be

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Table 2. Cultural information for selected plants of use in quail food plots.

Plant	Establishment Source	Establishment Time	Fertilizer [a]
Browntop millet	10[b] seed; 25 [c] seed	Summer	500 lb./ac 6-12-6
Doveweed (wooly croton)	15 [c] seed	Spring	200 lb./ac 6-12-6
Florida beggarweed	10 [c] seed	Spring	400 lb./ac 0-14-14
Annual lespedezas	10 [c] seed	Early Spring	250 lb./ac 0-14-14
Partridge peas	15 [c] seed	Late Winter	250 lb./ac 0-20-20
Sesbania	15 [c] seed	Spring	250 lb./ac 0-20-20
Vetches	25 [c] seed	Sept.-Oct.	500 lb./ac 0-16-12
Clover (crimson)	20 [c] seed	Late Aug.–Early Oct.	500 lb./ac 0-16-12
Bush lespedezas	5 b seed; 15 [c] seed; seedlings [d]	Winter	400 lb./ac 0-14-14
Bush honeysuckles	Seedlings 10 ft. spacing	Dec.–Feb.	Per plant: ¼ lb. 6-12-12
Plums	Seedlings 10 ft. spacing	Dec.–Feb.	Per plant: ¼ lb. 6-12-12

[a] Adjust PH by adding lime (one to two tons/acre may be needed).
[b] Pound per acre in rows 2 ½ to 3 feet apart, later cultivated between rows
[c] pounds per acre
[d] one-year-old seedlings planted 18 to 24 inches apart in rows 3 to 3 ½ feet apart.

(Taken from Landers and Mueller 1992).

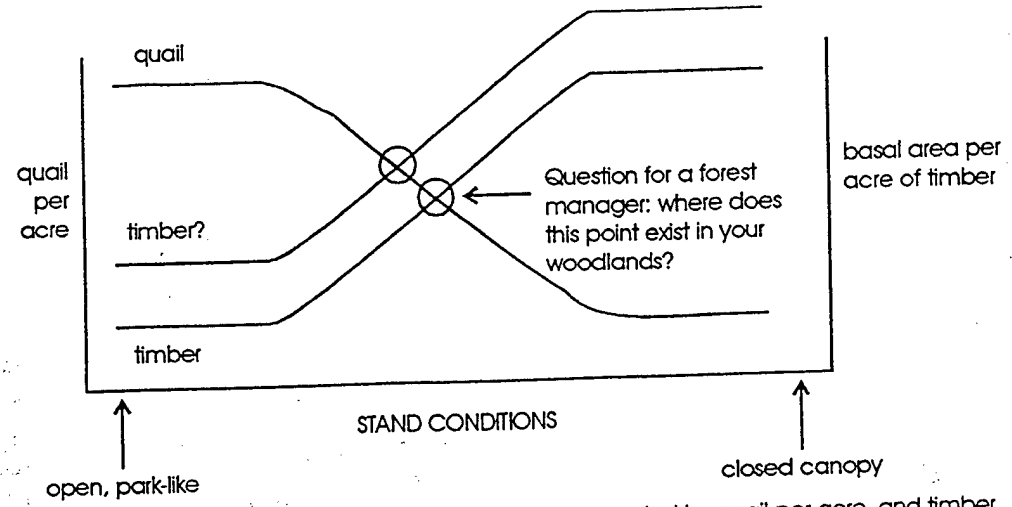


Figure 1. A theoretical diagram of tradeoffs between quail productivity, represented by quail per acre, and timber productivity, represented by basal area of timber per acre. There is a very strong interrelationship between the amount of timber in the overstory and its effect on quail habitat, which, in turn impacts the amount of shootable quail. Where the tree canopy covers more than 50 percent of the ground, quail numbers drop dramatically.

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directed at the objectives of the landowner. On some properties, the objective is to maximize the number of shootable quail on the site. Other landowners want to emphasize timber management, while providing for some quail hunting. Still others want a moderate amount of annual timber income along with a moderate amount of quail. No matter the objective, a quail management program should integrate forest management into its objectives for ecological, economic and aesthetic reasons.

Figure 1 shows that there is a tradeoff between quail management and timber management. You cannot maximize both quail and timber on the same piece of land. A high basal area results in full occupancy of the site, a greater degree of self-pruning leading to fewer quality-reducing knots. Such a forest management strategy will allow almost no light or moisture to support the cover and food plants that quail require. A lower basal area can lead to growth being concentrated on fewer trees, in some cases resulting in trees reaching sawlog size sooner, although there are fewer trees per acre. The landowner needs to choose: how much timber (quail) will he give up for a certain amount of quail (timber)?

A landowner interested in quail management should ask himself the following five questions:

- Is your land mainly forested or a mix of forest and agricultural fields?
- Is your forest young or mature?
- Are your trees at normal stocking or understocked?
- Are you interested in even-aged management or uneven-aged management?
- Are you willing to pay whatever it takes to get high quail numbers on your land?

We do not have enough space to answer all combinations of the aforementioned questions, but let's look at a few examples.

Example 1:
If you have a mature even-aged stand

If you have a mature even-aged stand, you can begin quail management by thinning now, reducing the overstory basal area. On good sites, even-aged stands can run to 120 square feet basal area per acre. Such stocking levels allow little light or moisture for the ground cover and are too dense for quail habitat. On the shooting plantations in the Red Hills region of southern Georgia and northern Florida, forestland managed exclusively for quail generally has 35 to 50 square feet per acre. In other parts of the South, even-aged stands with at least some quail on them have an overstory that can vary from 30 to 90 square feet per acre. Well-burned stands in the Ouachita Mountains of Arkansas can carry 70 to 75 square feet of basal area on sites where hunters can find up to 10 coveys per day. Uneven-aged stands may vary from 45 to 80 square feet per acre. Conventional wisdom among wildlife biologists is to keep the basal area at levels equal to the site index—25. For example, such calculations would result in a residual basal area of 60 in a stand with a site index of 85. Where quail management is the principal focus, the canopy should not cover more than 50 percent of the ground. Start burning the understory on a short-interval cycle, say every one to two years. Begin disking on a wide-scale basis (10-30 percent of the ground cover). Smaller and more frequent harvests may be necessary to maintain several patches of habitat on the landscape. After harvesting, postpone replanting a year or two and reburn the cutover sites to maintain the herbaceous component.



Year 1	Year 2	Year 3	Year 4	Year 5
Second best year for quail (by slight margin over year three). Pine seedlings planted. Quail foods present are mostly annual plants, led by ragweed, followed by small partridge peas and crabgrass. Some perennial lespedezas begin to occur.	Best year for quail. Planted pines still too small to affect other vegetation. Annual plants continue to dominate, again led by ragweed. Next most common quail food is common lespedeza. Crabgrass and small partridge peas decrease while perennial lespedezas and beggarweeds increase.	Third best year for quail. Pine trees becoming significant in size, beginning to compete with quail food plants. Quail foods have peaked. Small partridge pea is most abundant quail food. Large partridge peas increase while ragweed and common lespedeza decrease in abundance. Perennial lespedezas and beggarweeds at maximum.	Quail now becoming scarce. Pine trees becoming a dominant species in the clearcut. Most quail foods declining, though small partridge peas continue to persist along with *lespedeza procumben.*	Virtually no quail to be found. Pine trees forming canopy and shading out ground. Quail food plants succumb to shading, pine needle accumulation and competition from hardwood sprouts, blackberries and broomsedge.

Figure 2. The impacts of clearcutting on quail populations.

Try to avoid using herbicides in site preparation for trees, particularly those chemicals targeting herbaceous species. You can also plant food plots to localize quail and improve your hunting. These tactics will bring your quail population up quickly, but they are expensive and must be maintained over the years.

Example 2: If a landowner has a young, normally stocked, even-aged stand

If a landowner has a young, normally stocked, even-aged stand, conduct prescribed fires starting 10 years after establishment. One can thin most planted stands between nine and 13 years after planting. Subsequent thinnings every eight to 12 years will remove poor-quality stems, favor growth of the crop trees and provide more light to the understory. Frequent burning will maintain the proper habitat (food and cover) for the quail. By age 30 on an average site, the stand will have about 60 to 70 square feet of basal area. At an age of 40 to 80 years, the final cut will remove saw logs. Manage all possible areas for brood and nesting cover, including the agricultural fields.

Example 2a:
If a landowner has a young, normally stocked, uneven-aged forest

If an owner desires to have an uneven-aged forest, the transition from the original even-aged stand to an uneven-aged forest is made over a period of years before the final harvest of the original overstory. Single-tree (loblolly-shortleaf) or group selection (longleaf) harvesting systems will allow the landowner to maintain quality quail habitat while retaining the opportunity of some economic returns from timber removals. These systems can reduce cash outlays for regeneration, concentrate growth on sawlog production and, once the stand structure is regulated, provide steady, but low, quail numbers and some timber income.

Example 3:
If you have large open areas

If you have large open areas, plant pines in strips to improve quail habitat. One property in coastal South Carolina broke up 20- to 30-acre crop fields with planted pine, laid out in strips eight to 12 rows wide. Although the original spacing was 8 by 8 feet, thinnings reduced the density so that light

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reaching the ground and moisture conditions were reduced, providing for quail food and cover plants. Also, the landowner kept a strip of grasses and legumes on both sides of this band of trees, supplying nesting cover through the middle of the fields.

Example 4:
In mixed woods and agricultural fields

To produce quail in mixed woods and agricultural fields, it may be more economical to relinquish some income from agricultural activities, than to intensively manage small- to medium-sized woodlots. These areas present special opportunities to manage for bobwhites. Crop land can be improved, especially grain crops, as summer habitat by providing fallow strips of vegetation 15-30 feet wide around each field. If fields are greater than 10 acres, consider leaving fallow strips down the center of fields. It is important that cover be present during the early spring and that these areas are not mowed each fall, but periodically disked to control hardwood encroachment. No-till management of crops, especially planting into wheat stubble or spring planted wheat, dramatically improves corn and soybean fields as brood and provides some nesting cover. Managing woodland edges in early successional habitats (i.e., small cutovers bordering fields that are periodically burned) provides winter cover and escape cover. Grain crops provide winter food resources. This should be combined with managing the larger upland blocks of forests in a more open state with prescribed burning and disking used to maintain the proper mix of groundstory vegetation types.

Logging and Herbicides: Implications for quail management

Harvesting in forest stands not only removes trees but also disturbs the soil, both of which are beneficial to quail woodlands. If the pre-harvest woodland was dense, a good boost in quail numbers might last from three to five years after harvest. After that,

Suggested Reading

The following publications will provide a more comprehensive explanation of the various aspects of quail habitat management. Landowners are strongly advised to use consulting foresters, state wildlife extension personnel or Quail Unlimited representatives before embarking upon a quail management plan.

Quail Management

Jackson J.J. 1989. Bobwhite quail on your land: Tips on management for Georgia and the Southeast. Athens GA: University of Georgia College of Agriculture Cooperative Extension Service Bulletin 950. 70 p.

Landers J.L., Mueller B.S. 1992. Bobwhite quail management: A habitat approach. 3rd ed. Tallahassee: Tall Timbers Research Station Misc. Pub. No. 6. 39 p.

Rosene W. 1984. The bobwhite quail: Its life and management. Augusta: Morris Communications Corp. 418 p.

Stoddard H.L. 1931. The bobwhite quail: its habits, preservation and increase. New York: Charles Scribner. 559 p.

Tall Timbers Research Station. Proceedings of various Annual Game Bird Seminars.

Prescribed Fire

Robbins L.E., Myers R.L. 1992. Seasonal effects of prescribed burning in Florida: A review. Tallahassee: Tall Timbers Research Station Miscellaneous Publication No. 8. 96 p.

Wade D.D. 1988. A guide for prescribed fire in southern forests. Asheville: US Forest Service Southern Region Technical Publication R8-TP 11. 56 p.

Merck L. 1991. Prescribed burning–a management tool. Athens GA: University of Georgia, College of Agriculture Cooperative Extension Service Bulletin 838. 18 p.

Forest Management, Thinning and Herbicides

Cooperative Extension Service. 1990. Georgia Forest Landowner's Manual. Athens GA: University of Georgia College of Agriculture Bulletin 950. 70 p.

McNeel J.F. 1986. Thinning your timber for profit. Athens GA: University of Georgia College of Agriculture Circular 781. 70 p.

Moorhead D.J. 1989. Regenerating southern pine in Georgia. Athens GA: University of Georgia College of Agriculture Circular 775. 11 p.

Nebeker T.E., Hodges J.D., Karr B.K., Moehring D.M. 1985. Thinning practices in southern pines–with pest recommendations. Atlanta: USDA Forest Service Technical Bulletin 1703. 36 p.

Uneven-aged Forest Management

Baker J.B., Cain M.D., Guldin J.M., Murphy P.A., Shelton M.A. 1996. Uneven-aged silviculture for the loblolly and shortleaf pine forest cover types. Asheville: US Forest Service Southern Research Station Genl Tech Rept 118. 65 p.

Farrar, Robert M. 1996. Fundamentals of uneven-aged management in southern pine. Moser W.K., Brennan L.A., editors. Tallahassee, FL: Tall Timbers Research Station Miscellaneous Publication No. 9. 66 p.



the forest management activities will determine the quail population dynamics. Large clearcuts will probably show an increase in quail numbers for a few years, but the vegetation will soon grow so thick as to become unsuitable for quail.

If there are thick growth and few quail, logging can be done at any time. Sites logged during the winter might see quail move in the following summer, but sites logged in the summer will not see any significant increase in quail numbers until the following nesting season. On sites with an open canopy and numerous quail, the sites should be logged from September to January if there is no hunting on the land. Sites should be logged from September to November and March to April, if there is to be hunting on the land. Harvesting during nesting season (late April to June) will cause abandonment of nesting and reduced and late hatches. After areas are logged, brush piles provide attractive nesting and loafing sites for quail for one to three years.

Herbicide use has long been an accepted practice in industrial forestry operations. Their prudent use can have a profound effect on planting survival and initial growth of pine seedlings. There is a very positive effect from using hexazinone (Velpar and Pronone) in first year release. Imazapyr (Arsenal) and triclopyr (Garlon) will also give excellent results when used with established seedlings. When used as release treatments, both hexazinone and imazapyr will help legumes, important quail food, by eliminating competitors. Herbicides are not uniform in their killing power, however, and may cause a successional buildup of species that "got away."

Conclusions

Quail management can be practiced simultaneously with forest management. However, landowners must decide how much timber they want vs. how much quail. A greater emphasis on timber returns would dictate denser stocking, whereas a quail emphasis would require a more open stocking. Once the overstory stocking levels are chosen, a disturbance regime of fire and/or mechanical disturbance, such as disking, is essential in maintaining the food and cover plants used by quail. The overstory species and understory growth will dictate the intervals between prescribed fires.

Whether you choose an even- or an uneven-aged system, the length of time the tree cover remains on the site must take into account the need to maintain the quail habitat. Once you decide on your quail to timber ratio, management of quail woodlands can provide timber income and quail hunting opportunities for the landowner.

Acknowledgements

The authors wish to thank Leonard Brennan, Bob Farrar, Jim Guldin, Steven Lindeman, Ron Myers and Rich Pouncey for their suggestions in the preparation of this article.

For more information: contact Tall Timbers Research Station, Route 1, Box 678, Tallahassee, FL 32312-9712.



Albany Area Game Management Project

A newsletter for plantation owners, managers, and hunters

Fall 1995

Inside this issue:

- ♦ Weather and "the hatch"
- ♦ Feeding study update
- ♦ Burning study update
- ♦ Pen-raised project update
- ♦ Insect study update

"Bird patch" study

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SUMMER WEATHER AND "THE HATCH"

Summer weather patterns have long been considered one of the most important factors affecting quail reproduction. We have been fortunate to have monitored a good sample of radio-tagged birds through the last four reproductive seasons over a wide range of summer weather patterns. Below is a table presenting data on the hatch from one of our study areas for that time period:

# radio-tagged birds (April)	110	110	120	80
# nests located	63	39	73	46
# nests hatched (%)	32 (51%)	10 (29%)	31 (43%)	23 (50%)
chicks survival (to 2 wks)	54%	34%	33%	39%
# double broods	5	0	4	4
# late hatches (after Aug 15)	15	0	9	5

The most significant information in this table is the low reproductive output in 1993. It's no coincidence that this was also the driest of the four years studied. The dry weather during this summer (only 64% of the normal rainfall) affected the birds, the habitat, and the hatch. The cover was light and the "buffer" foods are items that predators eat instead of quail. This light cover and lack of buffer foods apparently caused nesting success to be very low. Only 29% of nests hatched successfully due to increased depredation. These conditions also affected the physiology of the birds, causing them to basically shut down egg production

after July. Ceasing egg production prematurely accounts for the low nest production, lack of double broods, and little or no late summer hatch.

The summer of 1994 was the wettest on record but the hatch under those conditions was significantly better than during the drought year in 1993. The heavy rains apparently had no severe adverse effect on nesting and chick survival and also derived to produce abundant native feed, cover, insects, and "buffer" food sources for predators—all of which helped the hatch.

The heavy rains had no severe effects on nesting and chick survival

This year's hatch was similar to last year's 1994 effort on this study area. Although it was somewhat dry the second half of the summer (83% of normal rainfall), the drought was not as severe as the 1993 drought. Nest production, nest success, and chick survival were all good and there was a decent late summer hatch. This should equate to a bird population roughly the same year as last year's. In addition, it appears that we will not have a bumper live oak acorn crop like last year. Last year's abundant acorn crop made hunting difficult because food was everywhere and birds were hard to hem up. Rainfall patterns throughout the region were highly variable this summer with some areas experiencing severe droughts and some getting rainfall.

Expect quail populations and hunting success to vary depending on the local summer wet/dry patterns. The take home of this is: **wet is basically good and dry is basically bad for quail reproduction.**



FEEDING STUDY UPDATE

Two full years have now been completed on our supplemental feeding study. Previous newsletters have reported on the benefits of a well-planned feeding program. Reproductive output both years was initiated sooner on the fed area.

Total reproductive output was greater on fed areas

This past summer, following an abundant native feed supply during the winter, total nest production was about the same even though nesting started about a month earlier on the fed course. The dry weather apparently had no effect on the late hatch on this study area as there was not much nesting activity on either the fed or unfed course in August and September. Supplemental feeding is especially important in dry years in areas where native food and cover production is poor.

Plans this year are to begin feeding the course that has now been without any supplemental feed for two full years. There is no doubt that the quail population and hunting success have suffered over the past two years because of not having supplemental feed on this area. We wish to express our sincere appreciation to those involved who have suffered through our experiment. Additionally, plans are to add a high protein source to the supplement beginning on February to see of we can further boost the reproductive output of quail on this area. We will report on future newsletters.

BURNING STUDY UPDATE

In our summer 1995 newsletter we indicated that a study of post-fire cover effects on survival and nesting success had been initiated. We have now completed one nesting season with that study and preliminary results are very interesting.

On one hunting course a large number of small post-fire cover blocks was left. Traditionally, many quail managers create this type of small (less than 1 acre) ring-arounds to leave escape and nesting cover after spring burning. On another course post-fire cover was left in fewer large unburned blocks were laid out, the percent of the area left unburned was 12.4% on the small ring-around course and 23.4% on the large cover block course. Survival and reproductive output were monitored for a sample of radio-tagged birds on each course.

There was no difference on post-burn survival between the 2 courses; however, reproductive output was substantially different. On the course with a low unburned percentage, 27 radio-tagged birds produced 21 incubated nests of which only 9 hatched. None of the 7 May nests hatched on this course with the small unburned blocks (All were destroyed by predators). On the course with larger blocks of unburned cover, 21 radio-tagged birds produced 19 incubated nests of which

Predators find more and more nests in small burn blocks

12 hatched. Eight of these nests and four broods were produced in May.

These results strongly suggest that the way post-burn cover is managed can have a serious impact on nest production and success, especially early on the nesting season. We believe that predators have an easier time finding nests in the smaller blocks compared to the larger unburned blocks. Next spring, plans are to replicate this study by switching treatments on the two areas. If nest success is higher on the course with the larger post-burn blocks, this will demonstrate that larger blocks produce more quail.

PEN-RAISED PROJECT UPDATE

We are well underway in our study of pre-season release techniques and pen-raised bird survival. This study is designed to compare the effectiveness of a Smith/O'Neil type release system to a "dump" release. The Smith/O'Neil type release incorporates a permanent structure with feeder, waterer, and call bird. In the "dump" release birds are simply released into a thicket with some feed and water. After one month this study has shown that mortality from avian and mammalian predation is high on both areas but is higher on the dump site (survival: 39% dump, 51% Smith/O'Neil). Covey

Pen raised hens laid three nests, hatched, and raised two broods

integrity and localization of coveys appears to be maintained better under the Smith/O'Neil system. Besides survival and movement data we are maintaining records of costs of each system in terms of cash outlay and manpower. We plan to continue our studies of pre-season release techniques and will report more later.

SPECIAL RESEARCH NOTE :

From the 12 radio-tagged pen-raised birds remaining from the fall of 1994 release, we had 6 incubated nests and 3 broods produced over the summer. This included one 1994 pen-raised hen that incubated 3 different nests and successfully hatched and raised 2 broods. It appears to us that if fall-released, pen-raised quail survive until the spring breeding season, they are essentially "wild" quail.

Table 1. Listed below are the major management actions that Mr. Roger Croft, Manager of Sedgwick Land Company, and other workers conduct on the property each month.

JANUARY	FEBRUARY	MARCH
1. Feeding corn with spreaders. 2. Hunting - ducks, quail, deer. 3. Discussing and preparing for timber cutting. 4. Planting longleaf seedlings. 5. Ringing shortleaf and loblolly natural regeneration.	1. Hunting quail. 2. Preparing firebreaks. 3. Harrowing bird rings. 4. Feeding corn. 5. Usually begin timber cut.	1. Begin burning. 2. Timber cutting. 3. Harrowing food plots. 4. Feeding corn.
APRIL	**MAY**	**JUNE**
1. Continue burning. 2. Feed corn in rings and unburned areas. 3. Harrowing food plots.	1. Burning. 2. Begin planting food plots (Egyptian wheat).	1. Planting food plots-Egyptian wheat, chufas. 2. Some late burning. 3. Mowing drives; road work.
JULY	**AUGUST**	**SEPTEMBER**
1. Hardwood control - field edges and strips. 2. Repairing duck blinds, docks, etc. 3. Plant duck ponds. 4. Mowing drives.	1. Hardwood control; mowing. 2. Mowing drives.	1. Begin some chopping and mowing in bottoms. 2. Continued hardwood control.
OCTOBER	**NOVEMBER**	**DECEMBER**
1. Blocking in preparation for hunting. 2. Planting oats and wheat food plots. 3. Begin feeding corn.	1. Blocking. 2. Final preparation for hunting season. 3. Feeding corn.	1. Hunting. 2. Longleaf planting. 3. Feeding corn.

160 West Rhode Island Avenue
Southern Pines, NC 28387
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16 January 1997

Suzanne Oberholster
Forest Botanist
USDA Forest Service
1 Forest Drive
Brent, AL 35034-9593

Dear Suzanne,

Enclosed is a copy of a portion of my final report on the Alabama and Mississippi seepage bog survey. I have sent you the section which lists all Alabama sites that were surveyed, under which are given the rare plants found at each.

Although I was unable to survey all the known seepage bogs in the Conecuh National Forest, the ones listed in this report represent a large percentage. These include many of the ecologically most important bogs in the state. In my estimation, Curious Bog, Hines Lake Bog, Pleea Bog, and Wreck Bog rank up there with the best of the whole Gulf Coastal Plain. Crawford Bog is large and diverse and very likely harbors more rarities than I saw in my one visit; no doubt these will show up following a burn.

In 1997 I will be returning to the Gulf Coastal Plain to do survey work on longleaf pine communities. I will let you know if it will involve more work in the Conecuh NF.

Sincerely,

Bruce

Bruce A. Sorrie
Contract Botanist

Large Woody Debris – The Common Denominator For Integrated Environmental Management Of Forest Streams

C. Andrew Dolloff

INTRODUCTION

Knowledge about ecology and environmental issues has exploded in the last half of the 20th century. Concerns for environmental quality have become major political issues, and an increasingly informed public now demands comprehensive solutions to complex environmental problems. Such well publicized issues as preservation and recovery of individual endangered species have provoked the strongest reactions. Since passage of the Endangered Species Act, decision makers, scientists, and managers have been obliged to recognize that endangered species management may entail, among a host of other considerations, genetics research, captive breeding programs, and habitat manipulation. An integrated approach to resolving issues of environmental management should provide insights unavailable from the perspective of individual disciplines and help forestall-or at least foresee-potential future problems. The utility of an integrated approach to management extends far beyond concerns for the welfare of individual species to strategies for managing entire ecosystems. Nowhere is the need for integrated solutions greater than at the interface between terrestrial and aquatic systems, the riparian zone. And few features of

riparian zones in forested areas, aside from water and trees, are as conspicuous as large woody debris (LWD).

Today most stream ecologists recognize that a variety of aquatic species depend on the natural accumulation of trees, branches, and root wads collectively known as LWD. In the past, however, many managers treated LWD as a liability. Many Federal and state land management agencies and some private corporations had policies that mandated debris removal from watercourses or supported programs of clearing and snagging. Agency decision-makers invoked these policies in the name of flood prevention, habitat improvement or simply because LWD was unattractive. Although careful removal of individual trees and debris accumulations can be justified for safe, efficient navigation of large rivers and to protect property or individual stream and river crossings (bridges, fords etc.), wholesale removal of LWD from rivers and small streams disrupts ecological processes and radically changes habitats for a multitude of aquatic species. In this chapter I summarize the many functions of LWD in streams and describe the role of LWD in creating and maintaining fish habitat. I also outline the implications of past management of LWD in streams and waterways in the southern Appalachians.

WHAT IS LWD?

To many ecologists, any piece of wood 2.5 cm in diameter or greater is LWD.[1] Although pieces of wood this size and smaller play significant roles in stream ecology, they are more readily dislodged and moved downstream by flowing water and thus, have less influence on stream channel morphology and fish habitat. Based on its potential to influence channel morphology, LWD is any piece of wood at least 10 cm in diameter at the small end and 1.5 m in length. LWD can be whole trees with tops and root wads, branches, snags, or detached tree boles. In general, the larger the piece (both in diameter and length), the more likely it is to stabilize and influence stream channel morphology. Because of the anchoring effect of roots, entire trees with root wads attached are most likely to make long term contributions to habitat.

Even pieces that are not in the water at low or average flows can make important contributions to instream habitat: both bankside and suspended debris "bridges" (pieces that span the channel) and "ramps" (broken bridges or pieces that do not span the width of the channel) have the potential to influence stream channel morphology by deflecting flow and encouraging scour when streamflows approach bankfull.[2] Debris dams, typically composed of one or more pieces of LWD and many smaller pieces, slow the flow of water, trap sediment and organic matter and create microhabitats for fish and benthic macroinvertebrates. In larger rivers, snags and deadheads provide cover and enhanced feeding opportunities, attracting both prey and predator species.

LWD is not slash—typical logging residue composed of small trees, tops, and branches.[3] Except in the smallest of streams, slash tends to be unstable and contributes relatively little to instream habitat. Large amounts of fresh (green) slash and finely divided logging debris may even cause local depletion of dissolved oxygen[4] or buildup of toxic residues.[1,5,6] However, individual whole trees that accidentally enter a stream during logging operations should probably be considered LWD.

FUNCTIONS OF LWD

There are several excellent reviews that explore the ecology of LWD in detail[1,3,7] and while no attempt has been made to duplicate or supersede those efforts in this chapter, a brief overview of the roles played by LWD is necessary to appreciate its significance in stream and riparian ecology.

Many ecological processes are associated with LWD in streams, ranging from providing sites and raw material for primary and secondary production and the formation of critical habitat for fish, to control of water and sediment yield from watersheds (Table 1).[1,3] LWD provides both a grazing surface and food source for a host of microbes and aquatic invertebrates. Seston and inorganic sediments trapped and stored by debris dams or around LWD accumulations are more readily available for instream processing by macroinvertebrates and microbes.[8] During high flows sediments are trapped and stored, and downstream flood peaks may be delayed and damped by instream accumulations of LWD in the headwaters.

From the perspective of many fish species, pool formation probably is the most important function of LWD. Many species of fish are attracted to the lower water velocity and greater water depth in pools. In the pools of mountain streams, trout frequently occupy and defend positions in slow or slack water from which they make forays after insects and other food items in the faster flowing drift. Pools are especially important when fish are under stress, such as during conditions of extreme high or low flow.

Pools form around any material that creates friction and resists displacement by flowing water. While virtually everything in the channel creates friction, including the stream bottom and sides, LWD, boulders, and bedrock protrusions are the dominant pool forming elements. LWD is the most conspicuous of these elements, and may play a role in the

Table 1. Overview of functions and processes in streams influenced by LWD.

Physical	Biological
Habitat formation	Competition
Type	Inter- and intraspecific
Frequency	Predation
Sequence	Aquatic
Complexity	Terrestrial and avian
Water regime	Anglers
Storage	Primary and secondary production
Delivery	Substrate for microcosms
Quality	Source of fine organic material
Sediment regime	
Storage	
Delivery	

formation of up to 100% of pools in small to medium sized streams flowing through undisturbed forests.[1] Many mountain streams in the southern Appalachians flow through old clearcuts or fields and have lost much of their LWD through the natural processes of decay and downstream transport. The percent of pools formed by LWD tends to be much lower in streams flowing through these second- and younger growth forests because the immature streamside vegetation is not yet able to contribute large amounts of LWD. Recent research in the southern Appalachians, however, suggests that LWD is a component in at least 50% of pools in streams flowing through riparian zones ranging in age from 28 to over 300 years since establishment.[9]

Pools develop around LWD in a variety of ways.[10] Plunge pools result when water flow scours sediment from the downstream side of LWD that spans the channel, dam pools form when water is backed up behind one or more pieces of LWD, and backwater pools are created by eddies where the ends of pieces or rootwads jut into the flow (Figure 1). In general, the deepest pools form behind pieces that span the entire width of the channel near the water surface and are oriented perpendicular to flow.[11]

In addition to its role in pool formation, LWD in the form of overhanging logs, debris jams, and especially root wads serves as complex cover, protecting fish from predation, excessive competition and physical displacement. Fish in pools with complex cover have greater opportunities to be visually isolated, which may decrease the number of behavioral interactions and permit greater numbers of fish to coexist.[11] Complex cover in deep pools is especially valuable during times of increased stress such as winter.[11,16] Fish find shelter from high streamflows in winter by moving into or behind LWD accumulations and rootwads.[17]

THREE TYPES OF POOL

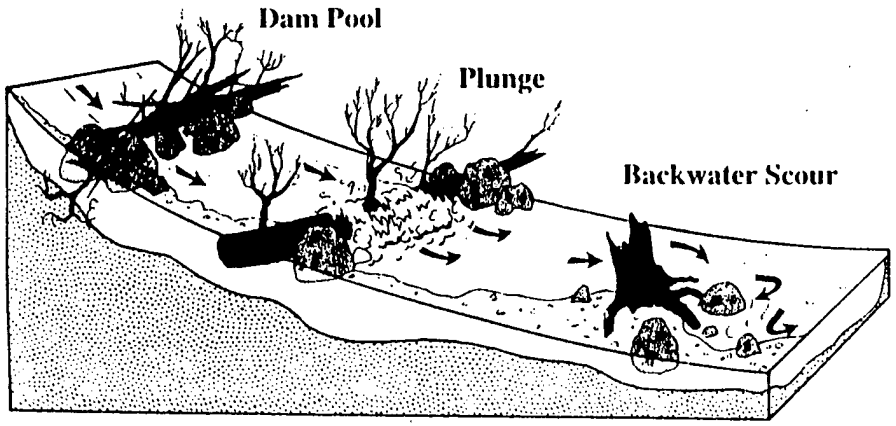


Figure 1. ...nes of pools formed by LWD.

Removal of LWD typically results in loss of pool habitat[18] and complexity[19] and low fish numbers, average size, and biomass for both warmwater[20] and coldwater fish species.[12,21,22,23] Habitat simplification following timber harvest and subsequent decreases residual LWD loading and input also has been linked to long term changes in the speci composition (diversity) of fish communities, including shifts in dominance and the disa pearance of formerly common species.[24]

Recent research on ecological disturbance and refugia - areas that remain habitat during extremes of drought, flood, or other disturbance - has emphasized the importan of maintaining connectivity among stream channels, accessory or side channels and rip ian zones as sources of LWD.[25] Refugia are fail-safe habitats from which fish and oth aquatic organisms recolonize following disturbances; the quality and frequency of refu greatly influences the stability and resilience of aquatic systems. LWD is a major featu of refugia across a multitude of habitat types and spatial scales, from individual pieces pools to large accumulations distributed across stream channels and floodplains of ent drainage basins. The variety and availability of refugia for aquatic organisms is grea reduced in streams and rivers that have been channelized, cut off from their floodplains, lack significant amounts of LWD. Fish assemblages in several flood-damaged watershe in the Blue Ridge Mountains of Virginia, for example, become isolated in individual poo when streams become intermittent because of low flows. Fish of several species pack in these residual pools, where they survive until flows return to normal, but are vulnerable predation and deteriorating water quality.[26] Researchers are attempting to increase surviv by decreasing fish densities per pool in a small stream on the George Washington Natio Forest by adding LWD to encourage the formation of additional refuge pools. Simi efforts are underway in other parts of the country to benefit trout, salmon and other nati fish species.

INPUT AND LOADING

Most LWD enters streams from a relatively narrow band on either bank; over 70% the LWD in streams flowing through mature and old-growth riparian zones in weste Washington and Oregon originated within 20 m of the stream bank.[27] Debris can be intr duced from more distant sources on floodplains and hillslopes, however, when transport by floods or debris torrents.[1,2,28,29] Large woody debris enters streams as the soil surrou ing root systems is eroded by flowing water. Bankside trees are then easily toppled further undercutting, windthrow or the extra weight of rain, ice or snow. Rates of LW input vary depending on factors such as size of receiving stream, age, species and health trees in the surrounding riparian zone, and historical land use.[2] When widespread, dise can greatly influence LWD loading. In the Eastern United States a blight has virtua eliminated the formerly common American chestnut, resulting in atypically high LW loads (except where valuable chestnut logs were salvage logged) composed primarily blight-killed chestnut trees.[9]

The greatest inputs of LWD can usually be traced to specific catastrophic events su as debris flows, floods, tornados and hurricanes.[1,5] LWD loading in the Basin Creek wat shed, for example, more than doubled over previous levels — from 39 to 88 pieces

kilometer of stream channel— after Hurricane Hugo swept over northwestern North Carolina in 1989. Much of this, however, was relatively small LWD reflecting the short time interval (~60 years) since the riparian zone began reverting to a forested condition.

In general, the proportional loading of LWD is higher and its contribution to structure and function is greater in headwater tributaries than major rivers.[30] Some low gradient large rivers in the southeastern United States, however, display trends of increasing instream LWD loading with increasing steam order.[31] The observed lack of LWD in many other large rivers is at least in part an artifact of river management. Over 800,000 snags (average length 40 m) were removed from the lower 1,650 km of the Mississippi River between 1830 and 1880 to improve navigation.[1] In later years, many other rivers across the United States received similar treatment.[1,32]

The particular arrangement of instream LWD is influenced by the dynamics of the addition process, stream size, and geomorphic characteristics of the site.[1,5] In small streams (first and second order), many patterns are possible but generally pieces do not move after input because small streams have little power to move larger pieces. The arrangement appears to be random but is determined by the source; pieces stay where they fall or move very little after input. Complex debris dams, composed of smaller LWD and wood fragments, leaves and forest litter are prominent features of small headwater streams in forested watersheds.[33]

Accumulations of LWD in streams of intermediate size (second to fourth order) tend to be clumped along the margins or at channel constrictions, creating secondary channels or meander cutoffs. Stream power is sufficient to float pieces from streambanks and upstream accumulations but many pieces may still span the width of the channel. Submerged pieces can remain in place for many years, influencing channel morphology and habitat formation by trapping or scouring sediments. In larger channels (4th order and greater), LWD forms tightly clumped accumulations at the heads of point bars and secondary channels, islands, and along the outside curve of meander bends.

Once in the channel, LWD may persist only until the next high flow or for hundreds of years depending on the attributes of the site (stream order, presence of channel constrictions, etc.) and relative size and quality (resistance to decay) of the LWD. Among other characteristics, smaller pieces have relatively higher surface area to volume ratios and lower proportions of decay resistant heartwood than large pieces; consequently, rates of fragmentation, abrasion and decomposition or disappearance through floatation may be higher for small versus large LWD.[1] LWD tends to exhibit a continual cycle of loss and replenishment in systems that have been undisturbed for a long time. As some pieces are lost or moved about, new pieces take their place, preserving the state of dynamic stability.

The highest loads of LWD usually are associated with coniferous forest types in riparian zones adjacent to streams in the Pacific Northwest;[1] up to 4500 m³/ha were estimated in a stream flowing through a redwood stand in northern California.[34] Outside of redwood country, typical LWD loads range from 2.5 to 1700 m³/ha. Estimates of LWD loading tend to be lower in southeastern streams (40-300 m³/ha),[1] owing in part to the long history of settlement and land clearing in the East. The most comprehensive inventory of LWD in southern Appalachian watersheds showed that loadings were highly variable depending on land use and disturbance histories, the number and variety of riparian tree species that

contribute to LWD accumulations, and the dynamics of American chestnut input relative to the chestnut blight.[9] LWD loadings, particularly those originating in mature and old-growth forests, were lower than expected and considerably lower than those in comparably sized Pacific Northwest streams.

In the absence of anthropogenic disturbances, streams flowing through Eastern forests probably would have substantial loads of LWD. Streams in unlogged watersheds in the Great Smoky Mountains National Park contain, on average, four times more LWD (338 vs. 84 m³/ha) than streams of comparable size in watersheds logged before the Park was established in the 1930s.[35] Elsewhere in the southern Appalachians, Flebbe and Dolloff[36] found higher loads of LWD in unmanaged (unlogged) versus managed (logged within the last 60-80 years) wilderness watersheds (Figure 2).

IMPACT OF PAST LAND USE

Of the many factors that affect LWD input to streams, perhaps the most significant is the legacy of past land use. Since antiquity, engineers have regarded LWD as a hinderance to navigation and commerce on large rivers and an impediment to efficient drainage of small watersheds. In more recent times, biologists have advocated debris

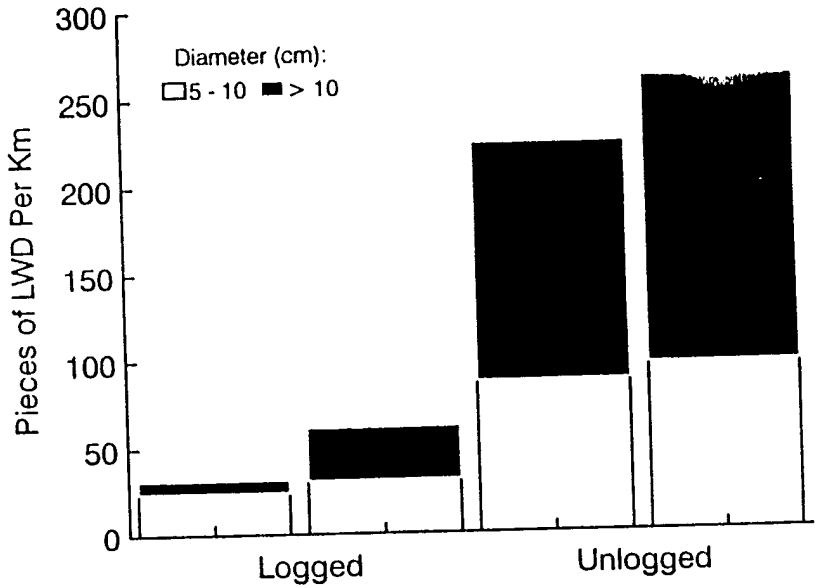


Figure 2. Loading of LWD in two streams flowing through second growth (logged 60-80 years ago) and two streams in old growth (never logged or cleared) wilderness areas in the southern Appalachians.

removal on the grounds that it might degrade water quality, harm fish habitat or block fish migration.[37,38] And even the most casual observers agree that wood debris in streams is unsightly.

We now understand the important role that LWD plays in stream ecosystems. Under natural conditions, LWD would be a key ecological component in most if not all river systems flowing through forested regions of the world. But centuries of forest and river management worldwide have changed the composition and appearance of most forested watersheds so that it is difficult for most people to appreciate the importance of LWD. Rivers and streams in Asia[39] and Europe[1] were cleared of boulders and debris hundreds of years ago to facilitate log driving. On the North American continent, land clearing and development of waterways as transportation networks began in the late 1600s. From 1867-1912, the U.S. Army Corps of Engineers oversaw the clearing and removal of many hundreds of thousands of snags, logs and debris piles from rivers all across the United States.[1]

Nearly all of our larger streams, rivers and lakes have been used to raft or drive logs to sawmills at some time over the last 300 years.[40,41] While the actual drives were responsible for significant damage to sensitive stream beds and banks and riparian areas, the stream improvements that preceded these drives were equally if not more destructive. Side channels and backwaters were blocked to keep logs in the main channel and ensure high water levels, and obstructions of all types were hauled, burned, or blasted out of the way.

The pattern of land clearing in the southern Appalachians generally proceeded from downstream to upstream. With the depletion of timber from floodplains and readily accessible lowlands adjacent to larger rivers, lumber companies were obliged to penetrate further into the mountains for supplies of their raw material. There they encountered rough country and small streams not well suited to traditional log driving activities. As was true in New England[42] the Great Lakes states,[43,44] parts of the Intermountain West,[45] and the Pacific Northwest,[46] splash dams, flumes and slides were common in parts of the southern Appalachians.[42,47-49]

One of the best documented examples of stream modification occurred from about 1907-1910 on the Russell Fork of the Big Sandy River in southwest Virginia.[47,50] There, near the Virginia-Kentucky State line, the Yellow Poplar Lumber Company constructed a 110 meter long, 7.5 meter high splash dam to help transport its supply of yellow poplar timber through the Breaks of Sandy into Kentucky and on to its mill in Coal Grove, Ohio. Over 50 million board feet of yellow poplar logs (average diameter 63.5 centimeters, length 0.5- 11.5 meters) passed through bays of the dam and down the Russell Fork during the few brief seasons of operation. Forty men labored for two months and used nearly 10,000 kilograms of dynamite to remove all obstructions in the 24 kilometers of stream immediately below the dam. The effect of the initial stream improvements and subsequent repeated torrents of wood and water totally transformed the character of the river; at the present time, the stream channel upstream and downstream of the dam (the main supports of which survive as the piers for a highway bridge) superficially resembles a u-shaped channel of glacial origin (Figure 3).

Many other rivers with headwaters in the Appalachians suffered similar fates, including the Tellico in Tennessee and West Fork Chattooga in Georgia. On a weekly schedule

until, after a few brief seasons the supply of logs was exhausted, water and logs were simultaneously released from behind three dams, each 122 meters long and 12 meters high, on the major forks of the Tellico.[51] Despite its current status as a Wild and Scenic Waterway, much of the watershed of the West Fork Chattooga River was logged and its timber transported by splash dams long before it received protective status or was included in the National Forest system.

Mountain streams continued to play an important role in resource extraction even after railroads had taken over much of the job of log transportation. Transportation by rail was



Figure 3. Splash dam at the head of the Breaks of Sandy, Russel Fork, Big Sandy River, Southwest Virginia, in 1910 and 1988.

more expensive than by water, which was used whenever conditions permitted. Companies frequently ran short lines to transport timber from remote coves and small drains to rollways and log dumps on the larger rivers. Transportation by rail did little to protect even the small streams, as stream gravels were mined to build roads and rails were frequently laid directly over stream channels.

Much of the cutover lands in the southern Appalachians eventually were acquired by the Federal Government in the 1920s and 30s. These "lands that nobody wanted" and the streams that drain them have largely reforested and are managed by the U. S. Departments of Interior and Agriculture in national parks and forests.[48] With the return of the forest, however, knowledge and understanding of the changes caused by past land use are fading from memory.

MANAGEMENT OF LWD

If we accept the premise that LWD is and will likely continue to be in short supply in many streams and rivers, then restoring loads and ensuring the future supply of LWD should be of major concern to managers. Arguments for maintaining or supplementing LWD loads include promotion of channel and habitat stability, habitat enhancement (holding, hiding areas), habitat restoration, and enhanced recreational use, primarily angling. On the minus side are the potential for localized damage from flooding, particularly at stream crossings, interference with fish passage, and conflicts with recreational uses such as canoeing and rafting. Because it influences so many ecosystem functions, criteria for LWD management should be based on input from many different disciplines, including (but not necessarily limited to) fisheries, stream and landscape ecology, geomorphology, hydrology, silviculture, and engineering. At all stages in the development of management plans, the public must be informed and given opportunities to voice concerns and opinions.

Of course, LWD is but one of a host of considerations in the broader domains of riparian and watershed management.[52,53] Riparian zones influence temperature, sedimentation, and basic ecological processes such as nutrient uptake and cycling. Many plant and animal species depend on the unique characteristics of riparian zones and wetlands to fulfill virtually all of their life history functions. Still other species rely on the relative security of riparian zones for nesting or rearing young or to facilitate movements and migrations among habitats. Along with an appreciation of the various natural functions and values of riparian zones has come increased human use. Riparian zones are now being managed for their ability to sequester nutrients, filter sediments, and grow specific agricultural and forest crops.[54,55] Lastly, because riparian zones form the highly visible boarders of streams and rivers, physical appearance is a major concern of managers who must respond to public perceptions and demands for recreation in aesthetically appealing settings.[55]

Other values notwithstanding, providing both current and future LWD for instream habitat is a legitimate objective of riparian management. In contrast to policies and practices that once allowed harvest of all streamside trees and mandated removal of all debris from stream channels, public land managers and some private industrial landowners have established standards and guidelines for riparian management and have even set goals for

LWD recruitment. This abrupt about-face has created some credibility problems for managers and biologists, who for many years demanded that loggers remove all debris, frequently including natural debris, from stream channels. Now they are told that not only is debris removal nearly always unwarranted but also that we should expend time and effort to deliberately put debris back in. The term "stream improvement," at one time used by loggers and rivermen to mean removal of any hindrance to free flow, including LWD and large rocks or boulders, now has exactly the opposite meaning.

Management of LWD will be most effective when approached from an entire watershed rather than an individual stream reach perspective. Examination of conditions at the watershed scale may expose stream reaches of exceptionally high or low quality that on the ground are indistinguishable from adjacent reaches. Information from aerial photographs, topographic maps, and ground-based inventories of habitat, riparian vegetation and LWD can be computerized in a geographic information system (GIS) and manipulated to produce graphic images of watershed conditions. A comprehensive plan for LWD management can then be developed with site specific goals and objectives.

How does one determine if LWD loading is "too low?" Where they exist at all, criteria for LWD loading are highly variable, depending on historic conditions, local topography, size and availability of tree species, and the composition and needs of the aquatic community. To date, there have been very few attempts to manipulate and link specific amounts of LWD to fish production. In general, however, LWD loadings are too low when the number and quality of pools and cover is low and the stream lacks hydraulic complexity.[5] Although the optimal amount and frequency of habitat types in mountain streams is probably unique for every stream, an approximate 1:1 ratio of pools to riffles is generally considered desirable.[56] The determination of what constitutes sufficient amounts of LWD is even more uncertain, but may be based on historic records or inventories of loadings in undisturbed watersheds. If such records or undisturbed areas do not exist, then loadings can be approximated by comparison with LWD loads in similar streams that appear to have "good" habitat, or by inference based on the outcome of controlled experimentation with different LWD loads in reference watersheds.

Techniques to modify stream structure range widely in expense and complexity. Engineered stream improvements such as wing deflectors, cribs and sills that are carefully designed to promote specific hydraulic action such as channel constriction or pool scouring are usually stable and effective but costly in both labor and time.[57] It also is possible to temporarily restore LWD by adding logs and rootwads, pulling or pushing over trees with winches or heavy equipment,[57] or toppling trees with strategically placed explosives.[58] But clearly, placement of individual stream improvement structures or trees is not feasible on a large scale. Alternatively, given enough time, many disturbed riparian areas will recover on their own, regain the characteristics of mature forest, and once again provide LWD. Unfortunately, "enough time" may mean at least 50[59] or as long as several hundred years. A flexible approach is therefore necessary, employing a mix of techniques to address both specific current conditions and long term goals for natural LWD recruitment.

In contrast to the relatively simple, if costly, techniques for actively inputting LWD, arriving at strategies for long term recruitment of LWD will tax the abilities of experts in many disciplines. The diversity of riparian zone functions and values suggests that advo-

cates for LWD must compete for their future raw material (trees) with proponents of other uses. It may be necessary to limit salvage of storm, fire or insect killed trees, for example, to a specified distance from the streambank to preserve sources of LWD until understory trees mature.[60]

Width of streamside management zones (SMZs) should be based on objective criteria including the probability of LWD recruitment. Except as a result of catastrophic additions such as debris flows or landslides, most LWD in the coniferous forests of the Pacific Northwest enters from a 20-30m wide band of riparian forest on both sides of the stream.[16] Similar relationships, although incompletely described, probably exist in other parts of the country as well. Robison and Beschta[61] suggest that a SMZ should be wide enough so that if a tree in the SMZ falls perpendicular to the stream channel, the portion of the tree that intersects the channel has the minimum diameter and height necessary to qualify as LWD. Models for LWD recruitment, such as those developed for watersheds in the Cascade Mountains of Oregon[62] and the coastal forests of southeast Alaska,[61] can be valuable tools for deciding the width of SMZs.

The appropriate species or mixture of species to be managed for LWD is an open question, depending on site suitability, resistance to decay, and other riparian management objectives. For example: in the southern Appalachians, northern red and white oak have high aesthetic value and produce hard mast and other benefits for wildlife, high quality timber, and decay-resistant LWD.[55] Eastern hemlock, while of lesser value for timber, provides thermal cover during both winter and summer and is very resistant to decay.

The emergence over the last 20 years of knowledge of the many roles played by LWD has contributed greatly to both the science and practice of riparian ecosystem management. Armed with this knowledge and an appreciation for the benefits of interdisciplinary, integrated approaches to management, present and future generations of managers will be better able to meet the increasing demands for traditional and potential new uses of riparian ecosystems.

SUMMARY

A variety of aquatic species depend on the natural accumulation of trees, branches, and root wads known as large woody debris (LWD). LWD slows the flow of water, dissipates energy, traps sediment and organic matter, and creates microhabitats for fish and macroinvertebrates. LWD in the form of overhanging logs, debris jams, and especially root wads forms pools and provides complex cover. Removal of LWD typically results in habitat simplification and fewer, smaller fish. Habitat simplification resulting from timber harvest and subsequent decreases in residual LWD loading and input has been linked to long term changes in the species composition of fish communities. LWD is a major feature of refugia across a multitude of habitat types and spatial scales.

Most LWD enters streams from a relatively narrow band on either bank. Debris can be introduced from more distant sources on floodplains and hillslopes, however, when transported by floods or debris torrents. Rates of LWD input vary depending on factors such as size of receiving stream, age, species and health of trees in the surrounding riparian zone, and historical land use. The greatest inputs of LWD can usually be traced to specific catastrophic events.

The particular arrangement of instream LWD is influenced by the dynamics of the addition process, stream size, and geomorphic characteristics of the site. Once in the channel, LWD may persist only until the next high flow or for hundreds of years. The highest loads of LWD usually are associated with coniferous forest types in undisturbed riparian zones adjacent to streams in the Pacific Northwest. Estimates of LWD loading tend to be lower in southeastern streams, owing in part to the long history of settlement and land clearing in the East.

Centuries of forest and river management worldwide have changed the composition and appearance most forested watersheds so that it is difficult for most people to appreciate the importance of LWD. As was true in other parts of the country, log driving and splash dams were common in parts of the southern Appalachians.

Riparian zones are now being managed for their ability to sequester nutrients, filter sediments, grow specific agricultural and forest crops and provide recreation as well as LWD. Criteria for LWD management should be based on input from many different disciplines, including fisheries, stream and landscape ecology, geomorphology, hydrology, silviculture, and engineering. Management of LWD will be most effective when approached from an entire watershed rather than an individual reach perspective.

Engineered stream and direct additions of LWD can be effective stream improvements but are costly in both labor and time. Many disturbed riparian areas if allowed to recover on their own will regain the ability provide LWD, given enough time. A mix of techniques is necessary to address both specific current conditions and long term goals for natural LWD recruitment.

The diversity of riparian zone functions and values suggests that advocates for LWD must compete for their future raw material (trees) with proponents of other uses. Width of streamside management zones (SMZs) should be based on objective criteria including the probability of LWD recruitment. Because of the different values associated with individual tree species, riparian species composition can be manipulated to meet specific management objectives.

Large woody debris is an effective model for implementing integrated environmental management.

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Herpetofaunal Drift-fence Survey of Steephead Ravines in Two River Drainages

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Abstract: A drift-fence survey of the herpetofauna of steephead ravines was conducted over 216 trapping days from 6 June 1995 to 6 June 1996 along first- and second-order streams in the Ochlockonee River drainage and along first- and third-order streams in the Apalachicola River drainage. Six drift-fence arrays in Apalachicola ravines had 1,223 captures of 34 species, whereas 6 arrays in the Ochlockonee ravine had 2,283 captures of 31 species. In the Ochlockonee ravine, more anurans were captured along the second-order than the first-order stream. In Apalachicola ravines, more Apalachicola dusky salamanders (Desmognathus apalachicolae) and turtles were captured along the third-order stream, whereas more southeastern slimy salamanders (Plethodon grobmani) and broadhead skinks (Eumeces laticeps) were captured along first-order streams. Along first-order streams, significantly more lizards were captured in Apalachicola ravines, whereas more three-lined salamanders (Eurycea guttolineata), southern red salamanders (Pseudotriton ruber), and anurans were captured in the Ochlockonee ravine. Salamander captures in both river drainages were significantly correlated with precipitation, but because of small sample sizes due to infrequent captures during the cooler months, anuran captures were not correlated with precipitation. Recaptures made up 11.1–12.8% of anuran and salamander captures in both drainages, whereas reptile recapture rates differed among drainages, with lizards and turtles being recaptured more frequently than snakes. The unique biotic communities in steephead ravines would be severely impacted by land-use practices or recreational activities that resulted in canopy disturbance, erosional siltation, water pollution, or reduction in the quantity of ground water feeding the seeps and streams.

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Steephead ravines occur in deep sands across Florida's Panhandle from the Ochlockonee River west to the Yellow River. Steephead ravines are formed by ground water leaking out on a sloping surface and undercutting the sand, creating a steep-walled amphitheater that erodes headward from the valley bottom (Sellards and Gunter 1918, Sharp 1938, Means 1975, Wolfe et al. 1988, Means 1991). The floor of steephead valleys may be 30 m below the surrounding flat or gently rolling sandhill habitat, and the sloping sides may be as steep as 45°. Many of the best-developed steepheads occur in the first-order branches (Strahler [1964]

classification) of Sweetwater and Beaverdam creeks north of Bristol, Liberty County (Means 1985). First-order streams are nearest to the stream source, whereas second-order streams are formed by the confluence of first-order streams.

Since the 1930s, many herpetologists have collected specimens in Apalachicola River ravines, but only 1 short-term drift fence-survey (ca. 3 months of summer sampling) has been conducted in gully-eroded ravines there (Means and Studenroth 1994). Gully-eroded ravines are formed by the scouring action of rainwater surface runoff, and water flows in the stream channels only during and shortly after a rainfall, unlike the permanent stream flow found in steephead ravines (Wolfe et al. 1988). No surveys have been conducted in the shorter and shallower Ochlockonee River steepheads, which represent the easternmost steephead ravines in the Panhandle (Means 1981), but drift-fence surveys have been conducted in this drainage in upland hardwood forest (Means and Campbell 1981, Enge 1998).

The cool, shaded, humid Apalachicola ravines contain a rich and often unique flora (Harper 1914, Kurz 1933, James 1961) and provide important refugia for northern herpetofauna (Carr 1940, Neill 1957, Means 1977). Many of the endemic and northern aquatic and semiaquatic wildlife taxa in the Apalachicola River drainage are probably present because its headwaters originate deep in the southern Appalachian Mountains, which provided refuge during Pleistocene sea level rises, and the river provided a convenient north-south dispersal route for species (Carr 1940, Neill 1957). The physical and vegetational characteristics of steepheads are relatively constant both within and between drainages, but more studies are needed of the comparative similarities and differences among steepheads (Means 1977).

The objectives of the study were to (1) identify the herpetofaunal taxa occurring in steephead ravines; (2) compare the herpetofaunal communities of steephead ravines in the Ochlockonee and Apalachicola river drainages; (3) identify potential threats to steephead ravine herpetofauna; and (4) assess the effectiveness of drift fences constructed of silt fencing for sampling the herpetofauna of seepage communities. I am indebted to D. T. Cobb, D. G. Cook, G. L. Sprandel, and K. Smith for help installing drift fences, K. Wood for help collecting habitat data, and D. T. Cobb, D. G. Cook, J. B. Jensen, D. B. Means, and P. E. Moler for providing comments on various drafts.

METHODS

Study Areas

The study area in the Ochlockonee River drainage was on Talquin Wildlife Management Area (WMA) in western Leon County, Florida. The steephead ravine surveyed originated 0.4 km north of State Road 20 and 1.0 km east of Coe's Landing Road. The seepage stream was ≈0.6 km long and flowed northwesterly into Lake Talquin, an impoundment of the Ochlockonee River. Steephead walls were ≈15 m high and had 30–45° slopes at the headwaters of the stream, but farther downstream, where the drift-fence arrays were located,

sidewall slopes were more gradual and the valley was wider.

The 3 sites surveyed in the Apalachicola River drainage were on Robert Brent WMA in northern Liberty County, Florida. Two arrays each were located along 2 first-order steephead streams whose headwaters were 0.75 km apart and situated ≈2 km west of County Road 271. The seepage streams were 0.3 km and 1.2 km north of State Road 12 and flowed westerly for 2.0 and 1.2 km before joining and flowing northwesterly for 1.3 km into Big Sweetwater Creek. Two arrays were farther downstream on terraces along Big Sweetwater Creek, where it was a third-order stream. The closest arrays between the 2 river drainages were 44 km apart.

Sampling Design

Each drift-fence array had 3 arms modified from a design of Jones (1986). A roll of 30.5-m long and 92-cm wide silt fencing (Enge 1997) was used to construct each array. The arms radiated outward from a center point at 120° angles, and 4 funnel traps (86 cm long) constructed of aluminum window screening fastened together with office staples were used per arm. Single-opening funnel traps (25 cm diameter, 6 cm funnel opening) were placed on both sides of each fence at the distal end, and double-opening funnel traps (20 cm diameter, 5 cm funnel opening) were placed ≈2.5 m from the centerpoint on both sides of each fence. To minimize mortality of trapped animals, funnel traps were provided with moistened sponges and shaded by 41 cm square boards of tempered masonite.

For ease of installation and to minimize erosion, arrays were located along relatively flat terraces adjacent to streams, preferably in areas with minimal microtopography and low streambanks. Along smaller streams, 1 arm of each array extended partially into the stream or into adjacent seepage areas, whereas the other 2 arms sampled either bottomland forest or slope forest habitat. Farther downstream, arrays were located on terraces adjacent to the larger streams, preferably in or near seepage areas.

In the Ochlockonee drainage, 2 arrays were located $>$130 m downstream from the headwaters of the first-order stream, where it was 0.5–1.5 m wide and 1–4 cm deep. The other 4 arrays were farther downstream below its confluence with another first-order stream (forming a second-order stream). Arrays were situated partially on 5° slopes and/or in sandy or mucky floodplain areas along the second-order stream, which was typically 1.0–1.8 m wide and 3–20 cm deep.

In the Apalachicola drainage, 2 arrays each were located along 2 first-order streams in different ravines. One arm of each of these 4 arrays intersected the stream and had end traps in the water, whereas the other 2 arms paralleled the stream or ascended sidewalls with 5–10° slopes. Arrays were $\geq$60 m downstream from the headwaters of the streams, which were 2.0–3.7 m wide and 3–13 cm deep. The remaining 2 arrays were located at the bottom of a 34-m deep ravine ≈2.4 km straight-line distance downstream from the nearest array in mucky seepage areas on opposite sides of the fast-flowing Big Sweetwater Creek, which was sand-bottomed, 3.7–6.0 m wide, and 10–80 cm deep.

Traps were opened 6 June 1995 and closed 1 August 1995 after 56 days of trapping. Because of time

and manpower constraints, subsequent trapping was conducted in alternate months (September/October, November, January, March, May) until trapping was terminated on 5 June 1996. Traps were open for a total of 216 days. Traps were checked twice per week during the initial sampling period, every 4 to 5 days in September/October and May, and every 7 days in November, January, and March, when trapping mortality and capture rates were lower. Captured animals were marked (except for hatchling turtles and small snakes) and released ≈3 m away on the opposite side of the fence. Larval amphibians were not included in capture totals. Precipitation, maximum/minimum air temperature, water temperature, and stream depth were recorded each time traps were checked.

Vegetation Description

The Ochlockonee steephead ravine had 10–30° slopes containing slope forest vegetation (see Florida Natural Areas Inventory 1990) consisting of predominantly xeric-adapted, deciduous trees at the top of the slope and mesic-adapted trees, such as swamp chestnut oak (Quercus michauxii), white oak (Q. alba), pignut hickory (Carya glabra), American beech (Fagus grandifolia), southern magnolia (Magnolia grandiflora), spruce pine (Pinus glabra), eastern hornbeam (Carpinus caroliniana), eastern hophornbeam (Ostrya virginica), and sweetgum (Liquidambar styraciflua), farther downslope. Bottomland forest habitat occurred along the second-order stream on the valley floor, where typical vegetation consisted of mesic-adapted tree species, sweetbay (Magnolia virginiana), tulip poplar (Liriodendron tulipifera), and red maple (Acer rubrum). The 2 arrays along the first-order stream had ≈80% canopy cover of mesic-adapted trees and 10–20% shrub cover. Grasses and sedges covered ≈5% of the area, and sphagnum (Sphagnum spp.), other mosses, and various ferns covered another 5%. The 4 arrays along the second-order stream had 80% canopy cover of mesic- and hydric-adapted species and 25–50% shrub cover that included canopy species, wax myrtle (Myrica cerifera), muscadine grape (Vitis rotundifolia), sparkleberry (Vaccinium arboreum), elderberry (Sambucus canadensis), American holly (Ilex opaca), and Virginia willow (Itea virginica). Grass/sedge and herbaceous ground cover ranged from 5 to 75% and often included netted chain fern (Woodwardia areolata), Virginia chain fern (W. virginica), southern shield fern (Dryopteris ludoviciana), lizard's-tail (Saururus cernuus), and marsh pennywort (Hydrocotyle umbellata).

The ridgetops above Apalachicola arrays had been planted in sand pine (Pinus clausa) on sandhill sites. The major vegetative difference from the Ochlockonee ravine was the presence of a dense evergreen shrub layer of predominately star anise (Illicium floridanum) and large gallberry (Ilex coriacea) along the lower slopes and first-order streams. Additional shrubs on slopes besides those found in Ochlockonee ravines were wild olive (Osmanthus americana), sweetleaf (Symplocos tinctoria), flowering dogwood (Cornus florida), and witch hazel (Hamamelis virginiana). Arrays along first-order Apalachicola streams had ≈80% canopy cover, 40–50% evergreen shrub cover, and 5–20% woody ground cover. The slopes above Big Sweetwater Creek differed from first-order streams in containing mountain laurel (Kalmia latifolia), Sebastian bush (Sebastiana fruticosa), and Florida yew (Taxus floridana) in the shrub layer. Arrays along Big Sweetwater Creek had 60–75% canopy

cover, 40–60% shrub cover of mountain laurel, fetterbush (Lyonia lucida), sweet pepperbush (Clethra alnifolia), star anise, wax myrtle, American holly, large gallberry, and Virginia willow. Woody ground cover was 15–20%, and sphagnum and other mosses carpeted 20% of the surface.

RESULTS AND DISCUSSION

Comparisons Between Stream Orders

Water Temperature—The constant flow of high-quality water of relatively constant temperature (≈21° C) in steephead streams and the protection of steep valley walls provide relatively constant year-round temperature and humidity (Means 1975, 1977). Much of the ravine-dwelling herpetofauna, particularly salamanders, occurs on ravine bottoms along seeps or streams where leaf litter accumulates (Wolfe et al. 1988). Steephead streams in the Panhandle have a diverse salamander community that utilizes different adult and larval microhabitats and has aquatic larval periods ranging from 6 months to 3 years (Means 1974, Means and Karlin 1989). The constant water flow in steephead streams allows salamanders, particularly ones with longer larval periods, to live year-round all the way to the headwaters (Wolfe et al. 1988).

I found relatively constant year-round water temperatures only at the source (seepage slope) of Ochlockonee steephead streams and in Apalachicola first-order steephead streams (5°C annual variation). Ambient air temperature affected the water temperature, especially in wintertime, of Ochlockonee first-order streams at the array locations (> 130 m downstream of the source) because of low volume of flow. Water temperatures in the Ochlockonee first-order stream ranged from 8.3–23.3°C, whereas a short, first-order stream in the vicinity had a greater volume of flow and a more restricted temperature range (18.9–20.0°C) that was probably near the temperature of the ground water in the subterranean perched aquifer. Water temperature ≥60 m downstream from the headwaters of Apalachicola first-order streams ranged from 18.3–23.3. Their greater volume of flow and closer proximity to the source apparently accounted for the more constant water temperature than in the Ochlockonee stream. Annual variations in water temperature were 11.1°C in the second-order Ochlockonee stream and 15.3°C in the Apalachicola third-order stream.

Species Composition and Relative Abundance—The variability of water temperatures throughout the year in Ochlockonee first-order streams apparently did not affect the presence of any amphibian species, because all species present along first-order Apalachicola steephead streams were also present along the Ochlockonee stream (Table 1). Amphibian species richness of first- and second-order Ochlockonee streams was similar (Table 1), despite differences in numbers of arrays used. In the Ochlockonee steephead, more anurans ($t = 3.34$, $P = 0.03$, $df = 4$) were captured per array in the second-order (100.8 ± 19.7) than in the first-order (51.0 ± 4.2) stream. Mean numbers of salamanders captured per array in the second-order (340.8 ± 223.6) and first-order (149.5 ± 54.4) Ochlockonee streams were not significantly different ($t = 1.13$, $P = 0.32$, $1 - \beta = 0.07$, $df = 4$) because of the high variance in captures among arrays. High variability in captures among arrays occurred

despite the close proximity of arrays, which sampled diverse microhabitats.

In the Apalachicola River drainage, significantly more Apalachicola dusky salamanders ($t = 3.66$, $P < 0.05$, $df = 4$) were trapped along the third-order stream than along the 2 first-order streams. In contrast, more southeastern slimy salamanders ($t = 4.22$, $P \leq 0.01$, $df = 4$) were trapped along first-order streams than the third-order stream. Apparent differences between stream orders in the mean number of captures per array were not statistically significant for any other amphibian species because of the high variance in captures among arrays. Although >6 times more anurans were captured per array along the third-order stream (72.0 $\pm$ 24.0) than along first-order streams (10.8 $\pm$ 5.6), this difference was not significant (Mann-Whitney rank sum test; $T = 11.0$, $P = 0.13$, $n_1 = 2$, $n_2 = 4$). Three more species of amphibians were captured along Big Sweetwater Creek than along first-order streams (Table 1).

In the Ochlockonee steephead, there were no differences between stream orders in the mean number of turtles ($t = 2.43$, $P = 0.07$, $1 - \beta = 0.39$, $df = 4$), lizards (Mann-Whitney rank sum test; $T = 7.0$, $P = 1.00$, $n_1 = 2$, $n_2 = 4$), or snakes ($t = 0.24$, $P = 0.82$, $1 - \beta = 0.05$, $df = 4$) captured per array. No reptile species was unique to the first-order stream, whereas 5 species were only captured along the second-order stream (Table 1). In Apalachicola steepheads, more broadhead skinks ($t = 7.57$, $P < 0.01$, $df = 4$) were captured per array along first-order (36.8 $\pm$ 5.9) than third-order (2.5 $\pm$ 2.1) streams. More lizards ($t = 11.5$, $P < 0.001$, $df = 4$) were captured per array along first-order streams (48.8 $\pm$ 5.3) than along Big Sweetwater Creek (3.5 $\pm$ 0.7), whereas more turtles ($t = 4.3$, $P \leq 0.01$, $df = 4$) were captured along Big Sweetwater Creek (4.5 $\pm$ 2.1) than along first-order streams (0.3 $\pm$ 0.5). Eight reptile species were only captured along first-order streams, whereas 3 species were only captured along Big Sweetwater Creek (Table 1).

Comparisons Between River Drainages

Species Composition and Relative Abundance—The herpetofaunal communities in steephead ravines in the 2 river drainages might be expected to differ in composition and relative abundance of various species because of differences in microhabitats and geological history. Near their headwaters, Apalachicola steephead ravines had greater depth, steeper slopes, more leaf litter, and a denser shrub understory than the Ochlockonee steephead ravine. First-order Apalachicola seepage streams tended to be larger, have more uniform temperatures, and contain more leaf beds and fewer mossy and mucky areas than Ochlockonee seepage streams. The fish faunas of the 2 river drainages are quite different because they have been physiographically independent for a long time, although Telogia Creek, a tributary of the Ochlockonee River, appears to have been captured from the Apalachicola River (Gilbert 1987). I found the amphibian species composition of steephead ravines in the 2 drainages to be similar, although relative abundance often differed. Some species captured in only 1 river drainage were relatively abundant there. For example, the eastern narrowmouth toad (Gastrophryne carolinensis) and eft stage of the central newt (Notophthalmus viridescens) were common in the Ochlockonee ravine, whereas the rusty mud salamander (Pseudotriton montanus) was common along Big

Sweetwater Creek (Table 1).

Comparing mean captures per array of species along first-order streams between the 2 river drainages, significantly more three-lined ($t = 13.4$, $P < 0.001$, $df = 4$) and southern red ($t = 4.44$, $P \leq 0.01$, $df = 4$) salamanders were captured in the Ochlockonee drainage, whereas more broadhead skinks ($t = 7.56$, $P < 0.01$, $df = 4$) were captured in the Apalachicola drainage. The scarcity of three-lined salamanders in Apalachicola steephead ravines ($n = 2$) was unusual because they accounted for 43.8% of all herpetofaunal captures ($n = 2,283$) in the Ochlockonee ravine, and this was reported to be one of the most common salamander species at the bottom of gully-eroded Apalachicola ravines in another study (Means and Studenroth 1994). Significantly more anurans ($t = 8.75$, $P < 0.001$, $df = 4$) were captured per array along the Ochlockonee first-order stream (51.0 ± 4.2) than along Apalachicola first-order streams (10.8 ± 5.6), which was primarily due to the scarcity of the Florida leopard (Rana sphenocephala) and bronze (R. clamitans) frogs along Apalachicola first-order streams (Table 1). There was no difference ($t = 0.59$, $P = 0.59$, $df = 4$, $1 - \beta = 0.05$) in the mean number of salamanders captured per array along first-order streams in the 2 river drainages.

Ochlockonee arrays captured 18 amphibian and 13 reptile species, whereas Apalachicola arrays captured 13 amphibian and 22 reptile species (Table 1). Twice as many snake species were captured in Apalachicola as in Ochlockonee ravines, but additional trapping probably would have yielded more snake species, especially in the Ochlockonee ravine. There were no significant differences in numbers of snakes captured between different stream orders within a river drainage nor between first-order streams in the 2 river drainages. Numerically, snakes were a minor component of the herpetofaunal community in steephead ravines, accounting for only 1.4% of all herpetofaunal captures in Ochlockonee ravines and 4.2% of all captures in Apalachicola ravines. The southern copperhead (Agkistrodon contortrix) appears to be largely restricted to ravines and floodplain forests in the Apalachicola River drainage, although there is a questionable record for the Ochlockonee River drainage north of the western end of Lake Talquin (Means 1992). Lizards dominated reptile captures in the Apalachicola steepheads because of the abundance of broadhead skinks. Turtles were scarce in first-order streams in both river drainages, occurring more frequently in downstream portions. The southern two-lined salamander (Eurycea cirrigera) was a predominant component of the herpetofaunal community in both river drainages.

The topographic gradient of slope forest habitat encompasses a broad soil moisture gradient that is potentially suitable for a wide spectrum of herpetofauna. Near the top of the slope, conditions are relatively dry and favor herpetofauna characteristic of xeric upland habitat. Farther down the slope, the vegetation is more characteristic of upland hardwood forest, and the increased soil moisture favors a more diverse amphibian community. Near the bottom of the slope, the bottomland forest habitat is suitable for semiaquatic amphibians, particularly along streams or seeps. Although only the lower slopes of ravines were sampled during this study, some reptiles more characteristic of xeric uplands (e.g., eastern coachwhip [Masticophis flagellum], eastern hognose snake [Heterodon platirhinos], and southern fence lizard [Sceloporus undulatus]) were occasionally

captured in Apalachicola ravines. Most terrestrial amphibian species (e.g., southeastern slimy salamander, eft stage of the central newt, eastern spadefoot [Scaphiopus holbrookii]) were trapped along arms of arrays on slopes adjacent to first-order streams.

Species composition of the amphibian community in the Ochlockonee steephead ravine was similar to that recorded from 2 other studies in the same drainage in Gadsden County, Florida. One study inventoried captures in September/October from a pipeline trench traversing slope forest habitat along a gully-eroded ravine (Enge et al. 1996), and the other was a drift-fence survey of upland hardwood forest and associated seepage streams (Enge 1998). The pipeline survey was much more effective than drift fences at capturing hylids (Acris, Hyla, and Pseudacris spp.), which comprised 67% of all herpetofaunal captures, including 2 species not recorded during this study (Enge et al. 1996). Amphibian and reptile species composition of the upland hardwood forest was similar to that of steephead ravines, with southern two-lined and three-lined salamanders being the most common species (Enge 1998). Both of these other studies captured bullfrogs (Rana catesbeiana) and marbled salamanders (Ambystoma opacum), which might have been detected in the steephead ravine with additional sampling.

In the Apalachicola River drainage, a short-term herpetofuanal survey of bottomland forest habitat along gully-eroded ravines in the Rock Creek Tract of Torreya State Park (Means and Studenroth 1994) found similar species to this survey, but the species list was much smaller (e.g., no turtles or snakes), probably because of limited sampling. The only species captured in gully-eroded ravines but not in steephead ravines were the eastern narrowmouth toad and southeastern five-lined skink (Eumeces inexpectatus). The eastern narrowmouth toad breeds in ephemeral wetlands, which might have been limited in the vicinity of the ravines along first-order streams, but suitable breeding habitat should have been available along Big Sweetwater Creek.

Seasonality of Captures—In both watersheds, more herpetofaunal species were captured during the warmer months (May, June, July, September/October) than during the cooler months (November, January, March). The most productive months for amphibian captures were July and September/October in both watersheds. Salamanders dominated amphibian captures during the cooler months, and the most productive months for anuran captures were May, June, and July. Many of the amphibian species were typically captured in greatest numbers during their breeding seasons. Most reptiles were captured during the warmer months; no lizards were captured during November and January. Sampling was conducted during the cooler months to detect winter-breeding amphibians, but the four-toed salamander (Hemidactylium scutatum) was the only winter-breeding species captured only in November or January.

Salamander captures per week were significantly correlated with the amount of precipitation in the Ochlockonee ($F = 24.0$, $P < 0.001$, $df = 30$) and Apalachicola ($F = 6.87$, $P < 0.05$, $df = 30$) steepheads, but there was no relation between weekly anuran captures and precipitation in the Ochlockonee ($F = 2.50$, $P = 0.12$, $df = 30$, $1 - \beta = 0.33$) and Apalachicola ($F = 0.19$, $P = 0.67$, $df = 30$, $1 - \beta = 0.06$) steepheads.

Salamanders were captured regardless of air temperature, but anurans were captured primarily during warmer weather. The seasonality of anuran captures partially accounted for the low correlation between anuran activity and precipitation.

Sampling Efficiency—During the first month of trapping, June, 74.2% of the total number of species (n = 31) were captured in the Ochlockonee study area but only 52.9% of the total number of species (n = 34) in the Apalachicola sites. However, after 2 months of trapping, 73.5% of the total number of species had been captured in the Apalachicola sites. Relatively few new species were added in November, January and March in either drainage. However, during the last month of trapping, May, 2 new species (one-toed amphiuma [Amphiuma pholeter] and five-lined skink [Eumeces fasciatus]) were added in Ochlockonee ravines and 4 new species (eastern spadefoot, Gulf Coast box turtle [Terrapene carolina], northern scarlet snake [Cemophora coccinea], and eastern coachwhip) in Apalachicola ravines. The addition of new species during the last month of trapping indicates that the trapping intensity (i.e., 6 arrays trapping for 216 days over the course of 1 year) was probably insufficient to compile a comprehensive species list of the herpetofauna occurring in steephead ravines.

Calculations of capture rates included recaptured individuals. Marked individuals represented 12.8% of all salamander captures (n = 1,574) in the Ochlockonee ravine. A similar proportion (11.9%) of recaptures was found for 646 salamander captures in the Apalachicola ravines. Of the more common salamander species captured in the 2 river drainages, the overall proportion of recaptures ranged from 9.4% for the southern red salamander (n = 64) to 15.8% for the Apalachicola dusky salamander (n = 190). Recapture rates of the 2 most common salamander species were 14.1% for the three-lined salamander (n = 960) and 11.0% for the southern two-lined salamander (n = 905).

Proportions of all anurans recaptured were also similar in the Ochlockonee (11.1%; n = 434) and Apalachicola (12.1%; n = 157) ravines. Recapture rates among commonly captured anuran species were more variable than among salamander species. The proportion of recaptures ranged from 0% for the spring peeper (n = 23) to 20.3% for the southern toad (Bufo terrestris) (n = 69). Only 3.9% of 154 Florida leopard frog captures were recaptures, whereas 11.5% of 279 bronze frog captures were recaptures. Leopard frogs were probably more transitory than bronze frogs, which resided along the streams. Lizards and turtles were recaptured more frequently than snakes. No snakes (n = 12) were recaptured in Ochlockonee ravines, whereas 6.3% of 32 snake captures in the Apalachicola ravines represented recaptures. In contrast, recaptures accounted for 15.0% of lizard captures (n = 40) in Ochlockonee ravines and 49.5% of lizard captures (n = 184) in Apalachicola ravines. The dissimilarity in lizard recapture rates between the 2 river drainages was attributable to the abundance of broadhead skinks in Apalachicola ravines. Overall, 55.8% of 154 broadhead skink captures in the 2 river drainages represented recaptures compared to 13.3% of green anole (Anolis carolinensis) captures (n = 45) and 15.6% of ground skink (Scincella lateralis) captures (n = 32). Recapture rates might have been

higher had there been no trapping mortality (6.1% for salamanders, 7.8% for anurans, 3.4% for turtles, 7.5% for lizards, and 2.1% for snakes), and recapture rates for salamanders were probably biased because of regeneration of toes during the study. Highest mortality occurred in trapped central newts (24.2%), green anoles (22.0%), southeastern slimy salamanders (19.3%), and bronze frogs (10.2%), primarily from desiccation.

Threats to Steephead Ravines and Management Implications

Although this study did not examine water quality, relative humidity, and soil characteristics, knowledge of the life history requirements of many of the herpetofaunal species found in the rare and vulnerable steephead habitat allows one to speculate concerning the potential impacts of various land-use practices and human activities. The aquatic and semiaquatic wildlife community along seepage streams may be affected by poor water quality resulting from the application of fertilizers or biocides on the surrounding uplands, or the dumping of hazardous wastes and other refuse within the drainage basin or steephead (Florida Natural Areas Inventory 1990). Illegal dumping of trash down easily accessible ravines is a common practice in the Panhandle (pers. obs.), but I suspect it is more of an aesthetic problem than a threat to wildlife, unless toxic materials or metal corrosion pollutes the streams.

The steepheads in this study occurred on lands formerly or presently owned by St. Joe Corporation, and ridges had been logged of longleaf pine and replanted in sand or slash pine. The latter species was often stunted because of unsuitable site conditions. Deforestation of adjacent uplands may result in increased erosion and sedimentation of the ravines, and the steep ravine slopes are very susceptible to erosion from even minor habitat disturbances, such as foot traffic. Logging of uplands or the upper slopes of ravines may increase insolation levels along streams, which may lead to higher temperatures and lower humidities unfavorable to herpetofauna preferring cool, moist conditions. Another byproduct of opening the canopy is increased shrub and/or emergent herbaceous vegetation along streams (Florida Natural Areas Inventory 1990).

The recent increase in prices for hardwood timber may make it economically feasible for commercial forestry operations to extract hardwood trees from the upper slopes of steepheads. The steep slopes have precluded the use of heavy logging equipment in the past and enabled most steepheads to retain their natural vegetation, although southern red cedars (Juniperus silicicola) have been removed from most ravines to make pencils (Means 1977, 1981). Timber harvesting of upland areas or hydrological manipulations may affect groundwater seepage; changes in the quantity of water entering seepage streams will alter the streamside and aquatic biotic communities. These first-order seepage streams are used by the larvae of several salamander species. Logging of hardwoods on the slopes would decrease shading, reduce leaf litter, increase soil-surface temperatures, reduce humidity, and reduce soil-surface moisture (Bury 1983, Ash 1988, Raphael 1988, Welsh 1990), conditions unfavorable for many of the amphibian species, especially if erosion results in sedimentation of streams (Corn and Bury 1989). Timber harvesting of southern Appalachian forests (Ash 1988, Petranka et al. 1993) and South Carolina bottomland swamps (Phelps and Lancia 1995) adversely affected many salamander

populations. The sunnier, drier conditions resulting from logging may benefit some lizard and snake species, especially those characteristic of the adjacent xeric uplands.

Impoundment of ravine streams has occurred in the Panhandle to create ponds for residential communities and for watering livestock. The larvae of most ravine-dwelling salamander species require flowing water or seepage areas and would be eliminated from impounded sections of streams. Impoundment would also interfere with movements of amphibians, reptiles, and fishes along streams and could adversely affect wildlife by changing the temperature and oxygen-carrying capacity of the water downstream.

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Table 1. Herpetofauna captured 6 June 1995–5 June 1996 by 2 drift-fence arrays along first-order (1st) and 4 arrays along second-order (2nd) steephead streams in the Ochlockonee River drainage, Leon County, Florida, and 4 arrays along first-order and 2 arrays along third-order (3rd = Big Sweetwater Creek) steephead streams in the Apalachicola River drainage, Liberty County, Florida. X indicates an observation rather than a capture. Taxa names follow Collins (1997).

	Ochlockonee		Apalachicola	
Taxon	1st	2nd	1st	3rd
Amphibians				
Florida cricket frog (Acris gryllus dorsalis)	2	9	0	0
One-toed amphiuma (Amphiuma pholeter)	0	2	0	0
Southern toad (Bufo terrestris)	17	31	22	13
Apalachicola dusky salamander (Desmognathus apalachicolae)	40	64	45	63
Southern two-lined salamander (Eurycea cirrigera)	151	308	428	118
Three-lined salamander (E. guttolineata)	75	925	1	1
Eastern narrowmouth toad (Gastrophryne carolinensis)	10	16	0	0
Four-toed salamander (Hemidactylium scutatum)	0	1	0	0
Cope's gray treefrog (Hyla chrysoscelis)	0	2	0	7
Green treefrog (H. cinerea)	1	4	0	0
Squirrel treefrog (H. squirella)	1	0	0	X
Central newt (Notophthalmus viridescens louisianensis)	2	31	0	0
Southeastern slimy salamander (Plethodon grobmani)	8	5	42	2
Spring peeper (Pseudacris crucifer)	1	10	1	14
Little grass frog (P. ocularis)	X	0	0	0
Rusty mud salamander (Pseudotriton montanus floridanus)	0	0	0	45
Southern red salamander (P. ruber vioscai)	23	29	3	15
Bullfrog (Rana catesbeiana)	0	0	1	2
Bronze frog (R. clamitans clamitans)	30	171	17	105
Florida leopard frog (R. sphenocephala sphenocephala)	34	147	2	2
Eastern spadefoot (Scaphiopus holbrookii)	6	13	0	1
Reptiles				
Southern copperhead (Agkistrodon contortrix contortrix)	0	0	2	3
Florida cottonmouth (A. piscivorus conanti)	0	1	1	2
Green anole (Anolis carolinensis)	5	24	28	2
Northern scarlet snake (Cemophora coccinea copei)	0	0	0	1
Snapping turtle (Chelydra serpentina)	0	10	0	3
Racer (Coluber constrictor)	7	4	11	1
Southern ringneck snake (Diadophis punctatus punctatus)	5	8	10	3
Corn snake (Elaphe guttata)	0	0	1	1
Gray rat snake (E. obsoleta spiloides)	0	1	4	0
Five-lined skink (Eumeces fasciatus)	2	2	0	0
Broadhead skink (E. laticeps)	4	5	147	5
Eastern mud snake (Farancia abacura abacura)	0	2	0	0
Eastern mud turtle (Kinosternon subrubrum subrubrum)	0	22	0	6
Eastern hognose snake (Heterodon platirhinos)	0	0	1	0
Eastern coachwhip (Masticophis flagellum flagellum)	0	0	1	0
Banded water snake (Nerodia fasciata fasciata)	0	1	7	3
Queen snake (Regina septemvittata)	0	0	1	3
Southern fence lizard (Sceloporus undulatus undulatus)	0	0	1	0

Ground skink (Scincella lateralis)	3	3	18	0
Dusky pigmy rattlesnake (Sistrurus miliarius barbouri)	0	0	1	0
Florida redbelly snake (Storeria occipitomaculata obscura)	3	2	2	1
Gulf Coast box turtle (Terrapene carolina major)	0	X	1	0
Eastern garter snake (Thamnophis sirtalis sirtalis)	0	0	1	0
Unidentified lizard	0	0	1	0
Grand total	430	1853	801	422

AN ENVIRONMENTAL REPORT ON THE BLACKWATER RIVER DRAINAGE BASIN IN SOUTHERN ALABAMA AND NORTHWESTERN FLORIDA.

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PRELIMINARY REPORT

August, 1979

An environmental report on the Blackwater River Drainage Basin in Southern Alabama and Northwestern Florida: SUMMARY.

A brief history of the Blackwater River and forest management practices which have preserved the river in its natural state are given.

The biology of the river is discussed:

— its productive sand habitats, a unique ecosystem, and

— its extremely high diversity of aquatic animals.

We give a brief list of plants, mammals and fishes which are endangered or threatened, and which would become more severely endangered is large amounts of the natural habitat were lost.

A temporary list of endangered invertebrates is presented, but since the invertebrate list for Florida is unpublished at this time, only mayflies can be discussed in any detail.

Other considerations are mentioned:

— that one of the threatened species of mayflies represents a family of insects nearly extinct in the world.

— that of only two fully protected rivers in the Southeastern coastal plain, the Blackwater is the only one available for recreational use by all.

— that historical consideration should be given to maintaining the Blackwater for future generations.

Some suggestions and recommendations for future protection of the river are included.

INTRODUCTION

The headwater tributaries of the Blackwater River lie in the Conecuh National Forest in southern Alabama and the river proper begins just north of the Florida and Alabama boundaries. The Blackwater River and its five major tributaries flow south through the Blackwater River State Forest to Blackwater Bay, at Milton, Florida.

A visitor to the river first notices the large bars of clean, shifting sand along the river. Streams and rivers with shifting sand bottoms are widespread within the Southeastern Coastal Plains; however, many are disturbed and the sand is biologically unproductive. As will be discussed in this report, the Blackwater River is still in a natural state for almost its entire length, and the shifting sand bottom and other river habitats are very productive.

Headwater tributaries of the Blackwater River have been entirely protected by the Conecuh National Forest since 1936. While the national forest offers multiple use, no agricultural or industrial use is near any of the headwater tributaries.

Almost the entire freshwater portion of the Blackwater River Drainage in Florida has been protected since the early 1930's. The area was originally owned by the U. S. government for a land-use project; however, the land was deeded to the Florida Board of Forestry in 1955. Today only a few small areas along the freshwater portions of the river and its tributaries are locally owned, mostly for agricultural or recreational purposes, and no to little

agricultural runoff enters the river. The remaining area is in the Blackwater River State Forest (administered by the Division of Forestry, Department of Agriculture and Consumer Services). The state forest offers multiple use including controlled operations in timber harvesting; however, the Division of Forestry does not allow harvesting within 100 feet either side of the Blackwater River or 50 feet either side of its tributaries. Based on the above statements, the banks of the freshwater portion of the Blackwater River and its tributaries are almost entirely protected.

The freshwater portion of the Blackwater River has never been channelized or dredged. Except for the occasional removal of fallen trees or log jams for small boats and the building of bridges, the entire aquatic habitats of the river remain natural. To my knowledge no extensive agricultural or industrial pollution has ever entered the freshwater portion of the river. Such cannc be said for any other sand bottom river in northwestern Florida. The only other fully protected sand bottom river in North America is Upper Three Runs Creek in South Carolina which is full protected and managed by E.I. DuPont de Nemours and Company.

Extensive research programs are now in progress at both the Blackwater River by Florida A & M University and Upper Three Runs Creek by Stroud Water Research Center of the Academy of Natural Sciences of Philadelphia. In both studies, emphasis concerns the biological uniqueness of natural sand bottom rivers. In the Blackwater River studies, scientists from many states and over 10

foreign countries have visted the river for biological studies under the Florida A & M University program (as an example, see Soldán 1979).

Stanford and Ward (1979) recently stated that intensive regulation of the world's river systems preceded consideration or understanding of the consequences of such actions. They further noted that rivers were harnessed without regard for the interrelationships of physical and biological components or interactions between terrestrial and aquatic systems. Certainly it is a rare occasion to have left intact a natural river system such as the Blackwater River. It should be scientifically studied in its natural state and then protected for use by future generations.

CHEMICAL AND PHYSICAL ASPECTS

The combined chemical, physical, and geological features of the Blackwater River are summarized by Beck (1973) and this publication is included herein as Appendix I. Chemically the river water is extremely soft, slightly mineralized, and low in dissolved nutrients, a fact that is reflected in sparse growth of aquatic plants. Due to steepheads, most of the normal flow of the river is ground water, not runoff water (surface drainage.) Beck (1965) indicated this results in a temporing effect on extremes of temperatures, keeping the Blackwater River cooler in summer and warmer in winter than waters of other origins. The effects of this modulated temperature on the biological productivity and diversity in the Blackwater River remains to be studied.

Yearly detailed discharge data and water chemistry analyses are published by the U.S. Department of Interior, Geological Survey (1978 and previous years). Recently Bass and Hitt (1977) summarized water chemistry analyses taken during 1976-1977 in a standing crop study of the Blackwater River system.

HISTORICAL AND BIOLOGICAL ASPECTS

The historical and general biological aspects of the Blackwater River are summarized by Peters and Jones (1973) and this publication is included herein as Appendix II. In this paper we identified five natural types of vegetation occurring along or near the Blackwater River. Further we discussed the major aquatic habitats within the Blackwater River Drainage and the insect communities living within the habitats. It is difficult to list the habitats in any river, as one habitat merges to another. Further, preliminary studies indicate the habitats and communities in several tributaries and head waters of the Blackwater River Drainage are significantly different than those in the river proper. Bass and Hitt (1977) indicated the Blackwater River Drainage is divisible into five aquatic environments based on physical features such as current flow, substrate type, depths, and vegetation. While this is correct, studies on aquatic insect communities have further defined the uniqueness of various tributaries and portions of the freshwater areas of the river proper (See Beck & Beck 1974, Berner 1978, and Stark & Gaufin 1979).

Several studies have now appeared which indicate the high diversity and biomass of aquatic insects in the Blackwater River Drainage. Tsui and Hubbard (1979) recently discussed the feeding

habitats of the predaceous nymph of Dolania americana in the Blackwater River. These nymphs live in the clean shifting sand and the bulk of their food is larval Chironomidae which also live in the sand. The relationship between predator and prey throughout the year is discussed. For most of the year the standing crop of both insects is exceptionally high (from original data and subsequent studies used by Tsui and Hubbard 1979 and Peters and Peters 1977, roughly 4-5 Dolania predators and 6,000-12,000 chironomid prey organisms per square meter in the sand habitat). Tsui and Hubbard (1979) is included herein as Appendix III as documentation that clean, shifting sand habitats are often biologically productive.

The diversity of aquatic insects in the Blackwater River is just becoming known and many new species have not yet been named and described. For example, Berner (1978) revised the mayfly genus Siphloplecton which occurs in North America. Of 8 species in the genus, one is endemic to the Blackwater River and three occur in this river and few other places. One other endemic species of mayfly (Stenacron floridense) from the Blackwater River was described by Lewis (1974) as part of an EPA study. Stark and Gaufin (1979) recently published the stoneflies of Florida. They recorded 26 species in Florida of which 21 species were collected from the Blackwater, more than any other Florida river. Further, although occurring in other states, four of these species were found in Florida only in the Blackwater River.

The diversity of aquatic insects in the Blackwater River Drainage can be seen in the following list of aquatic insects which have been identified. Data is from Peters and Jones 1973, Stark and Gaufin 1979, Beck and Beck 1974, Berner 1978, Lewis

1974, and lists supplied by the following specialists: Drs. Curtis Dunn, Joe Schuh, and Annelle Soponis.

33 species of Odonata (dragonflies and damselflies)

42 " " Ephemeroptera (mayflies)

21 " " Plecoptera (stoneflies)

24 " " Trichoptera (caddisflies), but not all groups have been studied

1 " " Neuroptera

3 " " Megaloptera (dobsonflies and fishflies)

12 " " Corixidae, a family of aquatic Hemiptera (bugs)

20 " " aquatic Coleoptera (beetles)

52 genera of Chironomidae, a family of aquatic Diptera (midges or blind mosquitoes)

We do not have data on other families of Hemiptera or Diptera, some of which are abundant in the Blackwater, nor do we have data on other arthropods (crayfish, fairy shrimp, isopods) which play an important role in the ecology of the river and its tributaries. Based on available data given above, the diversity of invertebrate species in the Blackwater River Drainage is obviously quite high. Few rivers in the world can produce a similar list.

ENDANGERED SPECIES

The Inventory of Rare and Endangered Plants and Animals of Florida is still mostly in preparation. However, enough manuscripts have been published to give a partial list of rare and endangered species occurring in the Blackwater River Drainage. Those species listed below have been selected by me to give a representative

list of various plants and animals, but this list is by no means complete.

1. Plants

Drosera intermedia Hayne in Schrad.

Water Sundew RARE

Kalmia latifolia L.

Mountain Laurel RARE

Lilium iridollae Henry

Panhandle Lily THREATENED

Rhododendron austrinum (Small)

(no known common name) THREATENED

Sarracenia leucophylla Raf.

White-top Pitcherplant THREATENED

2. Mammals

Felis concolor coryi Bangs

Florida Panther ENDANGERED

Ursus americanus floridanus Merriam

Florida Black Bear THREATENED

3. Fishes

Except for one report "of doubtful validity" of the Okaloosa darter (Etheostoma okaloosae) mentioned in Bass and Hitt (1977), there are no records of endangered species of fish from the Blackwater River. However, in discussing the Blackmouth shiner (Notropis new species) from Pond Creek near Milton, Gilbert (1978)

stated: "the range of this species probably encompasses the lower reaches of the adjacent Blackwater and Yellow rivers, as well as freshwater sections of Blackwater Bay itself, and a careful watch should be kept on these areas to ensure that they do not suffer environmental damage."

4. Aquatic Insects *

Pseudiron meridionalis Traver

(no common name) THREATENED

Dolania americana Edmunds and Traver

(no common name) THREATENED

Homoeoneuria dolani Edmunds et al.

(no common name) THREATENED

OTHER CONSIDERATIONS

1. In at least one case (that of the sand-burrowing mayfly Dolania americana), the "threatened" classification applies to the whole family Behningiidae. Nearing extinction (if not already extinct in Europe and with its status in the Amur and Ussuri basins (border between China and the USSR) in doubt, foreign scientists have been coming to Florida for comparative studies concerning the family (Riek 1973, Soldán 1979).

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* The list of endangered species of invertebrates has not yet been published. Having authored part of the mayfly section, I know some mayfly species which are being included.

2. Of the two protected coastal plain, sand-bottomed rivers in the Southeast (Blackwater River and Upper Three Runs), only the Blackwater is a complete river system available for scenic and recreational purposes. Upper Three Runs is on the Savannah River Plant of E. I. DuPont and admission is restricted. Further, Upper Three Runs is a tributary of the Savannah River and, because of differences in water flow, lacks the clean sand bars that characterize the banks of the Blackwater.

3. The Blackwater and its protected forest banks exist in essentially the same condition now as they did 200 years ago. Preservation for historical purposes should be considered.

FUTURE PROTECTION

For many years the Blackwater River Drainage was isolated and only the local citizens knew of the area. However, in recent years the effects of use are beginning to show as more and more persons are becoming aware of the river. Weekend vacationers alone travel as much as several hundred miles to use the Blackwater recreational facilities, such as the Blackwater River State Park which was developed in the late 1960's.

In the early 1970's the Blackwater River was designated a Florida Canoe Trail by the Florida Department of Natural Resources. Since then the river has had increasing use by canoeists and several professional outfitters rent canoes in the area.

As a professional zoologist and aquatic ecologist, I have noticed many changes along the Blackwater River in the 13 years I have been associated with it. The single most important environmenta

change in the past 13 years is the increasing amount of trash and litter left in the river or along the banks by an increasing number of visitors.

While the state park and state forest provide organized recreational facilities, every accessible area to the river is used by visitors and canoeists explore the entire length of the river. In these areas not even minimal facilities are provided for trash. Further, law enforcement is minimal, especially on the weekends when it is needed the most.

If the freshwater portion of the Blackwater River and its tributaries are to remain in their natural state, then an effective plan of protection must be developed. Such a plan should consider the protection of the natural state of both the river and its banks, but allow a visitor maximum use of the area for recreational purposes. This plan is needed <u>now</u> if the Blackwater River Drainage is to remain in its natural state.

The Florida Division of Recreation and Parks is seeking to designate portions of the Blackwater River as a State Wild River. While this state legislative mechanism is available to protect the river, I feel special consideration should be given several points in developing this plan. Some of these are discussed below:

1. The river proper and its tributaries should not be dammed, channelized, or dredges. These restrictions are most important if the physical structure of the river and its banks are to remain unchanged. Further no massive clearing of log jams in the river or its tributaries should be allowed.

2. No agricultural or industrial pollution should be allowed

to enter the freshwater portion of the river or its tributaries. Water quality should be maintained at all times.

3. Effective law enforcement should be maintained on the river system at all times, and more importantly, designation of enforcement responsibility should be clear. All state and county laws should be enforced.

4. Hunting should continue in the Blackwater River area as presently administered by the Florida Game and Fresh Water Fish Commission and the Florida Division of Forestry. I have often been asked if the training and use of dogs by hunters is detrimental to the area. I can see no way the area is harmed by hunting dogs as long as the hunters respect the area.

5. Boats should be allowed to be used on the Blackwater River area as long as they are regulated to fit into the natural environment. Due to the physical nature of the river's bottom small motor boats move slowly in the Blackwater River and do not destroy habitat. As long as motor boat operators regulate their speed, obey litter regulations, and restrict their boats from designated swimming areas, motor boats should continue to be used on the Blackwater River area. Further, canoes do not harm the Blackwater area; however, professional boat rental services and private owners should be well informed on all regulations concerning litter and conservation of the area. (See item 7 for education program.)

6. Sufficient trash containers and other services should be provided for the visitor in the Blackwater area. A visitor will uphold the protection regulations only if he or she is encouraged to do so.

7. An educational program on the natural state of the Blackwater River area and the protective regulations should be developed. All persons concerned in using the Blackwater River area should be fully informed of the program.

8. Any plan of protection for the Blackwater River area should be periodically reviewed by an Advisory Committee composed of state officials, scientists, and local citizens. No plan can be effective until the future protection and use is well planned by all concerned.

CLOSING REMARKS

The Blackwater River exists in its original state today only because of the enlightened management practices of the Forest Service of Florida. The Forest Service deserves a special commendation for preserving the river for this generation. Havi already proven its management capabilities, the Florida Forest Service would be my first choice as the agency responsible for preserving the forest and river for future generations.

The Nature Conservancy®
Florida Chapter

PRESS RELEASE
May 21, 1997

CONTACT: Melva Macfie
407/682-3664

LANDMARK CONSERVATION PARTNERSHIP ANNOUNCED TODAY WILL SUSTAIN 840,000 ACRES IN FLORIDA AND ALABAMA

Ecosystem Conservation Agreement includes Air Force, Champion International Corp., The Nature Conservancy and five public agencies in two states

SANTA ROSA COUNTY, FL -- Florida Environmental Policy Unit Analyst Rick Smith, Air Force Colonel James Shambo, Division of Forestry Director L. Earl Peterson and representatives from five other companies and agencies join local residents today to celebrate the Gulf Coastal Plain Ecosystem Partnership. The voluntary landowner partnership was formed last year to sustain 840,000 contiguous acres of longleaf pine habitat in northern Florida and Alabama.

The seven partners are Champion International Corporation, Eglin Air Force Base, Florida Division of Forestry, National Forests in Alabama, National Forests in Florida, the Northwest Florida Water Management District and The Nature Conservancy.

"This partnership was formed to help preserve the dwindling longleaf pine and wiregrass ecosystems, an extraordinary natural resource," said Earl Peterson, director of the Florida Division of Forestry, "and it is the right thing to do."

The seven partners meet today at Blackwater River State Forest to explain the details of their land management agreement to neighboring landowners and local officials in Florida and Alabama. The Memorandum of Understanding that each of the partners signed allows the partners to combine their expertise and resources to more effectively manage their individual properties and to meet the challenges of sustaining the larger ecosystems.

The lands and waters included in the partnership are managed for purposes ranging from intensive forestry to military training, from recreation to water resource protection. The partnership reflects the desire of local land managers to work cooperatively to sustain important ecological processes, provide timber products and jobs, meet the escalating demand for recreation and protect populations of game and imperiled species.

"As a partner in this cooperative landscape management effort, we see the opportunity to continue to manage our lands to provide trees, a renewable resource, needed for useful products," said Joann Cox, manager of Champion's Western Florida Region Forest Resources, "and work with other partners toward a common goal of sustaining a healthy ecosystem. We felt these basic forest management concepts go hand in hand."

- MORE -

The acreage within the Gulf Coastal Plain Ecosystem Partnership contains ecosystems that cut across geographic and political boundaries. They include portions of four major watersheds, more than 160 rare or imperiled plants and animals, a thriving timber industry, and important game and fish populations in Florida and Alabama.

The Memorandum of Understanding allows the partners to implement cooperative and voluntary strategies to conserve and restore the integrity of the ecosystems; ensure a continued supply of forest commodities, recreational opportunities, clean water and ecosystem services; and support the local communities that depend on these resources and services.

The partners have conducted several joint projects, including prescribed burns, siting of the Florida Scenic Trail and cooperative management of the federally endangered red-cockaded woodpecker.

Robert Bendick, The Nature Conservancy's Florida regional director, said "This cooperative effort shows how landowners can work together on a voluntary basis to achieve their individual goals for their land while at the same time protecting the economy and the environment of a larger area. Such cooperation means that there is hope for the future of the native plants and animals that are such an important part of our heritage in Florida and Alabama."

As part of the Memorandum of Understanding, the partners recognize the full rights of individual land managers and neighboring private property owners. They welcome the involvement of interested private landowners who wish to learn more about this joint effort.

- ## -

The mission of The Nature Conservancy is to preserve plants, animals and natural communities that represent the diversity of life on Earth by protecting the lands and waters they need to survive. To date, the Conservancy and its members have been responsible for protecting more than nine million acres in 50 states and Canada. It has helped like-minded partner organizations to preserve millions of acres in Latin America, the Caribbean, the Pacific and Asia. The Conservancy owns more than 1,500 preserves -- the largest private system of nature sanctuaries in the world. With the support of 42,000 individuals, foundations and corporations, the Florida Chapter has protected more than 650,000 acres across the state since 1959.

PENSACOLA
News Journal
MONDAY, NOVEMBER 16, 1998
SECTION C
To report a story: 435-8535

ENVIRONMENT

Bird lovers try to save woodpecker

$25,000 grant sparks efforts for preservation

By Jenny LaCoste
News Journal staff writer



Red-cockaded woodpeckers are still on the endangered species list.

There are days when the traditionally serene Blackwater State Forest echoes with the sound of dozens of volunteers working to pull a species back from the brink of extinction.

A $25,000 federal grant has renewed an interest among bird-lovers in the red-cockaded woodpecker, a bird that carves out its home in the heartwood of longleaf pines.

Although not as well known as the manatee or the Florida panther, the red-cockaded woodpecker is a charter member of the Endangered Species Act of 1973. Aggressive habitat restoration and breeding policies have boosted the population in some places in the Southeast, but in Blackwater State Forest the numbers have dropped precariously low.

MUNSON

"The population is very small. It's easy when you have a small number like that for it to decline rapidly," said Vernon Compton, project director for the Gulf Coastal Plain Ecosystem Partnership. "If this area is not intensively managed now, the population will be completely lost in about 30 years."

Tom Arrington, Blackwater's ecology unit supervisor, said there are about 18 families of the birds living there. A family, or cluster, usually consists of between one and five birds.

Arrington said people always tell him they've spotted one of the rare birds in their backyards. "I can never convince them they're probably wrong," he said.

The red-cockaded woodpeckers are the smallest of the woodpeckers and actually have very little red on them. They are usually about 7 inches long and their most distinguishing characteristic is a black head with white cheek patches. The male's head has two red cockade feathers – barely visible unless close up.

Arrington said he's had hundreds of offers from volunteers to help save the bird – some from college students studying forestry, others from those who are simply nature-lovers. They've helped with everything from watching the birds' flight patterns to clearing underbrush in the pine forests.

One of the greatest success

See WOODPECKER, 4C



Tony Giberson/News Journal

Patty Kelley waits for the red-cockaded woodpecker to come to roost for the evening in the Blackwater State Forest. State officials are trying to bolster the dwindling population.

Woodpecker still endangered

FROM 1C

stories for the red-cockaded woodpecker has been restoration efforts on Eglin Air Force Base. About 280 clusters thrive on Eglin's reservation and the population is climbing.

Arrington said the difference between Eglin and Blackwater is that Eglin has plenty of century-old longleaf pines. At Blackwater, most of the pines are too young.

A tree has to be a minimum of 60 years old to have heartwood, Arrington said. "Otherwise, if you carve out a hole, the hole will fill with sap."

Arrington has been tracking the population at Blackwater for five years, but this year, money from the U.S. Fish and Wildlife Service, volunteer help and other donations have allowed officials at Blackwater to get proactive.

This month, Arrington began placing wooden boxes into young longleaf pines for the birds to nest. He hikes out in the forest every day, either at sunrise or sunset, to monitor how many bird families have moved in.

"It's not new technology. It's been around a long time," Arrington said of the man-made inserts. "We just haven't had the money to do this."

Blackwater now has about 20 inserts, with half of them already in use.

"It's tough to climb that thing with a chain saw," he said, pointing to the skinny aluminum ladder he uses to scale the trees. Arrington hollows out a spot about 30 feet above the ground, places the box inside, and fills the gaps with putty. He paints the exterior the color of bark to fool the birds.

The activity at Blackwater has attracted attention from other organizations.

Patty Kelly, a research officer for U.S. Fish and Wildlife Service in Panama City, visits Blackwater State Forest about three times a week to help Arrington monitor the birds. Kelly makes the drive on her own time — either before daybreak or in the evenings after she leaves work.

Kelly and Arrington work as a team to trap the birds so they can be banded. Arrington crouches near the base of a pine and carefully raises a long aluminum pole with mosquito netting to cover the cavity about 30 feet above him. Kelly then beats on the tree with a hose and scrapes at the bark, hoping to flush any birds out.

They wait expectantly, then try another tree. And another.

On a recent trip, Kelly and Arrington had no luck catching any of the birds, but she wasn't disappointed.

"It's just part of it," she said. "Field work can be pretty unpredictable. I'm just glad to be able to get out of the office and help out."

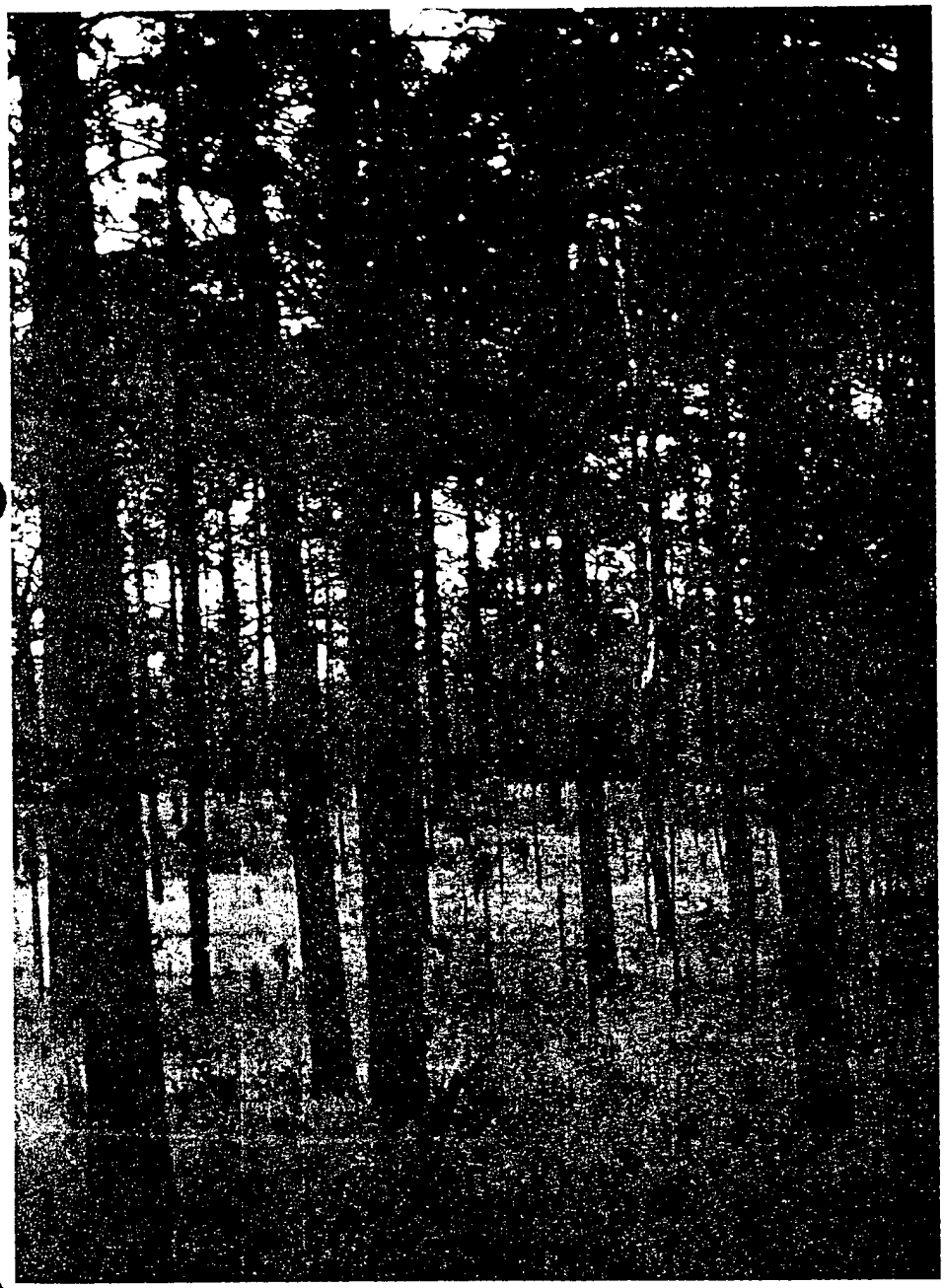
The local chapter of the Audubon Society pledged $4,000 to help efforts at Blackwater. "It's a hunk of money for us, but it's different than sending money to somewhere like Ducks Unlimited where the help goes somewhere up north," said chapter president, Dana Timmons. "That's a good program, but we need to do our part at home first."

To find out more about the red-cockaded woodpecker or to help with habitat restoration, call Compton at 983-7414.

Second In A Series

FLORIDA UPLANDS

Text and Photographs by D. Bruce Means, Ph. D.



Old-growth longleaf pine forest in Riverside Island, Ocala National Forest. Young trees are shown in the grass stage.

In the early summer of 1774, William Bartram rode on horseback from a trading post on the St. Johns River to the Seminole town of Talahasochte on the Suwannee River, making a transect across the upper Florida peninsula through Putnam, Alachua and Levy counties. At least 70 percent of the voyage was through forests of longleaf pine. Today, over the same transect, less than 5 percent is longleaf.

Now, 220 years after Bartram's visit to that part of British Florida, you can't hear the tooting of an ivory-bill nor the plaintive howl of the red wolf. Plains bison calves don't frolic the Alachua Savanna; the passenger pigeon doesn't fly south to Florida for the winter. The red-cockaded woodpecker is endangered; the bald eagle, indigo snake, gopher tortoise, pine snake, gopher frog and Florida mouse are all threatened or species of special concern. Most of these animals, to a greater or lesser extent, have depended upon Florida's extensive longleaf pine forests.

This is the story of Florida's most important natural ecosystem and the dozens of species of plants and animals that are highly adapted to and dependent upon longleaf pine forests. It is a marvelous story about the strongly beneficial role that fire plays in the ecological integrity of this forest. It is a story about connections in nature, and about Florida's rich biodiversity. It is a sad story, however.

Originally part of a vast forest ecosystem estimated at 70 million acres and stretching from Virginia to east Texas, Florida's longleaf pine forests already had shrunk substantially

Longleaf Pine Forests

by 1936, when the forest resources of the state were first inventoried. As late as the second census in 1949, longleaf pine forests were still the dominant forest type, covering 22 percent of the entire Florida landscape. Over the ensuing decades, longleaf pine steadily gave way to agriculture, silviculture, pasture and range, and urban and suburban development. By the last inventory in 1987, longleaf had suffered an 88 percent reduction from 1949 levels, over a mere 38 years. At this rate, it has been predicted that longleaf pine forests will disappear from all but public lands in Florida by next year, 1995!

Why? What is it about longleaf pine forests that makes them so vulnerable to human activities? Human beings are upland animals. We don't build roads, towns, shopping malls, parking lots – or our homes – in wetlands. We don't plant corn, cabbage, tomatoes, field peas or most other foodstuffs in wetlands, and we don't fence cattle and livestock into swamps, marshes or bogs. We do all these things in upland habitats; in Florida, that mostly means longleaf pine forest.

There is another reason the reduction of longleaf pine forest has been so rapid. To begin with, longleaf pine is by far the superior timber tree in the Southeast. Its wood is denser and more rot-resistant than all the other pines.

Foresters, however, tend to replace longleaf with slash, loblolly or sand pines, mostly because of several peculiarities of the natural history of longleaf. Longleaf pine's fire resistance, which would be a desireable property of any commercial forest tree, comes with a cost: slow growth when young. Instead of growing upward quickly, as most saplings do, longleaf seedlings sit flat on the ground in what is termed the "grass stage" for three to 15 years.

In the grass stage, a thick root collar with insulative bark protects the stem, and a dense ball of long needles surrounds the growing tip of the young pine, protecting it in some unknown way. When the needles burn down toward the bud, moisture liberated as steam may insulate the bud, or choke out fire in combination with a reduction of oxygen needed by the fire. Buds protected by the dense ball of needles are rarely killed, unless the fire is fanned by a strong wind.

During this time the young tree grows a long, thick taproot that reaches far down into sandy soil toward moisture. This taproot serves as a nutrient storage organ so that when the young plant finally starts its height growth, the stored nutrients in its taproot help it shoot up. During this upward growth, the tree delays putting out lateral branches, giving saplings a distinctive bottle-brush appearance. By growing rapidly upward, the young tree minimizes the time its sensitive terminal buds are exposed to ground fires that once were common in longleaf pine forests.

Early foresters could not see economic return in a species that delays height growth, but longleaf pine is also difficult to plant because of the ▷



Newly metamorphosed gopher frogs, Apalachicola National Forest.

long taproot, and the survival of planted saplings is often low. It is one of the few Southern pines that masts, which means that periodically all the trees produce cones and seeds in much greater quantities than in average years. For longleaf pine, a good seed crop comes along only once on an average of seven years, and foresters haven't yet learned when to expect a mast year. The large, heavy seeds are easily preyed upon by birds and beetles.

Because of these problems, foresters planted slash pine where longleaf pine used to be. By 1987 slash pine had become the dominant forest tree in the state, accounting for 69 percent of all commercial pine forests and 15 percent of the land area of Florida. It was not intuitively obvious that the replacement of one kind of pine by another would be ecologically harmful. Slash pine is a native species of Florida, too, but it has properties that grossly change the ecology of any site where slash pine plantations replace longleaf pine forest.

Unlike slash pines, which can be grown very densely, longleaf pines don't tolerate much crowding. The canopies of mature stands of longleaf are open and the forests form park-like vistas. Sunlight pours down on the forest floor, stimulating a rich groundcover flora. One of the fascinating paradoxes about longleaf pine forests is that while the tree species richness is very low, the overall species richness is very high. So high, in fact, that there we find the greatest number of flowering plants and the greatest number of breeding birds in Florida. The diverse groundcover supports a rich fauna of insects, amphibians, reptiles and mammals. The gopher tortoise, for instance, lives in longleaf pine forests because the open canopy allows its preferred groundcover foods to flourish.

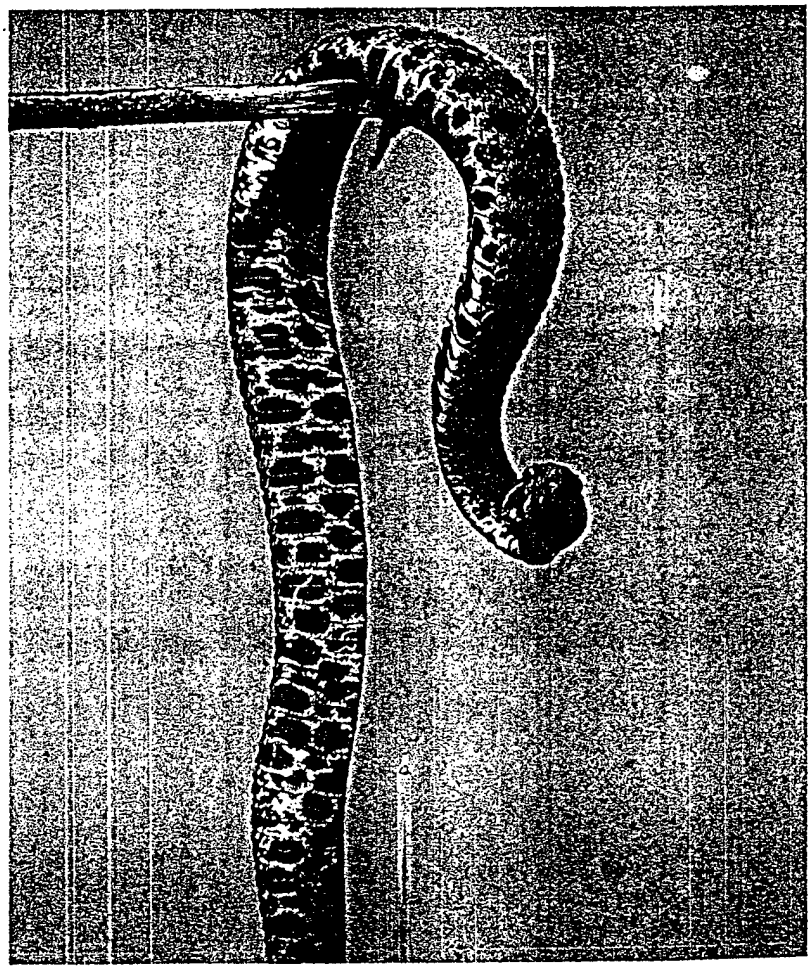
Slash pines can be grown together in rows so densely that after about 10 to 15 years the canopy closes and not enough sunlight reaches the ground to support the original groundcover diversity. The gopher tortoise, able to live in recently planted slash pine plantations, soon is forced to migrate to find food.

Shading alone, however, is not the whole problem. Because of slash pine's sensitivity to fire, the plantations are not allowed to burn, at least for the first 10 years. During this time many woody species such as gallberry dominate the groundcover and do their share to shade out other groundcover plants. Beyond 10 years, in the continued absence of fire, slash pine plantations become encroached by a more serious group of interlopers – hardwood species from the wetlands. Eventually the combination of dense tree canopy and hardwood encroachment causes a very different ecological condition than existed in the natural longleaf pine forest. Many of the native species associated with longleaf forests disappear.

Longleaf pine forests are not all alike. Tolerant of a wide range of soil conditions, this pine ranges ecologically from the highest, dryest sand ridges and clayhills in Florida, down gentle slopes, through dry and moist flatwoods, and even to the edge of seepage wetlands, the native habitat of slash pine. On sandy soils, longleaf pine associates with turkey and blackjack oaks, two scrubby understory trees. Here, where the soils are hot and dry, the gopher tortoise and other plants and animals tolerant of desert-like conditions thrive. On moister soils in flatwoods, saw palmetto and gallberry are principal associates. Throughout most of the range of longleaf pine in Georgia and Florida, a rolled-leaf bunchgrass called wiregrass is a major understory associate.

Next to the imperiled future of longleaf pine forests, the most important story about longleaf communities is their love affair with an agent of destruction, fire.

One would predict that nonflamma-



The pygmy rattlesnake is a common inhabitant of longleaf forests.



Cool fires burned for weeks at a time in original old-growth longleaf pine forests.

bility would evolve in plant parts as a major feature of resistance to death by fire. Not so. Longleaf produces needles that have more volatile resins and oils than any other Southern pine, rendering the needles extremely flammable. Wiregrass is also highly flammable. Forester Robert Mutch hypothesized that as longleaf pine adapted to insulate its vulnerable parts from heat, the highly flammable needle litter surrounding the tree gave longleaf a deadly advantage over fire-sensitive competitors. Any thin-barked young pine or hardwood tree, for example, was doomed if it chanced to germinate in a funeral pyre of shed longleaf pine needles.

Fire has been so important in the evolutionary structuring of longleaf pine ecosystems that the timing of flowering and seed production of most of the grasses (especially wiregrass) and many forbs are highly dependent upon fire. In other words, these grasses and forbs will not reproduce sexually in the absence of fire. More than that, not just any old fire will do. Only in the past two decades have we come to learn the importance of fires ignited in the season when natural fires were set by lightning, May-July. You can burn longleaf groundcover from September to April, as cattle graziers did for four centuries, but these plants will not flower. But if you burn from May to July, later in that very growing season, these plants will flower so profusely that the human eye will be overwhelmed with the difference. It is no coincidence that the flowering of these plants is tied to the natural lightning season.

Wander in the groundcover of longleaf pine forest. You can't see your feet because the groundcover is so rank. Wiregrass, especially, sprawls so densely over the ground as to create a springy mat, often calf deep. What chance for successful establishment would a seed have falling here? In the first place, a seed probably wouldn't make it to the soil because it would rest on deep, dry litter. Few seeds can germinate under these conditions. If a seed did reach the ground and germinate, how would it acquire the necessary sunlight to drive photosynthesis and enable it to grow, in the densest shade created by the groundcover and dead matter from previous growing seasons?

Enter fire. Fire completely eliminates the groundcover. The earth under longleaf pine forests after a fire is black and bare. Fire burns up every blade of grass, every leaf, most stems, green or dead...but it does not kill their roots. If the fire is followed immediately by a rain, fresh green growth can peek through the ashes the next day. Anyone who has watched this phenomenal recovery knows how fast it takes place. Within a couple of weeks a riot of new, lush greenery carpets the scene. If there has been plenty of rainfall to wash the carbon off the tree trunks, it can be difficult to tell the site was black and barren only a month previously.

From the point of view of a seed, think about the condition of the ground after a May-July burn. Dead litter doesn't choke out overhead sunlight, and there are large patches of bare mineral soil on which to germinate. An excess of nutrients are available in the soil, liberated from the dead and live plant tissues that were ashed. Over evolutionary time, those plants with sufficient growing season to produce seed quickly after a burn were more likely to get their offspring into the next generation than relatives who scattered seed on unburned groundcover. Wiregrass did this. So did longleaf pine, since, of all the Southern pines, it alone drops its seed in the fall. They germinate in late fall and winter.

The original longleaf forests did not require a lightning strike every square mile to burn the whole forest. In presettlement times the only barriers to fire were natural wetlands such as lakes, rivers and the steeper stream-valley bottomlands. And in those days, longleaf forests stretched for hundreds of square miles. Studies done in the 1880s reported that fires burned for weeks at a time, slowly moving over the landscape. The ▷

original longleaf pine forests probably burned every three to five years, sometimes more often, sometimes less.

Longleaf pine lives to the greatest age of any Southern pine, more than 450 years. Probably fewer than 3,000 acres (0.004 percent) of old-growth longleaf pine remains, scattered about in small patches over its original range, since almost all of the original timber was cut during the Great Depression and World War II. Second-growth longleaf pine is harvested when its commercial value peaks at about 50 years, so unless some conservation effort is made to allow some longleaf pines to live out their natural lives, there will be no more trees suitable for the red-cockaded woodpecker, nor any dead, standing snags for all the birds who utilize dead trees for their nesting cavities.

The more we study nature, the more we discover the importance of connections. Many people would not miss the red-cockaded woodpecker, which excavates its nesting cavity in old trees affected by the wood-softening heart-rot fungus, should it go extinct, but consider this: The red-headed woodpecker and the wood duck would miss it. So would the flying squirrel, the honey bee and numerous other animals that utilize their abandoned cavities. The gopher tortoise excavates a burrow averaging 30 feet long in longleaf pine forests – over 100 species of arthropods and vertebrates have been found to utilize this burrow. Both the woodpecker and the tortoise are vitally connected to the ecology and survival of other animals. Because animals and plants are intimately connected in nature, each species' worth far exceeds its own presence. The same goes for entire communities as well.

If any community in the world could be called a "keystone community," it is the longleaf pine ecosystem. Just one example of its importance to the survival of other communities should suffice. In sandy flatwoods from North Carolina to Texas, where gentle slopes intercept a shallow water table, seepage communities of great biodiversity are found. These herb bogs, where most of our carnivorous plants grow, contain up to 50 species of plants per square meter, more species than has ever been measured at that scale anywhere on earth.

Just downslope through the herb bogs another wetland community is dominated by evergreen shrubs in a dense tangle. These are all hardwood species sensitive to fire. In the absence of fires, these shrubs rapidly invade upslope into the herb bogs. Since all of the species of the herb bogs are heliophiles, sun lovers, they soon die and disappear from sites that have been invaded by shady evergreen shrubs. Where does the fire come from that keeps the shrub species out of the herb bogs? It usually burns downslope out of longleaf pine forests. No longleaf pine forests, no fire, no herb bogs. This vital connection between two species-rich plant communities has persisted so long that most of the grasses and many forbs in the herb bogs only flower and set seed vigorously after fires between May and July!

Longleaf pine forest contributes, more than any other ecosystem in Florida, to our state's biodiversity, both directly from its own species richness as well as indirectly through its "keystone" role in the maintenance of other communities. This connectedness should make us realize that people are connected with nature too. We have been ignoring those connections for a long time – so long that, for the longleaf pine, sadly, the eleventh hour has arrived.

D. Bruce Means, Ph.D. is an ecologist, and the founder and director of the Coastal Plains Institute. His feature on beech/magnolia forests, scheduled for our next issue, will conclude the upland series.



Characteristic Mammals and Birds of Longleaf Pine Forests

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ABSTRACT

The structure and plant species composition of natural longleaf pine (Pinus palustris) forests varies in response to disturbance (particularly fire and hurricanes), hydrology and soil quality. Bird and mammal community composition reflects this variation. To define the mammal and bird communities, I considered the entire distribution of longleaf pine, including the forests in eastern Texas and western Louisiana. Considerably more information is available for birds than for mammals. Based primarily on community-wide surveys, 36 mammal and 86 bird species (35 residents, 29 breeders and 22 winter visitors) are characteristic of longleaf pine forest. Three mammal species, bison (Bison bison), red wolf (Canis rufus) and mountain lion (Felis concolor), and one bird species, ivory-billed woodpecker (Campephilus principalis) have been extirpated from the distribution of longleaf since European settlement.

Species that largely are sympatric with longleaf pine and commonly use the habitat type are: southeastern pocket gopher (Geomys pinetis), southeastern fox squirrel (4 subspecies of Sciurus niger), red-cockaded woodpecker (Picoides borealis), brown-headed nuthatch (Sitta pusilla) and Bachman's sparrow (Aimophila aestivalis). Sixty-nine percent of the mammals and 36 percent of the characteristic bird species forage primarily on or near the ground in longleaf forest. This is one measure of the importance of the ground cover to the mammalian and avian communities. Fire is essential for maintaining this important component of the vegetation.

INTRODUCTION

The process of identifying bird and mammal species that are characteristic of longleaf pine forests is as difficult as defining the longleaf pine plant community. The broadest categories of longleaf forest, based primarily on soil and hydrological characteristics, are flatwoods, sandhills, and clayhills (Abrahamson and Hartnett 1990; Myers 1990). These have been subdivided into 12 natural community types east of the Mississippi River (Allard 1990) and seven types in the west Gulf Coastal Plain (Bridges and Orzell 1989). Wahlenberg (1946) described the overstory of undisturbed longleaf forest as a monoculture, but ground cover composition and the structure of longleaf pine community types vary. Savannas with few trees and a ground cover of palmettos, forest with tall trees and prairie-like ground cover, and sparsely vegetated scrub in deep sand are a few of the structural types. Bird and mammal communities of longleaf reflect these variations.

In addition to variation in natural longleaf communities, humans have eliminated large portions of the original habitat and modified much of the remainder. Possibly as little as 500 ha of old-growth longleaf pine forest remains (Davis 1990). Longleaf individuals can be found in suburban settings, dense commercial plantings or regeneration areas, and intermixed with hardwoods following fire exclusion, but natural longleaf forests maintained with frequent fires are increasingly rare (Means and Grow 1985).

Many longleaf communities were eliminated or severely disturbed before systematic community-level studies of vertebrates were undertaken. Also, structural components of old-growth forest, such as old trees, mixed age-class distribution and horizontal patchiness that existed before European settlement, have been lost in the remaining second-growth forests. Therefore, our knowledge of the mammal and bird communities of longleaf is incomplete.

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The purpose of this paper is to identify characteristic bird and mammal species of longleaf pine forests and to examine how some changes in habitat structure and composition have affected longleaf pine forest bird and mammal communities.

MAMMALS OF LONGLEAF

To compose the initial list of mammals, I first compared range maps of individual species (Hall 1981; Schmidly 1983) with the distribution of longleaf pine (Little 1971). This provided a comprehensive list of all potential members of the community. I determined habitat affinities of these species from a literature search and included a species if it was explicitly associated with longleaf. The habitat-specific, systematic surveys of mammals at St. Marks National Wildlife Refuge (United States Fish and Wildlife Service 1980) and along the proposed corridor for the Cross Florida Barge Canal (Florida Game and Fresh Water Fish Commission 1976) were particularly useful. Jennings (1958) provided most of the information about habitat preferences in bats. Thirty-seven species of mammals have ranges that both overlap with the distribution of longleaf pine and are associated with longleaf habitat in the literature (Table 1). Three species, plains pocket gopher, fulvous harvest mouse and northern pygmy mouse, are only sympatric with longleaf in Texas and Louisiana in the west Gulf Coastal Plain.

The mammal community of longleaf has changed over time. Four species, feral swine, northern pygmy mouse, armadillo, and coyote (Table 1) have spread into longleaf forests since European settlement. Swine escaped from Hernando DeSoto's expedition in 1539 and feral populations became established throughout the coastal plain (Hanson and Karstad 1959). Feral and free-ranging domestic swine were detrimental to longleaf reproduction during settlement of the coastal plain (Frost 1993). The northern pygmy mouse probably was restricted to the coastal prairie in eastern Texas before extensive habitat disturbance, but it spread northward into pine-oak forests in the 1970s (Schmidly 1983). First reported in southern Texas along the Rio Grande (Bailey 1905), the armadillo spread into the western Gulf Coastal Plain in the early 1900s and was introduced into Florida during World War I (McBee and Baker 1982). It currently is widespread throughout the Coastal Plain. The coyote, through a combination of range expansion and local introductions, is becoming increasingly common in the Southeast (Bekoff 1977).

In addition to the 36 species currently found in longleaf, three species, red wolf (Canis rufus), mountain lion (Felis concolor) and bison (Bison bison) have been extirpated. Although red wolves are being reintroduced into coastal North Carolina, this large predator has been reduced to such low numbers that it essentially has been eliminated from the distribution of longleaf. Only a small population of mountain lions exists in southern Florida south of the distribution of longleaf, although individuals were seen in central Florida in the mid-1970's (Florida Game and Fresh Water Fish Commission 1976). Bison were distributed widely "although in relatively dispersed and small populations" at the time of European settlement in the sixteenth century (McDonald 1981). The species was eliminated from the southeastern Coastal Plain by the early nineteenth century.

Four additional species, ringtail (Bassariscus astutus), gray wolf (Canis lupus), jaguar (Felis onca), and ocelot (Felis pardalis), which occurred in the western Gulf Coastal Plain in Texas and Louisiana (Bailey 1905), have been extirpated. The degree of use of longleaf habitat by these four species is unknown, but probably was small. The introduced black rat (Rattus rattus), has been recorded in longleaf flatwoods, but only as a transient (Layne 1974). Thirty-two additional mammal species overlap in range with longleaf, but use longleaf forests rarely or accidentally.

Foraging zones provide one indication of the importance of different structural aspects of longleaf forest to the mammal community. Most of the characteristic mammals (25 species, 69%) forage primarily on the ground. Seventeen percent are aerial feeders, 8% are subterranean and 6% feed at least partially in trees. Twenty-seven percent of the species are microtine or cricetine rodents that dwell in ground cover vegetation. These species in particular would be susceptible to alteration of the ground cover.

Of 36 species of mammals that are characteristic of longleaf pine forest, longleaf is used by some species more than others. Most of the species (29) either overlap with longleaf extensively, but have very large distributions of which longleaf is only a small part (eg. raccoon) or have distributions that are mostly peripheral to longleaf (eg. plains pocket gopher).

Seven species, Seminole bat, yellow bat, southeastern fox squirrel, southeastern pocket gopher, marsh rice rat, Florida mouse and oldfield mouse, share at least two-thirds of their distribution with

Table 1. Characteristic mammals of longleaf pine forest and references that describe the species' association with longleaf. Longleaf is not necessarily the primary habitat of the species listed below. Scientific names follow Jones et al. (1979).

Species	Reference
Virginia opossum (Didelphis virginiana)	FGFWFC (1976)[1]
Southeastern shrew (Sorex longirostris)	USFWS (1980)[2]
Southern short-tailed shrew (Blarina carolinensis)	USFWS (1980)
Least shrew (Cryptotis parva)	USFWS (1980)
Eastern mole (Scalopus aquaticus)	Golley (1962)
Eastern pipistrelle (Pipistrellus subflavus)	Jennings (1958)
Southeastern myotis (Myotis austroriparius)	FGFWFC (1976)
Red bat (Lasiurus borealis)	Jennings (1958)
Seminole bat (L. seminolus)	Jennings (1958)
Yellow bat (L. intermedius)	Jennings (1958)
Evening bat (Nycticeius humeralis)	Jennings (1958)
Nine-banded armadillo (Dasypus novemcinctus)	Fitch et al. (1952)
Eastern cottontail (Sylvilagus floridanus)	FGFWFC (1976)
Gray squirrel (Sciurus carolinensis)	FGFWFC (1976)
Fox squirrel (S. niger)[3]	Weigl et al. (1989)
Southern flying squirrel (Glaucomys volans)	FGFWFC (1976)
Southeastern pocket gopher (Geomys pinetis)	FGFWFC (1976)
Plains pocket gopher (G. bursarius)	Schmidly (1983)
Hispid cotton rat (Sigmodon hispidus)	FGFWFC (1976)
Eastern harvest mouse (Reithrodontomys humulis)	USFWS (1980)
Fulvous harvest mouse (R. fulvescens)	Schmidly (1983)
Marsh rice rat (Oryzomys palustris)	USFWS (1980)
Florida mouse (Podomys floridanus)	Stout et al. (1988)
Oldfield mouse (Peromyscus polionotus)	FGFWFC (1976)
Cotton mouse (P. gossypinus)	FGFWFC (1976)
Golden mouse (Ochrotomys nuttalli)	USFWS (1980)
Northern pygmy mouse (Baiomys taylori)	Schmidly (1983)
Pine vole (Microtus pinetorum)	USFWS (1980)
Raccoon (Procyon lotor)	FGFWFC (1976)
Long-tailed weasel (Mustela frenata)	Pournelle (1950)
Striped skunk (Mephitis mephitis)	FGFWFC (1976)
Coyote (Canis latrans)	Pers. obs.
Red fox (Vulpes vulpes)	Sunquist (1989)
Gray fox (Urocyon cinereoargenteus)	Sunquist (1989)
Wild boar (Sus scrofa)[4]	Hanson and Karstad (1959)
White-tailed deer (Odocoileus virginianus)	FGFWFC (1976)

[1] FGFWFC = Florida Game and Fresh Water Fish Commission
[2] USFWS = United States Fish and Wildlife Service.
[3] The southeastern fox squirrel is a combination of 4 subspecies. The entire range of fox squirrel is much larger. (See text).
[4] Introduced.

that of longleaf. Most of these species use a wide range of habitats, but for the fox squirrel and southeastern pocket gopher longleaf could be considered primary habitat.

Historically, the southeastern pocket gopher probably occurred most commonly in sandy soils associated with upland longleaf. Currently, pocket gopher burrows can be found in roadsides and pastures where longleaf has long since disappeared. The southeastern fox squirrel is an amalgamation of four subspecies (cinerea, niger, shermani, and bachmani) and is restricted to the southeastern Coastal Plain. These subspecies are significantly larger and have a more variable pelage than the "western" subspecies (Weigl et al. 1989). The southeastern fox squirrel occurs extensively in longleaf although it was probably rare in large stands of pure longleaf in Texas (Schmidly 1983).

The Florida mouse has a highly restricted distribution in peninsular Florida and is found mostly in sand pine (Pinus clausa) scrub (Stout 1981, Stout et al. 1988), but sandhill longleaf pine-turkey oak (Quercus laevis) woodland is also an important habitat.

BIRDS OF LONGLEAF

I composed the list of birds from 18 Breeding Bird Censuses (BBC) and 11 Winter Bird Population Studies (WBPS) that have been conducted in longleaf forests (Appendix I). All species that visited or held territories on at least one BBC or WBPS were considered characteristic species (Table 2). The foraging zones of the birds of the longleaf community were classified according Ehrlich et al. (1988).

The list of characteristic bird species of longleaf pine forest is subdivided into residents, breeders and winter visitors (Table 2). I did not include transients in this paper. Residents are those species that were found on at least one BBC and one WBPS. Most breeders are long-distance neotropical migrants, but also include species that shift to other habitats in the winter (eg. brown-headed cowbird). Winter visitors migrate from northern breeding grounds and use longleaf for foraging and roosting seasonally.

The standardized bird counts (BBC and WBPS) were made in a variety of structural types of longleaf. The habitats where the bird counts were made include a mature longleaf monoculture in rich clayey uplands (Thomasville, Georgia), sandhills (North Carolina and Gainesville, Florida), mixed hardwood-pine (Mississippi), and flatwoods (Okefenokee National Wildlife Refuge, Georgia).

BBCs have been conducted in longleaf at two sites in Florida, three sites in Georgia, one site in South Carolina, and one site in Mississippi. Fewer WBPSs have been conducted in longleaf, but winter counts have been made at one site in Florida, two sites in Georgia, and two sites in North Carolina (Appendix I). Unfortunately, no BBCs or WBPSs have been conducted in longleaf habitat in the western Gulf Coastal Plain.

All characteristic species were ranked according to abundance and frequency of occurrence (Table 2). Abundance categories for the breeding season were based on the maximum number of territories per 40 ha observed over all BBCs. The abundance categories (number of territories per 40 ha) are: 1 (visitor), 2 (0.5-5), 3 (5.5-10), 4 (10.5-15), and 5 (>15). Frequency of occurrence is the percentage of sites at which a species was observed. All years were pooled for each site. There were 7 BBC sites and 5 WBPS sites. Categories for frequency of occurrence (%) for both the breeding season and winter are the same: 1 (1-20), 2 (21-40), 3 (41-60), 4 (61-80), and 5 (81-100). Abundance categories for winter were based on the maximum number of individuals observed per visit standardized to the number expected on 40 ha. These categories (average number of individuals per 40 ha) are: 1 (<1), 2 (1-5), 3 (6-10), 4 (7-15), and 5 (>15).

Eighty-six species of birds (excluding migrants) occur in longleaf pine forests based on the BBC and WBPS. Thirty-five are residents, 29 are breeders, and 22 are winter visitors (Table 2). Of the breeders, 21 species migrate mostly to the neotropics. Eight species, Wild Turkey, Black Vulture, Barred Owl, Common Ground-dove, Fish Crow, Blue-gray Gnatcatcher, Field Sparrow and the Brown-headed Cowbird, either shift to other habitats or migrate to south Florida in the winter. The wild turkey, for example, uses longleaf seasonally for brood habitat (Sisson 1991).

Although BBC and WBPS sites were not randomly chosen, frequency of occurrence provides a measure of the relative likelihood that a species will be encountered on a longleaf site. Seven species, northern bobwhite, red-headed woodpecker, blue jay, Carolina wren, eastern bluebird, northern cardinal, and great crested flycatcher, were encountered on more than 80 percent of the sites in the breeding season. Brown-headed nuthatch, pine warbler, American robin, and yellow-rumped warbler, were seen on more than 80 percent of the sites in winter.

Table 2. Characteristic birds of longleaf pine forest. All residents were visitors or territorial on at least one BBC and WBPS; all breeders were visitors or territorial on at least one BBC; and all winter visitors were seen on at least one WBPS. Abundance and frequency of occurence of all species were ranked on a scale of one (low) to five (high) for the breeding season and winter. (See text.) Scientific names follow the American Ornithologists' Union (1983).

Residents	Foraging* Technique	Breeding Abun.	Breeding Freq.	Winter Abun.	Winter Freq.
Wood duck (Aix sponsa)	D	2	1	2	1
Turkey vulture (Cathartes aura)	P	1	1	2	2
Red-tailed hawk (Buteo jamaicensis)	P	1	1	1	1
Red-shouldered hawk (B. lineatus)	P	2	1	1	2
American kestrel (Falco sparvarius)	HP	1	1	1	3
Northern bobwhite (Colinus virginianus)	G	4	5	4	2
Mourning dove (Zenaida macroura)	G	4	3	2	3
Great horned owl (Bubo virginianus)	S	2	1	2	2
Red-bellied woodpecker (Melanerpes carolinus)	B	3	4	3	4
Red-headed woodpecker (M. erythrocephalus)	H	4	5	3	1
Downy woodpecker (Picoides pubescens)	B	2	3	2	4
Hairy woodpecker (P. villosus)	B	2	3	2	3
Red-cockaded woodpecker (P. borealis)	B	2	3	4	4
Northern flicker (Colaptes auratus)	G	3	4	3	2
Pileated woodpecker (Dryocopus pileatus)	B	2	1	2	2
Blue jay (Cyanocitta cristata)	G	3	5	3	2
American crow (Corvus brachyrhynchos)	G	3	2	3	3
Carolina chickadee (Parus carolinensis)	F	2	3	3	3
Tufted titmouse (P. bicolor)	F	5	3	4	3
White-breasted nuthatch (Sitta carolinensis)	B	3	2	3	3
Brown-headed nuthatch (S. pusilla)	B	5	4	5	5
Carolina wren (Thryothorus ludovicianus)	G	5	5	3	4
Eastern bluebird (Sialia sialis)	H	2	5	5	3
Gray catbird (Dumetella carolinensis)	G	1	1	2	1
Northern mockingbird (Mimus polyglottos)	G	5	3	1	2
Brown thrasher (Toxostoma rufum)	G	4	3	2	1
Loggerhead shrike (Lanius ludovicianus)	S	2	1	2	1
Pine warbler (Dendroica pinus)	F	5	4	5	5
Common yellowthroat (Geothlypis trichas)	F	5	3	5	2
Northern cardinal (Cardinalis cardinalis)	G	2	5	2	2
Rufous-sided towhee (Pipilo erythrophthalmus)	G	5	4	4	2
Bachman's sparrow (Aimophila aestivalis)	G	5	3	3	2
Eastern meadowlark (Sturnella magna)	G	4	3	5	2
Red-winged blackbird (Agelaius phoeniceus)	G	2	1	5	3
Common grackle (Quiscalus quiscula)	G	2	1	1	1
Breeders					
Black vulture (Coragyps atratus)	P	4	1		
Wild turkey (Melleagris gallopavo)	G	1	1		
Common Ground-dove (Columbina passerina)	G	2	1		
Yellow-billed cuckoo (Coccyzus americanus)	F	3	3		
Barred owl (Strix varia)	P	3	3		

Breeders, Cont'd.	Foraging Technique	Breeding Abun.	Breeding Freq.	Winter Abun.	Winter Freq.
Chimney swift (Chaetura pelagica)	A	1	2		
Common nighthawk (Chordeiles minor)	A	4	3		
Chuck-will's-widow (Caprimulgus carolinensis)	A	2	2		
Eastern wood-pewee (Contopus virens)	H	5	3		
Great crested flycatcher (Myiarchus crinitus)	H	5	5		
Eastern kingbird (Tyrannus tyrannus)	H	4	3		
Purple martin (Progne subis)	A	1	3		
Fish crow (Corvus ossifragus)	G	1	2		
Blue-gray gnatcatcher (Polioptila caerulea)	F	5	3		
Wood thrush (Hylocichla mustelina)	G	4	1		
White-eyed vireo (Vireo griseus)	F	5	1		
Yellow-throated vireo (Vireo flavifrons)	F	4	3		
Red-eyed vireo (Vireo olivaceus)	F	2	1		
Northern parula (Parula americana)	F	2	1		
Prairie warbler (Dendroica discolor)	F	2	2		
Yellow-throated warbler (D. dominica)	F	2	1		
Hooded warbler (Wilsonia citrina)	F	2	1		
Yellow-breasted chat (Icteria virens)	F	3	1		
Summer tanager (Piranga rubra)	F	5	4		
Blue grosbeak (Guiraca caerulea)	G	5	3		
Indigo bunting (Passerina cyanea)	F	5	3		
Field sparrow (Spizella pusilla)	G	3	1		
Brown-headed cowbird (Molothrus ater)	G	3	3		
Orchard oriole (Icterus spurius)	F	2	1		
Winter visitors					
Yellow-bellied sapsucker (Sphyrapicus varius)	B			3	4
Eastern phoebe (Sayornis phoebe)	H			2	3
Tree swallow (Tachycineta bicolor)	A			1	1
Brown creeper (Certhia americana)	B			1	1
Red-breasted nuthatch (Sitta canadensis)	B			1	1
House wren (Troglodytes aedon)	G			5	3
Golden-crowned kinglet (Regulus satrapa)	F			1	3
Ruby-crowned kinglet (R. calendula)	F			3	3
Hermit thrush (Catharus guttatus)	G			2	2
American robin (Turdus migratorius)	G			5	5
Cedar waxwing (Bombycilla cedrorum)	F			1	1
Solitary vireo (Vireo solitarius)	F			3	3
Orange-crowned warbler (Vermivora celata)	F			1	1
Yellow-rumped warbler (Dendroica coronata)	F			5	5
Palm warbler (D. palmarum)	G			3	3
Chipping sparrow (Spizella passerina)	G			1	2
Song sparrow (Melospiza melodia)	G			2	1
Swamp sparrow (M. georgiana)	G			5	2
Dark-eyed junco (Junco hyemalis)	G			1	1
White-throated sparrow (Zonotrichia albicollis)	G			2	1
Pine siskin (Carduelis pinus)	F			2	1
American goldfinch (C. tristis)	F			5	4

*Foraging techniques (based on Ehrlich et al. 1988): A=aerial forage, B=bark glean, D=dabble, F=foliage glean, G=ground glean, H=hawk, HP=hover and pounce, P=patrol, and S=swoop.

For most species ranks of abundance and frequency of occurrence were similar (ranks equal or less than one rank apart). Twenty-two species were locally abundant (abundance two or more ranks higher than frequency of occurrence) in either the winter or the breeding season (eg. common yellowthroat). Several residents show seasonal changes in use of longleaf or at least changes in detectability. For example, mourning dove, Carolina wren, northern mockingbird, brown thrasher, and Bachman's sparrow were more abundant or more detectable in the breeding season than in the winter. Eastern bluebird and red-winged blackbird were more abundant in the winter than in the breeding season. Although these data are crude, they are useful for an initial examination of patterns of abundance and distribution. A model that includes vegetation structure would be valuable.

Some relatively rare birds that use longleaf do not appear on the lists composed from BBC and WBPS data. The bald eagle (Haliaeetus leucocephalus) frequently uses tall living pines for its nest trees (Wood et al. 1989). The Florida sandhill crane (Grus canadensis pratensis) is sometimes found in open, wet flatwoods, but it prefers wet savannas and pastures (Williams 1978).

Two bird species, the ivory-billed woodpecker and the passenger pigeon (Ectopistes migratorius) have been extirpated from longleaf. The ivory-billed woodpecker was found in mature hardwood swamps and floodplain forests throughout most of its range. Evidence that the ivory-billed woodpecker used pine forests came from A. A. Allen and P. P. Kellogg, who found that this woodpecker nested in swamps and fed on fire-killed trees in the pinelands in Florida (pg.16, Tanner 1942). Tanner (1942) speculated that use of upland pine forests by the woodpecker explained why it was relatively more abundant in Florida than in other parts of its range.

The extent to which passenger pigeons used longleaf is unclear. Ridgway (in Mershon 1907) explicitly excludes the pigeon from longleaf. Jackson (1988), however, cites indirect evidence that pigeons ate turkey oak acorns, which is a common associate of longleaf. However, most accounts of pigeon habitat describe hardwood dominance.

Foraging techniques indicate structural aspects of longleaf forests that are important to birds. Nineteen bird species (22% of the characteristic species) forage in the air by aerial-foraging, hawking, patrolling, swooping or hover-pouncing. The number of perches and openness of the habitat are important to these birds. Ten species (12%) are primarily bark gleaners and 25 (29%) are foliage gleaners. Thirty-one species (36%) forage on or close to the ground. The importance of ground cover to the avian community of longleaf is indicated by this large number.

Of all the characteristic bird species, three are most closely associated with longleaf. Red-cockaded woodpecker, brown-headed nuthatch, and Bachman's sparrow use longleaf extensively and are sympatric with longleaf to a significant degree. The dependence of the red-cockaded woodpecker on older age-class pine trees for nesting sites is well-known (Wood 1983). Brown-headed nuthatches forage on the bark and needles of pines and nest in low snags. Bachman's sparrows nest and forage in dense ground cover of open pine forests. Although Bachman's sparrows will breed in clearcuts, they prefer open mature stands of timber with low, thick ground cover (Dunning and Watts 1990).

CHANGES IN FOREST STRUCTURE AND COMPOSITION

Not only has the longleaf pine ecosystem been dramatically reduced in size through conversion to other land uses, but virtually all of the remainder has been altered. Alteration of natural fire frequency and season, forest fragmentation, harvest of old trees, and elimination of native groundcover are some of the major changes. The effects of these changes are not well understood, although forest fragmentation and elimination of old trees (>100 years old) have been implicated in the decline of at least one bird species, the red-cockaded woodpecker (Anonymous 1990, Baker 1981).

Little research has been done on the effects of fire on mammals and birds of longleaf pine forests. However, the effects of fire exclusion on the mammal and bird communities were studied in an oldfield pine forest of loblolly (Pinus taeda) and shortleaf (P. echinata) pine that had a thick diverse ground cover (Engstrom et al. 1984). The gross structural changes following fire exclusion in longleaf pine forest would be similar to those observed in this oldfield forest. Forest structure changed dramatically following fire exclusion. In 15 years a thick midstory of sweetgum (Liquidambar styraciflua) and water oak (Quercus nigra) shaded out most of the ground cover vegetation and most of the young pines.

The small mammal and bird communities changed radically during the 15 years of fire exclusion on this oldfield forest. Virtually all small ground-dwelling mammals were eliminated from the community after 15 years without fire. The southern flying squirrel was the only species captured in small live-traps in the forest toward the end of the study (W.W. Baker pers. comm.). Bird species that typically nest in vegetation on the ground (Bachman's sparrow) or forage in open habitats (eastern kingbird) also disappeared within a few years of fire exclusion. Species that require more mesic conditions, such as hooded warbler and wood thrush, increased in abundance toward the end of the 15-year study period.

Hirth et al. (1991) described the bird community in an "old-growth" longleaf pine forest in central Florida that had not been burned in many years. Remnants of wiregrass (Aristida stricta) indicated a more abundant ground cover before fire exclusion (pers. obs.). Although no data on the bird community was available before fire exclusion, absence of the closest avian associates of longleaf (red-cockaded woodpecker, brown-headed nuthatch, and Bachman's sparrow) could have been caused by changes in forest structure.

The effects of fire exclusion on mammal and bird communities in southeastern upland pine forests are dramatic. But in longleaf forests that are burned, the effects of season of fire, especially growing season fires, are poorly understood. As interest increases in using growing season fire to enhance flowering of certain plant species or to control hardwoods, the direct and indirect effects of growing season fire on mammals and birds need to be documented. Maintenance of a schedule of frequent prescribed fire is essential for the long-term persistence of the characteristic mammals and birds of longleaf.

CONCLUSIONS

Although any list of mammals and birds for an entire forest type is incomplete and somewhat arbitrary, certain limited generalizations can be made from the lists provided. Significant portions of the mammal and bird communities forage on the ground. This indicates that the quality and composition of the ground cover should be important considerations for longleaf pine forest management. Fire is most important factor for ground cover management.

The mammal and bird species that have been extirpated from longleaf pine forest could not be called longleaf specialists. In fact most of them probably only used longleaf occasionally. Of the species that are most closely associated with longleaf only the red-cockaded woodpecker is federally endangered, although the Bachman's sparrow is under consideration for listing. Implementing ecologically sensitive land and timber management techniques will improve the long-term prospects for retaining the mammal and bird communities of the longleaf pine forest.

CONECUH NATIONAL FOREST UPDATE

Dear Friends and Neighbors, October 28, 1996

You no doubt have noticed all the burning done on the Forest. We have burned more in 1996 than anyone can remember. This last year has been very challenging: first with Hurricane Opal cleanup (roads, houses, timber salvage), then taking on the extra work of burning almost 30,000 acres since last January. Before all the storm cleanup was over, we started another big job of burning. Why did we take it upon ourselves to do all this extra prescribe burning? One reason: it was the right thing to do.

After losing so many of our bigger, older trees in Hurricane Opal, we were given a great gift . . . this year is going to be the biggest cone crop of longleaf pine since the 1940's. We had to take advantage of this tremendous opportunity! We are here to take care of the Forest - the best way we know how. By providing a healthy productive Forest, we can better serve our community by providing wildlife and fish, timber, camping, hunting, and clean water. The Conecuh is in the heart of "Longleaf Pine Country." Longleaf grows great on poorer soils, is resistant to disease/insect attacks, thrives on fire, and grows to be some of the strongest wood around. Without longleaf pine and fire, the Conecuh and its inhabitants would suffer.

To get these thousands and thousands of seeds to germinate, the seedbed first has to be prepared. The best and cheapest way I know to prepare the seedbed is to prescribe burn. The burning will not guarantee reforestation, but it is a necessary first step, and I know we have to try. Very young longleaf trees are susceptible to fire damage so we probably cannot burn these areas for 2-3 years. Burning will help reduce the fire hazard in these portions of the Conecuh.

I know that burning now is close to deer season and that may cause some conflicts with people wanting to enjoy their National Forest. Originally, I wanted to get much of this burning done in August and early September; however, during that time most of our work force was out West protecting homes and resources from devastating wildfires where fire has been excluded for many years.

Our efforts have been very successful. Prescribed burning is the most effective and cheapest habitat management tool we have for game, non-game, endangered species, and fuel hazard reduction. Helicopter burns done in the larger blocks contained many unburned patches which provided refuge for animals. Over the last 20 years we have been "re-learning" what Indians and settlers knew a long time ago. Much of the summer burning has already proven to be even more effective than winter burning at knocking back gallberry and brush and promoting the growth grasses, legumes, and other forage. These plants, in turn, provide better food for deer, turkey, quail, and many other animals. We hope to continue to this habitat restoration through our summer burning program and be prescribe burning for years to come.

The opportunity to get longleaf pine trees back in areas that lost trees is too valuable to pass up. Hopefully, many of these seeds will grow into trees for future generations to use and enjoy. A big part of taking care of the Conecuh involves caring about our community and neighbors. I wanted everyone to know what we were trying to accomplish with the prescribe burning. I hope this work does not inconvenience anyone. If you have concerns, please contact me or my staff at 222-2555 or come by the Ranger Station in Andalusia.

Sincerely,

United States Department of Agriculture
Forest Service
Conecuh Ranger District
Route 5, Box 157
Andalusia, Alabama 36420
(334) 222-2555

Conecuh National Forest - Flood Update

March 18, 1998

From Hurricanes to Floods

I am thankful that this recent weather did not involve high winds like we had from Hurricane Opal. I hope you, your family, and property are all okay. As far as National Forest roads, this storm has done more damage than Hurricane Opal. A possible reason is that when Hurricane Opal hit in October, 1995, we were in a drought period. The ground was much drier and able to absorb the heavy rains. This flood came at a time when the ground was already saturated with above average rainfall. When the rain came, flooding swiftly followed.

Road Repairs

We have assessed the road damage, blocked some roads, and will begin making repairs as soon as we can. These initial repairs will involve grading where possible. More extensive repairs on washouts, surface replacement, and culverts will take additional time. It may be 1-2 years before all repairs can be made. Right now, we are trying to secure funding for the repairs. I appreciate your patience during this time.



FEMA Assistance

If you have any damage, call 1-800-462-9029 (TDD 1-800-462-7585 for the speech and hearing impaired).

Safety

Please be cautious on the roads. The rains may keep coming for a while. Keep an eye out for hazards. When in doubt slow down. Do not drive in water where you cannot see the road surface. Please do not try to get across areas you are uncertain about. For your own safety, please do not try to go on any closed roads.



Turkey Hunters and Safety

You most likely will be traveling to your hunting spot in the dark. Please be extremely cautious. The flood has changed road conditions for the worse: there are signed blockades installed where the road is washed out. Also, there are rough washboard areas. Please drive slowly and be alert. Enjoy your hunt on the National Forest. As always, be safety conscious during your hunt, follow the State Game Laws, and be courteous to other hunters.

Your help is needed

If you need to report any hazards or if you have any concerns to share, please call 334-222-2555 or come by the Ranger Station on Highway 29 South.

Thank you again for your support and patience.

Sincerely,

Gary L. Taylor
District Ranger

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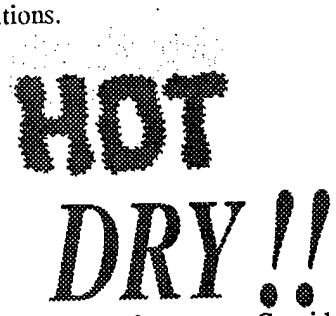
United States Department of Agriculture
Forest Service
Conecuh Ranger District
Route 5, Box 157
Andalusia, Alabama 36420
(334) 222-2555

Conecuh National Forest - Fire Danger Update

July 10, 1998

Fire Hazard

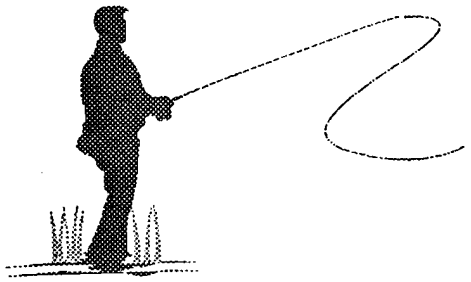
Our last update in March began by saying, "From Hurricanes to Floods." Now just a few months later, we are experiencing a severe drought. We have received less than 6 inches of rain in the last 3 months. Our drought index was over 700 for most of June - indicating severe drought. Although recent rains have helped, we are under extremely hazardous fire conditions.



So far we have been very fortunate. Considering the ***drought***, ***lightning***, and ***heat***, it is suprising that we have not had more wildfires. I am sure you have heard about the disastrous fires in Florida. We could be in the same emergency as Florida, had we not been prescribed burning all these years. The key difference between where wildfires are doing so much damage and here is that we have r**educed the hazardous fuel loadings and kept them low**.

The fuel loading (the amount of burnable material present) increases each year. The longer you wait between burns, the more the fuel builds up which leads to more severe wildfires.

Outdoor Safety



Be careful in the heat. Hikers, Anglers, and Campers need to remember to take precautions when outside. Avoid a lot of physical activity during the hottest parts of the day. Drink plenty of fluids, and remember there is no substitute for water.





Drought+ Lightning+ Fuel+ *Heat* = *Hot* Fires

Fire is a natural event. For thousands of years regular fires have shaped the South. The South is a fire-maintained ecosystem that offers one of the most diverse and species rich areas on Earth. From the abundant game to endangered species, all rely on fire in some way for their survival. Historically, the main cause of fires has been lightning occurring in the spring and summer. Native Americans also lit fires for agriculture and hunting. Their knowledge of the benefits of fire were passed on to the early pioneers that settled and farmed this area.

We are lucky that here in our area people have not lost this knowledge and appreciation for Nature and Fire.

Fire Safety



Please be careful when burning debris and with campfires Although we have not had many wildfires, there have been 7 to date. Two of these were escapes from people burning debris. The other 5 wildfires were caused by lightning. Most of the wildfires have been about 5 acres; however, we had a 23-acre and a 70-acre wildfire. The larger ones have typically been in areas with greater fuel loadings.

Mimicking Nature is the Key

You cannot fool Mother Nature. Sooner or later the woods will burn. We have been working hard to mimic nature through prescribed burning. Our goal has been to capture the benefits of fire without the devastating results uncontrolled wildfires can bring. On the Conecuh NF, we have been burning 20,000+ acres each year to keep the fuel loading down. We try to burn 50-60% of the areas during the lightning season when Nature burned, and the rest in the winter. Mimicking Natural fires through prescribed burning is helping to restore habitat for game and non-game animals as well as rare species such as the red-cockaded woodpecker, pitcher plant bogs, gopher tortoise, and bachman's sparrow to name a few. Even these prescribed burns get hot in places which shows the need to burn and reduce the fuel loading.

It is unfortunate that the drought has prevented us from prescribe burning. This has set us back on restoring and maintaining vital habitat and ecosystems. Hopefully, rain will come soon, and we can get some much needed prescribed burning done. Thank your for your time. If you need further information, please call 334-222-2555 or come by the Ranger Station on Highway 29 South, Andalusia.

Sincerely,

Gary L. Taylor
District Ranger

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CONECUH NATIONAL FOREST

NOT CLOSED FOR ROAD REPAIRS

I wanted to thank everyone that visits and enjoys the Conecuh National Forest for being so patient while we have repaired our roads following Hurricane Opal. First reactions after the Hurricane were that our roads were wrecked and could never be in good shape again. Trees blocked hundreds of miles of Forest roads, stream crossings were blown-out by flood waters, and heavy rains washed whole road surfaces away. We set out to fix what the Hurricane had wrecked. It was not easy, and there were many bumpy roads ahead for us. Over the last two years, you have been extremely supportive while we smoothed out those bumps. We greatly appreciate your understanding.

My staff has been working hard on the roads, and I wanted to update you on what has been done. Within 18 days after the Hurricane, Forest Service personnel from all over Alabama came to our aid and helped us clear trees from 34 miles of U.S. & State Highways, 104 miles of County Roads, and more than 250 miles of Forest Service roads. Since then, we have graded about 140 miles each year, totally reconstructed 14 miles, repaired 5 areas where roads were completely blown out, replaced more than 50 culverts, spread more than 4,000 tons of clay/gravel in mudholes, and seeded more than 50 miles.

Our seeding and water-barring have been very successful in reducing erosion which, in turn, has allowed us to keep many roads open. One of the first rules of maintaining roads is to keep the soil in place. I know water-bars can be annoying, but land is just too valuable to let wash away. Some were built too high, and we responded to concerns by making them smaller and smoother. We were able to make the adjustments without compromising our responsibility of protecting soil and water quality. Still, I apologize for any inconveniences you may have with them.

Despite the obstacles and challenges we faced after the storm, the roads are now in great shape. Maintaining hundreds of miles of Forest Roads will always be challenging, and there will always be a lot of work to do. I thank you all again for your support as we have repaired the roads. If you would like to discuss this further or need any information, please call me at 222-2555.

Sincerely,

Gary L. Taylor
District Ranger

FOREST SERVICE
US
DEPARTMENT OF AGRICULTURE

October 1, 1997

EGLIN FACT SHEET

Prescribed Fire

Historically, the landscape in and around Eglin Air Force Base was maintained by natural processes that included fire. Fires burned through the area every 3 to 10 years. The lightning-ignited fires worked as a natural forest management process. More recently, Native Americans used fire as a tool to aid in hunting and gathering of food. The frequent, low-level fires maintained the fire-resistant longleaf pines, thinned understory trees, and encouraged lush ground plants. These grasses and herbs stabilized the sandy soil. Ground plants, and the insects that lived in them, provided abundant food for wildlife.

In the late 1800s and early 1900s, new land uses caused the forest to change. Livestock grazing decreased native grasses which had carried earlier fires. Logging and roads broke up the continuity of natural forest ...ls which had carried fires. By the mid-... century, people began to actively put ... natural fires. Decades of excessive logging, insufficient replanting, and fire suppression have allowed competitive trees to encroach on over 20% of Eglin's original longleaf pine forests. This has reduced diversity and forage for wildlife. Fire suppression also increases the risk of catastrophic wildfire and forest disease and insect attack.

Many studies have been done to understand the role of fire in forest ecology. Research in southeastern longleaf pine forests shows that fire is very important in determining the types of trees that grow and in promoting plant reproduction. There is no way to imitate the beneficial effects of fire.

Eglin managers now are systematically reintroducing fire into the landscape using carefully planned **prescribed fire**. A prescribed burn is so named because managers write a "prescription" that must be met before burning can be done.



Based on many years of research and experience on Eglin and other areas, fire personnel have created a plan which specifies conditions that must be met so the fire will safely do what is needed. Factors that are monitored before and during a burn include temperature, fuel type and moisture, relative humidity, wind speed and direction, and smoke dispersal. If a fire strays from prescription, it is discontinued. All of Eglin's fires meet Florida prescribed burning standards.

Of course smoke is a concern for Eglin's military mission and for people in neighboring areas. Burns are planned for times when wind is expected to keep smoke away from adjacent communities, test missions, public highways, and airfields. As of January 1997, Eglin Air Force Base (and the entire Air Quality Control Region from Panama City to Mississippi) has air quality which exceeds federal Clean Air Act standards. The smoke from a prescribed burn only temporarily impacts air quality. Eglin's prescribed fires follow all federal, state, and local air quality regulations.

After a fire, the ground may look charred, but in just a few days grasses and plants begin to sprout with new life. If you visit a recently burned area a few weeks, months, or years later, you will see that prescribed fire is good for the health of Eglin's forest ecosystems.

What about wildlife? Observations have shown that most wildlife survives prescribed fire. Large animals simply walk away, while smaller ones find shelter in their own burrows or in gopher tortoise burrows. In fact, many of Eglin's threatened and endangered species depend on fire-maintained longleaf systems to survive.

The major objective of Eglin's prescribed fires is to restore the longleaf pine ecosystem. Prescribed fire strategies include:

- implement a 3- to 5-year fire cycle in Eglin's longleaf pine sandhill ecosystems;
- use prescribed fire as a cost-effective tool to support the military mission, manage wildlife habitat, and reduce fuel hazards;
- use unplanned fires as prescribed fires if conditions are right and management objectives can be met; and,
- scientifically monitor and learn from the results of various burning practices.

Prescribed fire is just one of the ways the Natural Resources Branch supports the military mission. This ecological approach to land stewardship, called "ecosystem management," is part of Eglin's 1993-1997 Natural Resources Management Plan and was mandated by the U.S. Air Force in 1994.

A forest ecosystem is only partly trees, animals, birds, and wildflowers. It is also all of the processes that make the system work, including fire. If you want more information on Eglin's prescribed fire and ecosystem management program, please contact the Natural Resources Branch.

Eglin Natural Resources Branch ● Jackson Guard Building
107 Highway 85 North ● Niceville, FL 32578 ● 904-882-4164

EGLIN FACT SHEET

The Benefits of Prescribed Fire

	Without Fire	With Fire
Result	Fire suppression eventually leads to uncontrolled wildfire.	Fires are controlled and managed according to prescription, to benefit forest ecosystems.
Military Mission	Unhealthy ecosystems result in less flexibility for the military mission.	Healthy ecosystems are more resilient and provide more flexibility for the military mission.
Eglin Neighbors	Neighboring property owners are at risk of property damage and personal injury from hazardous wildfire.	Prescribed fire protects neighboring landowners from the dangers of wildfire. Prescribed fire opens scenic vistas and reduces ticks, making the forest a more pleasant place to visit.
Air Quality and Smoke	Hot, damaging wildfire produces very heavy smoke, which may blanket highways or communities, causing health problems or accidents.	Prescribed fire produces much less smoke and is under specific guidelines for smoke management. Certified fire managers plan in advance to keep smoke away from highways, settlements, and other smoke sensitive areas. If the fire becomes too hot or winds shift, managers do their best to prevent negative impacts.
Ecosystem	The ecosystem becomes unhealthy and prone to wildfire.	Longleaf pine ecosystems are restored to a more natural condition and the ecosystem is healthy.
Animals	Without fire, grasses and herbs that provide food for animals do not grow or produce seed. Animals may be killed in the hot, fast-moving wildfire that results from fire suppression.	Native animals are adapted to slow-moving prescribed fire – they are able to walk away or shelter in burrows or wetlands. Prescribed fire is patchy, leaving some open areas where wildlife can feed, and some thickets where animals can hide. Initial studies in Eglin's Unit 16 suggest that white-tailed deer weigh more in areas that have been burned. Studies elsewhere have shown that growing season fire benefits quail more than winter fire. Ground nesting birds, like turkey and quail, make new nests after a fire.
Wildlife Habitat	Unburned forests become overgrown. Desirable plants and trees are displaced by competing vegetation. The forest changes and native animals are in danger of going extinct. Ensuing wildfire can destroy critical plant and animal habitats.	Habitat for native wildlife is improved with each prescribed fire. Deer, gopher tortoises, and other wildlife feed on new green growth, and other animals enjoy the fruits and seeds that are produced after a fire. Quail thrive on the insects that live in grassy, regularly burned longleaf pine forests. Fox squirrels, gopher tortoises, red-cockaded woodpeckers, and bluebirds are just a few native animals that depend on fire to maintain their habitat.
Fuels	Sooner or later, buildup of flammable fuels leads to hot, damaging wildfire.	Prescribed fire is a natural and practical way to reduce fuels like pine straw and leaves to safe levels. Areas that have had a prescribed fire are protected from wildfire damage.
Vegetation	Vegetation and trees are consumed and killed by hot, damaging wildfire. The trees that survive are susceptible to disease and insect attack.	Ground level vegetation is consumed, but not killed. Plants sprout with new growth after a prescribed fire. Tree diseases and insects are controlled. Fruit and seed production is stimulated. On Eglin, wiregrass, longleaf pine, wild flowers, and many other plants require regular fire to produce seeds and to maintain their habitat.
Nutrients	Nutrients are bound up in vegetation and fuel on the ground and are not available to support new plant growth.	Low-level fire changes fuel and vegetation to ash, releasing nutrients into the soil to support new plant growth, which is high in protein and very attractive to wildlife.

Eglin Natural Resources Branch ● Jackson Guard Building
107 Highway 85 North ● Niceville, FL 32578 ● 904-882-4164

Prepared by Dr. S.K. Jacobson and S.B. Marynowski of the University of Florida's Department of Wildlife Ecology and Conservation for Eglin's Natural Resources Branch.

United States Air Force

Air Force Materiel Command

Air Force Development Test Center, Office of Public Affairs

101 W. D Avenue, Suite 110, Eglin AFB, FL 32542-5498 Tel. (850) 882-3931

The Role of Wetlands

Introduction

Eglin Air Force Base is the largest air force base in the free world, including 724 square miles of land area and about 130,000 square miles of controlled airspace overlying land and water. In this setting, Eglin conducts its primary mission of full-service air armament development through weapons system research, development, testing and evaluation; training; space operations; and base and range support. While fulfilling its mission, Eglin also manages its natural resources, acting as a steward to protect plants and animals for future generations.

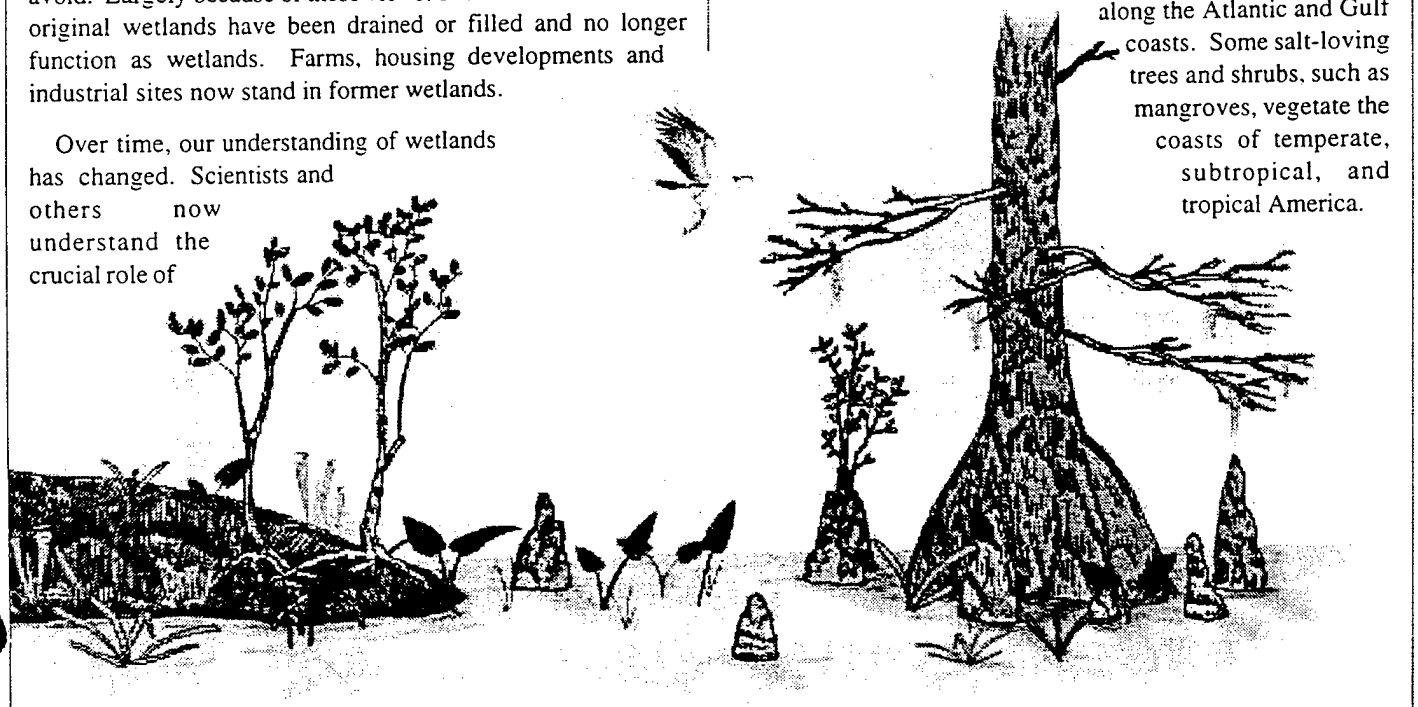
The base is home to a wide variety of plant and animal life specially adapted to Eglin's wetlands. Wetlands are areas with periodically waterlogged soil. About 7 percent of Eglin's lands, mostly flat bottomland or swamp areas, fit this category. At certain times of the year, these areas have standing water from a few inches to a foot or more in depth.

In the past, the importance of wetlands was not well understood, and wetlands were often regarded as wastelands to eliminate or avoid. Largely because of these views, over half of our nation's original wetlands have been drained or filled and no longer function as wetlands. Farms, housing developments and industrial sites now stand in former wetlands.

Over time, our understanding of wetlands has changed. Scientists and others now understand the crucial role of wetlands and the many important benefits they provide to the environment and people. Wetlands purify water by removing and retaining nutrients, processing wastes and trapping sediments. They help prevent floods in populated areas by absorbing floodwaters and then slowly releasing them. Wetlands also help to minimize land erosion. Coastal wetlands play a major role by absorbing the force of storms as they hit shore. Wetlands provide important habitat to fish and wildlife, and support hunting and fishing activities. In addition, wetlands serve as natural recreational and tourism sites.

Classes of Wetlands

There are two basic types of wetlands—coastal wetlands and inland wetlands. Coastal wetlands are linked to our nation's estuaries, where sea water mixes with fresh water. Many plants cannot tolerate this environment because of the salt water and the fluctuating water levels. As a result, some shallow coastal areas are unvegetated mud or sand flats. Some plants, however, have adapted successfully to this brackish environment. A few grasses and grass-like salt-loving plants cover large areas called "coastal marshes." These marshes are especially common along the Atlantic and Gulf coasts. Some salt-loving trees and shrubs, such as mangroves, vegetate the coasts of temperate, subtropical, and tropical America.



Inland wetlands are far larger in area and may be found throughout the nation's interior. They include floodplains along rivers and streams, isolated depressions surrounded by dry land, and the margins of lakes and ponds. Inland wetlands may also be found along the margins of coastal marshes where salt water does not extend. Inland wetlands include marshes, swamps, ponds, bogs, and bottomlands.

Wetlands Vary in Other Ways

Wetlands are not all alike, because they vary according to three additional characteristics: vegetation, soil and water saturation. If an area shows one or more of these wetland indicators, the area is most likely classified as a wetland.

Nearly 5,000 different plants may occur in U.S. wetlands. Wetland vegetation often includes plants such as cattails, bulrushes, cordgrass, sphagnum moss, sedges, rushes, arrowheads and water plantains. All of these plants are water-loving. Shallow rooted trees, such as bald cypress, willows and mangroves, may also be found.

Soils vary greatly from wetland to wetland—over 2,000 soil types have been found in wetlands. All of these are similar in that they formed in conditions where soil oxygen was limited because of soil saturation. They often include decomposed or decomposing plant matter and may smell sulfurous, like rotten eggs.

Threats to Biodiversity in Wetlands

Wildlife, shellfish and natural fisheries depend on wetlands for their very existence. About one-third of America's threatened and endangered species are supported by wetlands. Each species is tailored to the specific conditions found at the wetland, each interacting in a complex web of life. Ranging from plankton to raccoons, and from shrimp to birds, all play an important role in the food chain.

Wetlands have continued to diminish in recent decades, despite greater recognition of their importance and efforts to protect them. Nearly 11 million acres of marshes and swamps were destroyed between the mid-1950s and the mid-1970s. This is equivalent to an area three times the size of New Jersey. Most of the acreage, 87 percent, was converted to agricultural use. Urban and other development was largely responsible for the remaining losses. Coastal wetlands are most affected by urban development, except in Louisiana, where losses occur as waters rise in the Gulf of Mexico. Wetlands have also been threatened by chemical contamination and other pollution.

The loss of freshwater wetlands has affected states like Florida, Louisiana, Mississippi, Arkansas, North Dakota, South Dakota, Nebraska and Texas. For example, man-made channeling of the Mississippi and the draining of wetlands have led to increased flood damages. Waterfowl populations are also declining as a result of the loss of wetlands.

Laws Protecting Wetlands

A variety of laws have been passed to protect wetlands. The major federal program is Section 404 of the Clean Water Act, which regulates activities in wetlands. Under this law, the placement of dredged or fill material into national waters—including most wetlands—requires a permit from the Army Corps of Engineers. Civil and/or criminal penalties are possible if permits are not obtained or if permit terms are not followed. Under the Corps' procedure, a public notice of a permit application for a proposed project is issued and public comments are solicited. Permits are evaluated for environmental criteria and factors that determine if the project is in the public's best interest. Important as Section 404 has been, it does not regulate drainage or pumping operations. These processes can often drain a wetland without violating Section 404.

States and local municipalities have enacted laws in recent years to regulate and protect local wetlands. As a result of these regulations, many coastal states improved protection of their coastal wetlands. Fewer than 20 states, however, have laws specifically regulating activities of inland wetlands. Even when there are laws, inland wetland protection is often limited. Without strong formal programs to protect interior wetlands, the voluntary actions of citizens are crucial to wetland protection.

The regulation of wetlands is a controversial issue. Not everyone agrees that wetlands should go untouched. Property owners often want to develop their land in ways that require draining saturated land and clearing for construction. When state and federal laws prevent such development, land owners, in turn, want compensation. Sometimes alternative, more appropriate uses may be found that leave the wetlands largely intact. Examples include waterfowl production, hunting and trapping leases, and selective timber harvest. In addition, wetlands can be donated to conservation agencies for tax credit. Development projects may often be reserved for upland sites.

Wetlands are an important resource that continues to dwindle. While Eglin wetlands are protected as a result of defense needs and proactive stewardship, many areas are less fortunate. Conservation measures can slow wetlands loss and protect existing areas. Economic incentives for wetland protection, combined with economic disincentives for development, may also be designed. Together these measures can help ensure that wetlands, and the benefits they provide, endure.

This fact sheet is one in a series designed to inform the public about ecosystem and resource management activities at Eglin Air Force Base.
For more information, contact Environmental Public Affairs Coordinator, AFDTC/PAV, (904) 882-4436, Ext. 321.
This fact sheet is also available on the World Wide Web via the Eglin Homepage at http://www.eglin.af.mil

United States Air Force

Air Force Materiel Command

Air Force Development Test Center, Office of Public Affairs

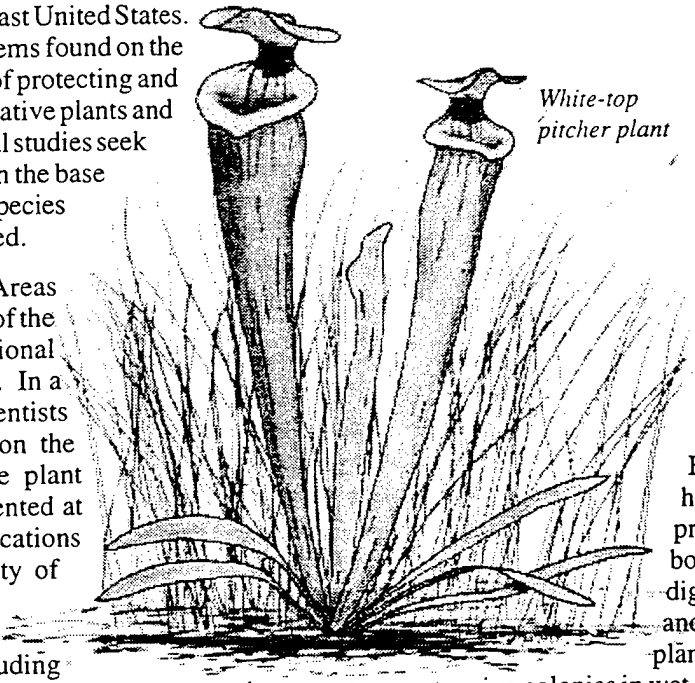
101 W. D Avenue, Suite 110, Eglin AFB, FL 32542-5498 Tel. (850) 882-3931

Rare Plant Species

Introduction

Eglin Air Force Base is the largest air force base in the free world, including 724 square miles of land area and about 130,000 square miles of controlled airspace overlying land and water. In this setting, Eglin conducts its primary mission of full-service air armament development through weapons system research, development, testing and evaluation; training; space operations; and base and range support. While fulfilling its mission, Eglin also manages its natural resources, acting as a steward to protect plants and animals for future generations.

Eglin contains some of the highest quality natural areas in Florida and in the Southeast United States. Within the various ecosystems found on the base, Eglin pursues a goal of protecting and enhancing populations of native plants and animals. Ongoing botanical studies seek to identify the rare plants on the base and to classify appropriate species as threatened or endangered.



White-top pitcher plant

The Florida Natural Areas Inventory (FNAI) is a part of the Nature Conservancy, a national conservation organization. In a study led by the FNAI, scientists surveyed over 300 sites on the base. A total of 60 rare plant species have been documented at Eglin, occurring at 1,747 locations across the base. A variety of natural communities have been identified which support these plants, including seepage slopes, wet flatwoods, dome swamps, bogs, wet prairies, sandhills, scrubs and blackwater streams. Twenty-five different community types in all were found to have rare plants. The diversity of plants within these communities is second only to that of a tropical rain forest.

Rare plants provide an essential connection in the network of plant and animal life. They offer protection and reproductive and hunting habitats for insects, aquatic mammals, waterfowl, and fish. Plants also contribute to human habitat by maintaining water quality. Plant-filled areas slow down floodwaters, filter out sediment, and absorb some of the potentially damaging nutrients and microbes. Rare plants contribute significantly to native biodiversity and often are indicators of healthy ecosystems.

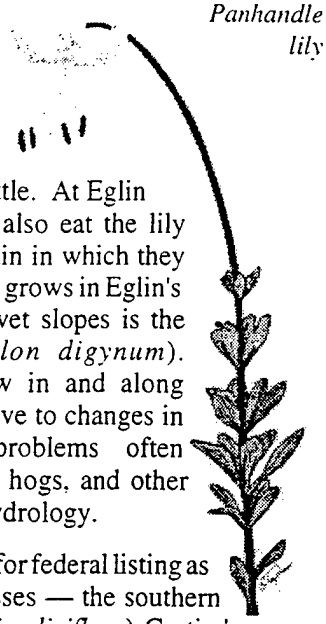
Rare plants at Eglin include one species listed by the federal government as endangered. Thirty other plant species believed to grow at Eglin are listed as candidates for federal threatened or endangered status. The state of Florida lists some of these 30 plants, plus eight others, as endangered.

Candidates for Federal Listing

One of these listed plants, the white-top pitcher plant (*Sarracenia leucophylla*) is a showy, insect-eating plant that lives in wet prairies, woodlands, and swamps and even along fire-swept slopes. The pitcher plant has elongated funnels or pitchers that hold liquid and hooded tops streaked with bright red. Insects, attracted by the color and the fragrance of the plant, crawl along the slippery rim of the pitcher and fall into the liquid. Because of downward pointing hairs along the pitcher's interior, prey cannot climb back out. The bodies of the insects are eventually digested by the enzymes of the liquid and the nutrients are absorbed by the plant. At Eglin, pitcher plants form extensive colonies in wet, highly acidic soil. Thousands of plants live along the partially open canopy of trees along creek beds. One impressive colony has grown together to form a large floating mat along a stream bank.

The panhandle lily (*Lilium iridollae*) also enjoys what botanists call "wet feet." The lily thrives in poorly drained soil along streams and bays. Its brightly colored flowers that appear in late summer attract bees, butterflies, and hummingbirds. The species has dwindled drastically

throughout the Florida Panhandle and adjacent counties in Alabama. It is sensitive to changes in drainage and water quality, and its flowers and bulbs are relished by deer and cattle. At Eglin and elsewhere, feral hogs also eat the lily bulbs and degrade the terrain in which they live. Another rare plant that grows in Eglin's swamps, bogs and along wet slopes is the bog-button (*Lachnocaulon digynum*). Because bog-buttons grow in and along streambeds, they are sensitive to changes in water flow and seepage, problems often caused by destructive feral hogs, and other disruptions in the natural hydrology.

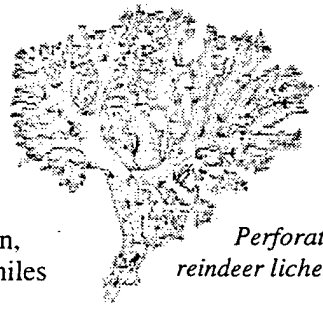


Panhandle lily

Also under consideration for federal listing as endangered are several grasses — the southern three awned grass (*Aristida simpliciflora*), Curtiss' sandgrass (*Calamovilfa curtissii*), naked-stemmed panic grass (*Panicum nudicaule*), and Drummond's yellow-eyed grass (*Xyris drummondii*). All of these grasses benefit from fires that reduce encroaching shrubs and other competition. All but the southern three awned grass grow in wet soil in open prairies or bogs. Songbirds and waterfowl use these grasses for protection and nesting, and they often feed upon the seeds.

An Endangered Lichen

Lichens are not true plants but are a combination of fungi and algae growing together. One lichen known to grow at Eglin, the perforate reindeer lichen (*Cladonia perforata*), is listed as a federally endangered species. This small, pale yellow-green ground lichen is found on Santa Rosa Island, a barrier island that is part of the Eglin base. Resource managers have identified one "mega" population and two other smaller populations of the slow-growing lichen on Santa Rosa Island. The perforate reindeer lichen prefers exposed patches of sand in coastal grassland and scrub and, other than at Eglin, is found several hundred miles away in south Florida.



Perforate reindeer lichen

Resource Management

Many of the rare plants at Eglin require specific growing conditions and can benefit from resource management activities. Natural resource managers can set controlled fires, for example, to maintain or alter vegetation composition in natural communities. Many plants and animals inhabiting the base are adapted to periodic fires, and several species depend on fire to eliminate competitive plants and to trigger their own reproduction. Fire also releases nutrients bound up in standing vegetation. Such releases stimulate flower and fruit production and are ideal for seed germination on fire-exposed soil.

Exotic plants not native to the area can threaten native vegetation and must be aggressively managed. On the base, the two most invasive and problematic plants are cogon grass and Chinese tallow trees. Cogon grass spreads rapidly, crowds out native grasses, and survives seasonal fires, dense pine needle ground cover and shade. The Chinese tallow tree was originally introduced as an ornamental but now must be eradicated because it too threatens native communities with its rapid growth. Management for these species includes mechanical removal and the use of herbicides to fight against the encroachment of these plants.

Habitat Protection: Key to Species Preservation

An important part of preserving a threatened or endangered plant species is preserving its habitat. Natural resource managers at Eglin have targeted their efforts to provide long-term species protection by encouraging a healthy ecosystem.

Eglin's natural resources program has been recognized through conservation awards from the Nature Conservancy, the Air Force, and the Office of the Secretary of Defense. Proactive measures and vigilance may well ensure the long-term survival of these rare plant species.

Endangered* and Potentially Endangered Plants

perforate reindeer lichen *
southern three awned grass
southern milkweed
Chapman's aster
snakeroot aster
hairy wild indigo
Curtiss' sandgrass
Baltzell's sedge
Godfrey's golden aster
Cruise's golden aster
Piedmont jointgrass
bog-button
West's flax
gulf coast lupine
Ashe?s magnolia
panhandle lily
bog spicebush
Alabama spiny-pod
Piedmont water-milfoil
west Florida cowlily
naked-stemmed panic grass
Chapman's butterwort
large-leaved jointweed
small-flowered meadowbeauty
panhandle meadowbeauty
hairy-peduncled beakrush
white-top pitcher plant
pineland hoary-pea
Drummond's yellow-eyed grass
Karst pond yellow-eyed grass
Harper?s yellow-eyed grass

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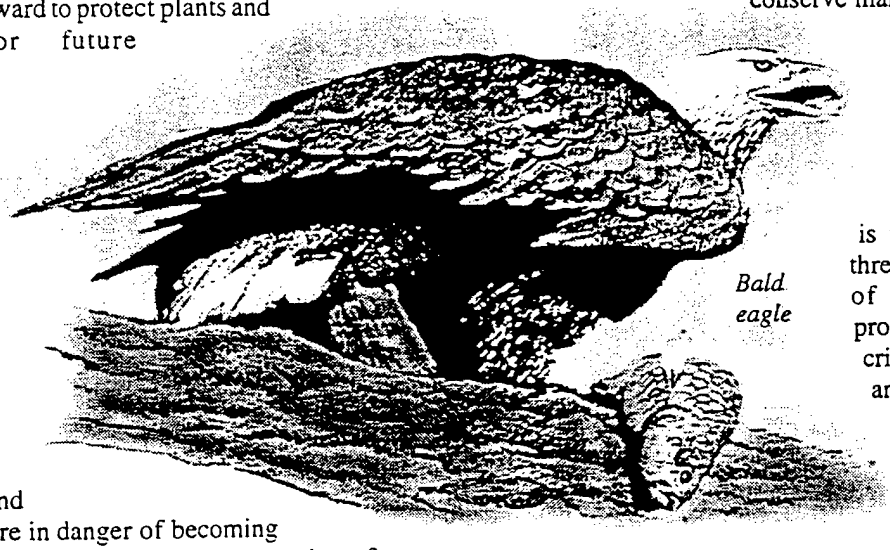
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Protecting Threatened and Endangered Species

Introduction

Eglin Air Force Base is the largest air force base in the free world, including 724 square miles of land area and about 130,000 square miles of controlled airspace overlying land and water. In this setting, Eglin conducts its primary mission of full-service air armament development through weapons system research, development, testing and evaluation; training; space operations; and base and range support. While fulfilling its mission, Eglin also manages its natural resources acting as a steward to protect plants and animals for future generations.

Eglin's habitat is crucial for a variety of threatened and endangered species of plants and animals. Endangered species are those plants and animals that are in danger of becoming extinct throughout all or a significant portion of their range. Threatened species are those likely to become endangered in the foreseeable future. Examples include the Eastern indigo snake and the bald eagle, which are both listed as threatened by the federal government. The federal list changes to reflect the latest available information about various species. The most up-to-date list is available from the U.S. Fish and Wildlife Service.



Bald eagle

Federal and State Law

Passage of the Endangered Species Act of 1973 gave the United States one of the most far-reaching laws ever enacted by any country to prevent the extinction of at risk animals and plants. Why should we save threatened and endangered species? Congress held that these species "are of aesthetic, ecological, educational, historical, recreational and scientific value to the Nation and its people." The primary goal of the Act is to return at risk species to the point where protection is no longer necessary under the Act.

Under the Act, the Secretary of the Interior, acting through the U.S. Fish and Wildlife Service, has broad powers to protect and conserve terrestrial and nonmarine wildlife and plants that the Secretary finds in serious jeopardy of extinction. The Secretary of Commerce, acting through the National Marine Fisheries Service, has similar authority to protect and conserve marine life.

The U.S. Fish and Wildlife Service and the National Marine Fisheries Service have established regulations to implement the law. Because habitat destruction is the most serious worldwide threat to wildlife and plants, many of the regulations require protection of habitat considered critical for these species, unless an exemption is granted.

Many states, including Florida, provide additional guidance in establishing and maintaining programs for the conservation of threatened and endangered species. Under a matching funds program, states have been able to increase their efforts to conserve threatened and endangered species through such measures as habitat protection, research and enforcement.

Managing Sensitive Species at Eglin

Eglin is working with federal, state, and other agencies to ensure its actions are not likely to jeopardize the continued existence of any threatened or endangered species.

In 1992, Eglin entered into a cooperative agreement with the U.S. Fish and Wildlife Service and the Florida Game and Fresh Water Fish Commission to manage individual species on the base. Eglin has also maintained ongoing relationships with the Florida Department of Environmental Protection

and the Nature Conservancy, which is a private non-profit organization dedicated to the conservation of plants, animals and intact ecosystems.

Eglin follows a natural resources management plan that echoes the goals of the Endangered Species Act. Specific objectives were established to help protect sensitive species. The plan called for an inventory of sensitive species and management activities designed for their protection.

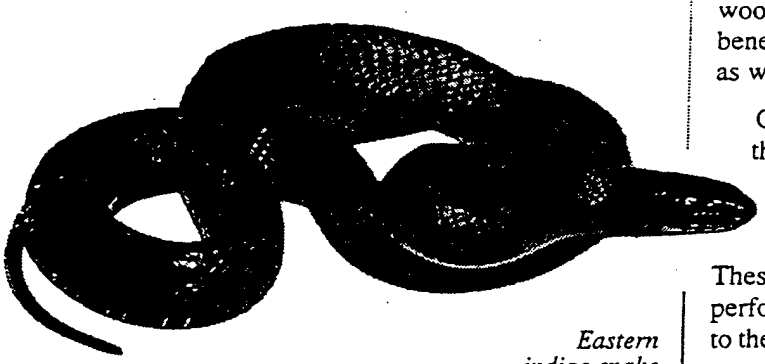
In preparing that inventory, Eglin relied in part upon state and federal lists of threatened and endangered species. Because of different methodologies, Florida's list of sensitive species varies from the federal list. Eglin tracks changes to these lists as new species are added, proposed, or removed from the lists. By knowing what species to watch for, Eglin can better plan its mission activities while preserving sensitive species.

Listing and Delisting Species

The U.S. Fish and Wildlife Service follows a formal "rulemaking" procedure to determine which species should be placed on the U.S. List of Endangered and Threatened Wildlife and Plants. Threatened or endangered species are placed on the list, reclassified or delisted through this procedure. The process for listing or reclassifying species involves the public, the scientific community, states, other federal agencies and sometimes foreign governments.

Key issues are evaluated when deciding if a species should be listed or reclassified. They include one or more of the following:

- Current or potential destruction, modification, or curtailment of habitat or range
- Overuse for commercial, recreational, scientific or educational purposes
- Disease or predation
- Adequacy of current regulatory mechanisms
- Other natural or manmade factors affecting continued existence.



Eastern indigo snake

Species may be proposed for listing under various priorities. The highest priority is reserved for those species whose at risk status is verified, as in peer-reviewed scientific journal articles by recognized experts. Verified information can also be used to remove a species from the list. A species may be delisted only if data substantiates that it is no longer threatened or endangered. Reasons could include extinction of the species, recovery of populations, or recognition that the original data used to classify the species was in error.

Careful Review Before Potential Actions

Whenever Eglin is considering a mission or other activities at a site, staff use the best scientific and commercial data available to determine the likely effect on sensitive species and habitat. Both federal and state lists are considered.

Informal consultations are held with the regulating agencies at first. If an agency requests additional information, that is provided and analyzed. If no further concerns are raised following formal review, the action may proceed following consultation with the U.S. Fish and Wildlife Service and/or National Marine Fisheries Service.

If concerns are found, mitigating measures or recommendations may be required before the action can be performed, or alternatives may be identified. If concerns remain after considering these measures, a jeopardy opinion would be issued, meaning that the proposed activity should not occur because of the potential to harm sensitive species. While an exemption to a jeopardy opinion can be sought, it is rarely used.

Through careful review, Eglin has been able to balance its primary mission of defense with its mission to improve and preserve habitat for sensitive species.

Habitat Protection: Key to Species Preservation

Natural resource managers at Eglin have targeted their conservation efforts to provide long-term species protection. Special Management Emphasis Areas have been named to focus and prioritize management efforts for the red-cockaded woodpecker and the Okaloosa darter. While these areas benefit the endangered species, they often favor other species as well.

Conservation is crucial for the long-term survival of threatened and endangered species. Eglin's natural resources program has been recognized through conservation awards from the Nature Conservancy, the Air Force and the Office of the Secretary of Defense. These awards are testaments to Eglin's commitment to performing its mission while preserving the environment and to the quality of Eglin's natural resources management team.

EGLIN FACT SHEET

Ecological Restoration

What is Ecological Restoration?

Some forests that you see at Eglin are not as nature intended them. Eglin's forests have changed due to factors such as suppression of natural fires and past overharvesting of longleaf pine trees.

During ecological restoration, managers restore native trees and natural processes like fire to Eglin's forests. Once processes like fire are added back into the ecosystem, native plants and wildlife thrive and the ecosystem returns to a more natural condition.

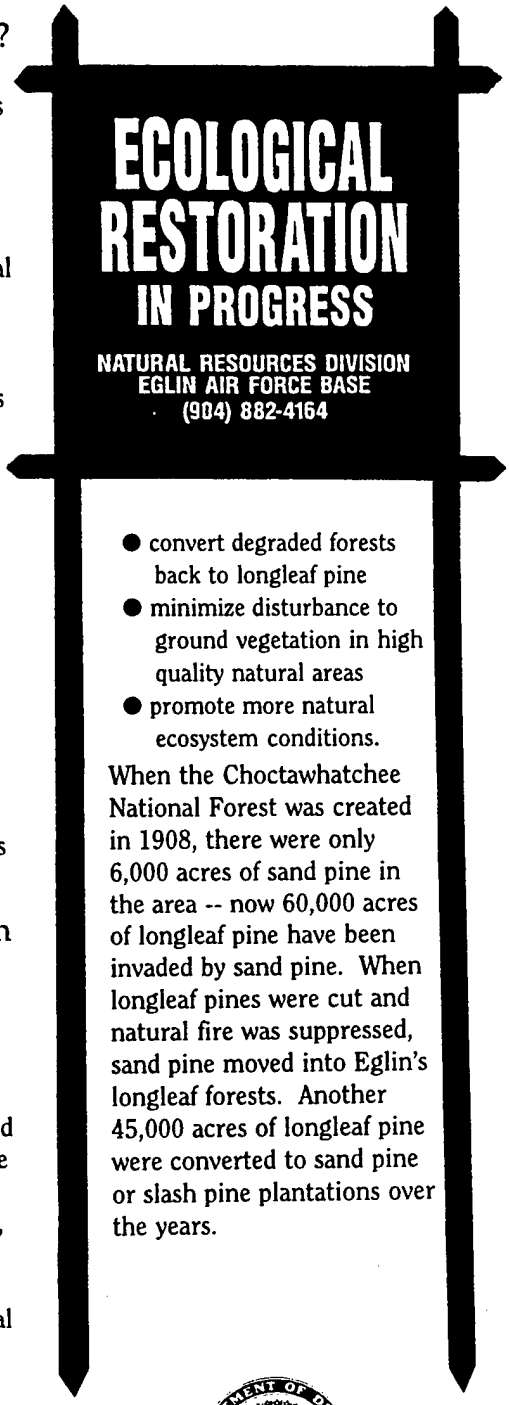
When you see the ECOLOGICAL RESTORATION sign, it means that managers are making progress toward healthier forest ecosystems on Eglin. This process of improving ecosystem health while managing for wildlife and military uses is called integrated ecosystem management. The idea is to bring together, or "integrate," all forestry, game, endangered species, and military management activities. The goal is to support Eglin's military mission while restoring longleaf pine forest ecosystems to a more natural condition.

Ecological Restoration on Eglin

Ecologically sound management includes techniques that mimic natural processes and which reduce long-term impacts to the ecosystem. In many areas, managers simply use prescribed fire to thin out overgrown shrubs and trees, and to encourage the growth of longleaf pine trees and native grasses and plants that provide food for wildlife. In other areas, non-native or off-site trees are removed and native trees are planted.

Management practices for ecological restoration on Eglin:

- encourage natural forest regeneration
- reintroduce natural processes like fire
- prevent the invasion of off-site pine or overgrown shrubs into longleaf areas



- convert degraded forests back to longleaf pine
- minimize disturbance to ground vegetation in high quality natural areas
- promote more natural ecosystem conditions.

When the Choctawhatchee National Forest was created in 1908, there were only 6,000 acres of sand pine in the area -- now 60,000 acres of longleaf pine have been invaded by sand pine. When longleaf pines were cut and natural fire was suppressed, sand pine moved into Eglin's longleaf forests. Another 45,000 acres of longleaf pine were converted to sand pine or slash pine plantations over the years.

Eglin managers currently are engaged in intensive restoration of longleaf pine ecosystems, and Eglin's longleaf pine coverage is increasing. Foresters plant an average of 2 million containerized longleaf pine seedlings each year on Eglin. Seedlings are planted in an irregular pattern to look like a natural forest. Eglin foresters plant so many trees that in some years they purchase 20% of the containerized longleaf pine seedlings produced!

Some techniques used by Eglin managers for longleaf pine restoration include:

- prescribed burning of longleaf pine areas to promote natural longleaf pine forest regeneration and restore wildlife habitat
- removing sand and slash pines from longleaf pine sites
- reducing the numbers of overgrown oaks on longleaf pine sites
- replanting longleaf pine seedlings

Eglin residents can visit ecological restoration areas that are being replanted with native longleaf pine. Longleaf pine seedlings stay in a grasslike stage while developing strong taproots. These seedlings then grow taller after several years.

A few years after longleaf pine seedlings are planted, managers reintroduce fire with prescribed burning. Fire once was a natural process in Eglin's longleaf pine forests, but now managers must use controlled fire to mimic natural fire. Longleaf pine seedlings and other forest plants and animals survive because they are adapted to fire. Visitors can see burned areas sprouting new growth just a few weeks after a fire. Fire encourages native ground cover plants and grasses to grow and reproduce. Prescribed fire also keeps scrub oaks and sand pines from invading Eglin's longleaf pine forests.

Eglin Natural Resources Branch ● Jackson Guard
107 Highway 85 North ● Niceville, FL 32578 ● 904-882-4164

EGLIN FACT SHEET

Restoring Eglin's Longleaf Pine Ecosystems

Eglin practices ecologically sound management based on ecosystem monitoring and the most up-to-date research available. Along with results from outside research, managers have studied Eglin's ecosystems in order to evaluate the current status of Eglin's ecosystems and identify the key processes (like fire) that form Eglin's ecosystems.

When Eglin managers begin ecological restoration, they look at many factors to determine the areas that were originally longleaf pine. Historic records, soil types, existing vegetation, and the presence of longleaf pine trees or stumps are all indicators that help managers determine the areas that once were longleaf pine forest on Eglin.

Researchers have identified a series of indicators which can be used to measure the ecological conditions of Eglin's longleaf pine ecosystems. Managers look at plant and animal species composition, endangered species population trends, forest structure, fire frequency, soil disturbance, and other indicators to assess ecological conditions and to guide longleaf pine forest restoration efforts.

Eglin's Longleaf Pine Ecosystems

Longleaf pine once covered about 90 million acres in the Southeast. Less than 3% of that total now remains. As a result, longleaf pine is an endangered ecosystem of the United States and many people are working to bring back healthy longleaf pine forests in the region.

Eglin has the best and largest remaining longleaf pine forest in the Southeast -- a resource of global importance! Eglin's forests support lots of native wildlife and they also support 22 animal and 67 plant species that are rare, threatened, or in danger of extinction. Just a few endangered animals that depend on Eglin's longleaf pine forests for habitat include the Red-Cockaded Woodpecker, Florida black bear, Sherman's fox squirrel, gopher tortoise, and indigo snake.

Eglin's ecosystem management plan focuses primarily on restoration and maintenance of the longleaf pine community, which covers over three-quarters of the Base. Because the forest is open and grassy, longleaf pine sandhill ecosystems are ideal for military training and testing operations. Restoring and protecting the health of Eglin's longleaf pine forests will provide support for the military mission while protecting and benefiting the species that depend on those forests. Longleaf pine forests also are important for their recreational and scenic qualities.

Values of Healthy Ecosystems

Restoration and maintenance of Eglin's forest ecosystems is good stewardship because it allows humans to continue to use Eglin's forests to achieve the military mission. Over the long-term, integrated ecosystem management will ensure the maximum return at minimum cost to the public of valuable ecosystem services like:

- land for military operations
- renewable natural resources
- clean air and water
- recreation and scenery
- wildlife habitat
- aesthetic and spiritual values

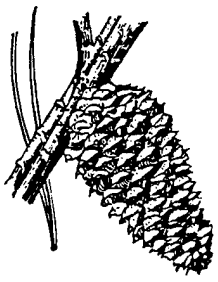
By returning Eglin's ecosystems to a more natural condition, managers provide for the military mission while protecting wildlife and endangered species.

What You Can Do....

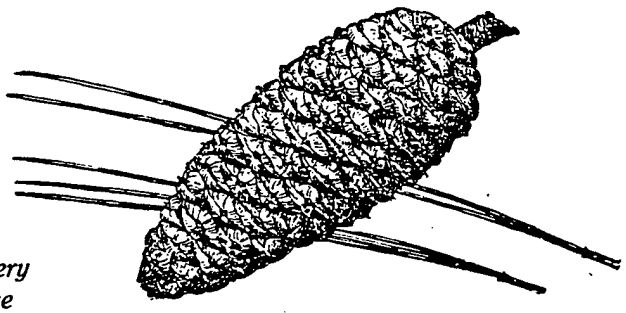
1. Learn to identify longleaf pine and Eglin's other native pine trees (see below).
2. Grow longleaf pine and other native plants and trees in your yard.
3. Contact Eglin's Grounds Section for native tree landscaping suggestions (904-882-8179).
4. Learn about creating a backyard wildlife habitat by contacting the Florida Game Commission's Wildlife Education Section (904-488-4676).



LONGLEAF PINE trees are tall and straight, with gray bark. Their shiny, dark green needles are 10-15" long in clusters of 3. The large cones are 6-10" long.



SAND PINE grow in very sandy soils, like those along the Gulf coast. The needles and cones are 2-3" long, and needles are in clusters of two.



SLASH PINE has a straight trunk and 8-12" long needles in clusters of 2 or 3. The shiny cones are 3-6" long. Slash pine do not grow very well in Eglin's deep sandy soils.

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107 Highway 85 North ● Niceville, FL 32578 ● 904-882-4164

Prepared by Dr. S.K. Jacobson and S.B. Marynowski of the University of Florida's Department of Wildlife Ecology and Conservation for Eglin's Natural Resources Branch.

United States Air Force

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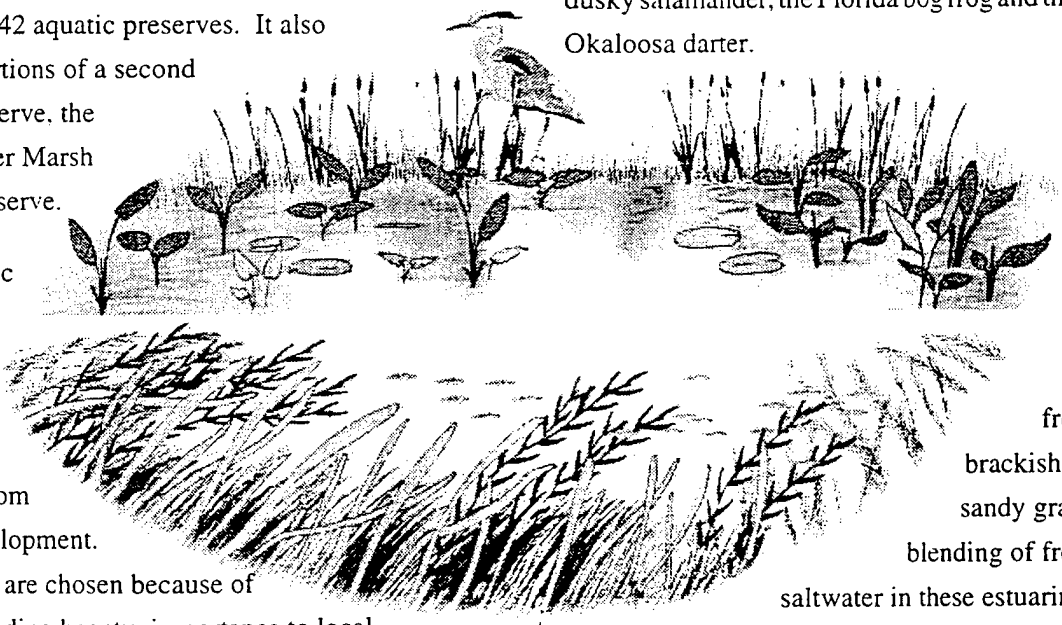
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Aquatic Preserves

Introduction

Eglin Air Force Base is the largest air force base in the free world, including 724 square miles of land area and about 130,000 square miles of controlled airspace overlying land and water. In this setting, Eglin conducts its primary mission of full-service air armament development through weapons system research, development, testing and evaluation; training; space operations; and base and range support. While fulfilling its mission, Eglin also manages its natural resources, acting as a steward to protect plants and animals for future generations.

Eglin Air Force Base borders Rocky Bayou, one of Florida's 42 aquatic preserves. It also contains portions of a second aquatic preserve, the Yellow River Marsh Aquatic Preserve.



An aquatic preserve is an area with submerged lands restricted from human development. These lands are chosen because of their outstanding beauty, importance to local ecology and their value to scientific research.

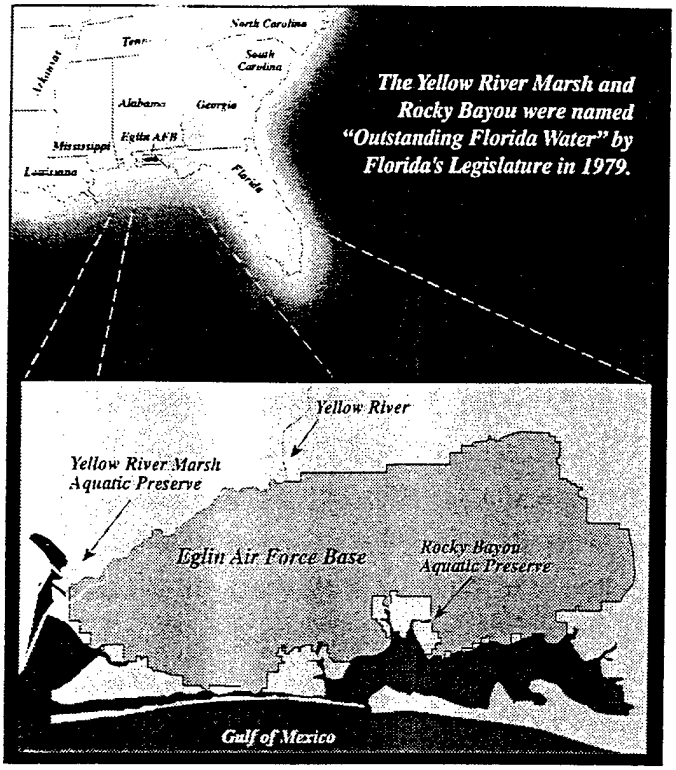
The Yellow River Marsh and Rocky Bayou were both named "Outstanding Florida Water" by Florida's legislature in 1979 and have been recognized by scientists as exceptional water resources. The Yellow River Marsh is fed by the fresh water of the Yellow River, the swiftest flowing river in Florida. This marsh encompasses about 16,435 acres, including about 2,500 acres of the western portion of Eglin. The Rocky Bayou Aquatic Preserve is much smaller, only about 480 acres. It receives its fresh water from two creeks and from several smaller "steephead" streams, areas where groundwater seeps up through sand to form a stream.

Steephead streams are found nowhere else in the world but this region. They support unique wildlife, including the dusky salamander, the Florida bog frog and the endangered Okaloosa darter.

Aquatic Preserves are complex communities made up of forested wetlands, freshwater and brackish marshes and sandy grassbeds. The blending of freshwater and saltwater in these estuarine and marsh communities creates a habitat that supports many plants, fish, reptiles, amphibians, birds and mammals.

Forested Wetlands

A forested wetland community supports trees that flourish



in poorly drained soils. The forests have an evergreen appearance and include laurel, live and water oaks, cypress, bay trees and pines. Luxurious vegetation shelters and feeds such animals as deer, otter, beaver, alligator, water snake, raccoon and bear. At the Rocky Bayou Aquatic Preserve, state recreation area rangers have observed nesting osprey, listed in Florida as a species of special concern. They have also observed the nest of a bald eagle, a species listed by the federal government as threatened.

Marshes

Marshes receive floodwater after heavy rains and undergo daily tidal water level changes. Many plants thrive in these marshes, including several types that grow under water. Pollutants, excess nutrients, and sediments are naturally filtered by floodwaters which wash through these marshes, thereby protecting area drinking water. Marshes also provide safe, sheltered habitats for marine and estuarine organisms to reproduce and develop. The wildlife of a marsh ranges from plankton, shrimp, crabs, and snails to fish, rodents and birds. Larger mammals include the raccoon, opossum and marsh rabbits. Wading birds, such as herons and egrets, feed primarily in the marsh edges and nest in forested wetlands.

Submerged Aquatic Vegetation

The wildlife in open water and seagrass bed habitats includes abundant fish and crustacean species. Some of these species require a saltwater/freshwater interface during their life cycles.

Submerged aquatic vegetation — underwater grassbeds — of the aquatic preserves appear to be at risk. Longtime residents and commercial fishermen have observed a significant reduction in the grassbeds, which are home to oysters, shrimp and fish. Scientists trace the problem to fungal parasites, poor water quality, heavy rainfall and dredging activities.

Impacts to Aquatic Preserves

Aquatic preserves' natural systems and the life they harbor are impacted by changes to the land that surrounds them. These changes include increased residential and commercial development which can deteriorate water quality. Additionally, the construction of roads and bridges creates more storm-water runoff.

Aquatic Preserves Uses

The Yellow River Marsh and Rocky Bayou Aquatic Preserves are enjoyed today as sites for recreational fishing, boating and swimming. Commercial fishing and navigation and limited adjacent land commerce (docks, bait shops, etc.) also impact these lands and waterways. The main objective of the resource management programs for the Yellow River Marsh and Rocky Bayou Aquatic Preserves is to protect the natural resources for the benefit of present day and future generations. Eglin joins the Aquatic Preserve management in efforts to protect these unique habitats.

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United States Air Force

Air Force Materiel Command

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Barrier Islands

Introduction

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Eglin's coastal barrier lands are located on Santa Rosa Island and at Cape San Blas*. The significance of these Eglin tracts is highlighted by the rapid spread of urban expansion beyond Eglin's boundaries. Beach front property is being rapidly developed for tourism, commercial and residential purposes. As more coastline is developed, Eglin's barrier islands will become increasingly significant for preserving the natural heritage of Florida's Gulf coast.

Barrier Islands

Barrier islands in the Eglin area are long, narrow accumulations of sediment—sand or gravel—that have formed in the shallow coastal zone and are separated from the mainland by some combination of coastal bays or lagoons and marshes. They are typically separated from each other by a tidal inlet, a channel of water. These islands protect the mainland from the ocean's energies and are constantly being changed by natural forces. While they occur throughout the world, the most extensive system of barrier islands lies along the Atlantic and Gulf coasts of the United States.

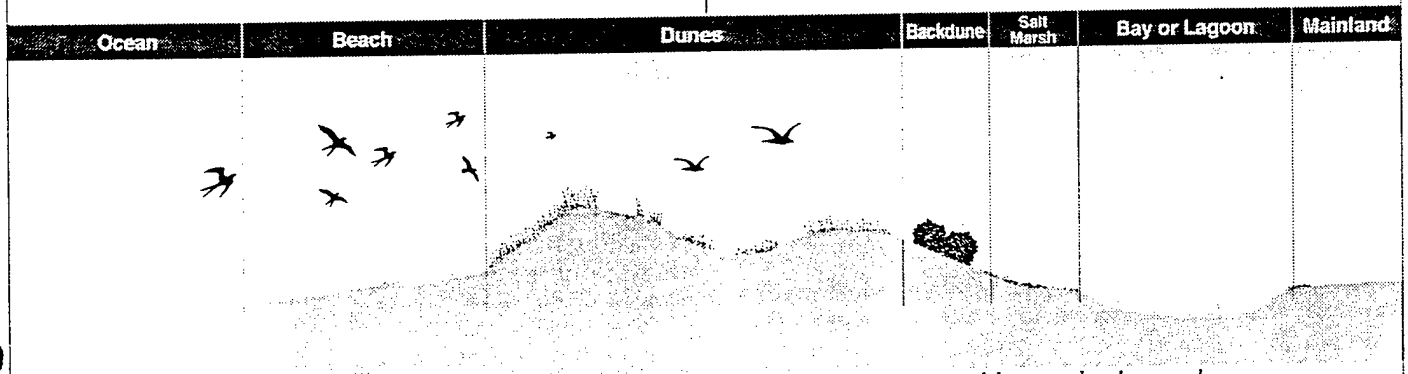
Formation of Barrier Islands

Over the years, scientists have developed various theories to explain how barrier islands formed. The presently accepted theory is that sediments carried by the rising sea level, along with submersion of beach ridges and headlands, made the first barrier islands. The ridges and headlands were eroded by wave action, forming spits or bars and lengthening the spits or bars. The spits or bars protected the lagoon behind them, allowing marshes to form. During storms or periods of high water, inlets formed, which provided nutrients and sediments for the new marshes.

Processes Affecting Barrier Islands

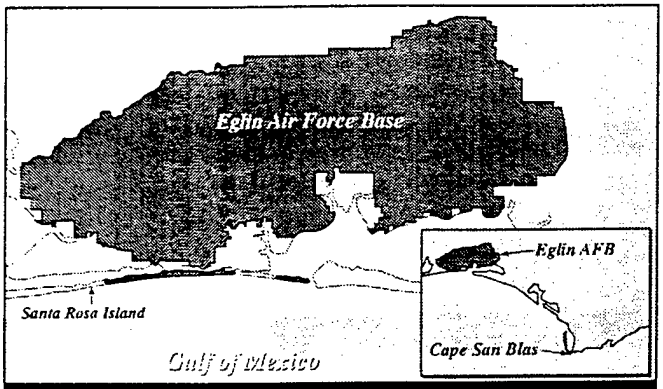
Every barrier island is unique, but the processes that affect and constantly change them are the same: waves, tides, currents, winds, sea level changes and storms.

- Waves—Waves usually break at an angle to the beach, an action that generates currents. Crashing waves may also cause temporary suspension of sediments, which can then be carried along the beach by currents. Waves are most active on the ocean side of the island but also occur on the bay side.
- Currents—Currents flow away from the angle where waves break and carry sediments along the beach. Strong currents, known as rip currents, run away from the beach back to the ocean and may also carry sediments out to sea. Tidal currents may carry large amounts of sediments through inlets and deposit them in the lagoon or marshes.
- Tides—Tides generate currents that move sediments. They may also flood low areas and deposit sediments in marshes or tidal flats.



A typical barrier island consists of the beach, dunes, the back dune, and the coastal bay and salt marsh.

* *Technically, because it is attached to the mainland, Cape San Blas is a barrier spit rather than a barrier island. The forces that form and affect barrier spits and barrier islands are the same.*



Eglin's coastal barrier lands include three narrow tracts in Santa Rosa, Okaloosa, and Gulf counties. The western tract is 13 miles long, and the central tract is 4 miles long. The eastern tract, known as Cape San Blas, is about 500 acres, with 3 miles of beach front.

- Winds—Wind energy far out to sea generates most waves. Onshore winds blow sediments from the beach, helping to form dunes. Winds carry sediments from dunes to marshes or bays.
- Sea Level Changes—Some scientists believe that change in sea level has the most important long-term effect on barrier islands. A continuing rise in sea level is the major reason that barrier islands move towards the mainland as time passes. During the past 50 years, sea levels have risen worldwide at an accelerating rate, believed to be partly due to the *greenhouse effect*. This term applies to the trapping of solar energy by water vapor, carbon dioxide (CO^2), and other naturally occurring gases that determine our climate. The burning of fossil fuels, cutting of forests, and other human activities are trapping more heat in the Earth's atmosphere. One result is an increased melting of glaciers and the polar ice caps, thus contributing to rising sea levels.
- Storms—The most dramatic changes in barrier islands are caused by storms, particularly hurricanes on the Gulf coast. The size, intensity, and speed of a storm, the tidal phase, and the storm's path influence overall impacts. Severe erosion is more likely to occur if there are two or more high tide cycles during the storm. *Storm surge*, an above-normal water level that results from low atmospheric pressure and high winds, can be especially damaging. Storms may also move sediments to the back dune by breaking through or over primary dunes. Generally, a storm flattens the beach and builds sandbars offshore. Natural forces usually rebuild the beach over time as wave action eventually pushes the sand ashore. This may take years. However, a rebuilt beach is not identical to the beach that existed before the storm.

The shape and position of the beach depends on waves, sediment/sand supply, and sea level changes. The natural balance of these three factors is called *dynamic equilibrium*. When one factor changes, the others adjust to maintain the natural balance.

Dune Building and Vegetation

Sand dunes are mounds or ridges of beach sand deposited by wind. Their shape is determined by the amount of sand available and the prevailing wind direction. Dunes occur when dry sand begins to build at some obstacle, such as plant debris or a shell. If a plant grows on the mound that results, the mound will begin to grow larger. As it blows around vegetation, the wind's speed is reduced, causing sand grains to drop. Plant roots help to stabilize the sand.

Few plant species are able to thrive in the harsh beach or dune environment. To survive, they must be able to tolerate salt spray, extreme heat, drought, sand blasting and burial, and low nutrient supply. Sea oats (*Uniola paniculata*) and bitter panicum (*Panicum amarum*) are two species that do well in this environment along the Gulf coast.

Importance of Dune Protection

Dunes are extremely important as barriers to waves or storm surges. They also can serve as a source of sand or sediment for rebuilding the beach and protect low areas behind them.

Even minor damage to the dune or dune vegetation can make the dune less stable. Once sand is free to move again, established plants may be covered with sand. Most dune plants cannot survive being covered by sand. If a plant dies, the stabilizing effect of the plant is lost. The dune may begin to disintegrate and may eventually return to its original unstable form. Water washing over the dune, storm surges, grazing and drought can also destroy vegetation and speed up erosion.

People are asked to stay off the dunes. Protection from foot and vehicle traffic cannot be overemphasized. Many studies have shown that dune grasses cannot tolerate trampling by foot or vehicle traffic. Driving off-road vehicles on dunes not only damages grasses but can even alter the dune profile. Foot traffic can be equally damaging. Visitors generally take the shortest and easiest path to the beach, often following existing trails over dunes. This foot traffic destroys plants. These trails in the dunes serve as paths storm waters surge through, allowing salt-water flooding of interior environments.

Santa Rosa Island

Santa Rosa Island hosts five different communities of vegetation: beach dunes; coastal grasslands; low-lying, usually wet areas called *swales*; habitat requiring moderate amounts or moisture (*mesic flatwoods*); and scrub (areas containing stunted trees or shrubs). All are in relatively pristine condition. During 1995, the island received extensive damage as a result of Hurricanes Erin and Opal. For example, dunes were 60-100 feet in some areas, and now they are gone. A brief study of the effects of these storms found that the beach dune, swales, and scrub vegetation were most damaged. Nevertheless, hurricane disturbance is a natural part of barrier island ecology. Although these areas have been altered, Eglin's barrier islands will continue to be some of the most pristine, ecologically significant coastal communities in Florida.

This fact sheet is one in a series designed to inform the public about ecosystem and resource management activities at Eglin Air Force Base.
For more information, contact Environmental Public Affairs Coordinator, AFDTC/PAV, (904) 882-4436, Ext. 321.
This fact sheet is also available on the World Wide Web via the Eglin Homepage at http://www.eglin.af.mil

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United States Air Force

Air Force Materiel Command

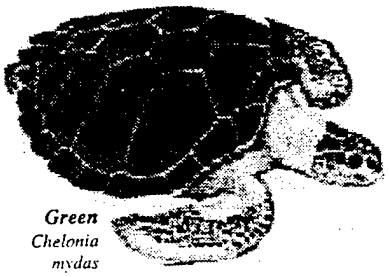
Air Force Development Test Center, Office of Public Affairs

101 W. D Avenue, Suite 110, Eglin AFB, FL 32542-5498 Tel. (850) 882-3931

Sea Turtles in the Gulf

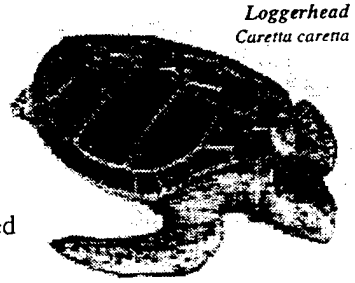
Introduction

Eglin Air Force Base is the largest air force base in the free world, including 724 square miles of land area and about 130,000 square miles of controlled airspace overlying land and water. In this setting, Eglin conducts its primary mission of full-service air armament development through weapons system research, development, testing and evaluation; training; space operations; and base and range support. While fulfilling its mission, Eglin also manages its natural resources, acting as a steward to protect plants and animals for future generations.



Green
Chelonia mydas

Eglin lies in northwestern Florida adjacent to the warm waters of the Gulf of Mexico. A variety of tropical life makes its home in this gulf, including several sea turtles. These ocean-going reptiles spend nearly all of their lives at sea, venturing to land when it is time to nest. While species range in ocean waters worldwide, Florida waters and beaches provide critical habitat. All sea turtles found in Florida are considered threatened or endangered. Eglin's undeveloped shoreline is a nesting habitat for the loggerhead and green sea turtles.



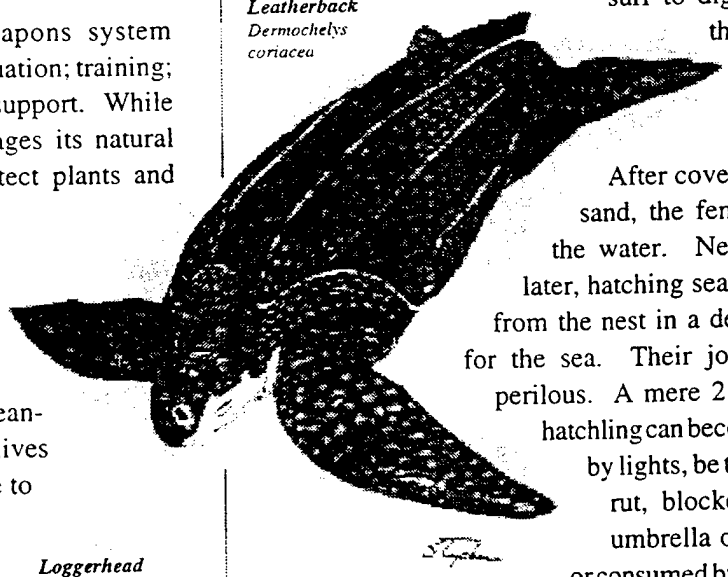
Loggerhead
Caretta caretta

Life in the Sea

Sea turtles are well adapted to life at sea. With powerful front flippers, they move easily through the water in search of a variety of foods. Their diets vary by species, but include jellyfish, sea squirts, shellfish, algae, seagrasses and mollusks. During the nesting season, females return from their feeding grounds to nesting beaches. The trip may be as long as 3,100 miles.

Each summer, Florida beaches host a variety of nesting sea turtles. Almost always coming ashore at night, females struggle through the surf to dig sand pits for their eggs. Each female can lay 60 or more eggs. After covering nests with sand, the females return to the water. Nearly 2 months later, hatching sea turtles emerge from the nest in a desperate search for the sea. Their journey is often perilous. A mere 2 inches long, a hatchling can become disoriented by lights, be trapped by a tire rut, blocked by a beach umbrella or a sand fence, or consumed by such predators as raccoons, wild pigs, feral cats and ghost crabs. At sea, the hatchling must survive marine predators and potential threats from human activities. Manmade debris (such as plastics, tar balls and styrofoam) is sometimes ingested and can cause death. Mature sea turtles can also get trapped in shrimp nets. In some parts of the world, people continue to eat the eggs or kill the turtles for food, oil and leather.

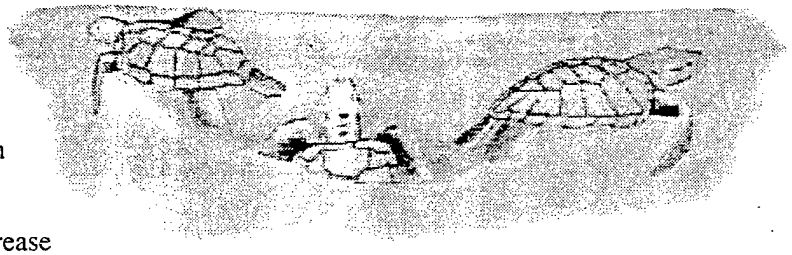
Leatherback
Dermochelys coriacea



As a result of habitat loss and human predation, many sea turtles are threatened or endangered.

Sea Turtles in the Gulf of Mexico

Five sea turtles may be found in the Gulf of Mexico. Two species are known to nest on Eglin beaches, the Atlantic loggerhead turtle and the Atlantic green turtle. The nesting season for both species is from mid-May through August.



Nearly 80% of the sea turtle hatchlings at Eglin reach the sea.

Natural resource managers at Eglin seek to increase sea turtle populations by increasing the number of hatchlings that reach the sea. This involves monitoring for nesting activity and minimizing possible threats to nests and hatchlings. As an example, nighttime mission activity requiring lights is carefully managed to minimize any disruptive effect on the turtles. Nests are screened to protect them from predators. If nests are threatened by imminent danger from tidal flooding or vehicle traffic, the eggs are relocated to safer areas. Natural resource managers from Eglin monitor sea turtle nesting on a daily basis along 17 miles of beach on Santa Rosa Island. Specially trained volunteers also perform periodic surveys at Cape San Blas.

Once any nest has been identified, it is checked every other day until hatching begins, at which time daily monitoring occurs. Nearly 80 percent of the eggs deposited on Eglin beaches mature to hatchlings which reach the sea. With luck, mature females will survive the rigors of the sea and begin the process again.

Sea Turtle	*Description*	*Status*	*Range*
Loggerhead 	- Adult size ranges from 36 to 38 inches in length; 200 to 350 pounds - Heavy head and jaw - Feeds on mollusks, shellfish, jellyfish, and plants	- Threatened	Found in temperate and subtropical waters worldwide
Green 	- Typical adult size is 39 inches in length; 330 pounds - Strictly herbivorous (plant-eating only) as adults	- Endangered on east coast of Florida and Pacific Coast of Mexico; threatened elsewhere - Eggs and meat eaten by humans	Primarily in tropical waters of Atlantic, Pacific, and Indian Oceans, Gulf of Mexico
Leatherback 	- Largest sea turtle, up to 6 feet in length; 1,300 pounds - Feeds chiefly on jellyfish - No hard shell	- Endangered	Subpolar to tropical waters of Atlantic, Pacific, and Indian Oceans, Gulf of Mexico
Hawksbill 	- Typical adult size 30 to 35 inches in length; 95 to 165 pounds - Feeds chiefly on sponges	- Endangered - Source of commercial tortoiseshell	Western Atlantic, from New England to Brazil
Kemps Ridley 	- Typical adult size 23 to 27.5 inches in length; 80 to 100 pounds - Feeds on crustaceans	- Endangered	Chiefly Gulf of Mexico, but also along Atlantic Coast to New England and Nova Scotia

The Skimmer

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Random Thoughts of Preservation of Rare Species and Their Habitats

James R. Burkhalter

It seems to me, in these times of rampant and accelerating urban development in Escambia County, and indeed throughout northwest Florida, that the importance of preserving natural habitats to protect and encourage rare species of plants and animals that live there cannot be over stressed or exaggerated. We must do all that we can possibly can to promote and implement such efforts and should not hesitate to allocate resources of time, effort, and money for such undertakings. And I wonder what the burgeoning Pensacola metropolis will be like in 50 to 100 years (or perhaps even sooner): essentially no vacant lots or unused spaces, and trees existing only as streetside plantings or in a few scattered parks.

I am particularly concerned about three outstanding local areas of special notice: the pitcher plant prairie area southwest of Pensacola, Santa Rosa Island east of Pensacola Beach, and the area east of Gulf Breeze by the south approach road to the new Garcon Point bridge.

The pitcher plant prairie area is especially noteworthy. There hundreds of acres of low wiregrass savannahs, flatwoods depressions, and other pitcher plant bogs occur. This is certainly one of the largest complexes of these unusual plant communities remaining undamaged in the state of Florida. What a magnificent natural treasure fate has bestowed upon us right here in our own backyard! Many thousands of rare white-topped pitcher plant (*Sarracenia leucophylla*) grow there together with parrot pitcher plant (*S. Psittacina*), purple pitcher plant (*S. purpurea*), and rare Chapman's butterwort (*Pinguicula plainfolia*). Other carnivorous species of genera *Drosera*, *Pinguicula*, and *Utricularia* also grow there, as well as several interesting species of orchids and other forbs. How can we as thinking and caring individuals do anything less than whatever is necessary to protect and preserve this assemblage of rare plant communities as a living legacy to future generations? Fortunately, the state of Florida is going to buy it and provide for its preservation.

On Santa Rosa Island, in the dry, sandy, harsh environment of the rear dunes, grow two of the rarest plants in the world: Godfrey's golden aster(Chrysopsis godfreyi) and Cruise's golden aster (C. cruiseana). Godfrey's golden aster occurs on Perdido Key and sparingly on the adjacent mainland, but Crusie's golden aster grows only on Santa Rosa Island east of Pensacola Beach. Godfrey's golden aster was recently listed as one of the 500 most endangered species of plants and animals in the United States by the Nature Conservancy. Is there any doubt that these two botanical rarities deserve to be protected? In fact, if steps are not taken to carefully plan and control coastal development activities these golden asters will be driven to extinction in the not-too-distant future.

Just south of the new approach road for the Garcon Point bridge is located one of the largest extant colonies of an exceedingly rare plant: Curtiss's sand grass(Calamovilfa curtissii). This plant grows only in Santa Rosa, Okaloosa and Brevard counties, Florida.–and no place else on earth. This site is certainly in need of protection, since they are currently completely surrounded by residential and commercial developments--a very precarious situation in which they could be easily wiped out by only a few hours of bulldozer activity. Perhaps, since it is designated as wetlands by the State of Florida, it might remain undisturbed indefinitely. Wetland protection laws only effectively prevent filling and excavation, not removal of vegetation.

Recently I searched Escambia County north of Pensacola for natural habitats that might support the rare orchid (*Peteroglossaspis ecristata*) which was found a few months ago by John Hays growing in

continued page 6 .....**Random Thoughts**

President's Message

Dana Timmons

Endangered Species and Audubon

On Thursday, November 5, the board of directors of the Francis M. Weston Chapter of the Audubon Society voted unanimously to assist the Blackwater River State Forest in its efforts to strengthen its population of **Red-cockaded Woodpeckers**. Vernon Compton, director of the Gulf Coastal Plains Ecosystem Partnership, during his presentation at our October program, mentioned the efforts being made in the forest on behalf of the woodpecker. Already workers in Blackwater are banding birds and enhancing cavities as well as installing new cavity inserts, but further steps must be taken to help the sinking population.The plan is to bring five female birds to influence five single male clusters. The cost of the move is $7,500 of which the US Fish and Wildlife Service has agreed to pay half. Our chapter has agreed to pay the additional half when the translocation permitting process has been completed.

The theme of our chapter meetings this year is endangered species. If you have not been attending our chapter meetings, you have missed out on some very interesting programs, and the best is yet to come. *Please take note of our January meeting date*. Instead of the fourth Thursday in January we have moved our program date to January 21st in order to accommodate the speaker, Dr. George Archibald, Director of the International Crane Foundation (ICF).



Since the founding of the ICF, he has studied the ecology of eight species of cranes in Australia, China, Iran, India, Japan, Korea, and the USA. Dr. Archibald helped organize nine Working Groups on Cranes, including more than 900 researchers in 64 nations. Under his direction, ICF has established a species bank of captive cranes and has been successful consistently breeding significant numbers of several endangered species of cranes.

Please mark your calenders with this date change and plan to attend this important meeting.

Education

Peggy Baker

Where the Birds Are!

The President's Message tells of FMWAS' undertaking to play cupid to the **Red-cockaded Woodpeckers** at Blackwater National Forest. In an effort to ensure the survival of the RCW there, we are supporting an attempt to move some female birds to "where the boys are."

The RCW has a social system that centers around a family group that creates a "cluster." The females usually travel to another cluster in search of mates. But unfortunately, the cluster at Blackwater is too isolated and there are young males there without mates. FMWAS will contribute financially to the translocation of five young females to establish some new breeding pairs into this cluster.

The RCW cluster in Blackwater State Forest is relatively easy to see. In the spring and early summer, these birds can be seen throughout the day as they return to the cavities to feed the young. In the fall and winter, they continue to use the cavity for night lodgings, so the best sighting time is late in the day.

To see these birds, take Hwy 87 north in Milton. Turn right on Hwy 191. Go north on Hwy 191, past the Spring Hill community, to Hwy 68 at the Blackwater horse stables. Look for the stables sign because the road may be unmarked. Turn left on Hwy 68 and then turn right on the first dirt road which is called Three Notch Road but it may also be unmarked. In approximately one mile, look for the pine trees that are ringed with white paint which denote nesting trees. One of these trees is literally on the roadway on the right. This road will take you to Hwy 4. Another cluster near a paved road is in Conecuh National Forest just north of the Florida state line. Exit I-10 at Holt and go right (east) on Hwy 90 and left (north) on Hwy 189. This road becomes Alabama Hwy 137 at the state line. At Wing, AL, turn left on Hwy 4 (note: this is AL Hwy 4, not Hwy 4 at Baker). On the right side of AL Hwy 4, about one mile from Wing, there will be white-ringed pine trees near the road . Turn right on the dirt road that goes beside these trees and listen for the Red-Cockaded's call.

Good luck on seeing these beautiful endangered creatures that need our help to survive!

PENSACOLA
News Journal
SUNDAY, MARCH 21, 1999

READER'S FORUM

To discuss an opinion, call 435-8545 or 435-8543

VIEWPOINT

Champion manages its 480,000 acres with future generations in mind



JOANN M. COX

Recently, community leaders suggested that Champion take a cue from St. Joe Company on how to manage and plan the future by setting aside land for development or preserves for public use.

The U.S. Constitution protects the right to own land, whether as a private individual or as a company, and allows landowners to choose how to use their land. The role of Champion's forest resources is to enhance the value of the land for its true owners, our shareholders.

Champion has long believed that practicing exemplary forest stewardship is the right thing to do, not only for the environment, but for our business. Our working forest supplies the renewable raw material for two existing manufacturing facilities and supports a variety of forestry contractors. As one of the largest landowners in Northwest Florida the company manages its 480,000 acres with future generations in mind.

Champion was a leader in the adoption of the American Forest and Paper Association's Sustainable Forestry Initiative (SFI), an ambitious set of principles and guidelines requiring companies to reforest promptly, provide wildlife habitat, improve water quality and ecosystem diversity and protect places of special significance.

The cornerstone for sustainable forestry is our land classification system. Each forest stand managed by Champion was reviewed and assigned to one of four classes: areas to be protected and preserved; restricted areas where water, wildlife and other values take precedence over timber production; areas where timber production is the primary objective, but other functions deserve special emphasis; and areas that are best suited for intensive tree culture. Approximately one-third of our total ownership falls in one of the first three categories.

Champion also uses a rigorous internal Best Management Practices (BMPs) audit system of our forestry practices to protect water quality. Champion's Western Florida Region is considered a role model in the implementation of sound and practical BMPs by our independent auditors.

Champion's commitment to sustainable forestry extends to ecological and social needs as well. For example:

- Champion is the only private industrial owner among the seven partners in the Gulf Coast Plain Ecosystem Partnership (GCPEP), a cooperative effort to maintain the economical and environmental health of a shared 845,800-acre ecosystem.
- In 1988, Champion assembled a team of natural-resource professionals to determine how to manage the company's river bottom land. Ultimately Champion conveyed 47,000 acres of river frontage along the Escambia, Yellow and Choctawhatchee rivers to the Northwest Florida Water Management District for the sustained management of water quality in the region.
- In November 1998, Champion was the first forest products company to commit to an independent review of all its forest lands in the United States within the next three years.
- On Feb. 25 the Governor's Council for Sustainable Florida presented Champion's Eastern and Western Forest Resource regions with the 1999 Sustainable Florida Award for Leadership. The award honors those who demonstrate the best performance standards in the integration of environmental, social and economic factors for the long-term sustainability of Florida.

As Northwest Florida grows, land use issues will continue to challenge community leaders and landowners.

I would like to suggest that the answer lies in the application of the principles of sustainability, as defined by the Governor's Council for Sustainable Florida: "sustainable should be understood to mean a fully integrated approach to the diverse but interrelated goals of a healthy environment, a prosperous economy, a satisfying quality of life, broad public participation and vibrant livable community."

Champion foresters, sustainable land use planners for decades, are more than willing to lend their experience to the process.

Joann Meyer Cox is the general manager, Western Florida Region for Champion International Corp.