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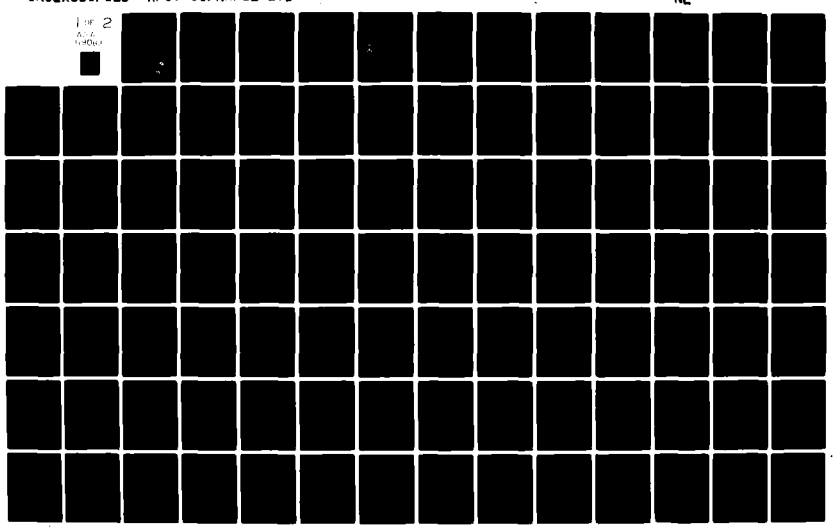

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LAWRENCE JOSEPH BIEVER
The Role of Mycorrhizal Fungi in Ecosystem Energetics
(Under the direction of EUGENE P. ODUM)

The vast majority of vascular plants in all nonhydric terrestrial ecosystems are mycorrhizal. While the effect of mycorrhizae on nutrition, survival and growth of plants (especially commercially important crops and trees) has been extensively investigated, little attention has been devoted to their role in the ecosystem as a whole. A review of the extensive literature has led me: (1) to conclude that energy flow through the mycorrhizal network represents a distinct and major food chain and (2) to test this hypothesis in a field study on experimental pine plantations.

Since mycorrhizal fungi obtain their energy directly from the vascular transport system in plant roots, the resultant energy flow does not fit into the traditional two-channel food chain model comprising grazing and detrital pathways. Accordingly, I developed an extended and more comprehensive energy flow model with four pathways: (1) grazing, (2) detritus, (3) exudation, and (4) active extraction, the latter to include the mycorrhizal pathway. Pathways 3 and 4, in contrast to 1 and 2, do not involve conversion of photosynthate to plant tissues prior to transfer to heterotrophic components in the food chain. The exudate and detritus flows are largely donor (plant) controlled while grazing and extraction pathway are more recipient controlled. Since photosynthate extracted by mycorrhizal fungi is exchanged for soil nutrients made available to the plant, the mycorrhizal network is a bidirectional energy and nutrient transport system that has the capacity to function as a major feedback control system for the ecosystem.

To obtain a minimum estimate of energy flow via the mycorrhizal path, sporocarps of Pisolithus tinctorium were harvested and annual production of woody tissue and needles measured in pine plantations on extremely poor soils at Copper Hill, Tennessee and at the Savannah River Plant, South Carolina. Addition of sporocarp production to tree growth increased the estimate of net primary production (NPP) by as much as 11%. Up to 10% of total NPP was estimated to pass through the sporocarps alone, an indication that total energy flow along this active extraction food chain can be quite large. The experiments, together with voluminous information in the literature, support the hypothesis that mycorrhizal fungi constitute a major energy flow pathway in terrestrial ecosystems.

INDEX WORDS: Mycorrhizae, Bisiodiocarps, Energy Flow, Model Food Chains, Pine Plantations.

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THE ROLE OF MYCORRHIZAL FUNGI IN ECOSYSTEM ENERGETICS

by

LAWRENCE JOSEPH BIEVER

B.S., South Dakota State University, 1965

M.S., South Dakota State University, 1967

A Dissertation Submitted to the Graduate Faculty

of the University of Georgia in Partial Fulfillment

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Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

1982

THE ROLE OF MYCORRHIZAL FUNGI IN ECOSYSTEM ENERGETICS

by

LAWRENCE JOSEPH BIEVER

Approved:

Eugene P. Odum Date March 31, 1982
Major Professor

[signature] Date March 31, 1983
Chairman, Reading Committee

Approved:

_____
Dean, Graduate School

_____
Date

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To the faculty, staff, and students of the University of Georgia and the Institute of Mycorrhizal Research. Every scientist searches for a view of nature which allows new understanding of the structure and function of nature. We aspire to the kind of event that occurred with Newton and Einstein in physics or with Darwin in biology. You gave me the opportunity to have such a vision for one small area of biology. Each of you gave me a piece of the puzzle, a view from your perspective based on your insight and the work of your contemporaries and those who have contributed before you. The effects of Dr. Marx, Dr. Berry and the other scientists and staff of the Institute of Mycorrhizal Research; and Dr. Odum and the other scientists and staff of the Institute of Ecology are obvious. Major components came from the opportunity to work with Dr. Swank, Dr. Crossley, and Dr. Todd; and to derive the benefits of their insight from the Coweeta project, and their personal experience. The personal input of Dr. Brown and his view from forestry and tree physiology are less obvious but no less important. Much of my systems view originated with Dr. Patten but has been modified by Dr. Golley's more mutualistic belief that components are not antagonistic but rather are harmonious. Dr. Wiegert's view of energy flow in ecosystems, Linda Wallace's understanding of energy capture and flow in plants, and Dr. Pomeroy's inquiries into energy flow in marine systems provided the raw material for my view of energy flow in ecosystems. I could not have

handled the mass of data without Thelma Richardson's help with computers. Each of you (the list above is far from complete) has contributed some of your life to this project. However, the other graduate students suffered the most. They put up with my tirade of wild ideas, sorted them, criticized them, modified them, and supported me. Of that group, I owe the most to Brent Haglund. As with all scientific endeavors, this one is built on the broad base of family, friends, teachers, and scientists who formulated my perceptions and shaped me into what I was before I came to Georgia -- you only modified and added to that. The individuals who contributed to the scientific basis of this work are, I hope, fairly represented in the bibliography.

I thank Dr. Crossley, Dr. Todd, Dr. Swank, Dr. Brown, and Dr. Golley for serving on my Ph.D. committee during the many phases of my degree program. Julie Fortson and Laurie Goldner were particularly helpful during the hectic days of completing the final manuscript.

I am especially grateful to four people: (1) my wife Helen, who not only suffers my insufficiencies daily but who also contributed much of the tedious technical laboratory work and typing; (2) a man whom I have never met, Dr. J. L. Harley. He had a similar vision of the role of mycorrhizae in ecosystems many years before me, without the benefit of most of the information presented in this dissertation; (3) Dr. Don Marx, who served on my committee and treated me as a friend and a contemporary. His knowledge about mycorrhizae, his insight into their function in forest ecosystems and his willingness to spend hours of his time with me were critical to my development; and (4) the chairman of my committee, Dr. Eugene Odum. He is an exceptional scientist and gentleman whom I am honored to call "a friend." He freely shared his vast knowledge

of ecology and his time, frequently at great personal inconvenience. His ability to refine ideas within a holistic context and his ability to express them clearly in writing were especially helpful.

The United States Air Force provided my salary and time off from my normal duties. The Institute of Ecology and the Institute of Mycorrhizal Research provided facilities and supplies for the research.

The dissertation that follows is my view of the role of mycorrhizae in ecosystems and what that might mean to ecological theory. It presents my support from logic, the literature, and experimentation for a view that mycorrhizae are important in ecosystem structure and function. I pass these ideas on to you here, incomplete as they are, because they are yours. I hope they are of use to you, I hope you will give them the test of scientific inquiry, criticism, and experimentation, and I hope you will correct and modify them such that they eventually reflect the true state of nature.

TABLE OF CONTENTS

TABLE OF CONTENTS continued.

LIST OF TABLES

LIST OF TABLES continued.

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Mycorrhizae mediated plant growth increases (yields) under adverse conditions, particularly in nutrient or moisture deficient soils, have obvious implications for food and fiber production because most plants important in agriculture and forestry form mycorrhizae. As a result, research on mycorrhizae has focused on the fungi, the infection process and the plant response under a wide range of environmental conditions. Although their importance as structural and functional components of ecosystems has been suggested (Harley, 1971, 1972; Trappe and Fogel, 1977) it has not been investigated. The affect of mycorrhizae on the heterotrophic portion of the ecosystem is little known, and mycorrhizae have not been incorporated into general ecological models and theories as they relate to succession, population and community dynamics, ecological genetics, nutrient cycling, cybernetics and energy flow. For example, it is not known whether the incidence of mycorrhizal mutualism increases as biomass and complexity accumulate during ecological succession; or how much energy may pass through a mycorrhizal network as compared to energy flow via other pathways.

Mycorrhizal fungi provide a physically continuous biological link between biotic and abiotic components of ecosystems. The hyphae are coenocytic or have simple or dolipore septae, and function as a cytoplasmic pipeline capable of bidirectional transport of energy and nutrients.

Because of their potential for enhancing connectance, they may play a quantitatively and qualitatively important role in ecosystem energy flow and nutrient cycling. Perhaps more important is their potential role as substructures that provide the internal feedback involved in ecosystem cybernetics (Patten and Odum, 1981).

Most individual members of the vast majority of vascular plant species in nonhydric terrestrial ecosystems of the world exist as a mutualistic association with mycorrhizal fungi (see Appendix 1, Prevalence of Mycorrhizae in the Biosphere). Interconnectivity between plants is facilitated by multiple infections of a single plant by as many as fifteen fungal species, fusing of compatible hyphae in the soil, and by colonization of more than one plant by continuous mycelium. The fungi effectively link the vascular systems in the roots of individual plants both within and between plant species. Mycorrhizal hyphae permeate the upper three meters of soil and provide a huge surface area for exchange. Accordingly, the fungi are a physical and physiological intermediary between plant roots and the soil environment. As a result, they affect, mostly in a positive manner, the survival, growth rate, and distribution of plants by mitigating the potentially limiting chemical, physical, and biological conditions in the soil. Table 1-1 summarizes plant benefits from the relationship as reported in the literature.

At the ecosystem level of organization, mycorrhizal structures provide a unique energy and nutrient transportation network whose importance has not been fully recognized. The fungal network can selectively acquire and concentrate a wide variety of inorganic nutrients from the soil column. They acquire energy directly from the vascular system of the plants, as early noted by Lewis and Harley (1965c), and distribute it within the

TABLE 1-1. Demonstrated Plant Responses to Mycorrhizae which Enhance Plant Growth Rate, Distribution and Survival.

(1) an expanded root system	(Slankis, 1973)
(2) increased longevity of feeder roots	(Meyer, 1974)
(3) resistance to feeder root pathogens	(Marx, 1973)
(4) resistance to high temperatures	(Marx et al., 1970, Marx and Bryan, 1971a)
(5) resistance to cold temperature	(Harley, 1969)
(6) increased tolerance to soil toxins	(Zak, 1971)
(7) drought resistance	(Trappe, 1962b)
(8) tolerance to adverse soil pH	(Marx, 1978)
(9) tolerance to adverse cationic and anionic concentrations	(Marx, 1978)
(10) selective absorbtion of certain ions from the soil	(Bowen, 1973)
(11) the ability to extract nutrients from normally inaccessable sources	(Bowen and Theodora, 1967)
(12) increased nutrient uptake. Mycorrhizae and/or mycorrhizal fungi have been demonstrated to absorb Ca^{++}, $H_2PO_4^-$, K^+, Rb^+, Cl^-, $SO^{=}$, Na^+, NO_3, NH_4^+, Mg^{++}, Fe^{++}, and Zn^{++}.	(See review by Bowen, 1973)

ecosystem biomass as fungal secretions. The hyphae transport nutrients and energy between plant roots, and between the soil column and roots, over considerable distances, as great as four meters according to Schramm (1966). Hyphae and fungal reproductive structures contribute nutrients and energy directly to decomposers and to a wide variety of micro and macro, above and belowground fungal grazers. The chemical form and proportional composition of resources available to plants from mycorrhizae appear to be significantly different from resources available through the detritus and grazing pathways.

Accordingly, mycorrhizal fungi constitute a qualitatively and quantitatively distinct alternative pathway or food chain for ecosystem energy flow and nutrient cycling. The pathway is spatially and temporally distinct from the detritus and grazing pathways currently used to describe ecosystem function. The mycorrhizal pathways have important implications for nutrient and energy budgets because these flows would not normally be accounted for, particularly when plant and animal biomass harvest methods are used to estimate energy flow. Because the mycorrhizal pathway embodies high interconnective, rapid transport rates, and bidirectional flow, it provides a potential feedback control mechanism between "downstream" consumers and "upstream" producers.

The literature on mycorrhizae suggests that the fungi have two other primary effects on ecosystem energetics. (1) They affect the plant species composition of ecosystems and the growth rate of individual plants, and thereby the total amount and physical-chemical nature of energy available within the ecosystem. (2) They affect plant morphology and therefore the partitioning of energy between above and belowground components.

Ecology has been defined as "the study of the relationship between structure and function in nature" (Odum, 1962). Currently mycorrhizae are considered in ecosystem models only as they facilitate nutrient uptake and cycling but not as ubiquitous ecosystem structures. Section II reviews the structural components of mycorrhizal associations and the related terminology as a basis for a structural model of the mycorrhizal pathway for energy flow. In Section III mycorrhizae are incorporated into a general model of ecosystem energy flow, consisting of four subsystems, namely plants, grazers, decomposers, and mycorrhizae. Such a model allows quantitative and qualitative comparisons, based on information available in the literature, of the various pathways (grazing, detritus, secretion, mycorrhizae) by which the energy of primary production is transferred to the heterotrophic components of the ecosystem.

Measurement of energy flow through most components of the mycorrhizal pathway is difficult because they are belowground and generally are microscopic. However, measurement of energy flow to the epigeous sporocarps of ectomycorrhizal fungi is feasible since the sporocarps (mushrooms) can be harvested and as the terminus of the mycorrhizal pathway their production represents a minimum estimate of energy flow through the pathway. A field study of sporocarp production in relation to energy flow through a pine plantation is reported in Section IV.

In summary, the objectives of this thesis are three-fold: (1) To develop and model the hypothesis that mycorrhizae constitute a distinct and important energy flow pathway in terrestrial ecosystems, and (2) to estimate energy partitioning between tree growth and sporocarp production as a means of validating the importance of this pathway. (3) To estimate

energetic benefits of the pathway to plant and to forest community as a whole.

CHAPTER II

MYCORRHIZAL FUNGI AS MAJOR STRUCTURAL COMPONENTS OF THE TERRESTRIAL ECOSYSTEM

"The study, understanding, and intelligent manipulation of our environment requires systematic investigation of the structure and function of ecological systems" (Odum, 1968). Since ecological systems are complex, one approach to their study involves simplification, generally in the form of modelling. The components of an ecosystem can be displayed as an array of groupings generally presented as state and transition functions -- the box and arrow diagrams common to systems ecology. However, "all significant populations and pathways must be known if the model is to have utility for understanding the real world" (Pomeroy, 1974). My contention is that mycorrhizal fungi are one of those significant components. This section describes the mycorrhizal components and develops a structural model that integrates them into a functional model of ecosystem energy flow.

Historically, studies of pathogenic and predator-prey relationships have dominated studies of symbiosis. Therefore, the terminology available is misleading or inappropriate when applied to mutualistic associations. For example, the term host is at best misleading when applied to either member of an obligate mutualistic association such as that between pines and mycorrhizal fungi or even between ruminant animals and their rumen microflora. The terms parasite or pathogen are totally inappropriate.

Therefore, Lewis (1973) suggested the terms phycobiont (plant symbiont) and mycobiont (fungal symbiont) to designate the partners in mycorrhizal associations.

For most mutualistic associations, there is no term equivalent to lichen for the structure composed of the combined organisms. For example, the term cow may alternatively mean the structure originating only from a single sperm and egg, or it may mean that structure plus all its associated microflora. Genetically cow is the former; but since cows cannot exist in nature without rumen microflora, functionally cow is the latter. The same can be said for a pine tree because of the obligate requirement for mycobionts. Lewis suggests the term symbiont to include both the phycobiont and the mycobiont in mycorrhizal associations. However, the term symbiont includes the entire range of symbiotic associations, including predator-prey, disease-host, and competition. Odum (personal communication) suggests the term mutualont to designate structures composed of two or more obligately mutualistic organisms.

The term mycorrhiza was coined by Frank (1885) to describe the composite fungus-plant root organ. It refers to a limited structure within the mutualont which includes only the colonized root and the surrounding mantle. The term mycorrhizae includes a wide variety of specific plant-fungus associations (see Appendix 1). Variations in the morphology have been used to categorize mycorrhizae as ectomycorrhizae, endomycorrhizae (frequently subdivided to ericalean, vesicular-arbuscular (VA), and orchidaceous) and ectendomycorrhizae (Appendix 2). Categories of mycorrhizae are broadly correlated with plant taxons (Appendix 1B) biome-type (Appendix 1C) and fungal taxons (Appendix 1D).

The structural components of the mycorrhizal association and the dominant flows of materials to and from those components are illustrated in Figure 2-1. All of the four fungal components, namely, cortical hyphae, mantle, soil hyphae, and reproductive structures constitute a physically continuous mass of hyphae. Furthermore, most of the fungal species have continuous cytoplasm throughout the thallus due to openings in the septae between cells within the hyphae. Ascomycetes have simple pores, Basidiomycetes have dolipores, and Endogonaceae are coenocytic. The boundaries between the components are not discrete, but are based on physical location and morphology which is correlated with functions within the association and the surrounding environment.

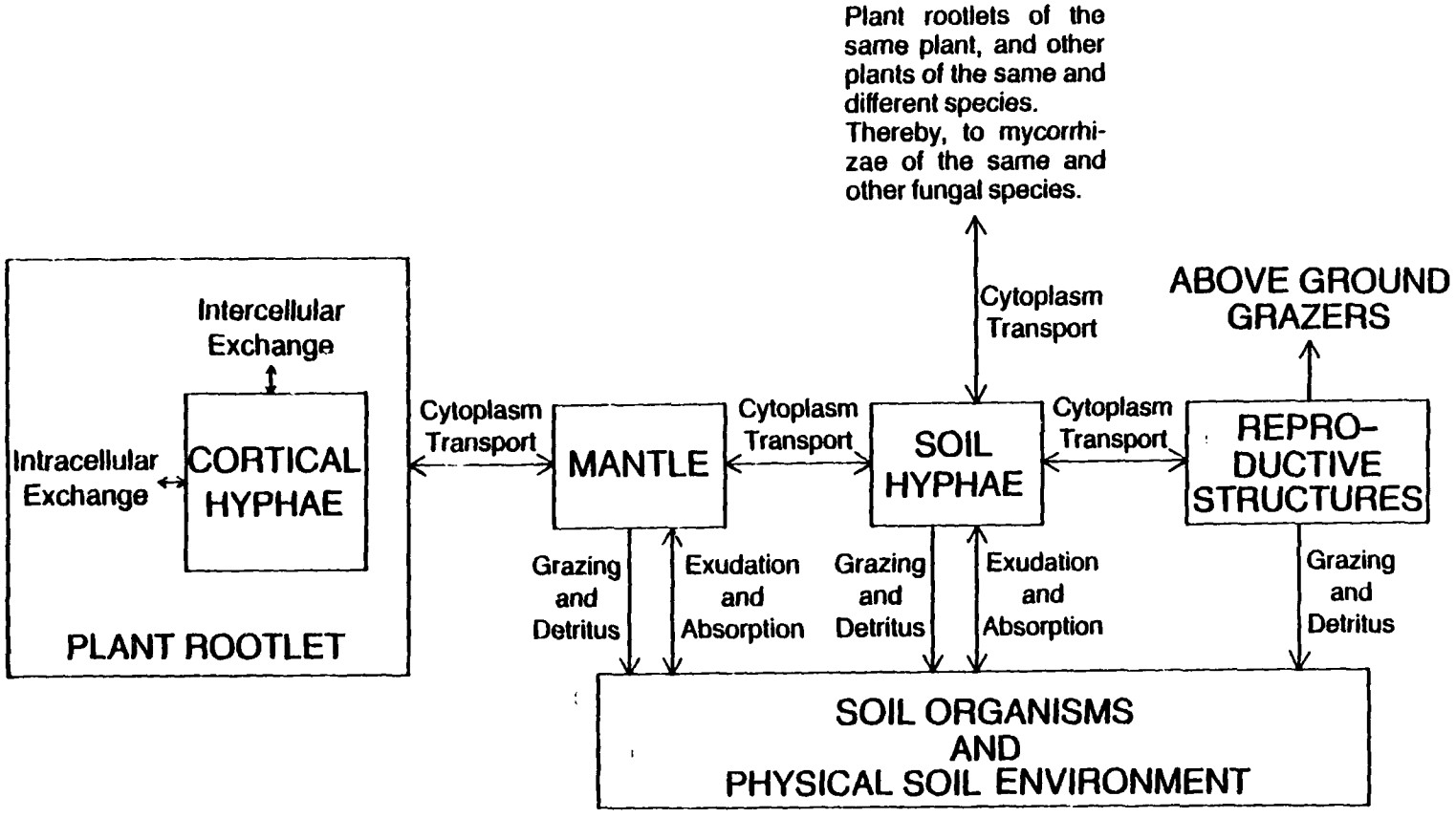
Cortical hyphae are restricted to the plant rootlet and do not penetrate the stele. They are the main organ of exchange between the plant and the mycorrhizal fungus. Intercellular hyphae are in direct contact with intercellular plant fluids. In endomycorrhizae, intracellular hyphae penetrate the plant cell wall but not the cell membrane. Exchange of materials is across both the fungal and plant cell membranes. Intercellular hyphae form specialized structures for exchange (arbuscules) and for storage (vesicles) (Gerdeman, 1974). For a more detailed discussion of inter- and intracellular hyphae, see Hayman (1978) and Mosse (1963).

In ectomycorrhizal associations a sheath of hyphae develops around the plant rootlets and forms the mantle. The mantle structure varies from a loose waft of hyphae to a 100 µm thick (Wilcox, 1968) dense pseudoparenchyma with a firm surface. The mantle is continuous with cortical hyphae. Mantle hyphae also exchange materials with soil organisms (including plant roots) and the physical soil environment by exudation and absorbtion.

For more detailed discussions of mantle structures, see Zak (1973) and Marks and Foster (1973).

Soil hyphae are continuous with cortical and mantle hyphae. Organized aggregates of soil hyphae (mycelial strands and rhizomorphs), and individual hyphae permeate the upper soil layers to depths of three meters (Meyer, 1973). Schramm (1966) traced soil hyphae which extended laterally for as far as four meters. The small diameter (2-4 μm) results in large surface areas (Bowen, 1973) which facilitates exchange with the physical soil environment and with soil organisms.

The soil mycorrhizal hyphae form an extensive network through the soil. Trappe (Trappe and Fogel, 1977) "traced a single hypha emerging from a Pseudotsuga - Cenococcum mycorrhiza in a rotten log. The hypha extended more than 2 m and had more than 120 lateral branches or fusions with other hyphae. At least 43 of these branches connected to other mycorrhizae; 34 of these connected to other mycorrhizae on the same tree and 9 to mycorrhizae of another tree species, Tsuga, roots growing in the same log. Sample counts on numerous mycorrhizae formed by Cenococcum with various host species showed that from 200 to 2,000 individual hyphae emerge from single mycorrhizae." Genetically compatible soil hyphae fuse readily. What emerges is a picture of a vast network of interconnected hyphae of one fungal species which physically connect mycorrhizae on the root systems of trees compatible with that species. The ability of mycorrhizae to link more than one plant species is dependent on phycobiont and mycobiont compatibility (see Appendix 1E). The compatibility of a single tree species with multiple fungal species, and a single fungal species with multiple tree species increases the physical interconnectivity.



There are C^{14} and P^{32} tracer demonstrations that the physical connection is functional (Melin and Nilsson, 1957; Bjorkman, 1960; Woods and Brock, 1964; Reid, 1971). Flows through the mycorrhizal fungi may be bidirectional for energy (Reid and Woods, 1969; Pearson and Read, 1973b) and nutrients (Pearson and Read, 1973b) although the dominant demonstrated flows are toward the fungus for energy and toward the plant for nutrients such as phosphate.

Reproductive structures are continuous with soil hyphae, and may be hypogenous or epigeous, dependent on the fungal species involved. There is no evidence that reproductive structures exchange materials with the surrounding environment by secretion or adsorption. Sporocarps as well as all of the other structures eventually contribute matter and energy to the grazing and detritivore food chains through mycovores (e.g., nematodes, arthropods, mollusks, and mammals (Ingold, 1971; Riffle, 1971) and saprovores after death.

In many ways the term mycorrhiza is misleading because it implies a single category of associations. It really refers to a broad spectrum of symbiotic associations where the fungi and plant species are unrelated taxonomically, the anatomy of the colonized roots varies widely, and the physiological interactions between phycobionts and mycobionts can differ markedly. Although there are obvious similarities between the groups of mycorrhiza, it is incorrect to assume that what is true for ectomycorrhizae is true for endomycorrhizae, or that what is true for VA mycorrhizae is true for ericalian or orchidaceous mycorrhizae and vice versa.

However, the variability does not detract from the fact that mycorrhizae form an interconnected energy and nutrient transportation pathway between the plant and its soil environment. Figure 2-1 serves as a

structural model of mycorrhizae as they physically exist in most terrestrial ecosystems.

CHAPTER III

HYPOTHESIS: MYCORRHIZAE CONSTITUTE A MAJOR ENERGY FLOW PATHWAY IN TERRESTRIAL ECOSYSTEMS

Energy flow is the central process in ecosystem function. Mycorrhizal fungi affect the flow of energy between autotrophs and heterotrophs by affecting the rate of production of plant biomass, and by affecting the partitioning of net production between above and belowground structures. In addition, I hypothesize that mycorrhizae constitute an energy pathway distinct from the grazing and detritus food chains because, energy is removed from the plant as phloem transport photosynthate rather than as cellular plant biomass, and because the temporal and spatial distribution of energy to heterotrophs is different.

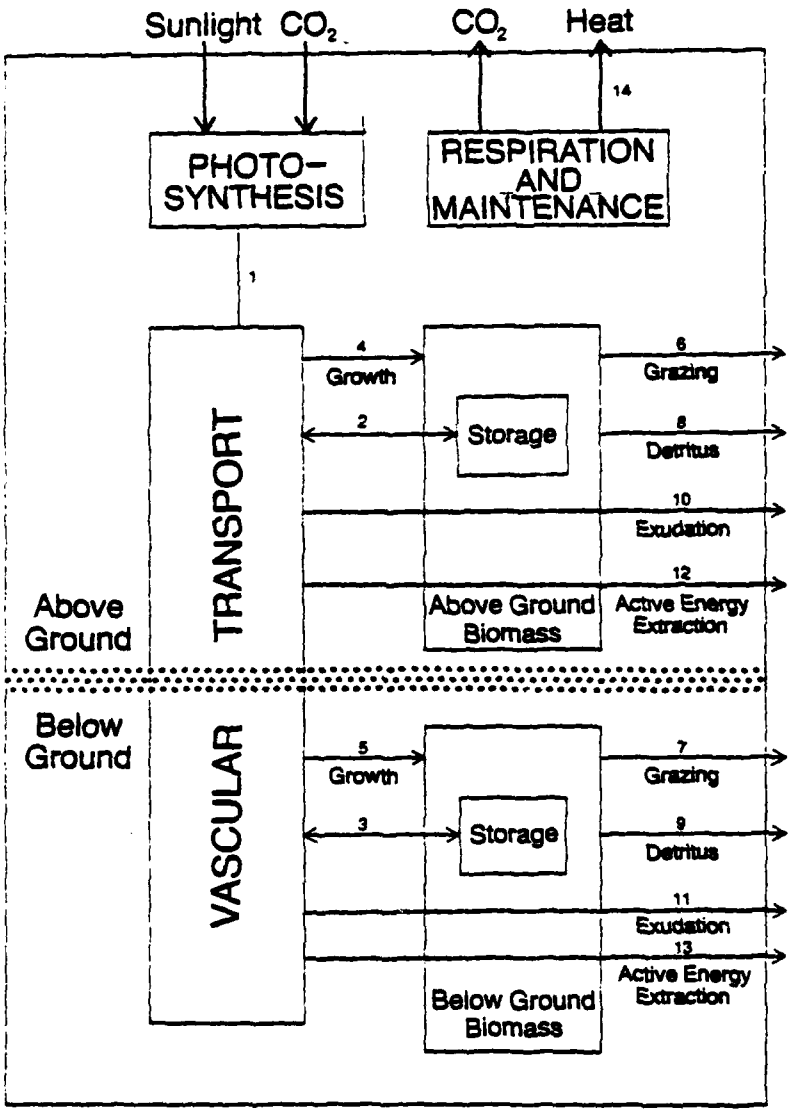
Quality as well as quantity of energy is important in determining availability to specific heterotrophic components. As reviewed by Swift et al. (1979), resource quality varies with: (1) chemical form of the energy source (whether sugar or cellulose, for example), (2) associated nutrients other than carbon, and (3) associated hormone-like substances, vitamins, antibiotics, etc. that stimulate or inhibit growth. Mycorrhizal fungi affect the quality of resources available as cellular plant biomass through the grazing and detritus pathways by affecting chemical composition of plants, plant species composition of the ecosystem, and by affecting partitioning of energy between components within individual plants. The quality of resources (fungal tissue and secretory products) distributed

through the mycorrhizal pathway is generally high. Composition varies with the mycobiont species involved.

The Plant Subsystem

Figure 3-1 is a box model of the plant subsystem, with four food chain outputs shown, two originating from plant biomass and two from the photosynthate in the vascular transport system. Above and belowground flows for each food chain are represented separately. Photosynthesis by vascular plants is the primary source of energy for most terrestrial ecosystems. Within the plant subsystem, photosynthesis captures sunlight and incorporates it in the carbon-carbon bonds of organic compounds which have a higher energy quality than sunlight. Flow 1 in Fig. 3-1 represents gross primary production or the total energy fixed by plants in photosynthesis. Photosynthetic products are converted to vascular transport molecules (principally sucrose, galactose, raffinose, stachyose or verbascose in trees; Kursanov, 1963) which are distributed and partitioned throughout the plant by the vascular system, primarily the phloem transport system. Some are stored within the plant biomass (flows 2 and 3) for future use. Biosynthesis of plant structure (flows 4 and 5) results in above and belowground biomass. This energy is eventually transferred to the heterotrophic portion of the ecosystem as cellular plant biomass by grazing (flows 6 and 7) or as detritus (flows 8 and 9). Some of the vascular photosynthate is transferred more directly to the heterotrophic portion of the ecosystem as soluble organic matter. Energy in the form of soluble organic matter is lost from the plant by exudation (flows 10 and 11) or is actively extracted by organisms such as aphids or mycorrhizae (flows

FIGURE 3-1. The Plant Subsystem


Sunlight
CO_2
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14
PHOTO-SYNTHESIS
RESPIRATION AND MAINTENANCE
1
TRANSPORT
4
Growth
2
Storage
6
Grazing
8
Detritus
10
Exudation
12
Active Energy Extraction
Above Ground
Above Ground Biomass
Below Ground
VASCULAR
5
Growth
3
Storage
7
Grazing
9
Detritus
11
Exudation
13
Active Energy Extraction
Below Ground Biomass

12 and 13. These latter flows are plant biomass for only the abbreviated time it takes to move through the plant.

The molecular rearrangement, energy transformations and work done in all of these plant processes result in the loss of energy as heat (Second Law of Thermodynamics). This loss of energy (flow 14) is commonly known as respiration and includes the energy cost of maintenance. Net primary production (NPP) is defined as gross primary production (flow 1) minus respiration and maintenance (flow 14). Alternatively, NPP is defined for a discrete time period as the change in biomass plus losses of energy-rich compounds from the plant subsystems (flows 6-13). Input to the heterotrophic portion of the ecosystem in any discrete time period is simply the sum of flows 6-13. What I have designated as the active energy extraction pathway (flows 12 and 13) is rarely considered or measured when net primary production is estimated; yet, as already noted, it may become a major flow when mycorrhizal structures are a functional component.

The Mycorrhizal Subsystem and its Effect on Production

Mycorrhizal fungi are a physical and functional intermediary between plant roots and the soil environment. Their ability to mitigate physical and chemical conditions in the soil directly affects the growth rate of plants and thereby affects the total amount of energy available for transfer from the plant subsystem to the grazing and detritus pathways. The effect on growth rate and survival ultimately affects plant species distribution. Since plant species have different growth rates, plant distribution also affects the total output of the plant subsystem. Likewise, plant species composition of the ecosystem affects quality of resources available to heterotrophic portions of the ecosystem.

Because of the obvious implications for food and fiber production, there is an extensive literature on plant response to both ectomycorrhizae (see for example, Harley, 1969; Mikola, 1970, 1973; Hacskaylo, 1971; Marks and Kozlowski, 1973; Marx, 1978) and VA mycorrhizae (see for example, Gerdemann, 1968; Harley, 1969; Hacskaylo, 1971; Mosse, 1973a; Sanders et al., 1974; Hayman, 1978). Most of the studies demonstrate that mycorrhizae increase general plant vigor, growth rate, and survival. In other words, benefits to plants more than compensate for loss of photosynthate extracted by mycorrhizae and resultant benefits vary with conditions in the soil environment, plant species, fungal species, and even strain of fungus (see Appendix 3).

Extrapolation of the results of experimental studies of mycorrhizal associations to natural systems requires great caution. Most of the available data on plant response comes from pot or controlled microplot studies which are not representative of conditions in natural systems. Even under those artificial conditions, relatively few phycobiont-mycobiont combinations have been studied in any detail. As of yet, even outplanting studies are short term as compared to the maturation time of woody plants. Therefore, the comparisons are relatively sound only for early developmental stages. Furthermore, the monoculture conditions of many experimental studies reduce the diversity of phycobionts and mycobionts found in natural systems. The mycorrhizal status of many naturally occurring fungal species is unknown or only suspected. The interconnectivity between plant and fungal species has rarely been addressed. Yet, some rather important implications for ecosystem energetics are evident.

First, there is little doubt that mycorrhizae are necessary for the survival, normal growth, and development of many plant species. As

Trappe and Fogel (1977) put it, "In nature, most woody plants require mycorrhizae to survive and most herbaceous plants need them to thrive."

Secondly, it has long been realized that plant species have different physiological requirements which result in the community composition associated with specific physiochemical environments. It appears that very specialized phycobiont-mycobiont (i.e., mutualont) combinations provide the adaptations required for existence in many natural environments. The combination of two or more separate genomes determines the growth rate of the mutualont in any given set of environmental conditions. Accordingly, some of the observed differences in plant requirements for nutrients and other environmental factors are likely to be a function of the mutualistically associated fungal genome or genomes. Adaptation to physical environments which are variable in space and time (succession) requires that two or more separate germ cells be appropriately distributed and coevolved in space and time. Competition between fungal symbionts may account for some of the observed phenomena formerly thought to be due to competition solely as a result of differences in plant genomes. Many aspects of the role of mycorrhizal fungi as mutualistic partners with plants raise interesting, unaddressed questions for plant physiologists, ecological geneticists, population and community ecologists. However, even limited research results so far accomplished leave little doubt that mycorrhizal fungi directly affect the growth rate and distribution of plants and thereby affect the output from the plant subsystem.

A Four-Pathway Food Chain Model

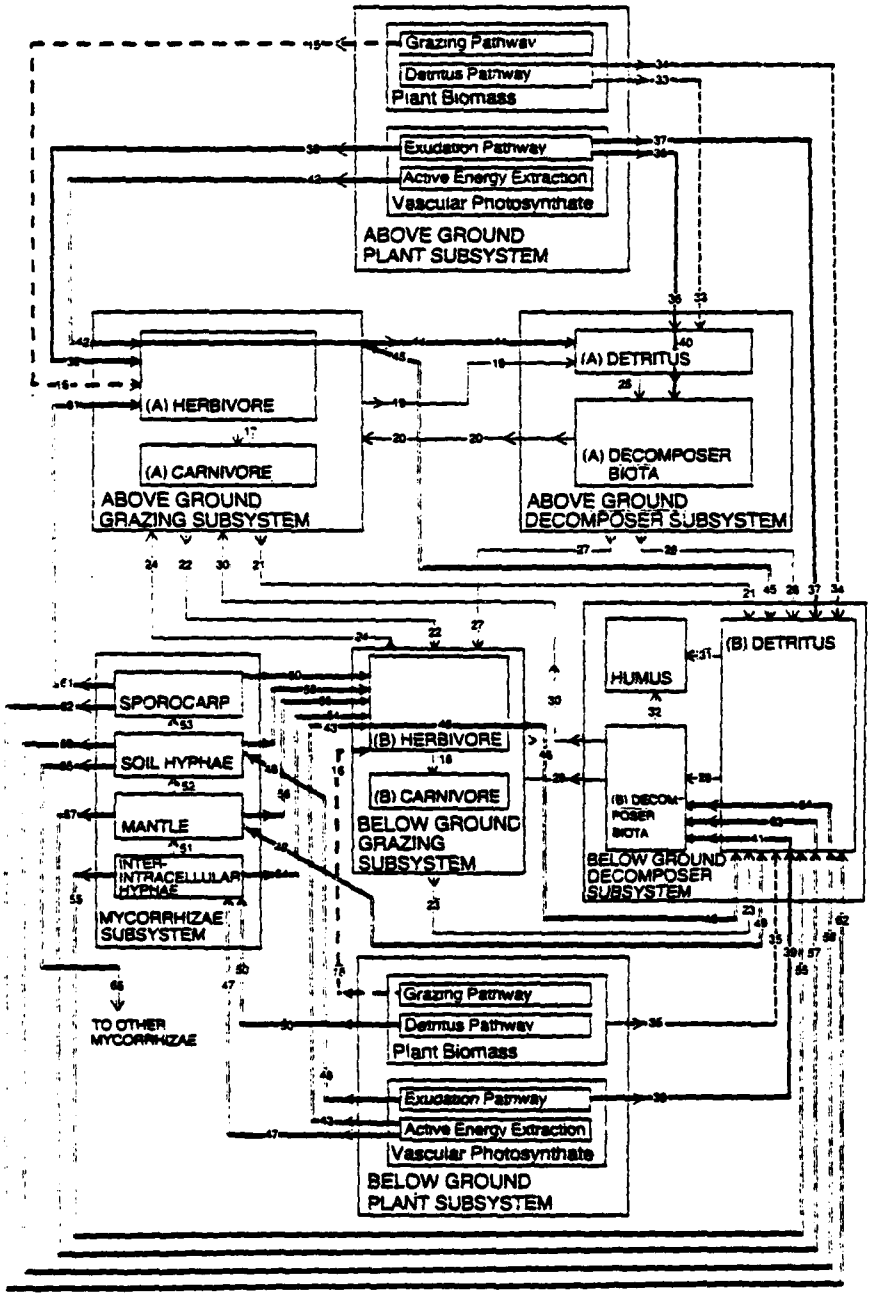
As already noted, it is traditional to diagram food chains in terms of two parallel pathways, the grazing and detrital flows which primarily originate from cellular plant biomass, see, for example Odum's (1971) text book. In Figure 3-2, the flows originating from above and belowground vascular photosynthate, namely, exudate and extraction pathways, are diagrammed along with grazing and detrital pathways. The mycorrhizal subsystem is depicted as a major terrestrial ecosystem component along with the plant, grazing and detrital subsystems. The model serves to emphasize the high degree of interconnectiveness of mycorrhizae with all other pathways and the importance of this heretheto little recognized energy flow pathway.

The Mycorrhizal Subsystem and Its Effect on Energy Distribution Through Cellular Plant Biomass

The grazing and detritus pathways diagrammed in Figure 3-2 are briefly described in Appendix 4. The quality and quantity of plant biomass available to heterotrophs through the various grazing and detritus pathways are dependent on the plant species composition of the ecosystem. Insofar as mycorrhizal fungi affect plant growth rate, survival, and distribution they affect the quality and quantity of resources available through cellular plant biomass pathways.

Mycorrhizae also affect partitioning to the pathways within a plant species by affecting the morphology of individual plants. Mycorrhizae are known to increase root development and thus change the root to shoot ratios (Marks and Foster, 1973), thereby modifying the partitioning of energy between above and belowground food chains. The effect may be the

FIGURE 3-2. Pathways of Energy Flow in the Ecosystem. Flows through the grazing (flows 15, 16; — — —) and detritus (flows 33-35; ——— —) pathways are described in Appendix 4. Effects of mycorrhizae on these pathways is discussed in the text. Flows 17-32 are interchanges of energy between heterotrophs which are common for all pathways. Flows through the exudation pathway (36, 41 ——————) are discussed in the text starting on pg. 26. The active energy extraction pathway, (═══) including aphid (flows 42-45) an mycorrhizae flows 46-65) mediated energy transfer are discussed in the text starting on pg. 27.


Grazing Pathway
Detritus Pathway
Plant Biomass
Exudation Pathway
Active Energy Extraction
Vascular Photosynthate
ABOVE GROUND
PLANT SUBSYSTEM
(A) HERBIVORE
(A) CARNIVORE
ABOVE GROUND
GRAZING SUBSYSTEM
(A) DETRITUS
(A) DECOMPOSER
BIOTA
ABOVE GROUND
DECOMPOSER SUBSYSTEM
HUMUS
(B) DETRITUS
SPOROCARP
SOIL HYPHAE
MANTLE
INTER-
INTRACELLULAR
HYPHAE
MYCORRHIZAE
SUBSYSTEM
(B) HERBIVORE
(B) CARNIVORE
BELOW GROUND
GRAZING
SUBSYSTEM
(B) DECOM-
POSER
BIOTA
BELOW GROUND
DECOMPOSER
SUBSYSTEM
TO OTHER
MYCORRHIZAE
Grazing Pathway
Detritus Pathway
Plant Biomass
Exudation Pathway
Active Energy Extraction
Vascular Photosynthate
BELOW GROUND
PLANT SUBSYSTEM

result of fungal production of auxins, cytokinins, gibberellins, and vitamins which affect the interaction between fungus and host (Moser, 1959; Bowen, 1973; Slankis, 1973). The hormones from fungal origin are homologous with those formed endogenously by the plants. The kinds and amounts vary between fungal species (Moser, 1959; Shemankhanova, 1962; Horak, 1963; Slankis, 1973; Crafts and Miller, 1974) and between varieties of a single fungal species (Moser, 1959).

Fungal hormones affect the growth rate of short and long roots; for example, they induce the typical dichotomous branching in pine root systems. Application of filtered extracts of fungi simulates mycorrhizal root structures and produces plant responses similar to infection with mycorrhizal fungi, namely, increased vigor, increased growth rate, and better color. Such hormone extracts increase root to shoot ratio as do mycorrhizal infections. Extracts from various fungal species differentially affect the roots of normal host and non-host plant species. In short, in addition to enhancing mineral uptake by the plant, hormonal influences by mycorrhizal fungi affect directly the growth form of plant species, and differentially affect the growth rate of roots and shoots.

Mycorrhizal fungi have been shown to alter what Swift et al. (1979) call resource quality within a plant species. Comparisons of mycorrhizal and non-mycorrhizal plants invariably reveal differences in the concentrations of inorganic nutrients, particularly phosphorus (i.e., Bowen and Theodorou, 1967) and nitrogen (i.e., Hatch, 1937). Krupa et al. (1973) demonstrated increased levels of such fungal products as glutamic acid and glutamine in ectomycorrhizal roots. Marx and Davey (1969) have found the antibiotics diatretyne nitrile and diatretyne-3 in the short roots of mycorrhizal pines. Since the fungal symbionts produce these

antibiotics in pure culture and non-mycorrhizal pines do not contain them, it is assumed that they are a product of the mycobiont. Colonization of roots by mycorrhizal fungi results in production and accumulation of volatile terpenes and sesquiterpenes in concentrations up to eight times greater than that found in non-mycorrhizal roots (Hillis and Ishikura, 1969; Krupa and Fries, 1971). Krywolap et al. (1964) and Grand and Ward (1969) have extracted from foliage of pines an antibiotic produced by the mycobiont Cennococcum graniforme.

The Exudation Pathway

Energy bearing compounds exudated aboveground are utilized either in the phyllosphere (flow 36) or in the soil column (flow 37). Use in the soil column is probably restricted to the surface layers because the sugars and other carbon materials are quickly available to microbes. Aboveground exudate input to the soil is spatially restricted to the circumference of the crown (stemflow and throughfall). Temporally the input is limited to the active growth periods for plants which occur during the summer months in temperate climates.

Nectar production is akin to exudation. Energy transferred to nectar feeders (flow 38) results in distributions similar to the grazing pathway.

Belowground exudation (flow 39) results in energy rich microsites throughout the range of root penetration in the soil column. Much of the well documented rhizosphere effect on soil populations is due to exudation (Balandreau and Knowles, 1978; Hale et al., 1978). Temporal distribution of exudates is dependent on plant species, conditions in the soil environment, and climate (Hale et al., 1978). Root exudation

from stored carbon reserves continues during early spring and late fall, when photosynthesis is not occurring.

Spatial and temporal linkage between plants and heterotrophs through the exudation pathway (flows 40, 41) is so tight that the microflora affect the rate of exudation. To that extent the exudation pathway is similar to active energy extraction since energy bearing compounds are never structurally part of the detritus pool.

The affect of mycorrhizal fungi on root exudation is uninvestigated. Exudation rate and above to belowground partitioning varies with plant species and nutritional status of the plant (Hale, 1978). To the extent that mycorrhizal fungi affect plant species composition of the system, morphological development of root systems and nutritional status of the plants they undoubtedly also affect energy distribution through the exudate pathway.

The Active Energy Extraction Pathway

(1) Sucking Insects. Energy extracted from the plant vascular system by above and belowground sucking insects (flows 42, 43) is transferred to the ecosystem in two forms - insect bodies and honey dew. Insect bodies distribute energy like the grazing chain. Carbon compounds which pass directly through the gut, and which are excreted as honey dew are distributed to the aboveground (flow 44) and belowground (flows 45, 46) decomposition subsystems, in similar manner as energy flow through the exudation pathway. Sucking insects are limited temporally to the seasons when there is active vascular transport, primarily while there is active photosynthesis. Transport by this mechanism could continue beyond leaf drop as long as plant storage reserves are sufficient.

(2) Mycorrhizal Fungi. Mycorrhizal fungi, by their effect on plant growth rate, survival, and development (morphology) affect the spatial and temporal distribution of energy through the grazing, detritus, and exudation pathways, but more importantly, they constitute a unique pathway for energy distribution.

Like all organisms, mycorrhizal fungi acquire energy, use energy in growth, respiration and maintenance, and serve as an energy source for other organisms. Mycorrhizal fungi as a group acquire energy from four sources - active energy extraction from the plant vascular system, plant root exudates, decomposition of detritus, and necrosis of living plant material.

Mycorrhizal fungi grown in pure culture can use simple carbohydrates including those exudated by plant roots (Hacskaylo, 1973; Hale et al., 1978). It is assumed that mantle and soil hyphae can utilize plant exudate carbohydrates from the rhizosphere (flow 48). This flow is likely to be of limited importance due to competition with bacteria which have much higher metabolic and reproductive rates.

The capacity of mycorrhizal fungi to produce enzymes such as cellulase, chitinase, lignase, pectinase, etc., which allow access to the less decomposable detritus (flow 49) varies greatly between fungal species (Theodorou, 1968; Laiho, 1970; Bowen, 1973; Hacskaylo, 1973; Lamb, 1974). Orchidaceous fungal species may rely heavily on such decomposition products (Smith, 1966; Hadley, 1969). They may even cause necrosis of host plant material (Alconero, 1969; Williams and Hadley, 1970) in what appears to be a tenuous balance between mutualism and parasitism. There are examples of ectomycorrhizal species which in pure culture produce decomposer enzymes (Young, 1947; Norkrans, 1950; Rawald, 1962; Ritter,

1964). Even in these species there is little indication of cellular disruption in the plant tissue of ectomycorrhiza. Norkrans (1950) suggested that cellulytic activity of the fungus is repressed in the presence of plant vascular photosynthate. Hacskaylo (1973) concluded that "In nature, ectomycorrhizal fungi depend primarily upon the roots of their hosts for carbohydrates, usually sucrose, glucose, and fructose. Certain species may, however, possess enzymes to hydrolyze cellulose and other complex carbohydrates, but this characteristic does not appear to be widespread." The case for VA mycorrhizae is similar (Hayman, 1978). The primary energy source, except for some orchidaceous mycorrhizae, is active energy extraction (flow 47) from the vascular system of plants (Melin and Nilsson, 1957; Shiroya et al., 1962; Lewis and Harley, 1965c; Harley, 1969; Wedding and Harley, 1976). The fungi remove vascular photosynthates from the plant and convert them to forms (e.g., mannitol and glycogen) which are not enzymatically accessible by plants (Lewis and Harley, 1965a,b,c).

Mycorrhizae are adapted to receive a carbon supply directly from the vascular transport products of photosynthesis in plants, rather than primarily or solely from dead tissue or by ingestion of cellular plant biomass. Thus, the mycorrhizal fungi constitute what Harley (1971) calls an energy "short-circuit" from photosynthate to heterotroph. Carbon compounds converted to fungal structures ultimately support a population of mycovores in the grazing chain or are contributed to soil detritus and support the decomposer pathway. Soil hyphae that form continuous cytoplasmic strands may constitute an additional short-circuit or shunt of energy. Energy-rich carbon compounds need not be converted to fungal

cellular structure to be directly available to soil organisms by way of hyphal "pipelines."

Mycorrhizal fungi do not fit the classical trophic role accorded the kingdom fungi, since they are neither pathogens nor decomposers, but mutualistic partners with vascular plants. Therefore, mycorrhizae do not fit into traditional models of ecosystem energy flow. For example, Odum (1971) divides ecosystem biotic components into: (1) "Producers, autotrophic organisms, largely green plants, which are able to manufacture food from simple inorganic substances;" (2) "Macroconsumers or phagotrophs (Phage = to eat), heterotrophic organisms, chiefly animals which ingest other organisms or particulate matter;" (3) "Microconsumers, saprotrophs (sapro= to decompose), or osmotrophs (osmo = to pass through a membrane), heterotrophic organisms, chiefly bacteria and fungi, which break down the complex compounds of dead protoplasm, absorb some of the decomposition products, and release inorganic nutrients that are useable by the producer together with organic substances, which may provide energy sources or which may be inhibitory or stimulatory to other biotic components of the ecosystem." Mycorrhizae certainly do not belong in category 1 or 2; and although they are "osmotrophs" they do not acquire energy by the breakdown of dead protoplasm. They are not parasites, pathogens, grazers, predators, or decomposers, but they are microconsumers that acquire their energy at the same energy level as non-photosynthesizing cells in green plants. In fact, one could consider them as part of the plant even though genetically and developmentally they have a separate origin.

Carbohydrate acquired from plant roots is passed from intercellular hyphae to mantle hyphae (flow 51) to soil hyphae (flow 52) to sporocarps

(flow 53). Energy is transferred to other ecosystem components in two forms - fungal biomass and fungal exudate.

Spatial distribution of inter- and intracellular hyphae is limited to distribution of fine roots in the soil. Energy in these hyphae is transferred to herbivores when fine roots are eaten (flow 54), or is transferred to the belowground decomposer subsystem when the fungi and fine roots senesce (flow 55).

Spatial distribution of mantle hyphae is limited to the surface of infected root tips in the top 3 m of soil. Mycorrhizal roots have extensive branching as compared to nonmycorrhizal roots (Zak, 1973).

Gobl (1965) found that the number of whole mycorrhizae in the A_F horizon ranged from 0 to 8,800/100 ml soil; A_H, 3,600 to 16,600; and B, 30 to 1,650. The profuse branching of individual mycorrhiza results in extensive distribution through the soil column. Interroot distances at the tap root are much shorter in mycorrhizal roots than in nonmycorrhizal roots (2.1 mm vs. 1.1 cm, Bowen, 1968). Therefore, input of both plant and fungal mantle biomass to the soil volume is more pervasive in mycorrhizal roots. Mantle biomass is fed on by mycovores (flow 56), or upon death is contributed to the belowground decomposer subsystem (flow 57).

Soil hyphae (including mycelial strands and rhizomorphs) penetrate the soil column for distances of up to at least 4 m beyond the area of root penetration (Schramm, 1966). As would be expected, distance of penetration varies with soil conditions (Skinner and Bowen, 1974). Extensive branching by mycelial strands, and individual hyphae growing into the soil along their length, result in profuse distribution of soil hyphae throughout the soil volume (see Bowen, 1973). The hyphae serve

as an energy source for mycovores (flow 58) and decomposers (flow 59) throughout the soil column.

Sporocarps may be hypogeous or epigeous. Their distribution is limited to the area of penetration of soil hyphae. Vertical distribution is species specific. Hypogeous sporocarps provide energy to belowground herbivores (flow 60) and belowground detritus (flow 62). There is also extensive harvesting of some hypogeous fungal species by aboveground herbivores (flow 61), such as e.g. squirrels. Epigeous sporocarps provide energy to aboveground herbivores (flow 61) and to belowground detritus (flow 62). Epigeous sporocarps enter belowground detritus pools in the same manner as plant detritus.

Each fungal species provides a short term pulse of energy to the grazing and detritus food chain in the form of sporocarps. Seasonal production of sporocarps is fungal species specific. Thacker's (1971) study of epigeous sporocarp production on a 70 year old hardwood-pine forest illustrates the variation in temporal distribution by fungal species (Table 3-1), while temporal distribution of sporocarp production varies as a function of forest type and maturity, as shown in Figures 3-3 and 3-4. Although species specific pulses of fungal sporocarps occur throughout the year, the major input of sporocarps is from late August to December. Sporocarp production also varies with climatic and soil conditions (Hora, 1959). Large sporocarps are produced very rapidly, sometimes literally overnight. Perennial mycelium are collecting and storing energy which is rapidly transformed to reproductive structures when suitable environmental conditions occur. In this regard, mycorrhizal fungi act as a capacitor for ecosystem functions driven by energy derived from sporocarps. Since sporocarps production is seasonal, they

TABLE 3-1. Epigeous sporocarp production in a 70 year old mixed pine-hardwood stand, by fungal species. Values are in grams/404m^2.

See Fig. 3-4 for site description. (Thacker, 1971)

Fungi	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Total
AGARICUS													
placomyces						44.8							44.8
sylvicola					156.1	23.0							179.1
unknown					.6	7.4							*8.0*
AMANITA													
brunnescens						190.7	17.9						208.6
caesarea					213.2	183.5							396.7
citrina							28.7	11.2					39.9
gemmata						6.0							6.0
muscaria					20.4								20.4
rubescens						33.8	7.9						41.7
solitaria					382.8	881.5	5.7						1270.0
verna						16.9							16.9
unknown					22.5	46.3	20.0						88.8
AMANITOPSIS													
unknown							29.2						29.2
AURICULARIA													
auricula											138.5	24.2	162.7
ARMILLARIA													
unknown							1.2						1.2
BOLETUS													
bicolor						62.2							62.2
luridus			37.7				13.8						51.5
luteus						210.6	73.0						*283.6*
unknown					210.6	207.3	245.4						662.7
CANTHARELLUS													
cinnabarinus						9.4							9.4
CLAVARIA													
pistillaris						35.8							35.8
unknown						137.1	11.5						148.6

TABLE 3-1 continued.

Fungi	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Total
CLITOCYBE													
unknown			.6			188.9	8.3	5.6					203.4
COLLYBIA													
dryophila					2.5								2.5
radicata					3.1	13.9							17.0
unknown		.1			13.3	449.4	108.8	3.7	27.7	7.6			610.6
CORTINARIUS													
unknown						471.5	132.6						604.1
ENTOLOMA													
strictius						11.3							11.3
unknown					2.6								2.6
EXIDIA													
glandulosa		2.6											2.6
FAVOLUS													
unknown	1.7												1.7
GRASTRUM													
unknown						20.0	22.0	.5					42.5
GOMPHIDIUS													
unknown								7.0					7.0
HELOTIUM													
unknown			5.4										5.4
HYGROPHORUS													
unknown						1.4	16.0	3.2	18.1				38.7
LACCARIA													
laccata						31.6	.3						31.9
unknown							.7						.7

TABLE 3-1 continued.

Fungi	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Total
LACTARIUS													
gerardii						7.6							7.6
lignyotus						127.1							127.1
piperatus						6.4							6.4
speciosus					4.5	4.8							9.3
volemus			10.6			29.0	17.2						56.6
unknown						253.3	69.4						322.7
LEOITA													
unknown			7.2			26.3							33.5
LEPIOTA													
unknown				52.3	2.7	13.4							68.4
LEPTONIA													
unknown						24.5							24.5
LYCOPERDON													
peckii					10.0	3.0							13.0
unknown					.2	16.5	6.9	2.4					26.0
MARASMIUS													
candidus					1.9								1.9
siccus					4.3	110.7	29.1	5.0					149.1
unknown		.1			.1	9.4	3.6		23.2	7.0			43.4
MUTINUS													
ravenelii						5.0							5.0
unknown						4.0							4.0
MYCENA													
unknown						.2		.4					.6
NOLANEA													
unknown						6.6			.9				7.5
PEZIZA													
unknown			117.8										117.8

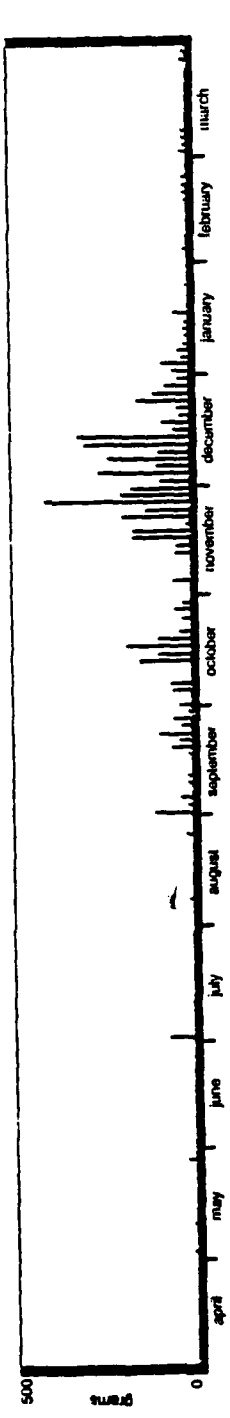
TABLE 3-1 continued.

Fungi	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Total
PLUTEUS													
cervinus						14.9							14.9
unknown									30.0	22.8			52.8
RUSSULA													
compacta						156.3							156.3
densifolia						4.8							4.8
emetica					24.0	776.2	69.6	21.1					890.9
foetens					11.7								11.7
fragilis		18.8	18.4		8.5	14.2	10.8						70.7
virescens						62.2							62.2
unknown					1.0	1487.3	258.8						1747.1
SCLERODERMA													
unknown						.6							.6
STROBILOMYCES													
strobilaceus						123.0							123.0
unknown						16.2	11.0						27.2
TREMELLA													
unknown		3.8				.7							4.5
TRICHOLOMA													
flavobrunneum								.8					.8
portentosum								.5	40.5				41.0
unknown						24.0	15.1	24.4					64.5
URNULA													
crateriun	15.9												15.9
UNKNOWN													
unknown		5.0	2.8		.4	248.3	60.2	3.6	7.1	.6			328.0
TOTAL	17.6	30.4	200.3	52.3	1096.4	6860.8	1294.7	90.4	147.5	38.0	138.5	24.2	9991.1

FIGURE 3-3. Epigeous sporocarp production in a 25 year old loblolly pine stand and in a 70 year old short leaf pine stand.

(A) 25 year old loblolly pine (*Pinus taeda*) stand; understory --wild plum (*Prunus* sp.), persimmon (*Diospyros virginiana*) and crataegus (*Crataegus* sp.); ground cover--mostly pine litter with sparce patches of honeysuckle (*Lonicera japonica*); soil--previously cultivated Madison sandy loam.

(B) 70 year old short leaf pine (*Pinus enchinata*); understory --scattered oak (*Quercus velutina*), wild plum (*Prunus* sp.) and wild cherry (*Prunus scrotina*); ground cover--mostly pine litter, hardwood litter near hardwoods, sparce patches of honeysuckle (*Lonicera japonica*); soil-previously cultivated Madison gravelly sandy loam (Thacker, 1971).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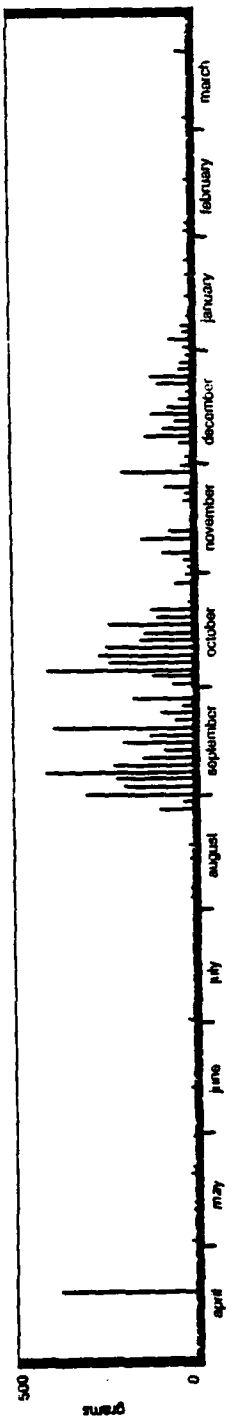
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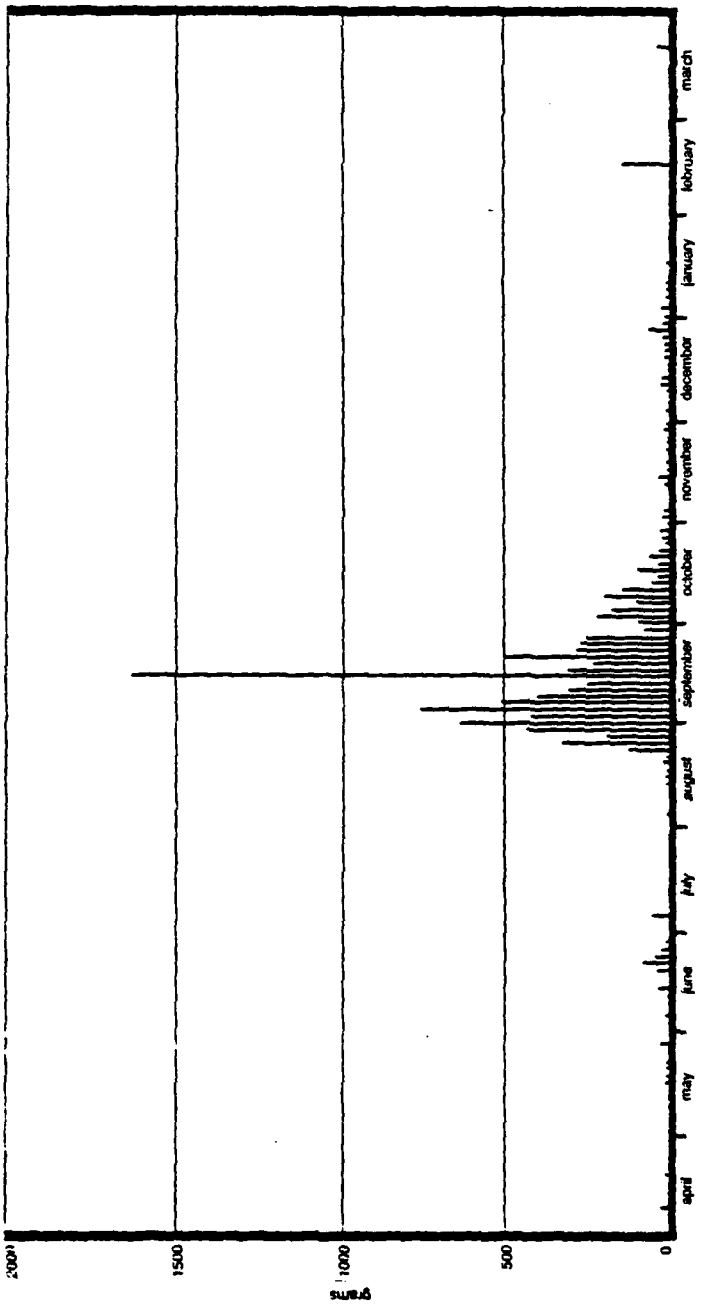
FIGURE 3-4. Epigeous Sporocarp Production in a seventy year old mixed hardwood-pine stand. Bars represent every other day collections on 20, 20.1m^2 plots (404m^2). Principal species --red oak (Quercus falcata), white oak (Quercus alba) and short leaf pine (Pinus enchinata); understory--dogwood (Cornus florida), winged elm (Ulmas alata) and wild cherry; ground cover--mostly hardwood litter with pine or pine-hardwood litter near pines, scattered patches of honeysuckle (Lonicera japonica); soil--cecil sandy loam and cecil clay loam, not previously cultivated (Thacker, 1971).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november
december
january
february
march

provide relatively large masses of temporally short term energy sources as compared to the other mycorrhizal structures.

Soil hyphae and mantle hyphae transfer energy to the belowground ecosystem as exudate (flows 57, 59). As a result, the area surrounding the mantle and hyphae (the mycorrhizosphere) has a rich source of relatively low molecular weight carbon compounds (Rambelli, 1973). The mycorrhizosphere may include a very large portion of the upper 1-3 m of soil volume (Meyer, 1973; Konoe, 1962). The large number of mycorrhizal root tips, with their profuse branching, results in a very large surface area for fungal exudation (see Bowen, 1973). Burgess and Nicholas (1961) estimated that a single millimeter of soil can contain as much as 4 m of hyphae. Bowen et al. (1975) calculated that 1 mg of hyphae of 10 μm diameter had the same length as 1600 mg of root of 400 μm diameter. Harley (1971) estimates that 1 gm dry wt. of hyphae would have 4.2 m^2 of surface area. There are no available measures of total surface area of mantle and hyphae in natural soils. However, there is no doubt that the mycorrhizosphere makes up an appreciable proportion of the soil volume.

As with the delivery of plant exudates (flows 40, 41) to rhizosphere and phyllosphere organisms, fungal exudates may be delivered directly to mycorrhizosphere biota (flows 63, 64) such that the energy rich carbon compounds never become part of the detritus pool.

Photosynthate which travels from the plant vascular system to hyphal secretion are roughly equivalent to direct plant secretion. Organisms which depend directly on plant and fungal secretion may not be very different from heterotrophic plant cells in terms of trophic position, but in terms of food chains they would be classed as primary consumers.

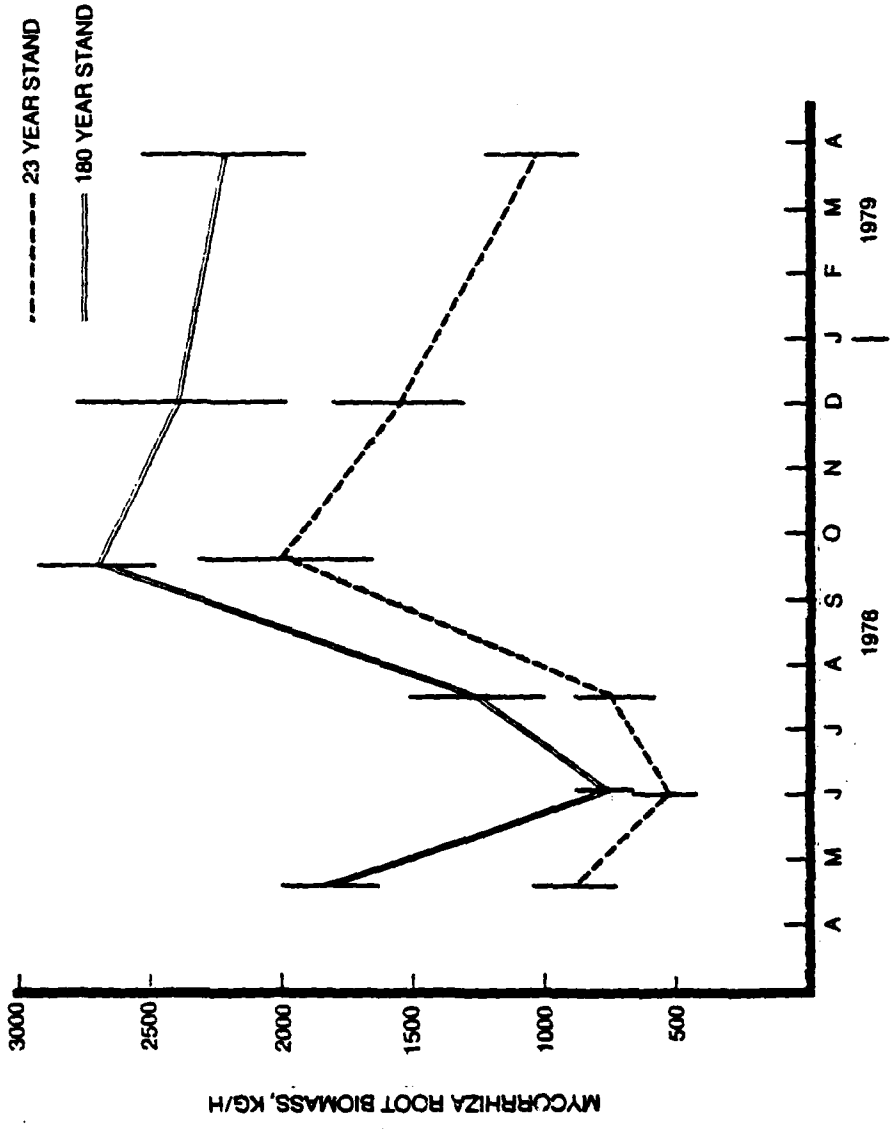
The mycorrhiza energy pathway results in temporal and spatial distributions of energy which are distinct from the grazing or detritus pathways (compare with Appendix 4). It provides energy resources of high quality to soil organisms, and in the case of epigeous sporocarps, also to aboveground consumers.

Temporal distribution of energy by the mycorrhizal pathway is even less well understood than spatial distribution. Observations are limited to measures of standing crop biomass. Except for sporocarps, there are yet no measures of turnover rate.

Temporal distribution of inter- and intracellular hyphae, and mantle can be assumed to be correlated with temporal distribution of mycorrhizal root tips (mycorrhiza). Number of mycorrhiza varies with tree species (Marks and Foster, 1973; Zak, 1973), fungal species (Marks and Foster, 1973; Zak, 1973), soil environment (Bowen, 1968), and season (Twaroski, 1963; Harvey et al., 1978; Fogel and Hunt, 1979).

Vogt et al. (1980) studied seasonal distribution of mycorrhiza in 23 and 180 year old Pacific silver fir stands in western Washington (Fig. 3-5). Both stands had maximal mycorrhizal root biomass in late September with a general decline from September to June, and increase from June to September. The 180 year old stand had significantly higher mycorrhizal root biomass than the 23 year old stand except when biomass was at a very low level in both stands. Proportion of fine roots which were mycorrhizal also varied with season. Temporal distribution of flow of biomass through the mycorrhizal pathway is unknown because turnover rate is unknown. Decreases in standing crop biomass of mycorrhizae from September to June (Vogt et al., 1980) does suggest seasonal growth followed by a dieback.

FIGURE 3-5. Seasonal distribution of mycorrhiza in 23 and 180 year old Pacific silver fir (Abies amabilis) stands. The young stand was almost entirely Pacific silver fir. The old stand was 80-85% silver fir associated with Tsuga mertensiana, Tsuga heterophylla. Common understory shrubs were Vaccinium ovalifolium, Vaccinium membranaceum, and Sorbus sitchensis. Ground cover species were Xerophyllum tenex, Clintonia uniflora, Cornus candensis, Rubus pedatus, Tiarella unifoliata, and Achyls triphylla (Vogt et al., 1980).


23 YEAR STAND
180 YEAR STAND
MYCORRHIZA ROOT BIOMASS, KG/H
3000
2500
2000
1500
1000
500
A M J J A S O N D J F M A
1978
1979

Nonmycorrhizal root hairs and short roots are known to have very short functional lives (rapid turnover rates). In contrast, mycorrhizal root tips have longevities ranging from several months to three or more years according to Harley (1969). Thus, mycorrhizae may temporarily delay the transfer of both plant root and fungal biomass to the decomposition subsystem. At the same time they may result in continuous availability to grazers and decomposers (sluffed cells and exudate) in a localized area.

Growth rate of soil hyphae and exudation production by mantle and soil hyphae are probably determined by carbohydrate availability in the phycobiont. Studies of carbohydrate translocation to roots have shown general seasonal patterns of carbon allocation (Nelson, 1964; Shiroya et al., 1966; Gordon and Larson, 1968; Schier, 1970; Ziemer, 1971; Ursino and Paul, 1973; Webb, 1977). Carbon is allocated to root growth prior to bud break in the early spring (Gordon and Larson, 1968). Carbon flow to developing buds and leaves reduces flow to roots (Gordon and Larson, 1968). As new leaves become a source of carbohydrate, translocation to roots resumes. Climatic conditions in the fall decrease (conifers) or terminate (deciduous plants) photosynthetic output. Translocation to the root system is restricted. Flow rates to belowground structures in the late fall, winter, and early spring are dependent on the availability of carbohydrates stored in plant roots; and on conditions in the soil environment. Species specific differences in fungal physiology (temperature requirements, etc.) probably result in a range of temporal distributions of energy as fungal biomass and fungal exudate throughout the year. The affect of energy storage by the fungi (e.g., glycogen) on growth rate and exudation is unknown.

The carbon products of photosynthesis routed through the mycorrhizal shunt never become cellular plant structure so that energy moving through this pathway is not accounted for when biomass increments are used to measure net primary production. The shunt of energy also escapes measurement in methods of measuring detrital input to the belowground ecosystem. Transport and turnover rates are so high that even radioactive carbon dioxide pulse tagging of photosynthetic products would not measure the flow unless sampling ensued at least within hours.

Obvious carbon inputs to the soil, namely, plant litter, excretion and secretion from the grazing chain are often inadequate to account for the rate of CO_2 release from the soil and the maintenance of the observed biomass of the soil organisms (Gray and Williams, 1971). Even including estimates of plant root exudates is insufficient to balance the energy budget (Barber and Gunn, 1974). Carbon input to the soil through the mycorrhizae pathway could account for the discrepancy.

Interspecific Transfers

Energy flow from mycorrhiza to external hyphae of other mycorrhiza (Fig. 3-2, flow 65) requires that the mycobiont be able to remove carbohydrates from one phycobiont and then release it to a second. Little is known about the effect of this flow on spatial and temporal distribution of energy in ecosystems. The potential for one plant to derive photosynthate from other plants raises some interesting questions in regard to shade tolerance, relationships between understory and dominant plant species, and mechanisms of replacement over successional time.

Interspecific flow is best understood in orchidaceous mycorrhizae. Some orchids can be raised in pure culture under laboratory conditions,

but in nature they all obtain their carbon supplies for early development from fungal symbionts that derive their energy directly from vascular plants or from detritus (Harvais and Hadley, 1967; Harley, 1969). In adult stages orchids form a series from obligate saprophytes to green orchids which are self-sufficient for carbon. Infection by mycorrhizae is common in saprophytic orchids, whereas green orchids may be almost uninfected in adult stages. Translocation of nutrients through the fungal hyphae is well documented (e.g., Smith, 1966, 1967).

Mycobiont-orchid mutualonts derive their energy source from either (1) decaying matter (Saprophytism) or (2) tree branches (Epiparasitism). The common mycobionts Rhizoctonia solani and Armillaria mellea can utilize cellulose and lignin (Smith, 1966). Many symbionts in this group are purely saprophytic (Harley, 1969). On the other hand, Gastrodia minor is epiparasitic on Leptospemum scoparium (Campbell, 1963). The mycobiont is non-pathogenic in G. minor but causes cortical damage in L. scoparium. The two major orchidaceous mycobionts, Armillaria mellea and Rhizoctonia solani, are species well known for their pathogenicity on many higher plants. The balance between parasitism and mutualism between the mycobiont and orchids is tenuous. In some cases the fungus may parasitize and kill the plant, in others the plant may digest and eliminate the fungus (Williams and Hadley, 1970).

Plants in the Ericales form a series from vigorous plants such as Rhododendron to less vigorous Pyrolaceae to achlorphyllous Monotropa (Henderson, 1919). Increased saprophytism and increased development of mycorrhiza characterizes this series (Hayman, 1978). Björkman (1960) has isolated mycorrhiza from Monotropa roots and synthesized mycorrhiza in pine culture. He also injected C^{14}-labelled glucose into conifers

and later detected the label in adjacent saprophytic plants of Monotropa hypopithys. He believes that M. hypopithys derives its nutrients from another plant with which it shares a common mycorrhizal fungus.

Fungal linkage between plant roots may be common. Most of the available studies suggest an epiparasitic relationship; possibly because work with orchidaceous mycorrhizae predominates such studies. It is easy to conceive three-way, mutually beneficial relationships where two plants benefit nutritionally from each other via a common mycobiont. Mycobionts and maybe the phycobionts could benefit from temporally separated photosynthesis in the phycobionts (e.g., an early season and a late season, or an understory and dominant plant in a deciduous forest linked by a common fungus). Is it possible that one plant species may be able to replace another simply by having better control of a common mycobiont, and thus better access to inorganic and organic nutrients? This area certainly deserves more attention from plant physiologists and ecologists.

Efficiency of Energy Transfer

Lindeman (1942) provided the first formal presentation of the idea that an ecosystem could be represented as a trophic pyramid or food web. Since then there has been great interest in trophic transfer or ecological efficiencies (see, for example, a review by Kozlovsky, 1968). Ecological efficiency has customarily been defined as the fraction of the energy ingested by a population that is passed on to the next trophic level (Kozlovsky, 1968; Turner, 1970). This definition is of little use for comparing the four major pathways of energy distribution. Gross primary production per se has little direct importance to the heterotrophs of an ecosystem since only potential energy in the form of chemical bonds left

over after plant activity (i.e., net primary production) is available to heterotrophs. Likewise, net primary production per se has little importance to a specific organism or process in an ecosystem since only the net energy delivered to that organism or process is of consequence to that organism. The important efficiency in ecosystem flow is the efficiency of transfer of the direct products of photosynthesis to specific organisms and therefore ecosystem processes.

Energy flow through the grazing and detritus pathways involves biochemical transformation of photosynthate to cellular biomass within the plant prior to export from the plant subsystem. Protoplasmic incorporation results in energy loss for respiration and maintenance. Efficiency of transfer from one trophic level to another that involves a photoplasmic incorporation, ranges from 5 to 15% (Wiegert, 1964). Ten percent efficiency (90% loss) is used as a general rule of thumb for transfer of energy from autotrophs to heterotrophs (Odum, 1971). As shown in Fig. 3-2, there are a large number of potential autotroph-heterotroph pathways that do not involve co : of conversion to plant tissue. For example, nitrogen fixation (N-fixing bacteria) can be driven by plant transport photosynthate in root nodules without an intervening protoplasmic incorporation. Energy provided by exudation directly to soil bacteria (flows 36→40 or 39→41 or 39→28 or 37→28) also do not incur the energy cost of conversion to plant tissue, since there is no intervening protoplasmic incorporation. The bacteria are supported by photosynthesis in the same manner as heterotrophic cells of the primary producer. And, of course, the mycorrhizae and other active energy extraction pathways involves energy transfer without tissue conversion by the plant. Accordingly, such transfers should be more energetically efficient than transfers

via the grazing or detritus pathways, both of which involve the additional step of conversion to plant biomass and frequently require an intervening heterotroph. Efficiency of energy transfer of plant photosynthate to heterotrophic microbes, sucking insects or nectar feeding insects could conceivably approach 100%. For the energy extraction pathway to be mutualistic, the heterotroph must provide an energetically valuable service that will more than compensate for the plant's loss of its high quality photosynthate that could otherwise be used to build up the plants own tissue and produce reproductive structures necessary for its own survival. Otherwise, the relationship would be one of detrimental parasitism. The nectar-feeding insects provide vital pollination services in return for their share of plants photosynthate while mycorrhizal networks supply the plant with phosphorus and other nutrients that would be unavailable to plant root systems alone. Sporocarps of mycorrhizal fungi are almost equivalent to plant tissue since they are produced as an extension of the plant's roots. In addition to reproductive function, the fleshy sporocarps provide food for squirrels and other animals which, in turn, may provide seed dispersal or other valuable services important to survival of the whole mutualont. As long as the transfer system enhances the productivity and fitness of all the partners, then the energy flow is efficient from the standpoint of the ecosystem as a whole.

When the ecosystem is viewed as a homeostatic entity, energy flow is seen as controlled production in chloroplasts, and controlled distribution throughout the ecosystem. From the standpoint of the plant subsystem, it is desirable to maximize photosynthetic rate and transfer of energy to the heterotrophic portion of the ecosystem as long as it does not ultimately decrease plant survival (competitive ability, reproduction,

etc.). This is particularly true if the energy can be directed to modifying or controlling the environment to the ultimate benefit of the plant (N-fixation, nutrient cycling, etc.). From the standpoint of the heterotrophs, it is desirable to maximize removal of energy from the plant subsystem as long as the removal doesn't ultimately decrease the flow of energy from the plant subsystem by detrimentally affecting plants. It is even desirable for heterotrophs to partition energy to particular ecosystem functions if they ultimately increase energy flow from the plant subsystem. The mycorrhizal pathway may be considered to be efficient because it minimizes the utilization of plant limiting essential nutrients in the transfer of energy to heterotrophs. The grazing pathway has relatively high requirements for nutrients because nutrient rich, actively growing plant tissue is removed from the plant. Additional nutrients are lost due to vascular and cellular leakage resulting from tissue damage. The detritus pathway reduces nutrient costs (increases nutrient efficiency) by active retraction of nutrients from plant tissue prior to removal from the plant subsystem. The exudation pathway may allow transfer of energy in the form of carbohydrates without accompanying essential nutrients. Control of nutrient release resides in the membranes of the plant. Energy transport through sucking insects may be relatively nutrient inefficient because the stylus non-selectively removes the contents of the phloem. The mycorrhizal pathway provides a supplement to mineral nutrition of the plant, rather than a sink.

The amount of energy which can be transferred from autotrophs to heterotrophs through the grazing and detritus pathways is limited by the availability of inorganic nutrients necessary for biosynthesis of plant tissue. Theoretically, rate of flow through exudation and mycorrhizal

pathways is only limited by availability of CO_2, H_2O, and sunlight and by the photosynthetic efficiency of available chloroplasts. Rate of flow through the grazing pathway is further limited when grazing removes actively photosynthesizing cells.

Exudation and active energy extraction pathways may be mechanisms for maximizing efficiency of energy capture for the ecosystem. Under conditions where photosynthetic capacity exceeds available sinks internal to the plant, secretion may constitute a mechanism for dumping excess photosynthate. When plant sinks become saturated, chlorophyll and accessory pigments continue to capture sunlight. Either the pigments must be degraded to prevent sunlight capture, or the energy must be reemitted, or the energy must be transferred to carbon-carbon bonds in the Calvin-Benson cycle. If H_2O, CO_2, and sunlight are available, and the photosynthetic mechanism is intact, dumping excess photosynthetic products is a simple way to balance energy supply and demand within the plant, and it costs the plant little in the way of scarce resources. By the same token, from the standpoint of the ecosystem, exudation may be a mechanism which maximizes the use of available energy capture machinery. Secretion and leakage of energy rich compounds are very common in aquatic ecosystems and it would appear that plants are not commonly energy limited in terrestrial ecosystems.

There is evidence that the mycobiont establishes a sugar gradient from the phycobiont to the fungus by rapidly converting transport carbohydrates to fungal storage and transport compounds such as manitol and glycogen (Lewis and Harley, 1965a). As long as the mycobiont is removing excess plant carbohydrates (similar to exudates) energy removal should not negatively affect photosynthetic rate or plant growth. If

photosynthetic capacity beyond available plant sinks results in shutdown of photosynthetic machinery, then removal of excess photosynthate increases total photosynthesis and availability of energy in the ecosystem. The possibility that photosynthesis is feedback inhibited by photosynthetic products (Geiger, 1976) raises another interesting possibility. Removal of the product (transport photosynthates) by mycorrhizal fungi might actually increase the rate of the reaction (photosynthesis).

Efficient ecosystem function requires controlled distribution of energy. The detritus and exudation pathways are primarily donor controlled. Grazing is primarily recipient controlled. The mycorrhizal pathway is donor-recipient controlled. The entire mutulont is controlled by hormones produced by both the phycobiont and the mycobiont. The primary site of hormonal production, especially auxin, may alternate between actively growing shoots on the plant during the summer season, and the fungal symbionts when the aboveground plant is dormant. Mycorrhizal fungi provide a physically controlled pathway for delivery of energy directly to specific belowground organisms and processes. They result in a short temporal linkage between chloroplasts and belowground heterotrophic processes. This pathway may be the source of fine control and high efficiency for the ecosystem.

In summary, it is clear that mycorrhizal fungi provide an energy efficient link between the plant subsystem and heterotrophic components of the ecosystem that is mutually beneficial in that the fungi and their associates get high quality energy and plants get vital mineral nutrients with both processes operating at very high efficiencies.

Effect of Mycorrhizal Fungi on Resource Quality

The quality of resources provided to heterotrophs by the mycorrhizal pathway can be strikingly different from the other pathways. For example, fungal structures which provide energy to grazers and detritovores have high levels of chitin and glycogen. Inorganic nutrient levels in the fungal biomass may be very high as compared to concentrations in the soil substrate or in plant tissue (Harley, 1971; Stark, 1972; Cromack et al., 1975; Byrne et al., 1976; Vogt and Edmonds, 1980a; Vogt and Edmonds, 1980b). Fungi are well known for their ability to produce both growth inhibitors (antibiotics) and growth stimulators (vitamins). Well over 100 species of ectomycorrhizal fungi have been shown to produce antiviral, antibacterial, and antifungal compounds in pure culture or in their basidiocarps (Marx, 1972).

There is no shortage of qualitative studies of exudation in the rhizosphere (see for example, Rambelli, 1973; Balandreau and Knowles, 1978; Hale et al., 1978). The list of exudates reads like the reagent list in a well equipped facility for producing biological growth media. Sugars include maltose, glucose, arabinose, xylose, ribose, rhamnose, galactose, deoxyribose, fructose (Vančura, 1964; Vančura and Hovadik, 1965). Amino acids include leucine, isoleucine, valine, glutamine, α-alanine, ρ-alanine asparigine, serine, glutamic acid, aspartic acid, glycine, phenylalanine, threonine, tyrosine, proline, lysine, methionine, cystathionine, α-aminobutrric acid, tryptophane, homoserine, cysteic acid, α-aminoadipic acid, and ρ-pyrazolylalanine (Scheffer et al., 1964; Vančura and Hovadik, 1965; Rambelli, 1973). Vitamins include biotin, thiamin, calcium pantathenate, niacin, riboflavin, choline, pyridoxine, p-aminobenzoic acid, inositol, and pyridoxine (Rovira, 1959; Sulochana, 1962). Organic acids include

formic, acetic, propionic, butyric, valeric, glycolic, oxalic, succinic, fumaric, malic, tartaric, nitric, pyruvic, oxalacetic, and citric (Rivière, 1959, 1960; Vančura, 1964; Vančura and Hovadik, 1965). The rhizosphere is generally rich in enzymes (Rambelli, 1973), growth stimulators, and allelopathic compounds (Hale et al., 1978). Resource quality varies with plant species, developmental stage of the plant, associated populations of organisms, light intensity, temperature, soil pH, soil CO_2 concentration, availability of nutrients, soil oxygen concentration, and availability of moisture (Hale et al., 1978).

Observed resource quality and diversity in the rhizosphere is due to the combined effects of plants and fungal exudation as modified by the rhizosphere population, and as influenced by light intensity, temperature, pH and so on (Hale et al., 1978). Spatial and temporal linkage between the three biological groups is so tight that any attempts to separate the effects in situ would be difficult. Separating the components experimentally in order to study them results in a highly artificial situation since each component affects the quantitative and qualitative output of the other (Rambelli, 1973; Hale et al., 1978).

Exudates from soil hyphae cannot be collected in natural systems. Studies of ectomycorrhizal species, where pure cultures of hyphae can be grown on artificial media, indicate high variability between species, and within species when media or physical conditions are changed. One has little confidence that pure culture studies represent exudate conditions in natural soils when the fungi are mutualistic with a plant.

The capacity of mycorrhizal fungi to produce antibiotics in pure culture is intriguing when considering that fungal biomass or exudation may be fed upon by heterotrophic populations. However, evidence that

the antibiotics are actually produced in the soil in natural systems is lacking. Some investigators feel that available techniques are not sensitive enough to detect their presence in the field.

There is a lot of uncertainty regarding the qualitative aspects of plant and fungal exudates. It appears that mycorrhizal fungal species distribute resources with unique quality which in turn specifies the heterotrophic populations. The best evidence for unique resource quality comes from comparisons of soil populations on mycorrhizal and non-mycorrhizal root systems of a single plant species under controlled populations.

The Effect of the Mycorrhizal Pathway on Heterotrophic Organisms and Nutrient Recycling

The disproportionately high concentration of microorganisms in the rhizosphere, as compared to the surrounding soil, is well known. There are often larger numbers of bacteria associated with mycorrhizae than with the rhizosphere (Kalznelson et al., 1962). Tribunskaya (1955) found nine to ten times more free living fungi in the rhizospheres of mycorrhizal pines than in non-mycorrhizal seedlings. The mycorrhizae have a selective effect on bacterial species. For example, Oswald and Ferchau (1963) studied aerobic bacteria associated with mycorrhizal and non-mycorrhizal rootlets of five pine species. They identified 51 species of bacteria in 253 isolates including 22 associated with mycorrhizae, 7 with non-mycorrhizal rootlets, and 22 common to both. Species of bacteria vary with species of mycobiont (Foster and Marks, 1967). As trees mature (successional time), rhizosphere and mycorrhizosphere populations of soil microorganisms change (Rambelli, 1973).

Many authors have speculated on the importance of antibiotics produced by fungi as determinants of mycorrhizosphere microbial populations. Mycobionts with strong antibiotic activity can inhibit populations of bacteria including actinomycetes (Ohara and Hamada, 1967). Marx (1972, 1978) has reviewed the considerable evidence that mycorrhizal fungi inhibit, and in some cases stimulate feeder root pathogens including bacteria, fungi, and nematodes.

Because of their diverse enzymatic capacity and rapid growth, reproductive, and metabolic rates, soil organisms are important in the processes of nutrient cycling. Little is known regarding the nutrient cycling affect of mycorrhizal fungi resulting from their impact on soil organisms. There are three major reasons for the lack of data: (1) The mycorrhizosphere is belowground. (2) Processes in the mycorrhizosphere are the complex result of the interplay of plant roots, one or more species of mycorrhizal fungi, and many species of bacteria and other soil organisms that live in the rhizospheres. It is very difficult, if it is indeed possible, to determine what organisms are causing what. (3) Most of the research has been directed at determining what the mycobionts per se are doing.

The one effect that has been repeatedly demonstrated is that mycorrhizal fungi, and associated mycorrhizosphere organisms, increase plant growth rate and tissue concentrations of inorganic nutrients. Much of the effect may be due simply to increased access to soil volume (Bowen, 1973). Exudates, including chelating compounds and the selective uptake capacities of the fungi, also contribute (Bowen, 1973). Nitrogen availability is enhanced by mycobionts and associated microorganisms which provide enzymatic access to many different chemical forms of nitrogen

(Bowen, 1973; Rambelli, 1973). But these mechanisms fail to explain the accretion of nitrogen in the ecosystem. As far as we know, nitrogen fixation is limited to prokaryotes which are dependent on plant production. Since mycorrhizal fungi increase nutrient availability to plants which increases primary production, they play a positive role in the improved nodulation and increased rates of N-fixation in plants observed when VA mycorrhizae are present (Crush, 1974; Mosse et al., 1976).

Nitrogen fixation is a high energy demanding process - 1 gm of carbohydrate may be metabolized per 10-30 mg of N fixed (Gibson, 1966; Bond, 1968; Pate et al., 1969; O'Toole and Knowles, 1973). Nodules in Pisum sativum utilize as much as 43% of the carbon translocated in roots (Minchin and Pate, 1973). Free living N-fixers do not enjoy direct access to plant phloem or production of the nodule and require more energy to fix a gram of N. It is generally believed that soil fixers are restricted by carbon availability, since no nitrogen fixing prokaryote has been demonstrated to have cellulytic capability. Therefore, they don't have direct access to detritus (Swift et al., 1979). Access to detritus carbon supplies, however, can be provided by association with decomposer organisms, but N-fixers would have to compete with the decomposers and other heterotrophic organisms for the breakdown products. Low nitrogen availability favors translocation of photosynthate to roots (Murata, 1969). N_2 fixing organisms grow more intensively in the root zone, and in desert soils they are found only in the vicinity of roots (Mishustin and Shilnikova, 1969). Such findings suggest that root exudation provides their means of existence (Warembourg and Morrall, 1978). If so, the energy requirements by exudation are very high. Balandreau and Fares-Hamad (1975) speculate that N_2 fixation in the rhizosphere of rice

required a root exudation of at least 23% of the carbon fixed by photosynthesis.

The mycorrhizosphere may be a unique microhabitat particularly suited to N_2 fixation. Rambelli (1970) isolated 24 strains of nitrogen fixing bacteria from non-mycorrhizal roots of Pinus radiata and 40 strains from mycorrhizal roots. Some of the strains of N-fixing bacteria were isolated from inside the mantle produced by Boletus granulatis. Strains from inside the mantle were not stimulated by root exudate but were stimulated by metabolites produced by B. granulatus. ^{15}N enrichment of mycorrhizal Pinus radiata, Pinus elliottii, and Pinus caribaea has been demonstrated (Stevenson, 1959; Richards and Voigt, 1964).

Nitrogen fixing bacteria survive better on roots with VA mycorrhiza than on noninfected roots (Barea et al., 1973). Under laboratory conditions, nitrogen fixing bacteria have been incorporated into hyphal cells of a mycorrhizal fungus (Giles and Whitehead, 1976). The bacteria continue metabolic activity within the fungal protoplasts.

The cycling of phosphate has drawn great attention in ecology because it is frequently the most limiting nutrient for the ecosystem as a whole. Virtually every experiment with mycorrhizal fungi in low phosphorous soils has demonstrated the ability of the fungi to enhance phosphorous nutrition of the plant. As with nitrogen, increased access to soil volume and selective ion uptake at least partially explain the enhancement. More than 95% of the phosphorous in unfertilized soils is relatively unavailable to plants (Hayman, 1975a). Mycorrhizal fungi readily solubilize mineral phosphate in laboratory media (Bowen and Theodorou, 1967). This solubilization may be due to high acid production in the presence of readily available carbohydrates. Extrapolation

to field conditions, as always, is risky. Bowen and Theodorou (1967) demonstrated a plant growth response to rock phosphate applications in both mycorrhizal and non-mycorrhizal Pinus radiata. Stone (1950) demonstrated similar responses with four mineral phosphates. These studies suggest that solubilization is likely due to interaction of rhizosphere and mycorrhizosphere organisms. Hayman and Mosse (1972a,b) found that onion plants fertilized with rock phosphate grew better with mycorrhizae than without. Mosse et al. (1976) compared the effects of rock phosphate and nodulation on mycorrhizal and non-mycorrhizal members of Stylosanthes, Centrosema and Trifolium. Mycorrhiza alone produced a growth greater than rock phosphate alone, while two treatments together acted synergistically, resulting in a 7 to 22-fold increase in dry weight.

Mycorrhizal fungi enhance plant uptake of many other macro, micro, and trace nutrients. As with N and P, it is not known whether the enhancement is the result of the mycobiont per se or to the synergism of all the mycorrhizosphere organisms.

There is considerable evidence that mycorrhizal fungi support populations of soil organisms beyond bacteria and fungi. Several plant-parasitic nematodes will feed on ectomycorrhizal fungi (Ruehle, 1962). Many mycophagous nematodes feed only on fungi (Riffle, 1971). Mycophagous animals in the soil include arthropods, mollusks, and mammals (Ingold, 1971). Some ectomycorrhizal mycobionts seem to produce attractants for root aphids (Zak, 1965).

Mycophagy is very common in small animals including insectivores, omnivores, herbivores, and carnivores. Fogel and Trappe (1978) present an extensive list of animal mycophagists and the fungal species they are known to feed on. Mammal mycophagists include members of the Sciuridae

(chipmunks and squirrels), Cricetidae (mice, rats, lemmings, voles), Zapodidae (jumping mice), Ochotonidae (pikas), Soricadae (shrews), Didelphidae (opposums), Peramelidae (bandicoots), Phascolomidae (wombats), Macropodidae (rat-kangaroos), Cynopithecinae (baboons), Dasypodidae (armadillos), Leporidae (rabbits and hares), Castoridae (beavers), and Mustelidae (weasels). Fungi account for as much as 72% of the annual dietary volume in some of these small mammal species. The red squirrel (Tamiasciurus hudsonicus) has been credited with eating mushrooms of 89 different fungal species, many of which are known to be mycorrhizal. Squirrels dry and cache sporocarps (Cram, 1924; Hardy, 1949). Mushroom eaters also include large mammals such as deer, bears, and baboons (Buller, 1920; Stroude, 1954; Miller and Halls, 1969; Fogel, 1975; Fogel and Peck, 1975). Many fungal species have limited ability to disperse spores and the mammals are adapted to find even the hypogeous sporocarps. Obligately, mycorrhizal plant species require simultaneous distribution of seeds and spores in time and space. Many small mammals (e.g., squirrels) feed on both seeds and sporocarps, suggesting a mutualistic relationship between the animal, fungus and seed plant.

Fruiting bodies of mycorrhizal fungi also serve as food sources for other organisms such as birds and lizards. They also provide unique breeding sites for insects, especially Diptera and Coleoptera (Pavoir-Smith, 1960; Elton, 1966; Fogel, 1975; Fogel and Peck, 1975). The range of mycophagy in Arthropoda is relatively unknown. To my knowledge, no one has looked at the interrelationship between mycorrhizal sporocarps, arthropods, and plant pollination.

CHAPTER IV

RATE OF ENERGY FLOW THROUGH THE MYCORRHIZAL PATHWAY IN YOUNG PINE PLANTATIONS AT COPPER HILL, TENNESSEE AND THE SAVANNAH RIVER PLANT (SRP), SOUTH CAROLINA

Pines planted at Copper Hill, Tennessee, on land denuded by fumes from ore smelters, and pines planted on a borrow pit at Savannah River Plant near Aiken, South Carolina provided an opportunity to estimate energy flow via the mycorrhizal pathway under extremely poor soil conditions where the mutualism between trees and fungal hyphae networks are vital to survival of the plantation. Data on annual stem, branch, and needle production of inoculated and non-inoculated pine trees were used to assess the effect of mycorrhizal fungi on rate of aboveground primary production. Annual production of aboveground sporocarps of mycorrhizae was estimated by harvesting them at short time intervals, and these data were used to estimate the partitioning of net primary production energy flow between tree growth, detritus production and mycorrhizal networks.

A. Materials and Methods

1. Site Description. The Copper Basin of Tennessee is located in the extreme southeastern corner of the state, just a few miles from the Georgia state line. The early history of the basin and conditions of the environment have been thoroughly reviewed by Seigworth (1943) and Allen (1950). Since 1843 mining and processing of ores has dominated

the area. Early methods of smelting resulted in removal of trees for ore roasting. Large quantities of sulfur dioxide produced in the smelting process, combined with frequent atmospheric inversions killed the remainder of the vegetation within a fifty square mile area. High levels of acid and frequent heavy rainfall resulted in severely eroded, excessively leached soils. Much of the area is devoid of topsoil and has very low levels of available nutrients. Conversion to modern refining facilities removed the demand for lumber and reduced the production of smoke; but atmospheric release of acid was still as high as 381 tons per day in the early 1900's. The industry was restricted to emission of 132 tons per day in the early 1920's. Reforestation efforts by the Civilian Conservation Corps, the Tennessee Valley Authority and mine owners met with little success except on the extreme margins of the basin. Even such exotic plants as weeping lovegrass and kudzu did not survive in the hostile environment.

Sulfur dioxide production has decreased since the acquisition of the mines by City Service Company in 1964, however, there are still episodes of SO_2 emission due to scrubber breakdown. Between 1972 and 1976 a series of pine plantations were established by Charles R. Berry and Donald H. Marx (Institute of Mycorrhizal Research and Development, U.S. Forest Service, Southeast Forest Experiment Station, Forestry Sciences Laboratory, Athens, Georgia) in cooperation with City Service Company. Two of their experimental sites, both located on the top of windswept ridges less than one mile apart were selected for this study. Description of the sites, methods of site preparation for planting, and procedures for mycorrhizal inoculation are reported in detail by Berry and Marx (1978) and Berry (1979, 1982). They report that at site No. 1, henceforth

designated as the "airport site," conditions prior to soil amendment and planting were: soil pH 4.3, cation exchange capacity 3.4 me/100g, organic content 0.29%, available phosphorus 1.0 ppm, and total nitrogen 240 ppm. Exchangeable concentrations of cations in ppm were K=17, CA=2.0, Mg=2.1, Mn=5.2, and S=560. On the second site designated as the "sludge site," soil pH was 4.4, cation exchange capacity was 3.3 me/100g, organic content was 0.83%, available phosphorus was 1.2 ppm, and total nitrogen was 300 ppm. Exchangeable concentrations of cations in ppm were K=12, Ca=2.9, Mg=2.0, Mn=3.2, and S=448.

The third site, designated as the "borrow pit site" was located on the Department of Energy's Savannah River Plant near Aiken, South Carolina. The borrow pit was formed by the removal of the A and B horizon for construction of a dam. Reclamation was attempted in 1953 by machine planting with loblolly pine seedlings. By 1976 many of the trees were windthrown and surviving trees were only 2.5 to 5 m tall. Surviving trees were severely stunted and yellow, with roots barely under the soil surface. Although a thin layer of litter was present, understory grasses and shrubs were absent. Basidiocarps of Pisolithus tinctorius were numerous and the mustard-yellow ectomycorrhizae were abundant on pine roots. Berry and Marx removed the remaining pine trees in 1975 and established new experimental pine plantations in 1976. Methods of site preparation for planting, seedling production, and site conditions have been previously reported by Berry and Marx (1980). They report that the exposed clay surfaces were highly compacted and eroded, impervious to root growth, and extremely low in available water, fertilizer, and organic matter. Chemical soil properties prior to planting were not investigated but conditions on the control plot in the third year of the new plantation were as follows:

soil pH 4.2, cation exchange capacity 1.4 me/100g, organic content 0.4%, available phosphorus 7.0 ppm, and total nitrogen 112 ppm. Exchangeable concentrations of cations in ppm were: K=6, Ca=4, Mg=11.

2. Plot Design. The airport site at Copper Hill consisted of six blocks of pine plantations. Each block contained four plots each, consisting of three rows of ten trees planted on 91 X 91 cm spacing. Plots were separated by 2 m and blocks by 6 m nonplanted strips. Prior to planting, the sites were subsoiled to a depth of 60 cm on 90 cm centers. Six hundred seventy two kg/ha of 10-10-10 fertilizer and 4,480 kg/ha of dolomitic limestone were broadcast and disced into the soil. Three blocks were covered with a three inch layer of chipped pine bark, which was at least 25% wood prior to planting. Plots without bark were designated as the "fertilizer treatment" and plots with both bark and fertilizer were designated as "bark treatment." The factoral design included Virginia vs loblolly pine either inoculated with mycorrhizal fungi or non-inoculated on pine bark amended or non-pine bark amended soils. The inoculated treatment (PT) consisted of trees that were inoculated with Pisolithus tinctorius in the nursery. Noninoculated (NI) trees acquired mycorrhizae (mainly Thelephora terrestris) which occur naturally in the nursery.

Soils on the sludge study site at Copper Hill were amended with 896 kg/ha of 10-10-10 fertilizer and 1,417 kg/ha of burnt lime (fertilizer treatment) or 34,000 kg/ha of sewage sludge (sludge treatment). Fertilization rate was selected to be approximately the same level for sludge and fertilizer. PT inoculated Virginia pines were not available when the experiment was established. PT or NI treated, loblolly or shortleaf

pines and NI treated Virginia pines were established on five replica plots for each soil treatment tree species-inoculum combination. Each plot consisted of 36 trees planted on 0.9 m by 0.9 m spacing in four rows.

On the borrow pit site at SRP, the PT and NI mycorrhizal treatments were combined with the following nine fertility treatments: (1) no soil treatment (control); (2) fertilizer and lime; (3) fertilizer, lime, and tree bark; (4) fertilizer, lime, and ash; (5) fertilizer, lime, bark, and ash; (6) sewage sludge; (7) sewage sludge and bark; (8) sewage sludge and ash; (9) sewage sludge, bark, and ash. Fertilizer = 560 kg/ha of commercial 10-10-10 fertilizer; and lime = 2,240 kg/ha of dolmitic limestone. Sewage sludge, milled pine bark, and bottom furnace ash were applied at a rate of 125 m^3/ha, or approximately 1.3 cm deep. With sewage sludge this rate was equivalent to a dry weight of 34,000 kg/ha. There were five replica plots of each mycorrhizal-soil treatment combination. Plots consisted of 25 loblolly pine seedlings, in five rows, with a 1.2 X 1.2 m spacing. Plots were separated by aisles 3 m wide in one direction and 6 m wide in the other. All plots were subsoiled to a depth of 60 cm, disked and seeded with fescue the fall prior to planting seedlings.

3. Measurement of Annual Production of Aboveground Plant Production and Partitioning Between Stems, Needles, and Branches. Volumes of biomass calculated from diameter (D) and/or height (H) measurements are a common non-destructive means of following tree production over time (Swank and Schreuder, 1974; Madgwick and Satoo, 1975; Parker and Schneider, 1975). Volume calculated as D^2H has become the standard means of comparing mycorrhizae inoculated and non-inoculated trees (Marx, 1977a). For this study, diameter (D) and height (H) in cm were measured annually

during the dormant season. All measurements, except for the fifth year on the airport site, were taken by personnel at the Institute for Mycorrhizal Research and Development, U.S. Forest Service, Southeastern Forest Experiment Station, Forest Sciences Laboratory, Athens, Georgia. The author is indebted to the Institute for use of these data. Unfortunately, trees on the airport site were not measured during the third and fourth growing season. Harms and Langdon (1975) have demonstrated that the growth of young pines fits a log growth curve model with high correlation. D^2H was summed for each plot to calculate plot volume index (PVI). Regressions for tree growth [Log_n (PVI) = a+b (years of growth) by treatment on all sites have r^2 values above 0.98. Therefore, wood volume for the third and fourth years on the airport could be estimated by fitting first, second, and fifth year measurements to a log normal growth curve. PVI provides a non-destructive means of comparing affect of different treatments on both the survival and growth rate of trees over multiple growing seasons.

Using allometric measures to estimate aboveground biomass introduces errors since Harms and Langdon (1976, 1977) found that the relationship between D^2H and plant biomass in young pines is not constant. Their studies demonstrate a negative relationship between seedling density and the needle biomass to tree volume (D^2H) ratio. Branch and needle growth is not always proportional to stem growth, therefore, thirty trees were harvested from the airport site to determine the relationship between stem volume (D^2H), total production and biomass of stem, needles, and branches. PT and NI, loblolly and Virginia pines from the fertilizer treatment were categorized into 10 tree volume ranks (small to large) for each tree species-mycorrhizal treatment based on D^2H determinations

at the end of the last growing season. Trees were randomly selected from the 1st, 3rd, 5th, 7th, and 10th rank for each tree species-mycorrhizal treatment. Tree parts of selected trees were harvested separately, forced air oven dried to constant weight at 55°C, and weighed. Independent regression lines (dry weight = a+b (D^2H)) were calculated for stems, needles, and branches of loblolly and Virginia pines under both PT and NI treatments. Standing crop biomass by tree part of all trees at the beginning and end of the growing season (4th and 5th year airport site, 3rd and 4th year sludge site, 2nd and 3rd year borrow pit site) were calculated from tree volume measurements using these regressions. Annual biomass production was determined by difference.

Stem, needles, and branches of each harvested tree were separately homogenized, ground, and pelletized for caloric determination. Acid corrected calorie content was determined with a Phillipson microbomb. Mean calorie content per gm was calculated for each tree part-tree species-mycorrhizal treatment combination. Annual production in calories was determined by multiplying annual production in gm/m^2 times the appropriate calorie content/gm ratio.

Trees from other treatments could not be harvested without disrupting ongoing experiments. Therefore, tree volume to biomass regressions and calorie content determinations from harvested trees at the airport site were used to calculate biomass and calorie content for all other sites.

4. Estimates of Annual Production of Aboveground Sporocarps of Mycorrhizal Fungi. Sporocarps were harvested biweekly, and were pooled by plot and by fungal species. Sporocarps were allowed to surface dry and adhering foreign material was blown off with an air hose fitted with

a Pasteur pipette as a nozzle. Collections were force air oven dried at 55°C to constant weight to obtain dry weight. Individual collections were ground and homogenized for caloric determination. Acid corrected calorie content was determined with a Phillipson microbomb. Ash content was determined by exposure of paired samples to 500°C in a muffle furnace for five hours.

B. Results and Discussion

1. Affect of Inoculation with Mycorrhizal Fungi on Production of Plant Biomass Over Time. Means and standard errors for stem volumes in the Copper Hill study plots are summarized in Table 4-1. Previous experiments (Marx et al., 1981) have demonstrated that the growth response resulting from inoculation of trees with mycorrhizal fungi varies as a function of site, tree species, and soil treatment. Experiments are confounded by changes in availability of soil nutrients and interactions between aboveground plant parts over time. As the trees increase in size, competitive interactions within plots tend to obscure soil treatment and inoculation effects. With time, natural dissemination of fungal spores between plots and from the surrounding environment obfuscates inoculation treatment affects. Furthermore, variability within plots and between plots within treatments is usually very high, frequently precluding clear statistical demonstration of differences between treatments. As reported by Berry and Marx (1978) and Berry (1982), and as can be seen in Table 4-1, the Copper Hill experiments were no exception. The treatment that produced the largest standing crop differed according to age of the stand. Within treatment, variability was high; there were no statistically significant ($P = .05$) differences in standing crop (stem volume) of trees between treatments on the airport site at the

TABLE 4-1. Tree Growth Rate Over Time as Measured by Tree Volume (cm^3). Values are $\bar{x}$ (Σ diameter^2 X height) by plot and (standard error of the mean). Airport site (n = 3 plots, each plot = 30 trees, 25 m^2). Sludge site (n = 5 plots, each plot = 36 trees, 30 m^2). PT = trees inoculated with Pisolithus tinctorius in the nursery. NI = trees which naturally acquired mycorrhizae in the nursery. First year measurements were on seedlings which had been grown for 10 months in the nursery and were graded to 3.0 - 4.5 mm root collar diameters and 16 to 19 cm heights prior to planting. Seedlings were planted in March and measured in October. Third and fourth year volumes on the airport site are estimated from a log normal fit of D^2H determinations from years 1, 2, and 5. Statistical comparisons are within year, site, and tree species by treatment. Treatments followed by the same letter do not differ significantly at P = .05 (analysis of variance, Duncan multiple range test).

	YEAR				
	1	2	3	4	5
Airport Site					
Loblolly-Fertilizer					
PT	50.8 A	2470.8 A	3478.1	17748.4	65637.2 A
	(3.7)	(777.1)			(20233.9)
NI	48.4 A	1986.3 A	2904.2	14273.9	51810.8 A
	(4.6)	(499.3)			(16245.5)
Loblolly-Bark					
PT	48.9 A	1082.0 AB	2870.9	16477.4	77982.1 A
	(2.0)	(126.7)			(16649.6)
NI	37.2 B	257.3 B	1186.8	6344.0	32682.7 A
	(1.8)	(34.0)			(4612.4)
Virginia-Fertilizer					
PT	43.5 B	3866.2 A	4145.1	22156.7	79259.1 A
	(2.3)	(1178.6)			(26274.0)
NI	55.3 A	3072.3 AB	3933.4	19833.1	70988.1 A
	(5.1)	(344.4)			(7647.3)
Virginia-Bark					
PT	37.3 B	1132.5 BC	2806.5	17304.8	89458.4 A
	(2.7)	(351.1)			(14082.8)
NI	36.0 B	599.9 C	2096.5	12933.6	69223.5 A
	(1.8)	(91.9)			(11445.4)
Sludge Site					
Loblolly-Fertilizer					
PT	1663.0 AB	7616.3 A	20194.2 B	59646.7 B	
	(187.0)	(1094.6)	(3880.7)	(15617.5)	
NI	1774.4 A	7199.5 A	16085.7 B	39710.7 B	
	(120.2)	(543.3)	(1475.1)	(8223.4)	
Loblolly-Sludge					
PT	1628.3 AB	10961.3 A	46088.2 AB	154122.7 A	
	(135.4)	(1238.0)	(8609.1)	(22963.5)	
NI	1163.9 B	9199.7 A	57222.0 A	184067.4 A	
	(234.0)	(2671.3)	(20159.0)	(48323.2)	
Shortleaf-Fertilizer					
PT	355.0 A	1986.0 A	5614.0 A	17021.0 A	
	(9.0)	(175.0)	(975.0)	(4068.0)	
NI	416.0 A	1778.0 A	3864.0 A	10525.0 A	
	(52.0)	(250.0)	(555.0)	(1745.0)	
Shortleaf-Sludge					
PT	239.0 A	1704.0 A	7694.0 A	30079.0 A	
	(45.0)	(366.0)	(1240.0)	(4150.0)	
NI	310.0 A	1671.0 A	8449.0 A	30238.0 A	
	(87.0)	(541.0)	(3891.0)	(10898.0)	

TABLE 4-1 continued.

Virginia-Fertilizer				
NI	1625.0 A (235.0)	6981.0 A (801.0)	16094.0 B (1856.0)	41130.0 B (6889.0)
Virginia-Sludge				
NI	1405.0 A (320.0)	9575.0 A (2254.0)	43575.0 A (7746.0)	133875.0 A (19707.0)

end of the fifth growing season. However, PT trees were from 1:11 to 2.38 times larger than NI trees of the same species and soil treatment.

At the end of the fourth year on the sludge study site, soil amendment with sewage sludge produced a statistically significant (P = .05) increase in PVI of loblolly and Virginia pine, regardless of mycorrhizal treatment (see column 4, Table 4-1). Shortleaf pines in sludge amended soils were twice as large on the average as those on fertilized treatments, but the difference was not statistically significant. The PT treatment showed nonstatistically significant positive growth effects on the fertilizer soil treatment. These data suggest that inoculation of trees with Pisolithus tinctorius or amendment of soils with sewage sludge increases the availability of energy in the form of woody plant tissue. The effects of inoculation and sludge might be expected to be similar because both increase nutrient availability to the tree.

At the borrow pit site, Marx and Berry (1980) evaluated seedling roots after the first growing season and found that Pisolithus tinctorius, indigenous in the soil from the previously attempted reclamation, had formed ectomycorrhizae on all trees, regardless of mycorrhizal treatment. Therefore, they analyzed only for the effects of soil amendment on tree growth. They demonstrated (Table 4-2) that the tree volume of seedlings grown on sludge amended plots was approximately 20 times greater than that of seedlings grown on sludge-free plots after three growing seasons.

2. Affect of Inoculation with Mycorrhizal Fungi on Annual Plant Production and Partitioning of Annual Plant Production to Stem, Branches, and Needles. Independent regressions of D^2H vs stems, needles, and branches of PT and NI, loblolly and Virginia pines from fertilizer plots at the airport site are given in Table 4-3. Regressions based on

TABLE 4-2. Mean Growth and Survival of Loblolly Pine Seedlings after 3 Years on a Subsoiled Borrow Pit as Influenced by Different Soil Amendments* (Berry and Marx, 1980)

Amendments†	Survival	Height	Root-collar diameter	Seedling volume
	%	m	cm	cm^3 X 10^2
Control	81 a	0.63 c	1.9 b	4 c
Fertilizer & lime	77 a	0.72 c	2.0 b	4 c
Bark + fertilizer & lime	79 a	0.57 c	1.6 b	2 c
Bark + ash + fertilizer & lime	86 a	0.59 c	1.6 b	3 c
Sewage sludge	74 a	2.23 ab	6.4 a	100 ab
Bark + sewage sludge	77 a	2.13 b	6.0 a	85 b
Ash + sewage sludge	72 a	2.30 a	6.2 a	104 a
Bark + ash + sewage sludge	75 a	2.37 a	6.3 a	107 a

*Means in a column followed by the same letter are not significantly different ($p = 0.05$).

†Fertilizer and lime: 560 kg/ha of 10-10-10 + 2.240 kg/ha of dolomitic limestone. Bark, bottom ash, and sewage sludge broadcast evenly on the soil surface to a depth equal to 1.25 cm per each material. All plots double disked to incorporate amendments.

TABLE 4-3. Relationship Between Tree Volume (D^2H) and Biomass of Stems, Needles, and Branches of PT and NI Treated Loblolly and Virginia Pines That Were Harvested at the End of the Fifth Growing Season. Trees were categorized into ten ranks based on D^2H for each tree species treatment. Harvested trees were randomly selected from the ranks 1, 3, 5, 7, 10. Regressions are of the form dry wt = a + b (D^2H) where D = diameter at root collar in cm and H = height in cm.

	n	a	b	r^2
Loblolly-PT				
Stem	8	38.2	.0798	90.1
Branch	8	52.7	.0373	85.3
Needle	8	192.0	.0547	64.2
Crown	8	244.0	.0919	76.9
Total	8	283.0	.1720	85.9
Loblolly-NI				
Stem	7	21.5	.0877	95.0
Branch	7	22.9	.0517	94.0
Needle	7	49.6	.1040	93.6
Crown	7	72.6	.1550	93.9
Total	7	94.1	.2430	95.3
Virginia-PT				
Stem	8	48.8	.1050	96.1
Branch	8	58.5	.1820*	91.8
Needle	8	86.0	.1880*	92.7
Crown	8	145.0	.3700*	92.4
Total	8	193.0	.4740*	95.6
Virginia-NI				
Stem	7	12.7	.1050	98.9
Branch	7	-23.7	.1620	97.5
Needle	7	88.3	.1540	97.5
Crown	7	64.7	.3160	97.3
Total	7	77.4	.4200	78.7

* indicates significant difference (P = .05) between slopes of PT treated trees and NI treated trees for the same tree part within tree species.

(D^2H) and $\log_n$ (biomass) result in r^2 values higher than the values in Table 4-3 but do not change the statistical comparisons. Slopes of regressions of dry weight of stem vs D^2H of PT vs NI treatments are not significantly different (P = .05) for either loblolly or Virginia pines. The slopes of regressions for total weights and for weights of needles, branches, and crowns (needles plus branches) vs D^2H are different (P = .05) for PT and NI Virginia pines. PT treated Virginia pines have more crown and more total weight per unit stem volume than NI trees.

The affect of PT inoculation on crown to stem ratio is not apparent in loblolly pines, perhaps because crown closure had already occurred on the loblolly plots, a conclusion supported by Harms' and Langdon's 1977 studies of nursery seedlings. Personnel at the Institute of Mycorrhizal Research are currently doing a study of the relationship between D^2H and biomass of PT and NI trees which includes hundreds of trees (Personal communications). Their interim data suggests that soil conditions, mycorrhizal treatment, tree planting density, and age of the stand all affect the relationship in a complex manner. The number of trees in this study was too small to address such a complex relationship.

As shown in Table 4-4, calorie content per gram of the individual plant parts of the harvested trees is not significantly different (P = .05) between mycorrhizal treatments within or between tree species.

The regressions in Table 4-3 and calorie values in Table 4-4 based on the harvested samples, provide a means of estimating the biomass and calorie content of stems, needles, and branches from D^2H for all of the trees on the fertilizer treated plots at the airport site. Application of these table values to trees on the bark treatment plots at the same

TABLE 4-4. Comparison of the Calorie Contents of Stems, Needles, and Branches by Mycorrhizal Treatment for Loblolly and Virginia Pines. Caloric determinations were for the same trees as those described in Table 4-3. Values in parentheses are standard deviations. Caloric content of tree parts is not statistically different (P = .05) between mycorrhizal treatments (Analysis of Variance, Duncan's multiple range test).

	n	Stem cal/gm	Branch cal/gm	Needle cal/gm
Loblolly - PT	8	4558.4 (243.0)	4638.7 (69.6)	4650.4 (100.2)
Loblolly - NI	7	4473.2 (150.6)	4535.6 (71.2)	4643.5 (90.1)
Loblolly Total	15	4512.2 (188.2)	4581.4 (85.5)	4646.5 (88.6)
Virginia - PT	8	4244.1 (204.6)	4598.6 (159.7)	4697.0 (69.0)
Virginia - NI	7	4348.7 (99.7)	4674.2 (117.9)	4750.1 (123.9)
Virginia Total	15	4290.6 (166.4)	4632.2 (139.9)	4720.6 (94.4)

site is justified since these trees are the same age and close to the same size (see Table 4-1).

Trees could not be harvested from the sludge site without disrupting ongoing experiments. Use of values in Tables 4-3 and 4-4 with loblolly and Virginia pines on the sludge study site is questionable, but no other data or regressions are available which independently relate D^2H to stem, branch, and needle weight in young pines. Since biomass to D^2H regressions and calorie contents are not available for shortleaf pine at Copper Hill, the common regression for PT and NI treatments of Virginia pine had to be used. Like the Virginia pine, the shortleaf pine had not yet reached crown closure. Accordingly, regressions are likely to underestimate biomass of PT-treated trees and overestimate biomass of NI trees. The calorie content of Virginia pine was used as an estimate for short leaf pine.

The values in Table 4-3 were used to convert NI (4th and 5th dormant season, airport site; 3rd and 4th dormant season, sludge site; 2nd and 3rd dormant season borrow pit site) to standing crop biomass of stems, needles, and branches. Values in Table 4-4 were used to convert dry weight to kilocalories. Annual increments of biomass in gm/m^2 and $Kcal/m^2$ of stems, needles, and branches were estimated by difference between subsequent annual standing crop measurements. Annual production of biomass on the Copper Hill sites is given in Appendix 5, Table 1. Total standing crop at the end of the last growing season and annual production of stems, needles, and branches in $Kcal/m^2$ are given in Table 4-5 for the Copper Hill sites and in Table 4-6 for the borrow pit site.

On the airport site there were no statistically significant differences within tree species between treatments in Kcal of total standing

TABLE 4-5. Tree Production on the Copper Hill Sites

	n	total standing crop kcal/m²	total annual production kcal/m²	annual needle production kcal/m²	annual stem production kcal/m²	annual branch production kcal/m²
Airport Site						
Loblolly-Fertilizer						
PT	3	3124.5 A	1372.3 A	438.3 A	632.9 A	301.0 A
		(1034.9)	(744.6)	(237.8)	(343.4)	(163.4)
NI	3	2428.6 A	1547.5 A	673.3 A	547.2 A	326.9 A
		(1107.2)	(873.1)	(379.8)	(308.8)	(184.4)
Loblolly-Bark						
PT	3	3244.9 A	1791.4 A	572.2 A	826.2 A	393.0 A
		(805.5)	(696.6)	(222.5)	(321.3)	(152.8)
NI	3	1561.5 A	1083.9 A	471.6 A	383.2 A	229.1 A
		(334.5)	(280.8)	(122.1)	(99.3)	(59.4)
Virginia-Fertilizer						
PT	3	7077.3 A	4503.0 A	1834.8 A	929.0 A	1739.1 A
		(3601.7)	(2701.2)	(1102.8)	(553.1)	(1045.2)
NI	3	6928.4 A	3542.3 A	1349.6 A	842.4 A	1350.3 A
		(3635.7)	(582.3)	(249.5)	(155.8)	(177.3)
Virginia-Bark						
PT	3	7543.9 A	5287.7 A	2166.1 A	1088.1 A	2043.5 A
		(1951.6)	(1466.9)	(598.1)	(301.8)	(566.9)
NI	3	5224.0 A	3957.6 A	1488.2 A	928.9 A	1540.5 A
		(1413.1)	(1155.3)	(434.4)	(271.1)	(449.7)
Sludge Site						
Loblolly-Fertilizer						
PT	5	2890.8 BC	1050.6 C	337.3 B	483.3 B	229.9 B
		(1174.5)	(695.8)	(223.5)	(320.1)	(152.2)
NI	5	1851.1 C	879.1 C	382.9 B	310.7 B	185.6 B
		(610.7)	(566.4)	(246.6)	(200.2)	(119.6)
Loblolly-Sludge						
PT	5	5389.2 AB	2850.7 B	915.6 B	1311.4 A	623.7 A
		(1517.7)	(859.7)	(276.1)	(395.6)	(188.0)
NI	5	7221.9 A	4700.6 A	2046.9 A	1661.2 A	992.5 A
		(4987.5)	(2364.1)	(1029.5)	(835.4)	(499.2)
Shortleaf-Fertilizer						
PT	5	1914.0 AB	777.5 AB	280.4 AB	172.8 AB	324.4 AB
		(682.6)	(477.0)	(172.0)	(106.0)	(199.0)
NI	5	969.1 C	437.0 B	165.6 B	102.1 B	169.3 B
		(270.9)	(176.7)	(64.5)	(42.2)	(70.0)
Shortleaf-Sludge						
PT	5	2716.3 A	1495.7 A	539.3 A	332.3 A	624.0 A
		(720.0)	(440.4)	(158.8)	(97.8)	(183.8)
NI	5	2191.8 AB	1396.7 A	525.2 A	327.8 A	543.7 A
		(1623.4)	(1069.3)	(402.2)	(250.9)	(416.3)
Virginia-Fertilizer						
NI	5	2927.0 B	1524.5 B	573.2 B	357.8 B	593.4 B
		(829.2)	(696.6)	(262.0)	(163.4)	(271.2)
Virginia-Sludge						
NI	5	8699.7 A	5644.6 A	2122.6 A	1324.9 A	2197.1 A
		(2682.2)	(1589.7)	(597.8)	(373.1)	(618.8)

TABLE 4-6. Tree Production on the Borrow Pit Site

		Total Standing Crop Kcal/m^2	Total Annual Production Kcal/m^2	Annual Needle Production Kcal/m^2	Annual Stem Production Kcal/m^2	Annual Branch Production Kcal/m^2
Control	PT	915.2 D	142.4 D	45.8 E	65.5 D	31.1 D
		(286.7)	(205.3)	(66.0)	(94.4)	(44.8)
	NI	478.1 D	160.0 D	69.6 E	56.6 D	33.8 D
		(190.8)	(141.5)	(61.6)	(50.0)	(29.9)
Fert., Lime	PT	856.6 D	102.8 D	33.1 E	47.3 D	22.5 D
		(103.8)	(41.5)	(13.3)	(19.1)	(9.1)
	NI	509.8 D	183.0 D	79.6 E	64.7 D	38.6 D
		(193.3)	(110.4)	(48.1)	(39.1)	(23.3)
Bark, Fert., Lime	PT	763.8 D	44.0 D	14.2 E	20.2 D	9.6 D
		(109.3)	(34.9)	(11.2)	(16.0)	(7.6)
	NI	434.7 D	147.4 D	64.1 E	52.1 D	31.1 D
		(91.2)	(104.7)	(45.6)	(37.0)	(22.1)
Fert., Lime, Ash	PT	867.8 D	114.1 D	36.7 E	52.4 D	24.9 D
		(236.1)	(82.1)	(26.4)	(37.7)	(17.9)
	NI	497.1 D	152.9 D	66.5 E	54.1 D	32.3 D
		(198.8)	(124.9)	(54.3)	(44.1)	(26.4)
Fert., Lime, Bark, Ash	PT	952.5 D	116.4 D	37.4 E	53.5 D	25.5 D
		(168.1)	(93.4)	(30.0)	(42.9)	(20.4)
	NI	351.9 D	64.5 D	27.2 E	22.1 D	13.2 D
		(86.7)	(59.6)	(25.9)	(21.1)	(12.6)
Sludge	PT	4814.7 BC	3359.5 BC	1080.1 CD	1554.6 BC	734.7 BC
		(2010.4)	(1459.4)	(469.2)	(671.0)	(319.2)
	NI	5893.4 AB	4498.4 AB	1957.3 AB	1590.7 BC	950.4 AB
		(1610.6)	(1014.9)	(441.6)	(385.9)	(214.4)
Sludge, Bark	PT	3970.4 C	2699.2 C	867.9 D	1241.0 C	590.3 C
		(1091.7)	(782.0)	(251.4)	(359.5)	(171.0)
	NI	5746.0 AB	4549.1 AB	1979.4 AB	1608.6 BC	961.1 AB
		(2285.0)	(1717.4)	(747.2)	(607.3)	(362.8)
Sludge, Ash	PT	6586.4 A	4837.7 A	1555.4 BC	2224.3 A	1058.0 A
		(1519.2)	(1140.7)	(366.8)	(524.5)	(249.5)
	NI	3742.4 C	2297.7 C	1304.3 CD	1060.0 C	633.3 C
		(1552.7)	(1282.5)	(558.0)	(453.5)	(271.0)
Sludge, Ash Bark	PT	4810.4 BC	3391.1 BC	1090.3 CD	1559.1 BC	741.6 BC
		(2575.9)	(2137.7)	(687.3)	(982.9)	(467.5)
	NI	6910.8 A	5421.6 A	2359.0 A	1917.2 AB	1145.4 A
		(1864.2)	(1361.2)	(592.3)	(481.3)	(287.6)

crop, in total annual production, or in production of individual plant parts. PT treated trees had 1.02 to 2.07 times as much standing crop as NI treated trees of the same tree species and soil treatment. Annual production of PT treated trees was from 1.33 to 1.65 times larger than NI trees in Virginia pines and in loblolly pines on bark soil treatment. Likewise, PT treated Virginia pines and loblolly pines on bark treated soils had greater production of stems, needles, and branches than NI treated trees. PT treated loblolly pines on fertilizer treated soils had larger standing crops and greater annual stem production than NI treated trees. However, the PT trees had less total annual production, less needle production, and less branch production than NI trees.

At the end of the third growing season on the borrow pit site, trees on sludge ammended soils had a greater ($P = .05$) standing crop in $kcal/m^2$ than trees on soils without sludge. Differences between mycorrhizal treatments were not significant, probably because trees on non-inoculated plots were heavily colonized by Pisolithus tinctorius remaining from the prior plantation (Berry and Marx (1982). However, total production of NI trees was frequently greater than production of PT trees on sludge ammended soils and the reverse was true on soils not ammended with sludge.

Partitioning of annual production to individual tree parts for the fertilizer treatment on the airport site are estimated on Table 4-7. Production of tree parts was calculated from the plant part-treatment specific regression values in Table 4-3 and calorie values in Table 4-4 as:

$$\text{Kcal of tree part} = [a + b\ (PVI)] \times \text{cal/gm}$$

Therefore, the percentage distributions in Table 4-7 are defined by the regression values in Table 4-3. As a result, the percentage distribution

TABLE 4-7. Distribution of Annual Production to Stems, Branches and Needles. Values are for the fertilizer treatment on the airport site during the fifth growing season.

	% Stem	% Branch	% Needles
Loblolly-PT	46.1	21.9	31.9
Loblolly-NI	35.4	21.1	43.5
Virginia-PT	20.6	38.6	40.8
Virginia-NI	23.5	38.9	37.6

for all other treatments are within a few one hundredths of a percent of the values in Table 4-7. The data in Figure 4-7 suggests that inoculation affects partitioning of annual production to aboveground tree parts. However, as with the regression values in Table 4-3, crown closure in the Virginia pines and in the larger PT treated loblolly pines masks the response.

In summary, standing crop, total annual production, and production of individual tree parts all demonstrate a similar response to inoculation and soil treatments. Within tree species sludge-NI>sludge PT>Fert PT>Fert NI. Although the data in Table 4-5 are inconclusive, they suggest that inoculated trees are at least as large or are up to twice as large as noninoculated trees of the same species and soil treatment except on sludge amended soils. Tables 4-3 and 4-7 suggest that mycorrhizal inoculation increases the crown (stem + needle) to stem ratio in trees which are not subject to the competitive affects of crown closure.

3. Flow of Energy Through the Mycorrhizal Pathway Estimated on the Basis of Sporocarp Production. There were no sporocarps produced prior to 14 June or after 25 November on the Copper Hill sites; or prior to 4 August or after 11 November on the borrow pit site. Temporal distribution of sporocarp biomass from 14 June to 25 November is graphed in Appendix V, Figures 4-1 to 4-4. Quantity and time of appearance varies between sites, tree species, fungal species, and soil treatments. Accordingly, quantity and quality of fungal biomass in the form of sporocarps available to grazing and detritus food chains is strongly pulsed. Total production of fungal biomass and number of sporocarps by treatment are given in Tables 4-8 and 4-9 for the Copper Hill sites and in Tables 4-10 and 4-11 for the borrow pit site. Although the values are not always

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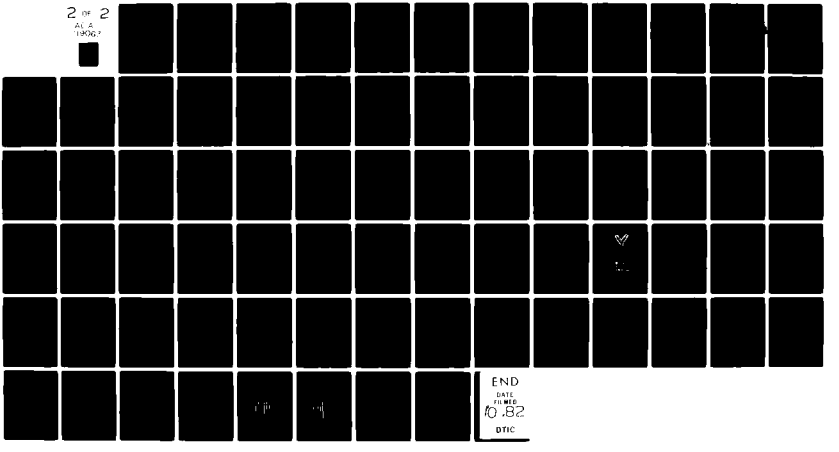

TABLE 4-8. Annual Production of Sporocarp Biomass on the Copper Hill sites; dry wt in gms/m^2. n = number of replicate plots; No. in parenthesis = standard deviation.

	n	*Pisolithus tinctorius*	*Rhizopogon* sp.	*Suillus luteus*
Airport Site				
Loblolly-Fertilizer				
FT	3	41.0 A (37.4)	.03 (.04)	0.0
NI	3	22.8 A (11.7)	.06 (.06)	0.0
Loblolly-Bark	3	39.2 A (12.9)	0.0	0.0
NI	3	10.4 A (9.1)	0.0	0.0
Virginia-Fertilizer				
FT	3	46.8 A (32.0)	.03 (.04)	0.0
NI	3	21.8 AB (7.9)	.09 (.10)	0.0
Virginia-Bark				
FT	3	38.4 AB (11.7)	0.0	0.0
NI	3	5.6 B (9.7)	0.0	0.0
Sludge Site				
Loblolly-Fertilizer				
FT	5	9.6 B (3.3)	.28 (.36	0.0
NI	5	.15C (.26)	.07 (.12)	.03 (.08)
Loblolly-Sludge				
FT	5	15.1 A (1.5)	.03 (.07)	.45 (.97)
NI	5	.7 C (.98)	.08 (.17)	1.25 (1.24)
Shortleaf-Fertilizer				
FT	5	16.2 A (5.7)	.25 (.34)	0.0
NI	5	.49B (.73)	.23 (.25)	0.0
Shortleaf-Sludge				
FT	5	11.5 A (5.0)	.08 (.13)	0.0
NI	5	0.0 B	.06 (.10)	0.0
Virginia-Fertilizer				
FT	5	NA	NA	NA
NI	5	0.0	.12 (.28)	0.0
Virginia-Sludge				
FT	5	NA	NA	NA
NI	5	.34 (.49)	.07 (.12)	.21 (.23)

TABLE 4-9. Annual Number of Sporocarps Produced on the Copper Hill Sites. sc = sporocarps/m^2; # of plots = observation of a species on a plot at least once during the year.

	n	*Pisolithus tinctorius* sc/m	*Pisolithus tinctorius* # of plots	*Rhizopogon* sp. sc/m	*Rhizopogon* sp. # of plots	*Suillus luteus* # of plots	*Thelephora terrestris* # of plots
Airport Site							
Loblolly Fertilizer							
PT	3	1.37 A (1.24)	2	.04 (.04)	2	0	2
NT	3	.95 A (.55)	3	.11 (.55)	2	0	3
Loblolly-Bark							
PT	3	1.33 A (.66)	3	0.0	0	0	1
NT	3	.36 A (.32)	2	0.0	0	0	2
Virginia-Fertilizer							
PT	3	1.97 A (1.62)	3	0.3 (0.04)	1	0	3
NT	3	.35 A (.18)	3	.11 (.09)	2	0	3
Virginia-Bark							
PT	3	1.57 A (.83)	3	0.0	0	0	3
NT	3	.16 A (.3)	1	0.0	0	0	3
Sludge Site							
Loblolly-Fertilizer							
PT	5	.45 A (.18)	5	.06 (.06)	4	0	1
NT	5	.01 B (.02)	2	.03 (.04)	2	1	4
Loblolly-Sludge							
PT	5	.95 A (.55)	5	.03 (.07)	2	2	4
NT	5	.03 B (.03)	5	.06 (.12)	2	3	4
Shortleaf-Fertilizer							
PT	5	.48 A (.20)	5	.15 (.20)	3	0	1
NT	5	.03 B (.03)	3	.15 (.20)	4	0	4
Shortleaf-Sludge							
PT	5	.62 A (.38)	5	.09 (.16)	2	0	0
NT	5	0.0 B	0	.06 (.10)	2	0	2
Virginia-Fertilizer							
PT	5	NA	NA	NA	NA	NA	NA
NT	5	0.0		.07	1	0	4
Verginia-Sludge							
PT	5	NA	NA	NA	NA	NA	NA
NT	5	.04 (.05)	2	.08 (.14)	2	3	5

TABLE 4-10. Annual Production of Sporocarp Biomass on the Borrow Pit Site; Dry Weight in gms/m^2. n = Five Replicate Plots; No. in parenthesis = Standard Deviation

		Pisolithus tinctorius	Suillus luteus
Control	PT	.226 CD (.505)	0 A
	NI	.798 BCD (1.14)	.115 A (.257)
Fert., Lime	PT	0 D	0 A
	NI	0 D	0 A
Bark, Fert., Lime	PT	.054 D (.122)	0 A
	NI	.174 CD (.389)	0 A
Fert., Lime, Ash	PT	.342 CD (.765)	0 A
	NI	.359 CD (.802)	0 A
Fert., Lime, Bark, Ash	PT	.057 D (.087)	0 A
	NI	.206 CD (.462)	0 A
Sludge	PT	3.18 ABCD (3.90)	.032 A (.070)
	NI	3.20 ABCD (2.89)	.096 A (.213)
Sludge, Bark	PT	3.57 ABC (2.16)	.137 A (.202)
	NI	5.98 A (3.67)	.082 A (.184)
Sludge, Ash	PT	3.45 ABCD (2.80)	.039 A (.088)
	NI	1.97 BCD (1.98)	.008 A (.018)
Sludge, Ash, Bark	PT	3.92 AB (1.24)	.054 A (.121)
	NI	6.04 A (6.14)	.142 A (.208)

TABLE 4-11. Annual Number of Sporocarps Produced on the Borrow Pit Site SC = Sporocarps/m^2; # of Plots = Observation of a Species on a Plot at Least Once During the Year. n = 5 Plots

		Pisolithus tinctorius		*Suillus luteus*	
		SC/m^2	# of Plots	SC/m^2	# of Plots
Control	PT	.022 C (.049)	1	0 C	0
	NI	.022 C (.030)	2	.016 C (.037)	1
Fert., Lime	PT	.001 C (.012)	1	.001 C (.012)	1
	NI	0 C	0	0 C	0
Bark, Fert., Lime	PT	.011 C (.025)	1	0 C	0
	NI	.005 C (.012)	1	0 C	0
Fert., Lime, Ash	PT	.017 C (.037)	1	.005 C (.012)	0
	NI	.011 C (.015)	2	0 C	0
Fert., Lime, Bark, Ash	PT	.017 C (.025)	2	.005 C (.012)	1
	NI	.017 C (.025)	2	0 C	1
Sludge	PT	.172 AB (.151)	4	.244 AB (.189)	5
	NI	.189 AB (.156)	4	.183 ABC (.349)	3
Sludge, Bark	PT	.244 A (.123)	5	.239 AB (.279)	5
	NI	.272 A (.115)	5	.083 BC (.113)	2
Sludge, Ash	PT	.228 A (.135)	5	.039 BC (.042)	3
	NI	.078 BC (.041)	5	.106 BC (.160)	2
Sludge, ash, bark	PT	.178 AB (.093)	5	.094 BC (.099)	3
	NI	.311 A (.218)	5	.356 A (.281)	5

significantly different, PT plots always produced greater numbers and biomass of Pisolithus tinctorius sporocarps than comparable NI plots at Copper Hill. As can be seen by the standard deviations in Tables 4-8 and 4-10, the biomass of sporocarps produced varies greatly between plots within treatments. Sporocarps may be absent or scarce on some plots, while other plots in the same treatment produce large numbers of sporocarps (see Tables 4-9 and 4-11). All values underestimate sporocarp biomass because: (1) It is not possible to quantitatively harvest Thelephora terrestris since these sporocarps are imbedded in the soil matrix. (2) Suillus luteus sporocarps are short-lived and were often degraded or partially gone when sampled. (3) Rhizopogon sporocarps were often partially or totally liquified. (4) Pisolithus tinctorius sporocarps mature and disseminate spores from the apex as the base matures. Collected specimens had often lost biomass through dissemination of spores (in many cases more than half of their volume) or were immature. (5) Sporocarps of P. tinctorius originating from trees on the plots occurred outside the plot boundaries. I have observed sporocarps more than 10 meters from the closest stem on other sites.

All in all, Pisolithus sporocarps are most available to production estimates based on harvest procedures. To assess the magnitude of production outside the plots, sporocarps were collected from a 3 meter wide area surrounding the fertilizer and bark plots at the airport site (see Table 4-12). Even without the first three collection dates, which had high production on the plots, sporocarp production off the plots would add an average of 8.9 gm/m^2 to bark treated plots and 12.4 gm/m^2 to fertilizer treated plots. Even though these sporocarps assuredly originated from trees on the plots, their biomass is not included in Table

TABLE 4-12. Biomass of Pisolithus tinctorius Sporocarps Which Originate from the Test Plots but are Produced Outside the Plots. Collections are composites from the area surrounding the bark treatment plots and fertilizer treatment plots on the airport site.

	Bark plots gms	Fertilizer Plots gms
28 June	Not collected	Not collected
27 July	Not collected	Not collected
13 August	Not collected	Not collected
25 August	1240	1530
6 September	819	1570
23 September	293	131
8 October	151	138
21 October	97	301
4 November	61	56
TOTAL	2661	3726

4-8 because it is impossible to determine which trees on which plots are the source of their energy. It might be assumed that plots with high sporocarp production produced a similar proportion of the off-plot biomass.

As can be seen in Table 4-13, the percent ash and calorie content per gram of sporocarp for one field collection (Aug. 25) differed according to treatment and tree species (significant at the P = .05 level). However, cal/gm ash-free dry weight differed only between the two species.

Comparison of sporocarps produced on the same plot at different times in the growing season, as shown in Table 4-14, revealed differences as great as that found between plots. The sporocarp matures from the apex down to the base. Therefore, individual sporocarps will vary in the proportion of mature and immature spores. And, as shown in Table 4-15, calorie and ash content of mature spores and immature spores and bases differed with the latter having a much higher ash content and consequently a lower cal/gm dry weight. Accordingly, differences in sporocarp age explain some of the variation found in the plot samples (Tables 4-13 and 4-14).

The mean calorie content of all samples of P. tinctorius sporocarps (Tables 4-13 and 4-14) was 3185 cal/gm dry weight, a value that was used to convert dry weight to calories per plot for all treatments and dates. Based on this conversion, annual production of P. tinctorius basidiocarps in kcal/m^2 was calculated as shown in the first column of Tables 4-16 and 4-17. In most cases, trees inoculated with P. tinctorius in the nursery produced more calories of P. tinctorius sporocarps than non-inoculated trees even four or five years after transplanting to the field.

TABLE 4-13. Variation in Energy Content of *Pisolithus tinctorius* Basidiocarps by Treatment.

	n	% Ash	cal/gm dry wt.	cal/gm ash free dry wt.
Virginia				
NI	5	53.4 a	2128.3 d	4555.4 b
		(1.7)	(25.04)	(44.43)
PT	5	7.4 d	4522.8 a	4884.9 b
		(1.0)	(42.87)	(46.27)
Loblolly				
NI	5	33.9 b	3245.9 c	5205.0 a
		(2.0)	(65.99)	(289.30)
PT	5	11.9 c	4041.0 b	4934.0 a
		(0.9)	(18.88)	(23.04)

TABLE 4-14. Variation in Energy Content of Pisolithus tinctorius Basidiocarps as a Function of Date of Collection. Sporocarps from a single plot (PT-Fertilizer-Airport) were composited, homogenized, and analyzed by date of collection. Values are the means and standard deviations (in parentheses) of three subsamples from each date.

Date Mo.	Day	% Ash	cal/gm dry wt.	cal/gm ash free dry wt.
Jun.	28	23.5	3111.5 (141.25)	4066.0 (184.59)
Jul.	27	40.8	1366.5 (89.88)	2307.6 (151.77)
Aug.	13	30.2	2681.8 (176.08)	3840.3 (252.15)
Sept.	25	30.7	3567.8 (79.66)	5146.0 (114.89)
Oct.	6	28.5	4224.7 (77.40)	5911.6 (108.33)
Nov.	8	41.1	2338.4 (87.77)	3973.1 (149.09)
Nov.	21	33.9	3238.1 (126.44)	4902.0 (191.38)

TABLE 4-15. Variation in Energy Content of Mature and Immature Portions of Pisolithus tinctorius Basidiocarps. Sporocarps were collected from a loblolly pine plantation approximately 100 meters from the airport site. Approximately 50 sporocarps were separated into mature spores (.933 kg dry wt.) and immature spores plus bases (3.089 kg dry wt.). The two samples were independently ground and homogenized. Values are the means and standard deviations (in parentheses) of 3 subsamples from each source.

	% Ash	cal/gm dry wt.	cal/gm/ash free dry wt.	n
Mature spores	5.34	5652.2 (67.72)	5971.0 (71.5)	3
Immature spores and bases	64.10	1888.2 (112.84)	5262.0 (314.5)	3

TABLE 4-16. Total Annual Production of Trees and Pisolithus Sporocrops at Copper Hill.

	n	Sporocarp kcal/m^2	Sporocarp and tree kcal/m^2	Percent increase NPP	Percent needles	Percent stem & branch	Percent sporocarp
Airport Site							
Loblolly-Fertilizer							
PT	3	130.6 A	1502.7 A	8.38 A	29.50 A	62.85 A	7.64 A
		(119.1)	(862.0)	(3.99)	(1.09)	(2.34)	(3.44)
NI	3	72.6 A	1620.3 A	4.80 B	41.52 A	53.90 B	4.58 A
		(37.3)	(908.7)	(0.61)	(0.24)	(0.31)	(0.55)
Loblolly-Bark							
PT	3	124.9 A	1915.0 A	7.04 A	29.83 B	63.57 A	6.60 A
		(41.4)	(731.6)	(1.24)	(0.33)	(0.70)	(1.03)
NI	3	33.1 A	1117.2 A	3.59 B	42.03 A	54.58 B	3.39 A
		(30.0)	(263.7)	(3.45)	(1.41)	(1.83)	(3.23)
Virginia-Fertilizer							
PT	3	149.1 A	4651.9 A	3.27 A	39.44 A	57.40 C	3.17 A
		(101.0)	(2800.3)	(0.73)	(0.34)	(0.36)	(0.69)
NI	3	69.4 AB	3611.6 A	1.95 AB	37.29 B	60.80 B	1.91 AB
		(25.2)	(597.2)	(0.65)	(0.71)	(0.86)	(0.63)
Virginia-Bark							
PT	3	122.3 AB	5409.8 A	2.41 A	39.81 A	57.83 C	2.35 A
		(37.3)	(1480.5)	(0.86)	(0.34)	(0.49)	(0.82)
NI	3	17.8 B	3975.5 A	0.63 B	37.37 B	62.01 A	0.62 B
		(31.0)	(1129.5)	(1.09)	(0.40)	(0.67)	(1.06)
Sludge Site							
Loblolly-Fertilizer							
PT	5	30.6 B	1081.2 C	4.69 A	30.70 C	64.93 B	4.37 A
		(10.5)	(687.8)	(4.01)	(1.17)	(2.42)	(3.59)
NI	5	0.5 C	879.6 C	0.06 B	43.53 A	56.41 C	0.06 B
		(0.8)	(566.3)	(0.10)	(0.05)	(0.05)	(0.10)
Loblolly-Sludge							
PT	5	48.1 A	2898.6 B	1.78 B	31.56 B	66.69 A	1.75 B
		(4.8)	(864.1)	(0.46)	(0.14)	(0.30)	(0.44)
NI	5	2.2 C	4702.7 A	0.04 B	43.53 B	56.43 C	0.04 B
		(3.1)	(2364.5)	(0.07)	(0.03)	(3.90)	(0.07)
Shortleaf-Fertilizer							
PT	5	51.6 A	829.1 AB	8.60 A	33.25 C	58.97 B	6.71 A
		(18.1)	(488.1)	(4.88)	(1.46)	(2.59)	(2.43)
NI	5	1.6 B	438.6 B	0.47 B	38.02 A	61.51 A	0.47 C
		(2.3)	(175.9)	(0.62)	(1.22)	(1.54)	(0.62)
Shortleaf-Sludge							
PT	5	36.6 A	1532.2 A	2.43 B	35.20 B	62.41 A	2.38 B
		(15.9)	(451.1)	(0.85)	(0.29)	(0.52)	(0.81)
NI	5	0.0 B	1396.7 A	0.0 B	37.59 A	62.40 A	0.0 C
			(1069.3)		(0.02)	(0.01)	
Virginia-Fertilizer							
NI	5	(0.0)	1524.5	0.0	37.60	62.40	0.0
			(696.6)		(0.01)	(0.01)	
Virginia-Sludge							
NI	5	1.1	5745.7	0.02	37.59	62.38	0.02
		(1.6)	(1589.4)	(0.04)	(0.01)	(0.03)	(0.04)

TABLE 4-17. Total Annual Production of Trees and *Pisolithus* Sporocarps at the Borrow Pit Site.

		Sporocarps kcal/m^2	Sporocarp and tree kcal/m^2	Percent Increase NPP	Percent Needles	Percent Stem & Branch	Percent Sporocarp
Control	PT	0.7 CD	143.1 D	1.50 B	31.71 C	66.91 A	1.40 AB
		(1.6)	(204.9)	(3.36)	(1.01)	(2.12)	(3.12)
	NI	2.5 BCD	162.6 D	4.58 A	41.83 B	54.31 C	3.86 A
		(3.6)	(143.1)	(9.10)	(3.3)	(4.2)	(7.5)
Fert., Lime	PT	0.0 D	102.8 D	0.0 B	32.15 C	67.85 A	0.00 B
			(41.5)		(0.01)	(0.01)	
	NI	0.0 D	183.0 D	0.0 B	43.51 A	56.49 B	0.00 B
			(110.4)		(0.01)	(0.01)	
Bark, Fert., Lime	PT	0.2 D	44.2 D	0.18 B	32.08 C	67.74 A	0.18 B
		(0.4)	(35.2)	(0.40)	(0.12)	(0.28)	(0.40)
	NI	0.5 CD	148.0 D	0.43 B	43.33 A	56.24 A	0.42 C
		(1.2)	(104.6)	(0.97)	(0.41)	(0.53)	(0.94)
Fert., Lime, Ash	PT	1.1 CD	115.2 D	0.94 B	31.87 C	67.25 A	0.90 B
		(2.4)	(82.2)	(2.09)	(0.65)	(1.37)	(2.01)
	NI	1.1 CD	154.1 D	0.72 B	43.32 A	56.09 B	0.69 B
		(2.5)	(124.9)	(1.61)	(0.68)	(0.88)	(1.55)
Fert., Lime, Bark, Ash	PT	0.2 D	116.6 D	0.08 B	32.12 C	67.79 A	0.18 B
		(0.3)	(93.6)	(0.12)	(0.04)	(0.08)	(0.11)
	NI	0.6 CD	63.1 D	0.41 B	43.34 A	56.25 B	0.41 B
		(1.5)	(61.0)	(0.93)	(0.40)	(0.51)	(0.91)
Sludge	PT	10.1 ABCD	3369.6 BC	0.30 B	32.06 C	67.65 A	0.30 B
		(12.4)	(1462.5)	(0.37)	(0.12)	(0.25)	(0.37)
	NI	10.2 ABCD	4508.6 AB	0.25 B	43.40 B	56.35 B	0.25 B
		(9.2)	(1012.7)	(0.25)	(0.11)	(0.14)	(0.24)
Sludge, bark	PT	11.4 ABC	2710.6 C	0.41 B	32.02 C	67.57 A	0.41 B
		(6.9)	(786.2)	(0.21)	(0.06)	(0.14)	(0.20)
	NI	19.0 A	4568.2 AB	0.41 B	43.33 A	56.26 B	0.41 B
		(11.7)	(1726.7)	(0.16)	(0.07)	(0.09)	(0.16)
Sludge, ash	PT	10.7 ABCD	4848.3 A	0.21 B	32.08 C	67.70 A	0.21 B
		(8.9)	(1146.1)	(0.15)	(0.01)	(0.10)	(0.15)
	NI	6.3 BCD	3004.0 C	0.37 B	43.35 A	56.28 B	0.36 B
		(6.3)	(1277.7)	(0.57)	(0.24)	(0.32)	(0.56)
Sludge, Ash, Bark	PT	12.5 AB	3403.5 BC	0.51 B	31.99 C	67.50 A	0.51 B
		(3.9)	(2137.6)	(0.37)	(0.12)	(0.25)	(0.36)
	NI	13.2 A	5440.8 A	0.34 B	43.36 A	56.30 B	0.34 B
		(19.5)	(1366.0)	(0.37)	(0.16)	(0.21)	(0.37)

4. Partitioning of Annual Primary Production to Plant Growth Detritus and the Mycorrhizal Pathway. Previous experiments (Appendix 3) clearly demonstrate that inoculation with mycorrhizal fungi before planting can increase primary production in young pine plantations. Inoculation with Pisolithus at the Copper Hill site did result in bigger trees after a 4 or 5 year growth period, as compared with non-inoculated seedlings, even though differences were not statistically significant. Since there were no trees without ectomycorrhizae, these experiments did not directly demonstrate that the fungus increases plant growth. However, it may be assumed that benefits to the plants outweigh the cost of photosynthate lost to mycobionts.

Since no aphids and few grazers were observed on these sites, practically all plant production is currently flowing through the detritus and mycorrhizal pathways. The current production of woody tissue (stems and branches) will not be available as detritus until sometime in the future. Current annual needle production will become detritus next year. Current year plant detritus input is the result of needle and branch fall from prior years production on plants which were at least an order of magnitude smaller (see Table 4-1). Litter fall as a measure of flow through the detritus pathway was not measured directly. Total annual production of needles could be considered as an estimate of detritus production in the current year. Energy in the detritus pathway actually used (decomposed) in the current year would be considerably less.

Energy flow through the mycorrhizal pathway, in the form of sporocarps and hyphal exudation, is available in the soil in the current year. Mantle and soil hyphae are partitioned between current and future years use. Sporocarps appear and disappear (consumed or decomposed) within

the current year. For reasons already discussed, sporocarp production is a minimal estimate of annual energy flow through the mycorrhizal pathway. Soil organic content on these sites was very low prior to establishment of these plots. At the end of the study, the non-bark and non-sludge plots still had organic contents of less than 0.66% at both Copper Hill and SRP. Therefore, the energy source for biosynthesis of fungal tissue has to be current photosynthesis.

Since sporocarps are produced from current photosynthate, they are part of the current year's NPP. Addition of annual fungal biomass (Column 1, Tables 4-16 and 4-17) to annual plant production (from Column 2, Tables 4-5 and 4-6) increases estimates of annual NPP by as much as 8.38% (Columns 2 and 3, Table 4-16). Inclusion of sporocarps originating from the plots, but produced outside the plot bounds (Table 4-12), averaged across all plots, results in estimates of NPP that are as much as 11.0% greater than tree biomass alone. Individual plots with high annual plant production rates also tended to have high sporocarp production rates. Since photosynthesis by inoculated plants produced more plant biomass and sporocarps, the fungi must either increase the photosynthetic rate or improve the efficiency of energy utilization or both.

Partitioning of energy between needles, stems and branches, and sporocarps is shown in Tables 4-16 and 4-17, Columns 4, 5, and 6. As much as 7.64% (average of 4.94%) of NPP (Table 4-16, Column 6) was shunted through the sporocarp portion of the mycorrhizal pathway on inoculated plots at the airport site. Inclusion of sporocarps produced outside the plot bounds raised this value to 10%. As previously discussed, this value is a very low estimate of Pisolithus sporocarp production, and does not include the sporocarps of other ectomycorrhizal fungal species

present on these plots. In comparison, needle production on the same plots is only 29.5% of NPP. Values for younger trees at SRP (Table 4-17) are smaller. These estimates of energy flow through the mycorrhizal pathway did not include fungal respiration or the biomass of intra cortical, mantle, and soil hyphae. The data show that the sporocarps of mycorrhizal fungi alone represent a large flow of primary production energy in the pine plantation ecosystems.

Total energy flow through the mycorrhizal pathway is obviously much larger than that estimated, based on sporocarp production alone. It is interesting to speculate on the total flow of energy through the mycorrhizal pathway when the other flows not assessed in this study (see Fig. 2-1) are included. Hepper (1977) found that 17% of the weight of heavily infected roots can be fungal biomass. Vogt and Edmonds (1980b) found that as much as 29% of the dry weight of fine roots was mycorrhizae. Harley (1971) estimates that approximately 10% of the matter usually reported as dry weight biomass of roots is actually fungal mantle. If the top to root ratio is estimated as 1:1, then using Harley's value the standing crop of mantle for the airport-loblolly - fertilizer-PT treatment would be on the order of 312 kcal/m^2. Vogt and Edmonds (1980b) studies indicate that approximately 70% of the mycorrhizae are turned over every year. Thus, annual production of mantle hyphae can be estimated to be on the order of 218 kcal/m^2/yr. This is a low estimate because it does not presuppose any increase in fungal biomass with age of the tree stand and plant biomass is expanding exponentially. Belowground tree production would likewise be estimated at 1235 kcal/m^2/yr.

There are very few estimates of the standing crop of soil hyphae of mycorrhizal fungi in the literature. Estimates of basidiocarp to

belowground hyphae ratios range from 1:10 to 1:1000 (Hurley, 1972). For this study a 1:10 ratio would place total standing crop of belowground hyphal biomass at 1300 kcal/m^2. This estimate places standing crop of soil hyphae (total belowground hyphae minus mantle) at 31 kcal/m^2.

Soil hyphae must turn over at least as fast as the mycorrhizae from which they originate (70%/yr, Vogt and Edmonds, 1982). In all likelihood these very small structures turn over much faster, maybe even several times per year. All estimates are speculative, but an estimate of 50 kcal/m^2/yr would be conservative for these pine plantations.

For the airport-loblolly-fertilizer-PT plots, we can estimate net plant production at 2607 kcal/m^2/yr (1372 kcal/m^2/yr aboveground measured plus 1235 kcal/m^2/yr belowground estimated). Similarly, annual fungal biomass production would come to 438 kcal/m^2/yr (sporocarps on plots 130.6 kcal/m^2/yr measured, mantle 218 kcal/m^2/yr estimated, soil hyphae 50 kcal/m^2/yr estimated). Adding fungal production to the estimate of tree production gives an estimate of total net production of 3045 kcal/m^2/yr. According to these calculations, 14.4% of the current photosynthate is being distributed as fungal biomass, not including plant exudation, fungal exudation, and fungal respiration and maintenance.

Admittedly, these estimates relate only to ectomycorrhizae on young pine trees at a unique site. Mycorrhizal fungi are present in mature systems (see Appendix 1), and produce large quantities of mycorrhizae (Vogt and Edmonds, 1980b) and sporocarps (Thacker, 1971; Vogt and Edmonds, 1980a). It seems likely that we will find that the mycorrhizal pathway is important through all stages of succession in most terrestrial ecosystems. The fungal species composition of mutualonts probably changes to reflect the change in soil environment over successional time. For

for example, in these studies Suillus lueteus was rarely observed on plots prior to crown closure; whereas Thelephra terrestris, Rhizopogon sp., and Pisolithus tinctorius were frequently observed with the smallest trees in the most open stands. The experiments reported here and the voluminous information in the literature support the hypothesis that mycorrhizal fungi are a major pathway for distribution of energy in terrestrial ecosystems. It is probable that enhanced photosynthetic capability of plants resulting from mycorrhizae more than offsets the energy cost of this pathway. Paul and Kucey (1981) found that photosynthesis per unit of plant tissue in mycorrhizal plants was 7% greater than non-mycorrhizal control plants. Furthermore, the pathway is qualitatively important because it distributes unique combinations of resources to soil heterotrophs in localized sites through a physically controlled pipeline which links abiotic and biotic ecosystem components on a very short time scale as compared with detritus and grazing pathways.

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APPENDICES

APPENDIX 1.

PREVALENCE OF MYCORRHIZAE IN THE BIOSPHERE

Mycorrhizae have only been known to man since the mid 1800's (Vittadini, 1842; Kamienski, 1881; Frank, 1885). There is now evidence that they have been present for some 300 million years. Importance in ecosystem processes is dependent on the prevalence of mycorrhizae as structures in ecosystems. They are present on most individuals in the vast majority of vascular plant species in all major terrestrial biomes of the world (see review by Meyer, 1973). The only exceptions to a general presence of mycorrhizae appear to be aquatic systems and systems on soils which are normally water saturated.

A. Fossil Record

Not only are mycorrhizae common in ecosystems today, it appears that they have been so over evolutionary time. "Fungal infections in fossilized roots from the Devonian and Carboniferous periods (Osborn, 1909; Kidston and Lang, 1921; Boullard and Lemoigne, 1971) look remarkably like some vesicular-arbuscular (VA) infections in living roots of today. Rootlets of the Palaeozoic gymnosperm genus Cordaites, for example, were often found to contain a fungal endophyte with vesicles and large, mainly aseptate hyphae (Osborn, 1909). Some cortical cells contained dark masses interpreted as fungal clumps and resembling arbuscules. This interpretation, however, was questioned by Cridland (1962) who did not consider the endophyte to be mycorrhizal. As in present-day

VA mycorrhizal infections, the fungus occurred in the root cortex but not in the endodermis and stele, and the infected roots appeared undamaged. Some of the large fungal spores recovered from Pleistocene deposits in North America (Dowding, 1959; Srivastava, 1968) could be mistaken for present-day spores of Endogone, the VA mycorrhizal fungus par excellence. These ancient spores, sometimes called Rhizophagites, were around 50 to 80 μm in diameter and thus similar in size to the smaller or their modern relatives" (Hayman, 1978).

The earliest records of even the precursors of modern roots include mycorrhizae. Lewis (1973) suggests that biological invasion of primordial land was faced with the compounded problem of limited energy (fixed carbon compounds) nitrogen, and phosphorus. He suggests that the problem may have been solved by a three organism mutualism between a carbon fixer (algae like), a nitrogen fixer (capacity still restricted to bacteria), and a fungi (mycorrhizae as a class mitigate P deficiencies in plants); and that this is the evolutionary source of modern mycorrhizal associations.

B. Prevalence of Mycorrhizal Associations in Vascular Plants

Mycorrhizal associations are so common in non-aquatic vascular plants that non-mycorrhizal species are the exception. Only a few plants, such as sedges and crucifers, do not normally form mycorrhizae.

Ectomycorrhizae are common in both Gymnosperms (Pinaceae, Cupressanceae) and Angiosperms (Salicaceae, Betulacceae, Fagaceae, Juglandaceae, Ulmaceae, Rosaceae, Leguminosae, Sapendaceae, Aceraceae, Tilinaceae, and Ericaceae) (Meyer, 1973). They typify only about 5% of the world's plant species (Trappe, 1971; Gerdemann and Trappe, 1974). But, ectomycorrhizal associations predominate in tree species which are economically important

for lumber and pulp production, and are important in ornamentals and nut crops.

Ericalean mycorrhizae have not been well-studied, but it is likely that most members of the five families in the Ericales are mycorrhizal (Hayman, 1978).

Orchidaceous mycorrhizae are restricted to one plant family although they may be similar to mycorrhizae in Gentianacea and in the bryophyte Aneura (Hayman, 1978).

VA mycorrhizae form associations with far more species, families, and orders of plants than all other types of endo- and ectomycorrhizae combined (Hayman, 1978).

> "They occur in most cultivated crops and in most plant species growing in natural ecosystems. Important crops with VA mycorrhiza include wheat, maize, potatoes, beans, soybeans, tomatoes, strawberries, apples, oranges, grapes, cotton, tobacco, tea, coffee, cacao, sugarcane, sugar maple and rubber trees (see Gerdemann, 1968). Wild plants with VA mycorrhiza (see Stelz, 1968; Khan, 1974; Mejstrik, 1972; Mosse and Hayman, 1977) include trees such as ash and oak, shrubs such as hazel, climbers such as honeysuckle, and a multitude of herbaceous plants of woodland and meadow, mountain and seashore. VA mycorrhizae are especially widespread in tropical tree species (Redhead, 1968). In addition to angiosperms and gymnosperms, they are found in pteridophytes and bryophytes. Very few of the many plant families examined do not have VA mycorrhizae (Maeda, 1954; Boullard, 1968; Gerdemann, 1968; Harley, 1969). Only the Ericales, Orchidaceae and certain ectomycorrhizal families such as the Pinaceae and Betulaceae are believed to definitely lack VA mycorrhiza, although it may be rare or absent from many species in such families as the Cruciferae, Chenopodiaceae, Caryophyllaceae, Cyperaceae and Polygonaceae, Swedes, for example, seem to be non-mycorrhizal (Hayman et al., 1975). It is widespread in the two major crop families, the Gramineae and Leguminosae." (Hayman, 1968)

C. Distribution and Frequencies of Mycorrhizae in Biomes.

Distribution of type of mycorrhizae is broadly correlated to biome type. Most shrubs and grasses are endomycorrhizal. Ectomycorrhizae are more profuse in temperate forests and VA mycorrhizae are more common in

tropical forests (Hayman, 1978). They are generally absent only in aquatic ecosystems and terrestrial ecosystems with very wet habitats (Maeda, 1954; Konoe, 1962; Mejstrik, 1965). They are ubiquitous components of arctic, temperate, and tropical ecosystems (Maeda, 1954; Gerdemann, 1968). The prevalence of mycorrhizae in ecosystems is evident from the list of mycorrhizal plant species in the preceding section. Furthermore, the vast majority of individuals in plant species which form mycorrhizae are found to be mycorrhizal in nature.

D. Fungal Species as Mycobionts

"It is estimated that more tha 2100 species of fungi form ectomycorrhizae with forest trees in North America. Most of these fungi are members of the higher Basidiomycetes that produce mushrooms or puffballs. Certain Ascomycetes, such as truffles, also form ectomycorrhizae (Trappe, 1971). Among the Basidiomycetes there are Hymenomycetes such as Boletus, Cortinarius, Suillus, Leccinum, Amanita, Tricholoma, Laccaris and Lactarius. The Gasteromycetes include such examples as Rhizopogon, Pisolithus, and Scleroderma (Smith, 1971). According to Trappe (1971), there are three orders of ectomycorrhizal ascomycetes -- Eurotiales (Cenococcum graniforme) Tuberales (truffles) and the Pezizales" (Marx and Krupa, 1978). Entire genera and even families consist of obligate mycobionts (Trappe and Fogel, 1977). The taxonomy of ectomycorrhizal fungi is based on the sexual reproduction structures. Many attempts have been made to correlate form and color of the mycorrhiza to fungal species (Zak, 1973). Because morphological characteristics vary with tree species and soil environment, these classification systems have been of limited use. However, they can be useful with some fungal species in known environments in association with known phycobionts (Marx, 1978).

Little is known about the taxonomy of the mycobionts in ericalean mycorrhizae. It has been possible to isolate fungal hyphae from the mycorrhizae, culture them, and establish typical mycorrhizae in Ericales by aseptic inoculation. However, the fungi persist as sterile hyphae (Freisleben, 1936; Pearson and Read, 1973a). Pearson and Read (1973a) have obtained the sexual stage of Pezizella ericae from ericalean mycorrhizae. There is controversial evidence that a species of Phoma is an ericalean mycobiont (Ternetz, 1907; Rayner and Smith, 1929; Rayner and Levisohn, 1940. Sevoir et al. (1973)) have shown a serological relationship between basidiocarps of Clavaria sp., which are constantly and specifically associated with Rhododendron and Erica, and the pelotons of ericalean mycorrhizae in thos plant species.

Unlike other endomycorrhizal fungi, the mycobiont of orchidaceous mycorrhizae can be readily isolated and maintained in pure culture. The isolation and identification of orchidaceous mycobionts is comprehensively reviewed by Harley (1969). The two major mycobionts are Armillaria millea and Rhizoctonia sodani. The perfect stages of many of the Rhizoctonia were identified by Warcup and Talbot (1967) as species of Ceratobasidium, Sebacium, Thanatephorus and Tullasnella.

Taxonomic study of VA fungi is difficult because the mycobionts are all obligately mutualistic and have not been grown in pure culture. They have usually been assigned to the genus Endogone, family Endogonaceae, order Mucorales. This order is currently placed in Zygomycotina because the term phycomycetes is now considered taxonomically defunct (Hayman, 1978). Studies on the various possible VA fungi, culminating in the acceptance of Endogone as the VA endophyte, are comprehensively reviewed by Butler (1939), Mosse (1963), Gerdemann (1968) and Harley (1969).

Species of Endogone are distinguished by the morphology of their resting spores. Two major systems of taxonomy based on spore type are currently in use (Mosse and Bowen, 1968; Gerdemann and Trappe, 1974). Therefore, at present there is some confusion regarding genera and species names of VA mycobionts. I will use the name used by the original author.

E. Phycobiont and Mycobiont Specificity

Although some fungal species may be phycobiont species specific, others have a broad host range. For example, in the ectomycorrhizae Suillus gravillei and Suillus tridentinus are host specific on Larix (Meyer, 1973) and Cortinarius hemitrichus is specific for birch (Lange, 1923). Host specificity of certain mycorrhizal fungi is an important characteristic for mycological taxonomists (Trappe, 1962b; Singer, 1975; Thiers, 1975). On the other hand Cenococcum graniforme is capable of forming ectomycorrhizae with over 200 species of plants throughout the world (Trappe, 1964, 1971). Pisolithus tinctorius is known to form ectomycorrhizae on 73 species of forest trees including Abies, Betula, Carya, Eucalyptus, Quercus, Tsuga, and Pinus (Marx, 1977b). Endogone species appear to lack specificity. For example, a single isolate can establish VA mycorrhizae on completely unrelated plants such as onion, strawberry, violet, sweetgum, and diverse legumes and grasses. Furthermore, it is not uncommon for a single species, an individual plant, or even a small segment of root to have many species of fungi. As many as three species of fungi have been isolated from a single ectomycorrhiza (Zak and Marx, 1964). Trappe (1977) has observed hundreds of roots in natural forests ranging from subalpine and timberline habitats to tropical pine and oak stands in North America, Europe, and Japan. "Individual trees usually have at least two different types of mycorrhizae (often five or more) on

their roots by the end of their first growing season. Trees beyond the sapling stage typically have at least five and often dozens of mycorrhizal fungi." Some plant species form mycorrhizal associations with a broad range of fungal species. For example, Trappe (1977) estimates "that some 2,000 species of fungi are potential mycorrhizal associates of Douglas Fir (Pseudotsuga menziesii)". Some plant species form more than one kind of mycorrhizae. Arbutus menziesii is an Ericaceae but it has been shown to form ectendomycorrhizae with Cortinarius zakii (Zak, 1974) and with at least six other ectomycorrhizal fungi including Cenococcum graniforme (Trappe, 1971). Oak is a member of the traditionally ectomycorrhizal Fagaceae family, but it also forms VA mycorrhizae (Grand, 1969). Conversely, Photinia glabra, in the Rosaceae which are commonly endomycorrhizal, forms ectomycorrhizae with Cenococcum graniforme (Grand, 1971). Many woody plants have both ecto- and endomycorrhiza (Meyer, 1973). These include Corylus, Eucalyptus, Juniperces, Liquidamber, Liriodendron and Populus. These two types of infection usually occur on separate roots, but in some plants such as Leptospermun (Baylis, 1962) there can be a double infection with an ectomycorrhizal sheath enclosing a root cortex containing arbuscules of Endogone. Alnus may form ectomycorrhizae and endomycorrhizae, as well as nitrogen-fixing nodules.

APPENDIX 2

MORPHOLOGICAL CATEGORIES OF MYCORRHIZAE

Mycorrhizae have traditionally been separated into three major categories (ectomycorrhizae, endomycorrhizae, and ectendomycorrhizae) based on the morphology of infected roots and presence of a mantle.

Ectomycorrhizae are characterized by penetration of fungal cells between the outer cortical cells of the rootlet, but not into the stele or into the cortex cells themselves. Fungal cells may completely enclose the outer cortical cells forming a net-like structure called the "Hartig net" (Fig. II-1). Ectomycorrhizae generally produce a sheath of fungal tissue around the rootlet called the "mantle." The mantle may take a variety of shapes and colors dependent on the combination of tree and fungal species involved, and dependent on conditions in the surrounding enviornment. For more detailed discussions of ectomycorrhizae structures see Marx and Krupa (1978) and Marks and Kozlowski (1973).

Endomycorrhizae do not produce a mantle, and do produce hyphal structures within the cortex cells of rootlets. Endomycorrhizae are further separated into three major groups -- ericalean, orchidaceous, and vesicular-arbuscular (VA).

Ericalean mycorrhizae are limited to the four or five plant families placed in Ericales. These mycorrhizae are characterized by fungal hyphae within the root cortex which form intracellular coils (pelotons) or hyphal masses, and by the development of an extensive mycelium in the

FIGURE II-1. Diagram of typical ecotmycorrhiza including the Hartig net, fungal mantle, and external hyphae (Ruehle and Marx, 1979).

FIGURE II-2. Diagram of typical endomycorrhiza including arbuscules, vesicules, and external hyphae with spores (Sanders, et al., 1971).

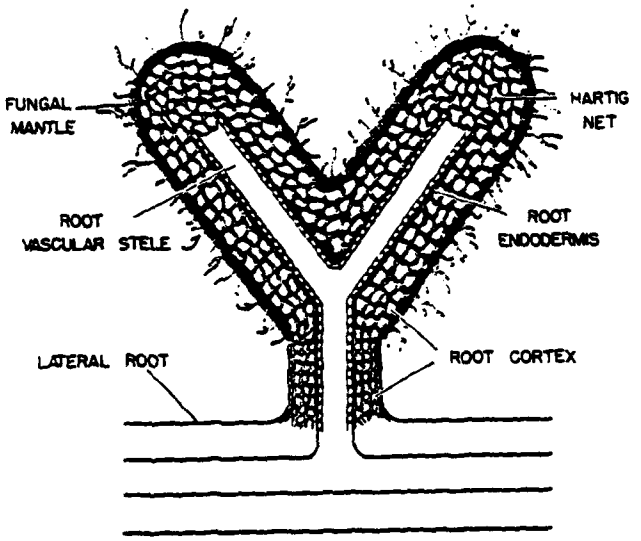


FIGURE II-1

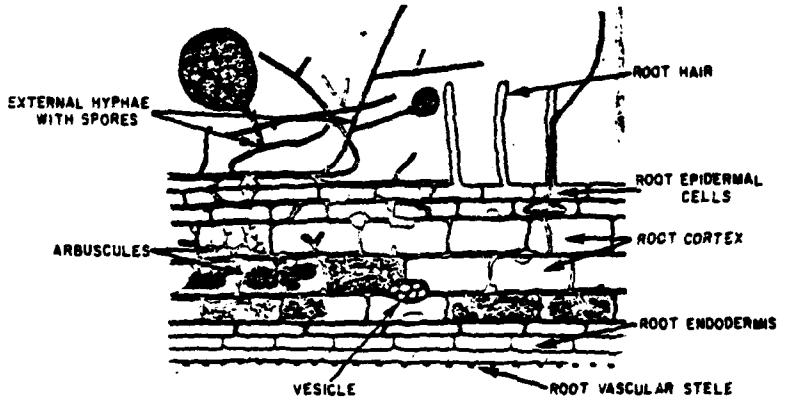


FIGURE II-2

soil and around the roots. Intracellular hyphae are alternately formed and digested during the growing season. In some cases, ericalean mycorrhizae have a mantle and are thus more like ectomycorrhizae. For a thorough review of ericalean mycorrhizae, see Hayman (1978).

Orchidaceous mycorrhizae are limited to a single plant family -- Orchidacea. Orchid embryos are infected in the early protocorm stage. The central region of the embryos become heavily colonized. As a vascular cylinder is formed, the fungus becomes restricted to the cortex. Characteristic hyphal coils (pelotons) are alternately formed and digested. Hyphae connect the cortical infection with external mycelium. As young roots are formed they become infected from fungi in the surrounding soil. For a review of Orchidaceous mycorrhizae, see Hayman (1978).

VA mycorrhizae are characterized by the presence of vesicles and arbuscules in the root cortex. Vesicles develop inter- or intracellularly as swellings along or at the tips of fungal hyphae (Fig. II-2). Arbuscules develop within a host cell by repeated dichotomous branching of invading hyphae to form clusters of fine filaments (Fig. II-2). Inter- and intracellular hyphae in the cortex are directly linked to external mycelium which spreads through the soil.

For more detailed discussions of endomycorrhizae, see Hayman (1978) and Sanders et al. (1974).

Because research on ectendomycorrhizae has been very limited (Mikola, 1965; Wilcox, 1971), very little is known about this class of mycorrhizae. Morphologically they have characteristics of both ecto- and endomycorrhizae. They are found on normally ectomycorrhizal trees when they occur. Because they appear to have limited distribution in

natural ecosystems, and because they are so poorly understood, they will not be considered further.

APPENDIX 3

EFFECT OF MYCORRHIZAE ON PLANT SURVIVAL AND GROWTH RATE

The magnitude of the plant growth response as a result of mycorrhizal symbionts varies with conditions in the soil environment, plant species, fungal species, and even fungal strain. The following examples are chosen to illustrate the magnitude of the response and some of the variables which affect it.

Plant response varies as a function of conditions in the soil. Under high nutrient conditions plant response may be limited or even absent. Even plants which are obligately mycorrhizal in nature (e.g., Pinus) can be grown successfully in the absence of mycorrhizae under "ideal" laboratory soil conditions (Melin, 1939; Schweers and Meyer, 1970). Plants which are already actively mycorrhizal will exclude the mycobiont if rich nutrient conditions are induced (Hatch, 1937; Bjorkman, 1942; Hacskaylo and Snow, 1959; Burgeff, 1961).

On the other extreme, under low nutrient or even highly fertile field conditions, many plant species cannot survive without mycorrhizae. The clearest evidence of the obligate need for mycorrhizae comes from attempts to establish normally ectomycorrhizal trees (e.g., Pinus) in areas of the world where their mycobionts don't occur naturally. Areas of the world without suitable ectomycorrhizal fungi include "The high Andes of Peru (Marx, 1975), regions of Australia (Bowen et al., 1973) and Asia (Oliveros, 1932), subalpine areas of Austria (Moser, 1963), Puerto Rico (Vosso and

Hacskaylo, 1971), Africa (Gibson, 1963), former agricultural soils of Poland (Dominik, 1961), oak shelterbelts on the steppes of Russia (Imshenetskii, 1967), and former treeless areas of the United States (Hatch, 1937)" (Marx, 1978). Forestation attempts there were either total or near failures until a mycobiont inoculum was introduced and mycorrhizae developed. When trees do survive in the absence of a suitable mycobiont they have very slow growth rates. For example, Briscoe (1959), in Puerto Rico, demonstrated that uninoculated seedlings of P. elliotti, P. taeda, and P. echinata grew only 12 cm in 4 years after out planting, while inoculated ones grew 149 centimeters.

Reduction of natural inoculum due to management practices, soil treatment, mining, and pollution generally result in poor plant performance due to a lack of mycorrhizae. Inoculation with appropriate mycorrhizal fungi increases plant survival and growth rates on these sites. For example:

(a) Soils under extended agricultural use. It is possible that failures of reforestation efforts in forest sites which have been denuded for harvest are due to destruction of fungal inoculum (Meyer, 1973; Mikola, 1973; Trappe, 1977). However, such problems are not likely unless the tree species being introduced are not native to the site, or the site is not planted back to trees for an extended period of time (Meyer, 1973; Mikola, 1973). Sites which have not supported forests for an extended time period do not have the appropriate fungi to support ectomycorrhizal trees. Ectomycorrhizal tree species do not generally thrive or survive well until mycorrhizal fungi are introduced (Dominik, 1961; Sobotka, 1963; Trappe and Strand, 1969).

(b) Soil fumigation and pesticide application. Nursery soils are frequently fumigated to eradicate soil borne pathogens. These treatments eliminate mycorrhizal fungi inoculum and decrease tree growth rate and survival. Introduction of appropriate endo- or ectomycorrhizae increase plant vigor and survival (Henderson and Stone, 1970; Iyer and Lipas, 1971; Kleinschmidt and Gerdemann, 1972; Iyer and Wojahn, 1976; Wojahn and Iyer, 1976; Marx et al., 1978).

Application of pesticides also detrimentally affects mycorrhizae development (Hacskaylo and Palmer, 1957; Ali, 1969; Nesheim and Linn, 1969; Hayman, 1970; Henderson and Stone, 1970; Iyer et al., 1971; Bowen et al., 1975; Jalali and Domsch, 1975; Wojahn and Iyer, 1976). In some cases differential susceptibility to pesticides will increase mycorrhizal development (Laiho and Mikola, 1964; Powell et al., 1968; Marx and Bryan, 1969, Bird et al., 1974).

(c) Air pollution. The harmful effect of industrial air pollutants on mycorrhizae has been observed in severely polluted areas (Sobotka, 1963; Meyer, 1973).

(d) Mine spoils. The ability of mycorrhizae to mitigate harsh soil environment and low soil nutrients has generated great interest in their use for mine reclamation. Schramm (1966) and Meyer (1968) demonstrated that only mycorrhizal trees survive and grow normally in coal mine spoils. Schramm also concluded that only a small portion of the numerous ectomycorrhizal fungi can survive in these harsh environments. Marx (1978) has since demonstrated that one of these species, Pisolithus tinctorius, is suitable for a wide range of industrially devastated sites. He has also demonstrated that fungal species have different abilities to colonize these harsh sites. The work of Daft et al. (1975) demonstrated similar benefits for VA mycorrhizae.

Plant response to inoculum results from the role mycorrhizae play as intermediaries between plant roots and the soil environment. See Table 1-1.

No single fungal species is able to provide all of the known benefits. There is great variability in the ability of mycobiont species to mitigate particular soil conditions. For example:

(a) Soil temperature. Temperature profoundly influences the growth, metabolism and colonization of roots by mycorrhizal fungi (Moser, 1958; Hacskaylo et al., 1965; Marx et al., 1970; Theodorou and Bowen, 1971). The optimal temperature for mycelial growth lies between 18°C and 27°C for the majority of fungi (Harley, 1969). Many fungi cease to grow below 5°C or above 35°C (Hacskaylo et al., 1965). Certain species such as Suillus variegatus and Paxillius involutus have been shown to grow at temperatures as low as -2°C to -4°C (Slankis, 1974). Maximal growth rate occurs at

temperatures lower than maximal respiratory rate (Hacskaylo et al., 1965). Cenococcum graniforme is broadly adapted to hot or cold environments (Trappe, 1962b). Pisolithus tinctorius does well in high soil temperatures (Marx, 1977b: Schramm, 1966). The differential response to temperature was graphically demonstrated by Marx and Bryan (1971a). Pinus taeda seedlings were inoculated with Thelephora terrestris and Pisolithus tinctorius. Seedlings with either fungal species grew well at 25C. When seedlings were held at 40C, those inoculated with T. terrestris either died or growth was severely reduced and most of their mycorrhizae died. Those inoculated with P. tinctorius thrived with generally healthy mycorrhizae.

(b) Soil moisture. Despite the importance for crop production, there has been little work on drought resistance. Phytogeographic data indicate that many mycorrhizal fungi don't fruit in droughty conditions. These data do not necessarily represent the ability of the mycobiont to grow and produce plant response. Cenococcum graniforme grows and forms mycorrhizae under more severe moisture stress than many other species (Worley and Hacskaylo, 1959; Trappe, 1962b; Mexal and Reid, 1973). Pisolithus tinctorius also produces vigorous mycorrhizae and increased plant growth on droughty sites (D. H. Marx, unpublished data).

Very wet or occasionally ponded sites present the opposite problem. Certain fungi appear to be adapted to these conditions. For example, Hymenogaster alnicola and Lactarius obscuratus occur with mycorrhizae of Alnus spp. in these conditions (Trappe, 1977). Cenococcum graniforme also tolerates periodically ponded sites (Trappe, 1962b).

(c) Soil pH. Relatively few mycorrhizal fungi tolerate extreme soil pH (Modess, 1941; Shemakhanova, 1962; Laiho, 1970). Most species show optimal growth at pH 4-6 (Modess, 1941). Some fungi, such as Suillus grow best at pH 3 (Hubsch, 1963). Strains of Paxillus involutus exhibit growth at pH 2.7 and others at pH 6.4 (Laiho, 1970). Pines with Pisolithus tinctorius have out performed those with Thelephora terrestris on sites with pHs as low as 3.4 (Marx, 1976). Cenococcum graniforme forms mycorrhizae in soils ranging from pH 3.4 to 7.5 (Trappe, 1962b).

(d) Soil nutrients. Mycorrhizal fungi affect the uptake of macro, micro, and trace nutrients. Mechanisms of uptake, specific nutrients, specificity of fungal species, and plant responses are reviewed in detail by Bowen (1973, 1978).

(e) Soil fertility. Mikola (1967) observed that an unidentified ectomycorrhizae suppressed growth of Pinus sylvestris on an unfertilized peat substrate, but promoted growth on fertilized peat. Krugner (1976) demonstrated that Pisolithus tinctorius and Thelephora terrestris respond differently to variation in soil fertility. Mycorrhizal fungal species clearly vary in their ability to uptake nutrients from the soil and make them available to plants (Bowen, 1973).

(f) Other soil conditions. Little is known about the toxicity of heavy metals to mycorrhizae. "Fungal species probably differ in tolerance to metals, as suggested by the decline in formation of ectomycorrhizae by some and the increase by others following application of a copper fungicide to seedlings (Göbel and Pümel, 1973)" (Trappe, 1977). Cenococcum graniforme grows well in high salt concentrations in coastal dune habitats (Saleh-Rastin, 1976). "Serpentine soils have been shown to support a rather different flora of mycorrhizal fungi than nearby nonserpentine soils (Mass and Stuntz, 1969). About 70 ectomycorrhizal fungal species occurred only on nonserpentine soil, 30 only on serpentine soil, and 25 on both soils" (Trappe, 1977). Levisohn (1960) has observed that Suillus bovinus grows well in soils with low organic content. Shemakhanova (1962) has indicated similar results for Boletus bovinus, Cenococcum graniforme, and Scleroderma verrucosum.

Relatively few of the many mycobiont species have been studied in any detail. Yet, it is clear from pot and microplot studies that there is a broad spectrum in the capabilities of fungal species to mitigate soil conditions. Studies of natural tree invasion of harsh sites, studies of fungal species on natural stands in different environments, experience with inoculum programs in forestry practice, and the limited number of controlled inoculum outplantings indicate that the fungal species specific capabilities hold true under field conditions. Pure culture studies with

mycorrhizal fungi suggest an even greater divergency in physiological ranges and optima.

Even the pure culture studies haven't tested the entire range because many ectomycorrhizal fungi cannot be grown in pure culture by existing methods, and some of those grow very slowly. Many of the available studies with ectomycorrhizae suffer because fungal species can only be identified from mature reproductive structures. Since spores generally cannot be germinated to produce mycelial growth on artificial media, isolation must be done from actively growing hyphae, from the sporocarp, or from mycorrhizae. These isolates cannot be taxonomically identified because they generally do not produce reproductive structures under artificial conditions. VA mycobionts cannot be grown in pure culture at all.

The plant response to a single fungal isolate varies for different tree species under the same environmental conditions (Young, 1940; Moser, 1956; Levisohn, 1957; Bowen, 1965; Krangauz, 1967; Lundegerg, 1970; Theodorou and Bowen, 1970; Vozzo and Hacskaylo, 1971; Marx, 1977a; Marx et al., 1977; Trappe, 1977). Marx and Bryan (1971b) reported that genotype of Pinus elliotti affected ability to form mycorrhizae. Likewise, the response for a single tree species varies for different fungal species (Melin, 1925; Levisohn, 1960; Shemakhanova, 1962; Krangauz, 1967; Lamb and Richards, 1971; Marx, 1977a; Marx et al., 1977; Trappe, 1977). Ecotypic variation within a fungal species may be as pronounced as the difference between fungal species (Marx, 1979) Moser (1956) demonstrated differences between high and low elevation ecotypes. Marx (1981) has tested numerous isolates of P. tinctorius from different tree hosts around the world and found one was far superior for mycorrhizal synthesis on southern pine in Georgia. Some isolates from oak formed

mycorrhizae on oak and pine, some did not produce mycorrhizae on pines at all (Marx, 1979). Similar ecotypic variations have been shown for a wide variety of conditions such as temperature and pH (Lindeberg, 1948; Moser, 1956, 1958; Levisohn, 1959; Trappe, 1962a; Laiho, 1970; Theodorou and Bowen, 1970, 1971; Göbl, 1975). Table III-1 gives examples of typical experiments demonstrating fungal species, plant species, and fungal isolate variation. As Table III-1 indicates, inoculation does not always stimulate plant growth. In other studies, inoculation with Paxillus involutus increased survival and growth of pine seedlings in the field (Laiho, 1970), whereas in experiments by Lundeberg (1967) the same fungus depressed growth. Likewise, Cenococcum graniforme has been very beneficial in some experiments (Sehmakhanova, 1962; Trappe, 1964) but has inhibited growth in others (Lundeberg, 1970).

A single plant in nature commonly has simultaneous mutualistic associations with many symbionts. Experience with inoculation of nursery trees for outplanting suggests that "because of the particular requirements of individual fungal species, a mixed population, i.e., soil inoculum, has often been superior to pure culture" (Mikola, 1973). Those results could be simply due to increasing the probability of having the right mycobiont for the environment and may not reflect the benefit of having multiple mycobionts on a single tree. Moser (1963) inoculated Pinus cembra with a mixture of four fungal species. Unfortunately, no assessment of mycorrhizal development was made. There are few results from studies of inoculation with multiple fungal species on a single plant. Sinclair (1974) found that Douglas Fir seedlings in nurseries grew better with two fungi forming their mycorrhizae than with one. Variability in results from multiple inoculations would be expected of

TABLE III-1. The relative affect of different fungi on growth of pine seedlings.[a] (Mikola, 1973).

Reference:	Haeskaylo & Vozzo (1971)		Theodorou & Bowen (1971)		Shemakhonova (1967)			Kranguaz (1967)		Björkman (1970)	Lamb & Richards (1971)	
Tree species:	P. Caribaea		P. radiata		P. silvestris			P. silvestris		P. silvestris	P. radiata	P. elliottii
Type of experiment:	Field Nursery		Field		Nursery			Pot		Pot	Pot	
Measurement:	Height		Height		Dry weight			Dry weight		Dry weight	Dry weight	
Age of seedlings:	40 weeks	43 weeks	15 months	43 months	1 year			1 year	2 years	1 year	8 months	
					b	c	d					
Boletus bovinus					166	134	117			93		
B. cothurnatus	151	120										
B. granulatus			144	133				115	90		153	608
B. luteus			122	114	105	99	99	112	244			
B. subtomentosus										144		
Cenococcum graniforme		119			231	127	118				209	581
Corticium bicolor	125	168										
Rhizopogon lutcolus 1			141	129								
Rhizopogon lutcolus 2			143	124								
Rh. roseolus	131	131									160	535
Scleroderma verrucosum					170	103	109					
Unidentified isol. P. radiata											296	231
Unidentified isol. P. elliottii											256	1080
Unidentified isol. P. radiata											324	200
Unidentified isol. P. radiata											497	427
Soil inoculum	141	121						139	157			

[a] 100 = uninoculated control

[b] Sandy soil

[c] Sandy soil, low humus content

[d] Sandy soil, high humus content

the species variability discussed above. But, synergistic effects from multiple mycobionts simultaneously solving independent problems of the phycobiont are theoretically likely, based purely on physiological differences between mycobiont species. Multiple symbiont species or varieties could also satisfy changing plant requirements over the growing season, and compensate for soil conditions (temperature, moisture, nutrient availability, etc.) as they change through the year. With VA mycorrhizae, changes in the percent of roots infected have been observed as a function of the growing season (Mason, 1964; Hayman, 1970). Large seasonal changes in the biomass of mycorrhizal roots have been observed (Twaroski, 1963; Harvey et al., 1978; Fogel and Hunt, 1979; Vogt et al., 1980). Different times of activity for individual fungal species in a multiple fungal species symbiont should be expected, based on differences in physiological requirements of the mycobionts.

Observations of fruiting bodies suggest that the mycobiont complement in a forest changes with successional time. Some mycorrhizal fungi such as Hebeloma crustuliniforme, Paxillus involutus, Rhizopogon spp., Thelephora terrestris, and Pisolithus tinctorius are able to fruit around young seedlings, whereas other species form sporocarps only in closed stands (Mikola, 1973). Schramm (1966), Meyer (1968), and Marx (1978) indicate that only a few species can survive in the conditions on mine spoils which can only be described as primary succession sites. Meyer (1973) suggested that early mycorrhizal trees improve the site so that other forms of mycorrhizal trees can follow. Physiological sensitivity of individual fungal species and strains would suggest a population change concurrent with changes in the soil environment over successional time. Sadly, little work has been done in this area.

The ability, or lack of ability, of particularly mycorrhizal fungus species to live in an environment most assuredly affects the ability of plant species to thrive, and, therefore, affects plant distribution and primary production. The effect on plant distribution may not be limited solely to the ability of the mycorrhizae to mitigate the soil environment. Although there has been little work done in the area, there is evidence of competition between fungal species. Ruehle and Marx (personal communications) have demonstrated that Thelephra terrestris infection inhibits subsequent infection by Pisolithus tinctorius. They suggest that once the limited number of infection sites on tender short roots are inhabited, physical limitation of available infection sites would inhibit subsequent infection. Seedlings inoculated with mycorrhizae in the nursery survive better on outplanting but the fungal species introduced in the nursery are gradually replaced by naturally occurring mycorrhizae in most forest soils (Mikola, 1965). The mechanism of displacement may simply be a difference in suitability of the mycobiont species for the physical site on the particular tree species. However, Handley (1963) suggests that the endomycorrhizae on Calluna heathland directly inhibit certain ectomycorrhizal species suitable for some pine species such as Pinus abies. Ectomycorrhizae (Leccinum scabrum) suitable for pine species that are able to live on the heath showed greater resistance to soil inhibiting factors associated with Calluna roots. Destruction of the Calluna allows subsequent introduction of pine species. Some species of ectomycorrhizal fungi produce considerable amounts of gibberellins (Slankis, 1973) which inhibit many other mycorrhizal species (Santoro and Casida, 1962). Inhibition between fungal species varies with the combination of fungal species and soil environment (Laiho, 1970).

Detailed studies with endomycorrhizae are not as common as the mainly ectomycorrhizal studies discussed above because: (1) Endomycorrhizae cannot be grown in pure culture or laboratory media. The requirement to maintain VA mycobionts on living plants makes pure culture work extremely difficult and greatly magnifies the difficulty of any comparable work. (2) They have little affect on root morphology. Roots must be stained and observed microscopically to distinguish mycorrhizal from nonmycorrhizal roots in endomycorrhizae. (3) Taxonomic identification of endomycorrhizae from microscopic reproductive structures is much more tedious than comparable work with macroscopic reproductive structures of ectomycorrhizae. Still, there are a large number of papers on the effects of VA endophytes on the growth rate of plants (Mosse, 1973a). The majority of the papers concern the effect of VA mycorrhizae on phosphate. Infection with Endogone can stimulate growth by several hundred percent. This stimulation of plant growth can occur in a wide range of soils (Hayman and Mosse, 1972b) and with many plant species (Gerdemann, 1968; Mosse, 1973b)." (Hayman, 1978) Table III-2 gives some examples.

VA mycorrhizae are also known to affect the uptake of zinc (Gilmore, 1971) and sulfur (Gray and Gerdemann, 1973). They can affect water transport (Safir et al., 1972). Occasionally VA infection may be detrimental to plant growth. This has been demonstrated under low light or low temperature conditions (Furlan and Fortin, 1973; Hayman, 1974). Crush (1973) and Mosse (1973b) have found that plants which give positive growth responses to VA infection in low soil nutrient conditions can give negative responses in high phosphorus experiments. Frequently plants growing in infertile soils have more mycorrhizae than plants growing in fertile

TABLE III-2. Growth responses of different plant species to vesicular-arbuscular mycorrhiza in soils containing various amounts of available (labile) phosphorus (Hayman, 1978).

Note: (1) Available soil P was estimated in 0.5 M NaHCO, extracts in the first four references and in dilute acid extracts in the last three.
(2) At low levels of available soil P, plants generally responded greatly to vesicular-arbuscular mycorrhiza; at high levels of available soil P, plants usually grew well irrespective of whether they were mycorrhizal.
(3) The level of available soil P at which a plant responds to mycorrhiza differs for different plant species.

Plant species	Site of soil collection	ppm available P	Plant dry weight (g)		Length of expt. (weeks)	Reference
			Mycorrhizal	Non-mycorrhizal		
Coprosma robusta[a]	Decid. copse	188	1.90	2.10	26	Hayman and Mosse (1971)
Coprosma robusta[a]	Arable fallow	12	1.50	0.10	26	
Allium cepa	Forest nursery	47	0.48	0.42	10	
Allium cepa	Arable fallow	26	0.47	0.36	10	
Allium cepa	Grassy common	18	0.65	0.07	10	
Allium cepa	Wheatfield	16	0.64	0.03	10	Hayman and Mosse (1972a)
Allium cepa	Decid. forest	10	0.23	0.17	10	
Allium cepa	Heath	8	0.16	0.01	10	
Allium cepa	Heath	5	0.12	0.07	10	
Melinis minutiflora	Decid. forest	6	1.04	0.77	10	
Melinis minutiflora	Brazilian cerrado	3	0.38	0.16	10	Mosse et al. (1973)
Centrosema pubescens	Brazilian cerrado	2	0.29	0.02	10	
Paspalum notatum	Brazilian cerrado	2	0.30	0.04	10	
Centrosema pubescens[b]	Wheatfield	13	3.88	1.67	4	
Stylosanthes guyanensis[b]	Wheatfield	13	1.63	0.47	4	
Trifolium repens[b]	Wheatfield	13	2.57	1.56	4	Crush (1974)
Lotus pedunculatus[b]	Wheatfield	13	2.01	2.54	4	
Lolium perenne[b]	Wheatfield	13	10.40	10.00	19	

TABLE III-2 continued.

Plant species	Site of soil collection	ppm available P	Plant dry weight (g)		Length of expt. (weeks)	Reference
			Mycorrhizal	Non-mycorrhizal		
Lolium perenne[a]	Tussock grassland	4	0.11	0.02	17-26	Crush (1973)
Lolium perenne[a]	Tussock grassland	8	0.08	0.10	17-26	
Dactylis glomerata[a]	Tussock grassland	4	0.17	0.02	17-26	
Dactylis glomerata[a]	*Tussock grassland*	8	0.11	0.12	17-26	
Anthoxanthum odoratum[a]	Tussock grassland	4	0.19	0.02	17-26	
Anthoxanthum odoratum[a]	Tussock grassland	8	0.15	0.41	17-26	
Glycine max	Arable	50	2561	1271	23	Ross (1971) and Ross and Gilliam, (1973)
Glycine max	Arable	162	2406	2282	23	

[a]Shoot dry weights.

[b]Total fresh weights.

soils; and plants growing in uncultivated soils have more than plants in fertilized cultivated soils (Hayman, 1978). Maize is heavily mycorrhizal, even in very fertile soils (Hayman, 1975b). Orchard and plantation crops generally have more mycorrhizae than annual field crops (Butler, 1939).

APPENDIX 4

FLOW OF CELLULAR PLANT BIOMASS THROUGH THE GRAZING AND DETRITUS PATHWAYS

(a) The Grazing Pathway. Carbon distribution through the grazing pathway is illustrated in Fig. 2-1. Spatial and temporal distribution of energy through the grazing pathway is a function of the species specific characteristics of the herbivores (flows 15, 16) and carnivores (flows 17, 18) in the particular ecosystem. Highly mobile grazers and carnivores (e.g., birds and mammals) may result in movement of the energy to points quite distant from the producers. Distribution may be clumped or dispersed depending on the behavioral characteristics of the animals involved. Less mobile grazers and carnivores (e.g., chewing and boring insects) result in energy distribution in the local area.

Partitioning between aboveground (flow 15) and belowground (flow 16) grazing chains is dependent on which plant species occupy the plant subsystem. Differences in above and belowground partitioning are very well documented for major biome types such as forests, as compared to prairie or tundra. Species specific characteristics of the plants, herbivores, and carnivores also affect temporal distributions. For example, in a temperate climate, deciduous woody plants only provide aboveground leaf biomass suitable for grazing in the active growing season of summer. Grasses also provide standing dead biomass suitable for grazing throughout the winter months.

Energy not utilized by the grazing subsystem eventually is passed to the aboveground and belowground decomposition subsystems as the result of excretion and death. Temporal and spatial distribution of inputs from the grazing subsystem to the aboveground (flow 19) and belowground (flows 21, 22, 23) decomposer subsystems are determined by the plant and animal species involved. These and other energy flows within the system (flows 24-30) eventually result in dispersion of the energy as heat or deposit of carbon compounds as biologically recalcitrant humus (flows 31, 32).

(b) The Detritus Pathway. Decomposition of dead plant tissue begins in the phyllosphere, while the tissue is still attached to the plant, and in standing dead (flow 33); but the majority of plant tissue is decomposed on and in the soil (flows 34, 35).

Root tissue (cells, root hairs, roots) from living plants is sluffed in the area immediately adjacent to active roots in the soil (flow 35, mainly to the rhizosphere). Area of distribution is limited to the circumference of the root system. Distribution through the soil column is limited to the physical location of roots. Temporal distribution of root detritus is seasonal (Edwards and Harris, 1977; Persson, 1978; Keyes, 1979).

Input from the aboveground plant subsystem (flow 34, leaves, small branches, fruiting structures, etc. from living plants) is also seasonal. Most of the material falls in the immediate area under the crown of the plant. Wind and water transport increase the area of dispersion. Over time, the material moves through the soil. The gradient with depth is obvious in the well known soil horizons.

Partitioning between above and belowground detritus input varies with biome type and plant species.

Temporal distribution of input is a function of life span and growth habit of the plant. Woody tissue accumulation results in long time delays between carbon fixation in the plant subsystem and transfer of that energy to the heterotrophic portions of the ecosystem.

APPENDIX 5

DATA FROM FIELD STUDIES OF INOCULATED AND NON-INOCULATED PINES AT COPPER HILL

TABLE V-1. Annual Production in gms/m^2 at Copper Hill. Numbers in parentheses are standard deviation. Values for airport site are fifth year of production. Values for sludge site are 4th year of production. Statistical comparisons are within tree species, within tree part, by treatment. Means followed by common letters are not statistically different (P = .05) between treatments (Analysis of variance, Duncan's multiple range test).

		Needle		Stem and Branch		Total	
Treatment	n	PT	NI	PT	NI	PT	NI
Airport Site							
Loblolly - Fertilizer	3	95.2 a (51.6)	145.0 a (81.8)	203.8 a (110.6)	183.6 a (109.0)	299.3 a (162.4)	338.8 a (191.2)
Loblolly - Bark	3	124.2 a (48.3)	101.6 a (26.3)	266.0 a (103.4)	136.2 a (35.3)	390.7 a (152.0)	237.3 a (61.5)
Virginia - Fertilizer	3	390.6 a (234.8)	284.1 a (52.5)	597.1 a (357.6)	482.6 a (73.8)	985.0 a (592.0)	774.9 a (143.2)
Virginia - Bark	3	459.1 a (127.4)	313.3 a (91.4)	700.8 a (194.4)	543.2 a (158.6)	1157.4 a (321.1)	854.4 a (249.4)
Sludge Site							
Loblolly Fertilizer	5	72.6 b (48.1)	82.3 b (53.0)	155.6 b (103.0)	110.3 b (71.1)	228.5 c (151.3)	192.4 c (123.9)
Loblolly Sludge	5	197.2 b (59.5)	440.2 a (221.4)	422.1 a (127.3)	590.0 a (296.7)	620.0 b (187.0)	1028.5 a (517.3)
Short Leaf Fertilizer	5	59.7 ab (36.6)	34.4 b (14.2)	111.3 ab (68.3)	59.7 b (24.7)	183.7 ab (112.7)	93.9 b (38.9)
Short Leaf Sludge	5	114.8 a (33.8)	110.6 a (84.7)	214.0 a (63.0)	191.7 a (146.7)	353.4 a (104.1)	301.5 a (230.9)
Virginia Fertilizer	5	NA NA	120.7 (55.1)	NA NA	208.8 (96.0)	NA NA	329.1 (150.4)
Virginia Sludge	5	NA NA	446.8 (125.8)	NA NA	774.7 (218.2)	NA NA	1218.7 (343.2)

FIGURES V-1 through V-4. Broad bars are production of *Pisolithus tinctorius* sporocarps collected on the dates specified. Narrow bars are production of *Rhizopogon roseolus*. Cross hatch bars are the means of sporocarp production on inoculated plots and solid bars are the means of production on non-inoculated plots. Bars above the dates are production on bark amended plots for the airport site and sludge amended plots for the sludge site. Bars below the dates are fertilizer treated plots for both sites. There were no inoculated plots on Virginia pines at the sludge study site. Sporocarp production on shortleaf pines at the sludge study site was too low to be meaningfully graphed.

FIGURE V-1. Airport - Loblolly

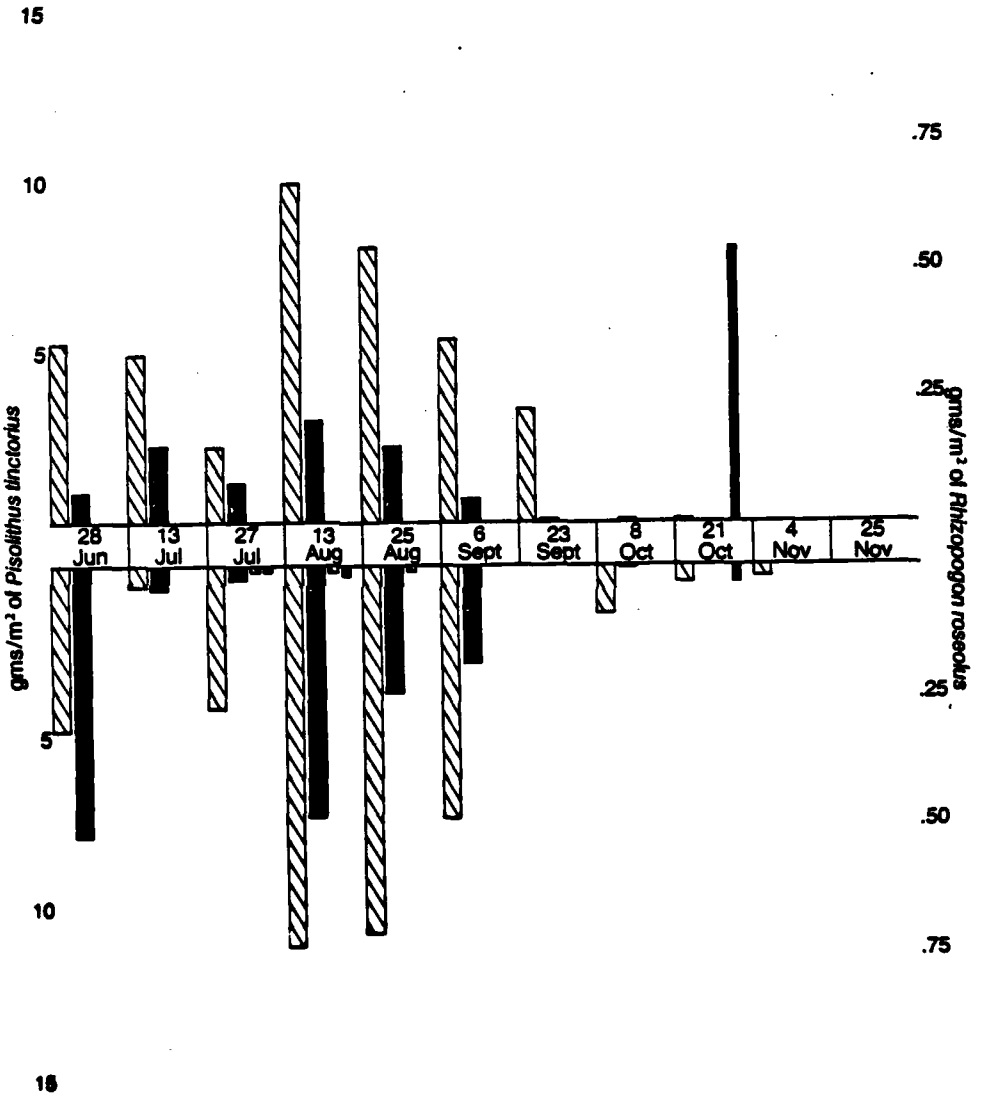


FIGURE V-2. Airport - Virginia

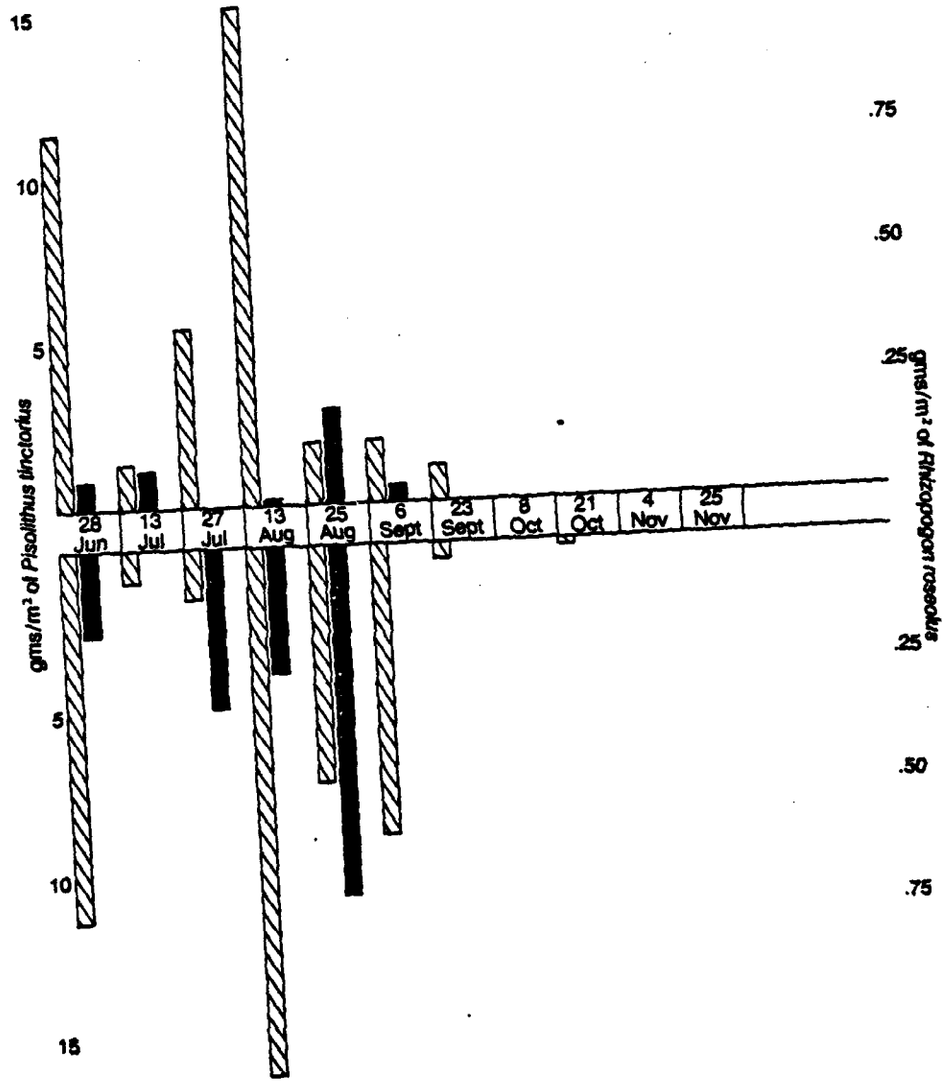


FIGURE V-3. Sludge Study - Loblolly

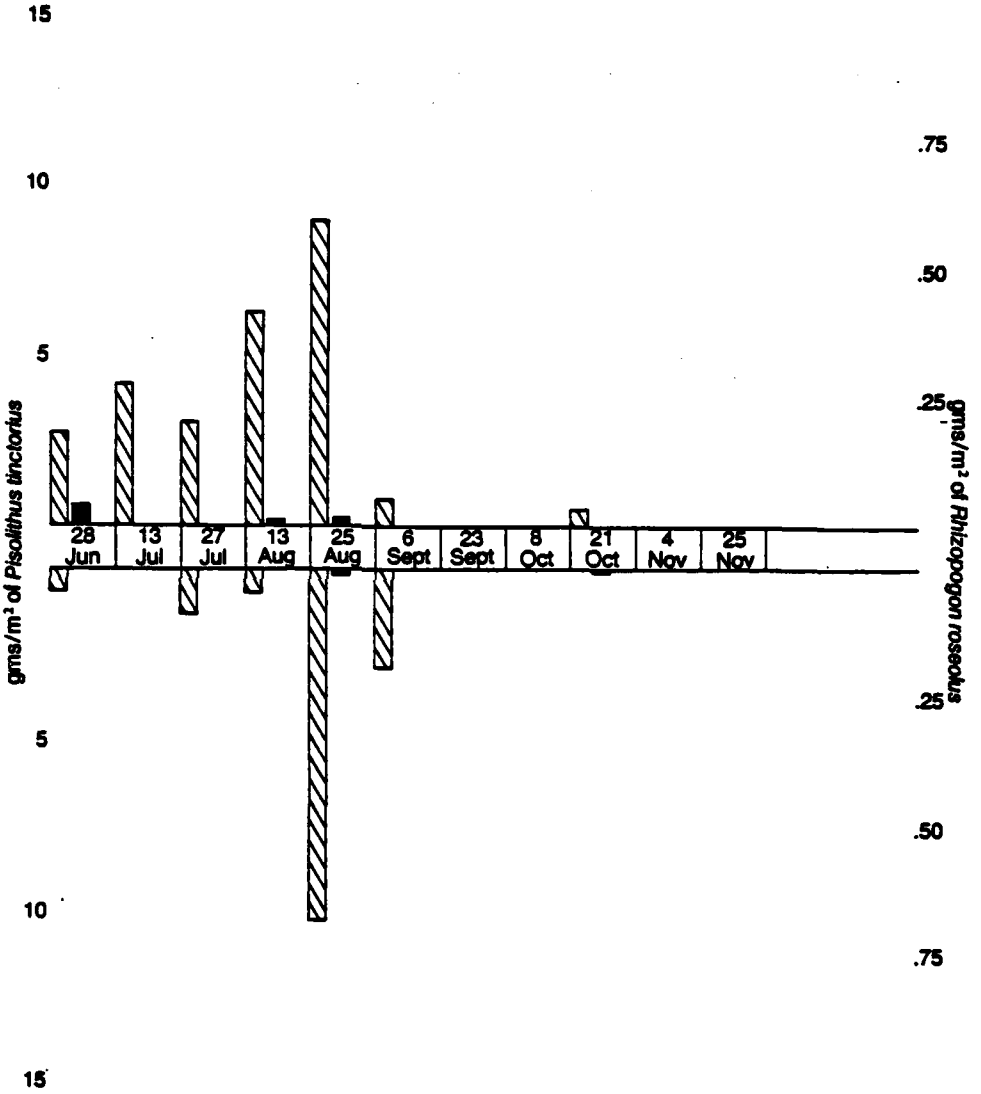
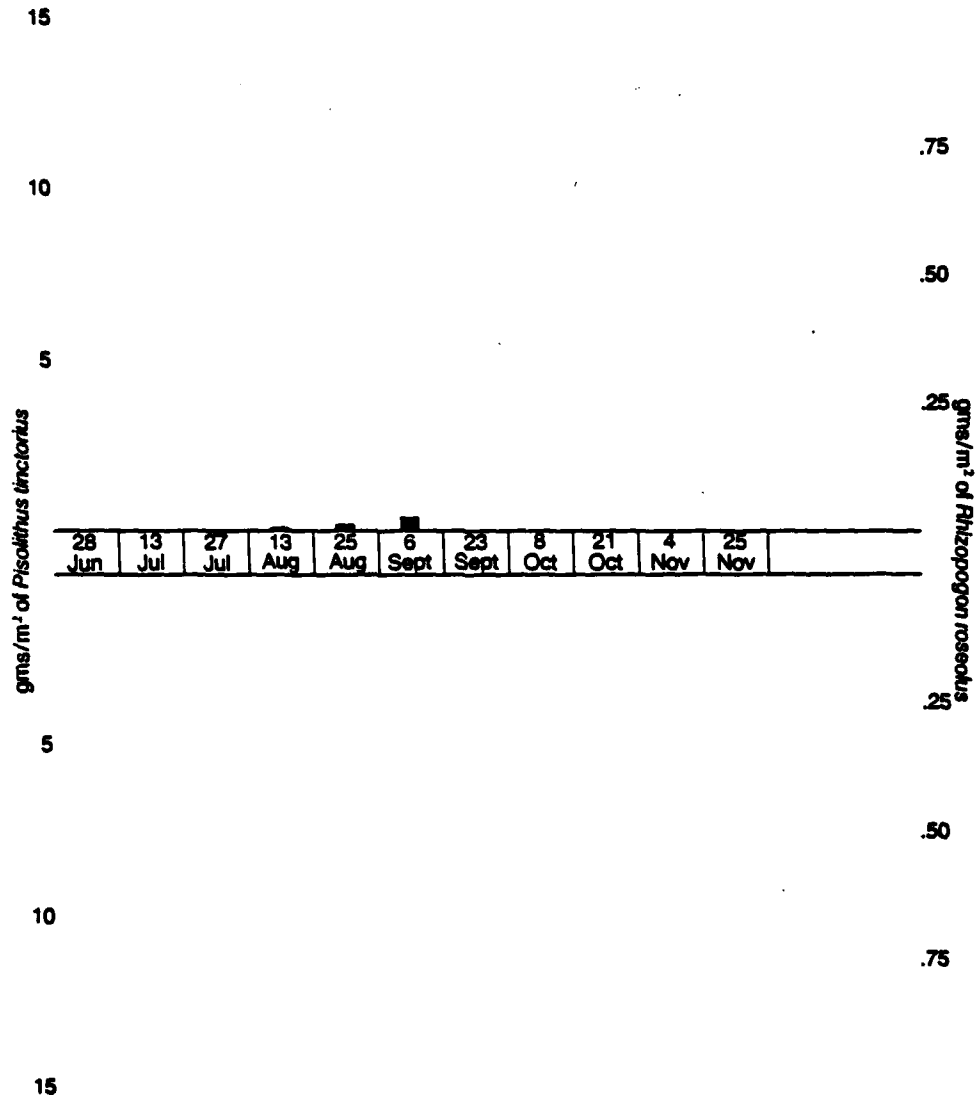


FIGURE V-4. Sludge Study - Virginia




FILME
0-8