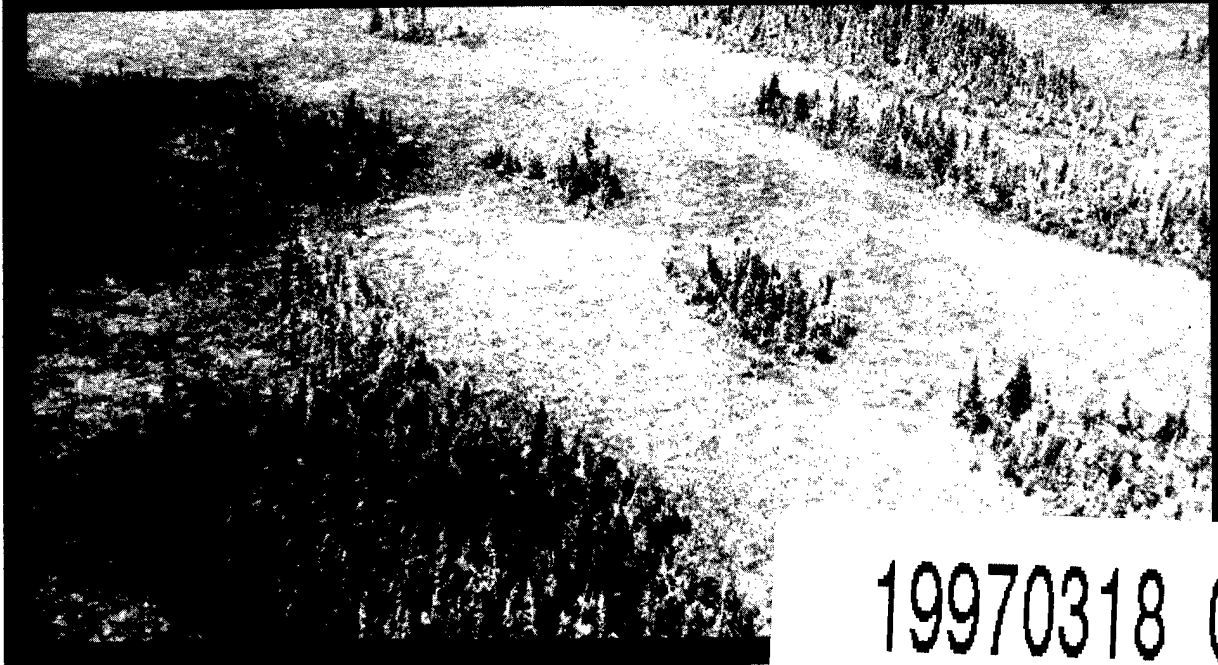
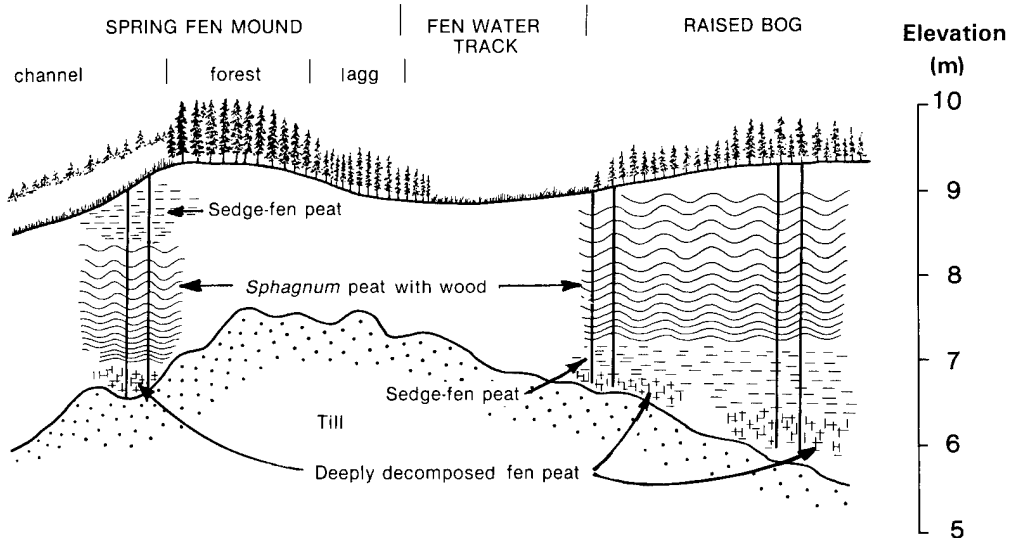


THE ECOLOGY OF PATTERNED BOREAL PEATLANDS OF NORTHERN MINNESOTA:

A COMMUNITY PROFILE



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**THE ECOLOGY OF PATTERNED BOREAL PEATLANDS OF NORTHERN MINNESOTA:
A COMMUNITY PROFILE**

by

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PREFACE

This monograph on the ecology of the patterned boreal peatlands of northern Minnesota is one of a series of U.S. Fish and Wildlife Service profiles of important freshwater wetland ecosystems of the United States. The purpose of this profile is to synthesize the literature available for patterned boreal peatlands of northern Minnesota and to describe the ecological structure and functioning of these freshwater wetlands.

Although vast areas of Canada and Alaska are covered by boreal forest, they extend southward into the Continental United States only in Minnesota. The cool continental climate of northern Minnesota, with seasonal maximum precipitation during the growing season, combines with the gentle topography of the region to favor the development of peatlands.

Peatlands are defined as areas having waterlogged substrates and at least 30 cm of peat. The accumulation of peat influences the landforms themselves, hydrology, nutrient accumulation, and nutrient availability, which in turn influences plant species which colonize peatlands. The most striking aspect of

peatlands is the landforms themselves, which are 3-dimensional in structure and, along with the vegetative communities, produce a patterned appearance when viewed from above.

This profile is intended to provide a useful reference to the scientific information available for the patterned boreal peatlands of northern Minnesota. The profile includes a description of the distribution of peatlands and physical setting in which they develop. It also discusses the physical properties of peat, peatland formation, and physical and chemical properties of peatlands. Several chapters are also devoted to the flora, fauna, and successional trends of peatlands. In the final chapter, human impacts and conservation are discussed.

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CONVERSION TABLE

Metric to U.S. Customary

<u>Multiply</u>	<u>By</u>	<u>To Obtain</u>
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m ²)	10.76	square feet
square kilometers (km ²)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m ³)	35.31	cubic feet
cubic meters (m ³)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft ²)	0.0929	square meters
square miles (mi ²)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft ³)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

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CHAPTER 1. INTRODUCTION

A peatland is defined as any ecosystem with a waterlogged substrate and at least 30 cm of peat (Kivinen and Pakarinen 1981). Once peat has accumulated to this depth the availability of essential nutrients falls sharply. Plant species are no longer rooted in mineral soil, and they must absorb all their mineral nutrients from within a waterlogged, anoxic, peat mass. Nutrients, however, are continually locked up within the peat, because the low levels of oxygen inhibit microbial activity and nutrient cycling. The supply of nutrients is therefore determined by transport processes that carry nutrients in from the (1) atmosphere, (2) adjacent mineral uplands, or (3) underlying mineral soil. These processes are strongly modified within a peatland by the physical properties of the peat and the active sequestering of ions by the living plants. The accumulation of peat therefore creates a uniquely integrated system in which there is a delicate balance between physical and biotic processes.

The most impressive products of peat accumulation are the peat landforms of boreal peatlands. These landforms have a 3-dimensional structure with a characteristic cross-sectional profile and surface pattern. The surface patterns are consistently oriented relative to the slope and appear as intricate networks of pools, peat ridges, or lines of trees or shrubs. In certain areas the patterns have the appearance of fluvial bedforms, such as islands, river channels, and ripple marks. The close relationship between the patterns and water movements is produced in part by the sensitive adaptations of the boreal mire flora to changing water levels and water chemistry. The small number of these species and their nearly circum-boreal distribution creates the impression

of a fairly uniform vegetation formation over broad geographic regions.

Boreal peatlands are common within the coniferous forest region of Canada and the interior of Alaska (Figure 1). In eastern Canada these peatlands are confined to small topographic depressions, but to the west peatlands cover vast areas of nearly level terrain (Zoltai and Pollet 1983). The major areas of peatland in North America occur in the Great Slave/Great Bear Lake region, the Hudson Bay lowlands, and the Glacial Lake Agassiz region. This major belt of peatlands extends southward to northern Minnesota.

The distribution of boreal peatlands was first determined from the ranges of such characteristic peatland taxa as *Drosera* (sundew), *Sarracenia* (pitcher plant), *Larix* (tamarack), *Ledum* (labrador tea), and *Chamaedaphne* (leather leaf) (Transeau 1903). Later the striking landform patterns were discovered from aerial photographs and the boreal affinities of these peatlands were more fully appreciated (Heinselman 1963, 1965; 1970; Grittinger 1971). Similar studies across the Great Lakes/St. Lawrence region have documented the southern limits of these peatlands in the eastern United States (Nichols 1919; Osvald 1955; Curtis 1959; Davis *et al.* 1983), but only in northern Minnesota have these peatlands spread over a large portion of the landscape.

The great size of these peatlands has largely protected them from exploitation, and today they represent the most pristine ecosystem in the State. Despite their significance as natural areas the ecology of these peatlands is still poorly understood. Ecologists have usually focused their attention on the upland forests and

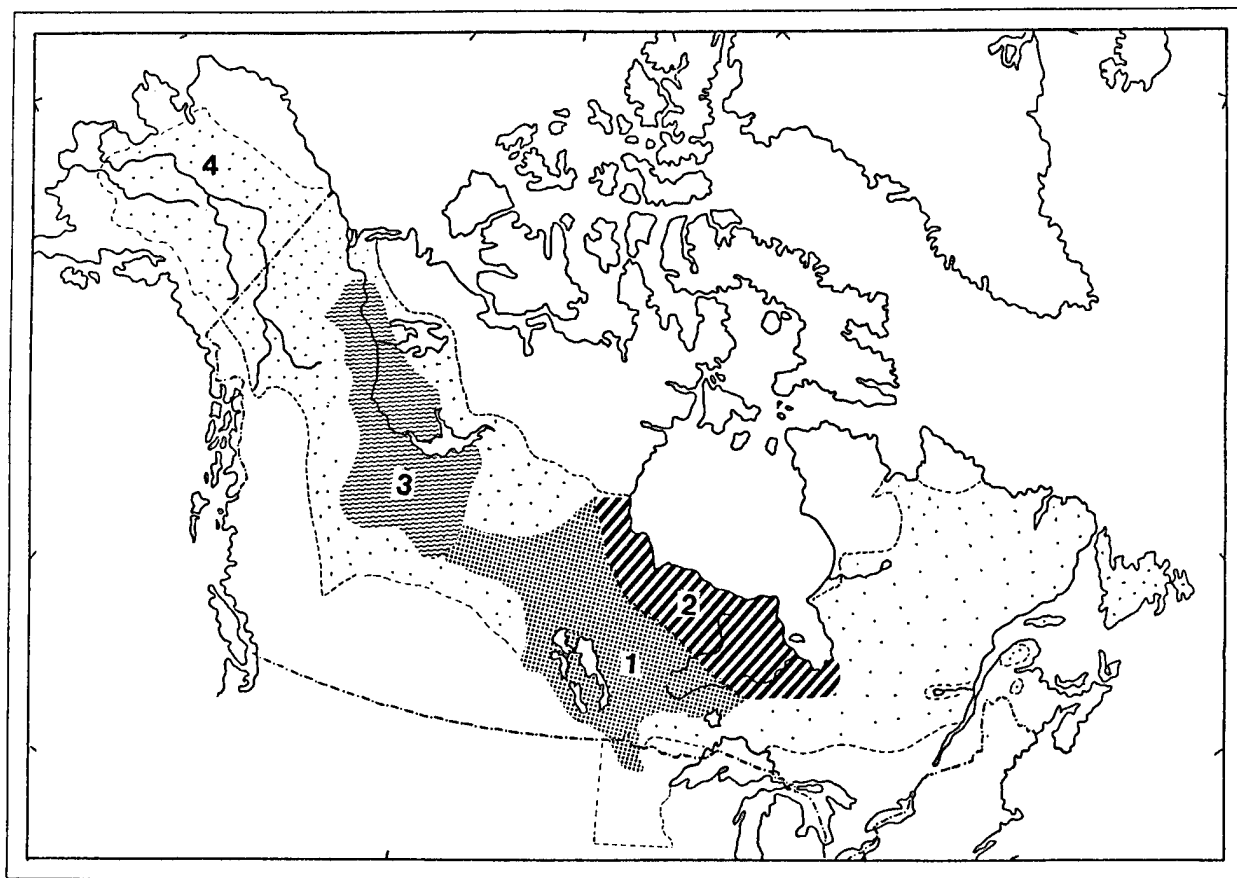


Figure 1. Major boreal peatlands of North America. The most extensive peatlands in North America are located in the (1) Glacial Lake Agassiz region, (2) Hudson Bay lowlands, (3) Great Bear/Great Slave Lake region, and (4) the interior of Alaska, where detailed peatland maps are not available. The lightly stippled area marks the boreal region of Alaska (from Viereck and Little 1972) and Canada (Rowe 1972). The major peatland areas are taken from Zoltai and Pollet (1983).

prairies, where the more variable environment and larger flora have produced more complex vegetation patterns. Ecological concepts derived from these systems may not be as suitable for patterned peatlands, where peat accumulation has created a more uniform environment (Glaser, In prep.a).

1.1 DISTRIBUTION

Prior to settlement approximately 10 million acres in Minnesota were mapped as unfit for agriculture because of poor drainage (Soper 1919). By 1919 Soper estimated that at least 7 million of these acres were peatlands as a result of his own extensive survey of peat in Minnesota. Most of these peatlands are concentrated on the beds of Glacial Lakes Agassiz,

Upham, and Aitken in northern Minnesota. These northern peatlands were originally recognized as boreal muskeg because of the prominence of black spruce (*Picea mariana*), bog ericads (*Ericaceae*), and *Sphagnum* moss.

Soper's peat map has since been greatly refined by the Minnesota Soil Atlas Series, which depicts soils and geomorphic landforms on 1:250,000 maps (University of Minnesota Agriculture Experiment Station 1971, 1977, 1980a, 1980b, 1981). The Peat Program of the Minnesota Department of Natural Resources (MN DNR) used these maps to compile a peat map for Minnesota (Figure 2). The distribution of peat landforms in these peatlands is presented in Figure 3 (Glaser, In prep.a).

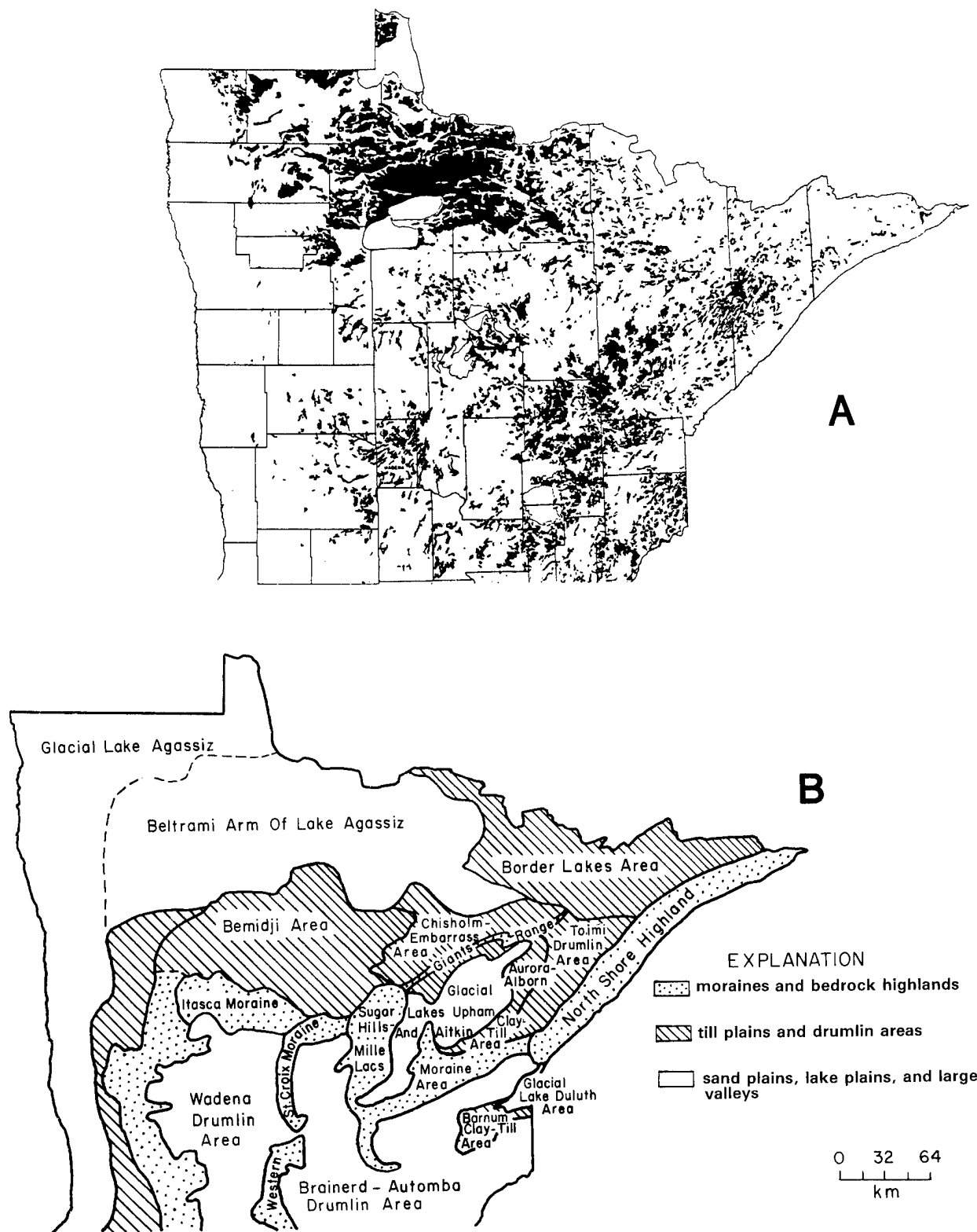


Figure 2. Peatlands and physiography in northern Minnesota. The peatlands are marked by the dark shading in A (MN DNR 1978), and the major physiographic areas are presented in B (Wright 1972a).

The Peat Program also initiated an inventory project to determine the quantity and quality of peat deposits in Minnesota. The inventories for Koochiching, Beltrami, and Lake of the Woods Counties in the Lake Agassiz region, for example, determined that peat depths

range from 3 to 5 m, with an average depth of 3 m in the central portion of the peatlands (MN DNR 1980, 1984b). Eastward peat depths are generally shallower, averaging 1 to 3 m, although deeper deposits underlie the raised bogs (MN DNR 1979a, b; 1982).

1.2 PHYSICAL SETTING

The spread of peatlands in northern Minnesota is favored by the gentle regional topography and moist cool climate. Elevation varies less than 240 m across the region, and the bedrock is generally covered by thick deposits of glacial till except in the extreme north-east, where bedrock outcrops are common (Figure 4). The three most important areas of peatland occur on the nearly level plains of Glacial Lakes Agassiz, Glacial Lakes Upham and Aitken, and on the northern portion of the Toimi drumlin area (Figure 3). Elsewhere peatlands are common but are more closely confined to local depressions in mineral uplands. The parent material under the Lake Agassiz plain is largely derived from calcareous drift, but eastward the till consists of

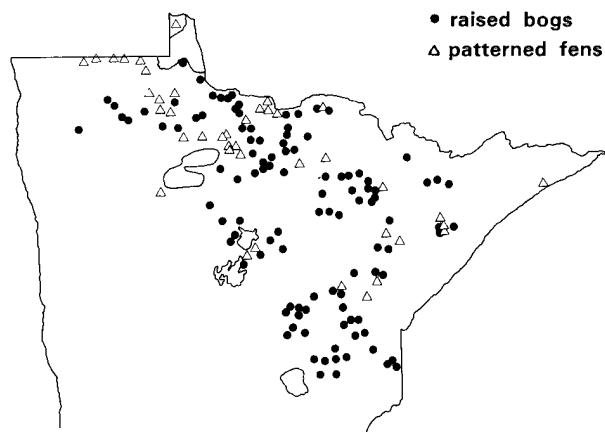


Figure 3. Distribution of the boreal peatlands with vegetation-landform patterns in Minnesota (Glaser, in prep.a).

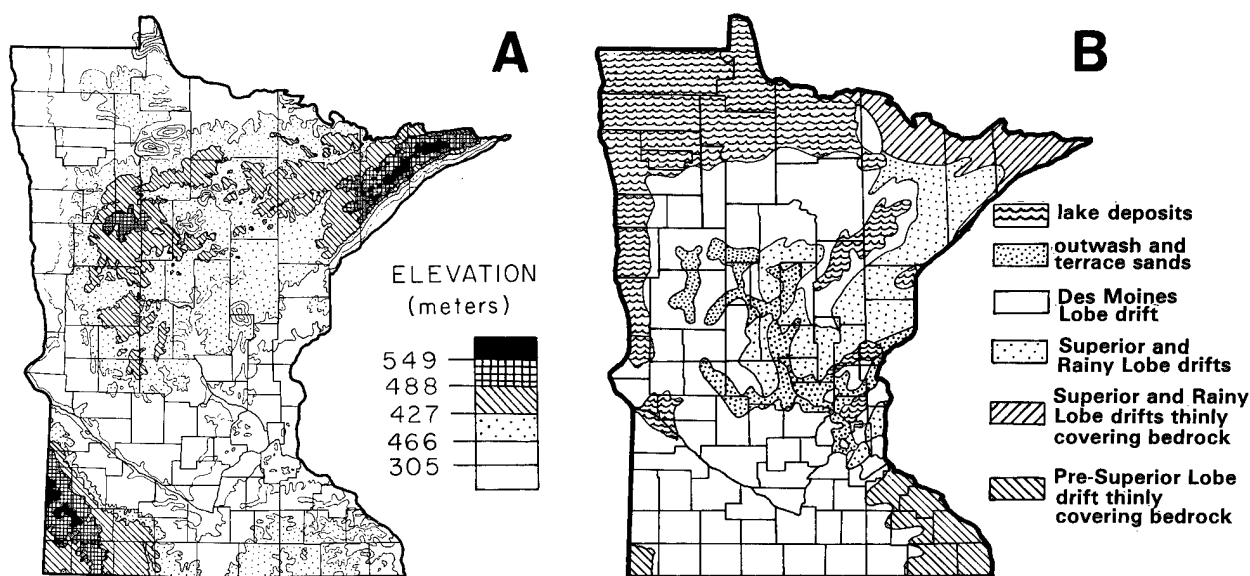


Figure 4. Elevation and soils in Minnesota. The topographic elevation map of Minnesota (A) is drawn from Baker and Strub (1963) and the surficial geological map (B) is adapted from Hogberg (1972). The lake deposits and till from the Des Moines Lobe are primarily calcareous; whereas the deposits and till from the Superior and Rainy Lobe range from noncalcareous to weakly calcareous.

noncalcareous to poorly calcareous material (Holowaychuk 1960; Figure. 4). Areas of sandy outwash are located largely in central and eastern Minnesota. A detailed account of the physiography and glacial history of Minnesota is given by Wright (1972a, b).

The climate of Minnesota is continental, with a precipitation maximum during the growing season (Kuehnast 1978). The landscape is generally covered with snow from November through March with a peak in storm hydrographs in April just after the flush of snowmelt (Baker et al. 1979). Northward there is a pronounced temperature gradient except along the north shore of Lake Superior, where temperature iso-

therms follow the shore. Westward the climate becomes progressively drier, and the important isotherm indicating a net moisture deficit occurs in northwestern Minnesota. However, direct measurements of the critical variable of evapotranspiration are not practical, and the indirect methods used all produce significantly different results. Actual evapotranspiration may also be seriously underestimated in areas where ground water recharges (Freeze and Cherry 1979). Despite these uncertainties the southern limit of boreal peatlands in Minnesota generally follows the 22" isopleth for evapotranspiration as calculated by the Thornwaite method. The distribution of the major climatic isopleths relative to the original presettlement vegetation is presented in Figure 5.

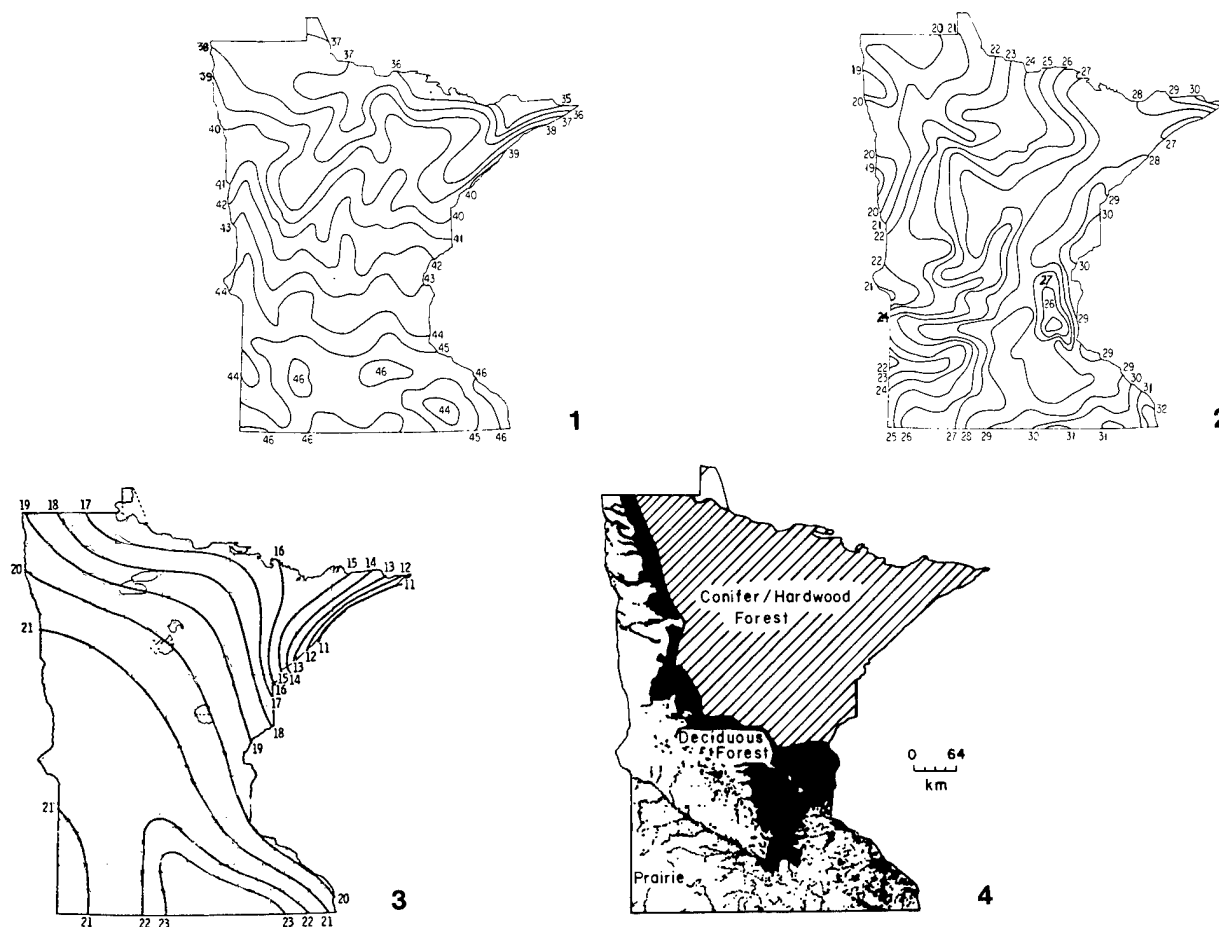


Figure 5. The climate and vegetation of Minnesota: (1) average annual temperature in °F (Baker and Strub 1965), (2) average annual precipitation in inches (Baker et al. 1967), (3) average annual evapotranspiration in inches (Baker et al. 1979), (4) presettlement vegetation of Minnesota (after Marschner map, Heinselman 1974).

CHAPTER 2. PHYSICAL PROPERTIES OF PEAT

2.1 DEFINITION

Organic deposits have traditionally been classified according to a genetic system that stresses the origin of the deposit from a source or "mother vegetation" (H. Von Post 1862; L. Von Post and Granlund 1926). A strong element of circularity is therefore present in the definitions of peat and peatlands, which cannot be defined exclusive of one another. In practice it is often impossible to distinguish lake sediments from highly humified peats unless diagnostic macro- or microfossils are present. The great variability of peatlands and the peat deposits they form also add to the difficulty of characterizing peats. To avoid these problems purely descriptive methods have been developed by Troels-Smith (1955), the United States Department of Agriculture Soil Survey Staff (1975), and the International Peat Society (IPS 1976).

2.2 COMPOSITION AND PHYSICAL PROPERTIES

Peat is composed of the partially decomposed remains of the plants and animals common to waterlogged soils. The organic content of peat is very high, and it is often possible to determine the types of taxa from which a specific deposit was derived. Small amounts of mineral material may also be present but these minerals never represent a majority of a peat sample. The most common mineral constituent in Minnesota peats is phytoliths that have apparently blown in from the surrounding uplands (Finney and Farnham 1970).

The major properties of peat that are of ecological interest are botanical composition, degree of decomposition (mea-

sured as humification, bulk density, and fiber content), hydraulic conductivity, and cation exchange capacity. The fiber content, which forms the basis of the USDA soil taxonomy for organic soils, also has important applications for engineering and hydrology.

Peats composed of bryophytes are called turfa or detritus bryophytica according to Troels-Smith or moss peat according to the IPS system. The most common type of moss peat in Minnesota contains a high percentage of Sphagnum and is found under raised bogs and certain poor fens. In Minnesota Sphagnum is often the major component of any peat horizon in which it occurs although it may be intermixed with fragments of sedges, wood, or other bryophytes.

The uppermost layers of Sphagnum peat in a profile are relatively undecomposed, with the majority of the leaves still attached to the stems. In Minnesota this very porous upper zone may extend as deep as 70 cm beneath the surface of nonforested bogs, although in forested sites this zone is generally shallower (Glaser and Janssens 1986). The upper porous zone generally gives way to more decomposed horizons at depth in which the Sphagnum leaves become detached from the stem, forming a more densely packed configuration. In more decomposed horizons the individual leaves are degraded to the point where they are difficult to detect within the more decomposed matrix of finer particles. Even where the detached leaves are virtually intact the macroscopic appearance of this peat is indistinguishable from that of decomposed sedge peat without microscopic identification. All Sphagnum peats in Minnesota are not necessarily derived from bogs or Sphagnum-dominated poor fens. In the Red Lake peatland J.A.

Janssens has identified horizons dominated by the minerotrophic Sphagnum subsecundum and S. contortum, which are associated with other rich fen indicators (Janssens and Glaser 1986).

The other type of moss peat in Minnesota is composed of members of the Amblystegiaceae and is collectively known as feather- or brown-moss peat (Cajander 1913; Auer 1933). This peat type is poorly developed in Minnesota, although minerotrophic Amblystegiaceae may be present as minor fractions in sedge-fen peats. The most common peat-former among this group in Minnesota is Scorpidium scorpioides and less commonly Calliergon trifarium, C. aftonianum, and Drepanocladus lapponicus (Janssens and Glaser 1986). In peats derived from rich fens Campylium stellatum is generally present as a minor fraction and is replaced by Calliergon stramineum in the poor-fen assemblages. A brown-moss sediment derived from the aquatic Drepanocladus has been identified by J.A. Janssens at the Marcell bog in north-eastern Minnesota. Without careful microscopic inspection this unusual lake sediment would normally be mistaken for a terrestrial peat.

Most fen peats in northern Minnesota are composed of sedge fragments in a generally decomposed state (turfa herbacea or detritus herbosus sensu Troels-Smith 1955). In the most fibrous state these peats consist of a porous network of rhizomes, rootlets, and leaf bases of Carex. With increasing humification the individual rootlets and sedge shoots become more fragmented and interspersed within a more finely decomposed matrix. Despite widespread reports of reed peat in Minnesota remains of Phragmites communis or various types of rushes (Scirpus, Juncus, Eleocharis, Rhynchospora, and Cladium) from the Juncaceae and Cyperaceae have yet to be documented. Seeds from these taxa, however, are often present in more finely decomposed peat that lacks larger sedge fragments.

Wood layers (turfa lignosa or detritus lignosus sensu Troels-Smith 1955) are common in the peatlands of northern Minnesota. Large pieces of wood are often found in layers of deeply humified peat in

which only the most resistant remains are identifiable, such as spruce and tamarack needles, wood fragments, occasional seeds, and mycorrhizae on rootlets.

In general the particle size of a peat horizon depends upon its botanical composition and degree of humification (Baden and Eggelsman 1963; Rycroft et al. 1975). Porosity generally decreases from the coarser sedge-reed and sedge brown-moss to the finer grained brown-moss peat. Sphagnum peats, however, have the finest particle size and thus the lowest hydraulic conductivity for any given degree of humification. The breakdown of the anatomical structure of these peat-formers by decomposition further decreases the particle size within a peat horizon and lowers its porosity. Various means have been devised to measure the degree to which peat is decomposed. The most common properties measured are fiber content, bulk density, and humification.

As peat decomposes the individual fragments are broken down into smaller particles, which become packed more closely together, resulting in a loss of void or pore space. Bulk density therefore provides a measure of decomposition by measuring the mass of organic matter in a sample as a function of volume. Profiles from raised bogs and water tracks in Minnesota generally have very low bulk-density values for the uppermost horizon, which consists of living plants and relatively undecomposed plant remains (Figure 6). This uppermost horizon of porous peat is generally known as the acrotelm, a term used by Ingram (1978) to describe a classification scheme developed by Soviet hydrologists (Ivanov 1981).

With increasing depth the peat becomes more evenly decomposed in Minnesota peatlands, but there is no linear relationship between bulk-density profiles and depth. This lower zone in a peat deposit has a high bulk density and corresponds to the catotelm of Ingram (1978) and Ivanov (1981). Bulk-density profiles for Minnesota peats have been determined by Boelter (1969), Boelter and Verry (1977), Chasson (1984), Chasson and Siegel (1986), Glaser and Janssens (1986), and

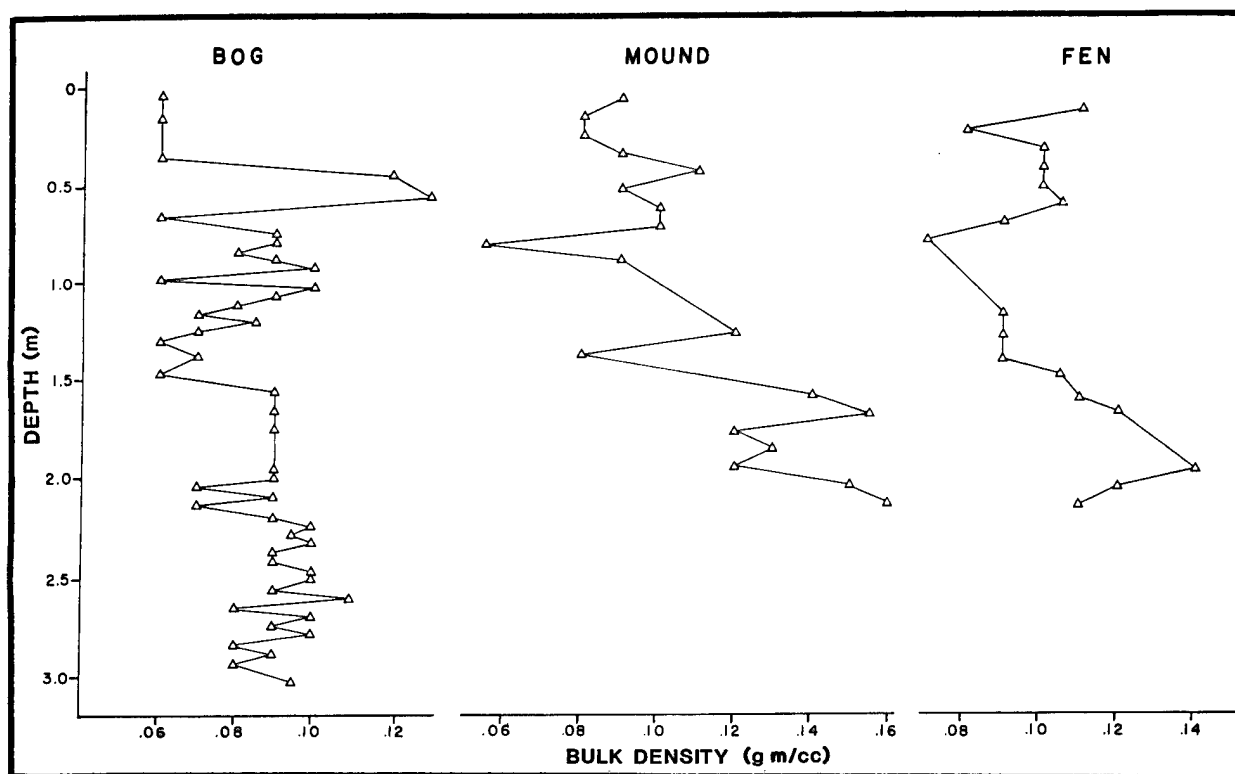


Figure 6. Bulk-density profiles from the Lost River peatland. The three profiles are from a raised bog, spring-fen mound, and fen water track (Chasson 1984; Chasson and Siegel 1986).

J.A. Janssens (University of Minnesota, Minneapolis; pers. comm.).

Decomposition also produces humic and fulvic acids that impart a dark color to peat waters. The concentration of these humic substances in a peat profile is therefore considered an important measure of the degree of decomposition (referred to as humification). Humification may be determined by (1) qualitative methods in which the color of water squeezed from a peat sample is compared to various states described by the Von Post scale (Von Post and Granlund 1926) and (2) quantitative techniques in which the concentration of humics extracted from a sample by an alkali solution are measured by spectroscopic means.

The humification of peat profiles from three different types of peatland at Lost River were determined by Chasson and Siegel (1986) and can be directly compared with bulk-density curves from the same

core (Figure 7). The curves for bulk density and humification coincide remarkably well for the upper 1 to 1.5 m of each core but then diverge greatly with depth. This pattern may be caused by factors other than the concentration of humics within a sample because the absorption spectra of humic compounds is also influenced by pH, by complexing with metals, and by the source of the humics, which may be diverse material (Tsutsuki and Kuwatsuka 1979a, b; Stevenson 1982).

Decomposition has a profound effect on the hydraulic properties of peat primarily by altering the size and geometry of the pores. The hydraulic conductivity of a peat horizon determines the resistance to the flow of water through a porous medium. The measurement of hydraulic conductivity in peat, however, is difficult because the natural bedding of the peat profile may be altered during the course of sampling. These problems are outlined by Rycroft *et al.* (1975), Boelter

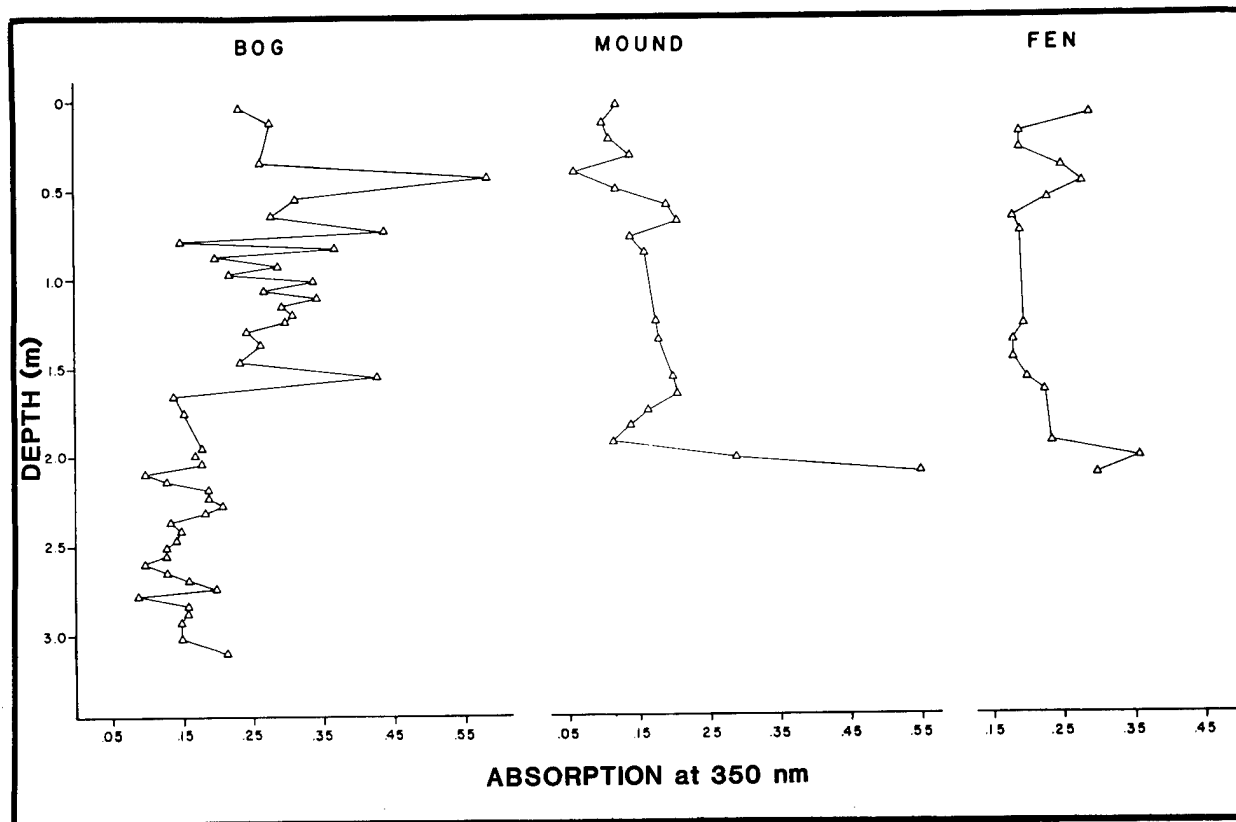


Figure 7. Humification profiles from the Lost River peatland. The profiles were obtained from the same cores as in Figure 6 using absorption of an alkali extract (Chasson and Siegel 1986).

(1965, 1970), Ingram (1983), and most recently by Chasson and Siegel (1986).

In Minnesota the first studies of hydraulic conductivity (K) in peat were made by Boelter (1965, 1969) in the Marcell Experimental Forest in northwestern Minnesota. Boelter found little difference between horizontal and vertical hydraulic conductivity within a profile, but his values of K were higher in the laboratory samples than those determined in the field. Boelter also found a direct relationship between K and decomposition as measured by bulk density and fiber content. The principal conclusion drawn was that most flow took place within the uppermost horizon of undecomposed peat in contrast to the negligible flow in the deeper decomposed layers. These findings are in agreement with the major literature in peatland hydrology, which distinguishes between an upper highly porous layer of peat (the acrotelm) and a lower more de-

composed layer (the catotelm), which acts as a confining layer by restricting water flow (Ivanov 1981; Ingram 1983).

Chasson and Siegel (1986), however, working in the Lost River peatland of northwestern Minnesota presented different conclusions based on laboratory and field measurements of horizontal (K_h) and vertical (K_v) conductivity (Figure 8). The ratio of K_h to K_v was extremely variable throughout the column of three peat cores taken from a bog, a fen, and a spring-fen mound. Values of K_h generally were 1 to 2 orders of magnitude greater than K_v . Chasson also found no statistically significant correlation between bulk density and humicity with depth or K at Lost River (Figure 8). Although they produced similar results, Chasson believed that bulk density gave a better estimate of decomposition than colorimetric methods.

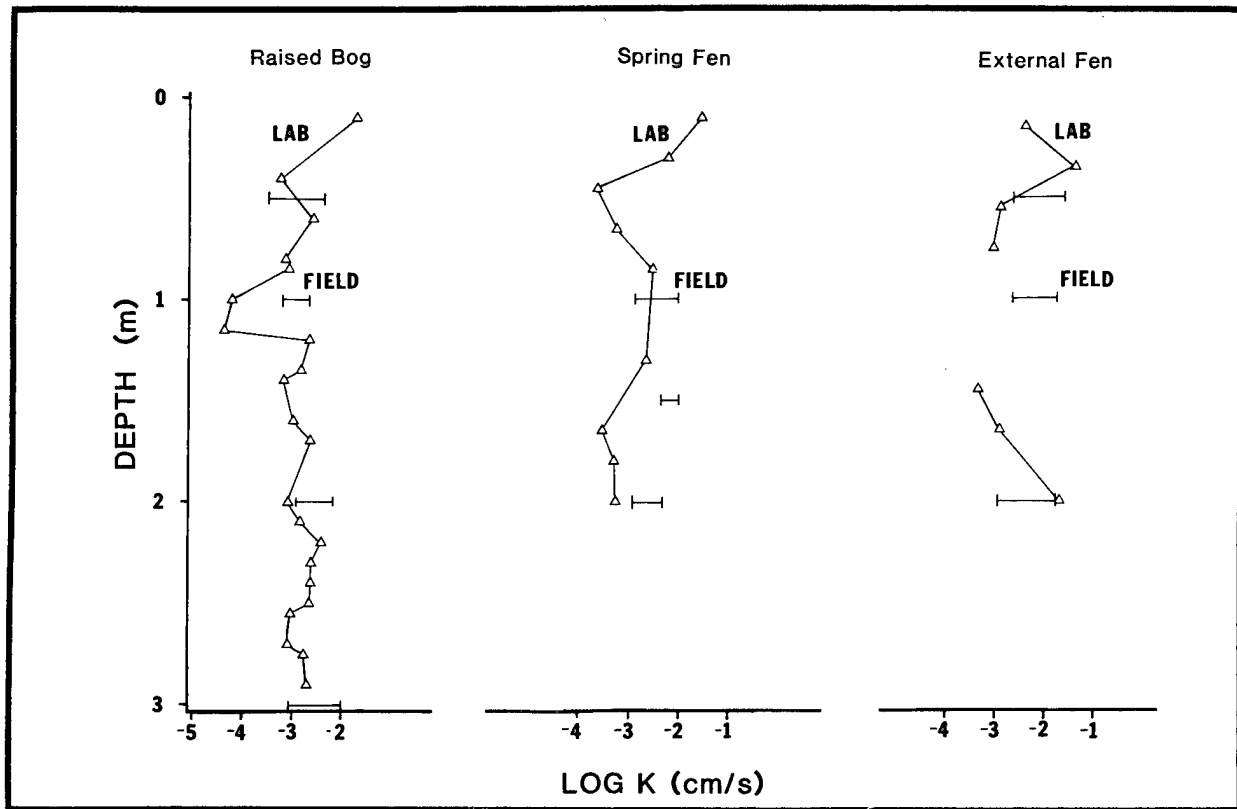


Figure 8. Hydraulic conductivity profiles from the Lost River peatland. The measurements of K were made from the same cores illustrated in Figures 6 and 7 (Chasson and Siegel 1986).

CHAPTER 3. PEATLAND FORMATION

3.1 TERRESTRIALIZATION AND PALUDIFICATION

Peatlands may develop directly over forest or prairie soils by the process of paludification (Versumpfung sensu Cajander 1913) or over lake sediments as a final step in lake-infilling or terrestrialization (Verlandung sensu Weber 1902). Both processes have been active in Minnesota, but the majority of peatlands in the State have developed by the paludification of the glacial lake plains (Figures 9 and 10).

Peat formation requires some factor to shift the balance between production and decomposition so that organic matter accumulates in the soil. The production of organic matter in peatlands is generally lower than that measured on adjacent upland sites, which indicates that decomposition rates must be lowered to permit peat to form (Reiners 1972; Clymo and Reddaway 1971). Decomposition rates are controlled by three major factors: (1) climate, (2) decomposer organisms, and (3) the quality of plant litter (Swift et al. 1979).

In boreal regions the activity of decomposers is severely restricted by low temperatures, a trend that increases toward the north. Thus in Alaska peat may accumulate on steep north-facing slopes, where the accumulation of a moss mat insulates the ground surface and allows the permafrost table to rise (Heilman 1966, 1968; Van Cleve and Viereck 1981). The cold temperature of the upper soil horizons depresses the activity of decomposer organisms and favors the accumulation of litter with low carbon to nitrogen (C:N) and carbon to phosphorus (C:P) ratios. Together with the increasing water retention of the soil these factors promote the

replacement of spruce forest by a nonforested peatland.

Elsewhere peat formation is believed to result from waterlogging, which creates anoxic conditions in the uppermost soil horizons. Poorly drained soils may become waterlogged as a result of many different factors that are directly or indirectly related to climate. A rise in the regional water table may be brought about by: (1) climatic changes that increase precipitation and decrease evapotranspiration (Godwin 1975), (2) forest clearance by man, which increases runoff and decreases evapotranspiration (Moore 1975; Frenzel 1983), (3) a rise in base level that accompanies a rise in eustatic sea level (Cajander 1913; Aario 1932; Godwin 1943; Oldfield 1960), and (4) development of an impervious hardpan by pedogenic processes (Hammond 1968; Mitchell 1976; Ugolini and Mann 1979; Taylor and Smith 1981).

In Minnesota paleoecological investigations have strongly indicated a climatic control on peat formation. Most peatlands in Minnesota formed after the end of the mid-Holocene, when the climate became cooler and moister. The great peatlands of the Lake Agassiz plain, for example began to form in the east about 4500 yr B.P. and then spread westward reaching Upper Red Lake area approximately 3000 yr B.P. (Glaser et al. 1981). The spread of these peatlands may have ended approximately 1900 yr B.P., which marks the youngest basal peat dates so far recorded in the Lake Agassiz region (Glaser et al. 1981).

The formation of Sphagnum mats around the margins of ponds is also dated from the mid-Holocene or earlier (Wright and Watts 1969; Janssen 1967a). Boreal conifers (Larix and Picea), bog ericads,

Landforms and Stratigraphy

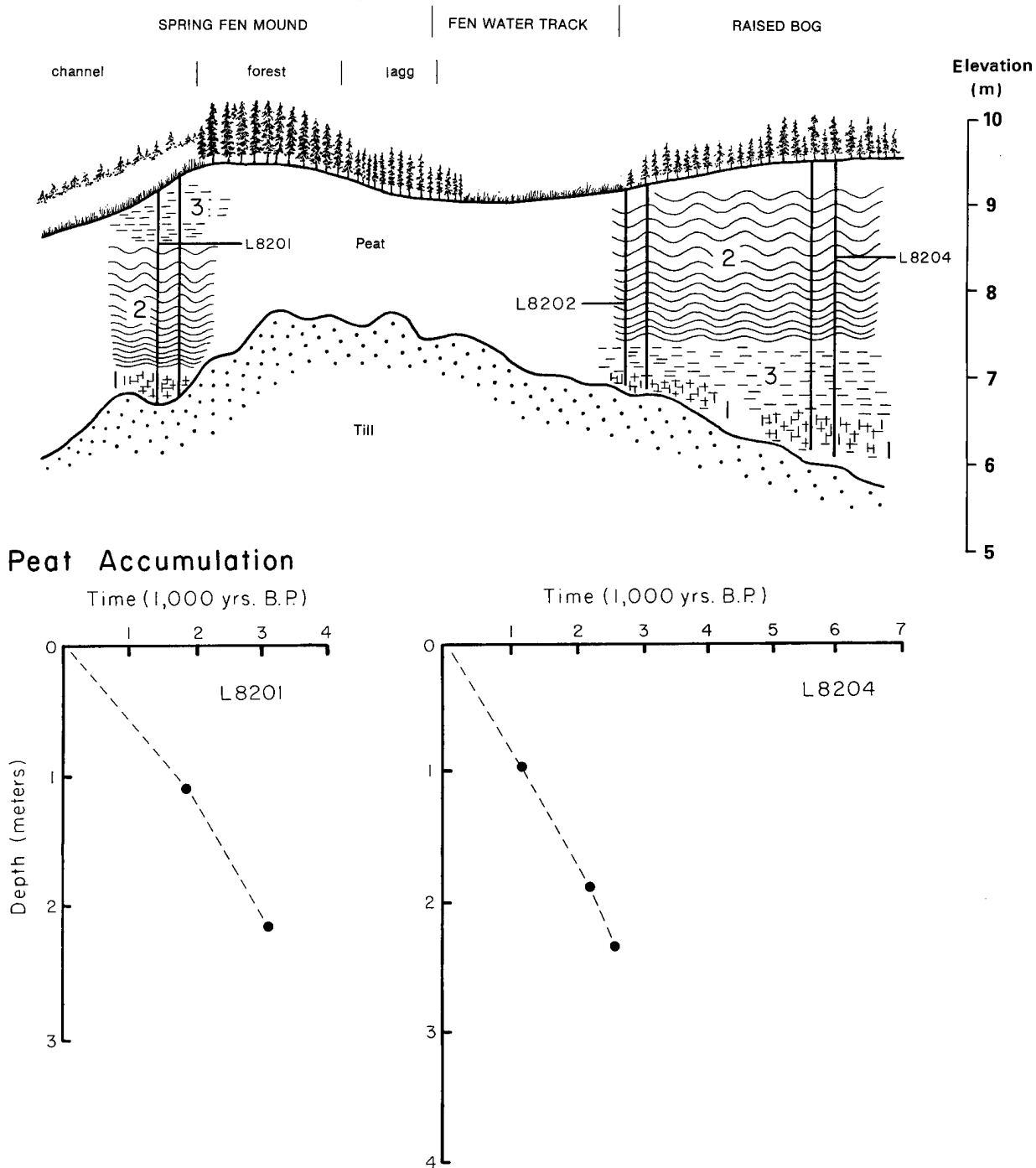


Figure 9. Paludification of sloping ground in the Lost River peatland, northwestern Minnesota. The spring-fen mound has developed over a rise in the mineral substrate, whereas the raised bog has grown over a depression (Almendinger et al. 1986). The peat stratigraphy from the three cores (L8201, L8204, and L8202) indicates that deeply decomposed fen peats (1) first accumulated in the peatland followed by *Sphagnum* peat with wood (2). In the upper 70 cm of the spring-fen core, however, woody *Sphagnum* peat is abruptly replaced by sedge-fen peat (3) indicating an abrupt change in the vegetation (Glaser et al., In prep.). Thus the spring-fen mound was once covered by a *Sphagnum*-dominated bog or poor fen that was abruptly replaced by a spring-fen channel less than 2,000 years ago. The cores in this diagram were collected adjacent to those in Figures 6, 7, and 8.

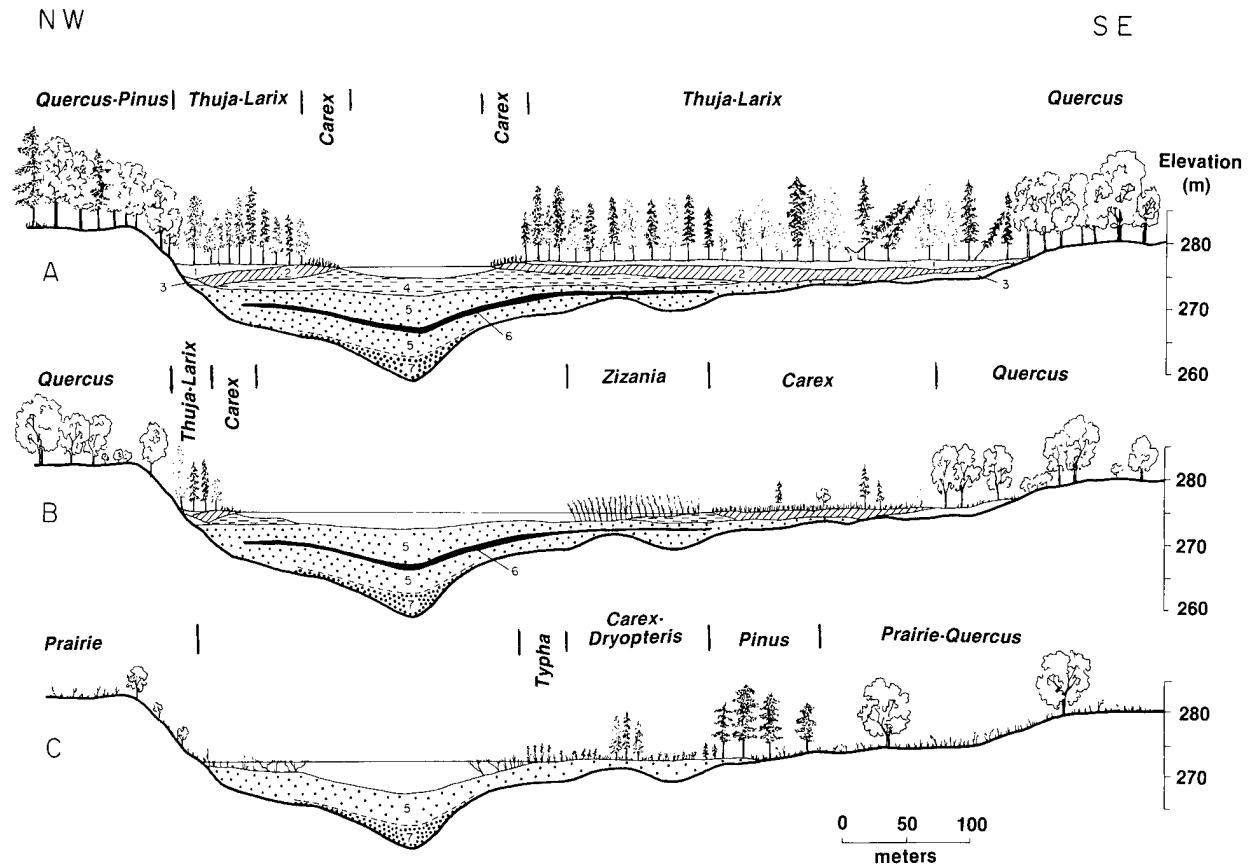


Figure 10. Terrestrialization at Cedar Bog Lake, south-central Minnesota. This reconstruction is slightly redrawn from Cushing (1963). The three stages represent (A) the present vegetation and lake level, (B) the inferred vegetation and lake level 4,000 years ago during the mid-Holocene, and (C) the inferred vegetation and stratigraphy during the early Holocene approximately 8,000 years ago. Cushing hypothesized that Cedar Bog Lake was 4 m lower during the early Holocene and the subsequent rise in the water table was followed by growth of the surrounding peatland. The sediment layers marked are (1) woody peat, (2) sedge peat, (3) sapropel, (4) coarse-detritus copropel, (5) marly copropel, (6) dark copropel, (7) sideritic copropel (Lindeman 1941; Cushing 1963). The sediment types are defined in Lindeman (1941). The elevations are height above sea-level.

and *Sphagnum* began to grow around the margins of lakes in northern and central Minnesota about 4000 yr B.P. following the end of the warmer and drier conditions that characterized the mid-Holocene. These boreal species again advanced over marly lake sediments in southern Minnesota after the end of the Little Ice Age (400 yr B.P.) when the climate became still cooler (Swain 1979).

A rise in the regional water table has been hypothesized to account for these changes, although the spread of a peat mat from the margins of a lake seems to require a lowering of the water table. Buell et al. (1968), for example, determined that the margin of the sedge mat at

Cedar Bog Lake in Anoka County has not changed its position in 30 years, and its further spread is limited by the water level in the lake. This conclusion is supported by Conway's (1949) studies in Itasca County.

The spread of the peat mat at Cedar Bog Lake has been investigated in more detail by the stratigraphic studies of Lindeman (1941) and Cushing (1963). Lindeman noted that the peatland surrounding Cedar Bog Lake is widest over the shallow southeast margin of the basin, which he attributed to protection from the prevailing winds and resulting wave action (Figure 10). Cushing, however, based his

reconstruction on water-table fluctuations, which he was able to infer from a detailed analysis of the lithology and fossil pollen assemblages of the sediments.

Cushing postulated that the lake level was 4 m below the present level approximately 8,000 yr B.P. when a *Dryopteris* and sedge-dominated wetland spread over the exposed mud flats at the southeast end of the basin (Figure 10). Progressively rising water levels after the middle Holocene then led to the development of a cedar swamp over the formerly exposed mud surface. The growth of this swamp forest apparently restricted the penetration of minerotrophic runoff from the surrounding uplands to the lake, because the sediments deposited at this time show a marked decline in carbonate content proceeding toward the top of the horizon.

Cushing's reconstruction therefore assumes that peat formation is always caused by waterlogging and that the distinction between terrestrialization and paludification is artificial. Around lake margins, however, peat formation must first be preceded by a fall in the water table that exposes part of the lake bottom. A subsequent rise in the water table will create a waterlogged substrate and favor the formation of peat. These conditions were probably created across northern Minnesota as a result of climatic changes during the Holocene (Grimm 1981; Webb et al. 1983; Almendinger 1985). Cushing's hypothesis explains the simultaneous formation of peatlands around lakes and over the glacial lake basins at the end of the mid-Holocene.

Peat formation may also be favored by a change in the chemistry of surface runoff. The reintroduction of the boreal mire flora in Minnesota coincided with the arrival of white pine (*Pinus strobus*), which migrated westward and replaced more xeric oak forest, oak savanna, or prairie (Jacobson 1979). Runoff draining from the more acidic and nutrient-poor litter of a pine forest could have promoted the spread of the less nutrient-demanding boreal species and lowered the decomposition rate of litter in low spots where water accumulated in the soil (Janssen 1967a, 1968; Wright and Watts 1969).

Basal peat dates from bogs and fens in eastern North America have similarly shown a relationship between the earliest peat formation and the establishment of pine forests or conifer forests on the uplands (Glaser, unpubl. data). Studies of runoff from the Marcell Experimental Forest, however, indicate that hardwood species actually remove more Ca from mineral soils than the pines (Alban 1982). The increase in precipitation at the end of the mid-Holocene may also have increased the leaching of the upper soil horizon and decreased the minerotrophy of runoff draining from the uplands.

3.2 PRIMARY PRODUCTIVITY

The current status of peat accumulation in Minnesota has been estimated from the rate at which organic matter and energy are cycled through various wetland communities. The most comprehensive studies of primary production in Minnesota were organized by D.B. Lawrence on a broad spectrum of plant communities on the Anoka sandplain 50 mi north of Minneapolis/Saint Paul (Bray et al. 1959; Bray 1963; Ovington et al. 1963; Ovington and Lawrence 1967; Reiners 1972). These studies provide the best comparison of primary production in different types of communities in Minnesota. More recently production, decomposition, and nutrient cycling have been investigated primarily at the Marcell Experimental Forest of the Chippewa National Forest in north-central Minnesota. These studies are part of a larger investigation of raised bogs in eastern North America organized by E. Gorham (1985).

The Anoka sandplain studies, however, provide the best comparison between production in peatland areas and adjacent upland communities. Reiners (1972), for example, estimated the primary productivity of three closely adjacent plant communities along a topographic gradient near Cedar Bog Lake. The above-ground net annual primary production totals for an oak forest (8.9 t/ha), forested lagg fen (7.1 t/ha), and cedar swamp forest (10.3 t/ha) closely followed the biomass estimates for these communities (125, 99, and 160 t/ha, respectively). Reiners also

determined that the basal area of the trees in these stands roughly paralleled the estimates of production and biomass.

Reiners then compared the productivity estimates for Cedar Creek with those reported for other types of upland and wetland ecosystems on the Anoka sandplain (Figure 11). The aboveground biomass data for the three forests at Cedar Creek seemed low in comparison with the other examples reported by Ovington *et al.* (1963) but the productivity data for the different oak woodlands were similar. The various types of ecosystems on the Anoka sandplain were classified by Reiners into two types: graminoid systems (wild rice stands, cattail stands, and prairie) with low biomass-to-production ratios, and the forest systems (oak woodland, oak forest, lagg forest, cedar swamp) with high biomass-to-production ratios. The aboveground biomass of these types had a 171-fold range, in contrast to the only 18-fold variation in productivity.

In northern Minnesota Grigal and colleagues (Grigal and Kernik 1984a, b; Grigal 1985a; Grigal *et al.*, In prep.) estimated the primary productivity of six forested bogs. A distinction was made between raised bogs, which cover large areas on glacial lake plains, and perched bogs (*sensu* Boelter and Verry 1977), which occupy smaller kettle-hole depressions. An allometric model was developed to estimate biomass of black spruce:

$$Y = aD^h \quad \text{and} \quad Y = aD^h H^c$$

where Y = mass in kg, D = diameter at breast height in cm, and H = height in m. Production in the tree stratum was also evaluated by means of the forest-growth and yield model STEMS (Grigal and Kernik 1984a, b).

Substantial differences were found between the perched and raised bogs for aboveground biomass (100.7 t/ha vs 31.0 t/ha) and total productivity (0.3 t/ha vs 1.3 t/ha). These values indicate a decline in the perched bog forest in contrast

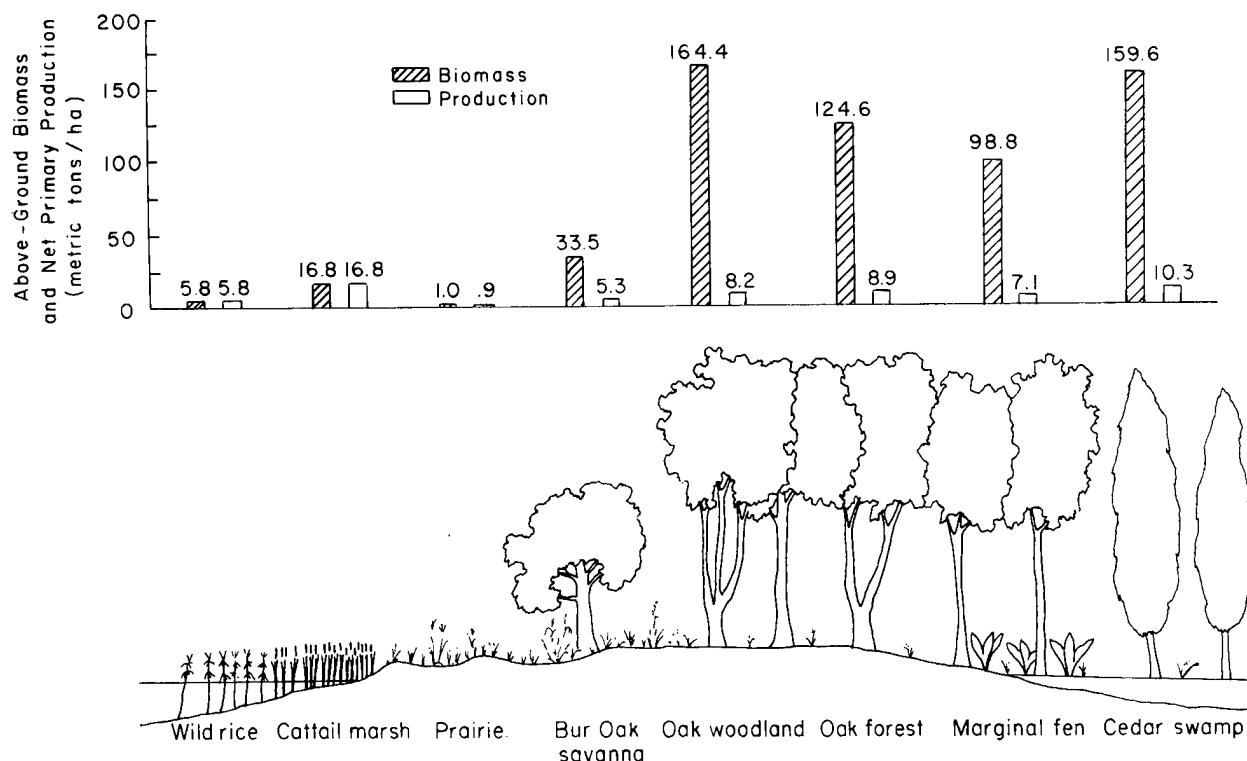


Figure 11. Comparison of net primary production and aboveground biomass from different communities on the Anoka Sandplain (Reiners 1972).

to a slight gain in the raised bog. Net primary production (NPP), however, was similar at both sites (3.6 vs 3.0). Grigal et al. (In prep.) note the exceptionally low values for NPP for these forested bogs compared to those of other forests in the Great Lakes region, and these values are half of those reported by Reiners (1972) on the Anoka sandplain.

Grigal (1985a) also made measurements of primary production in the *Sphagnum*-dominated ground layer over a 3 year period. On perched bogs *Sphagnum* production was estimated at $380 (+19\%) \text{ g/m}^2/\text{yr}$, in contrast to $320 (\pm 19\%) \text{ g/m}^2/\text{yr}$ on raised bogs. Production was much greater in the hollows (520 in hollows vs. $320 \text{ g/m}^2/\text{yr}$ in hummocks of perched bogs; and 320 in hollows vs. $300 \text{ g/m}^2/\text{yr}$ in hummocks on raised bogs). These data compare favorably with those of Elling and Knighton (1984), who obtained values of $390 \text{ g/m}^2/\text{yr}$ from a bog in northern Minnesota, and with those of Pakarinen and Gorham (1983), who reported values of $240 \text{ g/m}^2/\text{yr}$ for a bog in southern Manitoba. Grigal notes the general agreement in these values despite the different methods used. Elsewhere across the boreal zone values for peatlands range from 300 to $1000 \text{ g/m}^2/\text{yr}$ for peat bogs and mires (Bradbury and Grace 1983).

3.3 DECOMPOSITION

Decomposition may be estimated directly by the measurement of mass loss and gas evolution, or indirectly from numerical models or simulations of peat growth (Swift et al. 1979; Clymo 1983). At Cedar Bog Lake Reiners (1968) investigated decomposition by measuring CO_2 evolution from the floors of three forests ranging from an upland oak forest to a cedar swamp peatland. The rate of gas evolution in this study was closely related to soil temperature and secondarily to moisture conditions producing seasonal variations in the release of carbon. However, compensating mechanisms such as respiration from the tree roots produced nearly equal cumulative totals of CO_2 evolution in the three forest floors. Total CO_2 was over three times higher than expected from the equivalent amount of carbon released from annual litter fall. Reiners and Reiners

(1970) found that the forest floors generally increased in mass, organic matter, energy, and nutrient status in response to a rise in the water table. However, energy and nutrient flow through detritus pathways tended to converge in spite of the prominent differences in structure.

At Marcell decomposition was studied by means of decomposition strips placed at different depths in the peat profile and by laboratory experiments (Farrish and Grigal 1984). Decomposition not unexpectedly proceeded more rapidly at the bog surface and decreased with depth. The rate was also more rapid in the hummocks than in the hollows. Laboratory experiments showed an increase in decomposition with an increase in pH and K concentrations but no significant change with addition of N, P, and Ca. These findings at Marcell are reviewed by Gorham (1985).

3.4 PEAT ACCUMULATION

3.4.1 Physical Changes in Volume

The growth of a peat deposit is not a simple function of the yearly difference between gross primary production and total community respiration. The volume of a peat mass may also change significantly through time as a result of physical processes or decomposition that continues at slow rates throughout a profile (Clymo 1983; Dickinson 1983). Efforts to model the accumulation of a peat through time are therefore constrained by the difficulty of predicting the long-term stability of the mass-to-volume relationships of organic matter within a peatland.

A porous medium such as peat is subject to both compression and expansion according to the sum of forces exerted on it. At any given depth the stress equilibrium is determined by three forces: (1) the weight of the overlying material pressing down on the plane, which is borne by (2) the strength of the granular skeleton of the porous medium and by (3) the fluid pressure in the pores (Freeze and Cherry 1979). Consolidation occurs when the granular skeleton is rearranged into a more densely packed configuration. Consolidation commonly occurs in the upper portion of a peat profile but is restricted in the lower horizons by fluid pressure

in the pores. However, when a peatland is artificially drained by ditches the pores collapse and subsidence occurs. K. Bradof, for example, has measured substantial subsidence in the Red Lake peatland, where drainage ditches have been cut along Minnesota Highway 71 (K. Bradof, In prep.).

A rise in fluid pressure, however, may cause the peat mass to swell, a process known as mooratumung or "bog breathing" (Ingram 1983). An unusual example of mooratumung was recently described from the Lost River peatland, where over a period of 1 year the elevation of spikes driven into trees rose 10.7 cm on a raised bog and 6.1 cm on a spring-fen mound, in contrast to only minor changes in the intervening water track (Almendinger *et al.* 1986). The elastic expansion of the peat landforms at Lost River is probably related to a rise in pore pressure that was caused by the upward hydraulic-head gradients measured by Siegel and Glaser (In press). Expansion and consolidation of peat within a profile may therefore produce significant errors in estimating the growth or accumulation of a peat profile through time.

Peat may be removed from the interior of a peat deposit by means of underground pipes, which are common features on the blanket bogs of the British Isles (Gilman and Newson 1980; Jones 1981) and the raised bogs in eastern Canada (Glaser and Janssens 1986). Pipe drainage has never been reported for Minnesota peats although such pipes could locally alter the mass/volume relationships within a peat deposit.

3.4.2 Accumulation Estimates

Two techniques have been employed to determine the rate of peat accumulation in Minnesota peatlands: (1) measurements of mass and energy are used to estimate present turnover times, and (2) dating methods measure increments of organic matter in peat profiles as a function of time. The first method was employed by Reiners (1972) to estimate the accumulation of organic matter in the

floors of an oak forest, a lagg forest, and a cedar swamp at Cedar Creek. Organic matter increased markedly downslope along this topographic gradient (65, 323, and 917 t/ha), whereas the detrital inputs were approximately the same. Reiners concluded that turnover times (forest floor/input) for all components of the forest floors increased from oak to marginal lagg to cedar swamp (14, 73, and 184 t/ha for total weight) and represented 7, 46, and 90 years of aboveground production at current rates.

The first determinations of peat accumulation in Minnesota that used dating techniques were made by Leisman (1953, 1957) on small peatlands near Itasca State Park in northwestern Minnesota. Leisman used seedlings of *Larix laricina* to date peat accumulation over an 18 year period. Similar rates recorded at each station ranged from 1.38 cm to 1.73 cm/yr.

A more comprehensive study of peat accumulation has recently been made from peat cores collected between 1978 to 1984 with a specially modified Livingstone piston sampler (Wright *et al.* 1984). These cores have since been dated by ^{14}C methods. The dates indicate that peat accumulation in Minnesota is higher in ombrotrophic bogs than in minerotrophic fens. Moreover, the rate of peat accumulation in the Red Lake peatland in Minnesota is higher than that of other peatlands in North America and Europe (Gorham 1985).

In contrast to these rapid rates of accumulation of peat in the Glacial Lake Agassiz peatlands, the accumulation rate at the Alborn fen in northeastern Minnesota apparently stagnated during the past several thousand years. This fen is also exceptional because of its very old basal date of over 7,000 yr B.P. The old date is apparently related to its physiographic location in an abandoned drainage way of Glacial Lake Upham, because several comparably old basal dates have been obtained from nearby peatlands in similar drainage ways (Wasylikowa and Wright 1969).

CHAPTER 4. PHYSICAL AND CHEMICAL PROPERTIES OF PEATLANDS

4.1 BOG AND FEN

Boreal peatlands are separated into bogs or fens on the basis of four criteria: landforms, vegetation, water chemistry, and hydrology (Glaser 1983a; Glaser and Janssens 1986; Glaser and Janecky, In prep.). A major factor that determines the course of peatland succession is the supply of dissolved solids from outside sources. Fens, for example, are fed by waters that transport ions directly from a mineral source and consequently contain species more demanding in their nutrient requirements. Bogs, in contrast, are elevated above the influence of ground water and thus receive all their water and salts directly from the atmosphere. The very close relationships among these four criteria in Minnesota, however, enables an investigator to predict the nature of a patterned peatland from only one variable such as landform (Glaser *et al.* 1981; Glaser 1983a; Glaser and Janecky, In prep.).

4.2 HYDROLOGY

Hydrology has been recognized as a driving variable that controls the course of peatland succession (Von Post and Granlund 1925; Ingram 1967, 1983). Of the four fundamental properties of peatlands, however, hydrology is perhaps the least understood and is most often inferred from the interpretation of other peatland properties, particularly the water chemistry. Two schools of thought have developed on peatland hydrology: (1) the surface water approach that considers the deeper peats to be impervious to flow or (2) the ground water approach that considers a significant role for ground water (Figure 12).

The surface water approach was used by Von Post and Granlund (1926) to explain the development of a raised bog and its isolation from the underlying groundwater table. A more rigorous treatment of the role of surface waters in peatlands was presented by Boelter (1964, 1969) and particularly Ivanov (1981) who summarized the considerable Russian contributions in this field. According to this school water flow in a peatland is restricted to the uppermost layer of undecomposed porous peat (acrotelm) because the very low porosity and hydraulic conductivity of the deeper, more decomposed peat inhibits flow in a profile. A raised bog is therefore believed to be isolated from ground water by the confining layer of deeply humified peat. The bog-building *Sphagnum* will then spread outward from this center until continued expansion is checked by a eutrophic barrier presented by minerotrophic waters with a high pH and Ca concentration.

Recently the role of groundwater flow in peatland development has been examined by hydrological techniques such as (1) measuring of hydraulic head gradients with piezometer nests, (2) determining geochemical gradients in the interstitial water of peat profiles, and (3) computer simulation of groundwater flow patterns in peatlands (Siegel 1981, 1983; Boldt 1985; Siegel and Glaser, In press; Loiselle, In prep.). These methods have determined that significant flow of ground water does occur in the decomposed catotelm, and that ground water can have an important influence on the development of peatlands.

Computer simulations by Siegel (1981, 1983) and Boldt (1985) indicate that the growth of groundwater mounds under raised bogs in the Glacial Lake Agassiz region may generate sufficient hydraulic head to

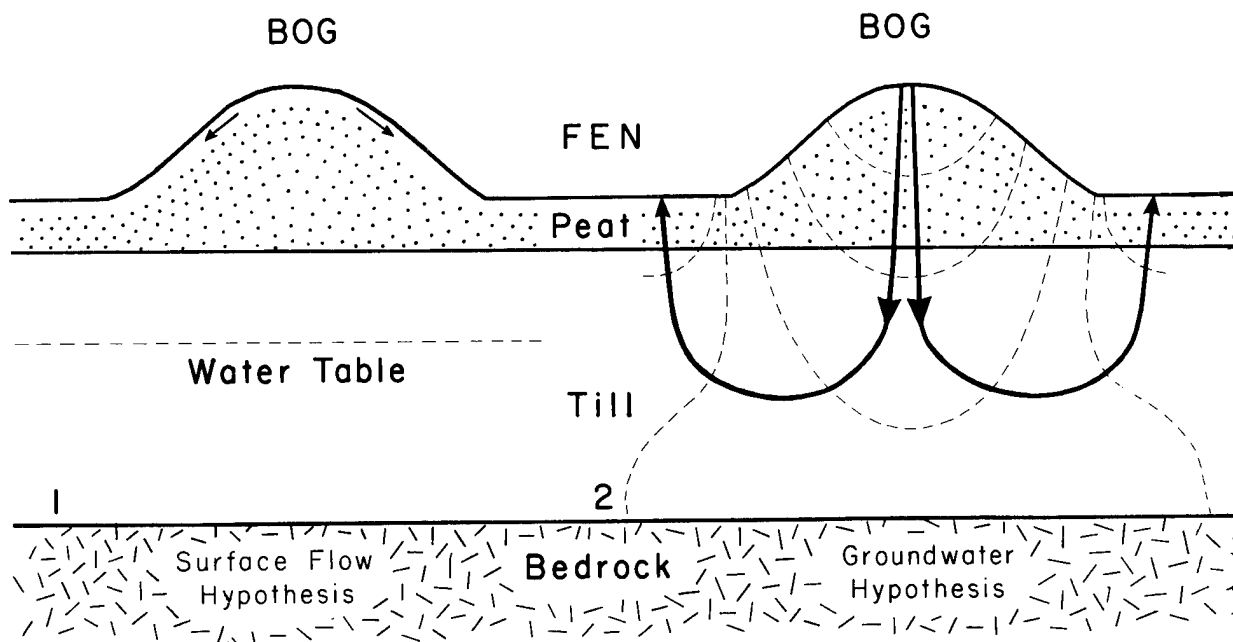


Figure 12. Role of ground water and surface drainage in controlling the outward growth of a raised bog. The surface flow hypothesis (1) assumes that a bog is isolated from the influences of ground water and that its outward growth is blocked by minerotrophic water draining from the adjacent uplands. The ground water hypothesis (2), in contrast, predicts that the outward spread of a bog may be blocked by the discharge of ground water at the bog margin. Thus the development of a ground water mound under a growing bog creates sufficient hydraulic head to drive flow cells, with water flowing from the bog crest downward into the underlying glacial till where the water picks up cations from the mineral substrate. The ground water in the cell then rises toward the surface and discharges at the bog margin. Both hypotheses assume that the outward growth of a bog is blocked by the high pH and calcium concentrations in surface water and differ only in their source of associated alkalinity.

drive local flow cells. The bogs according to this model then become recharge areas for ground water with water flowing down through the peat and underlying glacial till to the bedrock/till interface. Water flowing downward is then focused upward toward the surface where it discharges at the bog margin. The Siegel model therefore predicts an autogenic control on bog development in contrast to the largely allogenic controls assumed by the surface-flow hypothesis.

A field test for these two hydrological models was recently organized by P.H. Glaser and D.I. Siegel in the Lost River peatland of northern Minnesota. This study area contains two contrasting types of peatland: a spring-fen mound and a raised bog, which should be controlled by different hydrologic regimes (Figure 9). The first step in this study was to determine surface elevations across the peatland in order to accurately place the

piezometer nests. The survey showed that the peat mound is situated over a rise in the mineral substrate, whereas the adjacent bog is located over a depression in that substrate (Almendinger *et al.* 1986). The surface of the bog and spring-fen mound are raised above the water table in the adjacent water tracks, and therefore the surface of both features should be isolated from the influence of mineral ground water according to the surface-flow hypothesis.

The head measurements, however, indicated that all three landforms were in a discharge area for ground water, at least during part of the year (Siegel and Glaser, *In press*; Figure 13). The gradients were most pronounced in the spring-fen mound, where the surface-water chemistry also indicated groundwater discharge. The results from the raised bog, however, were very surprising. In the fall of 1983 all the water levels in the piezometer

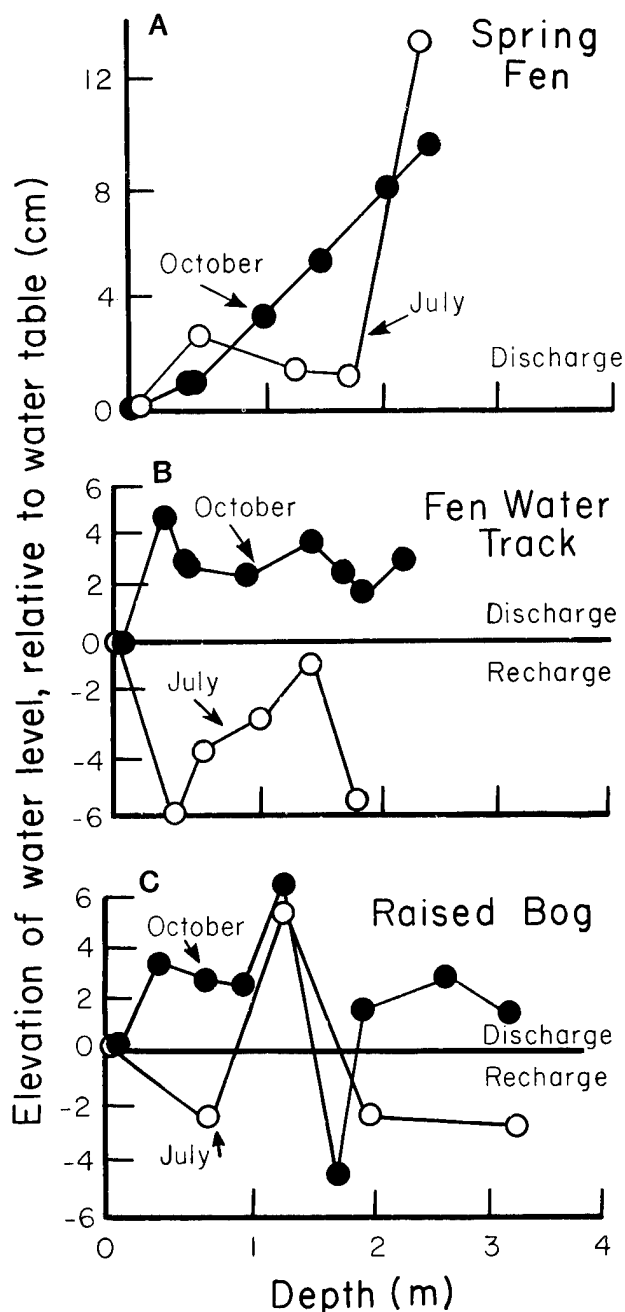


Figure 13. Head gradients from piezometer nests in the Lost River peatland, northwestern Minnesota. The elevation of water levels in the piezometer tubes inserted to different depths in the peat is presented relative to the water table (0 cm). Water levels above the water table indicate groundwater discharge, whereas water levels below the water table indicate groundwater recharge. Thus the gradients measured in the spring-fen mound (A) in July of 1982 and fall of 1983 indicate groundwater discharge, whereas the head gradients in the water track (B) and raised bog (C) indicate that these landforms were in discharge zones for ground water in the fall of 1983 and recharge zones in the summer of 1982.

nests on the raised bog were above the water table, indicating that the bog was in a discharge area for ground water at this time. During the summer of 1982, however, all the water levels in the piezometers were below the water table of the bog, indicating a recharge condition or reversal in gradient from the following summer.

The chemistry of interstitial waters collected from the piezometer tubes also indicated that the bog was located in a discharge area for ground water. At 50 cm depth the pH (7.0) and Ca concentration (100 mg/l) were similar to waters in the underlying calcareous till. Apparently the small volume of minerotrophic water rising from beneath the bog was diluted by rainwater and transformed by the growing *Sphagnum* in the upper 50 cm of peat to the point that it was chemically indistinguishable from typical ombrotrophic water. The instrumentation at Lost River therefore indicated that groundwater flow may have an important influence on the development of peatland patterns.

The groundwater model can also be applied to hydrological data acquired from the S-2 peatland in the Marcell Experimental Forest. Bay (1967) considered this peatland to be perched because its water table was 8 m above the regional water table in the underlying mineral soil. The water levels in his piezometers, however, could also be explained if the bog was a recharge area for ground water as predicted by the Siegel model. Verry and Timmons (1982), in fact, had to assume that at least one third of the water leaving S-2 was recharging the groundwater system in order to balance their hydrologic budget. Downward head gradients have also been found in bogs in Maine and elsewhere in Minnesota (Nichols 1984 a,b ; MN DNR unpubl. data).

Although ground water may have a significant impact on peatlands, the volume of water involved may be quite small. Siegel (1983) has calculated that the input of as little as 10% ground water into bog water from the Lake Agassiz region would raise the pH to 6.3 and the Ca concentration to 20 mmol/l. The very low hydraulic conductivity of peats in the

catotelm has also been challenged by measurements of vertical and horizontal hydraulic conductivity by Chasson and Siegel (1986) in the Lost River peatland. Chasson and Siegel discovered values of K_h and K_v that are as much as 100 times greater than that previously reported for northern Minnesota.

The greater volume of flow occurring in the acrotelm is strongly supported by the hydraulic conductivity of these upper layers, which may be as much as 10^2 to 10^4 times greater than that of the catotelm (Boelter and Verry 1977; Chasson 1984). The high conductivity of this zone is also demonstrated by the downward penetration of bomb tritium derived from atmospheric fallout at the crest of a raised bog in the Red Lake peatland in northern Minnesota (Gorham and Hofstetter 1971). Most of the water that falls on a peatland is rapidly carried away as runoff in the streams downslope. Storm hydrographs from various small peatland catchments in Minnesota clearly indicate the limited capacity of these peatlands to store water (Bay 1967, 1969; Verry 1975; Brooks *et al.* 1982).

4.3 WATER CHEMISTRY

The water chemistry in boreal peatlands is another important variable controlling the distribution of the vascular and cryptogamic flora. In Sweden Du Rietz (1949) and Sjörs (1946, 1948, 1952) established the close relationship between the distribution of many circumboreal mire species and the water chemistry. The sensitivity of certain species to pH and Ca concentration is so high, for example, that these species can be used as indicators for certain ranges in the water chemistry. Sjörs and Du Rietz therefore were able to construct a classification of peatlands that is largely defined by the water chemistry. Because this classification is partly independent of the more geographically variable mire flora, the Swedish system is applicable to peatlands across the boreal belt.

This classification scheme was first applied to Minnesota by Heinzelman (1963, 1970), who used slightly different ranges in pH to define the various peatland types. Heinzelman also made extensive use

of the Ca concentration of the mire waters to define his types and provided information on the principal plant species. A more detailed analysis of patterned peatlands in Minnesota has largely supported the types recognized by Heinzelman and Sjörs, which are summarized in Figure 14 (Glaser and Janecky, *In prep.*). The water samples in these newer studies also support the conclusion of Sjörs (1952) that the various types of peatland actually form a continuum rather than the sharply delimited types suggested by Du Rietz (1949).

Despite this continuous range in variation the Minnesota samples can generally be classified as either bog or fen waters. The bog waters all have a pH below 4.2 and Ca concentration below 2 mg/l although certain samples taken from pits may have slightly higher values. The acidity of bog waters is ultimately caused by their reputed isolation from cations supplied by ground water. However, the primary mechanism causing this acidity is a question of much debate. The most important sources of acidity considered in the literature are (1) cation exchange by *Sphagnum*, (2) acid atmospheric deposition, (3) biological uptake of nutrient ions, (4) oxidation and reduction of sulphur compounds, and (5) build-up of organic acids by decomposition.

The cation exchange system of *Sphagnum* has been championed as the most important mechanism causing acidity by Clymo (1963) and Clymo and Hayward (1982), but recently Gorham *et al.* (1984) has presented evidence that links the acidity of bogs to the accumulation of organic acids as a result of decomposition. A full review of this problem may be found in Clymo and Hayward (1982), Kilham (1982), and Gorham *et al.* (1984).

The rise in pH and Ca concentration in the fen waters is related to the input of cations from a mineral source, either from runoff or the discharge of ground water. Peatlands also receive a significant input of cations from atmospheric deposition, particularly Ca, which is transported as dust from the adjacent prairies (Munger and Eisenreich 1983; Gorham *et al.* 1984). The pH of precipitation in northern Minnesota, however,

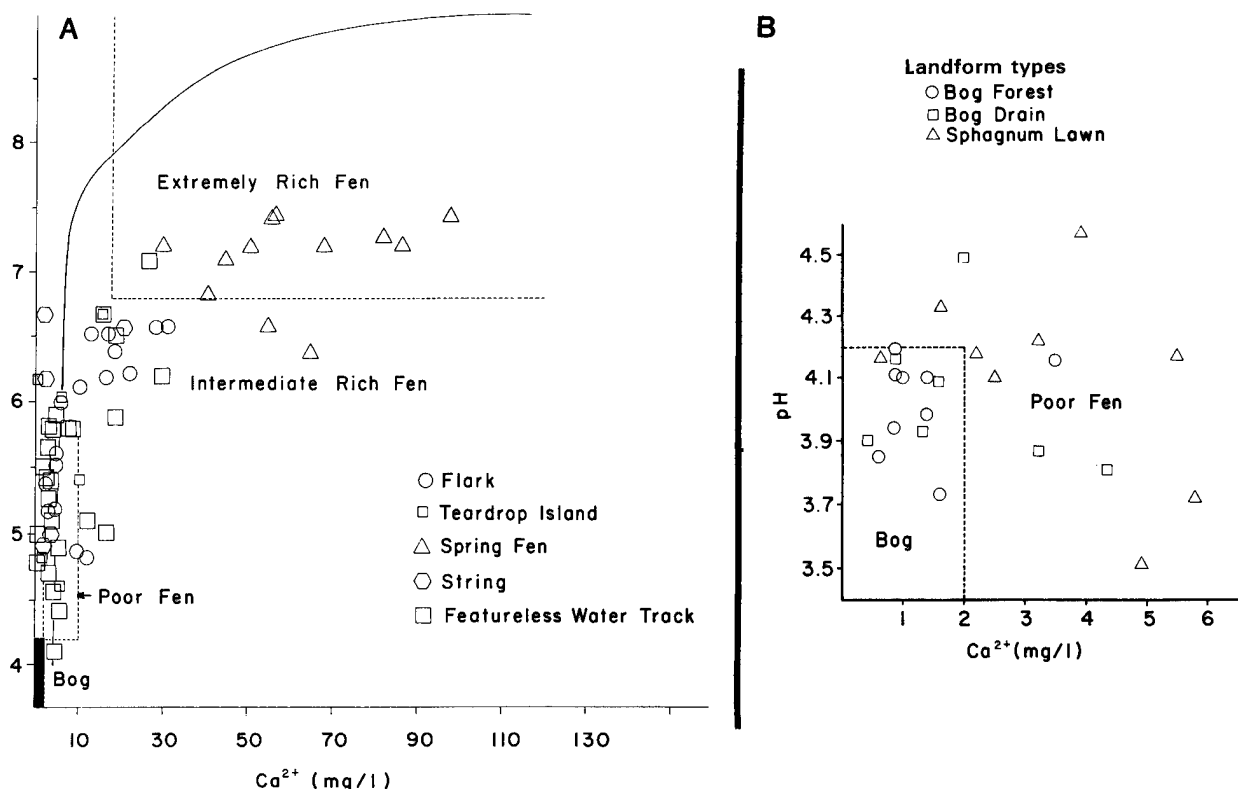


Figure 14. Water chemistry values for bog and fen samples in northern Minnesota. The complete range of water samples is shown in (A), with the pH and calcium values for specific ranges defined by the dashed lines. The samples in the more restricted bog range are shown in (B).

ranges from 5.0 to 5.1 and is insufficient to raise the alkalinity of fen waters to the levels found in the rich and extremely rich fens. Thus the very high pH (>7) and Ca concentration (>30 mg/l) in the extremely rich fens can only be maintained by a continuous discharge of ground water derived from calcareous till. Without the input of ground water the pH and Ca concentration of these surface waters would normally equilibrate to much lower levels because of the buffering capacity of atmospheric CO_2 .

The mechanisms that control the ranges in water chemistry observed in northern Minnesota are not well understood. Dissolved organic compounds, commonly known as humic acids pose a major difficulty in constructing a charge balance of the significant cations and anions. The general form of the curve for the water samples in northern Minnesota, however, fits the shape of a curve for

solutions in equilibrium with the atmosphere with a Ca balancing charge (Figure 14; Glaser and Janecky, In prep.). The fen samples from northern Minnesota, however, diverge from this ideal curve in the rich fen range, with the Ca concentration rising to 30 mg/l at a pH that is significantly lower than that predicted by the calculated curve. These samples are apparently oversaturated with respect to calcite, in response to complexing of the Ca^{2+} to organics or the release of anions from an organic source.

4.4 GEOCHEMISTRY AND NUTRIENT CYCLING

The surface-water chemistry of peatlands can only be understood within the broader context of the geochemistry and nutrient cycling of a peatland watershed. At Cedar Bog Lake Reiners and Reiners (1970) compared the total accumulation and

flux of nutrients in the floor of three types of forest from upland oak forest to a lowland cedar swamp. The nutrient flux in these three types of forest varied little, and therefore nutrient turnover times were proportional to the mass of the pools, which increased downslope with increasingly wet conditions. The turnover times of anions such as N and P were much slower than those of cations such as Ca and Mg, indicating a greater degree of retention by perennial vascular plants and soil microflora.

A more comprehensive study of the input and output of geochemical constituents in peatlands was made at the Marcell S-2 watershed as a result of long-term research by the U.S. Forest Service under E.S. Verry and by investigators at the University of Minnesota under the direction of S. Eisenreich and E. Gorham. Verry (1975) compared the water quality of streams draining from five perched raised bogs and one groundwater fen in the Marcell Experimental Forest. The concentration of organic ions was highest in streamflow from the perched peatlands and most ions were inversely related to streamflow. In the groundwater fen, however, ions derived from an organic source were in lower concentrations compared to ions derived from the solution of aquifer materials, such as calcium. The concentration of chemical constituents in streamflow draining from the fens was not related to flow rate. Annual nutrient yields (kg/ha/yr) for these two types of peatland were generally low and surprisingly similar to values obtained for other upland forested areas in North America.

The accumulation of metals in the uppermost horizons of peat was investi-

gated by Eisenreich and coworkers in the S-2 watershed at Marcell. Some elements such as K, Mn, Pb, Zn, Ca, and Mg were enriched in the uppermost zone of growing moss, probably by either active or passive biological uptake. Other elements, such as Fe and Al, were enriched in the zone of the minimum water-table fluctuation by a combination of washdown, dust inputs, and active redox processes. The preliminary results on the geochemical studies at Marcell are summarized in Gorham (1985).

A detailed hydrogen budget was constructed for this site to determine the relative importance of the various sources of acidity (Urban *et al.*, In press). The dominant source of acidity was determined to be organic acids (263 meq/m²/yr) produced by the decomposition of peat. The sequestering of elements in the peat represented another important source of acidity (42.9 meq/m²/yr). The most important source of alkalinity, in contrast, was derived from the weathering of dustfall (<76 meq/m²/yr) blown in from adjacent agricultural areas. Alkalinity derived from the reduction of nitrate and sulphate (<39.2 meq/m²/yr) was less important because of the low inputs of NO₃ and SO₄.

The N cycle at Marcell was investigated by Urban (1983), who determined the total input of N at 16 kg/ha/yr. A mass balance of N indicated that 40% of the total N was derived from atmospheric deposition, 30% from upland runoff, and 22% from nitrogen fixation. Most N lost from the system was in the form of organic N in streamflow. Denitrification losses were small and resulted from the absence of nitrification. Urban concluded that the bog is therefore a large sink for N, retaining 52% of the input within the peat deposit.

CHAPTER 5. VEGETATION OF PEATLANDS

5.1 VEGETATION-LANDFORM PATTERNS

A landform is any element of the Earth's surface that is characterized by a distinctive surface expression or internal structure (Howard and Spock 1940; Fairbridge 1968). Surface patterns on boreal peatlands may accurately be described as landforms because of the recurrence of similar pattern forms across broad geographic areas (Glaser 1983a; Glaser and Janssens 1986). Unlike geological features, however, the peatland landforms are composed entirely of the past and present remains of plant communities and therefore are largely the products of biotic rather than purely physical processes in the environment.

In Minnesota the study of patterned peatlands has been integrated around vegetation-landform patterns, with the field sampling aimed at delimiting the vegetation, water chemistry, and physiographic setting of different landform types (Heinselman 1963, 1970; Hofstetter 1969; Janssen 1967b; Griffin 1975, 1977; Glaser et al. 1981; Glaser 1983a, b, c; Wright and Glaser 1983; Glaser, In prep.a). Regional peatland studies in Minnesota demonstrated that the various landforms are composed of relatively uniform stands of vegetation that display comparatively little variation across the region (Glaser, In prep.a). The landforms can therefore be used to accurately predict the vegetation and water chemistry of a site. Transitions in the landform patterns also have been used to discern potential developmental trends that can be tested by stratigraphic analyses (Glaser et al. 1981; Glaser and Janssens 1986; Glaser, In prep.a).

Three major categories of landforms are found in northern Minnesota: raised

bog, water track, and spring fen (Glaser, In prep.a). Although these landform types are strikingly delimited on aerial photographs, they represent little vertical relief on the ground because the landscape is almost flat. The very subtle changes in elevation on these peatlands emphasize the sensitivity of these systems to small hydrological factors.

Many raised bogs in Minnesota develop a linear crest, which can be detected on aerial photographs by the radiating lines of spruce forest (Figure 15). The morphometry of the crest has been confirmed by topographic leveling at different sites in Minnesota (Farnham and Grubich 1966; Heinselman 1970; Almendinger et al. 1986) and by the contour interval on orthophotomaps of the U.S. Geological Survey. The forest cover is thinner on the lower flanks of these bogs and grades into a broad featureless nonforested *Sphagnum* lawn. On the larger bogs strips of minerotrophic seeps appear on the lower bog flanks, and these seeps may develop into distinct water tracks. On the largest bogs these water tracks convert the lower bog flanks into ovoid forms that have the appearance of ovoid islands. The best examples of ovoid islands in Minnesota are found in the Red Lake peatland (Figure 16).

A water track is defined as any zone in which minerotrophic runoff is channeled across a peatland. Originally described from areas of bog in Sweden (Sjörs 1948) these features were subsequently discovered in the Hudson Bay lowlands (Sjörs 1963) and in both bog and fen peatlands in Minnesota (Heinselman 1963, 1970). In Minnesota water tracks are distinguished by vegetation patterns that simulate the appearance of braided streams or networks of rills. In large forested swamps water

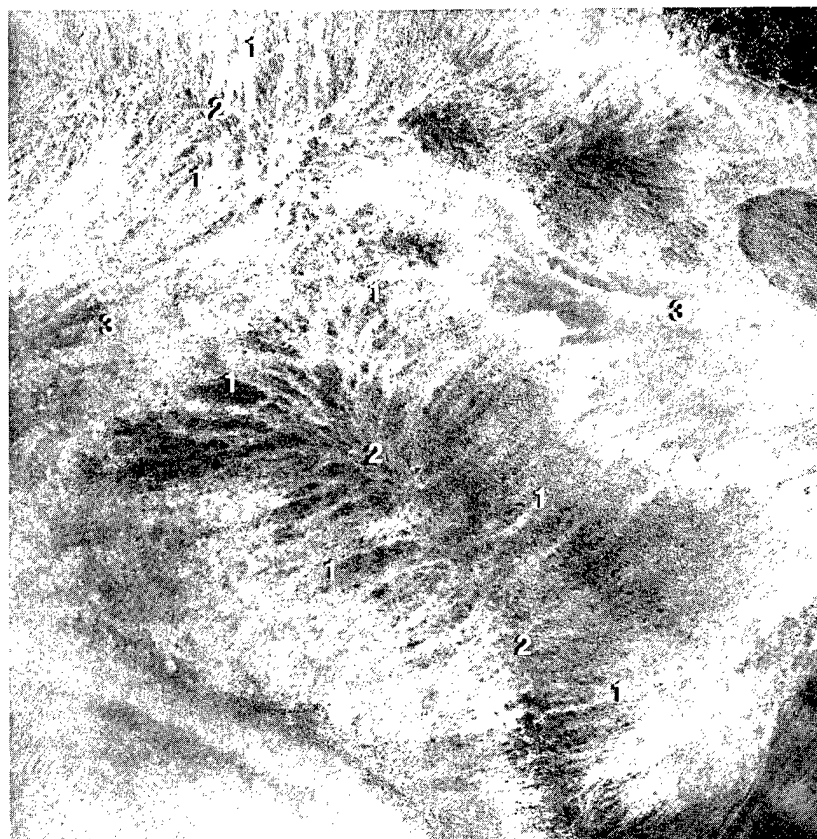


Figure 15. Radiating forest patterns on a raised bog. The features marked are (1) radiating lines of forest, (2) linear crest, and (3) *Sphagnum* lawns on the lower bog flanks. The photograph was taken from the Myrtle Lake peatland and covers an area 2.5 km across.

tracks appear as treeless zones of sedges or shrubs that form long streamlined bands parallel to the prevailing slope (Figure 17). The most highly patterned tracks, however, have networks of peat ridges (strings) and pools (flarks) oriented perpendicular to the slope. These patterns characterize the circumboreal aapamoor (*sensu* Cajander 1913) and represent one of the most distinctive features of the boreal region. In Minnesota and the North American interior they may also contain fields of tree islands entirely composed of peat (Figure 18).

A specialized type of water track is the spring-fen channel, which is generally restricted to the Glacial Lake Agassiz peatlands (Glaser 1983b; Glaser, In prep.a). Spring fens are characterized by

anastomosing networks of nonforested channels that drain through a rich swamp forest (Figure 19). The surface waters in these channels have a pH of 7 or greater and Ca concentrations of 30 mg/l, factors that strongly indicate the discharge of groundwater from calcareous parent material.

The larger peatlands in Minnesota usually contain areas of both bog and fen and may therefore best be described as mire complexes. Despite the complexity of the physiography and soils in the State only a few types of complexes can be recognized (Glaser, In prep.a). The types are illustrated in Figures 20 and 21 and should be regarded as reference points along a continuous spectrum of pattern variations.



Figure 16. Aerial photograph of ovoid islands in the Red Lake peatland. The features marked are (1) the bog crest, (2) *Sphagnum* lawns on the lower flanks, (3) internal water tracks, and (4) large ovoid islands with a horseshoe ring of spruce forest. The area is cut by drainage ditches spaced approximately 2 km apart. Water drains from the lower portion of the photo to the upper portion.



Figure 17. Featureless water tracks from the North Black River peatland in northern Minnesota. The features marked are (1) ovoid raised bogs, (1a) a mineral island that protrudes through the peat, (1b) internal water tracks, and (2) featureless water tracks. Human alterations to the peatland are Christmas tree cutter lanes (3) and muskeg tractor scars (4).

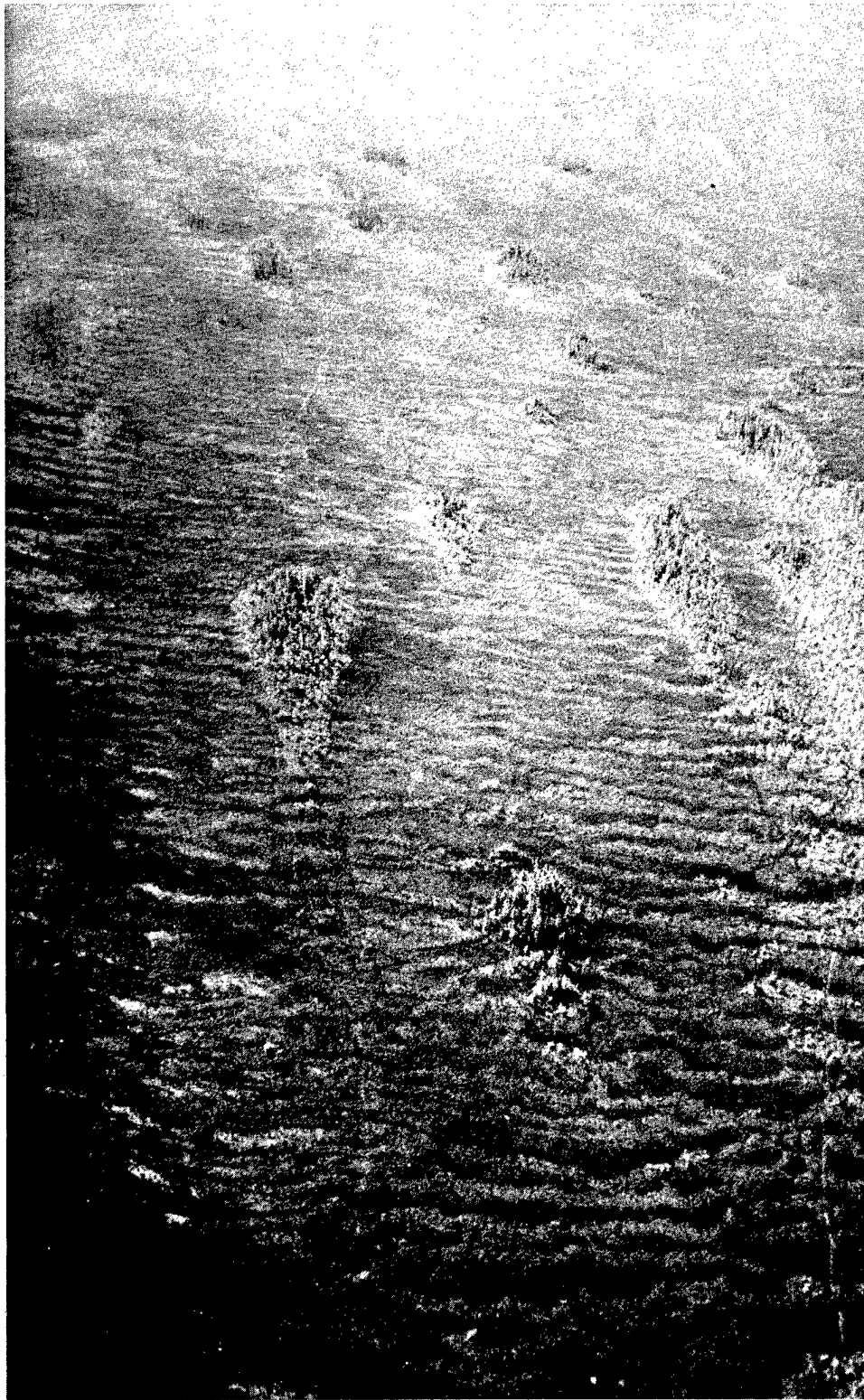


Figure 18. Patterned water track with fields of tree islands. Notice the network of flarks (pools) and strings (peat ridges) oriented transverse to the slope. This oblique aerial photograph was taken from the Lost River area in northwestern Minnesota.

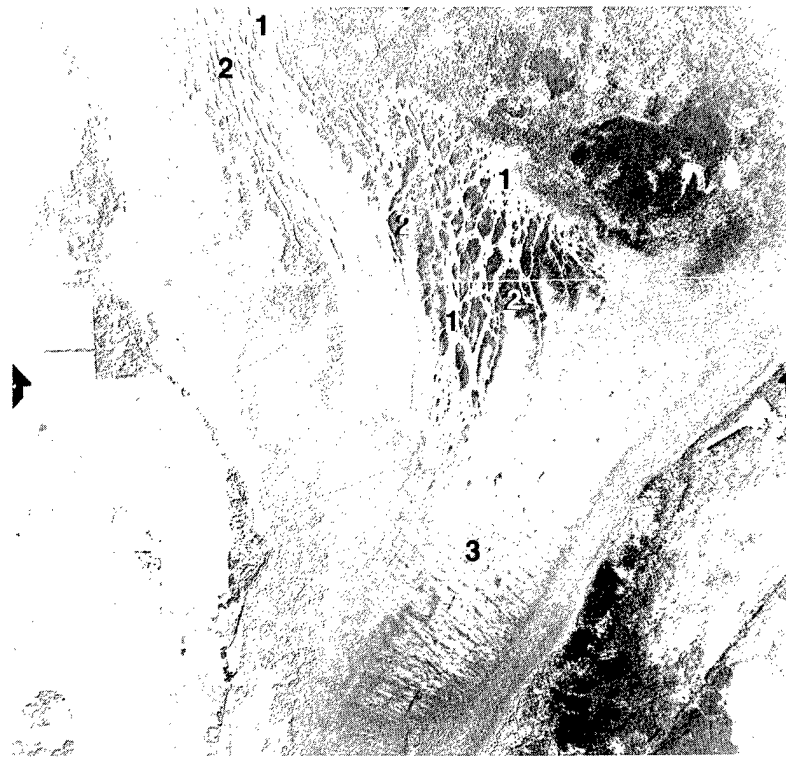


Figure 19. Spring-fen landforms. The networks of anastomosing channels (1) drain southward through a swamp forest (2) and grade into a patterned fen downslope (3). The photograph covers an area approximately 2.6 km across (Pine Creek peatland, northwestern Minnesota).

In the discontinuous peatlands the physiographic setting of the watershed is directly related to the area of bog and fen downslope. As the area of the mineral catchment at the head of a watershed increases there is a corresponding increase in the area of water track relative to that of bogs in the peatland. Thus the various mire-complex types in Figure 20 represent a sequence, which culminates in the huge water tracks of type 4, or in the single water track of type 7.

The continuous mire-complex types are found in the Lake Agassiz peatlands, in which peat covers over 75% of the landscape between the Big Fork River and Upper Red Lake (Figure 21). The various types consist of semicircular bogs with bifurcating water tracks, large bog complexes with internal water tracks and ovoid islands, huge water tracks, and spring-fen

mounds. The very small area of mineral soil in these peatlands probably represents an insignificant source of mineral ions leaching onto the peatlands, which instead may be supplied by groundwater discharge. A more thorough discussion of these types may be found in Glaser *et al.* (1981), Glaser (1983a), Glaser (In prep.a).

5.2 VEGETATION

Patterned peatlands are distinguished by relatively simple vegetation patterns that lack the spatial variability commonly associated with upland vegetation (Glaser and Janecky, In prep.). Only a few vegetation types are found in these patterned areas and these types exhibit a high fidelity to a particular landform type. The vast Red Lake peatland, for

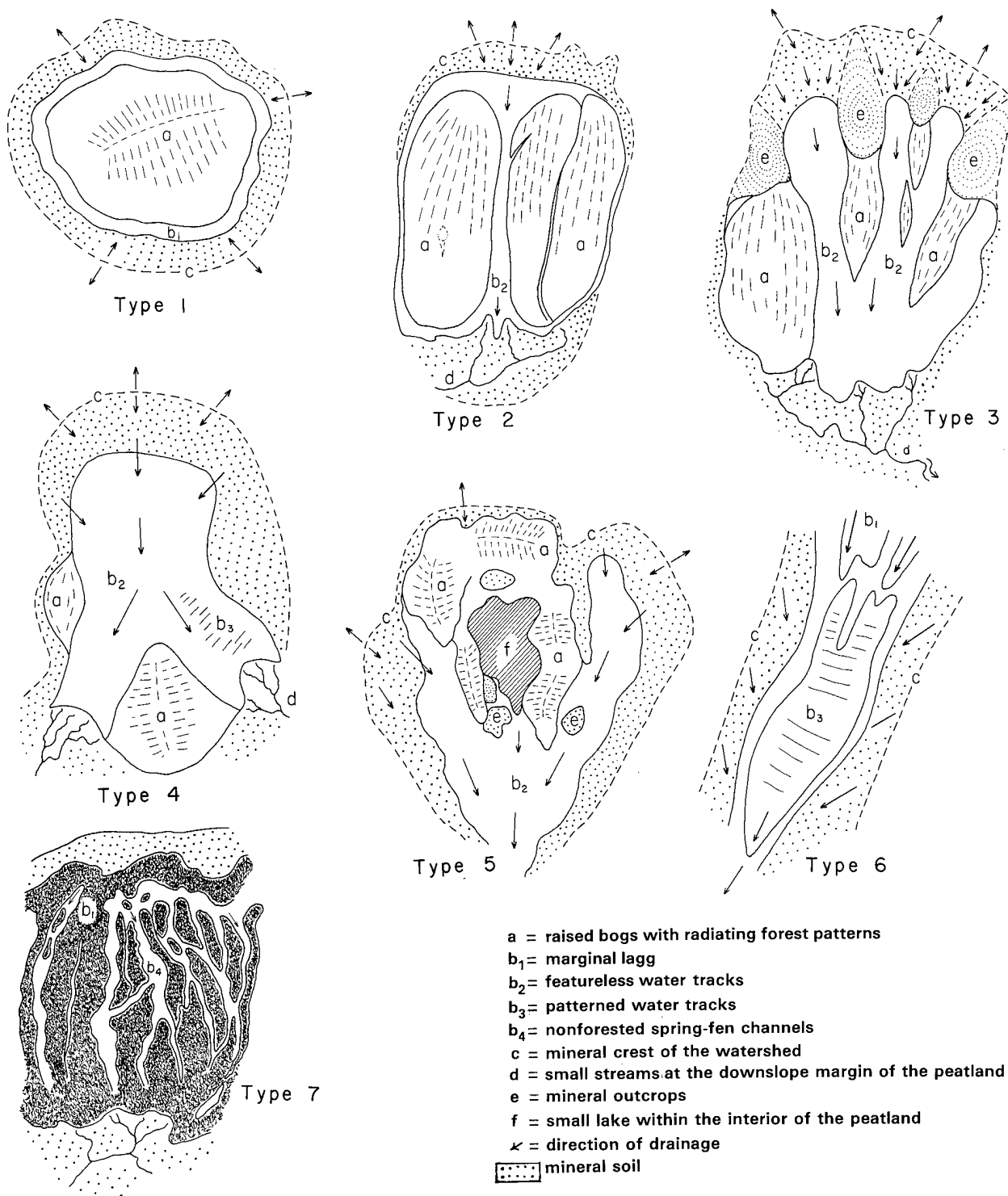


Figure 20. Mire-complex types of discontinuous peatlands, northern Minnesota. The types represent reference points on a continuous range of variation. In types 1-5 the area of fen relative to bog increases, culminating in the very large water tracks of type 4.

example, covers over 1,200 km² and contains only seven major vegetation types (Glaser et al. 1981). The flora for this area is similarly restricted to less than 200 species of vascular plants (Wheeler et al.

1983). A smaller, 728 km² area of uplands and wetlands in Itasca County, in contrast, contained over 700 species of vascular plants and over 14 major vegetation types (Glaser and Wheeler 1977).

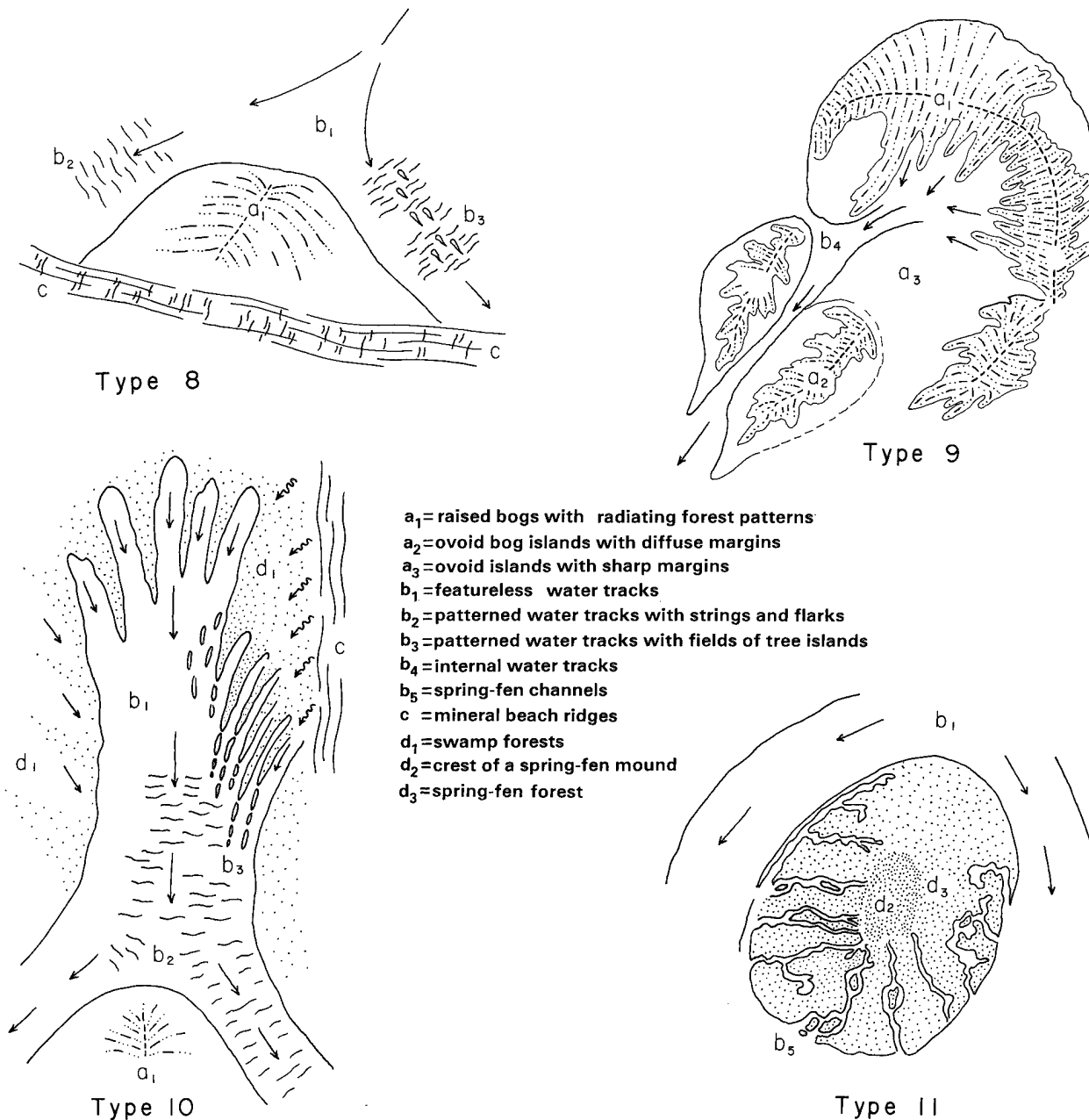


Figure 21. Mire-complex types of the continuous peatlands, northern Minnesota.

The two major types of vegetation in patterned peatlands are ombrotrophic bog and minerotrophic fen. Bogs and fens usually have very different species assemblages but transitional types can always be critically separated by the recognition of indicator species. Certain species cannot grow in mire waters in which the pH is below 4.2 and the Ca concentration is lower than 2 mg/l (Sjörs 1963; Glaser *et al.* 1981; Wheeler *et al.* 1983; Gorham *et al.*, In press; Glaser and Janecky, In prep). The presence of these species therefore indicates minerotrophic fen. Unfortunately, no species are solely restricted to ombrotrophic bogs, and thus raised bogs are recognized by the absence of these fen-indicator species.

5.3 OMBROTROPHIC BOG VEGETATION

The vegetation of raised bogs in Minnesota is characterized by a generally

continuous mat of *Sphagnum* and a relatively simple assemblage of species (Table 1). Lichen cover is rare except on dead trees and areas that have recently burned. The major factors controlling vegetation patterns on Minnesota bogs appear to be the elevation of the water table, the degree of light penetration, and the successional status of the stand. The water chemistry plays only a minimal role in differentiating types of raised bogs because of its very narrow range in pH and Ca concentration. The two most important disturbances are wildfires and drainage ditches. A common but minor disturbance is infections of dwarf mistletoe (*Arceuthobium pusillum*), which produce expanding circular zones of stunted trees bearing the characteristic "witches brooms."

5.3.1 Forested Bogs

Most raised bogs in Minnesota are covered with a stunted forest of black

Table 1. Major plant communities in the boreal patterned peatlands of northern Minnesota (DNR 1984).

CHARACTERISTICS	BOG (Ombrotrophic)		RICH FEN (Minerotrophic)		
PLANT COMMUNITY TYPE	Forested Bog	Open Bog	Fen-flark	Fen-string	Forested Island
DOMINANT SPECIES	Black spruce (<i>Picea mariana</i>) —varying density Ericaceous shrubs— Swamp laurel (<i>Kalmia polifolia</i>) Bog rosemary (<i>Andromeda glaucophylla</i>) Labrador tea (<i>Ledum groenlandicum</i>) Leatherleaf (<i>Chamaedaphne calyculata</i>) Sphagnum mosses (<i>Sphagnum spp.</i>)	Sedge (<i>Carex oligosperma</i>) Ericaceous shrubs (same as forested bog)	Sedges (<i>Carex lasiocarpa</i>) (<i>C. livida</i>) (<i>C. limosa</i>) Buckbean (<i>Menyanthes trifoliata</i>) White beak rush (<i>Rhynchospora alba</i>)	Bog birch (<i>Betula pumila</i>) Bog rosemary (<i>Andromeda glaucophylla</i>) Small cranberry (<i>Vaccinium oxycoccus</i>) Leatherleaf (<i>Chamaedaphne calyculata</i>)	Tamarack (<i>Larix laricina</i>) Black spruce (<i>Picea mariana</i>) Variable ground cover species
CHARACTERISTIC SPECIES	Sedge (<i>Carex trisperma</i>) Lingberry (<i>Vaccinium vitis-idaea</i>) 3-leaved false Solomon's seal (<i>Smilacina trifolia</i>) Feathermosses (<i>Pleurozium schreberi</i>) (<i>Dicranum sp.</i>)	Sedge (<i>Carex oligosperma</i>)	Marsh arrow grass (<i>Triglochin maritima</i>) Intermediate bladderwort (<i>Utricularia intermedia</i>) Intermediate sundew (<i>Drosera intermedia</i>)	Shrubby cinquefoil (<i>Potentilla fruticosa</i>) Sedge (<i>Carex cephalantha</i>)	Sedges (<i>Carex pseudo-cyperus</i>) Black chokeberry (<i>Aronia melanocarpa</i>) Dwarf raspberry (<i>Rubus pubescens</i>) Velvet honeysuckle (<i>Lonicera villosa</i>)
pH	—very acidic (pH less than 4.2)		—slightly acidic to neutral (pH greater than 5.2)		
SALT CONCENTRATION	—very low (e.g., Ca < 2.2 mg)		—moderate to high (e.g., Ca > 4.3 mg)		
SPECIES DIVERSITY	—very low (9-13 plant species)		—generally moderate to high (12-58 plant species)		
ASSOCIATED PEATLAND LANDFORMS	—raised bogs, ovoid islands		—water track features such as ribbed fens, teardrop islands, circular islands		

spruce (*Picea mariana*). The forest cover is generally best developed along the crest of a bog with the trees becoming more stunted and restricted to linear strips radiating downslope from the crest. The forest contains occasional trees of tamarack (*Larix laricina*) but otherwise black spruce is the only tree species. The water table fluctuates during the growing season, but generally the trees grow best in the driest and best-drained sites.

The understory contains the principal bog ericads, particularly Labrador-tea (*Ledum groenlandicum*) and leatherleaf (*Chamaedaphne calyculata*). Species generally restricted to a shaded understory on ombrotrophic sites are three-seeded sedge (*Carex trisperma*), lingberry (*Vaccinium vitis-idaea*), creeping snowberry (*Gaultheria hispidula*), and three-leaved Solomon's-seal (*Smilacina trifolia*). The forest floor generally contains a continuous mat of *Sphagnum magellanicum*, *S. angustifolium*, *S. capillifolium*, *S. fuscum*, and *Pleurozium schreberi*. These species grow in poorly differentiated hummocks and hollows that are highly compressible. Under the trees the dominant *Sphagnum* species commonly give way to small clumps of *Dicranum undulatum*, *Polytrichum strictum*, and *Pleurozium schreberi*.

5.3.2 Nonforested Bogs

The forest cover on most Minnesota bogs is not continuous. Near the bog crest the radiating lines of forest are separated by nonforested strips called bog drains. The vegetation in these drains is very similar to that found in the forested areas, except that the tree cover is replaced by a lawn dominated by few-seeded sedge (*Carex oligosperma*). Most of the forest species are present on these lawns except for the few species that require the shade of trees. The lawns often contain scattered clumps of trees that gradually become more widely spaced and depauperate downslope. The bog drains contain a continuous mat of *Sphagnum* that grows in a subtle hummock and hollow pattern. The position of the water table is variable, but after heavy rains it is usually close to the surface. Very similar communities occur within the non-

forested centers of ovoid islands in the Red Lake peatland.

The largest bogs in Minnesota are generally fringed by a nonforested apron that contains vegetation similar to that found in the bog drains. These aprons, however, are distinguished by a downslope transition from ombrotrophic bog to poor fen on the lower flanks. The first evidence of this change is the appearance of fen-indicator species; such as pale lead-colored sedge (*Carex livida*), aquatic sedge (*C. aquatilis*), chord-like root sedge (*C. chordorrhiza*), and bog birch (*Betula pumila* var. *glandulifera*). These poor-fen aprons are otherwise dominated by *Carex oligosperma* and are quite similar in appearance to the bog drains. The poor-fen lawns contain a continuous mat of *Sphagnum*, but *Sphagnum papillosum*, *S. fallax*, and *S. capillifolium* are the most abundant bryophytes. They may grade downslope into fen water tracks that contain a conspicuously different assemblage of species.

5.4 MINEROTROPHIC-FEN VEGETATION

Minerotrophic fens are distinguished from bogs by their richer assemblage of species, conspicuous presence of fen-indicator species, and generally greater cover of feather mosses in the field layer (Table 1). The fen vegetation may also be separated into more vegetation types than those found on bogs, primarily because of the greater range in water chemistry and position of the water table. Nevertheless, the fen vegetation associated with a particular landform type is remarkably uniform across Minnesota, particularly with regard to the flarks and spring-fen channels (Glaser 1983d; Glaser and Janecky, In press). The major gradients affecting the relative abundance of the dominant species are the position of the water table and the water chemistry (Figure 22).

5.4.1. Forested Fens

The driest fen landforms are the forested fen fingers, tree islands, and spring-fen forests. The surface of these landforms consists of moss hummocks surrounding the base of trees, along with occasional water-filled hollows. Fallen

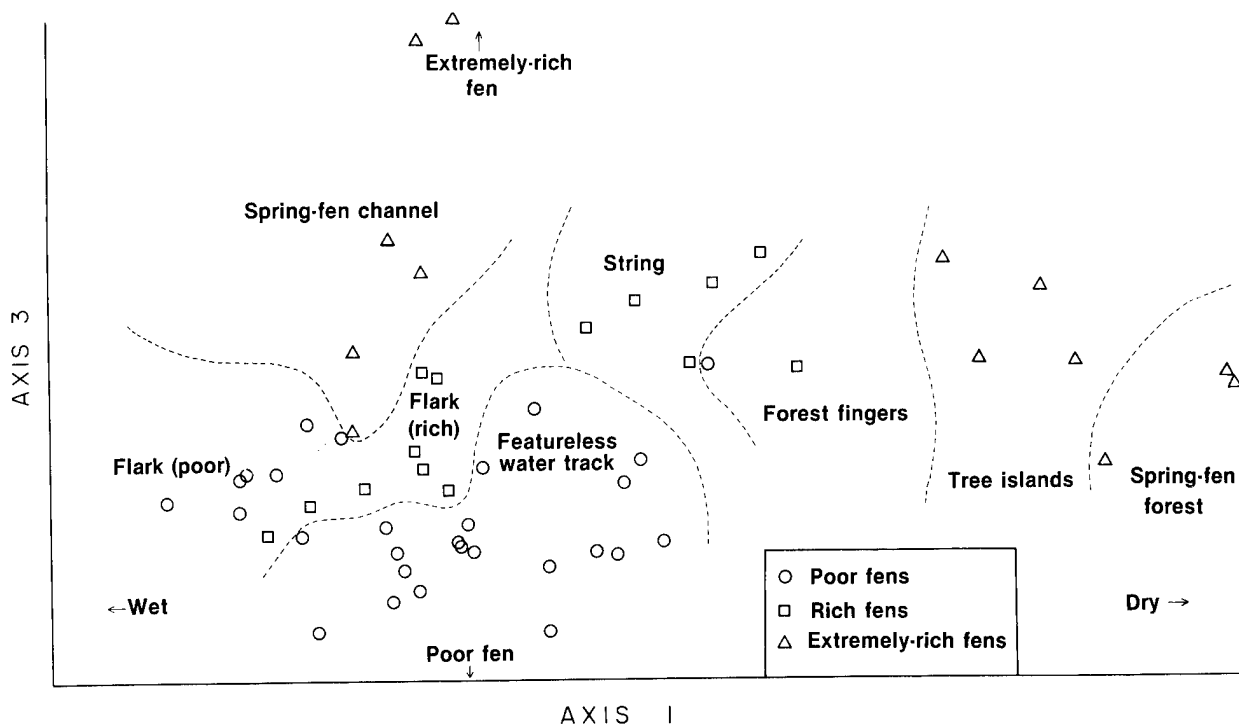


Figure 22. Detrended Correspondence Analysis of water track and spring-fen relevés in northern Minnesota (Glaser and Janecky, In prep.). The ordination sorts most relevés according to landform, particularly along a wet-to-dry gradient (axis 1) and secondarily by water chemistry (axis 3).

trees soon become overgrown with moss and greatly increase the heterogeneity of the substrate. The spring-fen forests are dominated by *Picea mariana* with occasional trees of *Larix laricina*, white cedar (*Thuja occidentalis*), and balsam fir (*Abies balsamea*). The forested fingers and tree islands, in contrast, are dominated by *Larix*, although scattered trees of *Picea mariana* may also be present. The understory of these landforms is fairly rich with the bog ericads and shrubs of willow (*Salix*).

The moss cover in the spring-fen forests is dominated by *Sphagnum nemoreum*, *S. angustifolium*, *Pleurozium schreberi*, and *Hylocomnium splendens*. The bryophyte cover in the forest fingers and tree islands, in contrast are usually dominated by *Sphagnum teres*, *S. centrale*, *S. angustifolium*, and *Pohlia* spp.

5.4.2 Nonforested Fens

The nonforested fen landforms are generally associated with a high water

table and are dominated by sedges. The three landforms with the highest water tables are the spring-fen channels, flarks, and water tracks. The spring-fen channels are associated with a very high water table and water chemistry typical of extremely rich fens (pH > 7; Ca concentration > 20 mg/l). The spring-fen channels are dominated by tussock bulrush (*Scirpus cespitosus*) and meagre sedge (*Carex exilis*) growing in mud sedge (*C. limosa*), hairy-fruited sedge (*C. lasiocarpa*), and bog rosemary (*Andromeda glaucophylla*). Twig-rush (*Cladium mariscoides*), a rare plant in Minnesota is very common in these channels, which also contain rich-fen indicators such as Hudson Bay bulrush (*Scirpus hudsonianus*), grass of parnassus (*Parnassia palustris*), and Kalm's lobelia (*Lobelia kalmii*). The channels generally have a mud bottom composed of decaying sedge shoots. The principal bryophytes are *Campylium stellatum*, *Scorpidium scorpioides*, and *Drepanocladus revolvens*, which are submerged and are often difficult to see without sampling the substrate.

The vegetation in the flarks is very similar to that found in the spring-fen channels. The dominant species, however, are the sedges Carex lasiocarpa, C. limosa, and white beakrush (Rhynchospora alba). Carex livida is consistently present along with buckbean (Menyanthes trifoliata), Scheuchzeria (Scheuchzeria palustris), Carex chordorrhiza, and Andromeda glaucophylla. The wettest flarks are characterized by the rare plants English sundew (Drosera anglica) and linear sundew (Drosera linearis), which are generally restricted to relatively pristine sites.

The flarks generally have standing water throughout the growing season and the substrate consists of fallen sedge shoots. The submerged bryophyte cover varies and is often difficult to estimate below the water surface. The most common bryophytes are Campylium stellatum, Scorpidium scorpioides, Riccardia spp., and Sphagnum contortum. In unusual situations Sphagnum may form mats across the flark substrate. At Alborn, for example, Sphagnum papillosum is spreading across the flarks in exanding circular clones, and at Grand Marais (Glaser 1983d) Sphagnum majus forms an almost continuous mat.

The vegetation in the featureless water tracks is very similar to that found in the flarks. Carex lasiocarpa, C. limosa, C. chordorrhiza, and Andromeda glaucophylla are the major species, but aquatic species such as the sundews are absent. The substrate of the water tracks

is variable, ranging from a mosaic of sedge tussocks and pools to a continuous mat of Sphagnum or feather moss. The principal bryophytes are Campylium stellatum, Scorpidium scorpioides, Sphagnum contortum, S. majus, and S. angustifolium.

The driest landforms in the non-forested fens are the strings, which are more variable than the adjacent flarks. In the wettest water tracks the strings are barely perceptible from the ground and consist of denser stands of Carex lasiocarpa growing on firmer peat. In drier water tracks, however, particularly those in which the water table has been lowered by drainage ditches, the strings have been significantly raised above the water table by the growth of Sphagnum and other mosses. These drier strings are usually dominated by Betula pumila var. glandulifera associated with marsh fern (Thelypteris palustris var. pubescens), shrubby cinquefoil (Potentilla fruticosa), and pale violet (Viola pallens var. mackloskeyi).

The major bryophyte species are closely adjusted to micro-site characteristics and therefore create more variable spatial patterns than the more deeply rooted vascular plants. The principal bryophyte species can be used to distinguish many of the landform types in patterned peatlands (Janssens and Glaser 1986), but the species generally produce a much finer scale of pattern than the vascular plants (Vitt and Slack 1984; Glaser et al., In prep.).

CHAPTER 6. AUTECOLOGY OF THE MAJOR PEAT-FORMERS

6.1 SPHAGNUM

Members of the genus Sphagnum are renowned for their ability to alter the physical environment (Skene 1915; Watson 1918; Clymo 1967; Clymo and Hayward 1982). A unique set of morphological, anatomical, and physiological adaptations enable a growing mat of Sphagnum to (1) increase its retention of water, (2) acidify interstitial water in the mat, and (3) slow decomposition rates. It is therefore not surprising that Sphagnum is the major agent of bog formation in boreal regions and represents one of the most important peat-formers in the world (Clymo and Hayward 1982; Clymo 1983).

The water-holding adaptations of Sphagnum are unique to the genus and represent important taxonomic characters. These characters include the compactness of the growing habit, imbrication of the leaves on pendant branches that act as wicks, drawing water up the stem, enrolled branch leaves that form capillary tubes, arrangement of branches in fascicles appressed to the stem, and the intermixture of empty hyaline cells with those containing protoplasts (Watson 1918). The empty hyaline cells are reinforced with fibrils and contain arrangements of pores that are highly diagnostic of different taxa. Collectively these adaptations permit Sphagnum to hold up to 15-23 times its dry weight in water (Vitt et al. 1975a).

The ability of Sphagnum to acidify its environment has long been recognized by field and laboratory observations. The mechanism for this ability is its cation-exchange matrix, which is correlated to polygalacturonic acids located on the cell walls (Clymo 1963; Clymo and Hayward 1982). The exceptionally high cation-exchange capacity of Sphagnum is approxi-

mately double that found in other bryophytes and is correlated with the concentration of uronic acid residues in the polymers. The uronic acid concentrations are lowest in the more aquatic forms (Sphagnum cuspidatum) and highest in the species inhabiting the more xerophytic hummocks (S. fuscum) indicating an important correlation between cation-exchange capacity and habitat (Vitt et al. 1975b).

The significance of the cation exchange for growing Sphagnum is a matter of debate. The cation-exchange process may be essential for maintaining a higher pH and cation concentration in the protoplasts of the living hyaline cells than in the surrounding external water. Brehm (1968), for example, has found that Sphagnum can maintain a fairly constant concentration of cations in its cytoplasm despite large changes in its external environment. The maximum activity of a peroxidase enzyme extracted from Sphagnum magellanicum was measured at a pH of 5, which was substantially above that of its preferred habitat (Tutschek 1979). The cation-exchange system could also protect the plasmalemma from excessive loading of cations, as suggested by Brown (1982). The contrary opinion stresses the ecological role of the exchange mechanism that creates an acid environment around the plant and thus excludes competitors.

The importance of Sphagnum as a peat-former is based on its exceptionally slow decomposition rate. The productivity of Sphagnum in its various habitats is not exceptionally high, but a very large percentage of production is preserved. Thus Clymo and Reddaway (1971) determined that up to 71% of the annual production on lawns in the Moor House Nature Reserve in England accumulated as peat. The very low decomposition rate of Sphagnum is caused

by: (1) its very low nitrogen content, (2) the acid-conditions produced by Sphagnum, (3) reduced aeration in its wet environment, and (4) the presence of phenolic compounds, such as sphagnol, that inhibit microbial activity (Clymo and Hayward 1982; Clymo 1983; Dickinson 1983).

The ability of Sphagnum to alter its environment is supported by a number of studies that correlate the distribution of various Sphagnum species to environmental gradients. The most important of these gradients is moisture (measured as capitulum height above the water table) and water chemistry (particularly pH and Ca concentration). The important thresholds that permit the initial colonization of a site by Sphagnum and the succession of various species in place of one another remain to be documented. Conway (1949), however, expressed the commonly accepted view that the spread of Sphagnum over a sedge mat is restricted by the general availability of cations. Thus in highly minerotrophic lakes Sphagnum colonizes sites where the mat is widest. However, Tallis (1973) has presented stratigraphic data from Cheshire in England in which the rise in abundance of Sphagnum remains within a core is preceded by a rise in the pH.

The distribution of the various species according to moisture and chemistry is documented in studies in Europe (Rose 1953; Ratcliff and Walker 1958; Sjörs 1948, 1983) and North America, particularly the work of Vitt and his associates in Michigan and Alberta (Vitt et al. 1975b; Vitt and Slack 1984; Horton et al. 1979; Slack et al. 1980). In Minnesota the ecological distribution of the various Sphagnum was described by Conway (1949) and more recently by Vitt and Slack (1984) and Janssens and Glaser (1986). The latter publication also describes the response of other important bryophytes to shade and moisture gradients (Figure 23).

6.2 VASCULAR PLANTS

6.2.1 Trees

The muskegs of boreal America are predominantly forested peatlands that have no real counterpart in the boreal region

of Europe except for areas in Finland and eastern Europe. In eastern Europe scotch pine (Pinus sylvestris) may form a canopy on raised bogs but only where the water table is low as a result of drainage projects or slow accumulation rates and a high moisture deficit (Katz 1926; Kulczynski 1949; Masing 1982). In North America, however, a number of conifer species have adaptations that permit the trees to adjust to the rising water table of actively growing peatlands. A high water table is otherwise lethal for the root systems of woody plants because of the accumulation of toxic metabolites from anaerobic respiration (Crawford 1983).

The two most important tree species in Minnesota peatlands are Picea mariana and Larix laricina, which adjust to a rising moss surface and water table by (1) layering, (2) production of adventitious roots from the stem, and less commonly (3) root sprouts (Cooper 1911; Fuller 1913; Gates 1938; Roe 1957; Fowells 1965; Horton and Lees 1961).

Picea mariana and Larix laricina readily develop adventitious roots whenever the lower branches come into contact with a wet moss substrate. This form of vegetative reproduction, called layering, results in a dense clumped growth form and is indicative of peatlands with a rapidly growing surface. Both species are also capable of producing adventitious roots from the stem, and trees in actively growing peatlands typically send out new layers of roots to replace the deeper roots killed by a rising water table (Rigg and Harrar 1931; Le Barron 1945; Hustich 1954, 1955; Horton and Lees 1961). Black spruce also has the ability to sprout from the roots and to form upright stems from wind-thrown trees. This type of vegetative reproduction results in apparent rows of trees that originate from the same moss-covered fallen log.

Thuja occidentalis also displays most of these adaptive characteristics but is more demanding in its nutrient requirements and is therefore less common in the patterned peatlands of Minnesota. The other major tree species in Minnesota peatlands is Abies balsamea, which does not reproduce readily by vegetative means and is less capable of growing on actively

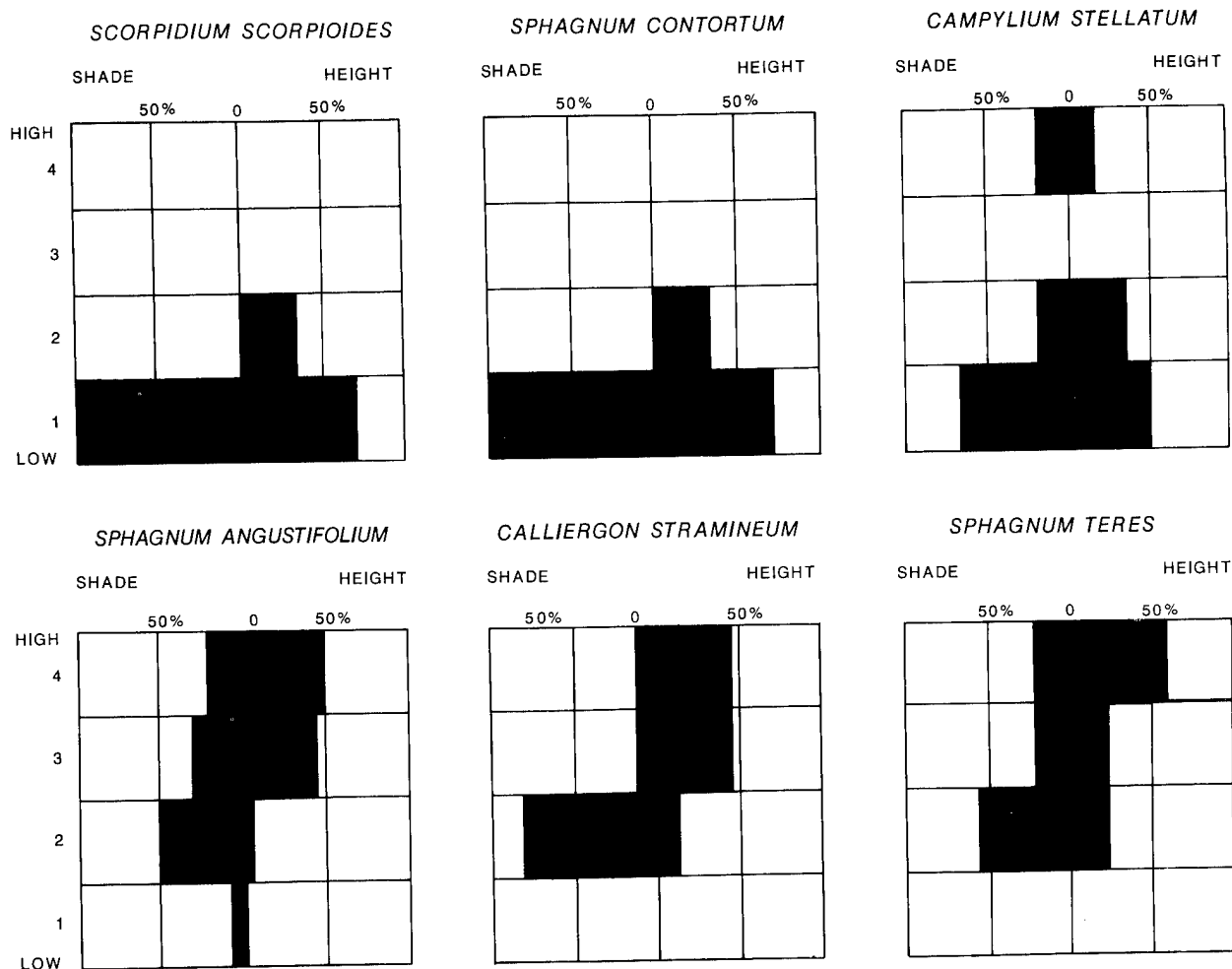


Figure 23. The cover value of the major peat-forming bryophytes in the Red Lake peatland in relation to shade and height above the water table (Janssens and Glaser 1986). The cover values are according to the Braun-Blanquet scale: (1) plentiful but at small cover value (2) covering up to 5% of the area, (3) 25-50% of the area, (4) 50-75% of the area.

growing peat (Fowells 1965). Fir also requires more minerotrophic sites and is relatively uncommon in patterned peatlands.

Picea mariana and *Larix laricina* are tolerant to changes in water chemistry and attain dominance wherever the water table is low or where there is sufficient drainage for proper root growth. *Picea mariana* is the dominant species in both bogs and spring-fen forests, which represent the opposite ends of the water-chemistry gradient in peatlands (Glaser and Janecky, In prep.; Figure 24). *Larix* is less common

in forested bogs because of its greater intolerance to shading, but clumps of *Larix* generally replace spruce on the more open and wetter *Sphagnum* lawns. The dominance of *Picea mariana* in bog forests compared to its replacement by tamarack in the more open fens led Heinzelman to suggest that these species could be used as indicator species (Heinzelman 1970). However, their indicator value is probably more related to landform and the position of the water table than to water chemistry, as the direct gradient analysis shows (Glaser and Janecky, In prep.; Figure 24). Heinzelman (1970) considered *Thuja occidentalis* to be an extremely rich fen-indicator in the Myrtle Lake peatland, but

this species may also occur sporadically in poor fens as well. The simplicity of the tree flora in the most actively growing peatlands attests to the apparent difficulty of evolving adaptations to adjust to a rapidly rising peat surface.

6.2.2 Shrubs

The most characteristic shrubs in boreal peatlands are the bog ericads,

which are immediately identified by their xeromorphic leaves, short stature, and showy flowers or berries. The largely circumboreal distribution of such species as *Ledum groenlandicum*, *Chamaedaphne calyculata*, bog laurel (*Kalmia polifolia*), *Andromeda glaucophylla*, *Vaccinium vitis-idaea*, small cranberry (*V. oxycoccus*), and *Gaultheria hispidula* provides a broad geographic continuity to the peatland vegetation of the boreal zone. Probably the most studied aspect of these plants is

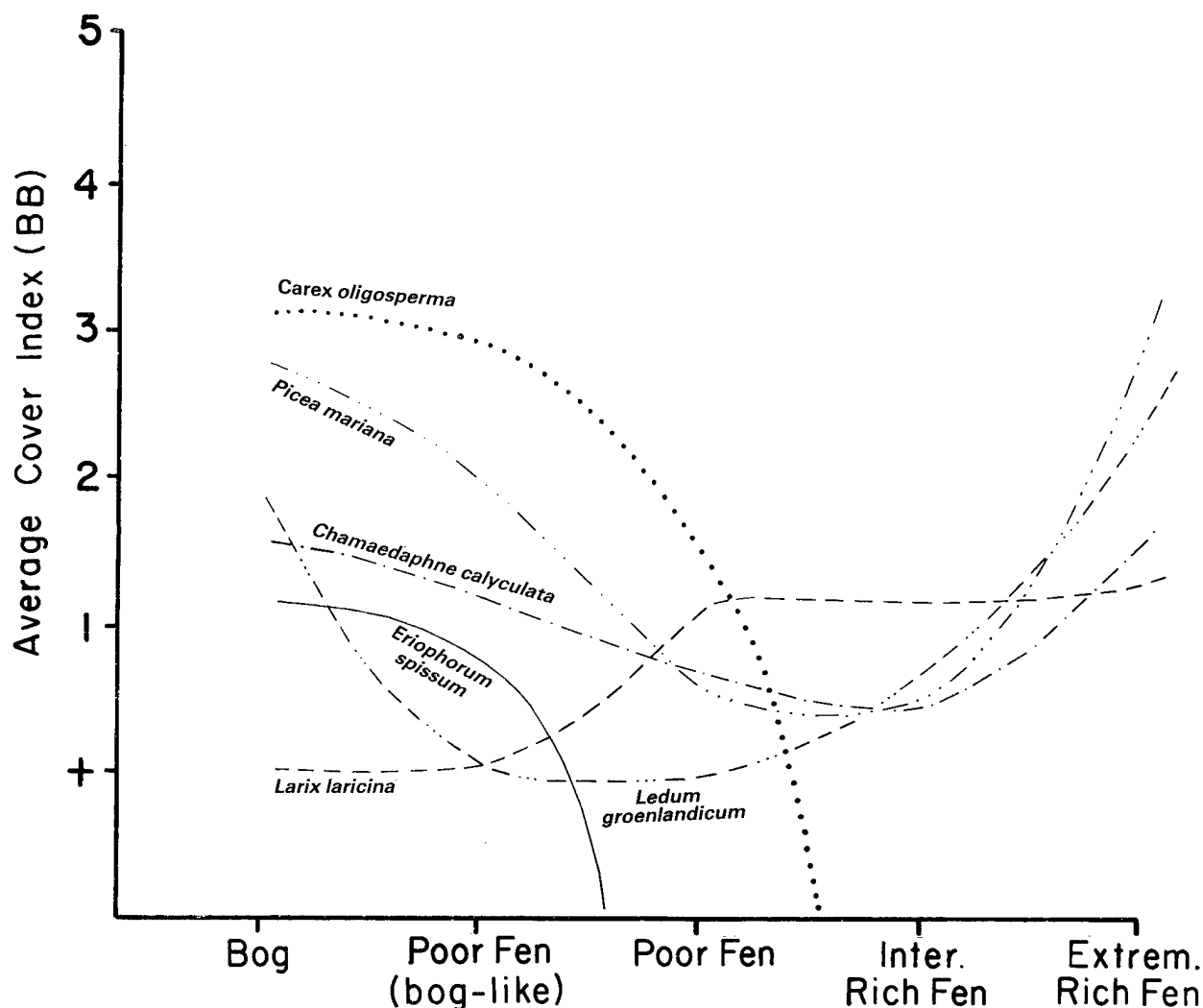


Figure 24. Direct gradient analysis of the major vascular plants that occur in both bogs and fens. The dual peaks in cover for *Picea mariana*, *Chamaedaphne calyculata* and *Ledum groenlandicum* indicate that these species are insensitive to changes in water chemistry but instead respond to another gradient such as water level or shading. The other species shown are *Carex oligosperma*, *Eriophorum spissum*, and *Larix laricina*. The average cover values represent the standard Braun-Blanquet symbols. The ranges in water chemistry are bog (pH <4.2; Ca <2 mg/l), poor fen (bog-like) (pH 4.1-4.6; Ca 1.5-5.5 mg/l), poor fen (fen-like) (pH 4.1-5.8; Ca <10 mg/l), intermediate rich fen (pH 5.8-6.7; Ca 10-32 mg/l), extremely rich fen (pH >6.7; Ca > 30 mg/l).

the apparent paradox of xeromorphic features in plants that grow in predominantly wet habitats. The concept that these species are actually physiologically stressed by the low availability of water was advanced by Schimper (1898), Gates (1914), Yapp (1912), and Caughey (1945). These authors noted that the availability of water in peatlands may be limited by low temperatures, the adsorption of water onto the peat, the presence of toxic compounds, low oxygen supply, and the periodic drying out of the upper peat surface. Actual measurements of transpiration rates, however, revealed little difference with the rates measured in mesophytic

plants (Maximov 1929; Shields 1950; Beadle 1966; Small 1972). The xeromorphic characters may instead be related to the conservation of nutrients, which generally characterizes plants in nutrient-poor habitats (Monk 1966; Beadle 1954; 1966; Loveless 1961, 1962).

The bog ericads occur on a wide range of peatland sites from ombrotrophic bogs to extremely rich fens (Figures 24 and 25). These shrubs can also tolerate waterlogging as depauperate individuals may be found on slightly elevated tussocks in the wettest flarks. However, the relative abundance of these species is always

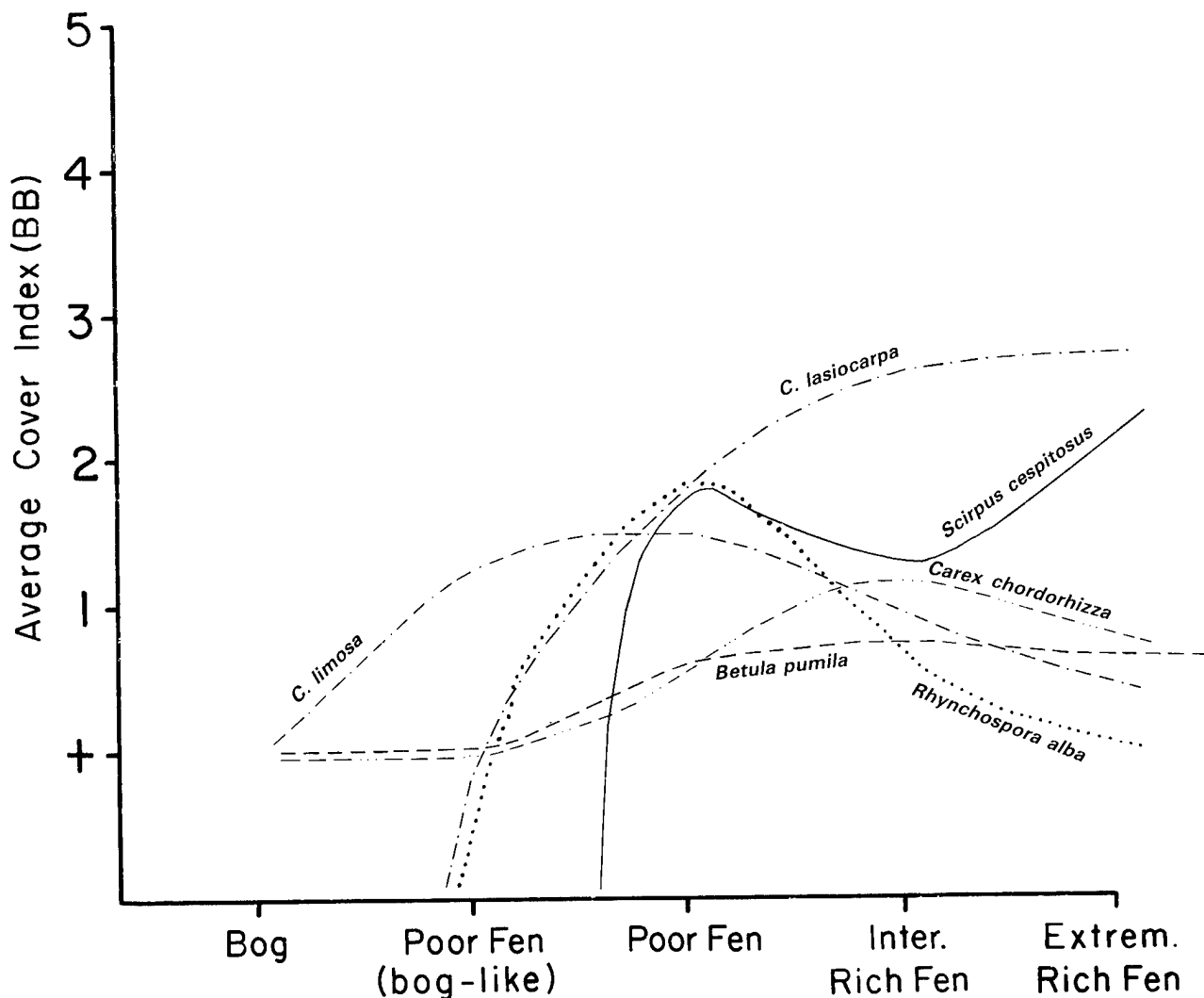


Figure 25. Direct gradient analysis of major fen species along a chemical gradient.

highest on the driest sites either in the shade of Picea mariana and Larix laricina or in sunny openings. Ledum, however, seems to prefer shaded sites in contrast to Chamaedaphne, which is more often the dominant in the open. These species have no intrinsic value as indicators of water chemistry although their distribution in particular peatlands makes such a usage tempting (Heinselman 1970).

The other important shrub species in Minnesota peatlands is Betula pumila var. glandulifera, which attains dominance on the string landforms. Although Betula pumila var. glandulifera is a minerotrophic indicator in Minnesota peatlands, water chemistry seems to have little influence on its relative abundance within the range from poor to extremely rich fen (Figure 25). Within minerotrophic fens water level and shading are the most important factors controlling the abundance

of bog birch. Thus Betula pumila var. glandulifera becomes dominant only on the driest strings, particularly those found in ditched peatlands. In those water tracks where the water table has been considerably lowered by drainage ditches Betula pumila var. glandulifera may spread out onto the adjacent flarks and form a continuous shrubland (Figures 26-29).

6.2.3 Sedges

The life-history characteristics of the dominant sedges in boreal peatlands has been relatively neglected, despite their considerable importance as components of the vegetation and as peat-formers. Bernard and Gorham (1978) described the life-history characteristics of two sedges that extend into the boreal zone but are major peat-formers only in more southerly and temperate regions: Carex lacustris (lake margin sedge) shoots



Figure 26. A pristine patterned fen in the Myrtle Lake peatland. The characteristic strings and flarks are dominated by sedges.



Figure 27. The invasion of a water track by shrubs. Where ditches have lowered the water table, shrubs generally cover the strings (Norris Camp peatland).

have a life span of 4-5 months, 9-11 months, or 11-12 months, depending upon when they emerge during the season; *Carex rostrata* (beaked sedge) shoots have an average 2-year lifespan. Bernard and Gorham noted that these species contain a considerable green standing crop in winter but also have a very high mortality rate in winter, with as many as 80%-90% of the shoots dying before reaching maturity. Similar studies on the major sedge peat-formers in boreal patterned peatlands are urgently needed before the dynamics of these communities can be understood.

The relative sensitivity of the major sedge species to water chemistry enhances their importance in distinguishing different peatland types (Figures 24, 25, and 30). In Minnesota the most important species reach their maximum abundance along a gradient represented by the position of the water table and the water

chemistry. *Carex oligosperma* and *Eriophorum spissum* reach their maximum abundance in ombrotrophic bogs and extremely poor fens. These species are replaced by *Rhynchospora alba* and *Carex limosa* in poor fens, and in turn they give way to *Carex chordorrhiza* and *Carex lasiocarpa* in the richer fens. The sensitivity of these species to water chemistry in Minnesota is not necessarily indicative of their preferences across their geographic range. A large number of exclusively fen plants in Minnesota also grow on ombrotrophic bogs in the Maritime Provinces of eastern Canada (Glaser 1983c; Glaser, In prep.b). A list of these plants is presented in Table 2.

As peat-formers the sedges are second in importance only to *Sphagnum* in the boreal peatlands of Minnesota. The most important is apparently *Carex lasiocarpa*, which reproduces vigorously by vegetative

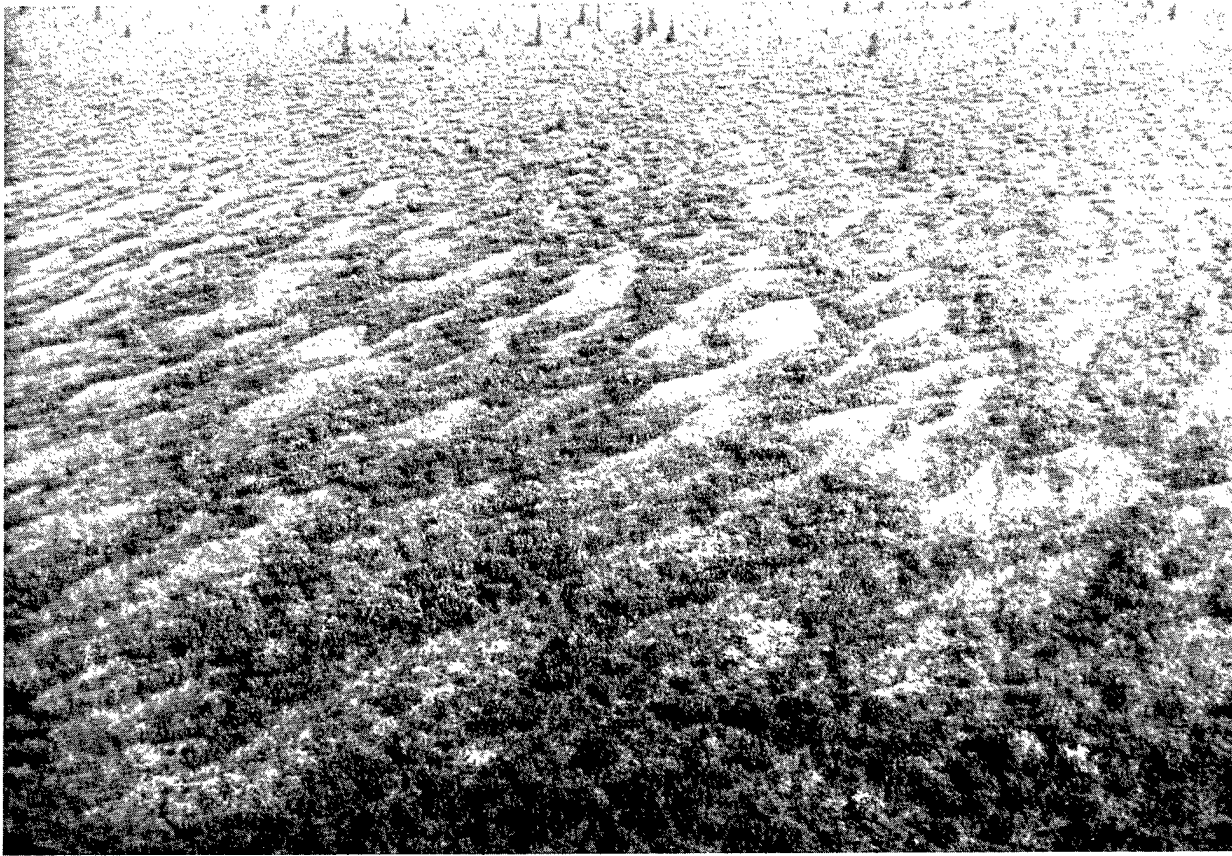


Figure 28. The invasion of a water track by shrubs. Where ditches have considerably lowered the water table, shrubs have spread from the strings to the adjacent flarks (Winter Road Lake peatland).

means and in the process establishes extensive networks of rhizomes and rootlets. The permeability of this rhizomatous peat is largely responsible for the channeling of water movements and the development of water tracks in Minnesota peatlands. The peat developed by *Rhynchospora alba* and *Carex limosa*, both of which reach dominance in flarks, is less fibrous because of the weakly rhizomatous nature of these species. The more decomposed peats formed by these species may contribute to the low infiltration capacity of the peat underlying the flark landforms and to the formation of a pool.

6.3 RARE PLANTS

A number of rare species in Minnesota are largely or entirely restricted to patterned peatlands (Wheeler and Glaser 1979, 1982a, b; Glaser 1983a, b; Wheeler

1983, 1984; Wheeler et al. 1983, Janssens and Glaser 1983a, b). Some of these species, such as *Carex exilis*, *Rhynchospora fusca* (sooty beak-rush), *Cladium mariscoides*, and *Eleocharis rostellata* (small beak spike-rush) are often the dominant species at their stations because of their strongly caespitose or rhizomatous growth forms. Of these plants *Carex exilis* and *Rhynchospora fusca* are the most restricted geographically, being limited to only a few sites outside the large Red Lake peatland (Glaser 1983c; Wheeler 1984). However, in actual numbers of individuals the circumboreal *Juncus stygius* (bog rush) is probably the rarest vascular species in Minnesota peatlands. Although it occurs in a number of sites it is usually represented by only a few individuals that grow in isolated patches. Along with the similarly inconspicuous *Xyris montana*

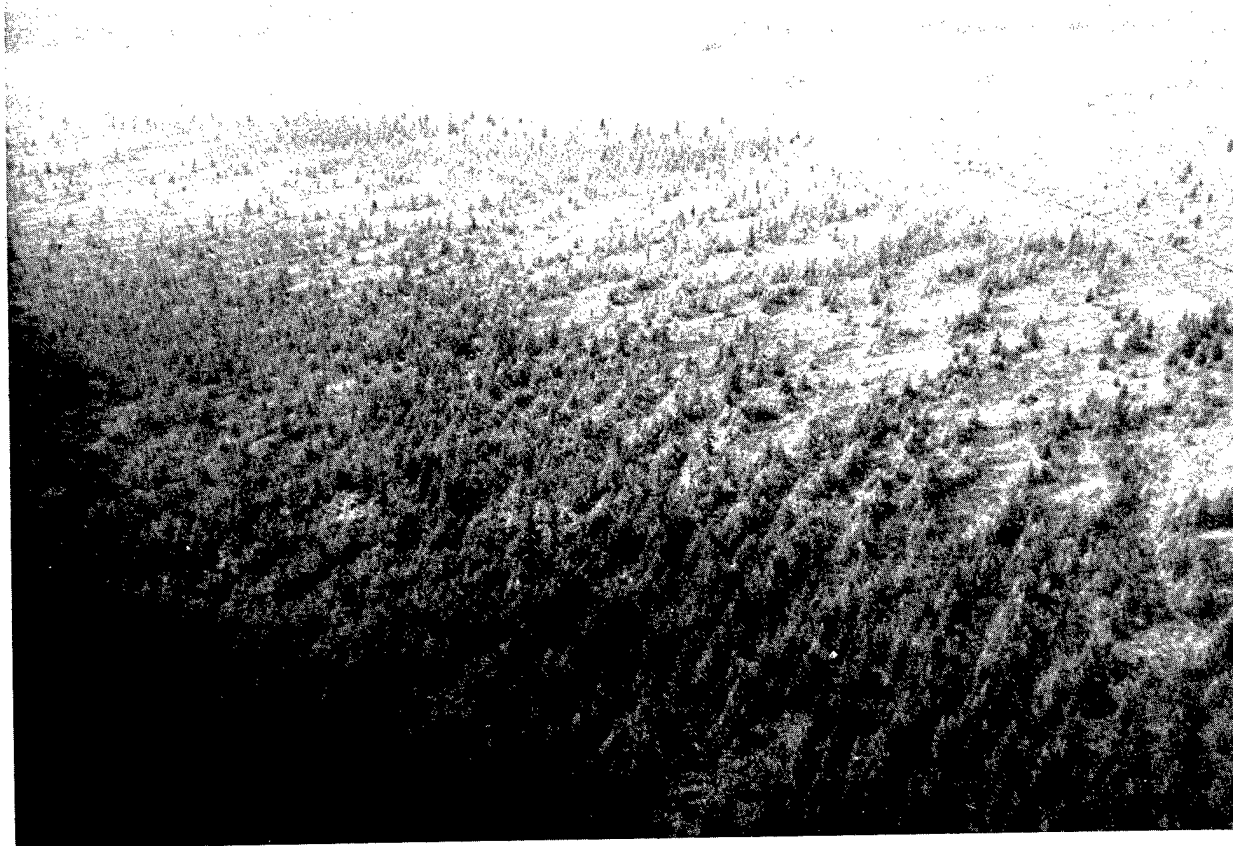


Figure 29. The invasion of a water track by trees. Where drainage ditches have considerably lowered the water table, black spruce trees have spread out from the strings and the water track is reverting to a swamp forest.

(mountain yellow-eyed grass) these species appear to grow in fugitive habitats where disturbance or high water levels have limited the competition from the larger more aggressive sedges.

The two rare sundews Drosera anglica and D. linearis are similarly restricted to sites with a high water table, but in this case these species only grow in the deepest flarks of pristine peatlands (Wheeler and Glaser 1979; Glaser unpubl. data). Of the two D. linearis has the more restricted distribution, as D. anglica is occasionally found in water tracks that have been ditched. Cladium mariscoides is similarly restricted to spring fens that have been minimally disturbed by drainage ditches although large populations occur in the altered Roseau Wildlife Refuge in northwestern Minnesota and along the northern edge of the western

water track in the Red Lake peatland. Cladium, however, was once much more abundant in areas such as the Red Lake peatland where achenes of this species are common in the basal peat layers, which apparently represent a wet prairie marsh or rich fen (Griffin 1977; Janssens and Glaser, In prep.).

The two most important habitats for these rare species in Minnesota are therefore (1) patterned fens within the largest peatlands and (2) spring fens where the impact of drainage ditches and other human modifications are limited. Most of these rare species, for example, are found within the Red Lake peatland in northwestern Minnesota where the great expanse of peat has limited the effects of drainage ditches. Spring fens also contain a large number of rare species including Eleocharis rostellata, sticky false

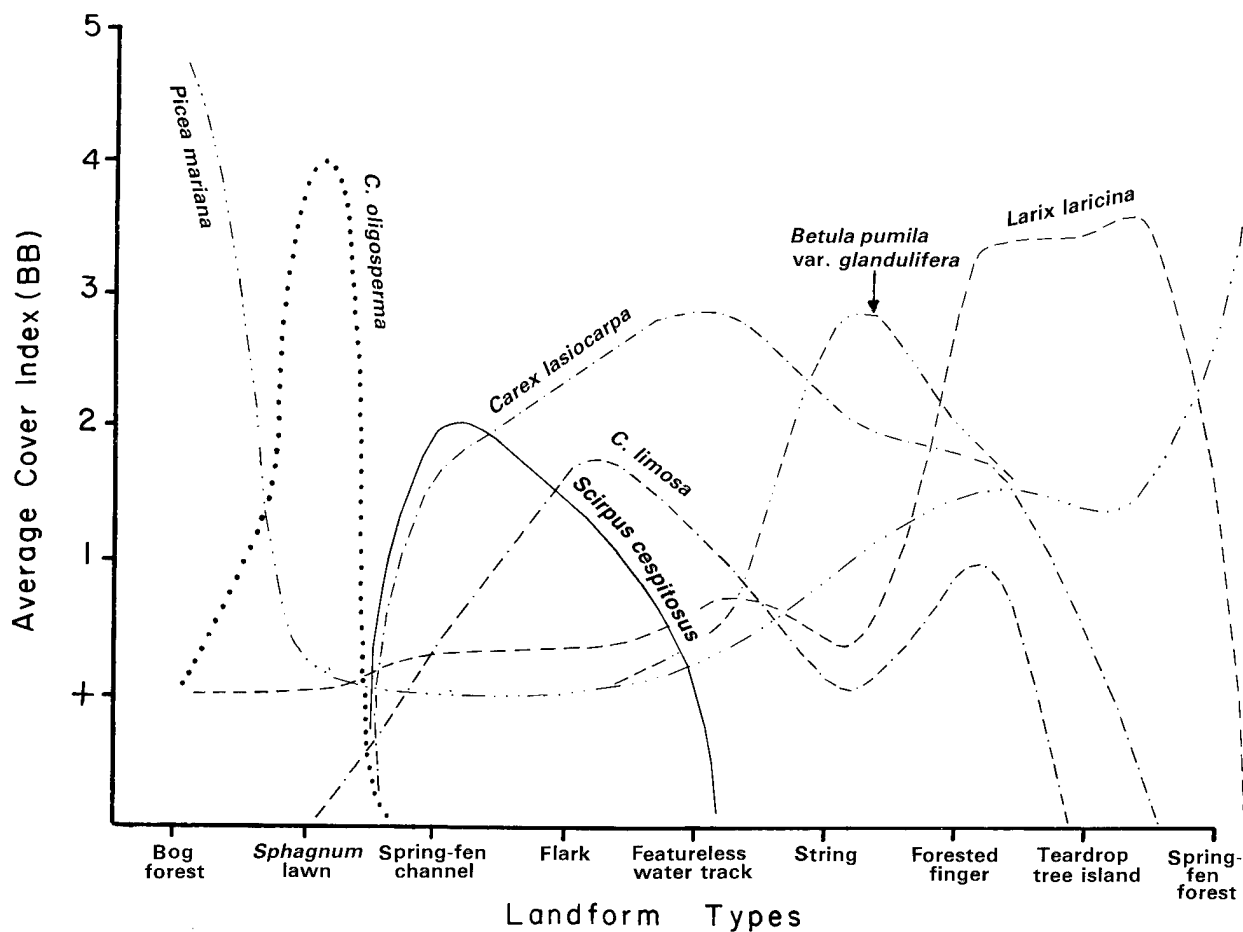


Figure 30. The relative dominance of the major species of vascular plants relative to the landforms. Different species attain dominance on different landform types in response to changes in water table and shade.

Table 2. Continental fen plants that grow on ombrotrophic bogs in the Maritime Provinces of Canada (Glaser, In prep.).

Hummocks	Pools	Lawn/mud/bottoms
<u>Cornus canadensis</u>	<u>Eriocaulon septangulare</u>	<u>Scirpus cespitosus</u>
<u>Melampyrum lineare</u>	<u>Nuphar variegatum</u>	<u>Calamagrostis inexpansa</u>
<u>Trientalis borealis</u>	<u>Nymphaea odorata</u>	<u>Carex exilis</u>
<u>Gaultheria procumbens</u>		<u>Juncus pelecarpus</u>
<u>Maianthemum canadense</u>		<u>Xyris montana</u>
<u>Juniperus communis</u>		<u>Arethusa bulbosa</u>
<u>Myrica gale</u>		<u>Calopogon pulchellus</u>
<u>Pyrus melanocarpa</u>		<u>Pogonia ophioglossoides</u>
<u>Nemopanthus mucronatus</u>		<u>Drosera anglica</u>
<u>Solidago uliginosa</u>		<u>Drosera intermedia</u>
<u>Aster nemoralis</u>		<u>Vaccinium macrocarpon</u>

asphodel (Tofieldia glutinosa), and marsh arrow-grass (Triglochin palustris), which have not been found in other types of patterned peatland in Minnesota.

An exception to this rule is the small patterned fen at Alborn, which contains populations of Carex exilis, Rhynchospora fusca, and Xyris montana. This peatland was altered by drainage ditches cut through the fen in 1937 to provide drainage for the old roadway of County Road 7. According to Louis Tremblay, who has lived near the fen for 80 years, the ditches substantially lowered the water table in the fen and permitted the invasion of trees such as Larix laricina, Pinus strobus, and Betula papyrifera onto the drier peat surface. According to the ^{14}C dates, however, the accumulation rate of peat in this fen had apparently begun to slow down several thousand years before the ditching project, so it is not clear exactly what impact the ditches have had on the local dominance of so many rare species. The poor-fen range of the water chemistry, however, is consistent with chemistry associated with the stations of these rare plants in other patterned fens. The history of the rare plants at this site is currently under investigation by means of pollen analysis.

The Minnesota stations for many of these rare species represent the border of their geographic ranges. The predominantly boreal Juncus stygius, Drosera anglica, and D. linearis reach their southern range limits in Minnesota peatlands, whereas the coastal plain elements Carex exilis, Rhynchospora fusca, and Xyris montana are centered in the Maritime Provinces of Canada and reach their western limit in Minnesota.

During the past 5 years a number of rare bryophyte species have been discovered in the boreal peatlands of northern Minnesota (Wheeler and Glaser 1982b; Janssens and Glaser 1983a, b, 1986). The most remarkable of these plants is Calliergon aftonianum, which was previously believed to be extinct since the Pleistocene (Janssens and Glaser 1986; Janssens unpubl. MS.). The fossil remains of a number of bryophytes, such as Calliergon trifarium and Drepanocladus lapponicus, are abundant in cores from the Red Lake peatland but are presently absent from the living vegetation (Janssens & Glaser 1986; Janssens and Glaser, In prep.). The list of rare bryophyte species in Minnesota peatlands will no doubt increase in the future with more detailed field sampling in the more remote areas.

CHAPTER 7. FAUNA OF PEATLANDS

The literature on the boreal peatland fauna of northern Minnesota has recently been summarized in reports issued by the Peat Program of the Minnesota Department of Natural Resources (Marshall and Miquelle 1978; MN DNR 1981a, 1984a). These reports stress the importance of peatlands as wildlife habitat in the State, particularly in regions where agriculture has eliminated the natural vegetation from the better drained soils. In northern Minnesota, peatlands may be important for the survival of certain species, such as the water shrew (Sorex palustris), southern bog lemming (Synaptomys cooperi), and northern bog lemming (S. borealis), which are primarily restricted to peatlands in Minnesota. Peatlands also provide crucial shelter for whitetail deer (Odocoileus virginianus) in winter and are an essential source of fat deposition for many bird species prior to migration.

7.1 LARGE MAMMALS

A summary of the use of peatlands by large mammals has been prepared by Marshall and Miquelle (1978) and the Minnesota DNR (1981a). The woodland caribou (Rangifer tarandus) was the only large mammal species largely restricted to peatlands in the State, but by 1936 caribou had disappeared from its last refuge in the Red Lake peatland (Nelson 1947). The caribou was not replaced by other large mammals, implying that man was responsible for its local extinction.

Moose (Alces alces) in northern Minnesota are frequently found in smaller peatlands, but they seldom enter the larger peatlands of the Glacial Lake Agassiz region. An occasional animal is sighted near the southern edge of the western

water track in the Red Lake peatland among browse of willow (Salix spp.) and bog birch. At present prime areas of moose habitat on the margins of large peatlands in northwestern Minnesota are being converted to agriculture, which may restrict the expansion of the moose population in the State.

Whitetail deer tend to avoid peatlands during the summer but in the winter they depend on dense stands of northern white cedar for their survival. The dense cover in these stands maintains a warmer average temperature than that found on the adjacent uplands and a narrower range in temperature fluctuations. The cedar stands also provide protection from wind and prevent the accumulation of a deep hard snowpack. Northern white cedar further provides the highest quality of browse for deer in winter, but the yards where the deer congregate are often heavily browsed, and the deer must therefore depend upon nearby uplands for food.

The location of the deer yards seems to be related to the activity of the eastern timber wolf (Canis lupis), because the yards are commonly located along the borders of wolf pack territories. The territories of timber wolves are related to the availability of prey, but wolf packs commonly use small areas of nonforested peatland as buffer zones between the territories of rival packs. Wolves have also been sited traveling along the drainage ditches of the larger peatlands, apparently in search of beaver in summer or as a means of easy transit, especially in winter when the ditches are frozen.

Several species of mammals, however, are more dependent on peatlands within the State, particularly lynx (Lynx canadensis), fishers (Martes pennanti),

and snowshoe hares (*Lepus americanus*). Most Lynx in Minnesota have probably migrated from Canada and are usually restricted to conifer swamps. The fisher also prefers this habitat in Minnesota, whereas the snowshoe hare uses a variety of upland areas as well. During periods of low population, however, the hare is generally restricted to swamp forests or peatland thickets where there is an adequate food supply of black spruce, balsam fir, cedar, aspen, birch, and alder (*Alnus*). A recent migrant into the peatlands are beaver (*Castor canadensis*) that migrate along the drainage ditches. Their expansion into the larger peatlands, however, is generally limited to the marginal areas where willows, birch, and some aspen have colonized the spoil banks.

7.2 SMALL MAMMALS

Most of the data on small mammals in Minnesota have been collected by Nordquist

and Birney (1980) and by the Minnesota DNR (1984a; Table 3). Eighteen species of small mammals were found in 10 peatland habitat types, and the size and diversity of the animal populations are strongly related to the corresponding floristic diversity of the vegetation. The largest number of animals was found in tamarack swamps (40) and the lowest numbers in non-forested bogs (12) or fens (13). The number of species in these habitats was low (13 in tamarack swamps and 8 in forested bogs) compared to nearby uplands (35-106 individuals and 8-17 species). Of the species recorded by Nordquist and Birney only the water shrew, southern bog lemming, and northern bog lemming were restricted to peatlands in the State.

7.3 BIRDS

The literature on birds occurring in the smaller peatlands of Minnesota was reviewed by Marshall and Miquelle (1978),

Table 3. Relationship of small mammals to general peatland types in northern Minnesota (Nordquist and Birney 1980; MN DNR 1984).

Common Name	Fen	Swamp thicket	Swamp forest	Forested bog	Open bog	Adjacent upland	Scientific Name
Masked shrew	4	4	4	4	4	4	<i>Sorex cinereus</i>
Water shrew	2				2		<i>Sorex palustris</i>
Arctic shrew	4	4	1-4		1	1	<i>Sorex arcticus</i>
Pygmy shrew	2-4	3	2-3	3	2	3	<i>Sorex hoyi</i>
Short-tailed shrew	2-4	4	3-4	2	1	4	<i>Blarina brevicauda</i>
Star-nosed mole		2	0-4				<i>Condylura cristata</i>
Eastern chipmunk	0-1		0-1			4	<i>Tamias striatus</i>
Least chipmunk	0-1		0-2			3	<i>Eutamias minimus</i>
Franklin ground squirrel	0-1				1	1	<i>Spermophilus franklinii</i>
Red squirrel	0-1	1	4	4		4	<i>Tamiasciurus hudsonicus</i>
Northern flying squirrel			0-2			3	<i>Glaucomys sabrinus</i>
Deer mouse			3-4	1	1	4	<i>Peromyscus maniculatus</i>
White-footed mouse	1	2	2-3			4	<i>Peromyscus leucopus</i>
Southern red-backed vole	4	4	4	4	4	4	<i>Clethrionomys gapperi</i>
Heather vole*							<i>Phenacomys intermedius</i>
Meadow vole	2-4	4	1-3	1	4	1	<i>Microtus pennsylvanicus</i>
Southern bog lemming			0-4	0-4	2		<i>Synaptomys cooperi</i>
Northern bog lemming	0-1				2		<i>Synaptomys borealis</i>
Meadow jumping mouse	2	3	0-3		1	3	<i>Zapus hudsonius</i>
Least weasel*							<i>Mustela nivalis</i>

Key

4—characteristic
3—frequent

2—occasional
1—occurred

0 or blank—not found
*—reported to occur in peatlands

and the avifauna of the extensive Red Lake peatland has been investigated by Warner and Wells (1980), Neimi (1985), Neimi and Hanowski (1984), and Neimi et al. (1984). The Minnesota DNR (1981a) has prepared a review of these findings that are presented in Table 4. In the Red Lake peatland Warner and Wells found 70 species of birds in 12 vegetation types during the breeding season. The highest

concentration of species was found in cedar-spruce swamps (32) in contrast to the nonforested bogs (4); population densities showed a similar decline from swamp thickets (387 birds/40.5 ha) to nonforested bog (40 birds/40.5 ha).

Although the peatland vegetation types were used unequally by breeding populations of birds, some vegetation

Table 4. Distribution of bird species in peatland habitats during the breeding season in northern Minnesota (Warner and Wells 1980; MN DNR 1984).

	Open Bog	Fen	Swamp Thicket	Swamp and Bog Forest		Open Bog	Fen	Swamp Thicket	Swamp and Bog Forest
American bittern		X			Cedar waxwing			X	X
Mallard	X	X	X	X	Solitary vireo				X
Blue-winged teal		X			Red-eyed vireo			X	X
Marsh hawk*				X	Black and white warbler			X	X
Spruce grouse				X	Golden-winged warbler			X	
Ruffed grouse			X	X	Tennessee warbler			X	X
Sharp-tailed grouse	X			X	Nashville warbler			X	X
Sora		X			Northern parula				X
Yellow rail		X			Yellow warbler			X	
Common snipe	X	X	X	X	Magnolia warbler				X
Mourning dove	X		X	X	Yellow-rumped warbler	X			X
Black-billed cuckoo			X	X	Black-throated green warbler				X
Barred owl*				X	Blackburnian warbler				X
Great gray owl*				X	Chestnut-sided warbler			X	
Short-eared owl*		X	X		Palm warbler	X			X
Common flicker			X	X	Ovenbird				X
Black-backed					Connecticut warbler			X	X
3-toed woodpecker				X	Mourning warbler				X
Great crested flycatcher			X	X	Common yellowthroat		X	X	X
Yellow-bellied flycatcher				X	Wilson's warbler			X	
Alder flycatcher			X		Bobolink	X	X		
Least flycatcher			X		Red-winged blackbird		X		
Olive-sided flycatcher			X	X	Brewer's blackbird	X			
Tree swallow	X	X	X		Common grackle			X	
Gray jay			X	X	Brown-headed cowbird			X	X
Blue jay			X	X	Rose-breasted grosbeak			X	
Black-capped chickadee			X	X	Purple finch				X
Boreal chickadee				X	Pine siskin			X	
Red-breasted nuthatch				X	American goldfinch	X			X
Brown creeper				X	Savannah sparrow	X	X		X
House wren			X		LeConte's sparrow	X	X	X	X
Winter wren				X	Sharp-tailed sparrow		X		
Short-billed marshwren	X		X		Dark-eyed junco	X			
Gray catbird			X		Chipping sparrow	X			
American robin			X		Clay-colored sparrow		X	X	
Hermit thrush				X	White-throated sparrow			X	
Swainson's thrush				X	Lincoln's sparrow		X	X	X
Veery			X	X	Swamp sparrow		X	X	
Golden-crowned kinglet				X	Song sparrow			X	
Ruby-crowned kinglet				X					

*Reported to occur by other sources

types provided food resources during critical periods, such as the molting period and the period of fat deposition prior to fall migration. The forested bog habitat, for example, had the lowest populations of breeding birds but the highest number of birds during those critical times.

Most of the bird species cited in these reports are common on upland sites, but a few depend upon peatlands for their survival. These species include the greater sandhill crane (*Grus canadensis tabida*), great gray owl (*Strix nebulosa*), short-eared owl (*Asio flammeus*), sora rail (*Porzana carolina*), and sharp-tailed sparrow (*Ammodramus caudacuta*). Species most common in peatlands but not restrict-

ed to this habitat type are the palm warbler (*Denroica pinus*) and Connecticut warbler (*Oporonis agilis*).

7.4 AMPHIBIANS AND REPTILES

Only seven species of amphibians and four reptiles are found in Minnesota peatlands (Karns 1979; Table 5). Although all of these species also occur in uplands they are often extremely abundant in certain peatlands. Their major limiting factor was determined to be acid mire waters with a pH below 5, which prevent the hatching and development of embryos for most species except the wood frog (*Rana sylvatica*).

Table 5. Relationship of amphibians and reptiles to peatland habitats in northern Minnesota (Karns 1979; MN DNR 1984).

Common Name	Open Bog	Forested Bog	Forested Swamp	Open Fen/ Swamp Thicket	Adjacent Uplands	Scientific Name
AMPHIBIANS						
Northern spring peeper		1	1	1	1	<i>Hyla c. crucifer</i>
Chorus frog			0-1		2	<i>Pseudacris triseriata</i>
Wood frog	1-2	1	2-3	3	2	<i>Rana sylvatica</i>
Northern leopard frog			1	1		<i>Rana pipiens</i>
American toad	1-2	1	2-3	2	2	<i>Bufo a. americanus</i>
Blue-spotted salamander	1	1	0-1	1	2	<i>Ambystoma laterale</i>
Mudpuppy*						<i>Necturus m. maculosus</i>
REPTILES						
Eastern garter snake	1		0-1			<i>Thamnophis s. sirtalis</i>
Northern red-bellied snake	**	**		1	1	<i>Storeria o. occipitamaculata</i>
Western painted turtle*						<i>Chrysemys picta belli</i>
Common snapping turtle*						<i>Chelydra s. serpentina</i>

Relative Population Levels

3—High

2—Moderate

1—Low

*—can occur in ditches or receiving waters

**—reported to occur in the literature

CHAPTER 8. PEATLANDS: SUCCESSIONAL TRENDS

The development of patterned peatlands in Minnesota has been inferred from three different lines of evidence: (1) landform patterns, (2) hydrologic models, and (3) stratigraphic analyses of peat cores (Glaser and Wheeler 1980; Glaser *et al.* 1981; Glaser 1983a, b; Siegel 1981, 1983; Siegel and Glaser, In press; Glaser, In prep.a; Janssens and Glaser, In prep.). The relative simplicity of these systems compared to upland communities should make these peatlands an ideal subject for discerning the role of autogenic vs. allogenic controls on vegetation development.

8.1 BOGS AND WATER TRACKS

The boundaries between bogs and water tracks in northern Minnesota are generally sharp, with only a few meters separating these contrasting landforms. The development of these two major vegetation-landform types is related to the pattern of surface runoff draining across a peatland or in some cases to the location of groundwater discharge. Water flowing across a peatland is channeled into definite zones initially in response to topographic features at the crest of a watershed and later by the accumulation of peat with different hydraulic properties (Glaser and Wheeler 1980; Glaser *et al.* 1981; Glaser 1983a; Glaser, In prep.a). A water track will generally develop along the path of minerotrophic runoff, which favors the growth of the more nutrient-demanding sedges. The porous rhizomatous peat developed by the aggressive *Carex lasiocarpa* further promotes this channeling process and directly leads to the development of a patterned water track. The raised bogs, in contrast, will develop anywhere in a watershed where topographic obstructions divert the main path of runoff. Within these zones of stagnant flow

mats of *Sphagnum* may form and grow outward until their continued spread is blocked by the main zones of minerotrophic runoff. The boundary between bog and fen is sharpened by the accumulation of peat with radically different hydraulic properties (i.e. the porous, permeable sedge peat vs. the more dense less porous *Sphagnum* peat). This hypothesis as presented by Glaser (1983a, b) and Glaser (In prep.a) is consistent with the landform patterns observed in aerial photographs and the different types of mire-complex types.

8.2 VEGETATION PROCESSES

8.2.1 Bogs

The development of radiating forest patterns on raised bogs is apparently controlled by the channeling of runoff from the bog crest. Runoff from the crest initially flows into drains that favor *Sphagnum* growth rather than tree growth. Runoff is preferentially focused into fewer drains because of the rapid growth of *Sphagnum*, which lays down a loose and hydraulically conductive surface layer of peat. These drains continue to expand as the bog develops, and they eventually coalesce into nonforested *Sphagnum* lawns.

This hypothesis on bog-drain development is supported by several lines of evidence. LANDSAT imagery taken during the spring break-up of 1978 clearly shows the focusing of water flow into the drains (Glaser *et al.* 1981; Glaser, In prep.a). The vegetation of the bog forest also contains a zone of deteriorating forest growth around the margins of the drains extending toward the bog crest. Cores taken from the peat of the drains also indicate the former existence of bog forest, because the drains are underlain

by buried wood and Sphagnum (Figures 31 and 32).

The formation of large ovoid islands in Minnesota peatlands may take place by two different processes. In the largest bogs, such as those at Red Lake, ovoid islands may arise secondarily from what was once a more continuous expanse of bog as a byproduct of the origin of internal water tracks (Figures 33 and 34). The formation of these internal water tracks and ovoid islands is found on almost all bogs from Minnesota to Hudson Bay and seems to be part of a fundamental mechanism of bog development in the North American interior. This pattern is also found in smaller bogs but is less well developed. The modes of origin for these

water tracks is discussed more thoroughly in the hydrology section.

Ovoid bog islands may also arise in a primary fashion within a more discontinuous tract of peatland. These islands tend to form downslope from bedrock outcrops or other topographic obstructions that divert the path of minerotrophic runoff draining across a peatland (Figure 35). The Sphagnum mat that develops outward from such an island is stopped by the concentrated flux of cations in the adjacent water tracks and is shaped into an ovoid form if the mat is completely surrounded by water tracks.

8.2.2 Water Tracks: Strings and Flarks

The two most conspicuous landform patterns in water tracks are fields of tree islands and networks of strings and flarks. The origin of strings and flarks is a controversial subject that has been treated extensively in the literature. In Minnesota the development of flarks seems to be the primary agent in patterned fen formation, with the channeling of water movement as the controlling mechanism (Glaser *et al.* 1981; Glaser 1983c).

Patterned fens first begin to appear in nonforested water tracks as a series of scattered individual pools (Figure 36). The flarks are generally clustered on one side of the water track where the surface may be lower and wetter. In large water tracks the upslope portion of the track is generally nonpatterned, whereas downslope the flarks first start to appear as scattered pools, which coalesce farther downslope into a more continuous network. The flarks get progressively wetter downslope and eventually the intersecting strings are barely discernible on the ground as bands of dense growth of Carex lasiocarpa growing on firmer peat.

The development of patterned fens therefore seems to be related to a progressive flooding of the peat surface, which is inundated in low spots parallel to the contour interval. This flooding process is produced by (1) the channeling of runoff, which converges from a wide area into a narrow track, (2) the development of nearly level peat slopes as a

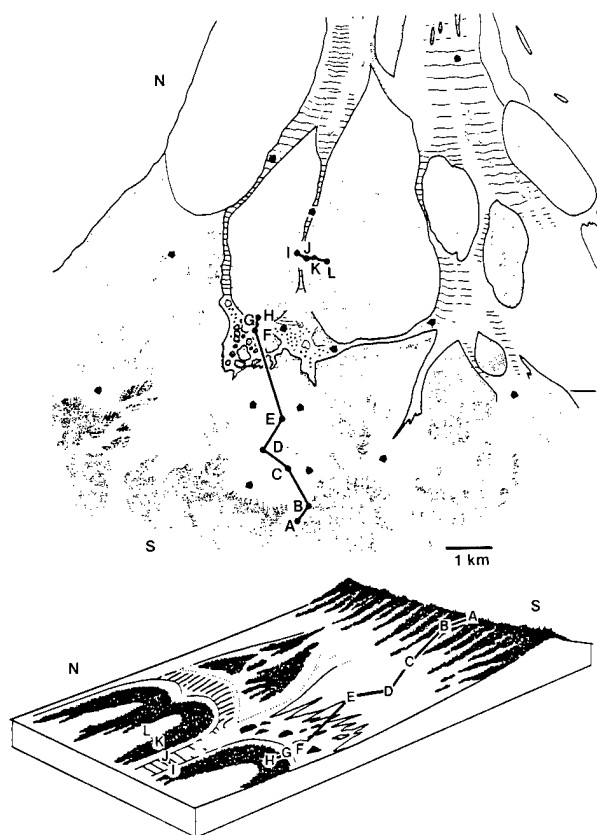


Figure 31. Diagram of Red Lake peatland, northern Minnesota (after Janssens and Glaser, *In prep.*). The stippled areas represent areas of bog forest or bog-like poor fens. The areas with transverse lines represent patterned water tracks. Water drainage is from the south to north. The peat stratigraphy of this area was studied along transects A-H and I-L.

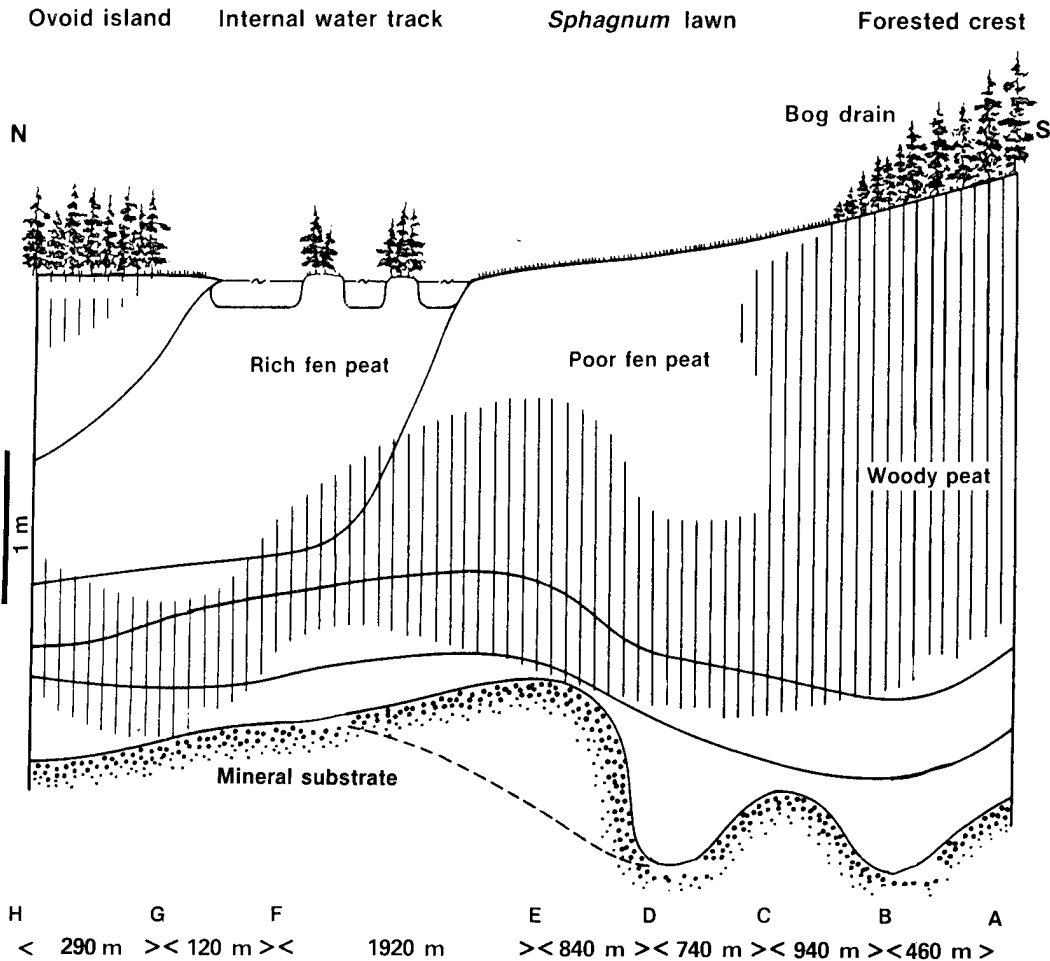


Figure 32. Diagram of the stratigraphy along a north/south transect in the Red Lake peatland (from Janssens and Glaser, in prep.). The water chemistry is inferred from the fossil bryophyte assemblages found in each zone. The internal water tracks are secondary features that developed over bog forest or bog-like poor fen peat. The distances between cores (A-H) taken along the transect are presented along the bottom of the diagram.

result of peat accumulation, and (3) the increasing resistance to infiltration produced by the development of more decomposed and less porous peat in the flarks. The flooding hypothesis is supported by the signs of progressive paludification of the adjacent tree islands discussed below and by the water chemistry.

This hypothesis is also supported by vegetational changes associated with the drainage ditches (Glaser *et al.* 1981). Drainage ditches locally lower the water table in a water track and permit various shrubs and trees to invade and eventually obscure the flark and string patterns.

Across a series of ditches the drier portions of the track then become covered with an increasing number of shrubs and trees until the characteristic landform patterns virtually disappear. (Figures 26-29; Glaser *et al.* 1981; Glaser 1983a). Thus the peatland reverts to the original state, in which better aeration in the surface layers of peat permits trees and shrubs to attain dominance.

8.2.3 Water Tracks: Tree Islands

Fields of tree islands are restricted to the large water tracks and smaller spring fens of the Glacial Lake Agassiz

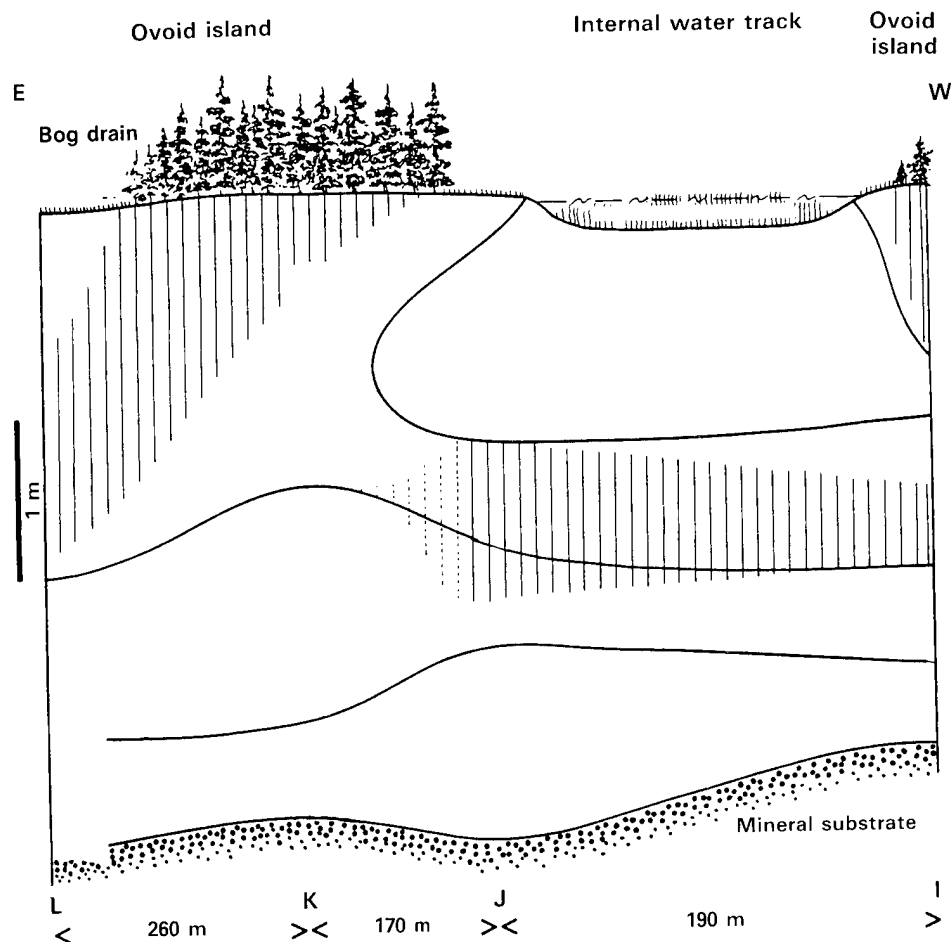


Figure 33. Diagram of the peat stratigraphy along an east/west transect between two ovoid islands in the Red Lake peatland, northern Minnesota (from Janssens and Glaser, In prep.). The bog peat is deepest in the center of the ovoid island and becomes shallower toward the outer margin. The rich-fen peat under the internal water track, however, is underlain by bog peat with wood, indicating a secondary origin for the track. The distance between cores (I-L) taken along the transect are listed at the bottom of the diagram.

peatlands. These islands seem to be the remnants of what was once a more continuous swamp forest that was replaced by nonforested sedge lawns in the expanding water tracks (Glaser and Wheeler 1980; Glaser et al. 1981). The large water tracks are fed by sinuous nonforested channels that arise at the margin of the peatland and converge downslope into a central track. The downslope expansion of these channels progressively restricts the forest into forested fingers that further fragment into discrete islands (Figures 37-40).

The islands are generally completely forested at the upslope margin of a water

track, but farther downslope the trees become restricted to a circular head with a tapering tail of brush trailing downslope (Figure 41 and 42). The trend from the crest to the lower flanks of these watersheds indicates a progressive flooding of the peat surface and restriction of trees to the smaller raised areas (Glaser In prep.a; Figure 37). This hypothesis is supported by stratigraphic evidence from nonforested channels in two different spring fens. The upper horizon of fibrous sedge peat is replaced below by woody *Sphagnum* peat indicating the prior existence of more continuous forest (Figure 9). Where drainage ditches have locally lowered the water table trees will

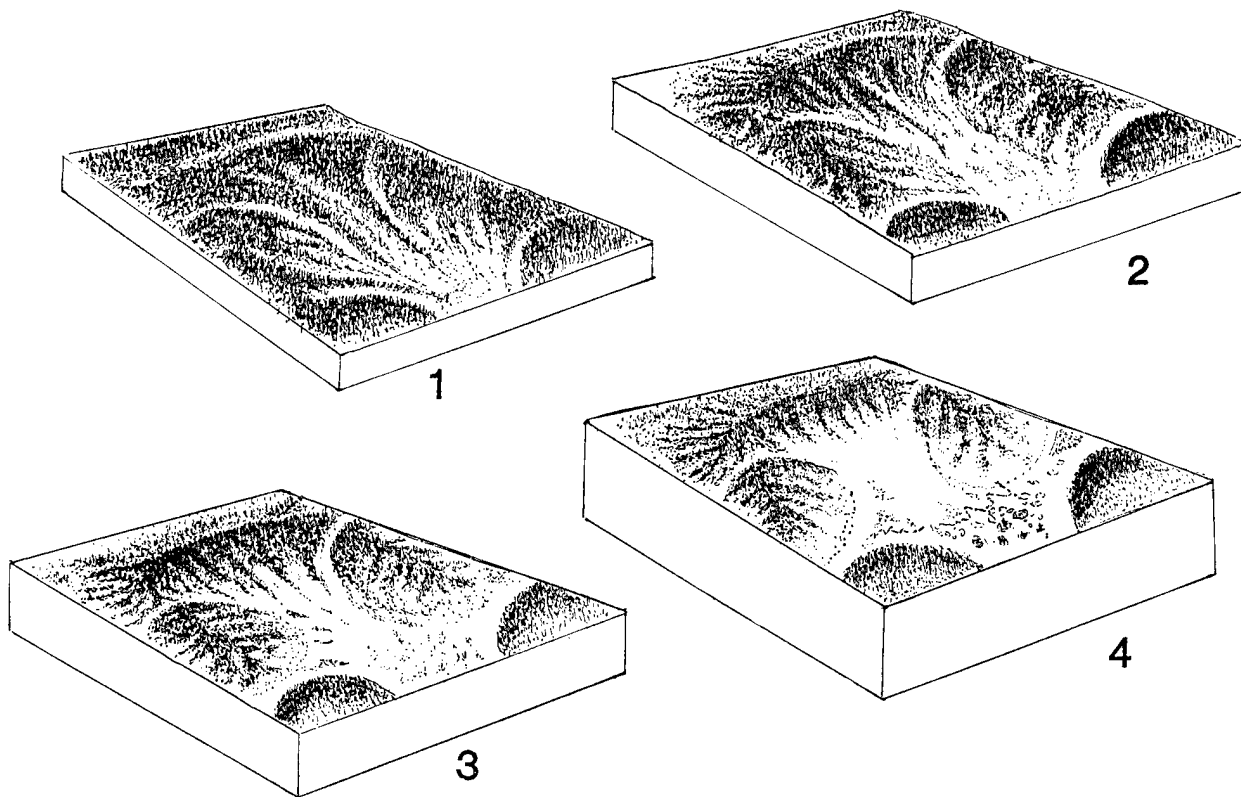


Figure 34. Diagram of the secondary development of ovoid islands within a large bog complex (from Glaser, In prep.a; adapted from Glaser and Wheeler 1980; Glaser et al. 1981). In step (1) a crest is beginning to form and water is being channeled into nonforested drains. The drains expand in step (2) and coalesce into large *Sphagnum* lawns, producing ovoid clumps of forest. Water draining across the open lawns is channeled into internal water tracks that converge around the ovoid clumps of forest step (3). The clumps are then sharply defined as ovoid islands step (4).

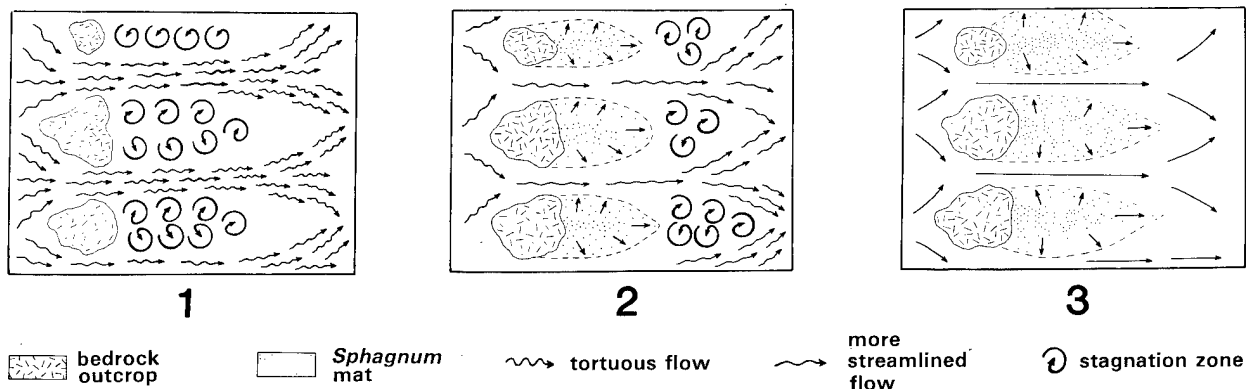
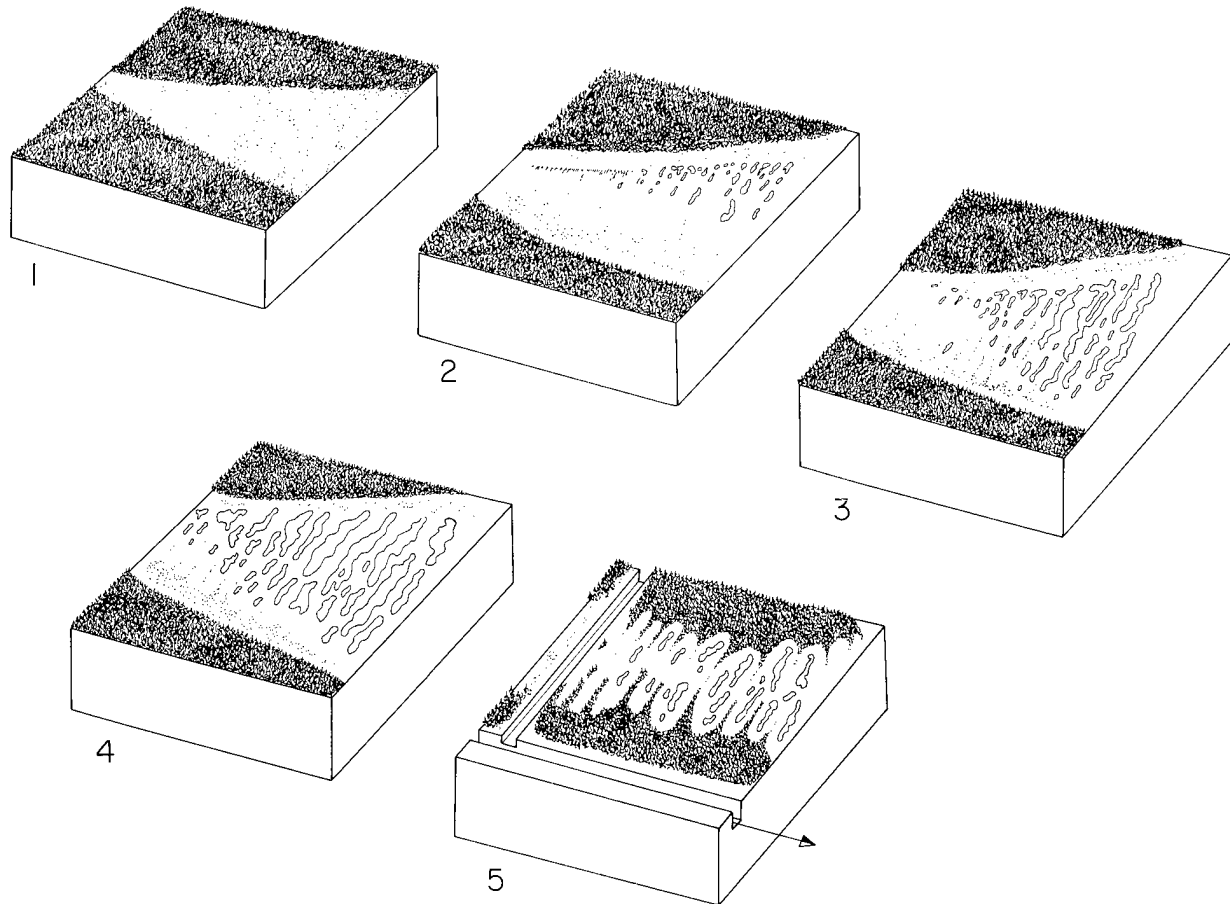
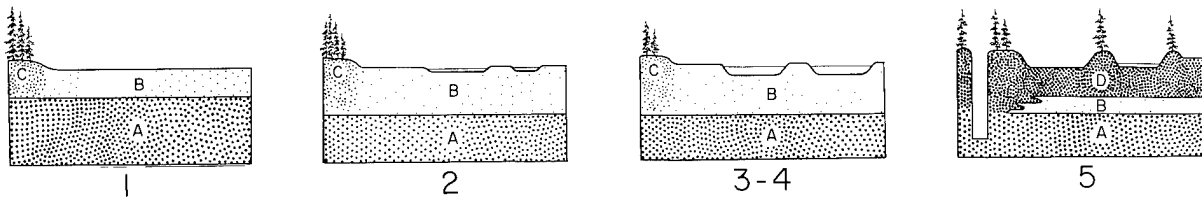


Figure 35. Diagram of the primary development of ovoid islands (from Glaser, In prep.a; adapted from Glaser 1983a). As peat spreads over a landscape, the path of geogenous drainage is diverted around obstructions (mineral outcrops), creating stagnation zones downslope (circular arrows in step 1). As peat continues to accumulate, *Sphagnum* mats form in these stagnation zones where the concentration flux of the water is lower (step 2). The *Sphagnum* mat will continue to spread outward until its continued growth is checked by the main path of geogenous water (step 3). The path of drainage continues to converge into a narrower path because of the difference in hydraulic conductivity between the *Sphagnum* peat under the bog and the *Carex lasiocarpa* peat in the tracks.

PLAN VIEW



CROSS-SECTIONAL VIEW



Peat types

- | | |
|---|---|
| A highly decomposed wood peat | C humified wood peat under the swamp forest |
| B porous sedge peat, particularly the rhizomatous network of <i>Carex lasiocarpa</i> | D highly humified and compacted peat near the drainage ditches |

Figure 36. Inferred development of a patterned fen in Minnesota (from Glaser, In prep.a; adapted in part from Glaser et al. 1981; Glaser 1983d). A patterned fen begins as a featureless water track in a swamp forest (step 1). The water track expands as drainage converges into the zone of very porous peat (B) that is deposited by the hydrophilous sedges growing in the track. The water table rises in the track and water ponds up at the surface because of the leveling of the slope and the convergence of surface drainage (step 2). The ponds expand parallel to the contour interval restricting the sedge lawn into very narrow sinuous ridges (steps 3 and 4). The progressive flooding of the track is checked, however, when drainage ditches lower the water table, permitting trees and shrubs to reinvade the water track (step 5).

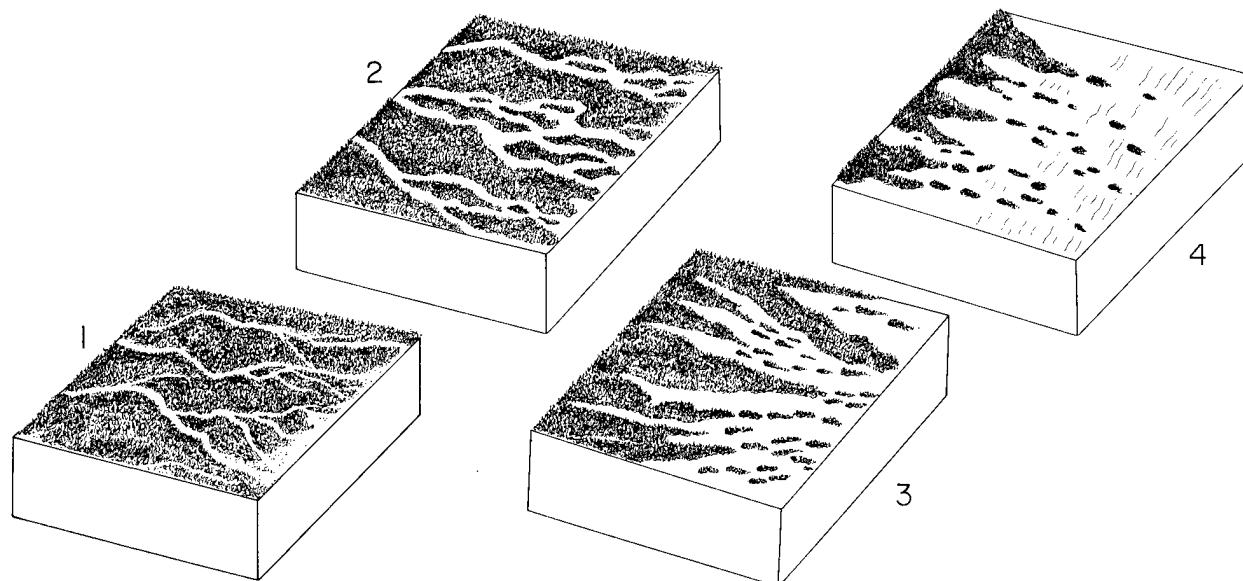


Figure 37. Transition from forested fingers to tree islands. Runoff within a swamp forest is first channeled into nonforested drains that fragment the swamp forest into linear forested fingers (step 1). The forest cover in the drains becomes thinner downslope because of the locally rising water table. This conclusion is supported by excavating the smaller trees in the drains, which have much larger stems and trunks under the peat. As the drains continue to expand, the forested fingers between the channels are constricted until clumps of forest are split off as discrete islands (steps 2 and 3). The drains coalesce farther downslope, forming a patterned water track in which remnants of the original forest appear as tree islands (step 4). The sequence of steps shown in 1-4 is observed in peatlands throughout the Lake Agassiz region and is controlled by two processes: (1) the channeling of drainage into the channels explained in Figure 36 and (2) the progressive rise in the water table that restricts tree growth to smaller clumps.



Figure 38. The initial phase of channel formation in a swamp forest. The channels are dominated by stunted *Larix* (Pine Creek peatland).

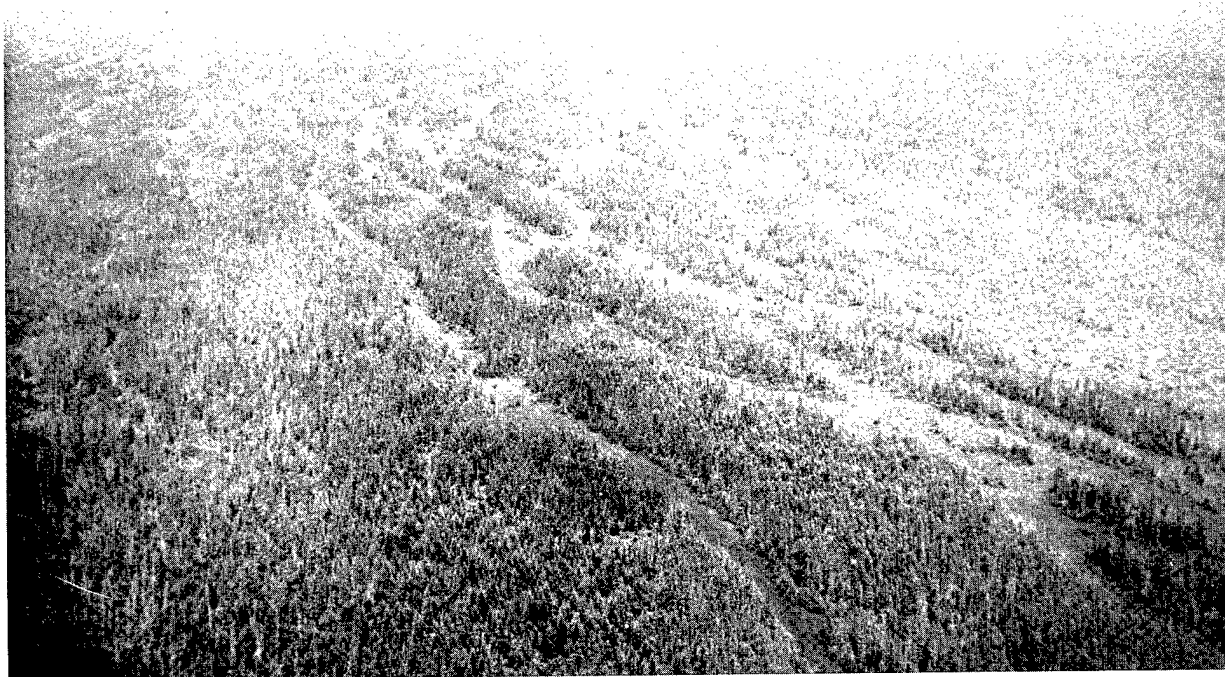


Figure 39. Later phase of channel development in a swamp forest. The channels have expanded and are now dominated by sedges. The forest, in contrast, is restricted into tapering fingers that fragment downslope into discrete "tree islands."



Figure 40. Final phase of channel development. The channels have now coalesced into a patterned water track with isolated "tree islands."



Figure 41. Types of minerotrophic tree islands from the Western Water Track of the Red Lake peatland, northern Minnesota. The islands (1) are completely forested nearest the marginal swamp forest. The water drains from the upper left side of the photograph to the lower right. The photograph covers an area over 2.5 km across.



Figure 42. Types of tree islands from the Western Water Track. Toward the wet center of the track the islands (2) consist of a small head of trees (2a) and tail of brush (2b) trailing downslope. Drainage ditches (1) have lowered the water table downslope as indicated by the lighter tones. The path of flow is indicated by the arrows. The photograph covers an area over 2.5 km across.

also spread over the entire island reversing the effects of flooding (Figure 43). Thus the tree islands form by the progressive flooding of the peat surface, which also produces the characteristic string-flark pattern.

In the Red Lake peatland stratigraphic work by Griffin (1977) provides less clear data on the formation of a tree island near the southern edge of the western water track. Griffin's cores indicate that the island forest and the adjacent water track dominated by *Carex lasiocarpa* arose at nearly the same time. Needles of *Larix* underlie the sedge peat zone that was interpreted as a *Carex lasiocarpa* meadow, but the needles occur in only a

shallow horizon. The *Carex diandra/Carex aquatilis* peat underneath this horizon has no analog in the Red Lake peatland today. Griffin's transect of cores also did not extend far from the margin of the island and therefore does not provide a conclusive test of the hypothesis presented above.

8.3 HYDROLOGIC PROCESSES

8.3.1 Surface Drainage Controls

The channeling of water across a peatland seems to be the most important factor controlling the development of vegetation in the patterned peatlands in

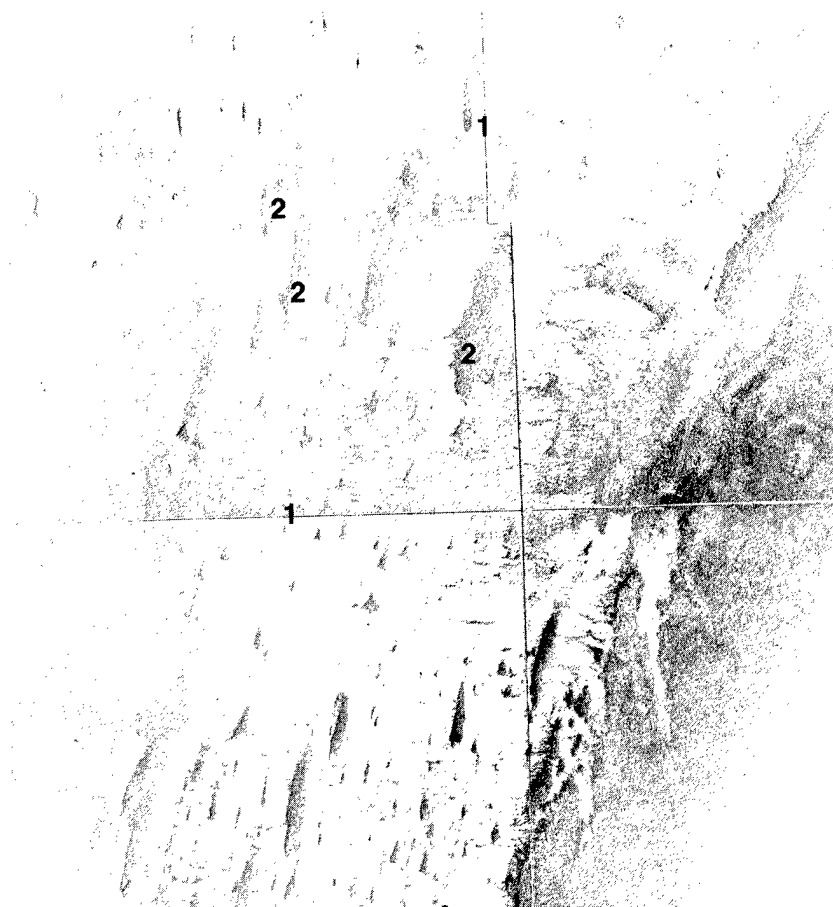


Figure 43. Types of tree islands from the Western Water Track. At the extreme downslope portion of the peatland where drainage ditches (1) have lowered the water table, the trees have spread back over the entire island (2). The photograph covers an area 2.5 km across.

Minnesota. The role of surface flow in peatland development is most apparent in the discontinuous tracts of peatland in northern Minnesota (Glaser 1983a; Glaser In prep.a; Figure 20). The landform patterns that develop in these watersheds are closely related to physiographic features at their crests that control the path of runoff draining onto the peatland downslope. Although storm hydrographs for these watersheds have not been established, a general relationship exists between the area of mineral soil at the crest of these watersheds and the size of bogs and water tracks on the peatlands downslope (Figures 44-47).

Bogs develop in those peatlands where the inflowing runoff contains a very low concentration of calcium and other dissolved solids. These conditions are created in peatlands where the area of mineral soil at the crest of a peatland

catchment is minimal or where runoff is diverted around a topographic obstruction (Figures 20 and 44-47). The larger water tracks, in contrast, receive runoff from larger mineral catchments draining directly onto the tracks. These water tracks originate downslope from swales or low valleys at the head of the watershed and drain into tributary streams at the downslope edge of the peatland; this alignment indicates an overriding control of surface flow on pattern development.

The bifurcating water tracks in the Glacial Lake Agassiz peatlands represent an inexplicable drainage feature (Figures 46 and 48). Water tracks in this region commonly split into two separate forks around the margins of a raised bog. Drainage systems on the uplands, in contrast, never assume such a pattern but instead converge downslope into progressively larger channels. In the Myrtle

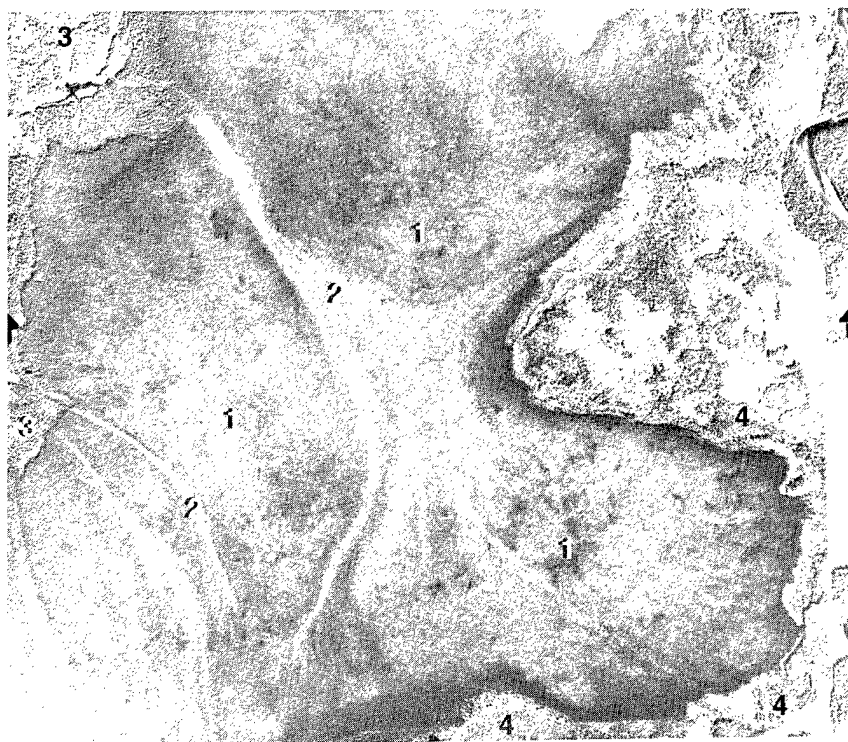


Figure 44. Aerial photograph of the Lindford peatland, north-central Minnesota (from Glaser, In prep.a). The peatland is almost completely covered by raised bogs (1) except for several narrow water tracks (2). The water tracks drain toward small streams (3) at the downslope margin of the peatland. The mineral crest (4) of the watershed is located very close to the margin of the peat land. This peatland is an example of mire-complex 2 on Figure 20. The photograph covers an area 2.5 km across.

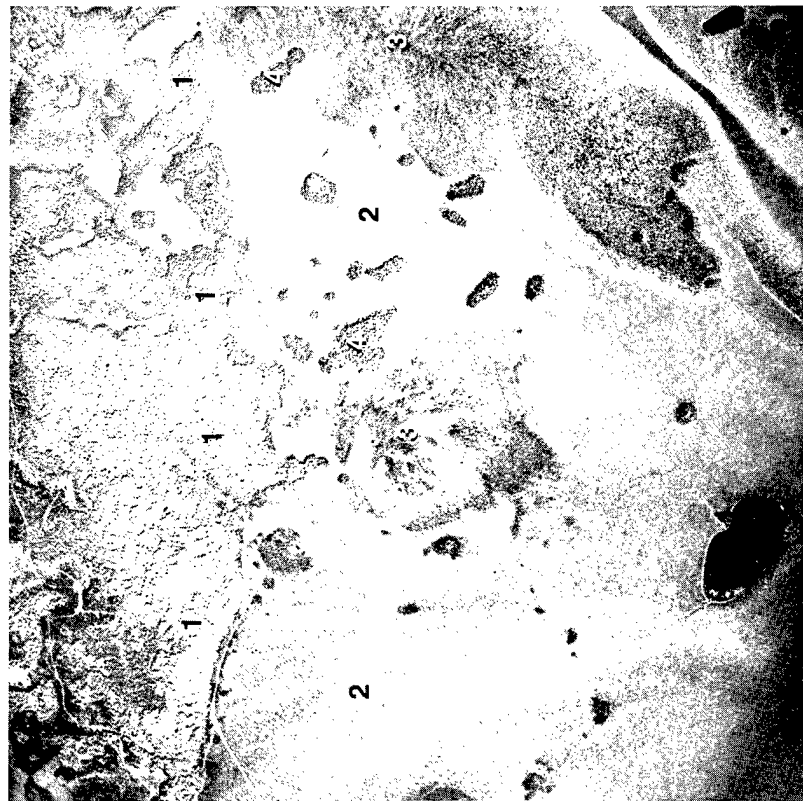


Figure 45. Aerial photograph of mire-complex type 3 (see Figure 20) near Sand Lake, northeastern Minnesota (from Glaser, In prep.a). Drainage from mineral soil (1) is channeled into featureless water tracks (2). Raised bogs (3), in contrast, have developed downslope from mineral outcrops (4) that divert the path of surface drainage. The path of runoff is indicated by the vegetation bands in the water tracks.



Figure 46. Aerial photograph of mire-complex type 4 (see Figure 20) at the Myrtle Lake peatland (from Glaser, In prep.a). The peatland contains a huge water track (1) that drains around the margin of a large raised bog (2) toward streams (3) at the downslope margin of the peatland. The photograph covers an area 14.4 km across.



Figure 47. Aerial photograph of a large patterned fen (mire-complex type 7 in Figure 20) near Mud Lake, northwestern Minnesota (from Glaser, In prep.a). Runoff from the uplands drains across this fen in the direction of Mud Lake (1). The peatland is distinguished by string/flark patterns (2) and is cut by drainage ditches (3).

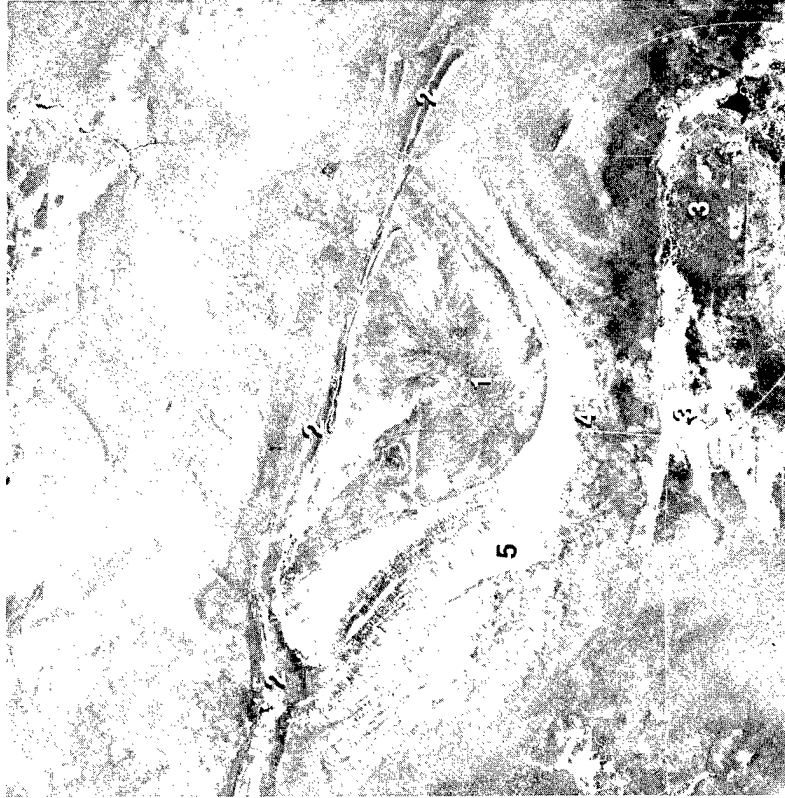


Figure 48. Aerial photograph of mire-complex type 8 (see Figure 20) in the Glacial Lake Agassiz peatlands, northern Minnesota (from Glaser, In prep.a). The peatland contains a large semicircular raised bog. (1) that has developed upslope from a narrow mineral beach ridge (2) that protrudes through the peat surface. Drainage from the mineral uplands (3) is channeled into a water track (4) that splits into two branches around the margin of the raised bog. One branch of the track (5) is differentiated into string/flark patterns and fields of tree islands.

Lake peatland Heinselman (1970) explained that this drainage pattern was caused by the stream piracy of a stream that had eroded headward into the downslope portion of the peatland. When the stream diverted flow from the main water track in a new direction, however, the piracy was not complete and surface drainage now flowed in two different directions.

The common occurrence of such bifurcating drainage patterns may also be explained by a subsurface mineral ridge that diverts water flow and promotes the growth of a bog on the ridge. The rate of peat accumulation in the adjacent water track may be sufficiently uniform over its surface to prevent stream capture and sustain the bifurcating flow system.

8.3.2 Groundwater Controls

In areas of nearly continuous peat cover the input of solutes from surface runoff may be insufficient to prevent the conversion of large areas of peatland into

ombrotrophic bog. However, the nearly continuous peatlands of the Glacial Lake Agassiz region are predominantly minerotrophic fens, indicating that groundwater discharge through the peat may provide a significant source for alkalinity and dissolved solutes in these mire-complex types (Figures 21 and 48-51).

At present the discharge of ground water has only been documented in the spring-fen mounds of the Glacial Lake Agassiz peatlands (Figure 51). The high pH and concentration of Ca in the surface waters of the spring-fen channels can only be sustained by the continual discharge of groundwater from calcareous parent material, a view supported by actual hydraulic-head gradients measured in these channels (Siegel and Glaser, In press). The role of groundwater discharge, however, is more difficult to distinguish in other mire-complex types from observations of the surface-water chemistry alone because the gradients observed are less pronounced.

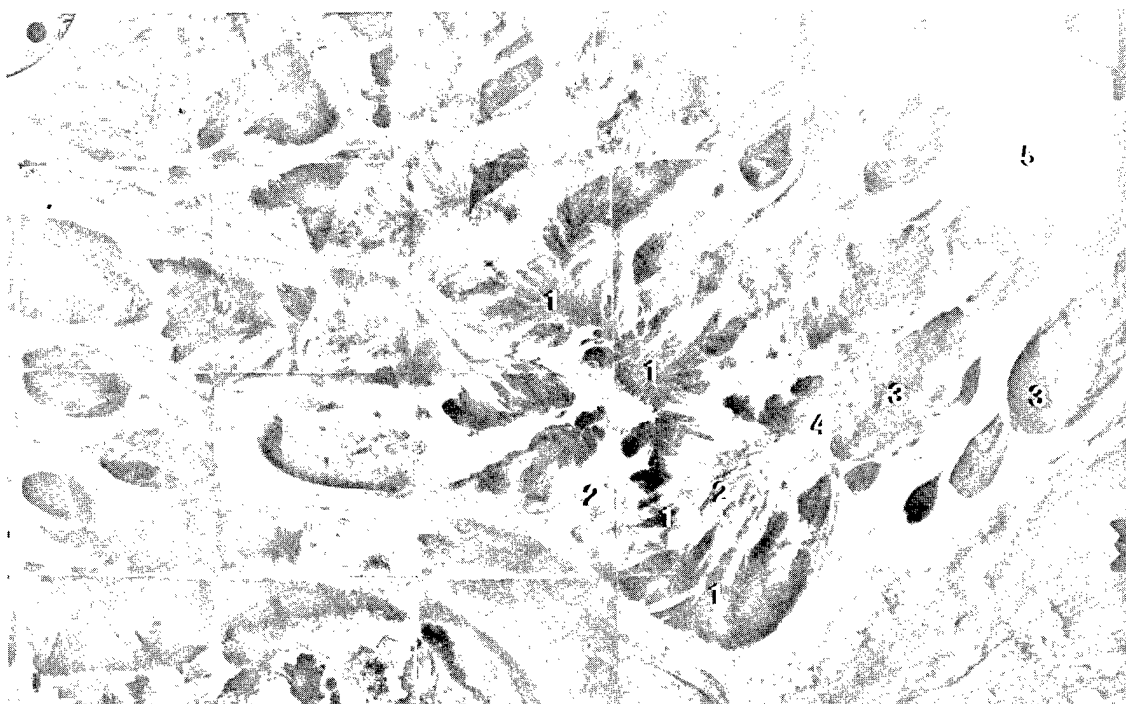


Figure 49. Aerial photograph of mire-complex type 9 from the Red Lake peatland, northern Minnesota. The peatland consists of a large raised bog complex that is differentiated into ovoid islands and internal water tracks. The features marked are (1) raised bog crest, (2) *Sphagnum* lawns on the lower flanks, (3) ovoid islands and (4) internal water tracks. Drainage ditches (5) are restricted to the lower portions of the watershed.

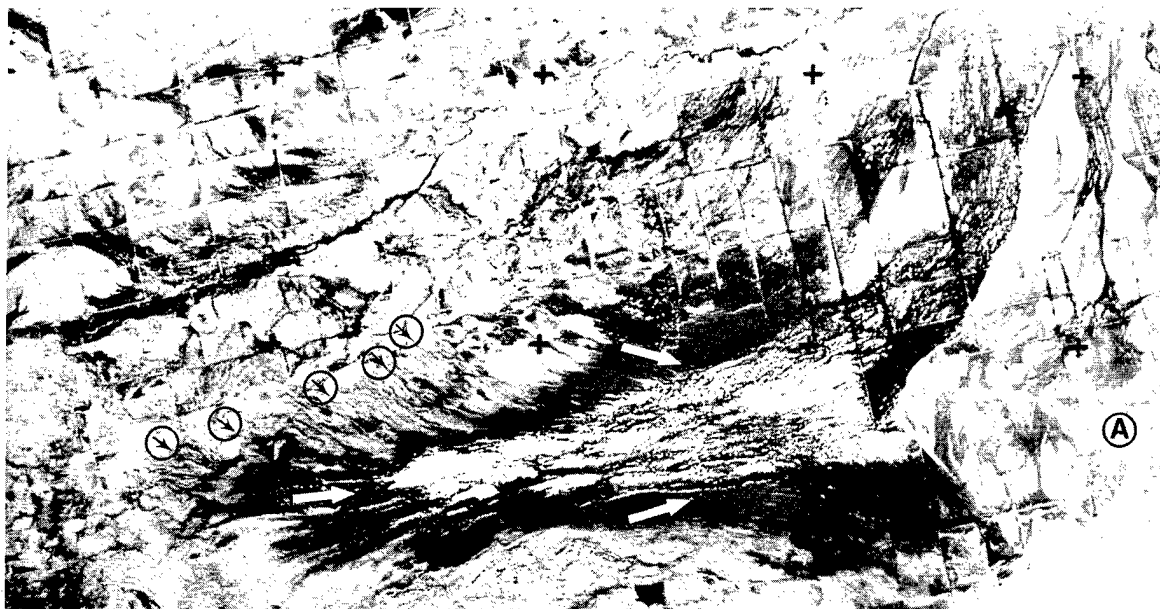


Figure 50. LANDSAT image of the Western Water Track (mire-complex type 10; see Figure 20) in the Red Lake peatland, northern Minnesota. The image was taken during spring break-up of 1978. The water track measures over 32 km long and 5 km wide. Drainage from the marginal beach ridge is focused in sinuous channels (small black arrows) that feed into the central portion of the water track (larger white arrows). The water drains toward the right-hand side of the photograph where it splits into two branches around a large bog complex (A) that is still snow-covered.



Figure 51. Aerial photograph of the Lost River peatland in northern Minnesota illustrating mire-complex type 11 (Figure 20) and an adjacent raised bog. The spring-fen mound on the left-hand side of the photograph is characterized by nonforested channels (1) that arise near the crest of the mound and drain through a swamp forest. The raised topography of the mound is indicated by the water track (2) that is diverted around the margin of the mound. The raised bog on the right-hand side of the photograph is indicated by the faint radiating lines of forest. A diagram of the topography and stratigraphy of this area is presented in Figure 9. The image covers an area approximately 2.5 km across.

The large water tracks with fields of tree islands may also be fed by groundwater discharge localized in the sinuous channels that arise around the outer margins of the track (Figure 50; Glaser In prep.a). Discharge appears to be focused at the heads of the sinuous channels that arise downslope from the beach ridges. The definite decline in minerotrophy from the margins of the water track to the patterned interior supports this view that groundwater discharge is restricted to specific foci rather than being distributed throughout the water track. The similarity of the channel and forest patterns in these two types of systems indicates a common mode of origin for their channel and island patterns.

The other potential zone for groundwater discharge is the internal water tracks of the raised bog complexes (Figure 49; Glaser In prep.a). The minerotrophic waters in these tracks are too dilute to indicate groundwater discharge without corroborating evidence from piezometer nests and geochemical profiles of the interstitial peat waters. The stratigraphy in these bog complexes demonstrates that these water tracks are of secondary origin with fen peat overlying bog peat

(Janssens and Glaser, In prep.; Figure 32). The sharp reversal from bog to fen, however, can be explained by either the groundwater hypothesis of Siegel (1981, 1983) or the surface flow hypothesis of Glaser et al. (1981). These two hypotheses, illustrated in Figure 52, may also explain the common occurrence of ovoid islands on bogs. The sharpness of the change could perhaps be most easily explained by a change in hydraulic head at the regional recharge area, causing groundwater to burst through in areas of shallow peat and in the water tracks (Siegel and Glaser, In press).

In the Glacial Lake Agassiz region groundwater discharge may therefore be an important force in the development of the peatland ecosystems. Because of the absence of significant relief on this vast lake plain, a rise in the water table under the raised bogs or on the regional recharge area for groundwater may significantly perturb the existing hydrologic regime and create new patterns of groundwater flow. Groundwater discharge has only been documented for the spring-fen landforms at present, but its influence may be more pervasive in the formation of landform patterns than formerly realized.

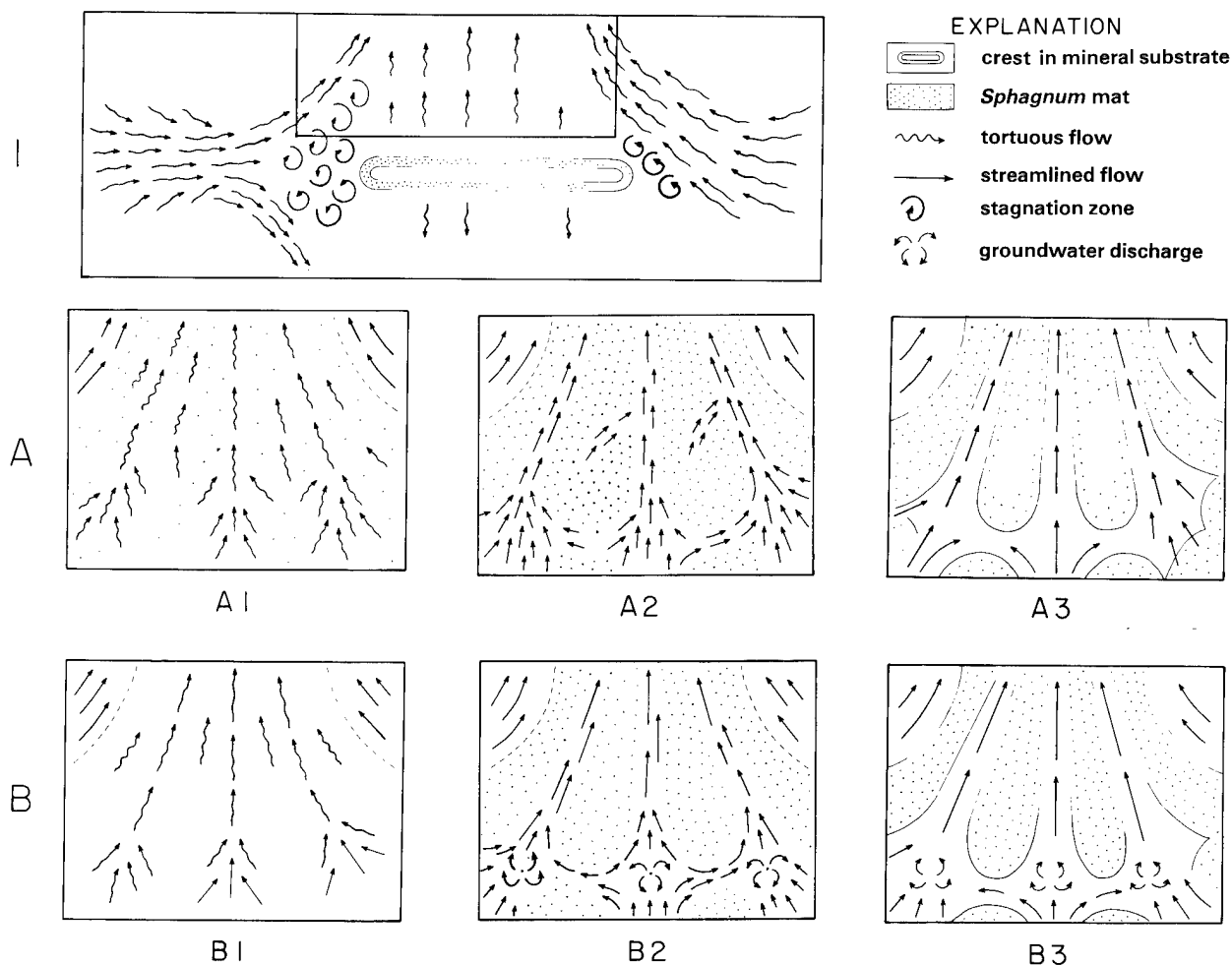


Figure 52. Two opposing models for the development of internal water tracks and raised bog complexes in Minnesota. Initially surface runoff is determined by topographic features in the mineral substrate. Flow paths indicated by the circular arrows are eddies or stagnation zones. In box 1 surface drainage is diverted around a beach ridge creating a zone of stagnant flow in which a *Sphagnum* mat may spread. The surface flow hypothesis (Glaser et al., 1981) is illustrated in (A). As *Sphagnum* spreads over the surface, drainage is progressively channeled into drains that become water tracks according to the process indicated in Figures 31, 32, and 33. The alkalinity in the internal water tracks is provided by the convergence of ions into the tracks from a larger expanse of bog and from enhanced decomposition along lines of flow. The groundwater hypothesis (Siegel 1981, 1983) illustrated in (B) proposes a different source for the alkalinity observed in the water tracks: the discharge of ground water from the calcareous mineral substrate. Once at the surface the geogenous water is channeled into water tracks fragmenting the bog into ovoid islands.

CHAPTER 9. HUMAN IMPACTS AND CONSERVATION

9.1 DRAINAGE PROJECTS

Prior to the First World War the northern counties in Minnesota undertook an ambitious project to drain and reclaim extensive areas of peatland. In the Glacial Lake Agassiz peatlands drainage ditches were cut along the surveyors' section lines in large areas of Koochiching, Beltrami, and Lake of the Woods Counties. As later demonstrated by Boelter (1972), these ditches were spaced too far apart to drain such extensive areas of peat, and the entire project ended in failure and bankruptcy for the northern counties. The State eventually paid for the ill-fated project and received title to these peatlands in compensation.

In northeastern Minnesota drainage ditches were later cut through smaller peatlands for reclamation and also to provide drainage for roadways. The damage to these peatlands was much more extensive than those in the larger Lake Agassiz peatlands. A thorough review of this failed reclamation plan with special emphasis on the Red Lake peatland in northern Minnesota is being prepared by K. Bradof of the University of Minnesota.

Drainage ditches alter a peatland by lowering the water table in the acrotelm and enhancing decomposition and compaction. Rutter (1955) and Boelter (1972) determined that a drainage ditch will produce a drawdown of the water table within the catotelm less than 3 m from the ditch. Where ditching is intensive substantial subsidence may take place: the most spectacular documented example of subsidence occurred in the Fenlands of England (Godwin 1978; Hutchinson 1980; Sheail and Wells 1983).

Drainage ditches have had a serious impact on peatland vegetation by promoting the growth of trees and shrubs at the expense of the more hydrophilous sedges and herbs. Glaser *et al.* (1981) described the striking changes in the landforms and vegetation that take place downslope from the ditches in the Red Lake peatland. The bog margins may have expanded in response to the ditching as *Sphagnum* first invaded the adjacent strings, where scaffolding was provided by the taller sedges and shrubs and later spread over the lower flarks (Glaser In prep.a; Figure 53 A and B). At Arlberg in northeastern Minnesota, for example, the flarks adjacent to a bog have been completely colonized by *Sphagnum* and *Carex oligosperma* immediately downslope from a drainage ditch (Glaser 1985).

In eastern Minnesota the string/flark patterns have almost disappeared in ditched peatlands because of the enhanced growth of various shrubs (particularly *Betula pumila* var. *glandulifera* and trees (Figures 26-29). Only at Alborn have the surface patterns and rare plant populations remained largely intact despite the ditching. The drainage ditches have had a substantial impact on the peatland vegetation, but the larger size of the Lake Agassiz peatlands has buffered these ecosystems from adverse effects to a larger degree.

9.2 PEAT MINING

After World War II several small peat-mining operations were started in northern Minnesota to extract peat for horticultural purposes. Approximately 1,400 acres of peatland were mined, with special emphasis on *Sphagnum* peat (MN DNR 1981). The limited availability of this

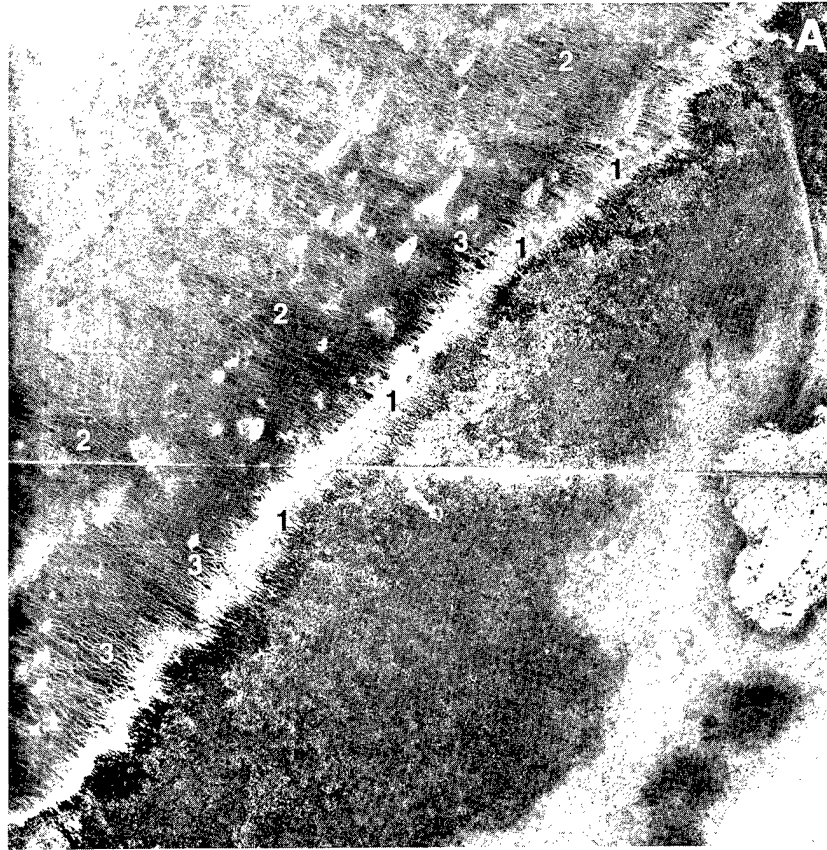


Figure 53. Aerial photographs of an expanding and contracting bog margin. The margin of a bog is controlled by the volume of water flowing in the adjacent water tracks. When water levels are lowered by drainage ditches (A) the bog margin will spread outward, producing a sawtooth pattern. In A the *Sphagnum* lawn (1) has spread out onto the adjacent water track (2) first along the strings (3) and then filling in the adjacent flarks. Trees from the bog forest will then grow out onto

higher-grade *Sphagnum* peat (only 112,000 to 129,000 acres in the State; MN DNR 1979b) and the intense competition from Canadian companies have limited the expansion of this industry in Minnesota.

In 1975, however, the Minnesota Gas Company (Minnegasco) requested a lease for over 200,000 acres of State-owned peatlands to mine peat for conversion into natural gas. The potential of a major impact on the environment prompted the State Legislature to set up the Peat Program in the Department of Natural Resources to evaluate the Minnegasco proposal. The mission of the Peat Program was later broadened to cover a survey of peat resources in the State and establish guidelines for their development and pre-

servation. The State of Minnesota was therefore in a strong position to manage future economic schemes for Minnesota peatlands. The Minnegasco proposal was later abandoned as economically and environmentally infeasible.

The impact of such a project could not be predicted from the smaller operations of northeastern Minnesota. The runoff leaving these small mined peatlands has higher levels of suspended sediment, acidity, organic N, and specific conductivity than the waters draining from peatlands that have not been mined (Brooks *et al.* 1982). However, the levels were not sufficiently elevated to violate drinking standards although they could promote eutrophication downstream.



the strings where the peat is higher. When water levels are raised, however, the bog margin will contract as in B. Here the water track (1) has been flooded by discharge from a drainage ditch (2) that is dammed by beavers. The large deep flarks are aligned to wet portions of the *Sphagnum* lawn (4) that have deeply intruded into the surrounding bog forest (5). Both aerial photographs are from the Red Lake peatland and each covers an area 2.5 km across.

The revegetation of mined peatlands in Minnesota is variable (Anderson and Kurmis 1981; Green 1983). Recovery is very slow if drainage ditches have lowered the water table and there is a low concentration of nutrients. If the ditches are blocked, however, the higher water table will promote a good recovery within 10 years. Trees will typically colonize spoil banks because of their deeper aerated zone. Green suggests that aluminum toxicity may be important in restricting plant colonization but the primary limiting factor seems to be the position of the water table.

These findings are difficult to apply to the vast peatlands of the Glacial Lake Agassiz region where the landscape is

nearly level. A large mining project would surely disturb the sensitively balanced flow systems that maintain the striking landform patterns. The removal of the raised bogs, for example, may alter the local flow systems that bring groundwater to the surface. Because of the nearly continuous expanse of peat it is impossible at present to predict the extent of any impact, which is more confined in the smaller peatlands to the east.

9.3 MINERAL EXPLORATION AND POWERLINES

Mineral exploration in northern Minnesota was greatly stimulated by the 1981 Hemloë gold strike near Thunder Bay,

Ontario. The Hemlo deposit is in the greenstone formation that extends across large areas of northern Minnesota, although in most cases it is covered by thick deposits of glacial till and a surface veneer of peat. Several peatlands are now being explored for mineral deposits, although the probability of finding a deposit that is economical to mine is not considered to be high.

A minor threat to the peatlands is the location of powerline right-of-ways. Powerlines were previously sited preferentially in peatlands to minimize the impact on humans and communications. The installation process may severely damage the peat surface locally and significantly alter the vegetation if heavy equipment is permitted to cross the peatland. At Toivola and Arlberg the powerline right-of-way is characterized by very wet vegetation--a result of local compaction by heavy equipment. In the Glacial Lake Agassiz peatlands, however, helicopters were used to install the powerline pylons and to string the cables; this method greatly minimized the impact of the powerline construction. The most significant impact was the removal of trees along the right-of-way, which locally altered the vegetation patterns (Grigal 1985b).

After World War II narrow lanes were cut across many peatlands in northern Minnesota to harvest small spruce for Christmas trees. Only the smallest trees were cut, and their stumps are now difficult to spot within the bog forests. All cutting has ceased, and the lanes are slowly being closed by windthrows and layering by the Picea mariana.

9.4 PRESERVATION PLANS

Collectively the various impacts on Minnesota peatlands are relatively minor compared to the extensive human alteration of the upland forests and prairies. Largely by default the peatlands in Minnesota have survived as relatively intact ecosystems that represent the most pristine stands of natural vegetation in the State. Through accidents, such as the

bankruptcy of the northern counties, the Minnesota Department of Natural Resources now controls the ownership of most of these peatlands. The State of Minnesota therefore is in a unique position to preserve a representative sample of these peatlands for scientific inquiry and the appreciation of future generations.

The Minnesota Department of Natural Resources has recently submitted a plan to the State Legislature to protect in various degrees the 18 most significant peatlands in the State. These peatlands have been ranked by a special task force according to their significance on regional, national, and international levels. Each peatland has also been divided into a core protection zone and watershed protection zone to categorize the degree of protection required for each area.

The Commissioner of the Minnesota Department of Natural Resources has the discretion of protecting these peatlands under several State statutes. The peatlands may be protected as Wilderness Areas, Scientific and Natural Areas, or Wildlife Management Areas. Other categories, such as State Forests, require approval of the State Legislature.

The Minnesota Department of Natural Resources has decided to recommend to the State Legislature a plan that would protect the core zones of these peatlands (totaling 156,600 acres) as Scientific and Natural Areas or Wilderness Areas, whereas the surrounding watershed protection zone (totaling 345,900 acres) would be protected by a less restrictive designation. Although these areas could be established directly by the Commissioner of the Minnesota Department of Natural Resources, the agency decided to request approval from the State Legislature because of the large extent of land involved. The peatland bill, however, was killed in committee by the State Legislature in 1985 and the plan no longer receives much attention. If eventually enacted the proposal would preserve a large intact example of one of America's outstanding natural areas.

GLOSSARY

- aapamoor - A term used by Cajander (1913) to describe patterned fens. See flarks, patterned fen, strangmoor, and strings below.
- acrotelm - The uppermost horizon in a peat profile that consists of relatively porous and undecomposed peat. The concept is largely based on the work of Soviet hydrologists, who divide a peat deposit into two layers with contrasting physical and biological properties (Ivanov 1981; Ingram 1978, 1983). The acrotelm or active layer is responsible for most water transmission through a peatland on account of its high hydraulic conductivity. It can also be defined as the zone of maximum water-table fluctuations and oxygen penetration from the atmosphere.
- accumulation - Growth of organic matter in an ecosystem as a result of the difference between gross primary productivity and total community respiration (Whittaker 1975).
- acidophilus - Plants adapted to habitats with dilute acid waters (pH <4.2).
- anastomosis - A network of interconnecting channels.
- bog - (i.e. raised bog, hochmoor, ombrotrophic bog). A major type of peatland distinguished by (1) acid, dilute waters (pH <4.2; Ca concentration <2 mg/l), (2) vegetation landforms that indicate a topographically elevated crest or plateau, (3) vegetation assemblages characterized by continuous mats of Sphagnum or other cryptogams and the absence of fen-indicator species, and, most important, (4) an atmospheric source for all water and salts (Glaser et al. 1981; Glaser 1983a; Glaser and Janssens 1986).
- bog drain - Bog drains are nonforested strips of vegetation that originate near the crest of a raised bog forest and radiate downslope eventually coalescing into a broad treeless lawn. The drains and lines of spruce forest make up the characteristic radiating forest patterns of raised bogs that are seen on aerial photographs.
- boreal region - A circumpolar forest region in the northern hemisphere that is generally dominated by conifer tree species. The boreal forest extends north to the treeless tundra and south to the mixed conifer/ deciduous forests or temperate grasslands. The position of the boreal forest in North America is presented for Canada by Rowe (1972) and for Alaska by Viereck and Little (1972).
- brown-moss peat - Organic sediments primarily composed of the brown mosses or Amblystegiaceae, such as Drepanocladus or Calliergon (Auer 1933).
- bulk density - The mass per unit volume of a soil sample that has been oven dried to constant weight at 105 °C.
- cation-exchange - Ability of a soil to adsorb or exchange positively charged ions on colloidal surfaces (Bohn et al. 1979).
- catotelm - The lower horizon of a peat profile, which consists of relatively deeply decomposed peat and has a correspondingly low hydraulic conductivity. The water content of this zone is therefore believed to be constant and water flow negligible. See acrotelm above.
- drawdown - The lowering of the water table as a result of pumping or enhanced drainage in a ditch (Freeze and Cherry 1979).

extremely rich fen - A type of fen vegetation with a very high pH (>7) and calcium concentration (>20 mg/l in Minnesota) and a characteristic species assemblage. Extremely rich fens are generally found in discharge zones for ground water.

fen - A major type of peatland that receives a significant input of water and dissolved solids from a mineral source, such as runoff from mineral soil or groundwater discharge. A fen is therefore considered to be geogenous and its vegetation minerotrophic. Fens are generally characterized by (1) surface waters with a pH above 4.2 and calcium concentration higher than 2 mg/l (2) a more diverse group of species, including many fen indicators, and (3) vegetation-landform patterns that are lower than the surrounding mineral uplands.

fiber content - A measure of peat decomposition that is determined by collecting the amount of material trapped in various-sized sieves and weighing the dried fraction that was trapped.

flark - A water-filled depression or pool that is elongate perpendicular to the prevailing slope. Flarks contain distinctive species assemblages, occur in linear or reticulate networks, and represent an important element of a patterned fen (aapamoor sensu Cajander 1913; strangmoor sensu Auer 1933).

geogenous - Water supplied from a mineral source (i.e. ground water, surface runoff).

hochmoor - A raised bog with ombrotrophic waters (Weber 1902). See bog above and ombrotrophic below.

Holocene - The last 10,000 to 12,000 years of geologic time, dating from the retreat of the last continental ice-sheets; also known as the post-glacial period.

humification - A measure of peat decomposition determined by measuring the concentration of humic materials extracted from a peat sample.

hydraulic conductivity - The constant of proportionality K in Darcy's law that defines the rate of flow through a porous medium:

$$q = K(H/L)$$

where H = difference between the 2 heads

L = length of the column containing the porous media

H/L = hydraulic gradient

internal water track - A zone of vegetation that contains fen-indicator species and minerotrophic waters and that is entirely surrounded by ombrotrophic bog vegetation.

lagg - A Swedish term to describe the margin of a peatland that receives runoff directly from the mineral uplands.

landform - Any feature of the earth's surface that has a consistent surface expression or internal structure. The vegetation landforms of boreal peatlands are vegetation patterns that recur across a geographic area as seen on aerial photographs. Peatland landforms often resemble fluvial landforms but are entirely composed of peat and living plant communities.

layering - The development of roots on the lower branches of trees where the branches come into contact with a wet moss substrate. Originally described by Cooper (1911) for black spruce growing on Isle Royale, Michigan.

minerotrophic - Plants that require waters that have been enriched by runoff or ground water derived from mineral soil. Minerotrophic indicator species are restricted to surface waters with a pH > 4.2 and a calcium concentration >2 mg/l. The term was originally coined by Du Rietz (1949) and popularized by Sjörs (1952, 1963, 1983).

mire complex - A term coined by Cajander (1913) to describe a peatland that contains large areas of both bog and fen.

muskeg - A term used to describe a black spruce and Sphagnum peatland in the boreal region of North America.

ombrotrophic - Plants that grow on a peatland that receives all its water and salts from the atmosphere (i.e. rain-nourished).

ovoid islands - A term used to describe large ovoid bogs that are completely surrounded by minerotrophic water tracks. The term was originally used by Heinzelman (1963) and Hofstetter (1969) to describe islands in the Red Lake peatland but later restricted to ombrotrophic landforms in the interior of North America by Glaser et al. (1981; Glaser 1983a; Glaser and Janssens 1986). Ovoid islands that contain permafrost have been referred to as peat plateaus by Brown (1967, 1968), Zoltai (1972), and Zoltai and Pollet (1983).

paludification - A term used by Cajander (1913) to describe the growth of peat over forest soils. Paludification has subsequently been used to describe the growth of peat over any upland soil such as the wet prairie soils that underlie the Red Lake peatland (Heinzelman 1963).

patterned fen - A minerotrophic peatland containing networks of pools (flarks) and ridges (strings) oriented perpendicular to the slope. See aapamoor and flark above and string and strangmoor below.

peat and peatland - A peatland is defined as any waterlogged area that contains at least 30 cm of peat in an undrained condition. Peat is an organic deposit that contains the dead remains of plants; it is distinguished from lake sediments by characteristic macro- or microfossils and from other terrestrial soils by the low percentage of mineral material. In this monograph boreal peatlands are distinguished by their boreal species assemblages and the characteristic landform patterns.

permafrost - Ground with temperatures continuously below freezing for many years.

piezometer - A field device for measuring hydraulic head. A piezometer consists of

a tube that is driven into the ground to a desired depth. The tube must be open to the atmosphere at top and to water flow at its base. The level of water in the tube is then an indicator of hydraulic head at the desired depth if the tube is sealed along its entire length and no seepage occurs down the outer edge of the tube.

poor fen - A type of fen vegetation that contains at least one minerotrophic indicator species and weakly geogenous surface waters. Originally described in Sweden by Sjörs (1952) as having a pH range of 3.8-5.7. The poor fens of Minnesota have a similar range in water chemistry (pH 4.2-5.8; calcium concentration 2-10 mg/l).

primary productivity - The total amount of organic matter synthesized or energy-fixed by photosynthesis in an ecosystem. Net primary productivity is the amount of energy remaining after plant respiration (Whittaker 1975).

rich fen - A type of fen vegetation that has a slightly higher range in pH (5.8-7.0) and calcium concentration (10-32 mg/l) than poor fens. In Minnesota the division between poor, rich, and extremely rich fens is not sharp but consists of a continuous range in variation.

Sphagnum lawn - A vegetation landform that forms a nonforested apron around the lower flanks of a raised bog (Glaser et al. 1981). The Sphagnum lawns become increasingly minerotrophic downslope and drain into internal water tracks on the largest bog complexes.

spring fen - A vegetation landform in peatlands that appears on aerial photographs as an anastomosing network of nonforested channels that drain through a swamp forest. This landform type occurs in discharge zones for ground water and has been previously described by Tarnocai (1974) and Glaser (1983c).

spring-fen mound - A vegetation landform in continuous areas of peatland that is similar to the spring fen but occurs on a raised mound of peat.

strangmoor - A term used by Auer (1920) to describe a patterned fen. Strangmoor,

which refers to an individual patterned fen differs slightly from the similar term aapamoor, which refers to a broader more regional vegetation unit.

string - A transverse peat ridge oriented perpendicular to the slope in a patterned fen. See flark and patterned fen above.

swamp - A forested peatland.

terrestrialization - A term used by Weber (1902) to describe the process by which a peatland spreads out over a lake.

tree islands - An area of forested peatland that is entirely surrounded by a water track. On aerial photographs these vegetation landforms have a streamlined shape giving rise to the term "island." In Minnesota the small tree islands have minerotrophic vegetation, whereas the larger (1-3 km long) ovoid islands have ombrotrophic bog vegetation. Heinselman (1963) originally used the term "teardrop island" to describe both the larger bog and smaller fen islands, whereas Glaser et al. (1981) restricted the term teardrop to just the fen islands. In view of the various shapes of minerotrophic tree islands in the interior of North America

the term teardrop tree island should perhaps be dropped as a useful term.

water track - A vegetation landform that represents a zone in which minerotrophic runoff is channeled across a mire expanse. Originally described in Sweden by Sjörs (1948) water tracks were identified in the Glacial Lake Agassiz region by Heinselman (1963). On aerial photographs water tracks appear as river-like landforms in which the vegetation patterns are streamlined in the direction of water flow. Featureless water tracks (sensu Glaser 1983a) are zones of nonforested sedge meadows that are sharply differentiated from a surrounding swamp forest. Patterned water tracks (sensu Glaser et al. 1981; Glaser 1983a), in contrast are distinguished by networks of pools and ridges oriented perpendicular to the slope (aapamoor) and by fields of tree islands oriented parallel to the slope. In each case the vegetation patterns indicate that drainage tends to converge into a central water track.

white-moss peat - Peat that is primarily composed of Sphagnum moss (Auer 1933).

xeromorphic - Structural and anatomical characteristics that are adaptations to arid habitats.

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APPENDIX A

VASCULAR PLANTS OF BOREAL PATTERNED PEATLANDS IN NORTHERN MINNESOTA

Scientific nomenclature follows Fernald (1970). Habitat notes are taken from Wheeler and Glaser 1982a, Wheeler (1983), Wheeler et al (1983), Glaser and Janecky (In prep.), and Glaser et al. (In prep.).

Habitat Designations

- 1 - Partially dried fen
- 2 - Drainage ditch
- 3 - Nonforested bog
- 4 - Forested bog
- 5 - Poor-fen margin
- 6 - Sphagnum lawn
- 7 - String
- 8 - Flark
- 9 - Tree island
- 10 - Spring-fen channel
- 11 - Spring-fen forest

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
Equisetaceae											
<u>Equisetum</u> <u>fluviatile</u>	-	X	-	-	X	-	-	X	-	-	-

(continued)

Appendix A. (Continued).

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
Osmundaceae											
<u>Osmunda cinnamomea</u>	-	-	-	-	-	-	-	-	X	X	-
Polypodiaceae											
<u>Athyrium filix-femina</u> var. <u>michauxii</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Dryopteris cristata</u>	-	-	-	-	-	-	X	-	X	-	-
<u>Dryopteris spinulosa</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Gymnocarpium dryopteris</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Thelypteris palustris</u> var. <u>pubescens</u>	-	-	-	-	X	X	X	X	X	-	-
Cupressaceae											
<u>Juniperus communis</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Thuja occidentalis</u>	-	-	-	-	-	-	-	-	X	-	-
Pinaceae											
<u>Abies balsamea</u>	-	-	-	-	-	-	-	-	X	-	X
<u>Larix laricina</u>	X	X	X	X	X	X	X	X	X	X	X
<u>Picea mariana</u>	X	X	X	X	X	X	X	X	X	X	X
<u>Pinus banksiana</u>	-	X	-	-	-	-	-	-	-	-	-
Apiaceae											
<u>Cicuta bulbifera</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Sium suave</u>	-	X	-	-	-	-	-	-	-	-	-
Apocynaceae											
<u>Apocynum cannabinum</u>	-	X	-	-	-	-	-	-	-	-	-
Araceae											
<u>Calla palustris</u>	-	-	-	-	-	-	-	X	X	-	-
Asclepiadaceae											
<u>Asclepias incarnata</u>	X	-	-	-	-	-	-	-	-	-	-
Asteraceae											
<u>Aster junciformis</u>	X	-	-	-	X	-	X	-	-	-	-
<u>Aster puniceus</u>	-	-	-	-	-	X	-	-	-	-	-
<u>Aster umbellatus</u> var. <u>pubens</u>	X	-	-	-	-	-	X	-	X	-	-
<u>Bidens cernua</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Bidens connata</u> var. <u>petiolata</u>	X	-	-	-	-	-	-	-	-	-	-

(continued)

Appendix A. (Continued).

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
<u>Cirsium arvense</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Cirsium muticum</u>	X	-	-	-	-	-	X	-	X	-	-
<u>Eupatorium maculatum</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Eupatorium perfoliatum</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Petasites sagittatus</u>	X	-	-	-	-	X	-	-	-	-	-
<u>Senecio pauperculus</u>	X	-	-	-	-	-	X	-	-	-	-
<u>Solidago canadensis</u>	X	-	-	-	-	-	X	-	-	-	-
<u>Solidago graminifolia</u>	X	-	-	-	-	-	-	-	X	-	-
<u>Solidago uliginosa</u>	-	-	-	-	X	X	X	X	X	-	-
<u>Sonchus arvensis</u>	-	-	-	-	-	-	-	-	X	-	-
<u>var. glabrescens</u>	-	-	-	-	-	-	-	-	X	-	-
Betulaceae											
<u>Alnus rugosa</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Betula papyrifera</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Betula pumila</u>	-	-	-	-	X	X	X	X	X	-	-
<u>var. glandulifera</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Betula X sandbergi</u>	-	X	-	-	-	-	-	-	-	-	-
Campanulaceae											
<u>Campanula aparinoides</u>	-	X	-	-	-	-	X	-	X	-	-
Caprifoliaceae											
<u>Lonicera oblongifolia</u>	-	X	-	-	-	-	-	-	X	-	-
<u>Lonicera villosa</u>	-	X	-	-	-	-	-	-	X	-	-
<u>var. solonis</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Virburnum trilobum</u>	-	X	-	-	-	-	-	-	-	-	-
Capryophyllaceae											
<u>Stellaria longifolia</u>	-	X	-	-	-	-	-	-	X	-	-
Cornaceae											
<u>Cornus canadensis</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Cornus rugosa</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Cornus stolonifera</u>	X	-	-	-	-	-	X	-	X	-	-
Cyperaceae											
<u>Carex aquatilis</u>	-	X	-	-	-	X	-	-	-	-	-
<u>var. altior</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Carex aurea</u>	-	2	-	-	-	-	-	-	-	-	-
<u>Carex bebbii</u>	-	2	-	-	-	-	-	-	-	-	-
<u>Carex brunnescens</u> var.	-	-	-	-	-	-	-	-	X	-	-
<u>sphaerostachya</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Carex buxbaumii</u>	X	-	-	-	-	-	-	X	-	-	-
<u>Carex canescens</u>	-	X	-	-	-	-	X	-	-	-	-
<u>var. disjuncta</u>	-	X	-	-	-	-	X	-	-	-	-

(continued)

Appendix A. (Continued).

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
<u>Carex cephalantha</u>	X	-	-	-	-	-	X	-	-	-	-
<u>Carex chordorrhiza</u>	-	-	-	-	X	X	X	X	X	-	-
<u>Carex diandra</u>	-	X	-	-	-	-	X	-	-	-	-
<u>Carex exilis</u>	-	-	-	-	X	-	X	-	-	-	-
<u>Carex interior</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Carex lacustris</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Carex lanuginosa</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Carex lasiocarpa</u>											
var. <u>americana</u>	X	X	-	-	X	-	X	X	-	-	-
<u>Carex leptalea</u>	-	-	-	-	-	-	-	X	X	-	-
<u>Carex timosa</u>	X	-	-	-	X	X	X	X	-	-	-
<u>Carex livida</u>											
var. <u>grayana</u>	X	-	-	-	X	X	-	X	-	-	-
<u>Carex oligosperma</u>	-	-	X	-	-	X	-	-	-	-	-
<u>Carex pauciflora</u>	-	-	X	X	X	-	-	-	-	-	-
<u>Carex paupercula</u>	-	-	-	X	X	-	-	-	X	-	-
<u>Carex projecta</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Carex pseudo-cyperus</u>	-	X	-	-	-	-	-	-	X	-	-
<u>Carex rostrata</u>											
var. <u>utriculata</u>	-	X	-	-	-	-	-	X	-	-	-
<u>Carex tenera</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Carex tenuiflora</u>	X	-	-	-	X	-	X	-	X	-	-
<u>Carex trisperma</u>	-	-	-	X	-	-	-	-	X	-	-
<u>Carex vaginata</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Carex viridula</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Cladium mariscoides</u>	-	-	-	-	-	-	-	X	-	X	-
<u>Dulichium arundinaceum</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Eleocharis compressa</u>	X	-	-	-	-	-	-	X	-	-	-
<u>Eleocharis rostellata</u>	-	-	-	-	-	-	-	-	-	X	-
<u>Eriophorum angustifolium</u>	X	-	-	-	-	-	-	X	-	-	-
<u>Eriophorum chamissonis</u>	X	-	-	-	X	-	-	-	-	-	-
<u>Eriophorum gracile</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Eriophorum spissum</u>	-	-	X	X	X	-	-	-	-	-	-
<u>Eriophorum tenellum</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Eriophorum virginicum</u>	-	-	X	X	X	-	-	-	-	-	-
<u>Eriophorum viridi-carinatum</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Rhynchospora alba</u>	X	-	-	-	X	-	-	X	-	-	-
<u>Rhynchospora capillacea</u>	-	-	-	-	-	-	-	-	-	X	-
<u>Rhynchospora fusca</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Scirpus atrocinctus</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Scirpus cespitosus</u>											
var. <u>callosus</u>	-	-	-	-	X	-	X	-	-	X	-
<u>Scirpus hudsonianus</u>	X	-	-	-	X	-	-	X	-	X	-
<u>Scirpus validus</u>	-	-	-	-	-	-	-	X	-	-	-

Droseraceae

<u>Drosera anglica</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Drosera intermedia</u>	X	-	-	-	X	-	-	X	-	-	-
<u>Drosera linearis</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Drosera rotundifolia</u>	-	-	X	X	-	-	X	-	X	-	-

(continued)

Appendix A. (Continued).

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
Ericaceae											
<u>Andromeda glaucophylla</u>	X	X	X	X	X	X	X	X	X	X	X
<u>Chamaedaphne calyculata</u>	X	X	X	X	X	X	X	X	X	X	X
<u>Gaultheria hispidula</u>	-	-	-	X	-	-	-	-	X	-	-
<u>Kalmia polifolia</u>	X	X	X	X	X	X	X	X	X	X	X
<u>Ledum groenlandicum</u>	X	X	X	X	X	X	X	X	X	X	X
<u>Vaccinium angustifolium</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Vaccinium myrtilloides</u>	-	-	X	X	-	-	-	-	X	-	-
<u>Vaccinium oxycoccos</u>	X	X	X	X	X	X	X	X	X	X	X
<u>Vaccinium vitis-idaea</u> var. <u>minus</u>	-	-	-	X	-	-	-	-	X	-	-
Gentianaceae											
<u>Gentiana rubricaulis</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Menyanthes trifoliata</u>	-	-	-	-	X	-	-	X	X	-	-
Hippuridaceae											
<u>Hippuris vulgaris</u>	-	X	-	-	-	-	-	-	-	-	-
Hypericaceae											
<u>Hypericum virginicum</u> var. <u>fraseri</u>	X	-	-	-	X	-	X	-	X	-	-
Iridaceae											
<u>Iris versicolor</u>	X	-	-	-	-	-	X	-	X	-	-
Juncaceae											
<u>Juncus alpinus</u> var. <u>rariflorus</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Juncus brevicaudatus</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Juncus canadensis</u>	X	-	-	-	-	-	-	X	-	-	-
<u>Juncus dudleyi</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Juncus nodosus</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Juncus pelocarpus</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Juncus stygius</u> var. <u>americanus</u>	-	-	-	-	-	-	-	X	-	-	-
Juncaginaceae											
<u>Scheuchzeria palustris</u> var. <u>americana</u>	-	-	-	-	X	X	-	X	-	-	-
<u>Triglochin maritima</u>	X	-	-	-	-	-	-	X	-	X	-
<u>Triglochin palustris</u>	-	-	-	-	-	-	-	-	-	X	-

(continued)

Appendix A. (Continued).

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
Laminaceae											
<u>Lycopus americanus</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Lycopus uniflorus</u>	X	-	-	-	-	-	X	-	X	-	-
<u>Scutellaria epilobiifolia</u>	-	X	-	-	-	-	X	-	X	-	-
Lentibulariaceae											
<u>Utricularia cornuta</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Utricularia intermedia</u>	-	X	-	-	X	-	-	X	-	-	-
<u>Utricularia minor</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Utricularia vulgaris</u>	-	X	-	-	-	-	-	-	-	-	-
Liliaceae											
<u>Maianthemum canadense</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Smilacina trifolia</u>	-	-	-	X	-	-	-	-	X	-	-
Lobeliaceae											
<u>Lobelia kalmii</u>	X	-	-	-	-	-	X	-	-	-	-
Loranthaceae											
<u>Arceuthobium pusillum</u>	-	-	-	X	-	-	-	-	-	-	-
Myricaceae											
<u>Myrica gale</u>	X	-	-	-	-	-	-	-	X	-	-
Nymphaeaceae											
<u>Nuphar variegatum</u>	-	X	-	-	-	-	-	-	-	-	-
Onagraceae											
<u>Epilobium angustifolium</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Epilobium leptophyllum</u>	X	-	-	-	-	-	X	-	X	-	-
Orchidaceae											
<u>Arethusa bulbosa</u>	-	-	-	-	-	-	X	-	-	-	-
<u>Cypripedium acaule</u>	-	-	-	X	-	-	-	-	X	-	-
<u>Habenaria lacera</u>	-	-	-	-	X	-	X	X	-	-	-
<u>Liparis loeselii</u>	-	-	-	-	-	-	X	-	-	-	-
<u>Liparis cordata</u>	-	-	-	X	-	-	-	-	-	-	-
<u>Malaxis unifolia</u>	-	-	-	-	-	-	X	-	-	-	-
<u>Pogonia ophioglossoides</u>	-	-	-	-	X	-	X	X	-	-	-
<u>Pogonia ophioglossoides</u> var. <u>albiflora</u>	-	-	-	-	-	-	-	X	-	-	-

(continued)

Appendix A. (Continued).

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
Poaceae											
<u>Agrostis scabra</u>	X	-	-	-	-	-	X	-	X	-	-
<u>Bromus ciliatus</u>	X	-	-	-	-	-	X	-	X	-	-
<u>Calamagrostis canadensis</u>	-	X	-	-	-	-	-	-	X	-	-
<u>Calamagrostis inexpansa</u>											
var. <u>brevior</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Calamagrostis neglecta</u>	-	X	-	-	-	-	-	-	X	-	-
<u>Cinna latifolia</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Glyceria borealis</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Glyceria striata</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Muhlenbergia glomerata</u>	X	-	-	-	-	-	X	-	X	-	-
<u>Phragmites communis</u>											
var. <u>berlandieri</u>	X	-	-	-	-	-	-	X	-	-	-
Polygonaceae											
<u>Polygonum sagittatum</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Rumex orbiculatus</u>	-	-	-	-	-	-	-	-	X	-	-
Primulaceae											
<u>Lysimachia terrestris</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Lysimachia thrysiflora</u>	X	-	-	-	-	-	-	-	X	-	-
<u>Trientalis borealis</u>	-	-	-	-	-	-	X	-	X	-	-
Pyrolaceae											
<u>Monotropa uniflora</u>	-	-	-	X	-	-	-	-	X	-	-
<u>Pyrola assarifolia</u>											
var. <u>purpurea</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Pyrola secunda</u>											
var. <u>obtusata</u>	-	-	-	-	-	-	-	-	X	-	-
Ranunculaceae											
<u>Caltha palustris</u>	X	-	-	-	-	-	-	-	X	-	-
<u>Ranunculus gmelini</u>											
var. <u>hookeri</u>	-	X	-	-	-	-	-	-	X	-	-
Rhamnaceae											
<u>Rhamnus alnifolia</u>	X	-	-	-	-	-	X	-	X	-	-
Rosaceae											
<u>Amelanchier humilis</u>											
var. <u>compacta</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Pyrus melanocarpa</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Geum aleppicum</u>											
var. <u>strictum</u>	X	-	-	-	-	-	-	-	X	-	-
<u>Potentilla fruticosa</u>	X	-	-	-	X	-	X	-	-	-	-

(continued)

Appendix A. (Continued).

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
<u>Potentilla palustris</u>	-	X	-	-	X	-	-	X	X	-	-
<u>Rubus acaulis</u>	X	-	-	-	-	-	X	-	X	-	-
<u>Rubus pubescens</u>	X	-	-	-	-	-	X	-	X	-	-
<u>Rubus strigosus</u>	X	-	-	-	-	-	-	-	X	-	-
<u>Spirea alba</u>	-	X	-	-	-	-	-	-	-	-	-
Rubiaceae											
<u>Galium labradoricum</u>	X	-	-	-	X	-	X	-	X	-	-
Salicaceae											
<u>Populus balsamifera</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Populus tremuloides</u>	-	X	-	-	-	-	-	-	X	-	-
<u>Salix bebbiana</u>	X	-	-	-	-	-	-	-	X	-	-
<u>Salix candida</u>	X	-	-	-	-	-	-	-	X	-	-
<u>Salix discolor</u>	X	-	-	-	-	-	-	-	X	-	-
<u>Salix gracilis</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Salix interior</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Salix lucida</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Salix pedicellaris</u>											
var. <u>hypoglauca</u>	X	-	-	-	X	-	X	X	-	-	-
<u>Salix planifolia</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Salix pyrifolia</u>	X	X	-	-	-	-	-	-	X	-	-
<u>Salix serissima</u>	-	X	-	-	-	-	-	-	-	-	-
Sarraceniaceae											
<u>Sarracenia purpurea</u>	X	X	X	X	X	X	X	X	X	X	X
Saxifragaceae											
<u>Parnassia glauca</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Parnassia palustris</u>											
var. <u>neogaea</u>	X	-	-	-	X	-	-	X	-	-	-
Scrophulariaceae											
<u>Gerardia paupercula</u>											
var. <u>borealis</u>	X	-	-	-	-	-	-	-	-	-	-
<u>Mimulus ringens</u>	-	X	-	-	-	-	-	-	-	-	-
<u>Pedicularis lanceolata</u>	X	-	-	-	X	-	X	X	-	-	-
Sparganiaceae											
<u>Sparganium minimum</u>	-	X	-	-	-	-	-	-	X	-	-
Typhaceae											
<u>Typha latifolia</u>	-	X	-	-	-	-	-	X	X	-	-

(continued)

Appendix A. (Concluded).

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
Violaceae											
<u>Viola incognita</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Viola pallens</u>	X	-	-	-	X	-	X	-	X	-	-
<u>Viola nephrophylla</u>	X	-	-	-	-	-	-	-	-	-	-
Xyridaceae											
<u>Xyris montana</u>	-	-	-	-	-	-	-	X	-	-	-
Zosteraceae											
<u>Potamogeton natans</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Potamogeton gramineus</u>	-	X	-	-	-	-	-	X	X	-	-

APPENDIX B

BRYOPHYTE FLORA OF BOREAL PATTERNED PEATLANDS IN NORTHERN MINNESOTA

Data from this appendix is derived primarily from the Red Lake peatland (Janssens and Glaser 1986), Lost River peatland (Janssens & Glaser 1983a,b; Janssens unpubl. MS.; Glaser et al. In prep.).

Habitat Designations

- 1 - Partially dried track
- 2 - Drainage ditch
- 3 - Nonforested bog
- 4 - Forested bog
- 5 - Poor-fen margin
- 6 - Sphagnum lawn
- 7 - Flark
- 8 - String
- 9 - Tree island
- 10 - Spring-fen channel
- 11 - Spring-fen forest

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
<u>Amblystegium serpens</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Aneura pinguis</u>	-	-	-	-	-	-	-	X	X	-	-
<u>Aulacomnium palustre</u>	-	-	X	X	-	-	-	-	-	X	X
<u>Brachythecium curtum</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Brachythecium salebrosum</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Bryum pseudotriquetrum</u>	-	-	-	-	-	-	-	X	X	X	X
<u>Callicladium haldanianum</u>	-	-	-	X	-	-	-	-	X	-	-
<u>Calliergon aptonianum</u>	-	-	-	-	-	-	-	-	-	-	X

(continued)

Appendix B. (Continued).

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
<u>Calliergon cordifolium</u>	-	-	-	-	-	-	-	-	X	-	X
<u>Calliergon giganteum</u>	-	-	-	-	-	-	-	-	X	-	X
<u>Calliergon richardsonii</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Calliergon stramineum</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Calliergon trifarium</u>	-	-	-	-	-	-	-	-	-	X	-
<u>Calliergonella cuspidata</u>	-	-	-	-	-	-	X	X	X	-	-
<u>Calypogeia integristipula</u>	-	-	X	X	-	-	-	-	-	-	X
<u>Campylium polygamum</u>	-	-	-	-	-	-	X	-	X	-	-
<u>Campylium hispidulum</u>	-	-	-	-	-	-	-	-	-	X	X
<u>Campylium stellatum</u>	-	-	-	-	-	-	X	X	X	-	-
<u>Cephalozia bicuspidata</u>											
<u>var. bicuspidata</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Cephalozia connivens</u>	-	-	-	-	-	-	-	-	X	-	X
<u>Cephalozia connivens</u>											
<u>var. connivens</u>	-	-	X	X	-	-	-	-	X	-	-
<u>Cephalozia connivens</u>											
<u>var. compacta</u>	-	-	X	X	-	-	-	-	-	-	-
<u>Cephalozia preniceps</u>											
<u>var. sphagnum</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Cephalozia elachista</u>	-	-	X	X	-	-	-	-	X	-	-
<u>Cinclidium stygium</u>	-	-	-	-	-	-	-	-	-	X	X
<u>Cladopodiella fluitans</u>	-	-	-	-	-	X	-	-	X	-	-
<u>Climacium dendroides</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Dicranum flagellare</u>	-	-	X	X	-	-	-	-	-	-	-
<u>Dicranum montanum</u>	-	-	-	X	-	-	-	-	-	-	X
<u>Dicranum ontariense</u>	-	-	X	X	-	-	-	-	-	-	-
<u>Dicranum polysetum</u>	-	-	X	X	-	-	-	-	-	-	-
<u>Dicranum undulatum</u>	-	-	X	X	-	-	-	-	-	-	-
<u>Drepanocladus aduncus</u>	-	-	-	-	-	-	X	X	-	-	-
<u>Drepanocladus exannulatus</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Drepanocladus fluitans</u>	-	-	-	-	-	-	X	X	-	-	-
<u>Drepanocladus revolvens</u>	-	-	-	-	-	-	-	-	X	X	X
<u>Drepanocladus uncinatus</u>	-	-	X	X	-	-	-	-	-	-	-
<u>Eurhynchium pulchellum</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Fissidens adiantoides</u>	-	-	-	-	-	-	-	-	X	X	X
<u>Fissidens cristatus</u>	-	-	-	-	-	-	X	X	-	-	-
<u>Fossombronia foveolata</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Hylocomnium splendens</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Hypnum linbergii</u>	-	-	-	-	-	-	-	-	X	-	X
<u>Hypnum pratense</u>	-	-	X	X	-	-	-	-	X	-	X
<u>Hypnum fertile</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Lepidozia reptans</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Leptodictyum riparium</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Lophocolea heterophylla</u>	-	-	-	-	-	-	X	-	X	X	X
<u>Lophocolea minor</u>	-	-	X	X	-	-	-	-	-	-	-
<u>Lophozia rutheana</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Meesia triquetra</u>	-	-	-	-	-	-	-	X	-	-	-
<u>Moerkia hibernica</u>	-	-	-	-	-	-	-	-	-	X	X
<u>Mylia anomala</u>	-	-	X	X	-	-	-	-	-	-	X
<u>Oncophorus virens</u>	-	-	X	X	-	-	-	-	-	-	-
<u>Pellia epiphylla</u>	-	-	-	-	-	-	X	X	-	-	-
<u>Plagiothecium laetum</u>	-	-	X	X	-	-	-	-	-	-	-

(continued)

Appendix B. (Concluded).

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
<u>Plagiothecium denticulatum</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Plagiomnium ellipticum</u>	-	-	-	-	-	-	-	-	X	-	X
<u>Pleurozium schreberi</u>	-	-	X	X	-	-	-	-	X	-	X
<u>Pohlia nutans</u>	-	-	X	X	-	-	-	-	X	-	-
<u>Polytrichum commune</u>	-	-	X	X	-	-	-	-	-	-	-
<u>Polytrichum strictum</u>	-	-	X	X	-	X	-	-	X	-	X
<u>Ptilidium ciliare</u>	-	-	-	-	-	-	X	-	-	-	-
<u>Ptilidium pulcherrimum</u>	-	-	X	X	-	-	-	-	X	-	X
<u>Ptilium crsita-castrensis</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Pylaisiella polyantha</u>	-	-	X	X	-	-	-	-	-	-	X
<u>Pylaisiella selwynii</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Rhizomnium gracile</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Rhizomnium pseudopunctatum</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Ricardia latrifrons</u>	-	-	-	-	-	-	-	-	-	X	X
<u>Rhytidiadelphus triquetrus</u>	-	-	-	-	-	-	-	-	-	-	X
<u>Scapania irregua</u>	-	-	-	-	-	-	X	-	X	-	-
<u>Scorpidium scorpiodes</u>	-	-	-	-	-	-	X	-	X	X	X
<u>Sphagnum angustifolium</u>	-	-	X	X	-	X	-	-	X	-	X
<u>Sphagnum centrale</u>	-	-	X	X	-	-	-	-	X	-	-
<u>Sphagnum contortum</u>	-	-	-	-	-	-	X	-	-	-	-
<u>Sphagnum fallax</u>	-	-	X	X	-	X	-	-	X	-	-
<u>Sphagnum fimbriatum</u>	-	-	-	-	-	-	X	-	-	-	-
<u>Sphagnum flexuosum</u>	-	-	-	-	-	X	-	-	-	-	-
<u>Sphagnum fuscum</u>	-	-	X	X	-	-	-	X	-	-	X
<u>Sphagnum magellanicum</u>	-	-	X	X	-	X	-	-	X	-	X
<u>Sphagnum majus</u>	-	-	-	-	-	X	-	-	-	-	-
<u>Sphagnum nemoreum</u>	-	-	X	X	-	-	-	-	-	-	X
<u>Sphagnum obtusum</u>	-	-	-	-	-	-	-	X	X	-	-
<u>Sphagnum papillosum</u>	-	-	X	X	-	X	-	-	X	-	-
<u>Sphagnum platyphyllum</u>	-	-	-	-	-	-	X	-	-	-	-
<u>Sphagnum riparium</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Sphagnum rubellum</u>	-	-	X	X	-	X	-	-	-	-	X
<u>Sphagnum russowii</u>	-	-	X	X	-	-	-	-	X	-	X
<u>Sphagnum squarrosum</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Sphagnum subfulvum</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Sphagnum subsecundum</u>	-	-	-	-	-	-	X	-	X	-	-
<u>Sphagnum teres</u>	-	-	X	X	-	-	-	-	X	-	-
<u>Sphagnum warnstorffii</u>	-	-	-	-	-	-	-	-	X	-	X
<u>Tetraphis pellucida</u>	-	-	X	X	-	-	-	-	X	-	-
<u>Thuidium recognitum</u>	-	-	-	-	-	-	-	-	X	-	-
<u>Tomenthypnum falcifolium</u>	-	-	-	-	-	-	-	-	X	-	X
<u>Tomenthypnum nitens</u>	-	-	-	-	-	-	-	X	X	X	X

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