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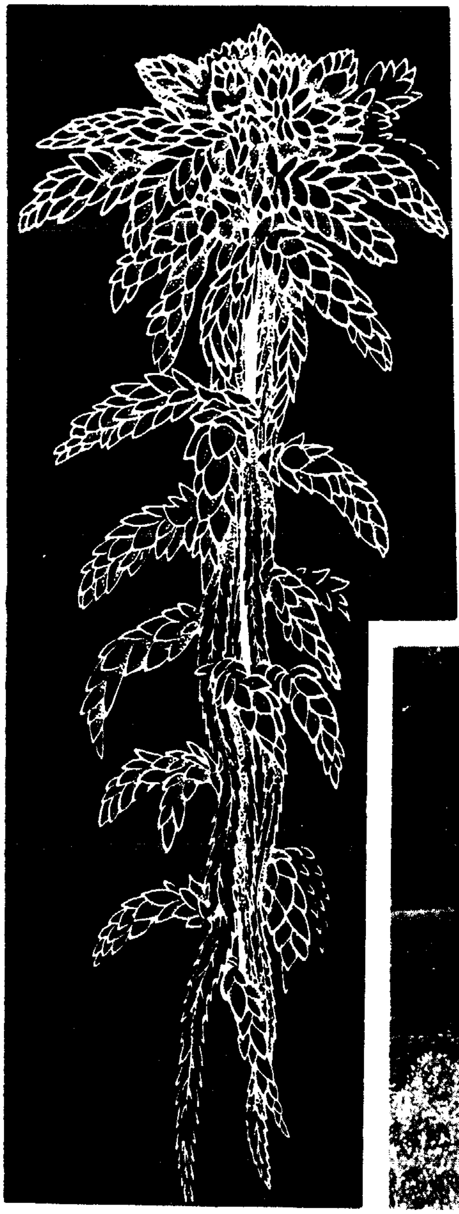

# THE ECOLOGY OF PEAT BOGS OF THE GLACIATED NORTHEASTERN UNITED STATES:

# A COMMUNITY PROFILE

Fish and Wildlife Service

U.S. Department of the Interior U.S. Environmental Protection Agency

U.S. FISH & WILDLIFE SERVICE
National Wetlands Research Center
NASA - Slidell Computer Complex
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Slidell, LA 70458

Cover:

Illustration of *Sphagnum magellanicum* by Mary Jane Spring.

The photo illustrates a pond border bog in Vermont with a well-developed floating mat.

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# THE ECOLOGY OF PEAT BOGS OF THE GLACIATED NORTHEASTERN UNITED STATES: A COMMUNITY PROFILE

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# PREFACE

This monograph on the ecology of peat bogs of the glaciated Northeastern United States 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 peat bogs of the glaciated portion of the Northeastern United States and to describe the ecological structure and functioning of these freshwater wetlands.

The glaciated portion of the Northeastern United States extends from the Canadian border in the north to the Pocono Mountains of Pennsylvania in the south. Peat bogs may be found scattered throughout this region where conditions favor peat development.

Peat bogs depend on acidic, nutrient-poor water for development and usually occur in areas underlain by sand, gravel, or nutrient-poor glacial till. The hydrologic characteristics and chemical composition of bog water influence both nutrient cycling and plant community development within bogs.

This profile is intended to provide a useful reference to the scientific information available for peat bogs of the glaciated Northeastern United States. The profile includes a description of the distribution of peatlands and the various types of peatlands. The authors also discuss the physical, chemical, and hydrologic properties of peat bogs as well as energy flow and nutrient fluxes associated with peat bogs. Several chapters are devoted to the biotic communities of peat bogs, human disturbances, and recommendations for future research.

Any questions or comments about or requests for this publication should be directed to:

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Slidell, Louisiana 70458

# CONVERSION TABLE

Metric to U.S. Customary

| Multiply | By | To Obtain |
|---|---|---|
| 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

| Multiply | By | To Obtain |
|---|---|---|
| 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) | 0.00045 | 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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# INTRODUCTION

Peat bogs support vegetation strikingly different from that of uplands as well as that of other wetlands. Conifers, ericaceous shrubs and peat mosses (Sphagnum spp.) are major components of the vegetation of bogs and usually determine their general appearance. Their superficial resemblance tends to hide the differences among them. Therefore, it is not always recognized that the conditions in peat bogs and the processes that maintain them can vary greatly.

This community profile describes the peat bogs of the glaciated northeastern United States. Information on these peat bogs is fragmented and major gaps in our knowledge about them exist. This applies to virtually all aspects of bogs. This publication synthesizes our knowledge about the vegetation, fauna, habitat conditions and ecological processes in these wetlands. Because of limited published information on peat bogs of the Northeast we included much unpublished data, especially on the vegetation. Regarding other aspects of these bogs, it was necessary to extrapolate from information on peatlands outside the region. Peat differs in many respects from other soils. For this reason, its special properties and their effect on retention, movement, and chemistry of the bog water are discussed. This knowledge is essential for understanding the present vegetation pattern, but it also provides an insight into the differences among bogs and the changes that can be anticipated as a result of disturbance in a peat bog or the surrounding uplands.

All bogs did not form in the same way. Their development is clearly expressed in their stratigraphy. However, the present conditions rather than their history of development control the vegetation, nutrient cycling, and water movement and whatever depends on them. Therefore, this community profile focuses on conditions and processes in existing bogs and deals only peripherally with development and peat stratigraphy, and only insofar as they affect present processes or further bog development.

Continued urbanization and recreational developments infringe upon many peat bogs. In recent years, there has also been a renewed interest in peat as an energy source, and several peat inventories have been carried out (Cameron 1970, 1974, 1975; Cameron and Anderson 1980; Cameron et al. undated). Research on peatlands has not kept up with this. This profile provides background information that can help us predict the effect of changes in the landscape and in land use, as well as explain changes taking place in peat bogs.

The nomenclature in this volume follows Fernald (1950) for vascular plants; Stotler and Crandall-Stotler (1977) for liverworts; Hale and Culberson (1966) for lichens; Crum et al. (1973) for mosses, except for Dicranum bergeri Bland. and D. leioneuron Kindb.; Andrus (1980) for Sphagnum, except for Sphagnum pulchricoma P. Beauv; Jones et al. (1982) for mammals; American Ornithologist's Union (1983) for birds; and Collins et al. (1982) for amphibians and reptiles.

# CHAPTER 1. DEFINITION AND GENERAL DESCRIPTION

## 1.1 DEFINITION OF PEAT BOGS AND RELATED PEATLANDS

The term "bog" in this community profile refers to nutrient-poor, acid peatlands with a vegetation in which peat mosses (Sphagnum spp.), ericaceous shrubs, and sedges (Cyperaceae) play a prominent role. Conifers, such as black spruce (Picea mariana), white pine (Pinus strobus), and larch (Larix laricina) are often present. The former can dominate the vegetation of some peat bogs.

Water is critical for the development and maintenance of all wetlands. Peatlands can be divided on the basis of the source of the water into wetlands receiving only rain water and snow (ombrotrophic bogs) and those influenced also by water that has been in contact with the mineral soil (minerotrophic peatlands). The water chemistry of the latter can vary greatly, and minerotrophic peatlands include a wide range of wetlands. Hydrologically and ecologically, the distinction between ombrotrophic and minerotrophic peatlands is important, especially in dealing with nutrient-poor peatlands. The boundary between these two types of peatlands, the mineral soil water limit (Du Rietz 1954), is usually marked by the appearance of more nutrient-demanding species. In recent years, there has been a tendency among peatland researchers to follow the Scandinavian practice of restricting the terms "bog" and "fen" to ombrotrophic and minerotrophic peatlands, respectively. This restrictive use of the term bog is unfortunate when dealing with vegetation, because weakly minerotrophic fens have a floristic composition and structure very similar to the vegetation of ombrotrophic peatlands, whereas floristically they have little in common with nutrient-rich fens (Malmer 1985).

In this community profile, "bogs" are peatlands with a well-developed moss carpet dominated by Sphagnum. Therefore, bogs include ombrotrophic and minerotrophic wetlands that are acid and nutrient-poor, and in which peat has accumulated. This terminology is also more in keeping with the conventional use of the word and with the definition in Webster's Dictionary, where a bog is described as "wet spongy ground, especially a poorly drained usually acid area rich in plant residues, frequently surrounding a body of open water, and having a characteristic flora of sedges, heaths, and Sphagnum."

Peatlands are landforms as well as vegetation types. As a landform, peatlands are complexes of plant communities. All peatlands include minerotrophic sites, at least in their margins. Therefore, the distinction between ombrotrophic and minerotrophic peatlands is of no value in dealing with peatlands as landscape units. A practical subdivision of peatlands as landforms can be based on the nature of the water that controls their development. This was originally suggested by von Post and Granlund (1926) for south Swedish peat deposits, and subsequently more clearly defined by Sjörs (1948). They distinguished ombrogenous, topogenous, limnogenous and soligenous peatlands. The major differences are shown in Figure 1.

Precipitation controls the development of ombrogenous peatlands. They are restricted to humid, temperate climates where peat can accumulate independently of ground water or seepage water. Topogenous peatlands develop in topographic positions where water accumulates, and they are maintained by a permanent ground-water table. These peatlands can occur under a wide range of climatic conditions from the tropics to the arctic. Limnogenous peatlands develop along lakes and slow-flowing

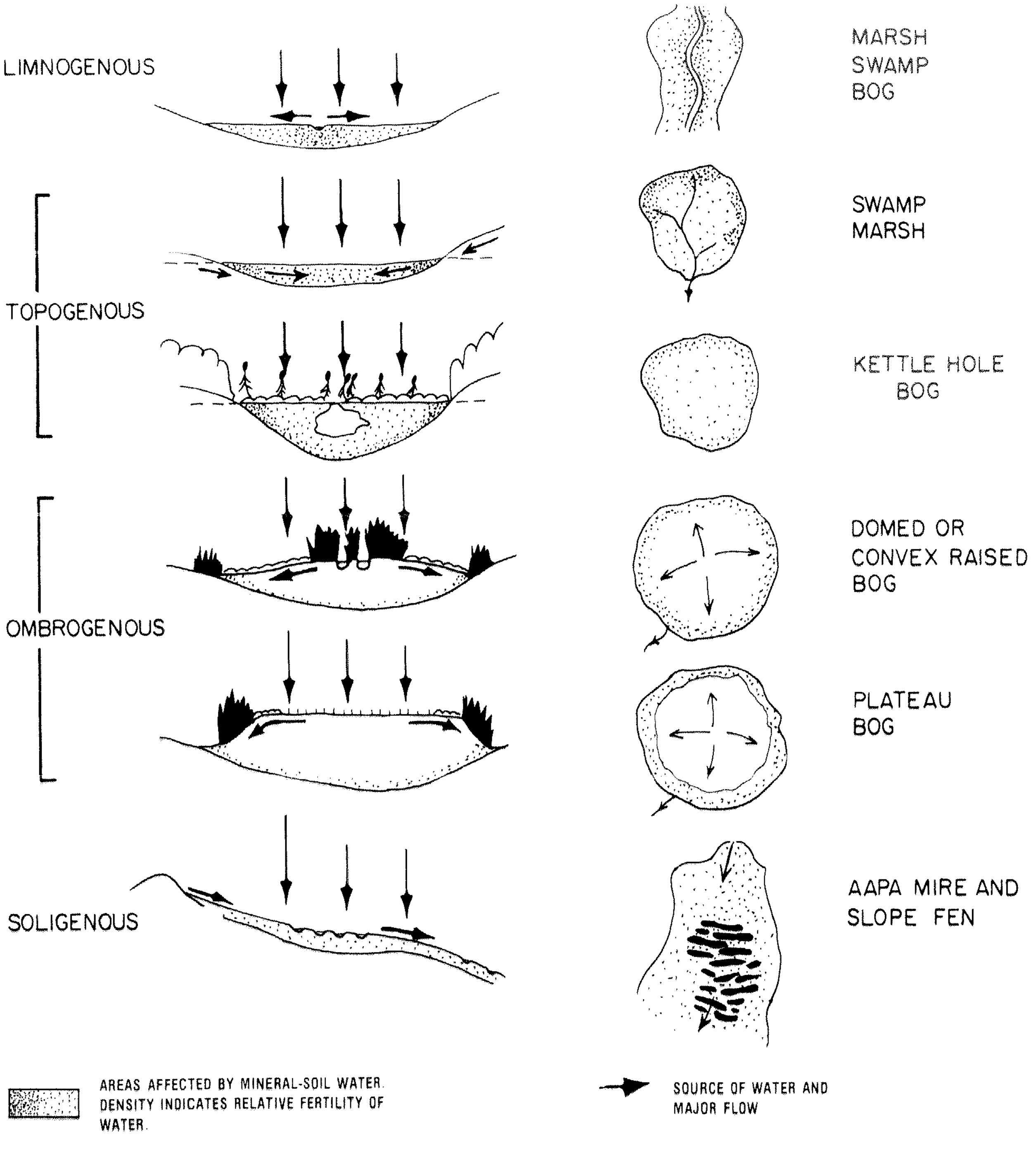


**Figure 1.** Major types of peatlands in relation to source of water. Note differences in the direction of water flow. Blanket bog, another ombrogenous peatland type, is not included.

streams under a wide variety of climatic conditions. Soligenous peatlands depend on a reliable source of minerotrophic seepage water. They are characterized by water that seeps through or over the surface peat and are most common in regions with a large surplus of precipitation over evapotranspiration. Therefore, soligenous peatlands become less common south of the zone with ombrogenous bogs, but some can be found even in Southern New England.

## 1.2 GEOGRAPHIC AND ECOLOGICAL RANGE OF PEAT BOGS INCLUDED

The southern limit of ombrogenous bogs in eastern North America is located within the Northern Hardwood Forest Zone (Figure 2). This boundary does not correspond with any clear vegetation boundary on upland sites, because the length and warmth of the vegetative season are the primary climatic controls on the zonation in the forest vegetation, whereas the type of bog development is determined primarily by the humidity of the climate (Eurola and Ruuhijärvi 1961; Damman 1979a). Raised bogs, including plateau and convex domed bogs, occur north of the ombrogenous bog limit (Damman 1977, 1978b; Damman and Dowhan 1981; Worley 1981), and soligenous bogs become common in the hilly, northwestern part of Maine (Sorensen 1986).

Geographically, this community profile includes New England, northeastern Pennsylvania, and the adjacent parts of New York. The Adirondacks are not included, although much of this information will also apply to bogs in that area. Ecologically, this profile deals mostly with oligotrophic Sphagnum-dominated bogs. Bog-like vegetation on mineral soil or on peat less than 30 cm deep is not included, and neither are the soligenous fens north of the southern limit of ombrogenous bogs (Figure 2).

This community profile focuses primarily on the topogenous and limnogenous peat bogs that occur throughout the glaciated northeastern United States. The vegetation of these bogs is influenced by minerotrophic water, although this water is nutrient-poor. The degree of minerotrophy varies spatially within a bog as well as seasonally. Dilution with rain water can cause conditions approaching ombrotrophy on the bog surface of the central part of a topogenous bog. However, truly ombrotrophic conditions do not appear to occur in these bogs.

The vegetation of the major types of raised bogs in the Northeast (Figure 3) is briefly described, mostly to emphasize how oligotrophic bogs differ and to provide an understanding of the geographical changes within this region. The hydrology of ombrogenous bogs differs fundamentally from that of topogenous and limnogenous bogs (Figure 1). It is discussed only peripherally here; more detailed information can be found in Ivanov (1975), Ingram (1982, 1983), Damman (1986a).

## 1.3 DISTRIBUTION IN THE LANDSCAPE

Peat bogs depend on acidic, nutrient-poor water. In northern and northeastern Maine they can be found in various landscapes, but south of the limit of ombrogenous bogs they are restricted primarily to two types of landscapes:

(1) Areas underlain by sands and gravels, occurring mainly in valleys and on coastal plains. These deposits are mostly of glaciofluvial origin, but locally they include marine and aeolian materials. Bogs occupy some of the depressions and kettle holes of this landscape. Their development is controlled by a water table maintained within these deposits.

(2) Areas underlain by glacial tills derived from acidic rocks such as gneiss, schist, sandstone, and granite. Here, bogs develop in depressions with a water table perched on compact till or bedrock. Conditions favorable for their development can occur at any elevation, including hill tops with depressional sites. In till landscapes, peat bogs are rare or absent in the larger valleys because the water is usually enriched by nutrients leached from the uplands.

Peat bogs develop also along lake shores and slow-flowing streams if the water is nutrient poor.

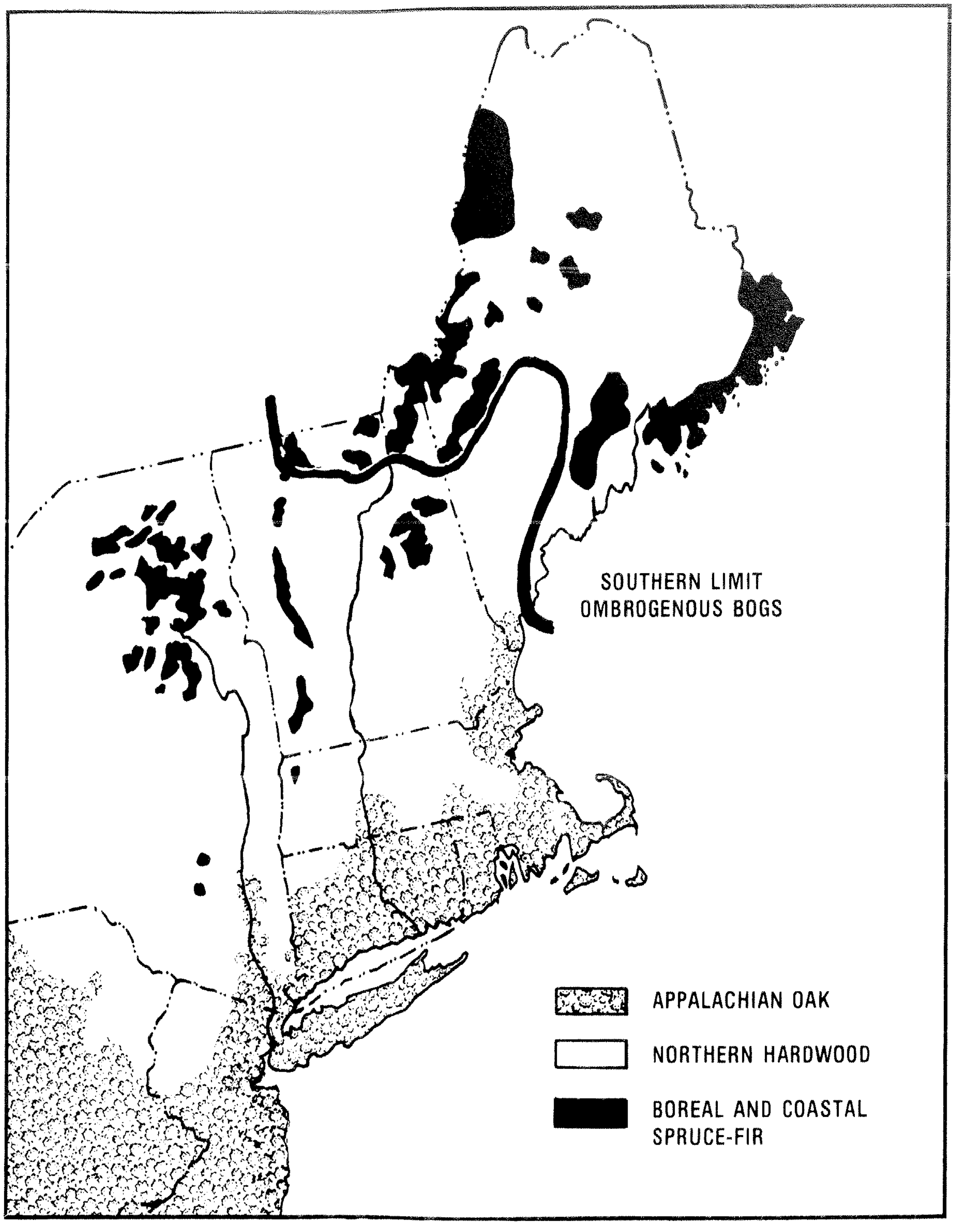


Figure 2. Southern boundary of ombrogenous bogs in relation to the major forest vegetation zones of the region.

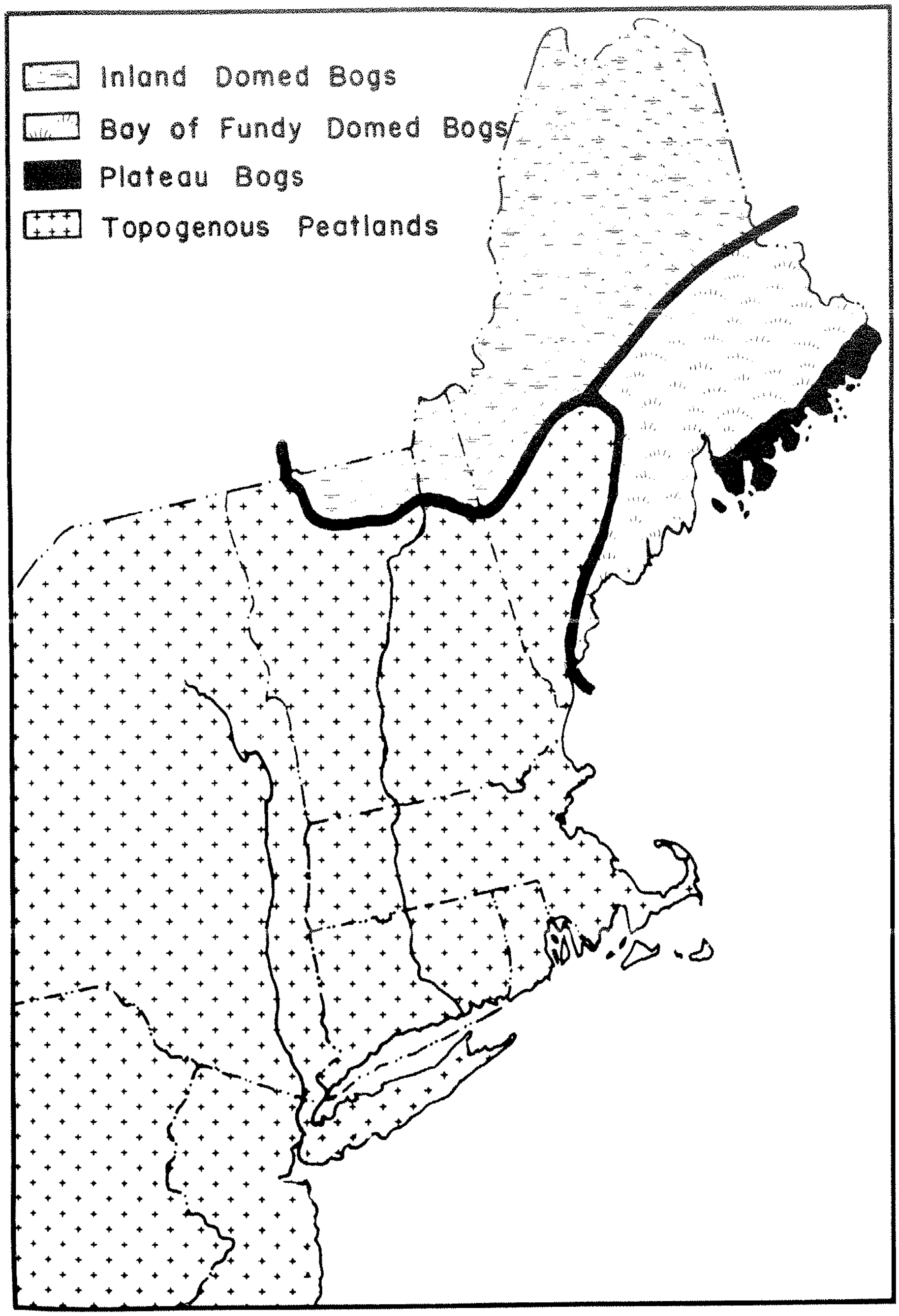


Figure 3. Major peatland zones in the northeastern United States.

## 1.4 MAJOR PHYSIOGNOMIC TYPES

The bogs in this community profile include five major physiognomic vegetation types. Three of these make up most of the bog vegetation:

Dwarf-shrub bogs. Dwarf-shrub bogs often contain scattered larch (*Larix laricina*) or black spruce (*Picea mariana*). The dwarf-shrub layer is dominated by evergreen ericaceous shrubs. According to the U.S. Fish and Wildlife Service (FWS) wetland classification (Cowardin et al. 1979) these bogs are classified as Palustrine, broad-leaved evergreen, scrub-shrub wetlands, saturated with fresh-acid water. In most of the region, leather leaf (*Chamaedaphne calyculata*) is commonly the dominant dwarf-shrub, and the soils are usually medifibrists or hemists of variable depth. Dwarf-shrub bogs occur mostly in glacial kettle holes, as quaking bogs along the margins of oligotrophic ponds, and along slow-flowing, oligotrophic brooks. In the northern part of the region and at higher elevations, sheep laurel (*Kalmia angustifolia*) is the dominant evergreen dwarf-shrub in most bogs. In this case the soils are often sphagnofibrists.

Tall-shrub thicket bogs. Tall-shrub thicket bogs are dominated by deciduous ericaceous shrubs, usually with black spruce, larch and a few red maples (*Acer rubrum*). According to the FWS wetland classification (Cowardin et al. 1979) these bogs are classified as Palustrine, broad-leaved deciduous, scrub-shrub wetlands, saturated with fresh-acid water. They occur on medifibrists or hemists. The dominant high shrub is highbush blueberry (*Vaccinium corymbosum*); winterberry (*Ilex verticillata*) can dominate on shallower peat and near the bog border. These thickets occur on organic soil with strong water level fluctuation and on the highest parts of quaking bog mats. This is a common bog vegetation in the southern part of the region but is absent in the northernmost part.

Forests. The typical bog forests are dominated by conifers, especially black spruce, with ericaceous shrubs and dwarf shrubs. They are classified as Palustrine, needle-leaved evergreen, forested wetlands (Cowardin et al. 1979). A variety of forested wetlands can occur on minerotrophic sites, especially in the bog border.

Moss carpets and communities with an abundance of Cyperaceae (lawns) are two other physiognomic types occurring commonly in peat bogs. Both are classified as Palustrine, moss-lichen wetlands (Cowardin et al. 1979), but some of the Cyperaceae-dominated communities on minerotrophic sites would be classified as Palustrine, persistent emergent wetlands. The bog lawns cover extensive areas only in the bogs of northern coastal Maine and in Canadian bogs. Moss carpets, including mud-bottoms, occur in most bogs but mostly as small, isolated patches.

## 1.5 PEAT BOGS AS LANDFORMS

The bog landforms recognized here show basic differences in their development, vegetation zonation, and hydrology. A classification like this is necessary for a discussion of processes maintaining or changing these landscape units. All can occur as distinct, clearly recognizable landforms. Nevertheless, it should be realized that not every peatland will fit into one category. Some are composites of two landforms, e.g., a perched water bog may adjoin a lake-fill bog. In other cases, two types may grade into each other. For instance, the water movement through a soligenous mire can become so insignificant that it cannot be distinguished from a perched water bog with stagnant water.

### 1.5.1. Peat Bog-Lake Systems

These include topogenous peat bogs resulting from primary succession in oligotrophic lakes, where lake water does not flood the bog surface. They represent the classical example of hydrarch succession leading to bog formation. These bogs develop most commonly in kettle-hole lakes in glacio-fluvial deposits, but they can be associated with other lakes that have nutrient-poor water. Conditions in the bog change drastically after the bog mat covers the lake. Therefore, bogs that have not completely filled in a pond need to be discussed separately. Three types are recognized (Figure 4).

Lake-fill bogs. These represent the final stage of filling in of a kettle-hole or other oligotrophic lake. Included here are those peat bogs without a remnant of the original pond in the central part of the bog. The vegetation of the bog center (Figure 5) can range from a forest to a dwarf shrub vegetation, and the bog surface can be grounded or quaking.

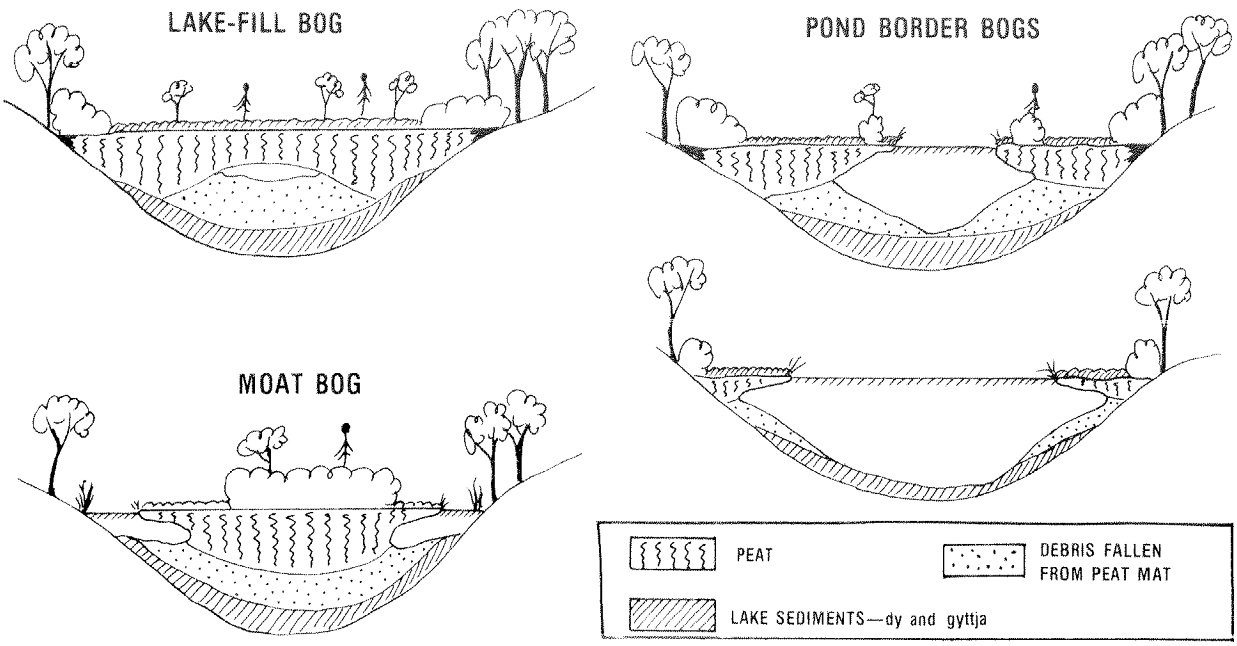


Figure 4. Types of peat bog-lake systems common in the region. Kratz and DeWitt (1986) provide further detail on the relation between peat types and lake-fill succession. The peat stratigraphy of moat bogs is poorly known. The diagram shows the probable sequence of peat types.

Figure 5. Bog vegetation in center of former lake. The vegetation is dominated by *Chamaedaphne calyculata* with scattered larch, pitch pine, white pine, and red maple trees.

Moat bogs. These bogs differ from the lake-fill bogs in that a well-developed moat (Figure 6) separates the bog from the uplands. This moat is filled with water most of the time. The bog adjacent to the moat is usually a quaking, floating mat. The central part of the bog is grounded and can be forested or have a dwarf shrub vegetation.

Pond-border bogs. These vary from narrow zones along the pond margin to peat bogs that have almost filled a lake (Figures 7 and 8). The latter differ from the lake-fill bogs in that a part of the original pond is still present. The bog mat is floating near the center but grounded along the landward side. The vegetation of the floating mat adjacent to the lake is usually enriched by lake water and differs from that of the remainder of the bog mat.

### 1.5.2. Perched Water-Peatland Systems

These occur in depressions and in valleys that have a perched water table that maintains conditions suitable for peat bog development. They can be associated with lakes, but their present development is not controlled by a lake. These peat bogs occur mostly in areas with shallow till or with compacted till. They receive water from the surrounding uplands; this water either seeps through the bog or stagnates in the basin. They can occur also in valleys and flats underlain by sands and gravels if water is perched on interbedded silt and clay layers, or if a reliable source of oligotrophic water is available.

Conditions in these peatland systems vary and depend mostly on the magnitude of the water-level changes in the basin, the

**Figure 6. Moat of moat bog during period of low water in late fall. The tussocks in the moat are *Carex stricta*; stems of *Typha angustifolia* are visible, especially in the background. In the far background at the bog side of the moat is a tall-shrub thicket with *Vaccinium corymbosum* and *Rhododendron viscosum* (Congamond Lake Bog, CT).**

Figure 7. Pond border bog with narrow strip of bog vegetation along opposite shore of lake (Gushee Pond, MA).

Figure 8. Pond border bog with well-developed floating mat (Molly Pond, VT).

water supply, and the flow through the peatland. Two types are recognized here.

Perched water bogs. These are topogenous bogs with stagnant, oligotrophic water perched on an only slightly permeable horizon, fragipan, or bedrock. The oligotrophic bog vegetation is separated from the surrounding upland by a swamp vegetation enriched by seepage water from the uplands. The width and floristic composition of this border zone varies, but this zone is usually forested. In bogs with large water-level fluctuations, flooding can occur at times of high water, mainly in spring and winter. This has a major effect on the bog vegetation.

Soligenous mires. The vegetation of these mires can vary greatly depending on the size of the bog and the amount and nature of the seepage water entering the mire. Only those with oligotrophic water allowing the development of a *Sphagnum*-dominated ground vegetation are discussed here.

In the southern part of the region, evapotranspiration losses are so great that oligotrophic soligenous mires seldom occur. They become more common northward as evapotranspiration losses decrease, and the moisture surplus increases. Nevertheless, these mires are not common in the landscape until the climate is sufficiently humid to allow raised bog formation. Soligenous mires can show a rather clear pool-string pattern in northern Maine (Davis et al. 1983; Sorensen 1986) and very impressive patterns farther north (Figure 9).

### 1.5.3. Peat Bog-Stream Systems

These are limnogenous mires flooded by a stream during high water. The water

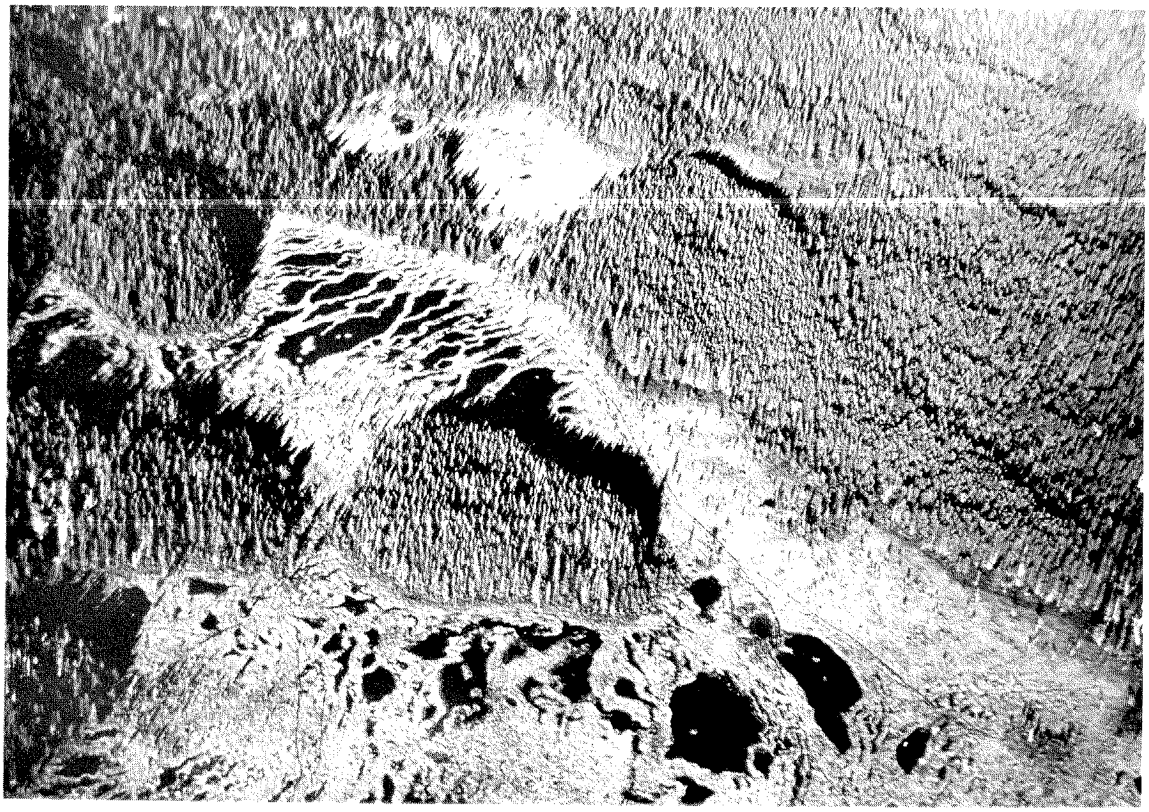

Figure 9. Soligenous mire with pronounced pool-string pattern. This is a small fen in the boreal forest of a hilly part of Western Newfoundland. The entire mire is influenced by minerotrophic water. Such mires occupy extensive areas on very gently sloping terrain.

chemistry and the duration, frequency, and depth of flooding are the primary factors controlling the vegetation of these mires. Only those mires flooded by oligotrophic water and with Sphagnum as a major ground cover are included here.

Limnogenous peat bogs. They occur along slow-flowing, nutrient-poor bog streams. As a rule, limnogenous peat bogs are associated with other types of peatlands. Their vegetation is usually dominated by leather leaf (Chamaedaphne calyculata), sedges (Carex lasiocarpa), or deciduous dwarf shrubs such as sweet gale (Myrica gale) or spiraea (Spiraea spp.). The moss layer is dominated by peat mosses (Sphagnum spp.).

### 1.5.4. Ombrogenous Peatland Systems

These are restricted to the northern part of the region and areas north of the Canadian border (Figure 10). Their ombrotrophic center is raised above the minerotrophic bog border or lagg (Figure 1). Their topography depends on climatic conditions, especially humidity (Granlund 1932; Damman 1979a). Three major types of ombrogenous peatland can be recognized in the northeast. They show a clear zonation from the coast to the interior (Figure 3).

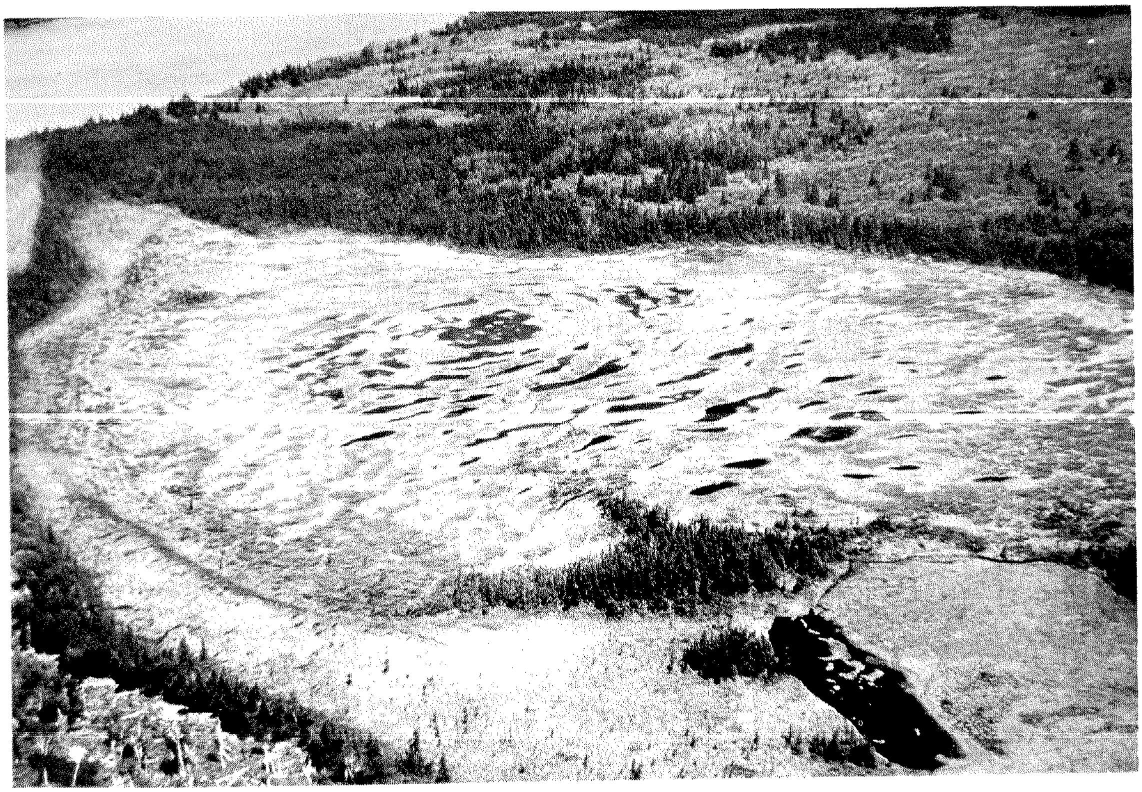

Figure 10. Ombrogenous peatland with almost concentric pool pattern in the ombrotrophic center (east of Roebuck's Lake, Central Newfoundland). A minerotrophic mire vegetation (fen) in the lagg separates the raised ombrotrophic bog center from the uplands. This is clearly visible at the left and bottom of the photograph.

# CHAPTER 2. FACTORS CONTROLLING PHYSICAL PROPERTIES

## 2.1 SUBSTRATE

Peatlands have an organic soil resulting from the slow and incomplete decomposition of organic matter. The fact that this organic matter has accumulated indicates that production exceeded decay during the development of the peatland. However, this does not necessarily mean that peat still accumulates in the peatland.

Peat consists of the partially decomposed remains of plant material produced by the present vegetation or by vegetation that occupied the site during earlier stages of bog development. The nature of the peat depends primarily on the type of plant material and the degree of decomposition or ultimately on the hydrology and water chemistry of the site. Vascular plant material is added to the peat as leaf litter and as dead roots, branches and stems. In contrast, a moss carpet, such as that of Sphagnum, grows at the surface and dies at the base. In many peatlands, these moss carpets determine the structure of the surface peat. Lichens and liverworts also grow in this way, but these plants decay so rapidly that they are an insignificant part of the peat.

The physical properties of peat change with time, i.e., with depth in the peat deposit, primarily because of decay and compaction. Decay breaks down the structure of the organic matter and increases the density of the peat. The weight of the overlying material compresses the peat and also increases its density. As a result, peat becomes denser and more humified with age (Figure 11). This does not always result in a uniform increase in humidification with depth because of changes in growth and decay during peat bog development. The rate of decay varies among peatlands, depending especially on aeration and fertility of the peat horizons. In addition, organic tissues decay at different rates. Wood and fibrous leaf bases are most resistant, and they may still be recognizable with the naked eye in peat thousands of years old. More importantly, this differential decomposition can lead to an overrepresentation of decay resistant materials, such as wood, in old peat horizons (Clymo 1983).

Peat is commonly classified on the basis of its botanical composition and the degree of humification or decay. These classifications compliment each other.

### 2.1.1. Classification Based on Botanical Composition

Based on botanical composition, at least five types should be distinguished:

Sphagnum peat. This consists mainly of the remnants of Sphagnum with varying amounts of sedges as well as branches and rhizomes of ericaceous dwarf shrubs. This peat type develops in nutrient-poor peatlands, such as ombrotrophic and oligotrophic bogs.

Moss and moss-sedge peat. This is made up mostly of other, mainly hypnoid, mosses and varying amounts of sedges. This peat is influenced by mineral-soil water, is more nutrient-rich than Sphagnum peat, and has a higher ash content.

Reed and sedge peat. Reed (Phragmites), cattails (Typha), and large sedges make up the bulk of this peat, which has a high ash content and develops in eutrophic peatlands.

Woody peat. This develops under forested peatlands, and contains undecayed wood. Woody peat is a heterogenous type,

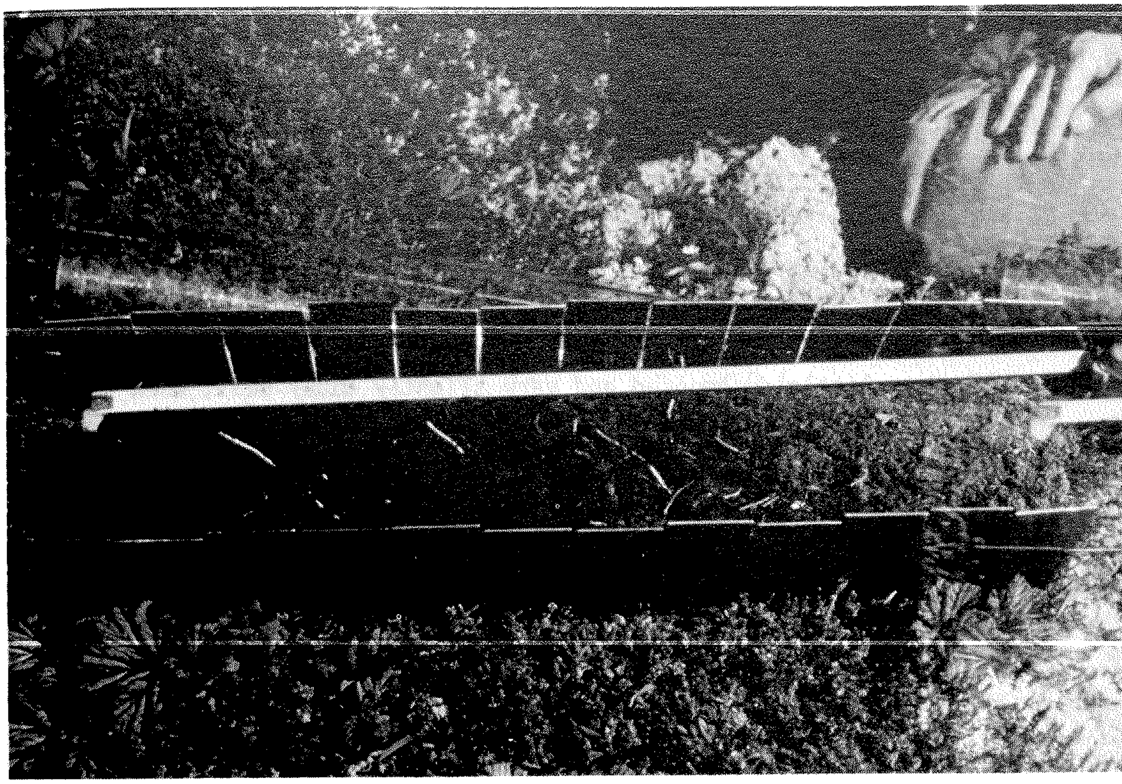

Figure 11. Core sample collected in the surface peat of an *Empetrum-Sphagnum fuscum* vegetation of a coastal plateau bog. Peat becomes denser and more humified with depth. The surface peat is loose and well-structured, but at 35-40 cm the structure of the *Sphagnum* plants is no longer visible. The peat at 40 cm is about 90 years old and at the bottom of the sample (60 cm; extreme left) about 360 years old (M.F. Fitzgerald, University of Connecticut; pers. comm.).

including peat developed under bog forests with Sphagnum peat, fen forests with moss-sedge peat, and swamp forests with a well-humified peat matrix. In dealing with woody peat, it is useful to recognize these three categories.

Limnic peat. This is a sedimentary peat or coprogenous sediment deposited in lakes and other water bodies. It consists mainly of organic matter derived from aquatic organisms or from aquatic plants. Gyttja and sapropel are forms of limnic peat.

The presence of layers of different peat will affect the characteristics of the peat deposit and will reveal the history of development of the peatland. Conversely, a knowledge of the history of development helps in understanding the hydrology of a peatland.

### 2.1.2. Classification Based on Degree of Decomposition

Degree of decomposition or humification of peat is often estimated according to von Post's H-scale (von Post and Granlund 1926). This scale is based on the color of the water, structure of the residue, and amount of peat that passes through the fingers when the fresh peat sample is squeezed (Table 1).

The U.S. Department of Agriculture Soil Conservation Service uses fiber content to determine the degree of decomposition in organic soils (histosols). Fibers are defined as fragments of plant tissue, excluding live roots and wood fragments larger than 2 cm in cross section, that are longer than 0.15 mm. Partially decayed fibers can be easily broken by

Table 1. Peat humification scale (von Post scale) based on properties that can be observed in the field. Translated from von Post and Granlund (1926).

| Scale | Properties |
|---|---|
| H1 | Completely undecomposed peat; only clear water can be squeezed out. |
| H2 | Almost undecomposed and mud-free peat; water that is squeezed out is almost clear and colorless. |
| H3 | Very little decomposed and very slightly muddy peat; when squeezed, water is obviously muddy but no peat passes through fingers. Residue retains structure of peat. |
| H4 | Poorly decomposed and somewhat muddy peat; when squeezed, water is muddy. Residue muddy but it clearly shows growth structure of peat. |
| H5 | Somewhat decomposed, rather muddy peat; growth structure visible but somewhat indistinct; when squeezed, some peat passes through fingers but mostly very muddy water. Pressed residue muddy. |
| H6 | Somewhat decomposed, rather muddy peat; growth structure indistinct; less than one-third of peat passes through fingers when squeezed. Residue very muddy, but growth structure more obvious than in unpressed peat. |
| H7 | Rather well-decomposed, very muddy peat; growth structure visible, about one-half of peat squeezed through fingers. If water is squeezed out, it is porridge-like. |
| H8 | Well-decomposed peat; growth structure very indistinct; about two-thirds of peat passes through fingers when pressed, and sometimes a somewhat porridge-like liquid. Residue consists mainly of roots and resistant fibers. |
| H9 | Almost completely decomposed and mud-like peat; almost no growth structure visible. Almost all peat passes through fingers as a homogeneous porridge if pressed. |
| H10 | Completely decomposed and muddy peat; no growth structure visible; entire peat mass can be squeezed through fingers. |

rubbing between thumb and fingers. Therefore, both rubbed and total fiber content need to be determined. Three major types of organic materials are recognized on the basis of their fiber content (Soil Survey Staff 1975). Figure 12 shows the criteria used in defining them as well as some of their properties.

## 2.2 PHYSICAL PROPERTIES

Physical properties of peat such as water-holding capacity, permeability, and hydraulic conductivity determine, to a very large extent, the hydrology of peatlands. These, in turn, depend on the

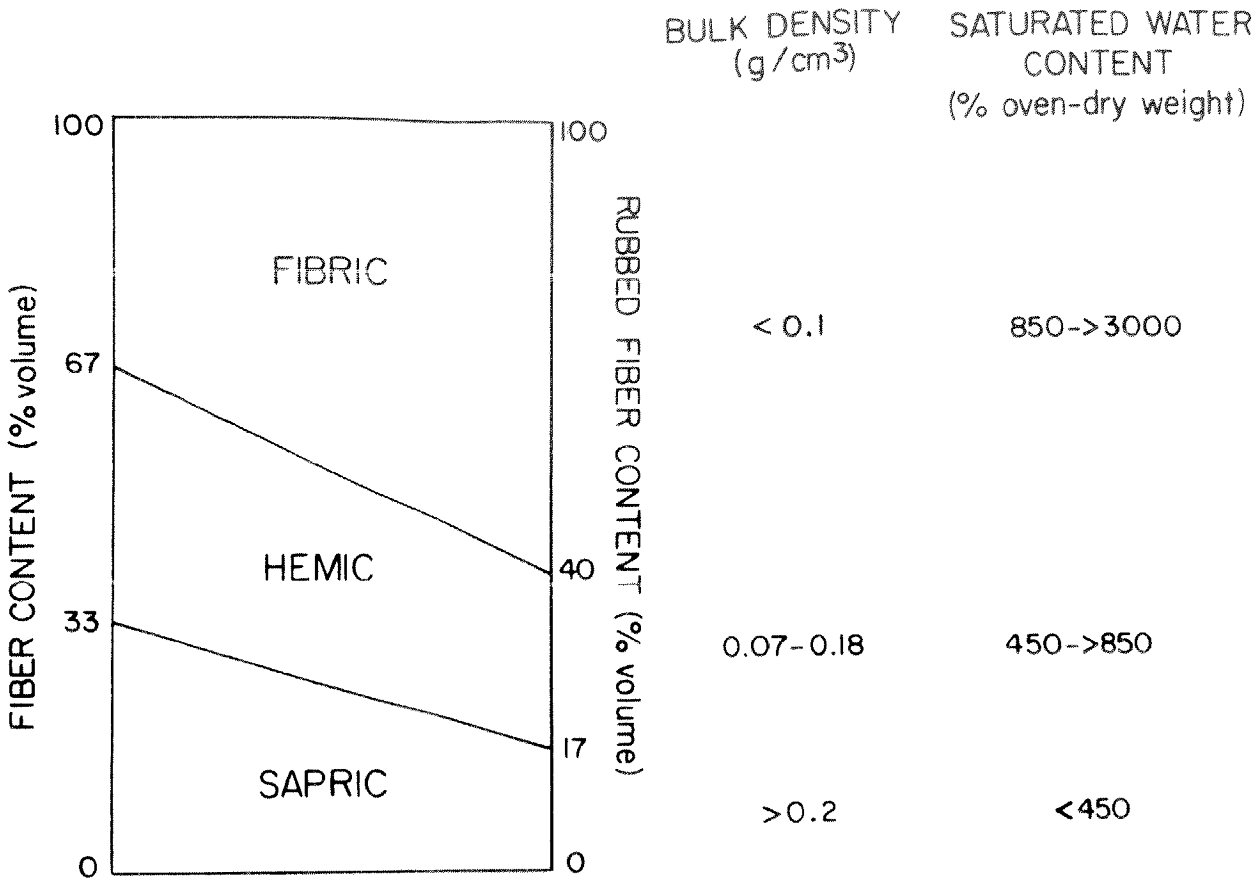


**Figure 12. Properties of fibric, hemic, and sapric peat as defined by Soil Survey, Soil Conservation Service, U.S. Department of Agriculture.**

botanical composition and degree of humification of the peat.

2.2.1. Water Content and Water Retention

Important are both the amount of water that the peat can contain and the tension at which water is held when the peat dries out. All saturated peat contains large amounts of water. However, the amount of water held at low tensions, which thus can be easily removed, decreases with decay and compaction of the peat. Boelter (1968, 1969) clearly demonstrated how the amount of water held at various tensions changes with bulk density and fiber content of peat (Figures 13 and 14). Since bulk density increases and fiber content decreases during decomposition, these diagrams also illustrate the effect of decay on the waterholding properties of peat.

Peat of different botanical composition differs in pore size and decay rate. Therefore, the water-retention properties differ among peat types. This relationship is shown in Figure 15. Water is held at much lower tensions in poorly decomposed or undecomposed Sphagnum peat than in other peat types. Nevertheless, saturated peats hold roughly equal amounts of water, so the amount of water removed from saturated peat when the water table is lowered is much greater for the poorly decomposed surface peat of Sphagnum bogs than for other peatlands. A rough impression of the differences in the amount of water that can be drained from various

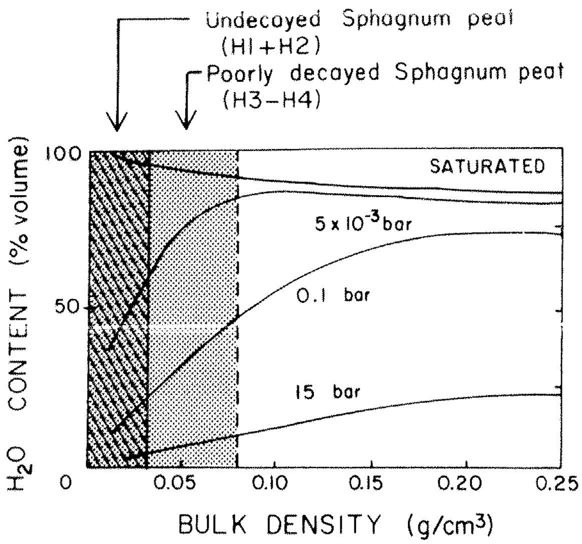


Figure 13. Relation between bulk density of peat and its water retention at various tensions (modified after Boelter 1968). Note that loose, poorly decayed peat with low bulk density holds the most water at low tensions.

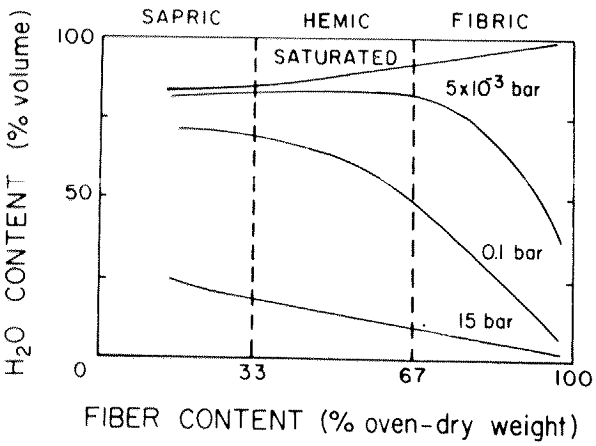


Figure 14. Relation between fiber content of peat and its water retention at various tensions (redrawn after Boelter 1968). Peat with high fiber content holds the largest amounts of water at low tensions.

peat types can be obtained from Figure 15 (Boelter 1968). Soil-water tension is at 0 bars when the peat is at its maximum retentive capacity and when all pores are filled with water. At field capacity, when all gravitational water has drained from the peat, water tension is about 0.1 bars in most mineral soil and slightly

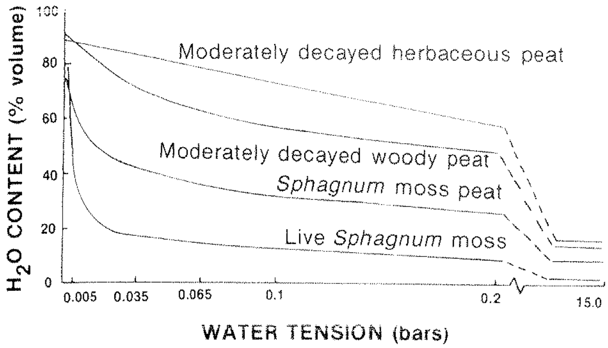


**Figure 15. Water retention in different peats (after Boelter 1968). The difference in the amount of water held by saturated peat (tension 0 bars) and drained peat at field capacity (about 0.1 bars) is largest for live *Sphagnum* moss and least for well-decomposed peat.**

higher in peat. Assume a water tension of 0.1 bars in fully drained peat; then the quantity of water that can be drained from saturated peat ranges from over 50% for the live, undecomposed Sphagnum peat to about 10% by volume for some of the other peat types. Water storage or water yield coefficient, the volume of water removed from a peat profile when the water table is lowered, will be somewhat higher since this includes also water in the capillary zone above the saturated peat.

### 2.2.2. Hydraulic Conductivity

Decay and compaction of peat also decrease its hydraulic conductivity, but this happens at different rates in each peat type. This was clearly shown in a study by Baden and Eggelsmann (1963) based on extensive field measurements of hydraulic conductivity with the auger-hole method (Hooghoudt 1937). The relationship between hydraulic conductivity and degree of decomposition, and density of the peat is shown in Figures 16 and 17. Several important conclusions can be drawn from these data.

(1) Live and undecomposed Sphagnum peat is very permeable, but decay decreases its hydraulic conductivity to a greater extent than that of other peat types.

(2) Within peats of similar botanic origin, the degree of decomposition based on the von Post scale

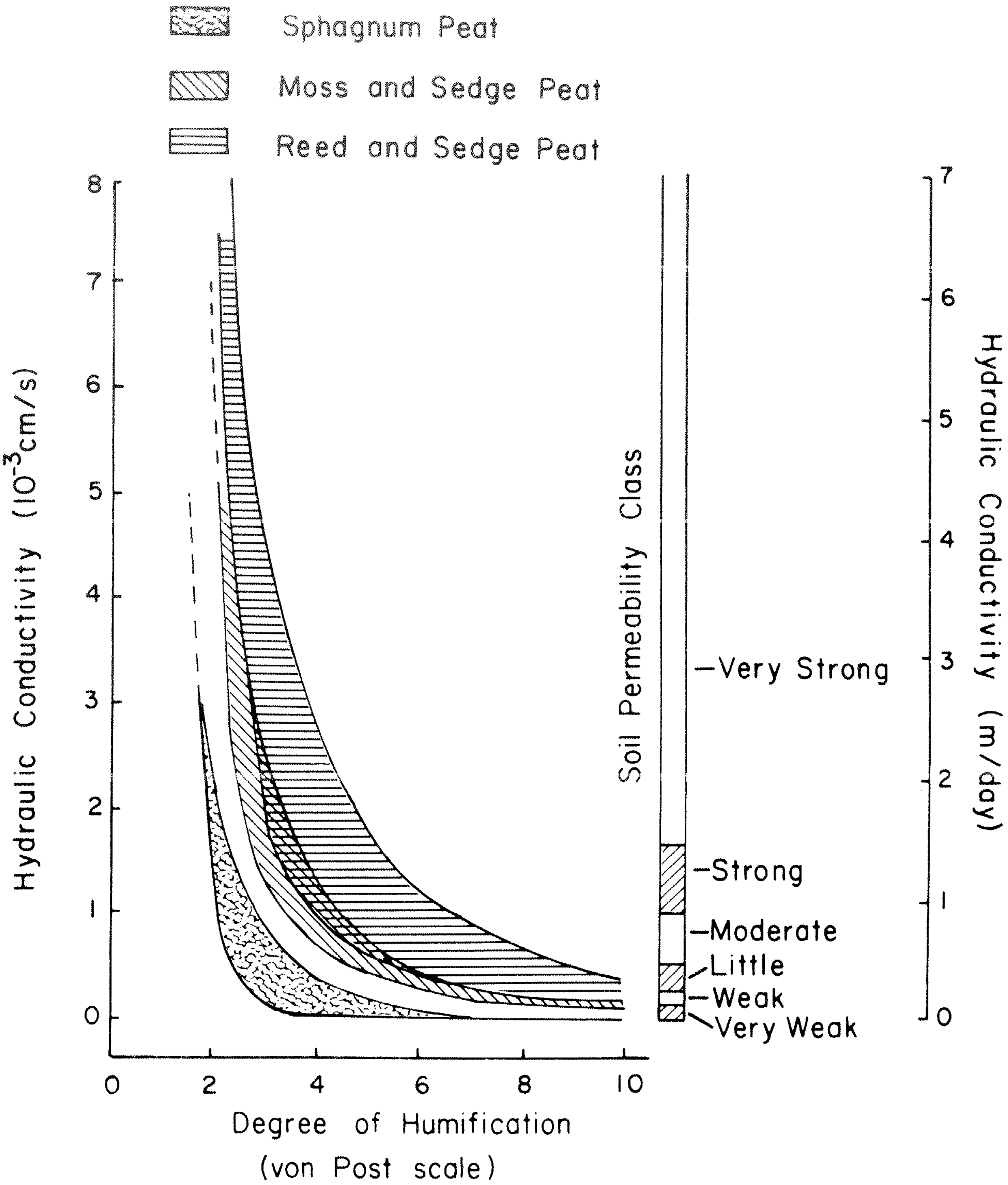


Figure 16. Relation between hydraulic conductivity and degree of humification of different peat types (redrawn after Baden and Eggelsmann 1963). The humification is based on the von Post scale (Table 1). The soil permeability classes are based on Sonneveld (1962, cited by Baden and Eggelsmann 1963). Wooded swamp peat not included because it is generally strongly to almost completely decomposed, except for wood fragments.

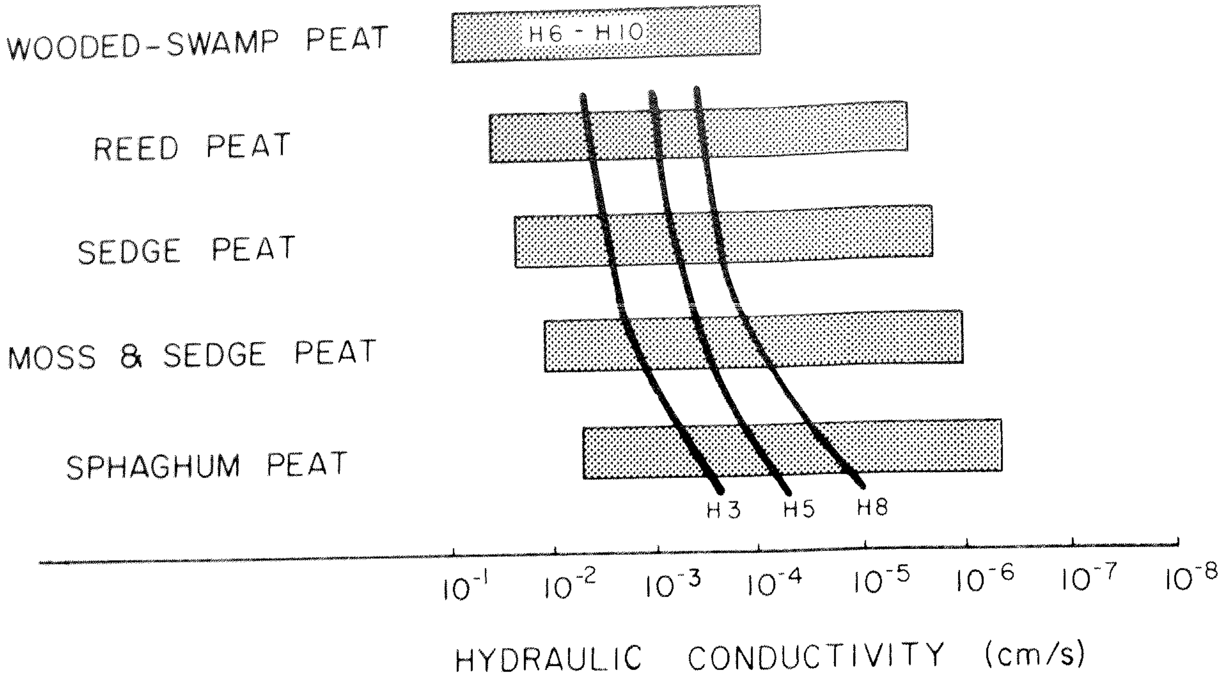


Figure 17. Relation between hydraulic conductivity and peat types (graphed from data in Baden and Eggelsmann 1963). H3, H5, etc. refer to humification according to the von Post scale (Table 1). In wooded-swamp peat, there is no consistent relation between decomposition and hydraulic conductivity.

is a rough indication of its hydraulic conductivity, but the hydraulic conductivity of peats with the same H-value increases in the order: *Sphagnum* peat, moss-sedge peat, sedge peat, and reed peat.

(3) Wood fragments increase the permeability of peat. Therefore, hydraulic conductivity of woody peat varies (Baden and Eggelsmann 1963) and is higher than the corresponding peat type without wood. This also explains why in wooded swamps the degree of decomposition is a poor indication of hydraulic conductivity.

# CHAPTER 3. HYDROLOGY AND WATER CHEMISTRY

## 3.1 WATER STORAGE

Throughout the northeastern United States precipitation exceeds water losses by evapotranspiration, at least on an annual basis. However, during the summer precipitation is often considerably less than the evapotranspiration losses. This applies also to the zone with ombrogenous bogs in northern Maine. Its southern boundary in eastern North America (Figure 2) occurs roughly where the cumulative deficiency of precipitation over potential evapotranspiration exceeds 100 mm (Damman 1977). When potential evapotranspiration exceeds precipitation, the vegetation will draw on water stored in the ecosystem or supplied from other sources. This will often result in a lowering of the water table during the summer and early fall.

Water is stored in the peat, in pools on the bog surface, as snow, and as intercepted water on the vegetation. The first two storage forms are most important during summer. The amount available in each depends on the physical properties of the peat and the microtopography of the bog surface. Bogs are saturated with water for most or all of the year. When saturated, their storage capacity is filled, and no additional water can be stored. The available storage capacity increases during the summer and will be highest at the lowest water level. In general, the water storage capacity of bogs is overestimated. In spite of popular belief, bogs regulate stream flow only to a limited extent, especially in humid areas (Goode et al. 1977).

It is useful to distinguish two major peat horizons: the acrotelm and catotelm. The former is the surface peat above the low-water table, and the latter is the permanently anaerobic peat below this level (Ingram 1978). Many hydrologically and ecologically important properties of the substrate are associated with this subdivision (Figure 18).

Water is stored in the acrotelm. Most of the changes in storage involve the free water in the zone of water-level fluctuation and the capillary water above the water table. Therefore, the depth and the physical properties of this layer affect water retention most.

The catotelm is constantly saturated with water, and therefore one would not expect any changes in water storage in this layer unless the peat bog is drained. Although this appears to be generally true, it does not apply to all bogs. In lake-fill bogs, a layer with loose, suspended organic matter occurs often at 1-2 m below the surface. During dry periods, this layer shrinks because water is withdrawn from it. This causes seasonal changes in surface level of these bogs similar to, but less dramatic than, those in the floating mat of pond-border bogs. There is also evidence of changes in surface level from bogs with solid peat deposits (Ganong 1897; Uhden 1956; Eggelsmann 1960). These surface level changes appear to be due to expansion of the peat during wet periods, perhaps due to increases in hydrostatic pressure (Ingram 1983). Increases in water content of the catotelm were also observed by Heikurainen et al. (1964).

## 3.2 WATER MOVEMENT IN BOGS

### 3.2.1. <u>Lateral Flow</u>

Within the acrotelm, the hydraulic conductivity decreases with depth because of decay and compaction of the peat. The reduction in hydraulic conductivity from the surface to the base of the acrotelm

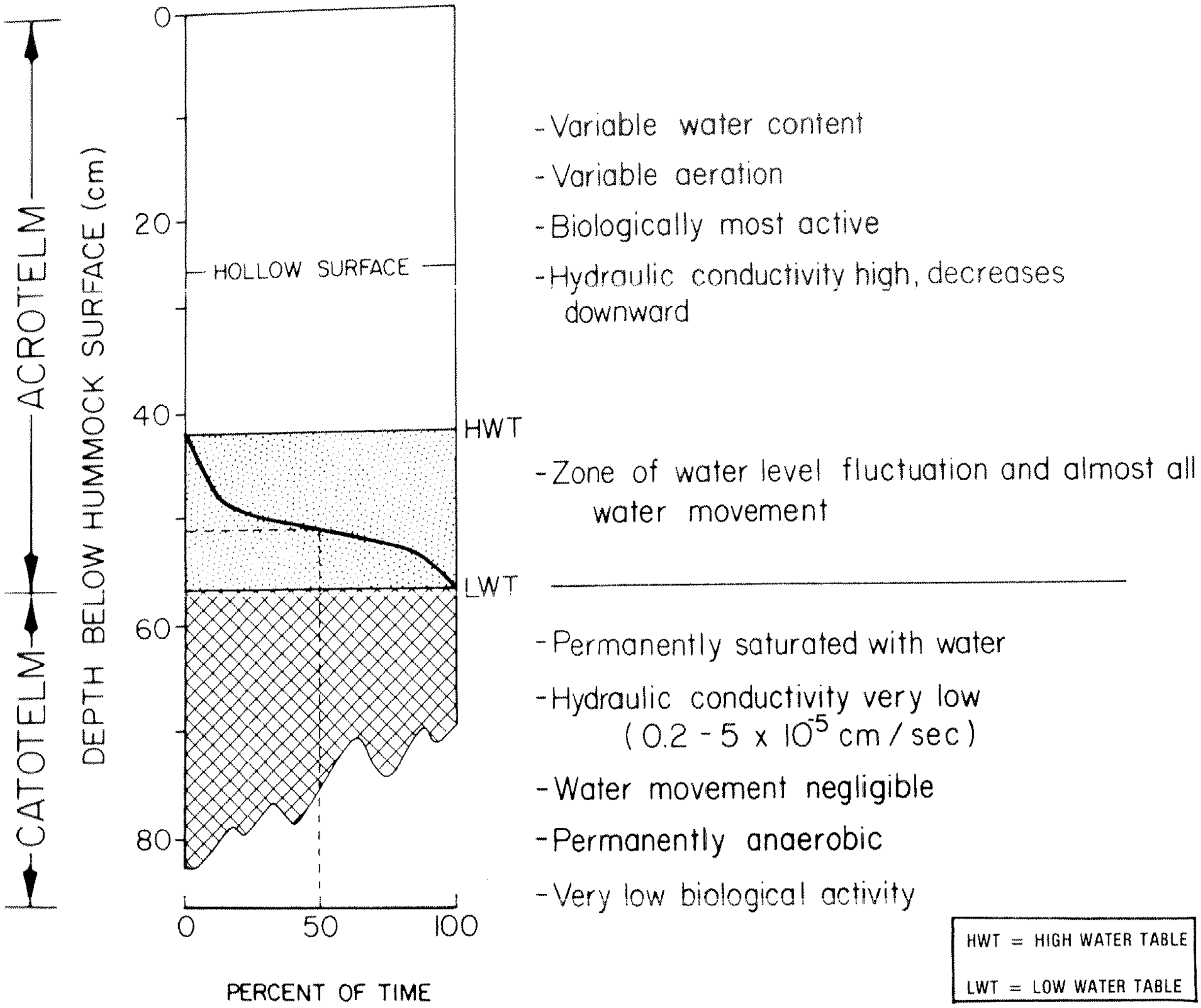


**Figure 18. Properties of acrotelm and catotelm of peat bogs. The heavy black line in the stippled horizon is the water level duration curve, indicating the percentage of time that the water table is at or above that level.**

tends to regulate water levels by increasing flow at high-water levels and reducing flow at low levels (Ivanov 1975). Consequently, water levels remain mostly around average levels and reach peaks for brief periods only. This is best expressed in Sphagnum peat of ombrotrophic bogs (Figure 18), where the acrotelm is thick and the peat poorly decomposed. In many oligotrophic bogs this regulation of water levels is less effective because of rapid decay of the peat or impeded drainage.

Small increases in nutrient level can greatly increase decay of the surface peat. Therefore, minerotrophic peatlands show a more rapid reduction in hydraulic conductivity with depth than do ombrotrophic bogs. Thus, Sphagnum peat influenced by weakly minerotrophic water can change within 25 cm from a layer of surface peat with H1 or H2 according to the von Post scale (Table 1) to H4 or H5. In red maple and cedar swamps, peat with H6 often occurs at the surface of the depressions.

Information on the relationship between hydraulic conductivity and botanical origin of the peat should be applied cautiously to field conditions. For instance, Sphagnum peat at H3 or over has lower hydraulic conductivities than other peat types (Figure 17). However, the living and undecomposed Sphagnum peat making up the surface peat has a very porous structure with organic matter occupying less than 20% of the volume (Clymo 1983), so water can move rapidly (Figure 19). In contrast, a layer with comparable permeability is absent in most swamps and marshes, and peat with H3 or over may occur at the surface. Therefore, flow through the Sphagnum peat can exceed that in other peatlands. Decay rates vary greatly among peatlands, and to avoid erroneous conclusions such changes should be considered in evaluating water movement. When the water table rises above the surface, water will drain rapidly from the peatland unless topography impedes drainage.

Impeded drainage from the peatland can cause high water tables in parts or all of a peatland. Consequently, water tables can be close to the surface in spite of a high hydraulic conductivity of the peat. Under these conditions water-level fluctuations depend on the balance between water losses (drainage and evapotranspiration) and inputs (precipitation, seepage, and possibly stream inputs).

### 3.2.2. Vertical Flow

Water movement driven by gravity and evaporation are important above the water table. This involves percolation of precipitation through the surface peat and upward movement of capillary water; both play a role in translocating elements.

Percolation of rain water through the peat depends on the permeability of the peat. It is controlled by the same processes that affect hydraulic conductivity. Water percolates easily through the live and undecomposed Sphagnum peat but very slowly through well-decomposed peat. If surface peat is well-decomposed, the water level is usually near the surface, and puddling on the surface is frequently due to a rise in water level. Well-decomposed peat can be found above the water table in drained peatlands and in bogs with strongly fluctuating, perched water tables. Under such conditions puddling occurs, and water flows mainly over the surface and through cracks that develop in the peat during drying.

Capillary water rises higher above a water table when pore size becomes smaller, but at the same time this reduces the rate of water movement. The capillaries through which water moves in peats are so small that the upper limit of the capillary zone is limited mostly by evaporation at the surface and uptake by vegetation. Sphagnum plants lack vascular tissue, and therefore water movement to the surface of a Sphagnum carpet is by physical processes. On a sunny day, evaporation losses can easily exceed transport of capillary water to the surface, and the Sphagnum surface will dry. The evaporation rate at the surface depends also on the morphology and anatomy of the Sphagnum species (Figures 19, 20, 21, 22, and 23) and the density of the carpet (Overbeck and Happach 1957; Hayward and Clymo 1982; Rydin and McDonald 1985; Andrus 1986). Drying out of the surface is, therefore, only partly controlled by the depth of the water table (Neuhäusl 1975).

## 3.3 WATER CHEMISTRY

### 3.3.1. Chemical Differences Between Meteoric and Telluric Water

Water in bogs comes from the atmosphere and the surrounding uplands. Atmospheric (meteoric) and terrestrial (telluric) water differ in chemical composition. It is important to distinguish these two sources when dealing with peatlands because their relative contribution varies within a peatland and among peatlands.

Some nutrients and other elements in precipitation are derived from the sea, but to these are added elements contributed by atmospheric pollution and natural fires as well as those in soil and organic dust, mostly from agricultural areas (Gorham 1961). The ionic composition of precipitation depends on the relative contribution from each of these sources, and it shows clear geographic trends (Munger and Eisenreich 1983). Precipitation in the northeastern United States is strongly

Figure 19. Loose surface peat with *Sphagnum magellanicum* and *S. angustifolium*. The surface peat is very porous, especially below the capitula (heads) of the *Sphagnum* plants.

modified by pollution, and to a lesser extent, by agricultural dust. Therefore, precipitation is greatly enriched with heavy metals (Groet 1976) and sulfur and nitrogen compounds (Junge 1958; Committee on Atmospheric Transport 1983). The deposition of all of these decreases roughly from south to north. Soil-derived elements such as Fe, Mn and Ca, are present in low concentrations compared to other parts of the United States (Munger and Eisenreich 1983).

Soil water is rain water that has been in contact with the mineral soil or bedrock. While seeping through the soil, it is enriched with elements supplied by weathering, solution, hydrolysis and cation exchange. This enrichment results in higher concentrations of most elements in telluric water than in rain water, especially of those elements occurring in large amounts in soils and rocks but in very low concentrations in sea water (Table 2). Foremost among the latter are Al, Si, Fe and Mn. Conversely, Na and Cl occur in much higher concentrations in seawater than in freshwater (Table 2). The ionic composition of telluric water depends on the type of rock and the length of time the water has been in contact with it. Consequently, ionic composition varies geographically and temporally. Ionic concentrations are lowest in areas with poor soils and rocks such as sandstones, schists, or granites and during periods of heavy flow. Superimposed on this variation are changes due to biological processes such as decay of organic matter and uptake by vegetation.

### 3.3.2. Chemical Composition of Ombrotrophic Bog Water

The ionic concentration of water derived from precipitation changes after it reaches the bog surface, even without coming into contact with telluric water.

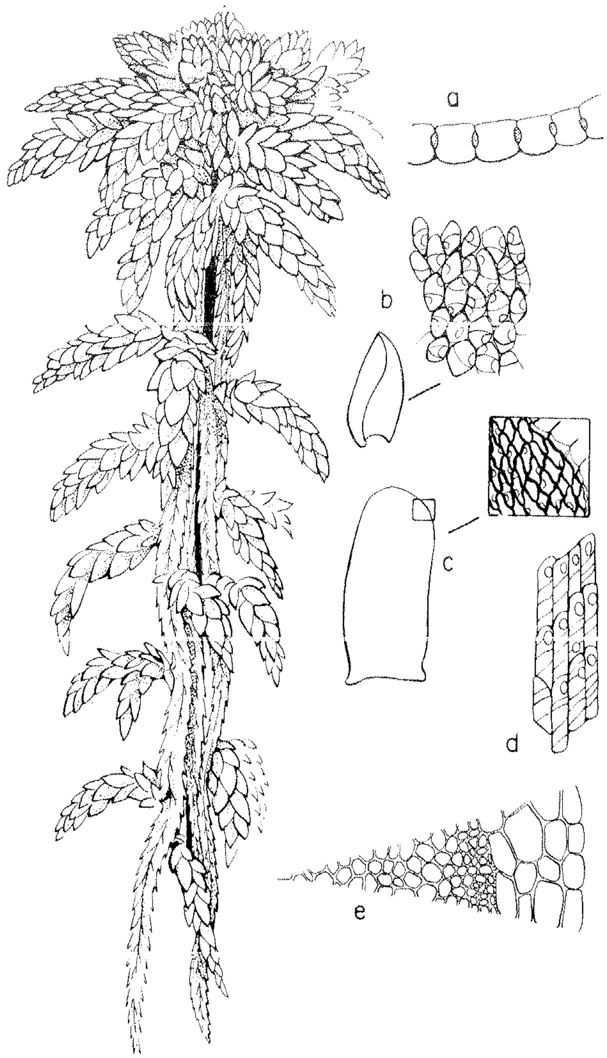


Figure 20. *Sphagnum magellanicum* Brid. (a) cross section of branch leaf, (b) branch leaf, (c) stem leaf, (d) branch cortex, (e) cross section of stem.

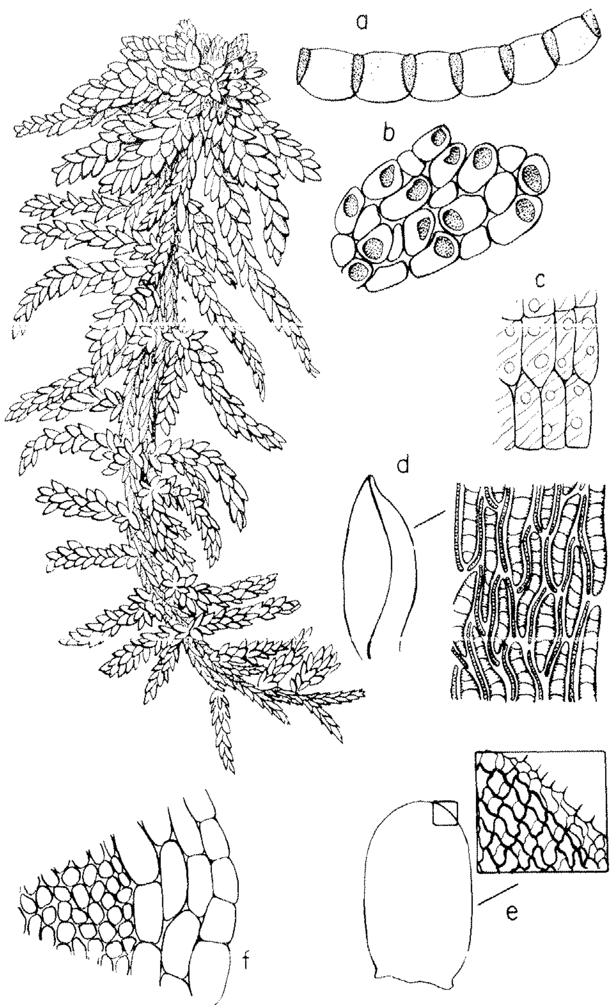


Figure 21. *Sphagnum papillosum* Lindb. (a) cross section of branch leaf, (b) convex surface of branch leaf as seen on electron microscope, (c) stem cortex, (d) branch leaf, (e) stem leaf, (f) cross section of stem.

Evapotranspiration at the bog surface, leachates from vascular plants, and decay of organic matter increase concentrations, whereas adsorption on peat and uptake by plants lower them. Most of these processes are temperature dependent, and therefore the concentrations of most elements vary seasonally (Damman 1986).

Evapotranspiration increases the ionic concentration of an element if the biological demand for the element is low, as for Na or Cl (Damman 1986). Even in humid climates their concentration in ombrotrophic bog water is many times that in the precipitation (Table 3). Other ions do not show this increase, because they are removed by uptake or cation exchange (Damman 1986). Seasonal variations in ionic concentrations are especially large for mobile ions such as K that can occur in concentrations below that in the precipitation during periods of active growth (Damman 1986), whereas concentrations reach high levels in early fall when it is leached from senescent and dead leaves (Malmer 1962b; Damman 1986). Ionic concentrations in ombrotrophic water are closest to that in the precipitation during periods of heavy rain or snow melt and deviate most during hot, dry spells.

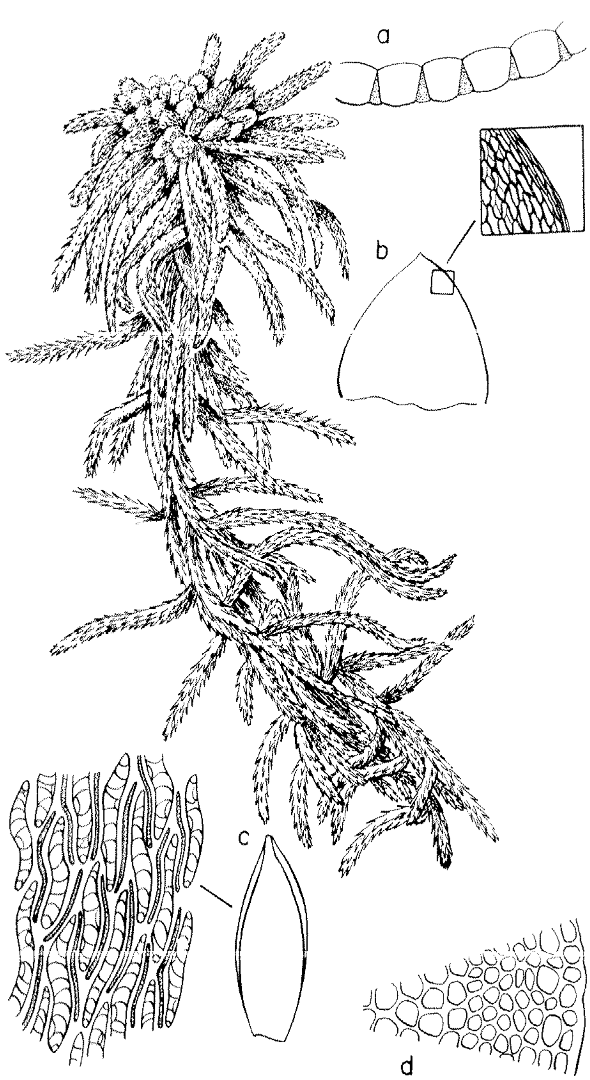


Figure 22. *Sphagnum fallax* (Klingr.) Klingr. (a) cross section of branch leaf, (b) stem leaf, (c) branch leaf, (d) cross section of stem.

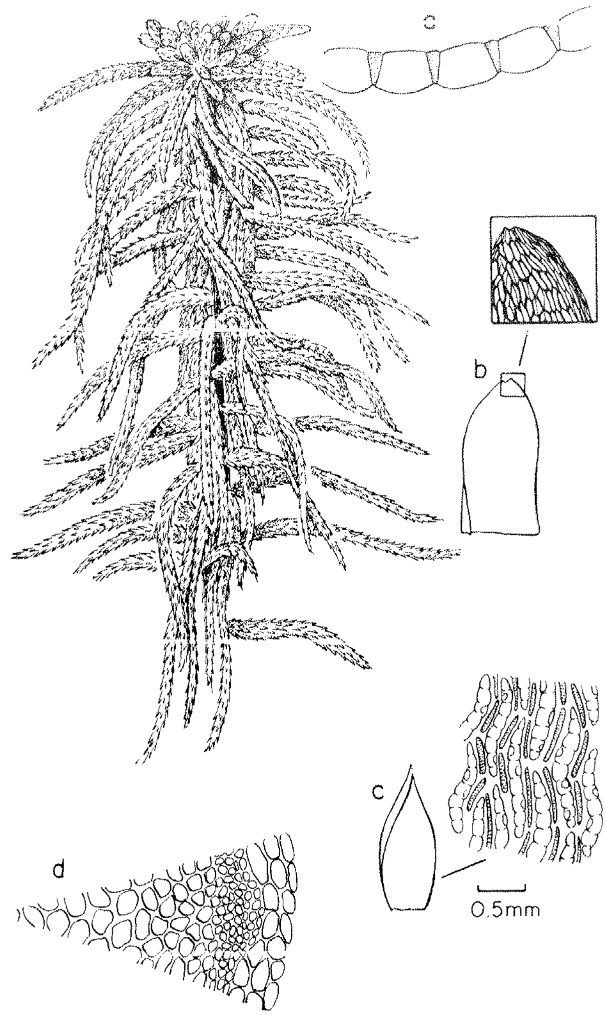


Figure 23. *Sphagnum rubellum* Wils. (a) cross section of branch leaf, (b) stem leaf, (c) branch leaf, (d) cross section of stem.

### 3.3.3. Chemical Composition of Minerotrophic Bog Water

The effect of the mineralogy of soils and bedrock on the ionic composition of telluric water is well documented (Clarke 1924; Troedsson 1952; Gorham 1961) and causes major differences in the chemistry of the water seeping into peatlands. Even on nutrient-poor sands the concentration of most nutrient elements is much higher than in the precipitation (Table 3). This is especially true for elements virtually absent in seawater such as Fe, Mn, and Si.

The ionic composition of mineral soil water flowing through a peatland is affected by the same processes discussed under ombrotrophic water. In addition, dilution by rainwater plays a major role here. The relative importance of evapotranspiration and dilution by rainwater on the ionic concentrations is controlled by climate, but in bogs receiving seepage water it depends also on the dimensions of the peatland.

Size of a peatland will affect surface-dependent factors such as precipitation and evapotranspiration to a much greater extent than border-dependent fac-

Table 2. The relative concentrations of the most abundant elements in the earth crust, soil, and water, excluding C, H and O. Values are percent (weight basis) of the total amount, calculated from mean and median concentrations reported by Bowen (1979).

| Element | Earth crust | Soils | Freshwater | Sea water |
|---|---|---|---|---|
| Al | 15.9 | 14.5 | 0.64 | $6 \times 10^{-6}$ |
| Ar | 0.0002 | - | 1.2 | $1 \times 10^{-3}$ |
| B | 0.002 | 0.004 | 0.03 | 0.01 |
| Br | $7 \times 10^{-5}$ | 0.002 | 0.03 | 0.2 |
| Ca | 7.9 | 3.1 | 33.2 | 1.2 |
| Cl | 0.03 | 0.02 | 15.0 | 58.3 |
| Fe | 7.9 | 8.2 | 1.0 | $6 \times 10^{-6}$ |
| K | 4.1 | 2.9 | 4.6 | 1.2 |
| Mg | 4.5 | 1.0 | 8.5 | 3.9 |
| Mn | 0.18 | 0.20 | 0.01 | $6 \times 10^{-7}$ |
| Na | 4.5 | 1.0 | 12.9 | 32.4 |
| P | 0.19 | 0.16 | 0.04 | 0.0002 |
| S | 0.05 | 0.14 | 7.9 | 2.7 |
| Si | 53.7 | 67.4 | 15.0 | 0.007 |
| Sr | 0.07 | 0.05 | 0.15 | 0.02 |
| Ti | 1.1 | 1.0 | 0.01 | $3 \times 10^{-6}$ |
| N | 0.005 | 0.41 | 0.10 | $1.5 \times 10^{-4}$ |

Table 3. Comparison of ionic composition of precipitation with that of ombrotrophic bog water and minerotrophic brook water for a peat bog at Stephenville Crossing, Newfoundland (May-September 1980). Mean concentrations ± standard error. Based on data in Damman (1986) and unpublished data.

| Water characteristics | n | Element (ppm) | | | | |
|---|---|---|---|---|---|---|
| | | K | Mg | Ca | Na | Fe |
| BULK PRECIPITATION | | | | | | |
| Volume weighted mean | 27 | 0.065 | 0.12 | 0.52 | 0.75 | 0.052 |
| Unweighted mean | 27 | 0.062±0.007 | 0.12±0.02 | 0.53±0.09 | 0.63±0.11 | 0.052±0.008 |
| OMBROTROPHIC | | | | | | |
| Pools on plateau bog | 48 | 0.10±0.02 | 0.46±0.02 | 0.25±0.02 | 3.89±0.10 | 0.065±0.009 |
| Bog brook | 16 | 0.17±0.06 | 0.52±0.03 | 0.27±0.01 | 3.81±0.12 | 0.079±0.008 |
| MINEROTROPHIC | | | | | | |
| Brook through nutrient-poor outwash | 7 | 0.22±0.03 | 1.11±0.06 | 2.80±0.36 | 5.76±0.26 | 0.47±0.07 |
| Regional brook | 8 | 0.63±0.03 | 4.5±0.2 | 18.5±1.0 | 6.18±0.20 | 0.18±0.03 |

tors such as seepage. This is especially noticeable in soligenous peatlands, which receive mineral-soil water mostly as seepage water rather than ground water. In such peatlands, the diluting effect of rain on ionic concentrations increases rapidly with the size of a peatland and the distance from the bog border. This effect is greatest in humid climates, where these peatlands are most common. During the fall, leachates from dead and senescent foliage will partly offset the lowering of ionic concentrations by rainfall and uptake by the vegetation.

# CHAPTER 4. STORAGE AND FLUXES OF ELEMENTS

## 4.1 INTRODUCTION

Our knowledge of energy flow and elemental fluxes in peat bogs is incomplete; this is especially true for North American peatlands. Quantitative data on elemental fluxes are virtually lacking for peat bogs in the northeastern United States and the situation is hardly better for information on amounts stored in the peat. Hemond (1980, 1983) provided estimates of fluxes for some elements in a kettle-hole bog, and Damman (1979b, 1986b), Laundre (1980) and Lyons (1981) showed amounts stored in the peat.

Extrapolation from data outside the region is complicated by differences in vegetation structure and climate, especially those affecting hydrology. For example, it is difficult to extrapolate from data for a well-studied, forested, perched peat bog in Minnesota (Verry 1975; Verry and Timmons 1982; Urban 1983; Grigal et al. 1986; Urban et al. 1986) information pertinent to open or shrub-covered bogs in the Northeast. In addition, the bogs within the region vary with respect to hydrology and inflow, and therefore they by no means represent a homogeneous group as far as fluxes are concerned.

This section is mainly on data collected elsewhere and interpreted in the light of our understanding of ecological processes in bogs. Therefore, this discussion is, to some extent, speculative. It indicates the general trends within the peat bogs of the Northeast and the expected geographical variation. Moreover, it points out how processes in peat bogs differ from those in the more-familiar upland ecosystems.

## 4.2 ENERGY FLOW

There have been no complete studies of energy flow in peat bogs. The studies providing the most detailed information were part of the International Biological Program (IBP) Tundra Biome Project in Moore House, a British blanket bog (Heal and Perkins 1978), and a subarctic mire in Swedish Lapland (Sonesson 1980).

The primary production of vascular plants, liverworts, mosses, and lichens in the bog vegetation provides the major input of organic matter. Additional inputs come from phytoplankton in bog pools and organic matter blown or washed in from areas outside the bog. The latter can contribute considerably in small peat bogs, but its role decreases with increasing size of the peatland. Little is known about phytoplankton productivity in bogs. This input increases with fertility of the peatland and with wetness, especially with the surface area of open water. Presumably, input from this source is small in bogs of the Northeast.

Among the vascular plants, ericaceous dwarf shrubs and sedges (Cyperaceae) are the most important primary producers (Forrest and Smith 1975; Svensson and Rosswall 1980), and much of this production is below-ground (Svensson and Rosswall 1980; Wallén 1983). Trees can also be major contributors in some bogs.

Productivity is rather low compared with other ecosystems (Reader and Stewart 1972; Forrest and Smith 1975; Grigal et al. 1986), but mosses and especially Sphagnum, can account for 1/3 - 1/2 of the total production (Forrest and Smith 1975; Grigal 1985), and probably more in some plant communities. Presumably, productivity increases with nutrient input and generally with inputs of mineral soil water into the peatland.

Herbivory is much less important in peat bogs than in other wetlands (Cragg 1961; Svensson and Rosswall 1980; Mason and Standen 1983), presumably because the organic matter of bogs is nutrient deficient (Bellamy and Rieley 1967; Small 1972; Damman 1978a) and the litter of the vascular plants is often sclerophyllous (Small 1973). Herbivory probably increases with the fertility of peat bogs.

Peat bogs are detritus-based ecosystems, and breakdown of organic matter is of major concern. Bacteria and fungi make up the major part of the decomposer complex (Svensson and Rosswall 1980). Fungi are mostly restricted to the aerobic peat, and Svensson and Rosswall (1980) found 90% of the mycelium in the upper 10 cm. Most decay also takes place above the water table (Clymo 1965; Malmer and Holm 1984).

Peat could not accumulate if productivity did not exceed decay. Although this has to be true over the entire period of bog development, this does not mean that productivity still exceeds decomposition. As long as accumulation takes place below a water table, decay will be very slow (Clymo 1965), and peat will accumulate in the bog. This situation clearly exists in may bog-lake systems that have not filled in completely. Above a water table, decay is accelerated, and generally, an equilibrium between production and decay is reached within 30-50 cm above the water level, unless the extreme nutrient deficiency of the peat limits decay (Damman 1979a, 1986). This can lead to a raised bog formation if climatic conditions cause a water mound to develop in the accumulated peat (Ivanov 1981; Ingram 1983). This happens in the zone of ombrogenous bogs in northern New England (Figures 1 and 2). Even in this case, there is a limit to peat accumulation (Damman 1979a; Clymo 1984).

## 4.3 FLUXES OF NUTRIENTS AND OTHER ELEMENTS

### 4.3.1. Causes of Differences with Upland Ecosystems

Peat bogs are characterized by slow decay of organic matter. This partially decayed litter forms the substrate in which plants root, and it also seals off the vegetation from direct contact with the mineral soil. Therefore, organic matter that is at the surface at any one time will gradually be buried under more and more peat as the moss layer continues to grow.

These conditions have several implications for nutrient cycling that distinguish peat bogs from upland sites:

(1) Nutrient turnover is slow because of nutrient deficiency of the litter and water-logging of the substrate. Therefore, in actively growing peat bogs the detritus cycle is poorly developed. Nutrient cycling increases when peat growth stagnates, and it is also more active in bogs receiving higher nutrient inputs.

(2) The amount of nutrients in the living biomass is small, but the amount stored in undecayed organic matter is far larger than in other ecosystems (Damman 1978a).

(3) Nutrients in peat below the rooting zone of the vegetation are unavailable to plants. Consequently, in bogs that actively accumulate peat, nutrients are continuously lost to peat stored below the rooting zone. This accumulation rate changes during bog development and varies spatially and temporally in existing bogs.

(4) Organic matter that makes up the surface changes its position with respect to the water table over time. Thus, organic matter appears to migrate with time from an aerobic horizon to one that is periodically anaerobic to a permanently anaerobic horizon. This causes redox-sensitive elements, as well as several other elements, to behave differently in organic soils than in mineral soils (Damman 1978a).

### 4.3.2. Inputs

The meteoric input of dust and rain is relatively more important as a nutrient source in peat bogs than in other ecosystems because of the absence of inputs by mineral weathering and the generally small telluric inputs. The importance of meteoric inputs increases as the decay rate of organic matter decreases and nutrient deficiency increases. Meteoric input is the sole input in ombrotrophic bogs. The chemical differences between telluric and meteoric water were discussed earlier.

Small bogs and bog borders receive significant additional inputs of nutrients from litter blown in from adjacent uplands. Import or export of nutrients by birds and mammals is unimportant in most bogs (Crisp 1966; Svensson and Rosswall 1980). Conspicuous exceptions are bogs used as roosting places by waterfowl or sea birds.

Nitrogen fixation by free-living micro-organisms appears to be insignificant (0.07-0.150 g $N/m^2/yr$) in ombrotrophic bogs (Granhall and Selander 1973; Waughman and Bellamy 1980) but becomes more important in minerotrophic mires. Hemond (1983) reported an input of 1 g $N/m^2/yr$ for an oligotrophic kettle-hole bog and Waughman and Bellamy (1980) found an average input of 0.53 and 2.1 g $N/m^2/yr$ in poor and intermediate fens, respectively. These values probably represent the upper limit of what can be expected in the bogs discussed here.

Symbiotic nitrogen fixation in bogs is limited to actinomycetes associated with *Myrica* and *Alnus*. These species do not occur in the most nutrient-poor bogs of the region. In minerotrophic mires N input from this source can be important. Schwintzer (1983) reported an addition of 3.53 g $N/m^2/yr$ in an oligotrophic *Sphagnum* bog with *Myrica gale*.

### 4.3.3. Temporal Changes in Elemental Fluxes

Seasonal changes in biological processes and periodic changes in water level are reflected in the elemental fluxes. Active growth and uptake of essential elements by the vegetation lower concentrations of these elements in the bog water. This is especially noticeable for elements that are in short supply and for which the biological demand is large. In ombrotrophic bogs, 70%-80% of the K and 20%-30% of the Mg is removed while water seeps through the bog (Damman 1986). Similar seasonal changes occur in N, P and Ca (Boatman et al. 1975), although changes in Ca are less conspicuous because Ca adsorption on peat is far more important than uptake by vegetation (Damman 1986). Potassium concentration in bog water peaks in early fall when K is leached from dead and senescent plants (Malmer 1962b; Damman 1986). Elements released mostly by microbial decay, such as N and P, do not show this so clearly. Such seasonal fluxes occur in all bogs, but their effect on water chemistry is less obvious when nutrient inputs are higher.

Sulfate concentrations are highest in bog water during the first rain after a dry spell as $H_2S$, oxidized to $H_2SO_4$ when the water level was low, is flushed out of the bog. This flushing of sulfates occurs in a wide range of mires (Gorham 1956; Malmer 1974), but presumably it is most pronounced in bogs experiencing large water-level fluctuations.

Reduction of Fe and Mn compounds during wet periods increases their solubility and exposes them to removal in the drainage water from the peatlands (Damman 1978a). Iron concentrations increase slightly in the drainage water of ombrotrophic bogs during high water levels in fall (Damman, unpubl.). This effect should be most obvious in bogs receiving telluric input.

The concentrations of ions for which the biological demand is low or negligible increase during warm and dry periods because of water losses by evapotranspiration. This increase is most clearly shown by Na and Cl (Gorham 1956; Boatman et al. 1975; Damman 1986).

### 4.3.4. Accumulation of Elements in Bogs

Elements are stored primarily in the living biomass of the primary producers and in the peat. The latter includes elements in undecayed organic matter and in the microbial biomass as well as ions adsorbed on the cation exchange complex of the peat. Some elements also occur in precipitated salts. Ionic concentrations in the bog water are in equilibrium with ions adsorbed on the peat; concentrations are relatively low in bogs but increase with the input of fertile, mineral-soil water.

Storage of elements in the living vegetation varies with its biomass, and it affects mostly the major nutrient elements. The amount is generally low compared with other ecosystems, but it is large in relation to inputs, especially in ombrotrophic bogs (Damman 1978a; Malmer and Nihlgård 1980). In bogs, N, P, and K are strongly conserved in the living Sphagnum plants (Damman 1978a; Pakarinen 1978a; Hemond 1980) and in the actively growing parts of vascular plants (Small 1972; Malmer and Nihlgard 1980), as they are in upland vegetation.

Enormous amounts of organic matter can accumulate as peat in bogs. In spite of the slow decay, and in contrast to popular belief, many elements are removed from the peat before it becomes anaerobic (Damman 1978a). The extent to which nutrients are retained depends mostly on the element and the time the peat remains above the summer water level. Nevertheless, storage can be considerable, because of the large amounts of peat, even for elements present in low concentrations. Accumulation in this ecosystem compartment increases with the rate of peat accumulation in the bog. This applies particularly to elements stored in organic form in undecayed peat.

Large amounts of C, N, and P are stored in the undecayed peat, but almost all of the N and P is unavailable to plants. Carbon accumulation is directly proportional to the amount of organic matter stored and depends on productivity and decay. The same applies to N, but the accumulation process is more complicated because of immobilization of N in the microbial biomass. Therefore, N concentrations in the peat can vary among peatlands.

In nutrient-rich, minerotrophic peatlands, N concentrations increase with depth because of N immobilization in the peat and generally remain rather constant after the C/N quotient is less than 20 (Damman 1987). This is comparable to changes in most decaying plant litter. In ombrotrophic bogs, N immobilization also occurs (Malmer and Holm 1984), but it is limited by the deficiency of other elements. Therefore, N concentrations decrease initially with depth, then increase slightly and generally stabilize at C/N quotients over 50 (Damman 1988). This corresponds roughly to peat with less than 1.2% N (Figure 24).

Most bogs discussed here fit between the strongly minerotrophic and the ombrotrophic peatlands. It is unlikely that C/N ratios will drop much below 30 in any of the peat bogs in the Northeast. In the oligotrophic floating and quaking bog-lake systems, N concentrations in the upper part of the bog mat (Figure 24) change with depth almost as in ombrotrophic bogs, but they increase abruptly in the gyttja deposited below the mat (Damman 1988).

Phosphorus accumulation in the peat shows a pattern similar to that of N, although the actual amounts of P are much smaller than for N. Magnesium and Ca are also retained in the undecayed peat, but for these ions adsorption on the cation exchange complex of the peat appears important. Magnesium can accumulate considerably in Sphagnum peat (Damman 1978a; Hemond 1980). Data on other peat types are few (Mörnsjö 1968; Tallis 1973; Lyons 1981), but concentrations appear similar. They are usually about 1 mg Mg/g in the deep peat except in inland regions where the concentration in ombrotrophic peat can be much lower (Damman, unpubl.). Calcium is also stored in large amounts in the peat. Concentrations are lowest in ombrotrophic Sphagnum peat of oceanic areas (Damman 1978a) and increase with distance from the coast. They are much higher in peat influenced by mineral soil water (Mörnsjö 1968; Tallis 1973; Lyons 1981).

Several elements are removed from the peat before it becomes anaerobic, and they accumulate in the zone of water level fluctuation (Fe, Al, Zn, Pb) or just above it (Mn) (Damman 1978a). In ombrotrophic bogs their concentration is very low in the anaerobic peat. However all, except Pb, occur in much higher concentrations in peat influenced by mineral soil water

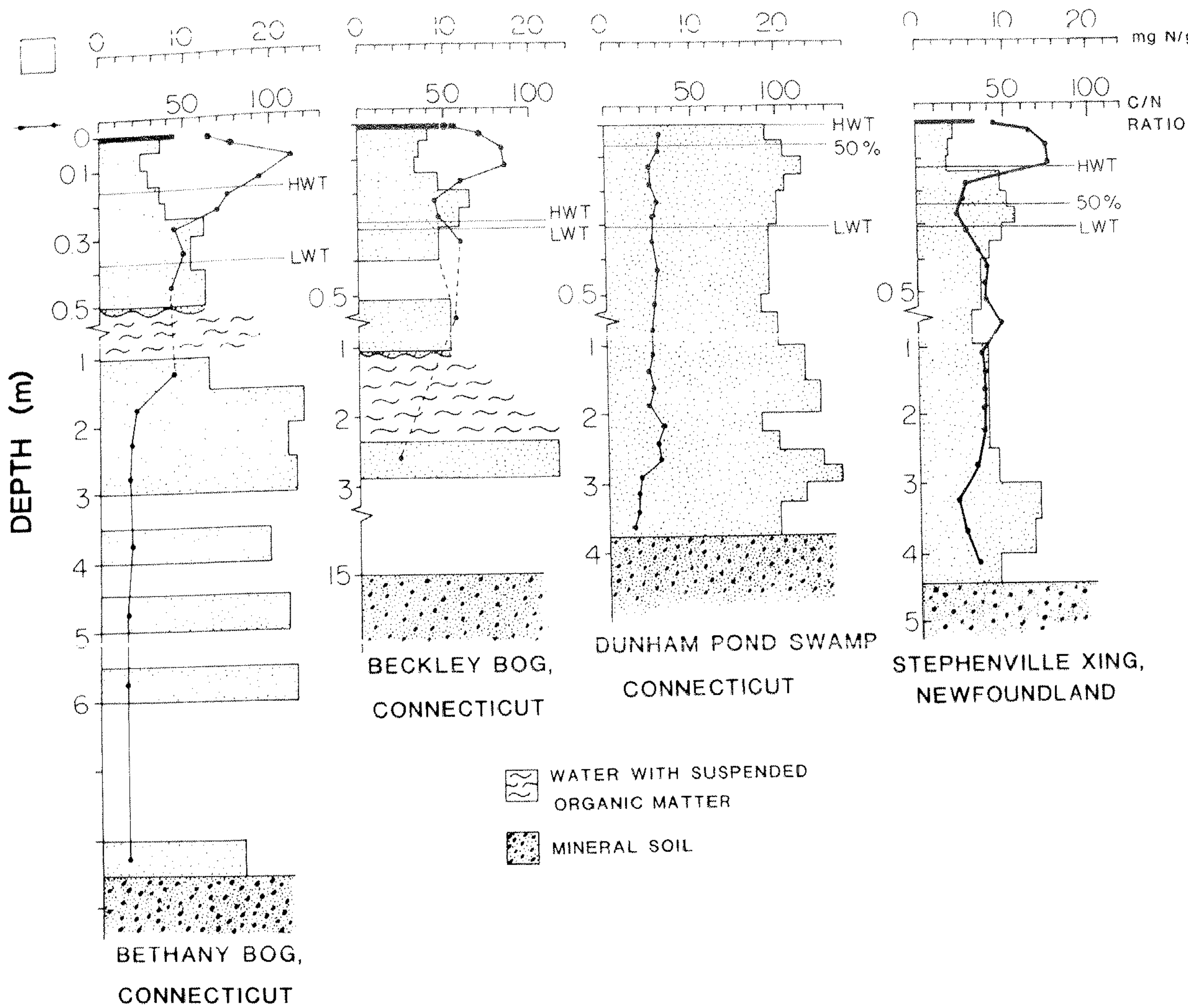


**Figure 24. Nitrogen concentration and C/N quotient in cores from an oligotrophic lake-fill bog (Bethany Bog), an oligotrophic floating mat (Beckley Bog), a mesotrophic red maple swamp (Dunham Pond) and an ombrotrophic bog (Stephenville Crossing). High water table (HWT) and low water table (LWT) are shown; 50% water table is the level at or above which the water table occurred for 50% of the 1980 vegetative season.**

(Damman 1979b; Laundre 1980; Damman and Dowhan 1981) and in other peat types (Mörnsjö 1968; Tallis 1973). Consequently, the concentrations of these elements in the peat vary among bogs, depending on mineral soil water input and water-level fluctuation.

Lead is derived mostly from atmospheric pollution. Therefore, concentrations in and above the zone of water-level fluctuation vary regionally, but concentrations in the deeper, anaerobic peat remain very low (Damman 1978a; Pakarinen 1978b; Damman 1979b; Laundre 1980). Livitt et al. (1979) and Hemond (1980) attributed the low Pb concentrations at greater depth to lower Pb fall-out at the time the older peat was deposited. However, this historical pattern seems to be usually overruled by the water-level effect (Damman 1978a). Even in isolated Southern Hemisphere bogs, which have not experienced an increase in Pb pollution, Pb concentrations are highest in the peat above the low water-level (Damman, unpubl.). Apparently, Pb accumulates in the peat of floating or quaking-bog mats with an almost stable water table as shown by Hemond's (1980) data.

Sodium occurs in low concentrations in the anaerobic peat (Mörnsjö 1968; Tallis 1973; Damman 1978a, 1979b; Laundre 1980), and amounts stored are relatively small. The same applies to K, except that its concentration can be high in peat influenced by mineral soil water (Mörnsjö 1968; Tallis 1973).

## 4.3.5. Elements Removed from Peat Bogs

Removal of elements, like their storage, depends on peat accumulation and bog type. Interpretation of the literature is further complicated by unknown inputs in all but the genuinely ombrotrophic bogs, as well as by seasonal variation in ionic concentrations of the drainage water that is rarely accounted for. Presumably, outputs will equal inputs as production equals decay, and no further bog growth takes place. However, this can require very long periods.

Low concentrations of dissolved N are present in the drainage water from bogs, and almost all of it occurs as $NH_4$ ions (Boatman et al. 1975; Urban 1983; Vitt and Bayley 1984). Most N appears to leave bogs as particulate organic N (Crisp 1966; Urban 1983) and probably also in dissolved organic matter. Denitrification losses from bogs are not well documented, but they are probably small, since nitrate concentrations are low and the pH is too low for nitrification (Rosswall and Granhall 1980; Hemond 1983). Urban (1983) attributed about 25% of the N output to denitrification, but this appears too high for most peat bogs. Both denitrification and losses of dissolved N are more important in peatlands with large nutrient inputs. About 20% of the N added was lost in the drainage water during the 2 years following fertilization of a blanket bog (Burke 1975).

Uptake of Cl by the vegetation is negligible and, as an anion, it is not adsorbed on the peat. Therefore, retention of Cl in bogs is limited and mostly in the water in pools and peat. It is flushed out at about the same rate it enters (Vitt and Bayley 1984). In large bogs, Cl concentrations increase as the water seeps through the bog because of water losses by evapotranspiration. Sodium behaves much the same way (Boatman et al. 1975; Damman 1986), but more of this element is stored in the peat and biomass (Mörnsjö 1968; Tallis 1973; Damman 1978a).

Most K leaves the bog in ionic form (Verry 1975; Burke 1975; Damman 1986), although Crisp (1966) also found large losses of K in particulate organic matter in an eroding blanket bog. The ability of bogs to retain K is limited since storage is mostly in the living biomass. This is also documented by the large losses of K after fertilization (Burke 1975). Under undisturbed condtions, K losses are largest from peatlands receiving substantial mineral soil water inputs.

Magnesium occurs in ionic form in the drainage water, but it is also strongly adsorbed on peat particles. The limited data on Mg outputs seems to suggest large regional differences. Apparently, losses in the drainage water are smaller in inland areas (Hemond 1980; Vitt and Bayley 1984) than in oceanic regions (Boatman et al. 1975; Damman 1986).

Most bogs are deficient in Ca and much of the input is retained (Boatman et al. 1975; Vitt and Bayley 1984) mostly by cation exchange (Damman 1986). Even a fertilized blanket bog (Burke 1975) lost only 4% and 8% of the added Ca from a drained and undrained area, respectively, in the two years following fertilization. Calcium concentrations are low in drainage water from nutrient-poor and actively growing peat bogs. They increase as telluric inputs increase. Among undisturbed bogs, higher concentrations can be expected in drainage water from bogs in inland areas than in coastal regions.

Phosphorus concentrations in bog water are low, and most P appears to be removed in particulate organic matter (Crisp 1966). Large amounts of P are stored in the peat, but the capacity of bogs for storage of additional amounts seems very limited (Malmer 1974; Burke 1975).

Urban et al. (1986) estimated that 60%-93% of the annual sulfur loadings are retained in bogs of eastern North America. Retention is clearly related to water-level fluctuations with permanently wet bogs storing more S than those with strongly fluctuating water levels. Regional differences in $SO_4$ inputs from air pollution are large (U.S.-Canada Workgroup 1982; Munger and Eisenreich 1983), and this is reflected in concentrations in the drainage water from bogs.

Concentrations of elements derived mainly from mineral soils, such as Fe, Mn, and Al, are highest in drainage water of bogs receiving telluric water. Lead occurs in bog water in much lower concentrations than in rain water (Hemond 1980), and input in runoff and seepage from upland areas is negligible (Damman 1979b). The distribution of Pb in peatlands (Damman 1978a; Laundre 1980) suggests that the highest concentrations can be expected in drainage from bogs with high water levels.

# CHAPTER 5. PEAT BOG VEGETATION

## 5.1 FLORISTIC COMPOSITION OF THE PLANT COMMUNITIES

Vegetation changes within a bog and the differences among bogs are controlled primarily by habitat conditions, especially hydrology and water chemistry. Climatic differences are reflected in the floristic composition of the vegetation of comparable habitats in different parts of the region. This community profile includes parts of three vegetation zones (Figure 2) and geographic changes in floristic composition can be considerable.

This section describes the major habitat-related variation in the peat bog vegetation, including the major geographic changes within the region. The distribution of the plant communities within the major peatland types is discussed in the following section.

The literature on peatland vegetation is fragmentary and inadequate, especially that on topogenous peat bogs. Reports on the vegetation of individual peat bogs have been numerous, but they consist mainly of incomplete species lists, sometimes with brief, superficial descriptions of the vegetation. Notable exceptions to this are the pioneering studies of Osvald (1928, 1955, 1970) on the North American peatland vegetation, which included floristic details on a number of bogs in the Northeast, and the work by Damman (1977). The latter dealt, however, only with the vegetation of the ombrogenous bogs of northeastern Maine. A few recent studies by Worley (1981) and Davis et al. (1983) provided a classification for the peatland vegetation of Maine, but their units are defined too broadly to reflect the floristic differences with respect to hydrology, water chemistry, and geographical location.

This lack of information hampered the preparation of this section, which is based primarily on my own unpublished data supplemented with whatever could be gleaned from the literature. Most helpful in this respect were the studies by Nichols (1915) and Osvald (1970), both carried out in the early part of this century.

Five major physiognomic vegetation units can be recognized in peatlands: forest, tall-shrub thickets, dwarf-shrub heath, vegetation dominated by grass-like plants (graminoids), and carpet or mud-bottom vegetation. In topogenous peatlands, the first three make up most of the vegetation. The last two play a minor role here, but they cover large areas in soligenous and northern ombrogenous peatlands (Sjörs 1961; Damman 1978b, 1979a; Glaser et al. 1981). Within the northeastern United States, they are important only in fens (Osvald 1970, Sorensen 1986) and in the plateau bogs along the northeast coast of Maine (Damman 1977).

On ombrotrophic peat the occurrence of these physiognomic vegetation units is closely tied to the depth of the water table (Malmer 1962a, Damman and Dowhan 1981), with the carpets and mud-bottoms occupying the wettest, most frequently flooded sites and the forests on the well-drained peat. The water-table depth controls the distribution of trees indirectly by its effect on nutrient supply. Nutrient uptake is improved on better-drained peat by increased decay and greater rooting depth.

On minerotrophic peatlands, the relationship between the physiognomy of the vegetation and water level is much more complex, because several tree species can grow on permanently inundated habitats if nutrient supply is adequate. Only excessive water level fluctuations may eliminate them here.

The floristic composition of the major peat bog community types of the region will be described within the framework of the major physiognomic vegetation units. This description will be limited mostly to the genuine bog vegetation. The bog border vegetation and other strongly minerotrophic vegetation vary widely in floristic composition depending on the mineralogy of the surrounding parent materials. Describing the floristic composition of this vegetation is beyond the scope of this community profile. However, some of these communities will be described in a general way in discussing the pattern of vegetation types within the major bog landforms of the region. In addition, Table 4 shows the effect of habitat changes on the dominant tree species in the bog border forests of each of the three forest zones of the region.

An overview of the floristic composition of the common plant community types of the bogs, and the differences among them, is given in Tables 5, 6, 7, and 8. These types are based on habitat-related differences in species composition and on data collected throughout the range of the types. There are clear phytogeographic changes within this region that are also reflected in the bog vegetation. This affects especially vegetation types with a large geographical range crossing major vegetation zones (Figures 2 and 3).

These geographic changes could not be adequately expressed in tabular form without describing each of the habitats separately for each vegetation zone. This approach would have resulted in an unwieldy number of vegetation types and would have confounded the discussion of the vegetation-habitat relationships. As an alternative, peat bog plants showing a clear geographic pattern within the region are listed in Table 9. This table shows the species that are present in certain parts of the region.

### 5.1.1. Forests

Forests occur extensively on peatlands but mostly on nutrient-enriched sites. These forests may be geographically associated with peat bogs, usually occupying the bog border, but they are not part of the bog vegetation proper. The composition of these forests varies with seepage flow and fertility of the surrounding uplands. Floristic composition will not be discussed here, but the major trends in the dominant tree species are shown in Table 4. In general, red maple (Acer rubrum) and Atlantic white cedar (Chamaecyparis thyoides) forests occupy the bog borders and dominate the forested swamps of the Appalachian Oak Zone (Nichols 1915;

**Table 4. Major trends in the dominant tree species in peatland forests with respect to nutrient regime and geographical location.**

| Zone | Eutrophic and mesotrophic seepage water | Mesotrophic stagnant water | Oligotrophic stagnant water |
|---|---|---|---|
| Appalachian Oak | Acer rubrum<br>Tsuga canadensis | Chamaecyparis thyoides<br>Acer rubrum | Picea mariana |
| Northern hardwoods | Acer rubrum<br>Thuja occidentalis<br>Tsuga canadensis | Acer rubrum<br>Thuja occidentalis | Picea mariana |
| Boreal and Coastal Spruce-fir | Picea mariana<br>Abies balsamea | Picea mariana | Picea mariana |

**Table 5. Floristic composition of the tall-shrub thickets and black spruce bog forests.**

| COMMUNITY | | 1 Highbush Blueberry Thicket | 2 Cinnamon Fern—Highbush Blueberry Thicket | 3 Mountain Holly—Black Spruce Thicket | 4 *Sphagnum magellanicum*—Black Spruce Forest | 5 *Carex trisperma*—Black Spruce Forest |
|---|---|---|---|---|---|---|
| TREE LAYER | Height (m) | 6-12 | 10-16 | 6-12 | 8-12 | 10-15 |
| | Cover (%) | <5 | 2-20 | 15-40 | >50 | >60 |
| *Acer rubrum* (Red Maple) | | ——— | ——— | - - - | - - - | |
| *Larix laricina* (Larch) | | - - - | - - - | ——— | ——— | - - - |
| *Picea mariana* (Black Spruce) | | - - - | - - - | ——— | ▨▨▨ | ▨▨▨ |
| *Pinus strobus* (White Pine) | | - - - | - - - | - - - | - - - | |
| *Pinus rigida* (Pitch Pine) S[a] | | - - - | - - - | | | |
| *Abies balsamea* (Balsam Fir) N | | | | - - - | | ——— |
| SHRUB LAYER (2-3 m) | Cover (%) | 80-100 | 80-100 | <50 | <10 | <10 |
| *Vaccinium corymbosum* (Highbush Blueberry) | | ███ | ███ | | - - - | |
| *Rhododendron viscosum* (Swamp Honeysuckle) | | ▨▨▨ | ▨▨▨ | | | |
| *Rhododendron nudiflorum* (Purple Honeysuckle) | | - - - | - - - | | | |
| *Lyonia ligustrina* (Maleberry) | | - - - | - - - | | | |
| *Pyrus arbutifolia* (Red Chokeberry) | | - - - | - - - | | | |
| *Clethra alnifolia* (Sweet Pepperbush) | | | - - - | | | |
| *Rhus vernix* (Poison Sumac) | | | - - - | | | |
| *Alnus serrulata* (Smooth Alder) | | | - - - | | | |
| *Alnus rugosa* (Speckled Alder) | | | - - - | | | - - - |
| *Ilex verticillata* (Common Winterberry) | | | ▨▨▨ | - - - | | - - - |
| *Viburnum cassinoides* (Wild-Raisin) | | | - - - | ——— | - - - | ——— |
| *Nemopanthus mucronata* (Mountain-Holly) | | | - - - | ▨▨▨ | ——— | ——— |
| HERB LAYER[b] | Cover (%) | <20 | 40-80 | <50 | 30-50 | 40-60 |
| *Chamaedaphne calyculata* | | ——— | - - - | ——— | ——— | - - - |
| *Kalmia angustifolia* | | - - - | - - - | ▨▨▨ | ——— | ——— |
| *Kalmia polifolia* | | | | ——— | - - - | - - - |
| *Ledum groenlandicum* N | | | | ▨▨▨ | ——— | ——— |
| *Rhododendron canadense* N | | | | ▨▨▨ | - - - | - - - |
| *Gaylussacia baccata* | | - - - | - - - | ——— | | |
| *Gaylussacia frondosa* S | | - - - | - - - | | | |
| *Vaccinium angustifolium* | | | | ——— | - - - | ——— |
| *Vaccinium oxycoccos* | | | | ——— | ——— | |
| *Drosera rotundifolia* | | | | ——— | ——— | - - - |
| *Sarracenia purpurea* | | | - - - | - - - | - - - | - - - |
| *Carex trisperma* var. *billingsii* | | - - - | - - - | - - - | ——— | |
| *Carex trisperma* | | | ——— | | ——— | ▨▨▨ |
| *Osmunda cinnamomea* | | | ▨▨▨ | | - - - | ——— |
| *Smilacina trifolia* N | | | | | | ——— |
| *Carex paupercula* N | | | | - - - | - - - | - - - |
| *Carex pauciflora* N | | | | ——— | | |
| *Cornus canadensis* | | | | ——— | - - - | ——— |
| *Maianthemum canadense* | | | - - - | - - - | - - - | ——— |
| *Coptis groenlandica* | | | - - - | - - - | - - - | ——— |
| *Trientalis borealis* | | | - - - | ——— | ——— | ——— |
| *Linnaea borealis* N | | | | - - - | - - - | ——— |
| *Gaultheria hispidula* N | | | | ——— | - - - | ——— |
| *Pyrola secunda* | | | | - - - | | ——— |
| *Clintonia borealis* | | | - - - | - - - | | ——— |
| *Aralia nudicaulis* | | | - - - | | | - - - |
| *Calla palustris* | | | ——— | | | - - - |
| *Dulichium arundinaceum* | | | - - - | | | |
| *Iris versicolor* | | | - - - | | | - - - |
| *Carex crinita* | | | - - - | | | - - - |
| *Carex folliculata* | | | - - - | | | - - - |
| *Carex stricta* | | | - - - | | | |
| *Dryopteris thelypteris* | | | - - - | | | ——— |
| *Symplocarpus foetidus* | | | - - - | | | |
| *Woodwardia virginica* | | | - - - | | | |
| *Carex howei* | | | - - - | | | |

(Continued)

Table 5. Concluded.

| COMMUNITY | | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|---|
| MOSS LAYER | Cover (%) | <60 | 60-80 | 80-100 | 90-100 | 80-100 |
| *Sphagnum magellanicum* | | ——— | ▨▨▨ | ▨▨▨ | ███ | ——— |
| *Sphagnum nemoreum* | | ——— | ——— | ▨▨▨ | ——— | ——— |
| *Sphagnum angustifolium* | | – – – | – – – | ▨▨▨ | ——— | ——— |
| *Sphagnum fallax* | | ▨▨▨ | ▨▨▨ | ——— | – – – | ▨▨▨ |
| *Sphagnum russowii* | | | – – – | | ——— | ——— |
| *Sphagnum fuscum* N | | | | – – – | – – – | |
| *Sphagnum palustre* | | | – – – | | | |
| *Sphagnum fimbriatum* | | – – – | ——— | | | – – – |
| *Sphagnum teres* | | | – – – | | | – – – |
| *Sphagnum centrale* | | | ▨▨▨ | | | – – – |
| *Sphagnum girgensohnii* | | | – – – | | | ▨▨▨ |
| *Sphagnum papillosum* | | – – – | – – – | | | |
| *Sphagnum imbricatum* | | | – – – | | | |
| *Sphagnum riparium* N | | | | | | – – – |
| *Dicranum scoparium* | | – – – | – – – | ——— | – – – | ——— |
| *Polytrichum commune* | | – – – | – – – | | | |
| *Aulacomnium palustre* | | – – – | ——— | – – – | | ——— |
| *Pleurozium schreberi* | | | – – – | ——— | – – – | ——— |
| *Bazzania trilobata* | | | – – – | ——— | ——— | ——— |
| *Dicranum polysetum* | | | – – – | ——— | – – – | ——— |
| *Hylocomium splendens* | | | – – – | ——— | | ——— |
| *Hypnum crista-castrensis* | | | | ——— | | – – – |
| *Ptilidium ciliare* | | | | ——— | – – – | |

███ Dominant; cover over 40%
▨▨▨ Sometimes dominant
——— Usually or always present; variable cover
– – – Occasionally to frequently present
"Blank" Absent or rare

[a]Geographical changes in species composition within a type are indicated as follows: N—occurs commonly in this community type in northern part of region but rare or absent in southern part except at higher elevation; S—occurs in this community type in southern part, rare or absent farther north.

[b]Herb layer includes vascular plants less than 60 cm tall, i.e., also dwarf shrubs and seedings of shrubs and trees.

Bromley 1935). Northern white cedar (Thuja occidentalis) and red maple dominate forested bog borders in the Northern Hardwood Zone, and black spruce (Picea mariana) dominates those in the Boreal Zone. Closed black spruce forests occur rarely in the peat bogs of the Appalachian Oak Zone, but they become common northward.

Two black spruce community types, the Sphagnum magellanicum-black spruce forest and the Carex trisperma-black spruce forest, are included in Table 5. The latter occurs on sites receiving telluric water from the surrounding uplands. It is a common black spruce forest on peat deposits in northern New England. It is included to emphasize the differences with the Sphagnum magellanicum-black spruce forest.

Sphagnum magellanicum-black spruce forest. This community type is found on oligotrophic peat throughout the region, although it is rare in the Appalachian Oak Zone. In northern Maine, this community type occurs also on genuinely ombrotrophic sites such as the slopes of plateau bogs and the centers of convex raised bogs (Damman 1977). This is an open-to-dense black spruce forest and the forest floor is covered with a well-developed Sphagnum carpet, dominated usually by S. magellanicum (Table 5). The density of the dwarf-shrub layer decreases with stand density. Ledum groenlandicum and Kalmia angustifolia are the dominant dwarf-shrubs in the north. The dwarf-shrub layer is impoverished in the Appalachian Oak Zone. Chamaedaphne calyculata is most common, and occasional shrubs of Vaccinium corymbosum are present.

Carex trisperma-black spruce forest. This is the common bog border forest of the Boreal zone and adjacent parts of the Northern Hardwood Zone. It is distinguished most easily by the abundance of Carex trisperma, the regular occurrence of Osmunda cinnamomea, and the well-developed Sphagnum carpet (Table 5). Balsam fir (Abies balsamea) is usually present in these forests.

## Table 6. Floristic composition of the dwarf-shrub bogs.[a]

| COMMUNITY | 1 *Empetrum-Sphagnum fuscum* | 2 *Sphagnum fuscum—Kalmia* | 3 *Sphagnum fuscum—Gaylussacia* | 4 *Sphagnum rubellum—Chamaedaphne*: Mat | 5 *Sphagnum rubellum—Chamaedaphne*: Lake border | 6 *Sphagnum fallax—Chamaedaphne* | 7 *Sphagnum centrale—Chamaedaphne* | 8 *Rhododendron canadense—Chamaedaphne* |
|---|---|---|---|---|---|---|---|---|
| SUBSTRATE | SOLID | | | FLOATING OR QUAKING | | | SOLID | |
| NUTRIENT REGIME | OMBROTROPHIC | | | OLIGOTROPHIC | | | | |
| TREE AND SHRUB LAYER Height (m) | - | 6 | 8 | - | 6 | 1.5 | 1.5 | 5 |
| Cover (%) | 0 | <5 | <5 | <1 | <25 | <2 | <20 | <1 |
| *Acer rubrum* (Red Maple) | | | | | — | - - - | | |
| *Larix laricina* (Larch) | | - - - | - - - | - - - | — | - - - | | - - - |
| *Picea mariana* (Black Spruce) | | - - - | - - - | - - - | — | | | - - - |
| *Pinus strobus* (White Pine) | | - - - | - - - | | - - - | - - - | | |
| *Vaccinium corymbosum* (Highbush Blueberry) | | | | - - - | — | - - - | - - - | |
| *Rhododendron viscosum* (Swamp Honeysuckle) | | | | | - - - | | - - - | |
| *Pyrus arbutifolia* (Red Chokeberry) | | | | | - - - | | | |
| *Alnus serrulata* (Smooth Alder) S[b] | | | | | - - - | | | |
| *Alnus rugosa* (Speckled Alder) | | | | | - - - | | | |
| *Nemopanthus mucronata* (Mountain-Holly) | | - - - | - - - | | - - - | | | |
| *Betula populifolia* (Gray Birch) | | | | | - - - | | | - - - |
| *Viburnum cassinoides* (Wild-Raisin) | | - - - | - - - | | | | | |
| HERB LAYER[c] Height (cm) | 10-15 | 30-60 | 30-70 | 40-60 | 60-90 | 50-70 | 60-80 | 40-60 |
| Cover (%) | 30-80 | 90-100 | 80-100 | 75-100 | 75-100 | 90-100 | 90-100 | 90-100 |
| *Chamaedaphne calyculata* | — | — | — | ▬ | ▬ | ▬ | ▬ | ▬ |
| *Gaylussacia baccata* | | - - - | ▬ | - - - | — | - - - | | |
| *Kalmia angustifolia* | — | ▬ | — | — | — | - - - | | — |
| *Kalmia polifolia* | — | — | — | — | — | - - - | | — |
| *Andromeda glaucophylla* | - - - | | | - - - | | | | - - - |
| *Ledum groenlandicum* N | — | — | — | - - - | - - - | | | — |
| *Rhododendron canadense* N | - - - | - - - | - - - | | | | - - - | — |
| *Vaccinium angustifolium* | — | — | — | | | | | - - - |
| *Eriophorum spissum* | — | — | — | - - - | | | | — |
| *Vaccinium oxycoccos* | — | — | — | — | — | - - - | - - - | — |
| *Drosera rotundifolia* | — | — | — | — | — | - - - | | |
| *Sarracenia purpurea* | — | — | — | — | — | - - - | - - - | — |
| *Pyrus floribunda*[d] | — | — | — | | — | | | — |
| *Cornus canadensis* | | - - - | - - - | | | | | |
| *Trientalis borealis* | — | — | — | | | | | |
| *Calopogon pulchellus* | — | - - - | - - - | - - - | | | | |
| *Melampyrum lineare* | — | - - - | - - - | | | | | |
| *Scirpus cespitosus* N | — | - - - | | | | | | |
| *Rubus chamaemorus* NC | — | — | | | | | | |
| *Empetrum nigrum* NC | — | — | | | | | | |
| *Gaylussacia dumosa* SC | - - - | - - - | - - - | - - - | - - - | | | |
| *Arethusa bulbosa* | | | | - - - | - - - | | | |
| *Solidago uliginosa* | — | - - - | - - - | | | | | |
| *Myrica gale* N | | | | - - - | — | - - - | - - - | - - - |
| *Pogonia ophioglossoides* | | | - - - | | - - - | - - - | | |
| *Cypripedium acaule* | | | - - - | | | | | |
| *Carex pauciflora* N | | | | - - - | - - - | | | |
| *Rhynchospora alba* | | | | — | — | - - - | | |
| *Eriophorum virginicum* | | | | — | — | - - - | | - - - |
| *Eriophorum angustifolium* N | | | | | | - - - | | — |
| *Vaccinium macrocarpon* | | | | | - - - | - - - | - - - | |
| *Carex trisperma* var. *billingsii* | | | | — | — | - - - | | |
| *Peltandra virginica* S | | | | | — | - - - | | |
| *Decodon verticillatus* S | | | | | — | - - - | | |
| *Cephalanthus occidentalis* S | | | | | — | - - - | - - - | |
| *Woodwardia virginica* S | | | | | - - - | | | |
| *Hypericum virginicum* | | | | | — | | - - - | |
| *Carex canescens* | | | | | — | | - - - | |
| *Carex lasiocarpa* | | | | | - - - | | - - - | - - - |
| *Carex oligosperma* N | | | | | - - - | | - - - | |
| *Spiraea latifolia* | | | | | - - - | | — | |
| *Spiraea tomentosa* | | | | | - - - | | — | |
| *Calla palustris* | | | | | - - - | - - - | - - - | |
| *Carex stricta* | | | | | | | - - - | |
| *Lysimachia terrestris* | | | | | - - - | | - - - | |
| *Carex rostrata* | | | | | | | - - - | - - - |
| *Calamagrostis canadensis* | | | | | | - - - | | |
| *Typha latifolia* | | | | | - - - | - - - | | |
| *Dulichium arundinaceum* | | | | | - - - | - - - | | |

(Continued)

Table 6. Concluded.

| COMMUNITY | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| MOSS LAYER Cover (%) | 90-100 | 60-100 | 60-100 | 90-100 | 80-100 | 90-100 | 30-100 | 75-100 |
| *Sphagnum fuscum* | ■■■ | ▨▨▨ | ▨▨▨ | – – – | – – – | | | ——— |
| *Sphagnum rubellum* | ——— | ——— | ——— | ▨▨▨ | ▨▨▨ | – – – | – – – | ▨▨▨ |
| *Sphagnum nemoreum* | – – – | ——— | ——— | ——— | – – – | – – – | – – – | – – – |
| *Sphagnum magellanicum* | ——— | ——— | ——— | ▨▨▨ | ▨▨▨ | ——— | ——— | ——— |
| *Dicranum bergeri* | ——— | ——— | ——— | – – – | | | | – – – |
| *Mylia anomala* | ——— | ——— | ——— | – – – | – – – | | | – – – |
| *Microlepidozia setacea* | ——— | ——— | ——— | – – – | – – – | | | – – – |
| *Pohlia nutans* | | – – – | – – – | | | | | – – – |
| *Cladonia rangiferina* | ——— | ——— | ——— | – – – | | | | – – – |
| *Cladonia arbuscula* | ——— | ——— | ——— | – – – | | | | |
| *Cladonia mitis* | – – – | – – – | – – – | | | | | |
| *Cladonia alpestris* | ——— | – – – | – – – | | | | | |
| *Polytrichum strictum* | ——— | ——— | ——— | | | | | ——— |
| *Sphagnum imbricatum* O | ——— | ——— | – – – | | | | | |
| *Icmadophila ericetorum* | ——— | – – – | – – – | | | | | |
| *Odontoschisma sphagni* | – – – | – – – | – – – | – – – | | | | |
| *Cladonia crispata* | ——— | ——— | ——— | | | | | |
| *Cladonia cristatella* | | – – – | – – – | | | | | |
| *Cladonia verticillata* | | – – – | – – – | | | | | |
| *Cladonia uncialis* | – – – | – – – | | | | | | |
| *Cladonia squamosa* | – – – | – – – | | – – – | | | | |
| *Cladonia chlorophaea* | | – – – | – – – | – – – | | | | |
| *Pleurozium schreberi* | | – – – | – – – | | | | | |
| *Dicranum scoparium* | | – – – | – – – | – – – | – – – | | | |
| *Sphagnum flavicomans* O | | ——— | | ——— | | ——— | | – – – |
| *Sphagnum tenellum* N | | | | – – – | | – – – | | |
| *Aulacomnium palustre* | | | | | – – – | – – – | – – – | – – – |
| *Sphagnum angustifolium* | | | | | – – – | ▨▨▨ | | – – – |
| *Sphagnum fallax* | | | | – – – | ——— | ▨▨▨ | ▨▨▨ | – – – |
| *Sphagnum papillosum* | | | | | ▨▨▨ | ▨▨▨ | – – – | – – – |
| *Sphagnum fimbriatum* | | | | | | ——— | ——— | – – – |
| *Sphagnum centrale* | | | | | – – – | | ——— | |
| *Sphagnum pulchrum* | | | | | | ——— | | |
| *Sphagnum flexuosum* | | | | | | – – – | | |
| *Sphagnum pulchricoma* S | | | | | | ——— | | |
| *Sphagnum russowii* | | | | | | – – – | | |
| *Sphagnum teres* | | | | | | | – – – | |
| *Sphagnum cuspidatum* | | | | | | | – – – | – – – |

[a]See Table 5 for explanation of symbols.
[b]Geographic differences in the floristic composition of the communities are indicated as follows: S—occurs in this community only in southern part of region; N—common in this community in northern part of region, absent or rare in south; NC—only in northern coastal parts of Maine; SC—only in this community in southern and coastal areas; O—only common in this community in bogs in coastal zones.
[c]Based on height only, includes all vascular plants less than 1 m tall, i.e., also woody species.
[d]This includes *Pyrus melanocarpa* which becomes more abundant in bogs farther inland.

5.1.2. Tall-Shrub Thickets

Tall-shrub thickets dominated by highbush blueberry (Vaccinium corymbosum) and swamp azalea (Rhododendron viscosum) are common in the bogs of the Appalachian Oak Zone and extend into the southern part of the Northern Hardwood Zone. Northward, shrub thickets are usually dominated by Mountain-Holly (Nemopanthus mucronata) and black spruce. Floristically and ecologically, these northern shrub thickets differ profoundly from the ericaceous southern tall-shrub thickets. They lack the southern species (Table 9), and ericaceous shrubs form a dwarf-shrub rather than a tall-shrub layer.

Highbush blueberry thicket. This is the most nutrient-poor of the two highbush blueberry thickets. It occurs mostly on peat soils with strong water-level fluctuations and occasionally on a quaking mat. It is flooded by weakly minerotrophic water but does not receive seepage water.

The ground vegetation is poorly developed and peat is exposed on much of the surface. The influence of weakly minerotrophic water is best expressed in the composition of the moss layer by the presence of Sphagnum fimbriatum, S. fallax, and Aulacomnium palustre (Table 5).

Cinnamon fern-highbush blueberry thicket. These thickets occur on peat soils with strong, seasonal water-level fluctuations, and are influenced by seepage water from the surrounding uplands or are otherwise influenced by minerotrophic

Table 7. Floristic composition of ombrotrophic and oligotrophic vegetation dominated by graminoids.[a]

| COMMUNITY | | 1 *Carex rostrata* fen | 2 Extremely poor fen | 3 *Sphagnum—Scirpus cespitosus* lawn |
|---|---|---|---|---|
| NUTRIENT REGIME | | OLIGOTROPHIC | | OMBROTROPHIC |
| TREE AND SHRUB LAYER | Height (m) | 10 | 5 | - |
| | Cover (%) | <20 | <1 | 0 |
| *Acer rubrum* (Red Maple) | | ——— | | |
| *Larix laricina* (Larch) | | - - - | - - - | |
| *Picea mariana* (Black Spruce) | | - - - | - - - | |
| *Pinus strobus* (White Pine) | | ——— | | |
| *Vaccinium corymbosum* (Highbush Blueberry) | | ——— | | |
| *Rhododendron viscosum* (Swamp Honeysuckle) | | ——— | | |
| *Alnus serrulata* (Smooth Alder) S[b] | | ——— | | |
| *Alnus rugosa* (Speckled Alder) | | ——— | | |
| *Nemopanthus mucronata* (Mountain-Holly) | | - - - | - - - | |
| *Betula populifolia* (Gray Birch) | | ——— | | |
| *Ilex verticillata* (Common Winterberry) | | ——— | | |
| *Lyonia ligustrina* (Maleberry) | | - - - | | |
| HERB LAYER[c] | Height (m) | 50-70 | 25-30 | 15-25 |
| | Cover (%) | 60-80 | 30-80 | 50-80 |
| *Chamaedaphne calyculata* | | ——— | ——— | ——— |
| *Kalmia angustifolia* | | | - - - | - - - |
| *Kalmia polifolia* | | | ——— | ——— |
| *Andromeda glaucophylla* | | | ——— | - - - |
| *Ledum groenlandicum* N | | | - - - | - - - |
| *Rhododendron canadense* N | | - - - | - - - | |
| *Eriophorum spissum* N | | | - - - | - - - |
| *Vaccinium oxycoccos* | | | ——— | ——— |
| *Drosera rotundifolia* | | ——— | ——— | ——— |
| *Sarracenia purpurea* | | - - - | ——— | - - - |
| *Pyrus floribunda*[d] | | - - - | ——— | - - - |
| *Rubus chamaemorus* NC | | | | ——— |
| *Empetrum nigrum* NC | | | | ——— |
| *Scirpus cespitosus* N | | | ——— | ███ |
| *Gaylussacia dumosa* | | | - - - | ——— |
| *Arethusa bulbosa* | | | - - - | ——— |
| *Calopogon pulchellus* | | | - - - | - - - |
| *Solidago uliginosa* | | | - - - | ——— |
| *Myrica gale* N | | ——— | ——— | |
| *Pogonia ophioglossoides* | | - - - | - - - | |
| *Carex oligosperma* N | | | - - - | |
| *Carex pauciflora* N | | | - - - | |
| *Rhynchospora alba* | | | - - - | |
| *Eriophorum virginicum* | | | - - - | |
| *Eriophorum angustifolium* N | | | ——— | |
| *Vaccinium macrocarpon* | | ——— | - - - | |
| *Peltandra virginica* S | | - - - | | |
| *Decodon verticillatus* S | | - - - | | |
| *Cephalanthus occidentalis* S | | - - - | | |
| *Carex lasiocarpa* | | ——— | | |
| *Spiraea latifolia* | | ——— | | |
| *Spiraea tomentosa* | | ——— | | |
| *Calla palustris* | | - - - | | |
| *Carex stricta* | | ——— | | |
| *Dryopteris thelypteris* | | ——— | | |
| *Lysimachia terrestris* | | ——— | | |
| *Carex rostrata* | | ▨ | | |
| *Calamagrostis canadensis* | | - - - | | |
| *Osmunda cinnamomea* | | ——— | | |
| *Osmunda regalis* | | - - - | | |
| *Typha latifolia* | | - - - | | |
| *Dulichium arundinaceum* | | - - - | | |
| *Galium palustre* | | - - - | | |
| *Symplocarpus foetidus* S | | - - - | | |
| MOSS LAYER | Cover (%) | 80-100 | 85-100 | 95-100 |
| *Sphagnum magellanicum* | | - - - | ——— | ——— |
| *Sphagnum rubellum* | | | ▨ | ▨ |
| *Sphagnum fuscum* N | | | ——— | ▨ |
| *Sphagnum fallax* | | ▨ | ▨ | |
| *Sphagnum papillosum* | | ▨ | ▨ | |
| *Sphagnum pulchrum* | | - - - | ▨ | |
| *Sphagnum flexuosum* | | - - - | - - - | |
| *Sphagnum pulchricoma* S | | ——— | | |
| *Sphagnum angustifolium* | | - - - | - - - | |
| *Sphagnum centrale* | | ——— | | |
| *Sphagnum cuspidatum* | | - - - | | |
| *Sphagnum teres* | | - - - | | |
| *Sphagnum fimbriatum* | | ——— | | |
| *Sphagnum russowii* | | - - - | | |
| *Sphagnum palustre* | | ——— | - - - | |
| *Polytrichum commune* | | - - - | | |
| *Sphagnum flavicomans* S | | | ——— | ——— |
| *Polytricum strictum* | | | - - - | ——— |
| *Mylia anomala* | | | - - - | ——— |
| *Sphagnum majus* N | | | ——— | |
| *Sphagnum tenellum* N | | | | - - - |
| *Sphagnum imbricatum* | | | | - - - |
| *Odontoschisma sphagni* | | | | ——— |
| *Cladonia rangiferina* | | | | ——— |
| *Cladonia mitis* | | | | ——— |
| *Cladonia arbuscula* | | | | ——— |
| *Cladonia terrae-novae* | | | | ——— |
| *Cladonia crispata* | | | | ——— |
| *Cladonia uncialis* | | | | - - - |
| *Dicranum leioneuron* | | | | - - - |
| *Dicranum bergeri* | | | - - - | ——— |

(Continued)

Table 7. Concluded.

[a]See Table 5 for explanation of symbols.

[b]Geographic differences in the floristic composition of the communities are indicated as follows: S—occurs in this community only in southern part of region; N—common in this community in northern part of region, absent or rare in south; NC—only in northern coastal parts of Maine.

[c]Includes all vascular plants less than 1 m tall, i.e., also woody species.

[d]This includes *Pyrus melanocarpa*, which becomes more abundant in bogs farther inland.

water. They often form a zone between the previous type and the upland.

The cinnamon fern-highbush blueberry thicket is distinguished from the highbush-blueberry thicket by a much better developed ground vegetation. It also contains many nutrient-demanding species (Table 5). Winterberry (Ilex verticillata) can be abundant in the shrub layer. A well-developed Sphagnum carpet usually covers most of the peat surface.

Mountain holly-black spruce thicket. This thicket often forms the transition from the open bog to the black spruce forests. It is floristically and geographically clearly separated from the highbush blueberry thickets (Table 5). Ericaceous dwarf-shrubs play an important role in the ground vegetation, and the Sphagnum carpet is dominated by species with low nutrient demands. This is the most nutrient-poor of the three tall-shrub thickets.

Table 8. Mud-bottom and *Sphagnum* carpet communities.

| COMMUNITY | | 1 *Rhynchospora alba* mud-bottom[a] | 2 *Carex rostrata* mud-bottom |
|---|---|---|---|
| HERB LAYER[b] | Cover (%) | 30–80 | 65–80 |
| | Height (cm) | 10 | 50 |
| *Rhynchospora alba* | | ——— | ——— |
| *Utricularia cornuta* | | ▬▬▬ | ——— |
| *Xyris montana* N | | - - - | |
| *Drosera intermedia* | | ——— | ——— |
| *Chamaedaphne calyculata* | | ——— | ——— |
| *Andromeda glaucophylla* | | ——— | ——— |
| *Kalmia polifolia* | | ——— | ——— |
| *Drosera rotundifolia* | | ——— | ——— |
| *Vaccinium oxycoccos* | | ——— | ——— |
| *Vaccinium macrocarpon* | | - - - | ——— |
| *Sarracenia purpurea* | | - - - | ——— |
| *Eriophorum virginicum* | | - - - | - - - |
| *Gaylussacia dumosa* SO | | - - - | |
| *Myrica gale* N | | | ——— |
| *Carex rostrata* | | | ▬▬▬ |
| *Phragmites communis* | | | - - - |
| *Pogonia ophioglossoides* | | | - - - |
| *Scirpus cespitosus* N | | - - - | |
| MOSS LAYER | Cover (%) | 100 | 100 |
| *Cladopodiella fluitans* | | ▬▬▬ | ——— |
| *Sphagnum cuspidatum* | | ▨▨▨ | ——— |
| *Sphagnum pulchrum* | | - - - | ▨▨▨ |
| *Sphagnum majus* N | | - - - | ▨▨▨ |
| *Sphagnum tenellum* N | | ——— | |
| *Sphagnum rubellum* | | ——— | ——— |
| *Sphagnum magellanicum* | | ——— | ▨▨▨ |
| *Sphagnum flavicomans* SO | | - - - | |
| *Sphagnum fallax* | | | ▨▨▨ |
| *Sphagnum papillosum* | | - - - | ▨▨▨ |
| *Drepanocladus fluitans* | | - - - | - - - |
| *Odontoschisma sphagni* | | ——— | |
| *Cephalozia connivens* | | - - - | - - - |
| *Microlepidozia setacea* | | - - - | - - - |

[a]*This represents the species composition on ombrotrophic and oligotrophic sites. On sites with stronger mineral soil-water influence, the moss layer is dominated by Sphagnum fallax, S. pulchrum,* or *S. majus*, and the following vascular plants are usually present in the Northern Hardwood Zone and northward: *Eriophorum angustifolium, Carex limosa, Scheuchzeria palustris,* and *Menyanthes trifoliata.*

[b]Distribution within the northeastern United States is indicated as follows: N—common in this community type in the northern part of the region, absent or rare in the south; SO—only in this community type in the southern part of the region and in coastal areas further north.

### 5.1.3. Dwarf-Shrub Heath

Ericaceous dwarf-shrubs make up the ground cover of many bogs (Figure 25). The dominant species depends primarily on the water level and its fluctuation, and secondarily on nutrient regime. With increasing wetness, the dwarf-shrub layer is dominated by Gaylussacia baccata, Kalmia angustifolia, and Chamaedaphne calyculata, respectively. The first two occupy rather well-defined sites in the ombrotrophic parts of bogs, whereas the Chamaedaphne calyculata-dominated dwarf-shrub heath occurs on various oligotrophic and ombrotrophic sites. This community type is very heterogeneous, both floristically and ecologically. It has been divided into five floristically distinct community types. Three of these develop on a floating or quaking mat and are never flooded; the floristic differences between these types are caused by differences in nutrient supply. The other two Chamaedaphne-dominated types are flooded regularly.

In regions with severe winters, ericaceous dwarf-shrubs grow poorly on exposed sites with a thin or erratic winter snow cover. This has a major effect on the floristic composition of the bog vegetation (Damman 1977; Johnson 1977). Such conditions exist in northern coastal Maine, where Empetrum nigrum replaces Kalmia as the dominant species. This is included here as a separate community type (Table 6). Ledum groenlandicum and Rhododendron canadense can be very abundant and occasionally dominant. Within the Northeastern United States, these species usualy dominate in semi-shaded sites such as forest borders and open forests.

The floristic composition of the dwarf-shrub community types is summarized in Table 6. The communities are further described as follows:

Empetrum nigrum-Sphagnum fuscum community (Figure 26). This community is restricted to the coastal areas of the Bay of Fundy, where it occurs in plateau bogs or other ombrotrophic sites. It occupies exposed sites with the maximum water level below the bog surface (Damman 1977). Physiognomically, it is clearly distinguished from other bog communities by the continuous Sphagnum fuscum carpet, the low height (10-15 cm) of the dwarf-shrubs, and the prominence of Rubus chamaemorus and Empetrum nigrum. Scirpus cespitosus is scattered throughout (Table 6). Cladonia species cover usually about half of the bog surface. In extreme coastal areas, Sphagnum imbricatum can be abundant, and Juniperus communis and Myrica gale can occur on the ombrotrophic bog surface. Osvald (1970) and Damman (1977) provided

**Table 9. Species showing clear regional differences in abundance within the region. The southern species are restricted to the southern half of the region, except as shown.**

| Habitat preference | Southern species | Northern species |
|---|---|---|
| Wide ecological amplitude, occur in many types | | Rhododendron canadense<br>Ledum groenlandicum<br>Myrica gale<br>Kalmia polifolia<br>Andromeda glaucophylla<br>Eriophorum angustifolium[d]<br>Carex pauciflora[d]<br>Scirpus cespitosus[d]<br>Dicranum bergeri |
| Dwarf-shrub bogs | Gaylussacia dumosa*[a]<br>Ilex glabra*<br>Myrica pensylvanica*<br>Sphagnum flavicomans*<br>Sphagnum bartlettianum | Cladina spp.[b, d]<br>Empetrum nigrum**, [d]<br>Rubus chamaemorus**, [d]<br>Eriophorum spissum<br>Geocaulon lividum[d]<br>Sphagnum fuscum<br>Icmadophila ericetorum[d]<br>Carex oligosperma[d] |
| Forested bog border and tall-shrub thickets | Vaccinium corymbosum<br>Rhododendron viscosum<br>Rhododendron nudiflorum<br>Lyonia ligustrina<br>Gaylussacia frondosa<br>Pinus rigida<br>Chamaecyparis thyoides<br>Rhus vernix<br>Clethra alnifolia<br>Alnus serrulata<br>Woodwardia virginica<br>Symplocarpus foetidus*<br>Pyrus arbutifolia<br>Carex howei<br>Sphagnum pulchricoma[c] | Nemopanthus mucronata<br>Viburnum cassinoides<br>Pinus banksiana[d]<br>Picea mariana<br>Larix laricina<br>Thuja occidentalis<br>Alnus rugosa<br>Alnus crispa**, [d]<br>Smiliana trifolia<br>Carex paupercula[d]<br>Linnaea borealis<br>Clintonia borealis<br>Gaultheria hispidula |
| Lake border of Chamaedaphne mat and Carex rostrata fen | Decodon verticillatus<br>Peltandra virginica<br>Cephalanthus occidentalis | |
| Mud-bottoms and shallow pools | Xyris caroliniana<br>Sphagnum torreyanum* | Xyris montana<br>Carex limosa<br>Menyanthes trifoliata<br>Sphagnum majus[d]<br>Sphagnum jensenii[d]<br>Sphagnum tenellum[d] |

[a]The following symbols are used to indicate additional geographic trends:

* = Southern species that also occurs in coastal areas farther north;
** = Northern species abundant only along the east coast of northern Maine.

[b]This includes: C. rangiferina, C. mitis, C. arbuscula, C. alpestris and C. terrae-novae. All of these reindeer mosses show the same pattern, with the last primarily occurring in the coastal areas of northern Maine.

[c]This is S. recurvum P. Beauv. The latter name has not been used here to avoid confusion since it is also used as a collective name to include S. angustifolium, S. fallax and S. flexuosum.

[d]Species occurring only in northern New England. Others in the column occur throughout the region but are much less common southward.


Figure 25. Ericaceous dwarf-shrubs common in peat bogs of the Northeast: (a) ***Kalmia polifolia***, (b) ***Kalmia angustifolia***, (c) ***Ledum groenlandicum***, (d) *Chamaedaphne calyculata*, (e) ***Andromeda glaucophylla***, (f) *Rhododendron canadense*, (g) *Gaylussacia baccata*, (h) *Gaylussacia dumosa*, (i) ***Vaccinium angustifolium***, (j) *Vaccinium macrocarpon*, (k) *Vaccinium oxycoccos*.

Figure 26. *Empetrum nigrum-Sphagnum fuscum* community (Quoddy Neck, ME). Note the low height of dwarf-shrubs, such as *Kalmia angustifolia*, the common occurrence of *Scirpus cespitosus* and the abundance of lichens.

further details on the floristic composition.

Sphagnum fuscum-Kalmia community (Figure 27). This is the most common dwarf-shrub community in the northern part of the region. It occurs on relatively well-drained peat and often covers the major part of a bog. Near the coast, this community is restricted to small bogs and sheltered parts of large bogs. Kalmia angustifolia forms a 30-40 cm high dwarf-shrub layer that determines the physiognomy of the vegetation and most easily separates it from other dwarf-shrub vegetation on ombrotrophic peat. In the coastal areas of Maine, Empetrum nigrum, Rubus chamaemorus, Sphagnum imbricatum, and S. flavicomans are found regularly in this community type.

Fire destroys the Sphagnum carpet and increases the Cladonia cover, especially that of Cladonia crispata (Damman 1977). Many bogs in northeastern Maine were frequently burnt until about 20 years ago. Depending on fire history, the Sphagnum cover varies greatly. Osvald's (1970) naked Kalmia angustifolia association probably refers to such burnt sites.

Sphagnum fuscum-Gaylussacia baccata community (Figure 28). This community occupies the driest parts of the bogs in the northern part of the region and covers large areas in the center of convex domed bogs (Damman 1977). It is absent in the bogs of the coastal zone of the Bay of Fundy. Gaylussacia baccata dominates the dwarf-shrub layer and is usually 50-60 cm high. Kalmia angustifolia is abundant throughout. This community shares with the two previous types many species of nutrient-poor sites (Table 6). Fires reduce the Sphagnum cover and increase the Cladonia cover as described for the Sphagnum fuscum-Kalmia type. Trees are often sparse in this type because of fire.

Figure 27. *Sphagnum fuscum-Kalmia angustifolia* community on the slope of a plateau bog (Jonesport Bog, ME). *Kalmia angustifolia* is the dominant dwarf-shrub.

Figure 28. *Sphagnum fuscum-Gaylussacia baccata* community in the center of a convex raised bog (Meddybemps Heath, ME). Fires have removed most of the trees in this part of the bog, but more trees survived the fires near the pools in the bog center (center background).

Sphagnum rubellum-Chamaedaphne community (Figure 29). This community represents the most nutrient-poor vegetation on floating or quaking bog mats throughout the region. Chamaedaphne calyculata and Sphagnum rubellum are always the dominant species; the abundance of many bog species with northern or southern affinities varies with geographic location (Tables 6 and 9). In contrast to the three previous types, lichens are never abundant here.

Toward the lake edge, the mat vegetation is enriched by lake water, especially on the windward side. This results in the presence of many species that are otherwise absent (Table 6). Low trees and shrubs are common in this zone (Fig. 30). The zone shows clear geographical changes in its floristic composition, since many species show southern affinities (Table 9), e.g., Peltandra virginica, Decodon verticillatus, and Cephalanthus occidentalis.

The most prominent difference with the other Chamaedaphne-dominated dwarf-shrub bogs is the dominance of Sphagnum rubellum, or occasionally S. magellanicum, in the moss carpet. In addition, the community lacks many more nutrient-demanding species, especially in the interior of the bog mat vegetation (Table 6). An impoverished form of this community type, in which Chamaedaphne is only 10 cm high, occurs in filled-in pools of ombrotrophic bogs (Damman 1977).

Sphagnum fallax-Chamaedaphne community (Figure 31). This community occurs on floating and quaking bog mats influenced by more nutrient-rich water than the Sphagnum rubellum-Chamaedaphne community. It is found throughout the region but is the most common bog mat vegetation in the southern part of the region. The moss carpet is dominated by either Sphagnum fallax or Sphagnum papillosum. Vaccinium macrocarpon is usually present, and other

Figure 29. *Sphagnum rubellum-Chamaedaphne calyculata* community on quaking bog mat (Beckley Bog, CT). *Chamaedaphne* is the dominant dwarf-shrub species; both *Ledum groenlandicum* and *Kalmia polifolia* are also visible on photograph.

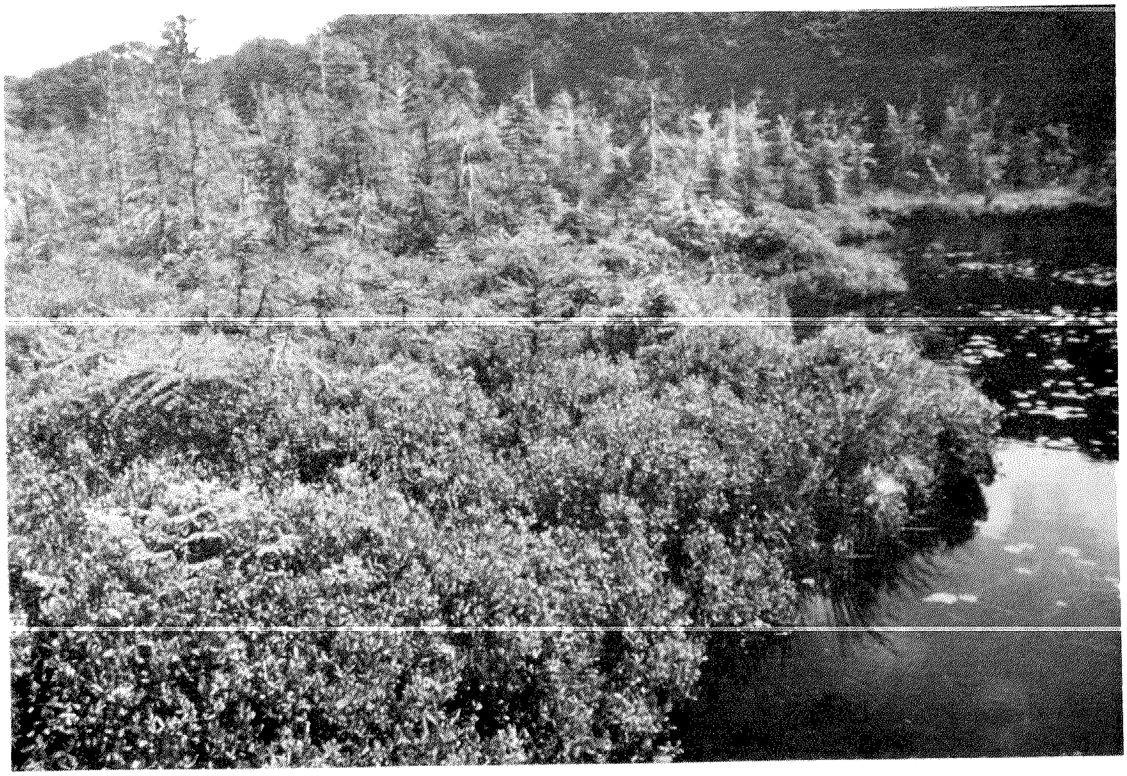

Figure 30. Margin of bog mat enriched by lake water. *Carex lasiocarpa* and many other more nutrient-demanding species are restricted to this part of the mat, and larch and black spruce occur as low trees in this zone (Pond Hill Pond Bog, CT).

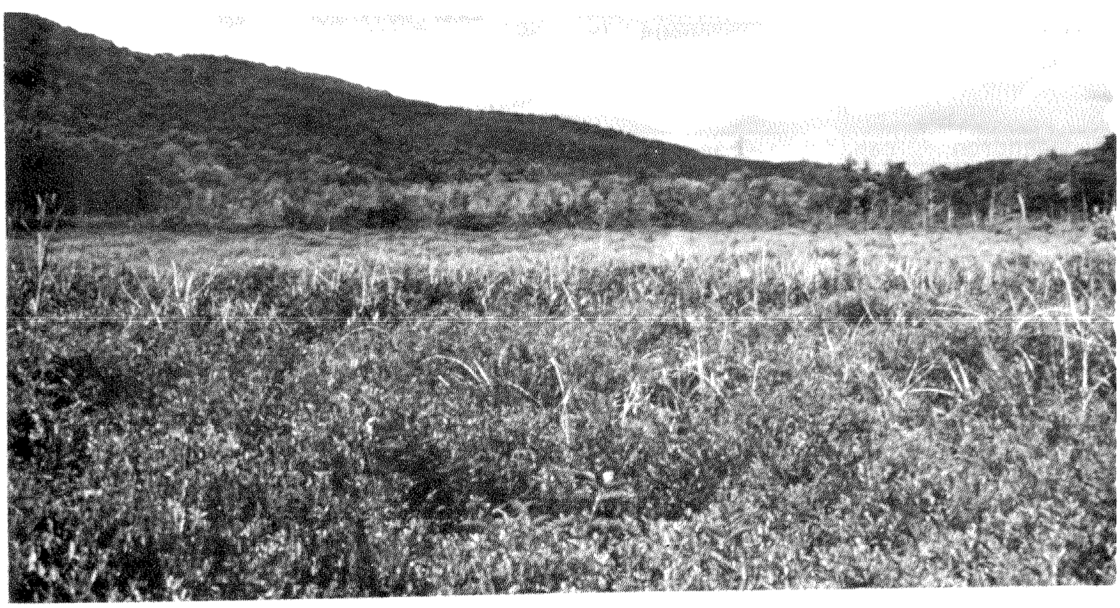

Figure 31. *Sphagnum fallax-Chamaedaphne calyculata* community. The arching shoots of water-willow (*Decodon verticillatus*) are scattered throughout the mat, and buttonbush (*Cephalanthus occidentalis*) can be seen in foreground (Cranberry Pond Bog, PA).

more nutrient-demanding species such as Dulichium arundinaceum occur frequently; other floristic differences are shown in Table 6. The community shows obvious geographic differences. Decodon verticillatus, Sphagnum flavicomans, and S. pulchricoma can be common in the southern bogs, and Eriophorum angustifolium is often abundant in the northern bogs (Tables 6 and 9).

Sphagnum centrale-Chamaedaphne community. This community, flooded regularly by nutrient-poor water, occurs in basins with large water-level fluctuations and more rarely along brooks. It is most common in the southern part of the region, probably because of large evapotranspiration losses and, consequently, larger water-level fluctuations. The community is most easily recognized by the irregular hummocky surface, the evidence of flooding, and its low species diversity. Chamaedaphne calyculata completely dominates the dwarf-shrub layer. Floristically, this is the poorest of the Chamaedaphne dwarf-shrub bogs. The cover of the moss layer varies and is frequently patchy. Sphagnum fallax is usually most abundant; S. centrale and S. fimbriatum are always present (Table 6). Carex stricta is often present on sites with relatively small water-level fluctuations. Low bushes of Spiraea spp., Vaccinium corymbosum, and Rhododendron viscosum are conspicuous in the south.

Rhododendron canadense-Chamaedaphne community. This community occurs in the northern parts of the region where it occupies bog sites flooded by very weakly minerotrophic water or by drainage water from ombrotrophic bogs. The community is found on the lower slope of raised bogs flooded only in the spring by meltwater (Damman 1977), in water tracks of ombrotrophic bogs, and along brooks draining ombrotrophic bogs.

The most conspicuous difference from the other Chamaedaphne dwarf-shrub bogs is the abundance of Eriophorum angustifolium and Rhododendron canadense. It has a well-developed moss carpet dominated by Sphagnum rubellum or S. magellanicum (Table 6).

### 5.1.4. Vegetation Dominated by Sedges

The communities included here are dominated by sedges and have a water table rising above the surface during wet periods. Floristically and ecologically, however, they form a heterogeneous group.

Carex rostrata community (Figure 32). This community is common on wet, nutrient-poor sites that receive seepage from the surrounding uplands. The peat is often less than 1 m deep. Although it is influenced by nutrient-poor minerotrophic water, it represents the most nutrient-rich of the three communities described here.

The Carex rostrata community is floristically and physiognomically clearly distinguished from the other communities described here. Carex rostrata, 60-70 cm high, dominates this vegetation, Chamaedaphne calyculata occurs with variable cover, and a variety of shrubs (Table 7) are scattered throughout. The moss carpet is mostly well developed and dominated by Sphagnum papillosum or S. fallax. Osmunda cinnamomea, Dryopteris thelypteris, Calamagrostis canadensis, Polytrichum commune, Sphagnum fimbriatum, and S. centrale are usually present (Table 7).

Extremely poor fen community (Figure 33). This typical lagg vegetation of the northern half of the region separates the bog vegetation from the surrounding mineral soil or from the shrub-covered minerotrophic bog-border vegetation. It also occurs alone on comparable habitats.

Several grass-like species, e.g., Carex exilis, Scirpus cespitosus, Rhynchospora alba, Eriophorum angustifolium, and E. virginicum, are abundant in the herb layer; nevertheless, the Sphagnum carpet determines the appearance of this community (Table 7). Four Sphagnum species, S. fallax, S. papillosum, S. rubellum, and S. pulchrum, are abundant and make up most of the moss carpet. Several other species, e.g., Aster nemoralis and Smilacina trifolia, clearly distinguish this community.

Sphagnum-Scirpus cespitosus community (Figure 34). This ombrotrophic lawn community occupies most of the center of the

Figure 32. *Carex rostrata* community on shallow minerotrophic peat with scattered larch, red maple, and highbush blueberry. Cinnamon fern (*Osmunda cinnamomea*) clumps are visible at left. Leather leaf (*Chamaedaphne calyculata*) is common but mostly hidden by the sedges (Tobyhanna, PA).

Figure 33. Extremely poor fen community covers an extensive area in this soligenous fen in northern Maine and occupies most of the foreground in the photograph. *Eriophorum angustifolium*, *Carex oligosperma*, and *C. exilis* are the most abundant sedges in this fen (Attean Lake, ME).

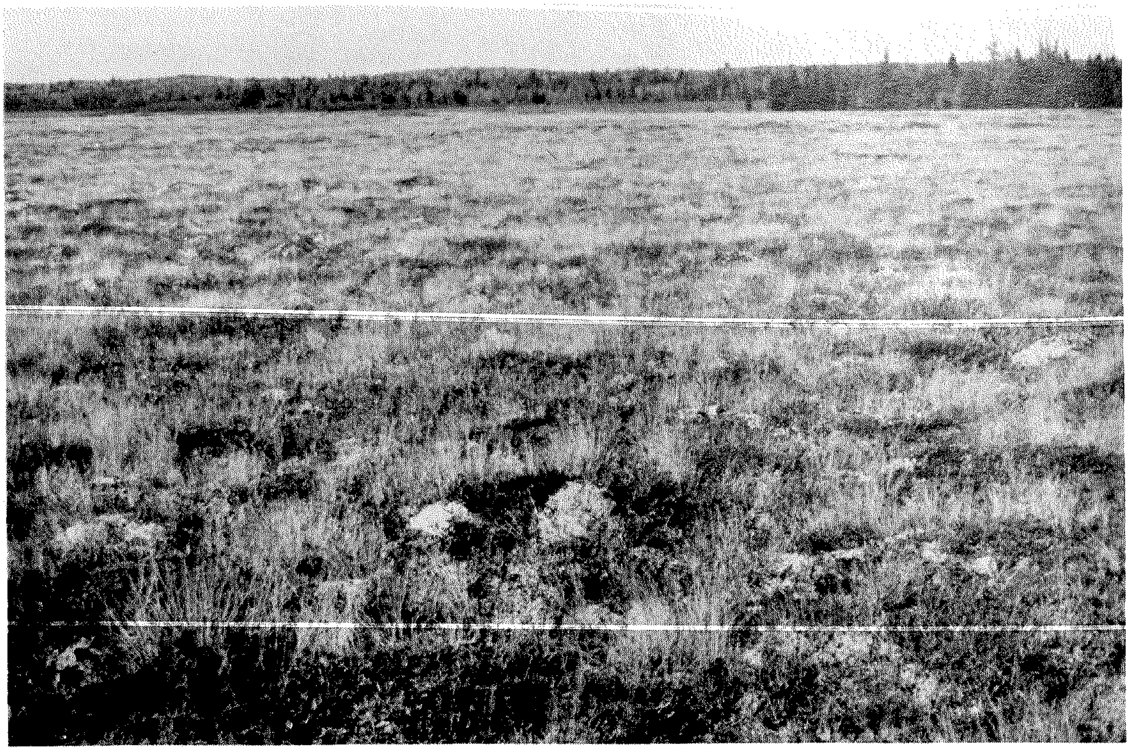

**Figure 34.** *Sphagnum-Scirpus cespitosus* community in the center of a plateau bog (Jonesport Bog, ME). Note the abundance of *Scirpus cespitosus* and lichens, mostly reindeer mosses.

plateau bogs along the Bay of Fundy (Damman 1977). It is widespread further north, but restricted to this area within the Northeastern United States.

The abundance of Scirpus cespitosus and Cladonia species (often over 25%) distinguishes this community, which represents a dry variant of the lawn community occupying the plateau bogs of Nova Scotia (Damman 1977). The species characterizing the oceanic plateau bogs appear in Maine only in a few bogs in extreme coastal locations (Damman and Dowhan 1981). Table 7 shows other floristic criteria separating this from the other communities.

### 5.1.5. Carpet and Mud-Bottom Vegetation

This includes communities of wet depressions consisting either of a very loose Sphagnum carpet or covered with liverworts and resembling surfaces with exposed peat. Carpet and mud-bottom vegetation occur on floating and quaking mats as well as solid peat in ombrotrophic bogs. Nowhere in the region do they cover large areas, but they form a conspicuous part of the bog vegetation. Two communities are described here.

Rhynchospora alba mud-bottom community (Figure 35). This is the normal mud bottom vegetation distributed throughout the region. This community can be dominated by either Cladopodiella fluitans, a liverwort, or by Sphagnum cuspidatum (Damman 1977). Utricularia cornuta is always abundant, but the small leaves are hidden in the moss carpet, and this species is only conspicuous when it is flowering.

Cladopodiella fluitans dominates if the community occupies shallow peaty depressions in the bog that dry up regularly; Sphagnum cuspidatum if it is situated along the margin of a pool or if the Sphagnum mat fluctuates with the water table. Table 8 shows the composition of this community if it occurs within the Sphagnum rubellum-Chamaedaphne community of nutrient-poor floating bog mats.

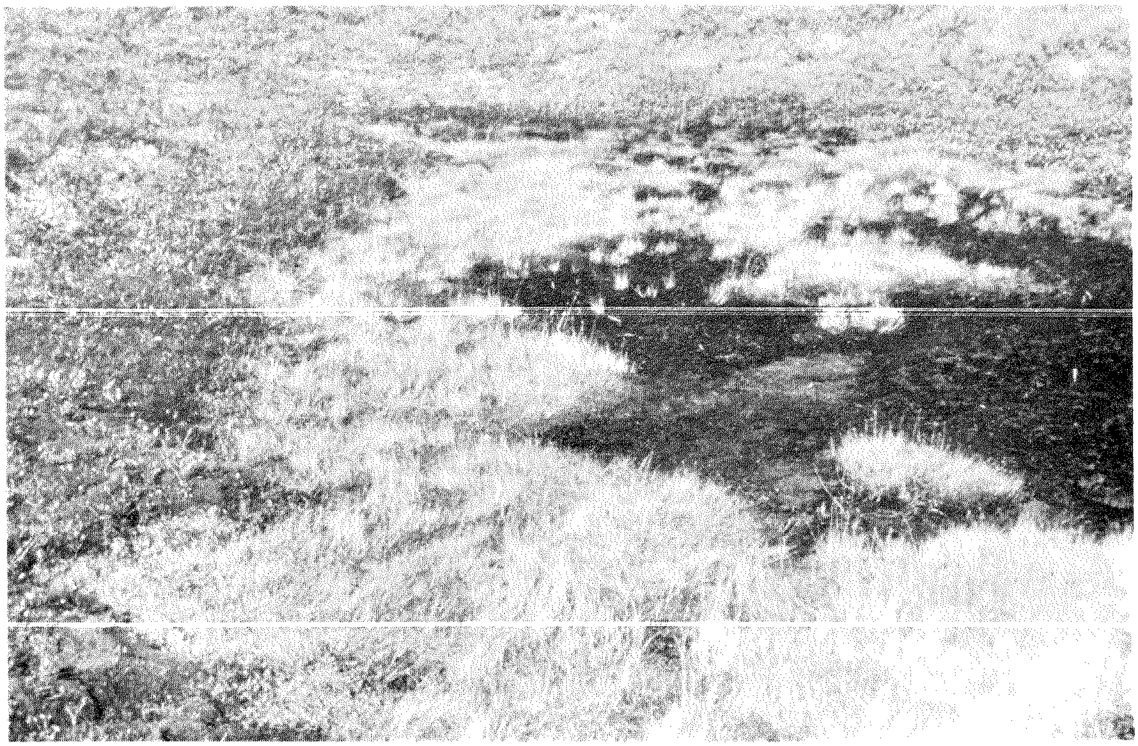

Figure 35. *Rhynchospora alba* mud-bottom community surrounded by dwarf-shrub vegetation (Meddybemps Heath, ME). The liverwort *Cladopodiella fluitans* covers most of the dark area in the right center. The light area surrounding this is dominated by *Rhynchospora alba* and *Sphagnum cuspidatum*. *Utriculara cornuta* is common in both zones but not visible in photographs. A *Sphagnum rubellum* carpet (dark tone) with some leather leaf (*Chamaedaphne calyculata*) separates the mud-bottom vegetation from the dwarf shrub bog.

Northward, Sphagnum tenellum, S. majus, and Xyris montana appear, and several species become more abundant (Table 9). On ombrotrophic bogs, the floristic composition of this community is similar (Damman 1977). In fens within the Northern Hardwood Zone and north, the moss layer is usually dominated by Sphagnum pulchrum, S. papillosum, S. fallax, or S. majus, and the following vascular plants are usually present: Eriophorum angustifolium, Carex limosa, Scheuchzeria palustris, and Menyanthes trifoliata.

Carex rostrata mud-bottom community (Figure 36). Locally Carex rostrata can dominate these mud-bottom sites. This happens most frequently on floating mats in the southern bogs where nutrient-rich lake water or telluric water reaches the bog surface. Such sites represent fen windows in the bog mat, and they develop usually on places where the bog mat is thin. Besides Carex rostrata, several other nutrient-demanding species can be present, e.g., Typha latifolia and Phragmites; the moss carpet has a different composition than in typical mud-bottoms (Table 8).

## 5.2 VEGETATION PATTERNS IN PEAT BOGS

### 5.2.1. Factors Controlling the Vegetation Pattern

Peat bog vegetation frequently shows a distinct zonation, which is often considered a result of hydrarch succession, and elaborate successional diagrams have been developed for plant communities in bogs (e.g., Dansereau and Segadas-Vianna 1952). Succession affects the structure and floristic composition in peat bog-lake systems with open water (Swan and Gill 1970). However, even in these systems much of the vegetation zonation observed is related to

Figure 36. A fen window in *Sphagnum rubellum-Chamaedaphne* vegetation on a quaking bog mat. The sedge *Carex rostrata* dominates the physiognomy of the mud-bottom vegetation in the fen window (Beckley Bog, CT).

the chemistry and flow of water in the bog. In bogs formed by swamping or paludification (Granlund 1932; Gore 1983) of dry land rather than filling-in of a lake, the vegetation pattern is completely controlled by the hydrology of the bog and the source of the water (Sjörs 1948; Malmer 1962a; Damman and Dowhan 1981).

Stratigraphic studies clearly show that succession has been important in controlling the vegetation pattern. However, at present many peatlands are in equilibrium with the climate, and by and large the vegetation zonation remains stable, unless the hydrology is changed. This applies to most of the soligenous and ombrogenous bogs in the northern part of the region but, apparently, is also true for many topogenous bogs. Once a lake is filled in, peat accumulation will not raise the surface much above the water table, unless the climatic conditions allow ombrogenous bog formation. Wetness combined with nutrient deficiency can keep forests from occupying these sites.

The vegetation patterns in bogs can be explained largely by water chemistry and water movement through the bog, and succession is less important in shaping the vegetation than is often assumed. The relation between water chemistry and floristic composition of the bog vegetation has been the subject of many studies (Sjörs 1950; Schwintzer and Tomberlin 1982; Vitt and Bayley 1984). The processes affecting water flow in peat are reasonably well understood; nevertheless, flow through peat bogs is poorly documented and limited mostly to input-output studies (Verry 1975; Hemond 1980). The large local variations in seepage along the bog border, combined with the vertical differences in hydraulic conductivity of the peat, hamper quantification of water flow. Published data on flow patterns within peat bogs are not available for the Northeast. However, this flow pattern determines the changes in water quality and vegetation within a peatland and causes the differences in vegetation patterns among peatlands.

Ivanov (1957, 1981) and Ingram (1983) discussed the various flow patterns in peatlands. Ivanov's elaborate classification is too complex to form the basis for a discussion of vegetation patterns. Also it does not include all conditions found in the bog-lake systems of our region. Nevertheless, his ideas and those of Ingram influenced the following discussion.

### 5.2.2. Vegetation Patterns in Relation to Water Flow and Habitat

The nature of the bog water and its flow pattern will be described for a few of the major peat bog landforms of the region. This information will then be related to the vegetation patterns in these peatlands. This section clarifies the essential features of the various bog landforms, highlights the differences among them, and provides an understanding of the causes of deviations from the patterns discussed here.

Peat bog-lake systems. These systems are all influenced by minerotrophic water, but its effect on the surface vegetation changes during their development. The successional changes in water movement are illustrated in Figure 37. Minerotrophic inputs to the bog come from the lake water and from telluric water seeping in at the bog border. The bogs develop in oligotrophic lakes and, therefore, the seepage water is more fertile. Its chemical composition depends mostly on the nature of the surrounding deposits and the length of the slopes. The amount of seepage is largest in landscapes with compacted till or bedrock near the soil surface, and it shows strong, seasonal variations. In early spring, surface runoff will add to the mineral-soil water input, which is mainly rainwater and melt water that have barely contacted the mineral soil. Consequently, the water is very weakly minerotrophic.

The bog mat floats, and this prevents flooding by the lake. The water table is almost stable, usually at 10-20 cm below the *Sphagnum* surface. Lake water is drawn to the surface by evaporation. At the margin of the mat, lake water can also be thrown on the surface by wave action. This marginal zone becomes more narrow as

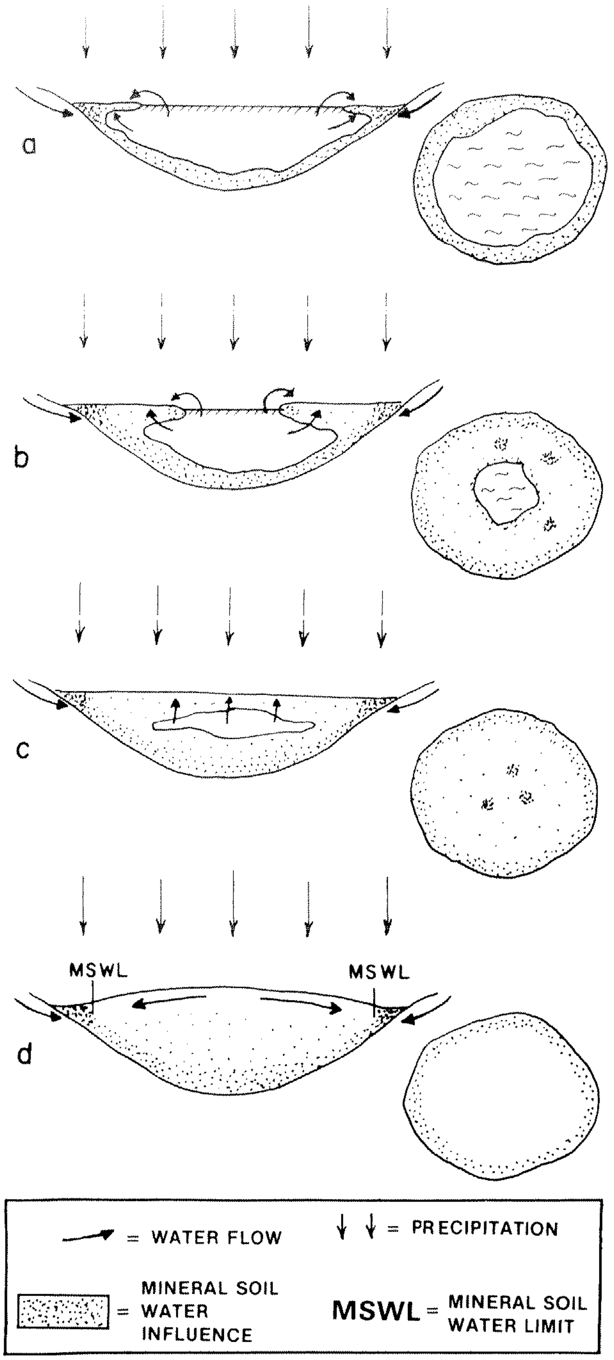


**Figure 37. Changes in water flow and nutrient input to the bog surface during hydrarch succession shown in cross section and plan view. Diagrams a, b, and c show bog development typical for most of the region; diagram d applies only to the three northern peatland zones (Figure 3). Seepage input is rarely uniform along the bog border. The dense clusters of dots in the plan views are fen windows where more nutrient-rich water reaches the bog surface.**

the bog mat grows, and the lake becomes smaller and wave action diminishes. Initially, the pond-border bog is influenced by minerotrophic water in several ways. However, when the mat becomes more extensive, three zones are recognizable (Figure 37): a border zone with seepage input--its effect decreases with distance from the border; a zone influenced by lake water through the bog mat -- its effect decreases with distance from the lake edge; and a zone along the edge of the mat enriched directly by lake water.

The associated vegetation pattern is shown in Figure 38. The diagram for the Appalachian Oak Zone and the southern part of the Northern Hardwood Zone shows the pattern most commonly found in the southern part of the region. In the southern coastal areas, the Atlantic white cedar (*Chamaecyparis thyoides*) can replace much of the *Osmunda*-highbush blueberry thicket. In this case, the cover of *Vaccinium corymbosum* and *Rhododendron viscosum* is much lower. Depending on the water chemistry, the bog mat can be either a *Sphagnum rubellum-Chamaedaphne* community (Figure 38) or the slightly more nutrient-demanding *Sphagnum fallax-Chamaedaphne* community. The occurrence of a *Decodon verticillatus* zone at the edge of the mat is characteristic for the southern bogs; it plays a major role in extending the bog mat into the lake (Nichols 1915). Mudbottoms occupy the low parts of the *Chamaedaphne* mat.

The influence of the lake water is weakest on the hummocks. The bog mat varies also in thickness, and the lake water influence is stronger in some depressions than in others. The *Carex rostrata* mudbottom community occupies thin parts of the mat (Figure 38) or other sites that contact more nutrient-rich water (fen windows). When the bog mat has completely covered the lake, the entire bog center becomes nutrient-poor, although more nutrient-rich depressions persist (Figure 37). Such bogs remain oligotrophic, although the surface peat of hummocks and raised parts can become locally ombrotrophic. At this stage, water with suspended organic matter is still present under the mat, and the bog mat rises and falls with the bog-water level. However, the mat has lost some flexibility and water levels fluctuate within the mat. Presumably, this becomes more pronounced as the bog mat thickens. During the earlier stages of mat development, one can observe a similar increase in water-level fluctuation from the pond edge to the mineral soil contact as the peat becomes grounded. In these filled-in lakes, the *Chamaedaphne* mat covers the entire bog center, but *Decodon verticillatus* often persists in some fen windows. Poorly growing black spruce, red maple, white pine, larch, and pitch pine (*Pinus rigida*) trees are scattered on the *Chamaedaphne* mat.

Major changes occur northward in the plant-community pattern of these bogs. First northern white cedar (*Thuja occidentalis*) replaces the red maple and Atlantic white cedar as the bog-border tree. Finally, black spruce replaces northern white cedar (Figure 38). The *Nemopanthus*-black spruce community forms the transition from the open *Chamaedaphne* mat to the spruce forest, and the *Decodon* zone is absent, so *Chamaedaphne* becomes the principal species extending the bog mat (Swan and Gill 1970).

In the initial stages of lake-fill succession, the process is controlled mainly by conditions in the lake and surrounding uplands. Initially, climate affects succession only indirectly. However, climatic conditions become progressively more important as the mat develops, resulting in geographical differences within the bogs of the Northeast. The relation between precipitation and evapotranspiration during the vegetative season is most important, since these factors control the upward and downward flow of water in the surface peat. Increased precipitation or lower evapotranspiration will make the *Sphagnum* carpet less dependent on water in the capillary zone above the lake-water level. Within the Northeast, this dependence decreases roughly with altitude and from south to north, until true ombrogenous bog development becomes possible in the northern half of Maine.

Moat bogs occur mostly in kettle holes in pitted outwash or kame deposits. They appear to be restricted to basins with

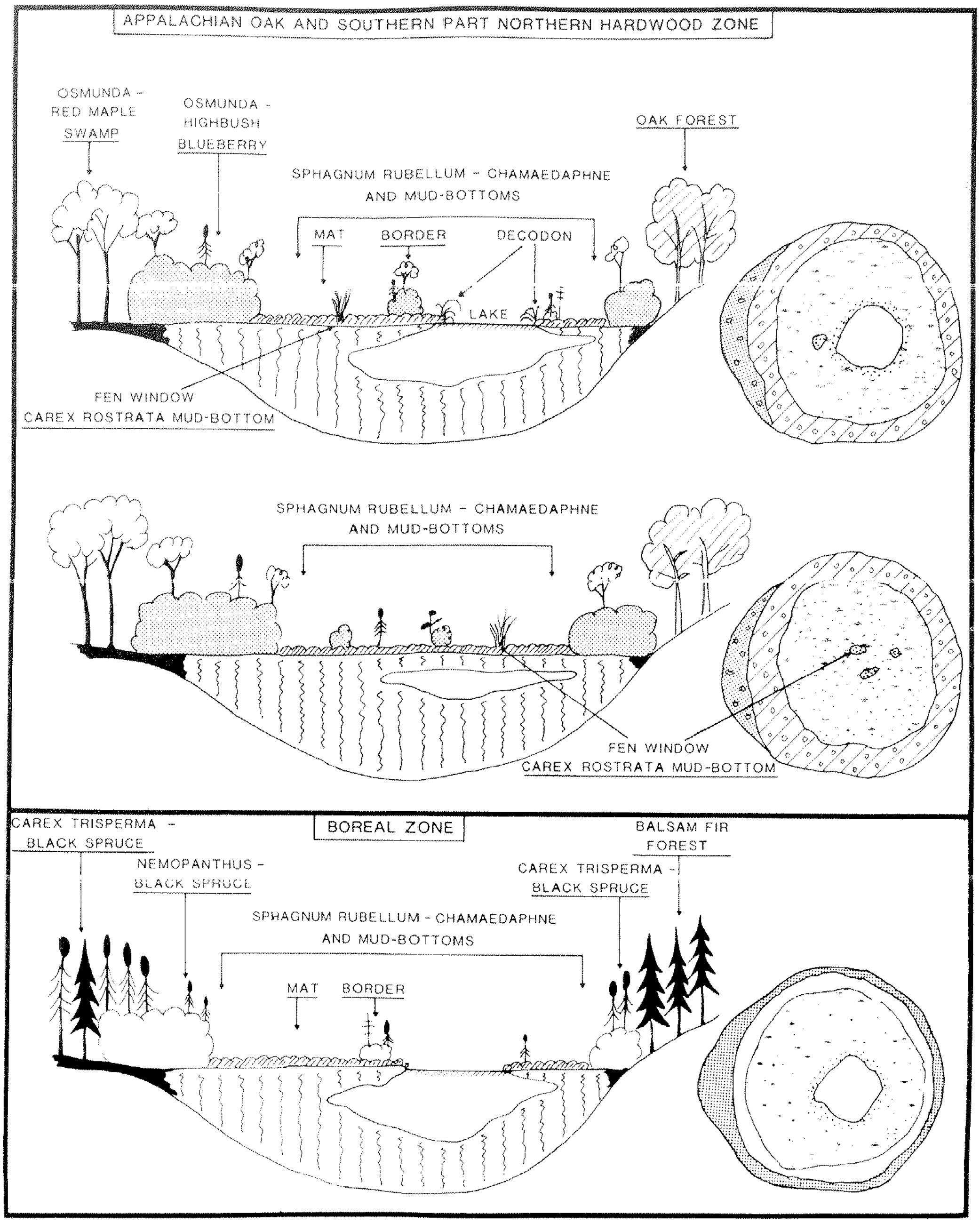


**Figure 38. Vegetation pattern of peat bog-lake systems in southern and northern part of region shown in cross section and plan view. Hemlock can also be common in the borders of bogs of the Appalachian-Oak and Northern Hardwood Zone (Table 4).**

strong water-level fluctuations. Reference to these bogs in the literature are few (Nichols 1915; Rigg 1940; Osvald 1970; Buell and Buell 1975), and their development is poorly understood. Presumably, the moat develops because during dry periods peat decays in the border of moat bogs to a greater depth than in the border of bogs with a more stable water table.

In lake-fill bogs, the bog water becomes gradually more nutrient-poor with distance from the border. The inflow from the upland areas varies, and this causes local fertility differences in the bog border. In contrast, in the moat of the moat bogs the water chemistry is fairly uniform, and the bog becomes more nutrient-poor from moat to bog center.

These moat bogs occur only in the southern part of the region, and therefore the vegetation does not show the geographical changes discussed above for the other peat bog-lake systems. The vegetation pattern of a moat bog is illustrated in Figure 39. The moat completely surrounds the bog mat and varies in width. It has a poorly developed vegetation; button bush (Cephalanthus occidentalis) usually dominates a zone in the moat, and Glyceria canadensis and Scirpus cyperinus are usually present. Carex canescens can dominate a zone along the edge of the floating mat. The vegetation on the floating mat is the Sphagnum fallax-Chamaedaphne community with Sphagnum papillosum often equally or more abundant than S. fallax. The grounded center is occupied by the highbush blueberry community and either the Sphagnum fallax-Chamaedaphne or

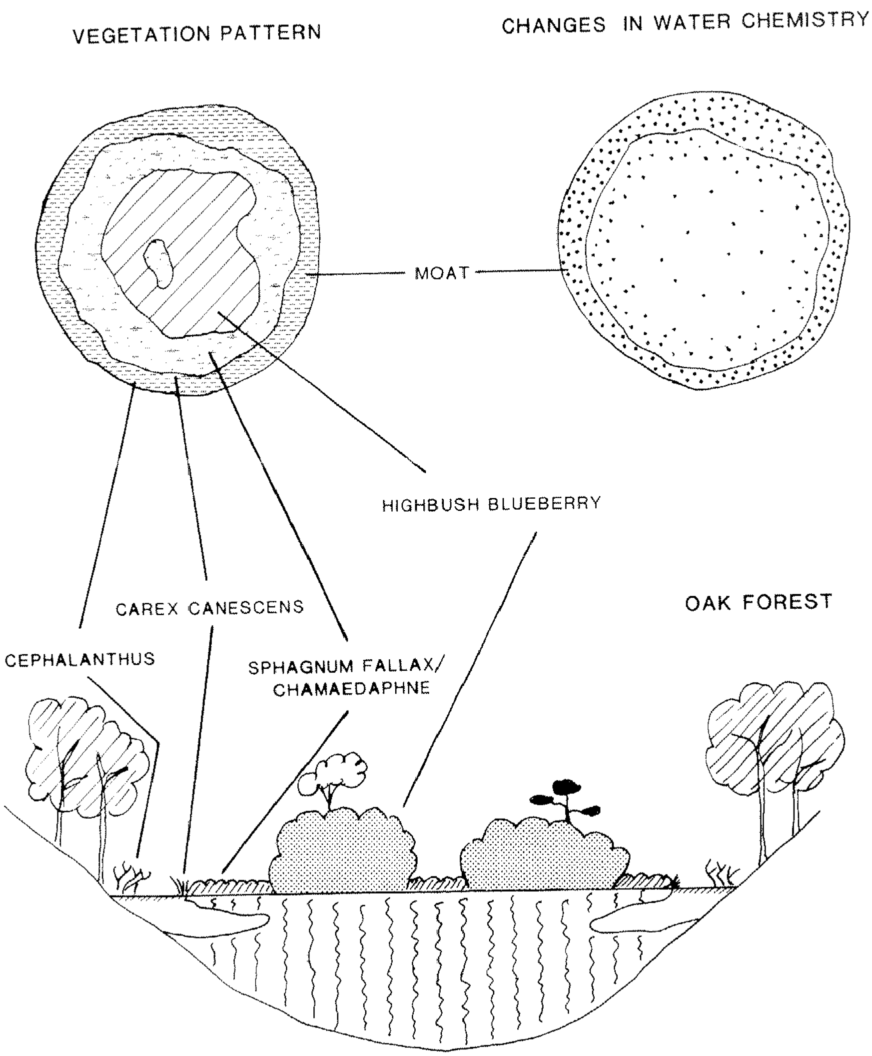


Figure 39. Vegetation pattern and changes in water chemistry in moat bogs. The density of stippling indicates degree of mineral-soil water influence. The nutrient regime in the moat is uniform, but the surface peat becomes more nutrient-poor from the edge of the bog mat to the bog center.

the Sphagnum rubellum-Chamaedaphne communities, depending on the ionic composition of the bog water.

Limnogenous bogs. The summer water-level of these bogs is maintained by streams or lakes. The limnogenous peat bogs occur mostly in association with other peatlands and this influences hydrology. Water movement is toward the stream or lake, but the bogs are also flooded by lake or stream water during high water (Figure 40). Therefore, the minerotrophic water affecting these bogs is derived from two sources. In the nutrient-poor limnogenous bogs, the flooded zone is invariably more nutrient-rich than the remainder of the bog.

The vegetation along the brook varies depending on the ionic composition of the brook water. It is mostly dominated by either Carex lasiocarpa and Sphagnum fallax or if the brook water is more nutrient-rich by Calamagrostis canadensis, sometimes with Carex stricta. Carex rostrata can also dominate this zone. The further sequence depends on the adjacent wetland. Figure 40 shows a sequence commonly encountered when the brook flows through a raised bog. In this case, ombrotrophic water draining from the bog dilutes the bog water in a zone above the Calamagrostis community. This zone is occupied by the Rhododendron-Chamaedaphne community if flooding by weakly minerotrophic water occurs only during very high water-levels, such as during snow melts. If summer flooding is common, this zone is occupied by a Sphagnum centrale-Chamaedaphne community with S. fallax as the major species in the moss carpet.

Oligotrophic peatlands outside lake basins. These minerotrophic peatlands are influenced by oligotrophic water. They have a solid, not quaking, bog surface that can be flooded, but not by lake or brook water. They have developed in various ways. The present conditions at the surface, rather than their origin, determine their hydrology and vegetation.

These bogs lack the large water reservoir of the peat bog-lake systems; therefore they depend more directly on precipitation and mineral-soil water to maintain their water levels. The mineral-soil water can be stagnant (topogenous bogs) or flow laterally through the peat (soligenous bogs). This distinction is not always clear, e.g., in peatlands that receive seepage but show no signs of lateral water movement through the bog.

The hydrology and water chemistry of these peatlands is controlled primarily by (1) the conditions within the watershed of the bog (size, deposit, relief); (2) the size of the peatland; and (3) the climate. The conditions in the watershed affect the amount and chemical properties of the water flowing into the bog. The size of the bog determines the relative effect of seepage and precipitation on water levels

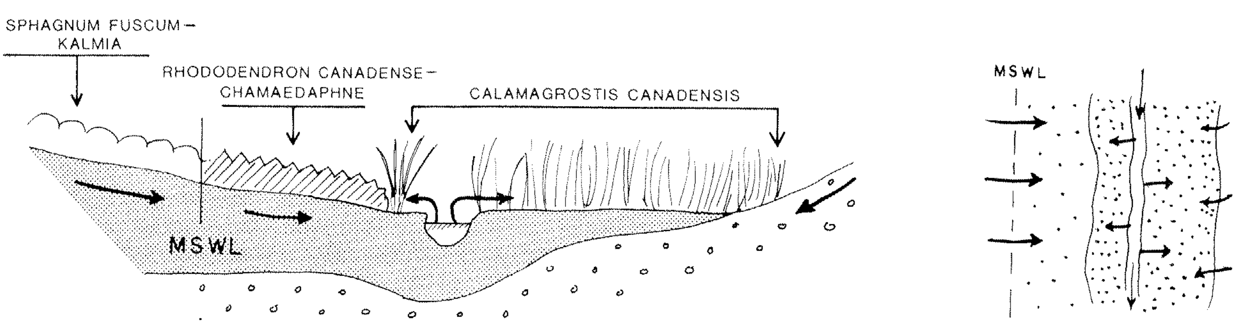


**Figure 40.** Vegetation pattern and water flow in limnogenous bog system associated with an ombrotrophic bog (at left). Inside the mineral-soil water limit (MSWL), the *Calamagrostis canadensis* vegetation is regularly flooded by the brook, but the *Rhododendron canadense-Chamaedaphne* vegetation is flooded only during high spring water levels and receives ombrotrophic water the remainder of the year.

and water chemistry. The climatic conditions, especially precipitation and evapotranspiration, influence both and are responsible for clear geographic trends in these peatlands.

Oligotrophic topogenous and soligenous peat bogs develop on nutrient-poor parent materials and have either small watersheds or are affected by water diluted considerably by rainwater, as in wet climates or large bogs. They can be associated with a lake, but peatland development cannot be attributed to the lake.

Hydrologically, three different conditions should be recognized:

(1) Bogs in basins that do not drain freely and that receive water primarily from precipitation (Figure 41). Water losses occur mostly by evapotranspiration so that water levels fluctuate strongly. These water-level changes are largest in regions with high summer temperatures where evapotranspiration losses are high. They occur most commonly in basins in sandy deposits underlain by clay or silt, or on bedrock if seepage along the slope is insignificant. Site conditions are rather uniform throughout this bog type because of spring flooding. Differences in the position of the peat surface relative to the summer water level are responsible for the largest habitat differences in these bogs. Slightly more nutrient rich conditions occur near the mineral soil contact in the bog border. The wettest sites are often found here because of more rapid decay of the peat.

Virtually no water flows through these bogs. During high-water levels, water may drain from the bog through a drainage channel or leave the bog through permeable deposits in the bog border. This happens mostly in late winter and early spring.

Basins of this type are occupied mostly by a dense highbush blueberry thicket in the Appalachian Oak Zone and the warmest parts of the Northern Hardwood Zone (Figure 41). The Osmunda-highbush blueberry community occupies a somewhat more nutrient rich belt in the bog border. The remainder is usualy occupied by the typical highbush blueberry community unless the bog is small. The *Sphagnum centrale*-*Chamaedaphne* community is found in openings in the thickets and locally along the border. *Calamagrostis canadense* and *Carex stricta* often dominate in a narrow zone between this and the mineral soil.

Basins with these large water-level fluctuations are uncommon northward. If they occur beyond the northern limit of dense *Vaccinium corymbosum* thickets, they are occupied by a *Chamaedaphne calyculata* vegetation.

(2) Bogs in drained basins with limited seepage input. These bogs receive their water supply from oligotrophic seepage water and precipitation. They are found in valleys in till landscapes underlain by acidic bedrock, most commonly in areas with shallow or compacted till. Seepage is seasonal and mostly restricted to the early part of the vegetative season. The surface-drainage pattern is poorly developed in these peatlands, but small brooks frequently drain the large ones. Water movement is through or over the peat and from the bog border to the center (Figure 41). Little is known about drainage into the underlying till; presumably, it is negligible.

The mineral-soil water influence in these basins is much stronger than in the undrained basins described above. Therefore, the *Osmunda*-highbush blueberry community occurs throughout (Figure 41). However, because the seepage flow is weak and seasonal, conditions become more nutrient poor as distance from the border increases. This is clearly visible in the vegetation, and the *Osmunda*-highbush blueberry community is floristically richest near the bog border. Apart from this border zone, the water chemistry seems to vary little, but it is clearly minerotrophic throughout these bogs.

Seepage inflow is usually restricted to certain sites along the bog border, and water flows mostly through channels in the bog. As a result, nutrient-poor pockets with a typical highbush-blueberry community and small patches of *Sphagnum magellanicum*-black spruce forest can occur locally (Figure 41).

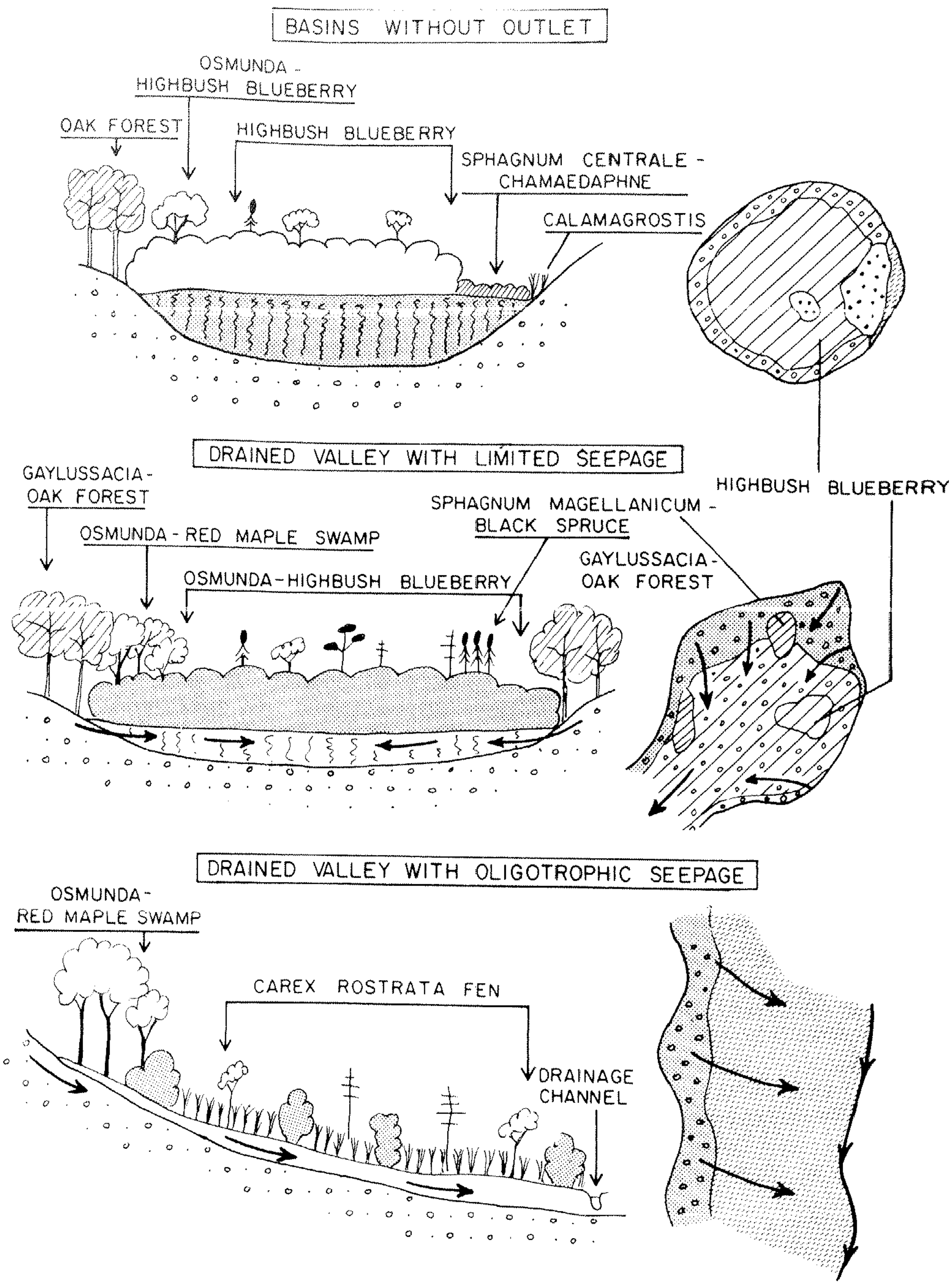


**Figure 41. Vegetation pattern and water flow in perched-water peatlands influenced by nutrient-poor minerotrophic water. The vegetation pattern is controlled by the flow rate and chemistry of the bog water. Hemlock can also be abundant in the border of these peatlands, especially those receiving seepage. See Table 4 for further details on bog border forests.**

This type of highbush blueberry bog is typical for the southern part of the region because dense highbush blueberry thickets do not develop northward. Also, topographically similar habitats receive much more seepage during the summer farther north and are fens or swamps.

(3) Bogs in drained basins with obvious but very nutrient-poor seepage input. These bogs also receive their water supply as oligotrophic seepage water and precipitation. However, here seepage water is supplied throughout most of the vegetative season, regulating water levels so that they fluctuate within narrower limits than in the previous two situations. In addition, the more continuous flow is clearly reflected in the vegetation, with nutrient-demanding plants in areas with higher flow rates. Differences in nutrient inputs are often not expressed in the ionic composition of the bog water except outside the vegetative season. At that time, K concentrations reflect input differences most clearly (Malmer 1962b; Damman 1986).

In the southern part of the region, evapotranspiration losses are so high that this type of soligenous mire can rarely develop. Conditions most closely resembling it in the Appalachian Oak Zone can develop on gentle lower slopes on nutrient-poor parent materials. If the sites remain moist during the summer and the seepage water is nutrient deficient, the Carex rostrata community will occupy such sites (Figure 41). Larch and red maple are scattered, and bushes of Vaccinium corymbosum and Rhododendron viscosum are common. The peat on these sites is usually less than 1 m deep and well decomposed.

Farther north, conditions for the development of soligenous mires with a fen vegetation become more favorable.

Ombrogenous bogs. These are the genuine peat bogs of the cold temperate zone with a topography controlled by differences in peat accumulation. They occur only in the northern part of this region (Figure 2), and are often associated with other peatlands. The vegetation patterns of the three major types of raised bogs (Figure 3) are shown in Figure 42. This illustrates the differences with the oligotrophic bogs that are the focal point of this community profile. The hydrology of ombrogenous bogs is discussed by Rycroft et al. (1975), Ivanov (1981), Ingram (1982, 1983), and Damman (1986). Their vegetation cover is described by Ganong (1897), Osvald (1970), Gauthier and Grandtner (1975), Damman (1977), and Worley (1981).

## 5.3 GEOGRAPHICAL CHANGES IN HYDROLOGY AND VEGETATION

Geographical differences in the hydrology of peatlands result from changes in the surplus of precipitation over evapotranspiration. In peat above a water table, upward movement of capillary water and percolation of rainwater are controlled by these processes when the bog is not frozen. If the moisture surplus increases, the bog surface will become more dependent on precipitation and more impoverished in nutrients. By itself, this process will not lead to ombrogenous bog development but, at most, to local ombrotrophy of the highest parts of the bog surface. Complete ombrotrophy rarely occurs on the hummocks of topogenous and soligenous mires, because vascular plant roots reach into the minerotrophic peat and enrich the surface with leachates and detritus.

Ombrogenous-bog development depends on the rise of the bog surface beyond the influence of minerotrophic water. Since water flows primarily through the relatively undecomposed surface peat or over the surface itself, minerotrophic water continues to affect the surface unless the topography of the bog prevents this water movement. So, in topogenous peatlands water flow has to be reversed to initiate ombrotrophic bog development (Figure 37). This requires a rise of the bog center and the development of a perched water table in the peat to prevent mineral-soil water from reaching the center.

For the bog surface to rise in the center, peat accumulation in this part of the bog has to exceed that in the border. Peat accumulation is the excess of production over decay, but it is due to slow decomposition rather than high production

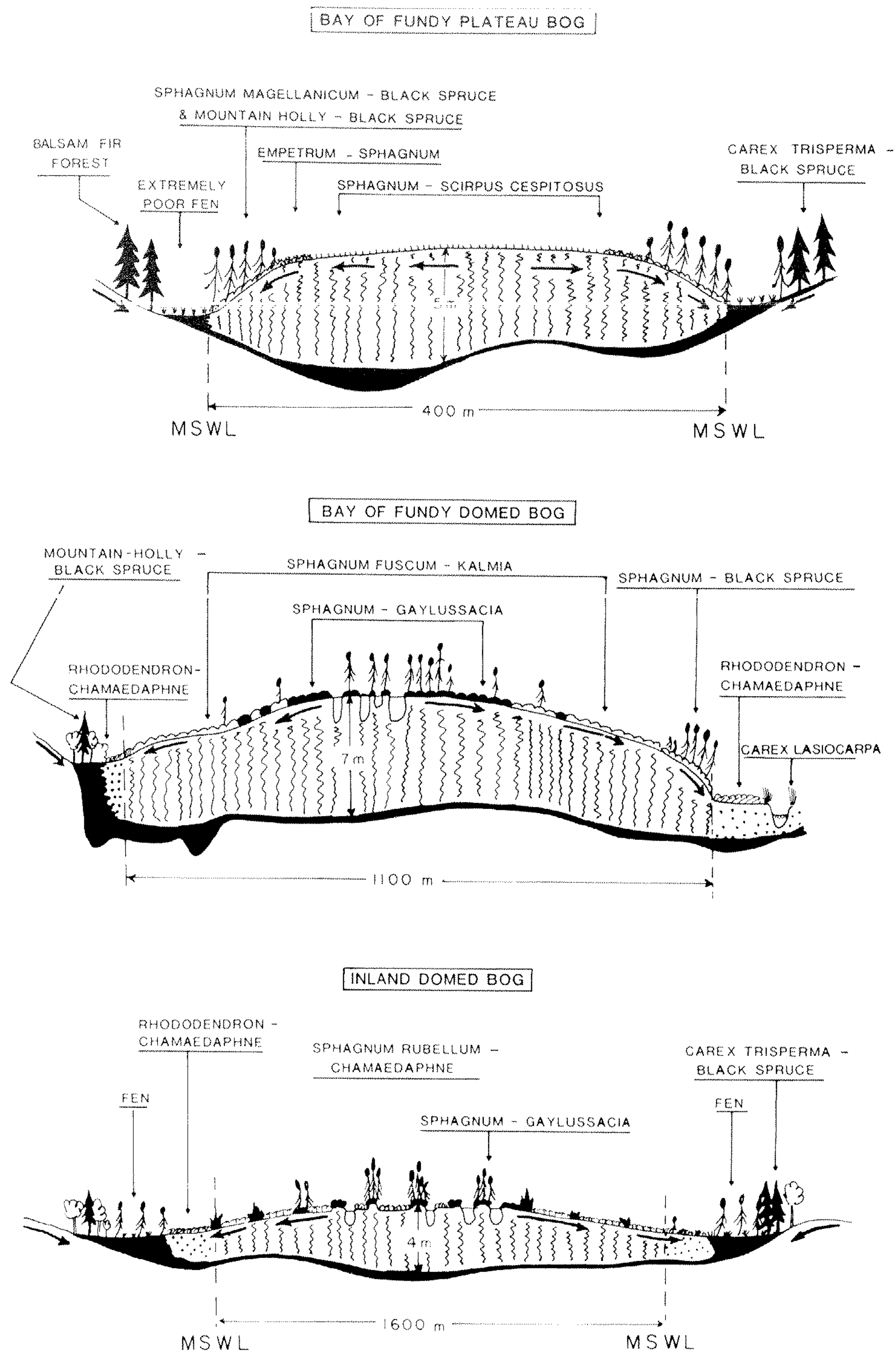


Figure 42. Vegetation pattern in the three major raised bog types of northern New England. The mineral-soil water limit (MSWL) is indicated in all diagrams. The *Sphagnum rubellum-Chamaedaphne* community of these bogs is the poor variant with low *Chamaedaphne* typical for ombrotrophic bogs.

(Damman 1979b, 1986; Clymo 1984). Decay below the water table is very slow, and these decay rates differ little between bog border and bog center. Therefore, we are concerned mainly with the decay within the aerobic acrotelm. This depends on the chemical composition of the organic matter and the thickness of the acrotelm, in particular the length of time the organic matter remains within the acrotelm (Clymo 1984). Low nutrient concentrations in the bog center can decrease decay to the extent that accumulation exceeds that in the bog border in spite of the reduced productivity (Damman 1979b, 1986). This explains the elevation of the bog surface but not that of the water table. The latter is raised if a water mound, maintained by precipitation, develops in the peat above the water table (Ivanov 1981; Ingram 1982). This development requires a low hydraulic conductivity of the peat in the lower part of the acrotelm. Under such conditions, the water mound rises with the bog surface until the critical level (Ivanov 1981) is reached; this level depends on the climatic conditions and the hydraulic conductivity of the peat above the water level in the bog border. The development of a water mound reduces the depth of the acrotelm and thus reduces decay and increases peat accumulation.

Local ombrotrophy, or near ombrotrophy, of hummock surfaces in topogenous and soligenous peatlands becomes progressively common with increasing altitude and latitude. However, it is followed by ombrogenous bog development only in the northern part of the region. The processes leading to local ombrotrophy and to ombrogenous bog development are distinct. The difference between them is most clearly expressed in the relationship between hummocks and hollows. As explained earlier, the initiation of ombrogenous bog development requires the rise of the bog surface so that a water mound can develop. When the water table in the bog center has been raised above that in the bog border, both hummocks and hollows will be ombrotrophic. In contrast, in topogenous and soligenous peatlands the hollows remain minerotrophic, whereas the hummocks may approach ombrotrophy. The small diameter of a hummock in these minerotrophic peatlands severely limits the maximum height of the water mound. Consequently, decay in the hummock soon equals production and limits further height growth above the minerotrophic peat surface.

# CHAPTER 6. ANIMAL COMMUNITY COMPOSITION

## 6.1 VERTEBRATES

Few studies have examined vertebrate assemblages in peatlands. The most complete studies have been conducted in Minnesota (Marshall and Buell 1955; Karns 1979; Nordquist and Birney 1980; Warner and Wells 1980), Michigan (Brewer 1967; Ewert 1982), Canada (Buckner 1957a, 1966; Erskin 1977; Muir 1977), and Scandinavia (Jarvinen and Sammalisto 1976; Henttonen et al. 1977; Bostrom and Hansson 1981). The only extensive studies of vertebrate assemblages in Northeastern peatlands are those of Stockwell and Hunter (1985) and Brooks et al. (1987).

The vertebrate fauna of peatlands has generally been considered rather depauperate. There are no endemic species, and few vertebrates use bogs as their primary habitat. However, the vertebrate species diversity may actually be greater within peatlands than in surrounding habitats because of the relatively great vegetational diversity.

### 6.1.1. Mammals

Most large mammal species in the Northeast move across peatlands, but few linger for long. Moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) and black bear (*Ursus americanus*) use peatlands more than other large mammal species. The edges of bogs provide good browse, and deer use is so heavy in some Maine bogs, that browse lines are apparent (Worley 1981). Some forested peatlands provide deer with winter yarding areas under dense stands of spruce or tamarack. Moose are perhaps the most frequent and best-adapted large mammals exploiting Northeastern peatland habitats. During the summer moose extensively use aquatic habitats including lakes, ponds, streams, and open bogs where they feed on aquatic vegetation (Dodds 1974; Crossley and Gilbert 1983). Water and open-bog habitats represent only 1.0% and 1.5%, respectively, of the total home range of moose in northern Maine, but these habitats are used significantly more than their relatively small availability suggests. Although areas of water and open bog were used heavily during the summer, they were not used at all during the winter (Crossley and Gilbert 1983).

Formerly, the woodland caribou (*Rangifer caribou*) occurred throughout eastern Canada and into northern Maine and extreme northern New Hampshire and Vermont where small herds fed extensively in the bogs and barrens (Allen 1972). Caribou were easily hunted and were eventually extirpated from the region. A few survived in the bogs of northern New Hampshire until at least 1885 and in Maine near the St. Johns River until 1916 (Allen 1972).

Bogs and other wetlands can be important habitat components for black bears in the Northeast by providing thick escape cover (Eveland 1973; Kordek 1973; Landers et al. 1979) and an abundance of succulent food in the post-denning period (Landers et al. 1979; Elowe 1984). The occurrence of swamps is considered a key component of bear range in the Pocono region of northeastern Pennsylvania (Eveland 1973; Lindzey et al. 1976; Alt et al. 1980) and the most important factor determining the size of bear range in northwestern Massachusetts (Elowe 1984). Isolation of wetland pockets by residential development and other means reduces the value of suitable bear habitat (Lindzey et al. 1976) and increases the vulnerability of bears by attracting hunters (Kordek 1973; Landers et al. 1979).

Beaver (*Castor canadensis*) are frequently found in peatlands with open water, particularly those with flowing water (Johnson 1985), but their importance to beaver has not been investigated in the northeastern United States. In Minnesota, Rebertus (1986) found evidence of current or previous beaver activity in 200 (42%) of 481 bogs surveyed. This included 102 colony sites with over-wintering lodges at the bog and 98 work areas with lodges in adjacent ponds or streams. Beaver use of sedge-moss, tall-shrub, and wooded bog cover types reflected their availability in the landscape. However when inhabiting bogs with moats, beavers showed a significant preference for sedge-moss and an avoidance of tall-shrub cover types. In bogs with flowage created by beaver dams, beaver rarely used sedge-moss because this vegetation occurred in kettle hole bogs that lacked sufficient ground water flow.

Flooding by beavers can seriously damage peatlands. Bogs with floating mats are least affected, because here rising water levels flood only the grounded mat near the upland margin of the bog.

The diversity and density of small mammal populations in peatlands depends largely on the structural diversity of the peatland vegetation. Stockwell and Hunter (1985) captured 12 species of small mammals in Maine peatlands. In their study of seven vegetation types, they captured as few as five species in moss-Chamaedaphne and as many as 11 species in lagg and forested bog. The greatest number of small mammal species was in the two vegetation types with the greatest structural diversity and closest to upland habitats, whereas the smallest number was in vegetation types with the least structural diversity and in the center of the peatlands, farthest from uplands.

Using pitfall traps, Stockwell and Hunter (1985) found the masked shrew (Sorex cinereus) to be the most abundant species (67% of captured specimens) in every vegetation type except the shrub thickets, where the meadow jumping mouse (Zapus hudsonius) was most abundant. It made up 13% of all captures and was the second-most abundant small mammal species in streamside meadows, pools, shrub heaths, and moss-Chamaedaphne habitats. The southern red-backed vole (Clethrionomys gapperi), most often found in spruce forests with relatively dry substrates, comprised 11% of the captures in the shrub thicket and 15% in the forested bog. The meadow vole (Microtus pennsylvanicus), a species of fields and wet meadows, accounted for 10% of the captures in laggs and 9% in streamside meadows. The water shrew (Sorex palustris), usually found along the edges of streams, lakes, and beaver ponds, has frequently been associated with peatlands. It made up 20% of the captures in laggs. Other small mammal species included the smoky shrew (Sorex fumeus), pygmy shrew (Sorex hoyi), short-tailed shrew (Blarina brevicauda), star-nosed mole (Condylura cristata), southern bog lemming (Synaptomys cooperi), deer mouse (Peromyscus maniculatus), and woodland jumping mouse (Napaeozapus insignis). The star-nosed mole is the most aquatic of the North American moles and was only found on sites with standing water (Stockwell and Hunter 1985). In the Northeast, this mole is found in various wetland habitats, but along the Atlantic Coastal Plain south to the Okefenokee Swamp, the southern edge of its range, it is mostly restricted to peatland habitats and has been found only in association with Sphagnum.

In a one-year study of six peatlands in the Pocono region of Pennsylvania (Brooks et al. 1987) found a total of 21 mammal species, with white-tailed deer being most frequently detected and present on all six sites. The three most abundant small mammal species were the southern red-backed vole (78 at 5 sites), white-footed mouse (Peromyscus leucopus) (69 at 6 sites), and the masked shrew (68 at 6 sites). Other documented small mammal species included the meadow vole (8 at 3 sites), deer mouse (6 at 4 sites), short-tailed shrew (6 at 2 sites), meadow jumping mouse (2 at 2 sites), and woodland jumping mouse (1).

The northern and southern bog lemmings (Synaptomys borealis and S. cooperi) are perhaps more closely associated with Sphagnum, although not necessarily peatlands, than any of the other Northeastern mammals. Preble (1899) named the subspecies of northern bog lemming found in the Northeast Synaptomys borealis sphagnicola because the type specimen was trapped in a runway in a dense carpet of (Sphagnum) moss at Fabyans, New Hampshire. Subsequent specimens have been trapped at several sites in New Hampshire and Maine, including an alpine spring on Mt. Katahdin, Maine (Dutcher 1903) and a spruce forest with a deep Sphagnum mat near the base of Mt. Katahdin (Garrett Clough and John J. Albright, The Nature Conservancy, Maine Chapter; pers. comm.). In Eastern Canada, the northern bog lemming primarily inhabits Sphagnum-Labrador tea-black spruce bogs, but it is also found in deep, mossy, spruce woods, wet alpine meadows, and alpine tundra (Banfield 1974).

The southern bog lemming was initially considered a bog-dwelling species, but now it is known to occupy a wide variety of wet and upland habitats throughout its range (Linzey 1983). However, in the northeastern United States and southern Canada it is mostly associated with Sphagnum bogs or heavily forested areas (Goodwin 1932; Hamilton 1941; Coventry 1942; Connor 1953; Buckner 1957b; Manville 1960). In Virginia, the southern bog lemming prefers habitats normally occupied by the meadow vole but, because of behavioral dominance by the meadow vole, the southern bog lemming gains access only to the poorest of these habitats during the low phase of the vole population cycle (Linzey 1984; Linzey and Cranford 1984). Habitats of marginal quality for meadow voles were unavailable to southern bog lemmings even if minimal densities of voles were present. In New Jersey, Connor (1959) found that southern bog lemming numbers surpassed those of the meadow vole only in Sphagnum bogs with shrub cover. Apparently, the same relationship exists between the southern bog lemming and the meadow vole in Northeastern bogs as well.

### 6.1.2. Birds

Avian species with boreal affinities are usually considered characteristic of Northeastern peatlands. Within the range limits of boreal species, they dominate peatland avifaunas. In Maine, boreal bird species represented 58% of the avifauna of peatlands but only 33% of surrounding habitats (Brewer 1967). A number of boreal bird species reach the southern edge of their ranges in either peatlands or alpine habitats (Figure 43). Within the Northeast, boreal bird species are an important component in peatlands of the Boreal and Coastal Spruce-Fir Zone of Maine, northern New Hampshire, northern Vermont, and the Adirondack Mountains of New York. South of the ranges of boreal species, peatlands are dominated by bird species from surrounding habitats (Figure 44). Birds that occupy wet meadows and marshes are found in fens, and species that inhabit shrubby forest openings also inhabit shrub heaths.

Stockwell and Hunter (1985) reported 104 bird species in a 2-year study of Maine peatlands. Within an individual peatland they found 29-69 species each year. Bird species richness in peatlands, expressed as the number of species present, was greater than that in surrounding habitats. They attributed this to the variety of vegetation types occurring in relatively small areas in most peatlands. For all peatlands, bird species richness is directly and independently correlated with vegetation diversity and size of peatland. Bird densities are also correlated with peatland vegetation diversity. Bird densities are lower in peatlands dominated by open patches than in peatlands dominated by arboreal patches. Foliage height diversity within a peatland is the best indicator of bird species richness, bird density, and bird species composition. As foliage height diversity increases, bird species richness increases, bird density increases, and bird species composition changes. The fewest bird species are found in fens and the most in wooded heaths. Most species occur in several peatlands and in several types of vegetation (Figure 45).

The common yellowthroat and Nashville warbler were present and abundant in all eight types of vegetation sampled (Stockwell and Hunter 1985). Fifteen species were common or abundant in three or more vegetation types and 20 species in 1-2 vegetation types. Most species, including some frequently associated with bogs (e.g., spruce grouse), were observed only rarely.

Stockwell and Hunter (1985) found that avian communities in bogs were distinctly divided into two groups associated with arboreal and non-arboreal vegetation.

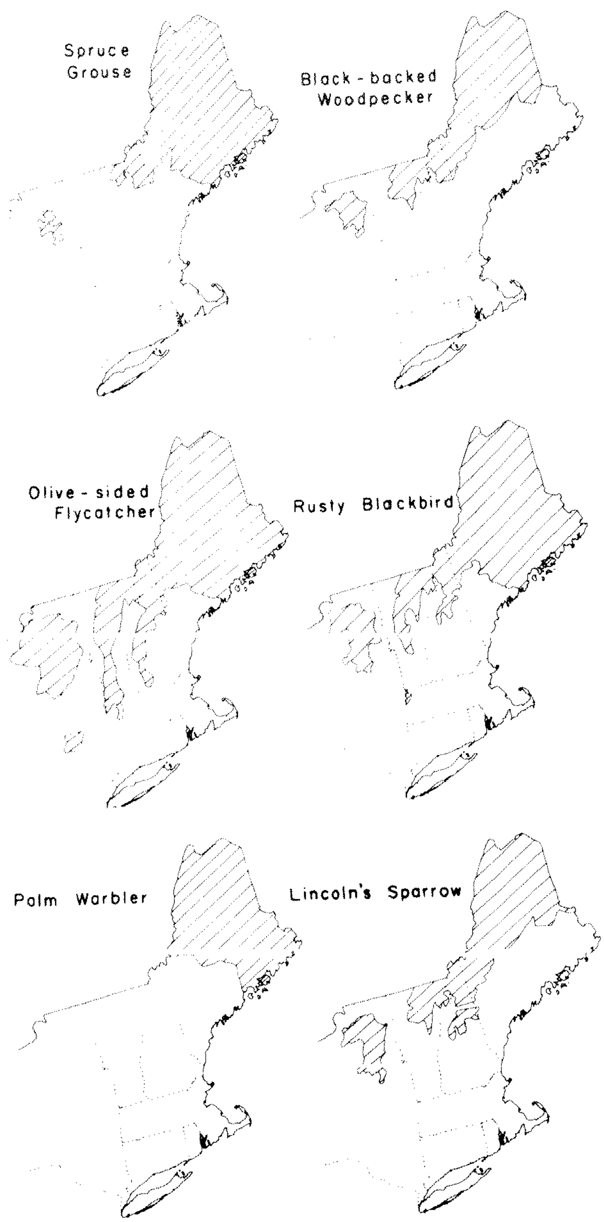


Figure 43. Northeastern United States breeding ranges of six boreal bird species characteristic of peatlands.

Vegetation types within these categories shared many of the same bird species, and the average degree of similarity between these two major groups was 0.63 (Figure 46). They observed certain bird species in only one or two peatland types and other species in several peatland types with similar vegetation characteristics.

Brooks et al. (1987) found 61 bird species in a one year study of six peatlands in the Pocono region of Pennsylvania. The 12 most frequent species included blue jay (90 at 6 sites), black-capped chickadee (76 at 6 sites), gray catbird (45 at 6 sites), cedar waxwing (29 at 6 sites), American crow (24 at 4 sites), red-winged blackbird (17 at 4 sites), rufus-sided towhee (15 at 4 sites), song sparrow (15 at 4 sites), northern flicker (14 at 5 sites), ruby-crowned kinglet (13 at 6 sites), common yellowthroat (11 at 5 sites), and white-throated sparrow (10 at 4 sites).

In the Adirondack Mountains of New York Hardin (1975) recorded 30 bird species on four peatland sites including two conifer bogs (18 species), an ericaceous shrub bog (10 species), and a bog sedge-meadow (14 species). Most abundant in each of these cover types were: the common yellowthroat (44) and song sparrow (50) in the two conifer bogs; bobolink (51) and song sparrow (10) in the ericaceous shrub bog; and bobolink (33), song sparrow (20), and savannah sparrow (10) in the bog sedge-meadow.

Although Northeastern peatlands generally lack a distinctive avifauna, certain boreal species such as the spruce grouse have been considered representative. Most are boreal species that typically inhabit cool, wet, brushy openings, or edges in spruce-fir forests. Included among these bird species are the spruce grouse, three-toed and black-backed woodpeckers, olive-sided and yellow-bellied flycatchers, gray jay, boreal chickadee, palm, Tennessee, Cape May, and bay-breasted warblers, Lincoln's sparrow, and rusty blackbird. Each of these species has a unique combination of habitat preferences, but they are all regularly found in association with peatlands in northern New England and the Adirondack Mountains of New York.

Among the boreal species that characterize northern New England bogs, the Lincoln's sparrow and the palm warbler are probably the two most restricted to this habitat. The palm warbler breeds in open Sphagnum bogs of northern Maine, and the Lincoln's sparrow is found on the brushy edges of these bogs as far south as northern New Hampshire, Vermont and New York

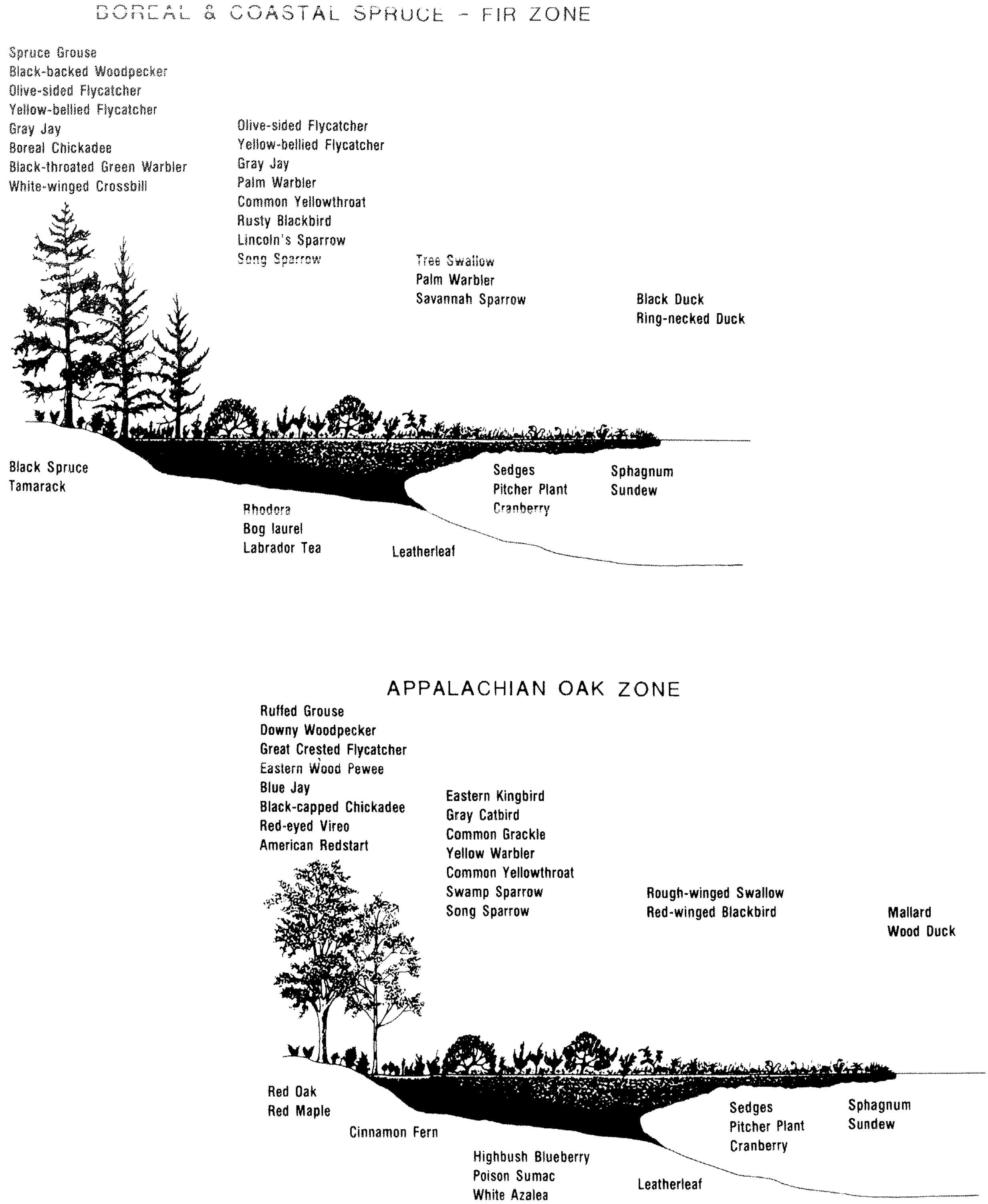


**Figure 44.** Comparison of bird distribution typical of a lake-border bog in the northern and southern part of the region.

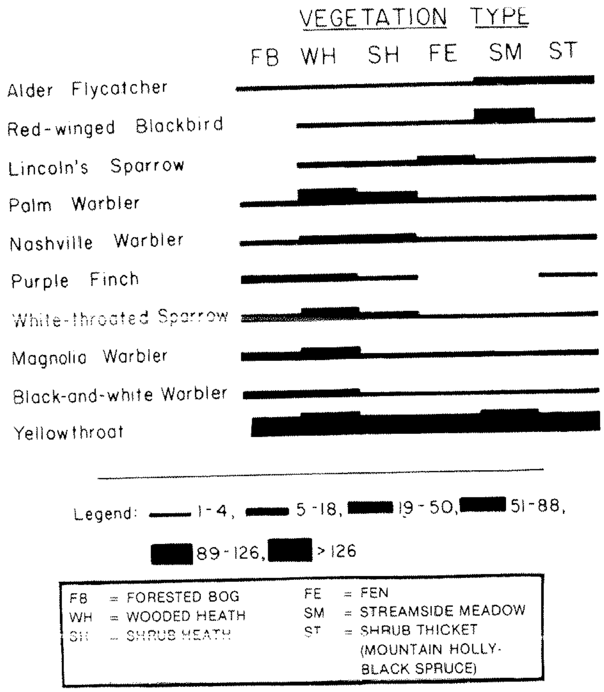


**Figure 45. Distribution of ten bird species in Maine peatlands (redrawn after Stockwell and Hunter 1985). Densities are expressed as number of individuals/40 ha based on 8 peatlands. Sample sizes for bog-border forest and wooded fen were too small to be included.**

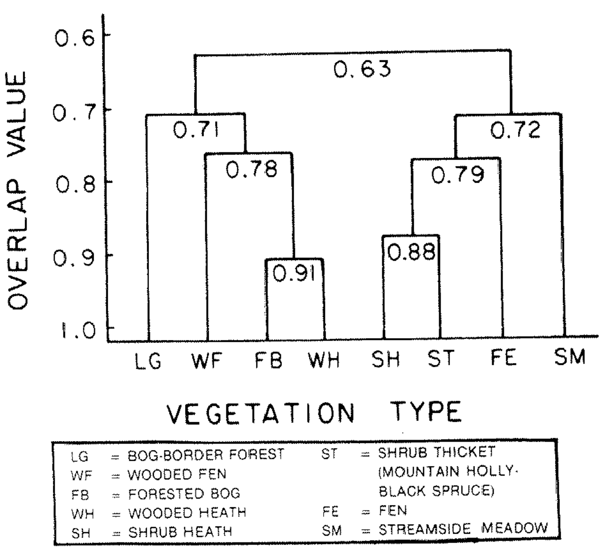


**Figure 46. Dendrogram of overlap of vegetation types based on similarities of 1983 and 1984 bird species composition on eight Maine peatlands (redrawn after Stockwell and Hunter 1985). Overlap values are calculated as $C_{AB} = (C_A + C_B)/2$ and range from 1 (identical) to 0 (completely different).**

(Brewster 1925; Forbush 1927; Palmer 1949; Spear 1976; Worley 1981; Laughlin and Kibbee 1985). Both species often place their nests in a mound of <u>Sphagnum</u> or cottongrass (Knight 1904; Bent 1953; Harrison 1978).

## 6.1.3. Amphibians and Reptiles

Few amphibians or reptiles can be considered peatland species, but many Northeastern species are found in peatlands. The low pH of the water, the cool microhabitats, the saturated substrates, and the occasional flooding make bogs unsuitable habitats for some species. The constant moisture content of the <u>Sphagnum</u> moss substrate is particularly favorable for others. Some amphibians may be attracted to the moist microhabitats, but the bog water may be too acid for breeding.

In the New Jersey pine barrens, Gosner and Black (1957) found that tadpoles of frog species occurring in acidic <u>Sphagnum</u> bogs were more tolerant of low pH than those of species occurring only in ponds with higher pH. In general, boreal species are more acid tolerant and most can be found in or around bogs. The wood frog (<u>Rana sylvatica</u>) appears to be particularly acid tolerant. Its eggs are able to survive and develop at pH 4.0 (Johnson 1985), although Karns (1979) never found wood frog larvae in water with a pH below 5.0. Tolerance extremes and pH of greatest hatching success for the spotted salamander (<u>Ambystoma maculatum</u>) under laboratory conditions were pH 6-10 and 7-9, respectively (Pough and Wilson 1976). Jefferson salamanders (<u>Ambystoma jeffersonianum</u>) tolerated more acidic conditions from pH 4 to 8, and achieved greatest hatching success between pH 5 and 6. Pough (1976) observed acid-tolerant egg masses of spotted salamanders in New York ponds between pH 4.5 and 5.0, where most egg masses of this species had not survived. Cook (1983) found one pond in the Connecticut River Valley, Massachusetts, where Jefferson and spotted salamanders were breeding successfully at pH 4.25.

In a study of eight vegetation types in nine Maine bogs (Stockwell and Hunter 1985) the wood frog was the most common amphibian, accounting for 59% of all amphibian and reptile captures in pitfall traps. These traps yielded 12 species of amphibians totalling 2,179 specimens and three specimens of eastern garter snake (Thamnophis sirtalis). The next four most frequently captured species were the green frog (Rana clamitans), (29% of total); northern leopard frog (Rana pipiens), 5% of total; blue-spotted salamander (Ambystoma laterale), 4% of total; and pickerel frog (Rana palustris), 1% of total. The remaining species were caught in low numbers in many vegetation types. Wood and green frogs were trapped in all vegetation types and at nearly all sites. Wood frogs were most abundant in forested bogs and least abundant in streamside meadows, where the northern leopard frog was the most abundant species. Green frogs were most abundant in wooded heath and least abundant in moss-Chamaedaphne. Streamside meadow was the only vegetation type where neither wood nor green frog dominated. Four-toed salamander (Hemidactylium scutatum) and mink frog (Rana septentrionalis), often considered bog associates, were not recorded!

The presence of amphibian breeding sites in or near the bogs studied by Stockwell and Hunter (1985) greatly influenced the number of individuals of each species present. The survival, emergence, and subsequent dispersal and capture of newly transformed juveniles contributed to high counts and great seasonal variation of species breeding nearby. Juveniles constituted 85% of all anurans captured and 18% of all salamanders captured.

Stockwell and Hunter (1985) found little variation in species composition or richness in six out of eight vegetation types studied. The presence of secondary pools did not increase species richness or abundance, nor alter species composition.

Brooks et al. (1987) found 13 species of amphibians and reptiles in six peatlands of the Pocono region of Pennsylvania. None of these species were common. The five most frequently encountered species were the red-spotted newt (Notophthalmus viridescens) (13 at 4 sites), bullfrog (Rana catesbeiana) (8 at 2 sites), spring peeper (Hyla crucifer) (5 at 2 sites), wood frog (3 at 3 sites), and green frog (3 at 2 sites).

Although no amphibian or reptile is limited to peatlands, several are frequently associated with this habitat. The four-toed salamander is the best example. This salamander is among the most secretive in the eastern United States, and it is infrequently collected even in areas where it is relatively common. Adults inhabit hardwood and, less often, coniferous forests most of the year, but they move to water in the spring. The eggs are usually deposited in a cavity within a clump of Sphagnum moss directly over water (Blanchard 1923; Bishop 1941). The moss may be in deep, shaded situations in mixed forests of hemlock, pine, and hardwoods, in open larch meadows, or in a Sphagnum-heath bordering bog ponds (Bishop 1941). Some nests have been found in fairly open bogs. The female usually stays with the eggs until just before they hatch (Breitenbach 1982). Communal nests may contain the eggs of several females but only one or two guard them.

The bog turtle (Clemmys muhlenbergii) occurs from Massachusetts, New York, and Connecticut south along the Appalachians to north Georgia and South Carolina. It is frequently associated with Sphagnum bogs (Barton and Price 1955; Ernst and Barbour 1972; Bury 1979), but open, sedgy, or shrubby fens and wet meadows are its typical habitats (Carr 1952; Arndt 1977). A muddy bottom seems to be the most important requirement (Barton and Price 1955). Arndt (1977) found bog turtle habitats in Delaware to be characterized by meadows with a substrate of deep mud, numerous small springs, constantly flowing clear and relatively cool water, and an anastomosing network of rivulets, shallow pools, and muskrat runways. The water temperature was usually lower than the air temperature. The pH ranged from 5.5 to 7.4 but was usually between 6.0 and 6.8. In the Northeast, however, the bog turtle is characteristic of calcareous, graminoid fens.

The spotted turtle (Clemmys guttata), a close relative of the bog turtle, is found throughout the Northeast in the sluggish water of bogs, swamps, and small ponds with muddy bottoms, as well as calcareous fens and other habitats (Pope 1939; Carr 1952; Ernst and Barbour 1972). In northern New England, bogs may be more important than farther south. At least, at the northern limit of its range in southern Ontario and Quebec, the spotted turtle finds its main or only refuge in small deep bog ponds and lakes with boggy margins (Cook et al. 1980).

## 6.2 INVERTEBRATES

Many invertebrates indigenous to bogs and barrens are derived from an arctic or subarctic fauna, but others are typical Canadian Zone species that feed upon spruce, tamarack, cranberry, or other bog plants (Ferguson 1955). A number of invertebrate species are restricted to peatlands, having obligate relationships with peatland plants. Aquatic invertebrates of bogs include species adapted to slow-moving, oxygen-depleted waters. The low pH of bogs is lethal to many invertebrates including earthworms, mayfly larvae, and aquatic mites (Svendsen 1957; Standen 1979). These acidic waters also prevent shell development on clams and snails that thrive in calcareous fens. Species occurring in bog waters, e.g., water boatmen (Corixidae) and whirligigs (Gyrinidae), can tolerate a pH as low as 3.5 (Johnson 1985).

Pitcher plants (Sarracenia spp.) are the obligate host to more invertebrate species than any other bog plant. At least 16 arthropod species are obligates, and many more are possible obligates or frequent associates of pitcher plants (Rymal and Folkerts 1982). Only the northern pitcher plant, Sarracenia purpurea, is found in peatlands of the northeastern states. At least eight arthropod species are found as obligate pitcher plant associates of S. purpurea, and four of these have been found only on this species (Rymal and Folkerts 1982). Obligate and probably obligate commensals found within the water-filled pitcher include a mosquito, a midge, two sarcophagid flies, and a mite. Species that feed exclusively on the tissue of the northern pitcher plant include an aphid and three moths (Figure 47). The pitcher plant mosquito (Wyeomyia smithii, including W. haynei Dodge 1947) is the most thoroughly studied species associated with S. purpurea (Smith 1902; Price 1958; Buffington 1970; Paterson 1971; Addicott 1974; Istock et al. 1975; Rymal and Folkerts 1982). The egg, larval and pupal stages of this mosquito are found within the water-filled pitcher. The larvae live in the upper water column where they feed on detritis.

The midge Metriocnemus knabi is frequently found sharing the same pitcher with W. smithii (Buffington 1970). Midge larvae occur in the lower portion of the pitcher fluid where they feed on the mass of entrapped prey (Knab 1905; Cameron et al. 1977; Fish and Hall 1978; Rymal and Folkerts 1982). The pupae are in a gelatinous mass attached to the pitcher wall above the water surface. The larvae of W. smithii and M. knabi can be frozen in the pitcher for months during the winter. During this time the larvae void their guts of food material that would facilitate water crystal formation and cause death. Overwintering mortality of midge and mosquito larvae frozen in the pitcher fluid is usually less than 5% (Paterson 1971).

The sarcophagid fly Blaesoxipha fletcheri is an obligate associate of pitcher plants, including S. purpurea, and Sarcophaga sarraciniae is probably an obligate. The larvae of these large flies develop in the pitcher where they feed on the entrapped prey mass. They often occur in most of the pitcher plants in a bog but usually singly within individual pitchers as a result of cannibalism (Forsyth and Robertson 1975; Rymal and Folkerts 1982).

The larvae of at least five species of moths feed exclusively on pitcher plants and three of these--two noctuids and a tortricid--are found on the northern pitcher plant. Larvae of the noctuid Exyra rolandiana usually girdle the pitcher with a narrow feeding canal and cause the upper portion of the leaf to wilt and fall over. Usually only one larva occurs in each leaf where it feeds on the inner portion, leaving the outer epidermis intact (Jones 1921; Rymal and Folkerts 1982). The noctuid root borer Papaipema appassionata feeds exclusively on the underground rhizomes of pitcher plants. The burrowing activities of this caterpillar are particularly damaging and frequently cause the entire clump of pitchers to wilt and die (Jones 1921; Rymal and Folkerts 1982). Although this

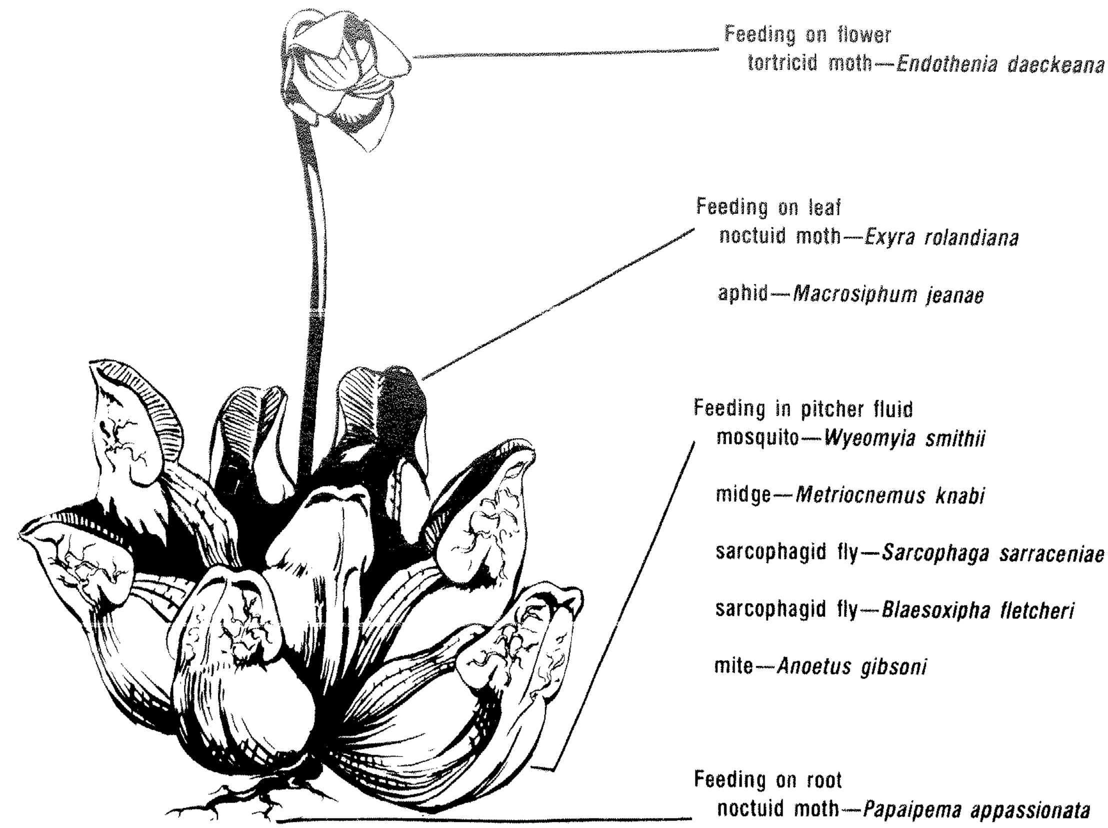


Figure 47. Invertebrate associates of the pitcher plant (*Sarracenia purpurea*).

is certainly the most damaging of the obligate herbivores of S. purpurea, it is rarely abundant enough to affect pitcher plant populations within a bog. The third obligate lepidopteran grazer is the tortricid moth Endothenia daeckeana. The larvae of this moth feed only on the flowers and developing fruit. Larvae bore into the ovary and consume the seeds. When mature, they bore down the flower stalk where they pupate and emerge in the spring through a pre-chewed exit hole (Jones 1921; Hilton 1982; Rymal and Folkerts 1982).

Other obligate associates include an aphid and a mite. The aphid Macrosiphum jeanae is currently known only from S. purpurea in Canadian bogs (Robinson 1972). All life stages of this aphid occur on the pitcher plant, and it is sometimes found in large numbers on the second-year leaves (Robinson 1972). The mite Anoetus gibsoni feeds on pitcher plant prey and is found on the pitcher walls beneath the surface of the liquid (Nesbitt 1954; Hughes and Jackson 1958; Rymal and Folkerts 1982).

Many lepidopteran species are found in bogs, and some are actually restricted to bogs (Forbes 1923, 1960; Ferguson 1955; Brower 1974; Howe 1975; Opler 1985). These are obligate associates of specific larval food plants and, in some species, of specific adult nectar sources as well. Typical bog butterflies include such species as the bog fritillary (Boloia eunomia dawsoni), bog elfin (Incisalia lanoraieensis), and bog copper (Lycaena epixanthe). Macrolepidopteran species characteristic of Northeastern bogs are listed in Table 10.

Many species of dragonflies and damselflies (order Odonata) are characteristic of Northeastern bogs (Howe 1921; Walker 1925, 1958; Garman 1927; Gibbs and Gibbs 1954; Needham and Westfall 1955;

Table 10. Macrolepidoptera characteristic of Northeastern peatlands. State abbreviation in parentheses indicates that the most recent record from that state is prior to 1965. In New England states, other than Connecticut, all such records are from before 1934. Source: Dale F. Schweitzer, The Nature Conservancy.

| Common name | Scientific name | Larval food plants in Northeast | Habitat[a] preference | Northeastern United States confirmed range[b] |
|---|---|---|---|---|
| BUTTERFLIES | PAPILIONOIDEA | | | |
| Bog fritillary | *Boloria eunomia dawsoni* | Unknown | 1 | ME |
| Jutta arctic | *Oeneis jutta* | Probably the sedge *Eriophorum spissum* | 1 | ME, NH |
| Bog elfin | *Incisalia lanoraiensis* | Black spruce | 1 | ME, (NH) |
| Western pine elfin | *Incisalia cryphon* subsp. | Probably black spruce | 1? | ME |
| Bog copper | *Lycoana epixanthe* | Cranberry | 2 | ME, NH, VT, NY, CT, RI, PA, MA |
| Hessel's hairstreak | *Mitoura hesseli* | Atlantic white cedar | 2 | NH, MA, RI, CT, NY |
| INCH WORMS | GEOMETRIDAE | | | |
| Chalky wave | *Scopula purata* | Unknown | 1 or 2 | ME, NH, MA, NY, PA? |
| | *Epilis truncataria* | Cranberry, other | 3 | ME, NH, MA, CT, NY |
| | *Itame sulphuraea* | Mostly cranberry | 2 | ME, MA, NH |
| Sharp lined powder moth | *Eufidonia discopilata* | Various shrubs | 3 | ME, NH, MA, CT, NY, PA? |
| Cranberry spanworm | *Ematurga amitaria* | Shrubs, esp. *Myrica*, heaths | 3 | ME, NH, MA, NY, PA |
| Projecta gray | *Cleora projecta* | Sweet gale | 3 | ME, MA, NY? |
| Blueberry gray | *Glena coanataria* | Blueberry, sand cherry, pin cherry | 3 | ME, NH, MA, (CT), NY, PA |
| | *Metarranthis* sp. *lateritiaria* of authors | Unknown | 2? | ME, MA, VT CT, NY |
| | *Metarranthis amyrissaria* | Unknown | 3 | ME, MA, NY, CT |

(continued)

Table 10. Continued.

| Common name | Scientific name | Larval food plants in Northeast | Habitat[a] preference | Northeastern United States confirmed range[b] |
|---|---|---|---|---|
| | SATURNIIDAE | | | |
| Columbia silkmoth | Hyalophora columbia | Larch | 2 | ME |
| TIGER MOTHS, WOOLLY BEARS | ARCTIIDAE | | | |
| Bog holomelina | Holomelina lamae | General | 1 | ME, VT? |
| Bog tiger moth | Grammia sp. (speciosa)? | General | 1 | NH, VT, MA CT |
| | NOCTUIDAE | | | |
| Sundew cutworm | Hemipachnobia subporphyrea monochromatea | Sundews, changing to heaths in late instars | 1 or 2 | ME, MA, CT, NY, PA |
| | Anomogyna imperita | Spruces? | 4 | ME, NH |
| | Anomogyna youngii | Blueberry, other heaths, larch | 2 | ME, NH, MA, CT, NY, PA |
| | Trichordestra rugosa | Chokeberry, probably others | 2 | ME, NY |
| Maroonwing | Sideridis maryx | Unknown | 3 | ME, NY, MA (RI), CT, NH, PA |
| | Lasionycta sp. | Unknown | 1? | ME, VT |
| Small dark yellow underwing | Anarta cordigera | Heaths | 1 | ME, NH, MA, CT |
| Thaxter's pinion | Lithophane thaxteri | Sweet gale, sweet fern | 3 | ME, NH, NY, MA RI, (CT), (PA) |
| Northern broad sallow | Xylotype acadia | Larch, several shrubs | 2 | ME, (NH?) |
| Cranberry blossomworm | Epiglaea apiata | Cranberry, blueberry | 3 | ME, NH, MA CT, RI, NY PA |
| | Oligia minuscula | Probably a sedge | 2 | ME, NY, (MA) (RI) |
| | Apamea commoda | Probably a sedge | 2? | ME |
| Pitcher plant borer | Papiapema appassionata | Pitcher plants | 2 | ME, MA, NY (CT) |

(continued)

Table 10. Concluded.

| Common name | Scientific name | Larval food plants in Northeast | Habitat[a] preference | Northeastern United States confirmed range[b] |
|---|---|---|---|---|
| Chain fern borer | *Papiapema stenocelis* | Chain fern | 2[c] | MA, NY? |
| | *Fagitana littera* | Ferns | 2? | (ME), MA, CT NY, (PA?) |
| Pitcher plant moth | *Exyra r. rolandiana* | Pitcher plants | 2 | ME, MA, NY, CT |
| | *Syngrapha microgamma nearctica* | Leatherleaf | 1 | ME, NH, NY |
| | *Syngrapha montana* | Unknown | 4 | ME, NH |
| | *Sungrapha surena* | Unknown | 1 or 3 | ME |
| Sweet gale underwing | *Catocala coelebs* | Sweet gale | 2 | ME, NH, NY |
| | *Macrochilo louisiana* | Probably sedges | 2[c] | ME, NH, MA |

[a]Habitats:

1 = bog obligate;
2 = found in bogs and other acidic peatlands;
3 = found also in pine barrens and occasionally other sites with abundant heaths; and
4 = found also in the alpine zones of New England.

[b]The region covered is northeastern Pennsylvania and all of New England and New York. Since virtually no records from northern New Jersey bogs are available and since the fauna of southern New Jersey is so different from the rest of the Northeast, that state is not considered here.

[c]Apparently a bog species in New England, but not restricted to bogs in most of its range.

Beatty and Beatty 1968, 1971; White and Morse 1973; Walker and Corbet 1975; Opler 1985). Examples of bog odonates include such species as the southern bog darner (*Gomphaeschna antilope*), banded bog skimmer (*Williamsonia lintneri*), and boreal bluet (*Enallagma boreale*) (Table 11). Odonate nymphs are obligate carnivores; therefore, the affinity of certain species to bogs is a result of the prey availability rather than the presence of food plants.

The banded bog skimmer is perhaps the most geographically restricted bog odonate in the Northeast. This dragonfly is a glacial relic species that has been collected at only a few coastal localities in New Jersey, New York, Connecticut, Rhode Island, and New Hampshire but at 13 sites in Massachusetts. Populations at many of these sites have been destroyed by urbanization, and several others in densely populated areas may be threatened in the near future. At least seven extant populations

Table 11. Odonates characteristic of Northeastern peatlands. This list contains only species showing a pronounced preference for peat bogs, and, therefore, not all species occurring in bogs are included. Source: Chris Leahy, Massachusetts Audubon Society.

| Species name | Habitat relationship[a] | Confirmed Northeastern range[b] | Forest zone[c] |
|---|---|---|---|
| Coenagrionidae | | | |
| *Amphiagrion saucium*[d] | BA | ME, NH, VT, MA, CT, RI, NY, PA, NJ | NH, AO |
| *Coenagrion interrogatum* | BO/BA | ME, VT | SF |
| *Enallagma boreale* | BA | ME, NH, VT, MA, CT, RI, NY | |
| *Nehalennia gracilis* | BO | ME, NH, VT, MA, CT, RI, NY, PA, NJ | SF, NH, AO |
| Aeshnidae | | | |
| *Gomphaeshna furcillata* | BO | ME, VT, NH, MA, CT, RI, NY, PA, NJ | NH, AO |
| *Aeshna interrupta* | BA | ME, NH, VT, MA, NY | SF, NH |
| *A. juncea* | BA | NH | SF |
| *A. sitchensis* | BO | ME | SF |
| *A. subarctica* | BO | ME, NH | SF |
| *A. tuberculifera* | BA | ME, NH, VT, MA, CT, RI, NY, PA | NH, AO |
| Corduliidae | | | |
| *Williamsonia fletcheri* | BO | ME, MA, VT | SF, NH |
| *W. lintneri*[e] | BO | MA, NH, (RI, NY, NJ)[f] | NH, AO |
| *Dorocordulia lepida* | BA | ME, Vt, NH, MA, CT, RI, NY, PA, NJ | NH, AO |
| *D. liberia* | BA | ME, NH, VT, MA, CT, RI, NY, PA, NJ | NH, AO |
| *Somatochlora albicincta* | BA | NH, NY | SF |
| *S. franklini* | BO | ME, NH | SF |
| *S. incurvata* | BO | ME | SF, NH |
| *S. kennedyi* | BO | ME, NH, MA, VT, NY | SF, NH, AO |
| *S. walshi*[g] | BA | ME, NH, VT, CT, NY, PA | SF, NH, AO |
| *Cordulia shurtleffi* | BA | ME, NH, VT, MA, CT, NY, PA, NJ | SF, NH, AO |
| *Epitheca cani* | BA | ME, NH, VT, MA, CT, NY, PA | SF, NH |
| Libellulidae | | | |
| *Nannothemis bella* | BO | ME, NH, VT, MA, CT, RI, NY, PA, NJ | SF, NH, AO |
| *Libellula quadrimaculata* | BA | ME, NH, VT, MA, CT, PA, NJ | SF, NH, AO |
| *L. julia* | BA | ME, NH, MA, VT, CT, NY, PA, NJ | NH, AO |

(continued)

Table 11. Concluded.

| Species name | Habitat relationship[a] | Confirmed Northeastern range[b] | Forest zone[c] |
|---|---|---|---|
| *Sympetrum danae* | BA | ME, NH, VT, NY | SF, NH |
| *Leucorrhinia frigida* | BA | ME, NH, VT, MA, CT, RI, NY, PA, NJ | SF, NH, AO |
| *L. glacialis* | BA | ME, NH, VT, MA, CT, NY, PA | SF, NH |
| *L. hudsonica* | BA | ME, NH, VT, MA, CT, RI, NY, PA | SF, NH |
| *L. proxima* | BA | ME, NH, VT, MA, CT, NY | SF, NH |

[a]BO = Bog obligate--Species breeds exclusively (or nearly so) in bog ponds/pools, *Sphagnum* ponds, slow streams flowing through bogs and/or spring bogs.

[b]BA = Bog associate--Species showing strong affinity for bog conditions (see above), and frequently encountered in such situations in the Northeast but having a more broadly defined ecotype. Includes some unpublished state records in the collection of Paul S. Miliotis.

[c]SF = Spruce-fir
NH = Northern hardwoods
AO = Appalachian oak

[d]Especially spring bogs.

[e]Candidate for endangered status.

[f]Known stations in these states no longer extant.

[g]Requires some flow.

are thought to remain--one in Connecticut, one in New Hampshire, and five in Massachusetts.

The nymph of the banded bog skimmer lives in deep, cold bog ponds and canals that do not dry up in late summer or freeze solid in winter (White and Raff 1970). This is a very early-flying dragonfly, and adults are seen from about the first of April to mid June, before most other species have emerged (Howe 1923). The adult is found in bogs or woodlands adjacent to *Sphagnum* bogs.

Bick (1983) listed the banded bog skimmer as "Vulnerable" in his list of "Odonata at risk in the conterminous United States and Canada." The banded bog skimmer is a candidate for listing on the Federal list of Threatened and Endangered Wildlife (Federal Register 1984), is proposed for State listing in New Hampshire, and is on the official State list in Massachusetts.

The sphagnum cricket (*Nemobius palustris*), the smallest cricket in New England, appears to be limited to bogs (Morse 1920).

Many groups of peatland invertebrates are still poorly known, and further study will undoubtedly reveal additional peatland obligates. Insect groups that warrant particular attention in future bog studies include Ephemeroptera (mayflies), Hemiptera (bugs), Homoptera (hoppers and aphids), Coleoptera (beetles), Diptera (flies), and Hymenoptera (wasps and ants). Arachnida (spiders and mites), Myriapoda (millipedes and centipedes), and Protozoa in peatlands are also poorly known.

# CHAPTER 7. HUMAN DISTURBANCES AND THREATENED BIOTA

## 7.1 PEAT MINING

Although peat has been used as a fuel for hundreds of years in other parts of the world, it has never been an important source of domestic fuel in North America. Nevertheless, it has been mined for this purpose in a few isolated bogs in the Northeast (Hills and Hollister 1912). In North America, peat is used mainly in horticulture and agriculture because of its ability to retain water. Most of it is used as a mulch, soil conditioner, or potting soil. The upper, mostly living parts of the Sphagnum plants are also used for air layering in greenhouses. Species of the Palustria group, e.g., Sphagnum papillosum and S. magellanicum (Figures 20 and 21), are most suitable for that purpose.

In recent years there has been an increased interest in peat as an energy source, especially for electric power plants. Bogs large enough for developments of this kind are found only in Maine. Thus far, none of them are used for this purpose.

Consequently, peat is mined on a small scale in most of the region. Horticultural peat moss is harvested on a commercial scale in northeastern Maine, and other peat mining operations are found in northeastern Pennsylvania. Peat mining involves three processes: clearing of the vegetation, draining and mining. It results in the destruction of the surface vegetation. Although Sphagnum plants can grow anywhere from 0.5 to over 10 cm per year, peat accumulates very slowly, usually less than 1 mm/yr. Therefore, peat is a nonrenewable resource, and mining results in the virtually permanent removal of the peat.

Peat-mining operations in the southern and central parts of the region generally leave an area of open water. Here, the fibric peat of peat bogs and the muck of mesotrophic cedar swamps are mined.

In the large raised bogs of northeastern Maine, peat is collected by large vacuum machines that suck up the dry peat. This method removes only thin layers of peat each year, but it requires harvesting over areas of 1000 acres or larger. Thus, extensive areas of peatland can be disturbed in a few years. Peat cutting was carried out in Maine up to about 1960. This operation disturbs smaller areas but leaves deep scars (Figure 48).

Regeneration of disturbed peatlands is very slow, even of bogs harvested by the vacuum method. It takes decades for a closed vegetation to develop on a denuded peat surface. Figure 49 shows the surface of a raised bog (plateau bog) 9 years after harvesting stopped. Eriophorum spissum is usually the first colonizer. Growth and establishment is slow because of the extreme nutrient deficiency of the peat and frost heaving of seedlings by ice needles in spring and fall. Regeneration after peat cutting (Figure 48) requires much more time (Mörnsjö 1969).

## 7.2 FIRES

Although some fires are caused by natural phenomena, most are caused by man. Fires are common in the peat bogs of the northern part of the region (Osvald 1928, 1955), and they greatly affect the vegetation.

Fires set in the high Calamagrostis vegetation of the lagg of a bog to improve conditions for deer hunting often also burned the bog vegetation. In addition, many bogs were burned to improve berry

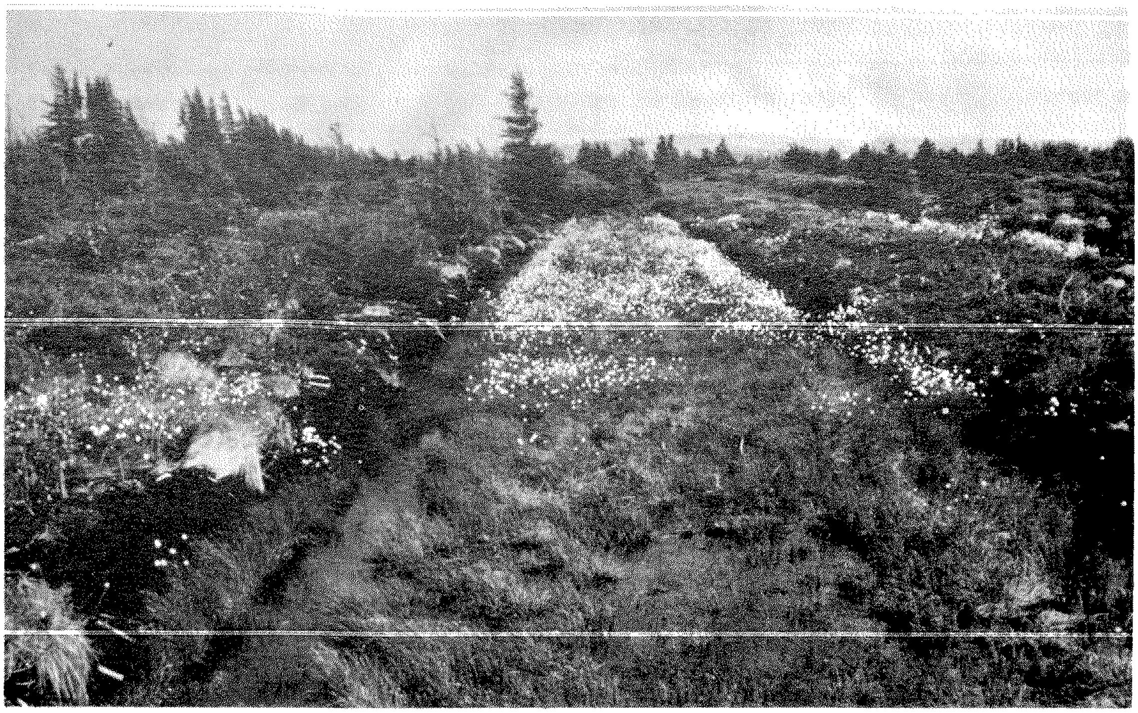

Figure 48. Raised bog from which peat was harvested by cutting. The ridges are the original peat bog surface. The trench is now occupied by *Sphagnum* species, *Carex canescens*, and *Eriophorum spissum*. The latter is especially abundant on the drier part in the background.

Figure 49. Raised bog surface harvested by vacuum method. Photograph taken 9 years after harvesting stopped in this area. The surface vegetation and only a very thin layer of peat was removed. *Eriophorum spissum* is virtually the only colonizer. Dead rhizomes of ericaceous dwarf shrubs are clearly visible between the *Eriophorum* tussocks.

picking. These practices have been discontinued, but their effects are still clearly visible in the present vegetation. Bogs are now burned by forest fires or by fires in adjacent blueberry barrens. Better fire control during the burning of the blueberry barrens has also reduced this risk.

Fires affect mostly the dry dwarf shrub and forest-covered parts of a bog. The dwarf shrubs recover easily from underground rhizomes and regain their original cover in 3-4 years. Large parts of many inland bogs formerly covered with an open forest now support a dwarf-shrub heath. Fires burn the reindeer mosses and kill most of the Sphagnum during the dry periods. Several lichens colonize the burnt crust, e.g., Cladonia crispata, C. cristatella, C. verticillata, and C. pyxidata, and can become very abundant after fires (Damman 1977). Burned dwarf-shrub bogs can be recognized for decades by the low Sphagnum cover and the abundance of Cladonia crispata.

Fires are uncommon in the topogenous and soligenous mires of the southern and central parts of the region because of the wet bog surface and the lower frequency of fires in the surrounding areas.

## 7.3 OTHER ANTHROPOGENIC EFFECTS

Housing and resort developments threaten peat bogs, and probably are the major threat in the densely populated southern part of the region. Peat bogs are destroyed directly by flooding or digging to create lakes, and indirectly by enrichment of the bog water by septic tank effluents. Bog water is very nutrient deficient, and nutrient additions cause drastic changes in the bog vegetation (Malmer 1974; Goffeng et al. 1979; Shaw and Reinecke 1983). The effect on the vegetation and the penetration into the bog depends on the properties of the effluent and especially the hydrology of the bog. In addition to the immediate effect on the vegetation, nutrient additions accelerate decay processes. This is particularly important in nutrient poor bogs where decay is stimulated most by nutrient additions. In these bogs, it can change also the topography of the bog surface.

Bogs are often considered biological nutrient filters (Richardson et al. 1976), but recent studies indicate that this may not be true and that the capacity for retention of certain elements, e.g., P can be very limited (Malmer 1974; Richardson et al. 1978; Shaw and Reinecke 1983). The ability of bogs to retain nutrients as well as other elements appears to be closely tied to their hydrology (Damman 1978a, 1979b). Removal and retention of elements will therefore depend on water-level fluctuations as well as water movement. This deserves further research.

## 7.4 RARE, THREATENED, AND ENDANGERED SPECIES

Peat bogs are wet, nutrient-deficient, and cold habitats strikingly different from the surrounding uplands, as well as from most other wetlands. Many plant species reach their southern limit in peat bogs. These species are often considered relics from an early postglacial period. However, they occur also in many recent bogs (Hemond 1980), and the unusual habitat conditions in these bogs appear to be the primary factor controlling their present distribution. The greatest threat to bog organisms is habitat destruction. This is not limited to disturbances such as peat harvesting or drainage. Because of the extreme nutrient deficiency of bogs, these ecosystems are sensitive to changes in the surrounding uplands that alter the nutrient input.

Since bogs become progressively smaller and less common southward, many bog species are considered rare in the southern part of the region and are included on state lists of rare and endangered species. This concerns mostly species that are widely distributed northward and become rare at the southern limit of their range. These species will not be listed here unless they are rare in the region as a whole. It should be emphasized, however, that their restricted distribution can be of concern at the state level (Dowhan and Craig 1976; Wiegman 1979; Crow et al. 1981). This applies to a large number of species in the bog flora; some of these are listed in Table 9.

Species common in the boreal zone but barely reaching into the northern part of the region make up a special category. These species (Table 12) are rare regionally and Rubus chamaemorus even nationally (Crow et al. 1981). The latter is common, however, in the bogs of the northeastern coastal parts of Maine (Damman 1977; Critical Areas Program 1981). Arethusa bulbosa occurs throughout the region and beyond, but it is now rare or declining because of habitat destruction and collecting. It reaches its northern limit in the Southern Boreal Zone. In contrast to the others, it does not have a primarily northern distribution. Its abundance in parts of Nova Scotia and Newfoundland results from the common occurrence of suitable habitat.

Several bog species with southern affinities reach their northern limit in the region, and several of the southern species in Table 9 are listed as rare in Maine (Critical Areas Program 1981). However, these species often reach their northern limit on more nutrient rich or drier sites rather than in bogs. Species of the New Jersey Pine Barren flora (Harshberger 1916; McCormick 1970), which reach into the region, do not occur in the peat bogs described here but favor Chamaecyparis swamps and open areas with mucky rather than peaty soils.

Most birds and other vertebrates require larger territories than can be found in the small bogs of the southern part of the region. Consequently, there are no vertebrates in the Northeast that occur only in bogs. However, there are a number of species closely associated with bog habitats that would be adversely affected by the loss of these habitats. Vertebrates associated with peat bogs are considered vulnerable and those proposed for listing on state rare or endangered species lists are listed in Table 13.

The minimum size of critical habitat for some invertebrate species may be quite small (Opler 1985). One Massachusetts colony of the bog copper butterfly (Lycoana epixantha) survives in a bog less than 0.1 acre in size (Dale Schweitzer, The Nature Conservancy, pers. comm.). The vulnerability of species dependent on bogs is illustrated by the probable extinction of 11 of the 17 known populations of the banded bog skimmer (Williamsonia lintneri) in the wake of urbanization (Mass. Natural Heritage Program files).

The present information on the distribution of bryophytes and fungi is too limited to indicate rare and endangered species for these groups. The same applies to the rare invertebrates. However, additional information on the distribution of some of these can be found in Chapter 6.

**Table 12. The distribution of nationally or regionally rare plant species in peat bogs of the northeastern United States. The following categories are used: R—rare; + present; – absent; EX—extirpated.**

| | State | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | ME | NH | VT | MA | RI | CT | NY | PA |
| Arethusa bulbosa | R[a] | R | R | R | + | R | + | R |
| Geocaulon lividum | R | R | R | - | - | - | R | - |
| Rubus chamaemorus | R[a] | R | - | EX | - | - | - | - |

[a]But frequent in bogs of northeastern coastal Maine.

**Table 13.** State rare and endangered vertebrates characteristic of northeastern peatlands. None of these species is listed as threatened (T) or endangered (E) at the national level. The following categories are used: S—species of special concern; R—rare; D—infrequent or declining; EX—extirpated; U—status undetermined. In addition, the presence (+) or absence (–) of a species is shown if it did not fall into any of the other categories. The categories for birds are based on breeding records.

| | State and Status of List | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | ME proposed | NH proposed | VT proposed | MA official | RI proposed | CT unofficial | NY official | PA official |
| Bog turtle | - | - | - | E | - | D | E | E |
| Spotted turtle | T | S | S | S | + | + | + | + |
| Four-toed salamander | + | + | S | S | + | + | + | + |
| Spruce grouse | + | + | S | - | - | - | T | + |
| Three-toed woodpecker | + | S | S | - | - | - | + | - |
| Black-backed woodpecker | + | + | S | - | - | - | + | - |
| Gray jay | + | S | S | - | - | - | + | - |
| Rusty blackbird | + | S | + | + | - | - | + | - |
| Pigmy shrew | + | + | + | - | - | - | + | U |
| Southern bog lemming | + | + | S | S | S | R | + | + |
| Northern bog lemming | T | E | - | - | - | - | - | - |
| Woodland caribou | EX | EX | EX | - | - | - | - | - |

# CHAPTER 8. RECOMMENDATIONS FOR RESEARCH

This study revealed many major and critical gaps in our knowledge about the peat bogs of the northeastern United States. This applies to virtually all aspects of these bogs and is especially true for the topogenous and soligenous peatlands, which are most abundant in the Northeast. Research is needed to fill these gaps and to understand the consequences of anthropogenic changes to these peat bogs. The general nature of the research needed is briefly discussed below.

## 8.1 CLASSIFICATION OF PEAT BOGS

The peat bogs in the northeastern United States include a wide range of conditions with respect to habitats, their development, and processes. Ecological processes and chemical fluxes are closely tied to hydrological conditions. Because of fundamental differences in hydrology among major peatland types, data obtained in one bog type may not apply to other types. Therefore, all research should be carried out in well-defined peatland types. For this reason, an adequate classification of peatlands is essential.

In this report we used a peatland classification system based on hydrology and vegetation type as a basis for a discussion of differences among bogs. However, this classification was based on a very limited survey and inadequate plant community data. Clearly, this classification needs to be refined to serve as a framework within which research can be carried out.

## 8.2 ECOLOGICAL PROCESSES

We clearly need to know more about nutrient and metal fluxes in peat bogs to learn about the consequences of nutrient additions and about the capacity of bogs to retain nutrients and heavy metals.

In addition to research on chemical fluxes for bogs as a whole, specific processes within peatlands need to be investigated. Differences in decay of organic matter affect surface topography, water flow, and nutrient release. In spite of its obvious importance, we know less about decay rates and the microbial processes involved than about any other peatland process.

Water chemistry changes rapidly after mineral-soil water enters a peatland, and this affects vegetation, peat chemistry, and decay. An understanding of these processes is critical for an evaluation of the impact of anthropogenic alterations to the peatland or the surrounding uplands.

## 8.3 HYDROLOGY

The hydrology of very few bogs has been studied in the northeastern United States. Although the principles controlling water movement through bogs are well-established, their application to actual bog sites is difficult. The lack of data on water flow within peatlands especially hampers our understanding of processes in topogenous and soligenous peatlands.

Research needs to be focused on seepage into and flow through bogs, and on evapotranspiration losses from bogs. Seepage and evapotranspiration, through their effect on water chemistry and water table fluctuations, have a major impact on ecological processes and vegetation patterns.

Variability in seepage flow along the bog border and difficulties in measuring seepage flow are major reasons for the limited information available. These problems need to be addressed by integrated studies of the hydrology, water chemistry and vegetation of bogs.

Evapotranspiration varies with vegetation and water level. Detailed analyses of the variation in evapotranspiration within a peatland are required to understand water chemistry changes in undisturbed peatlands and to determine the impact of drainage, peat removal, and artificial lakes.

## 8.4 VEGETATION

This report describes the common plant communities of peat bogs and related peatlands, but this classification is based on very limited data. This study revealed how poorly the bog vegetation of the northeastern United States has been investigated. Most botanical studies of peatlands have described their flora rather than plant communities and community dynamics. In addition, floristic surveys usually refer to bogs as a whole and pay little or no attention to habitat differences within bogs.

The floristic composition of the vegetation is a sensitive indicator of water chemistry, water flow, and water table fluctuations. Vegetation studies should focus on establishing the relationship between environmental factors and the floristic composition of the vegetation. This type of information is needed to:

(1) predict changes in vegetation resulting from anthropogenic alterations affecting the peatland;
(2) use vegetation as an indicator of habitat variation and to trace water flow within a peatland; and
(3) provide a vegetation-habitat classification that can be used as a framework for studies on ecological processes and the application of their results in wise management.

## 8.5 BOG DEVELOPMENT AND SUCCESSION

Our knowledge about succession in the peat bogs of the Northeast is based mainly on that in lake-fill bogs which represent only a subset of the different types of bogs. Succession of bogs in general is often erroneously interpreted from vegetation zonation in this subset of bog types. Careful stratigraphical studies are needed to reconstruct the development of other peatlands, especially moat bogs and peatlands resulting from paludification. Bryophytes are dominant in the surface vegetation and preserve well in peat. Consequently, subfossil bryophyte assemblages will show the sequence of vegetation changes on a site in much greater detail than vascular plant remains or traditional stratigraphic studies. Such investigations can indicate succession during bog development as well as recent vegetation changes.

## 8.6 FLORA AND FAUNA

The biology and ecology of peatland organisms are poorly studied. Research on the flora and fauna should emphasize the basic ecology of the dominant species and those of special concern, such as rare and endangered species.

The availability of a suitable habitat is a precondition for the occurrence of any organism. For rare and endangered species, the presence of the required habitat and its extent is critical for their survival. Therefore, efforts to protect these species should be habitat oriented rather than species oriented. Habitat conditions in bogs are coupled to processes in the surrounding uplands. These uplands have a greater effect as bog size decreases. Consequently, recommendations for preservation and management will have to differ with bog type and size, the nature of surrounding uplands, and climate. Restoration of bog habitats is almost impossible because of their sensitivity to changes in nutrient input and hydrology, and the emphasis in protecting rare species has to be on habitat preservation.

The distribution of some organisms in bogs is little known. This applies especially to fungi and soil invertebrates. Research on these organisms should be encouraged to provide a more complete picture of the floristic and faunistic composition of bog communities. This is also of biogeographic interest because bogs have cold microclimates and often represent the southernmost habitats for northern species.

The results of all of this research will be directly applicable to solving environmental problems concerning the peatlands of the Northeast. This research will supply basic facts necessary to assess how anthropogenic alterations in the landscape will affect peatlands. In addition, it will provide a much-needed framework for the application of research results and for evaluating the relative value of remaining peat bogs.

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## APPENDIX: GLOSSARY OF TERMS

Aapa mire - a type of soligenous peatland, also called string mire, characterized by alternating strings and pools along the contours of the slope (Figures 1 and 9).
Acrotelm - the zone of biologically active, aerobic or intermittently aerobic surface peat, through which almost all water movement takes place; the low water table is often used as the boundary with the catotelm (Figure 18).
Aerobic - characterized by the presence of free oxygen.
Anaerobic - characterized by the absence of free oxygen.
Blanket bog - a type of ombrogenous peatland developing in climates with a large moisture surplus, such as cool, temperate, maritime climates; the peat covers slopes and valleys, but outcrops of mineral soil result locally in minerotrophic conditions.
Bog - a nutrient-poor, acidic peatland with a moss layer dominated by *Sphagnum* mosses; ericaceous shrubs or conifers are often dominant.
Bog pool - a small body of stagnant water in a bog, often several meters deep; in most peatlands they are secondary features.
Capillary water - water drawn above the water table in the small pores of the soil; held more tightly than gravitational water, but available to plants.
Capitulum - the head of a *Sphagnum* moss plant, formed by the dense growth of the newest branches.
Catotelm - the zone of permanently anaerobic peat, characterized by negligible water movement and very low biological activity (Figure 18).
Convex domed bog - a type of raised ombrogenous peatland (Figure 1) with a gentle slope toward the center and a more gradual change from minerotrophic to ombrotrophic vegetation than in plateau bogs.
Coprogenous sediment - a lake sediment consisting largely of fecal pellets of bottom fauna; relatively dark in color, slightly viscous but not sticky, and normally devoid of recognizable plant fragments.
Detritus - dissolved and particulate dead organic matter.
Dy - a brown lake sediment consisting largely of amorphous humus gels and mostly derived from bogs associated with the lake; poorer in nutrients than gyttja.
Endemic species - a species restricted to a region or habitat.
Ericaceous - belonging to the heath family (Ericaceae).
Eutrophic - relatively rich in nutrients; generally referring to a habitat more nutrient-rich than oligotrophic or mesotrophic habitats.
Evapotranspiration - combined loss of water from surface evaporation and from transpiration by plants.
Fen - an open peatland, sometimes with scattered trees, occurring on minerotrophic sites; richer in nutrients and less acidic than a bog.
Fen window - a site in a bog where nutrient-rich minerotrophic water reaches the surface.
Fibrist - a suborder of organic soils (Histosols) characterized by a subsurface layer composed mainly of plant fibers, or by a surface layer

(top 60 cm) composed mainly of Sphagnum moss fibers; less decomposed than hemists or saprists.

Graminoid - grass-like; referring to grasses, sedges and rushes.

Gyttja - a form of coprogenous sediment occurring in waters enriched in nutrients and oxygen, consisting of a mixture of particulate organic matter, inorganic precipitates, and minerogenic matter.

Heath - an area in which the vegetation is dominated by ericaceous shrubs, growing on mineral or organic soil; used in Maine to refer to an ericaceous dwarf-shrub bog.

Hemist - a suborder of organic soils (Histosols) characterized by a subsurface layer dominated by mucky peat or peaty muck; more decomposed and generally more nutrient-rich than fibrists, but less than saprists.

Histosols - the soil order of organic soils.

Hollow - a microtopographic depression of various sizes in peatlands; covered with Sphagnum moss, liverworts, lichens or bare peat, and intermittently with standing water.

Humification - the process of decay of plant remains to amorphous organic matter.

Hummock - a moss-covered elevation in a peatland, usually less than 40 cm high, and varying from less than 1 square meter to over 10 square meters in area, usually with dwarf shrubs, and sometimes with shrubs or trees.

Hydrarch succession - the progression of communities occurring when a pond is transformed into a bog by filling and mat growth.

Hydraulic conductivity - the rate at which water flows through a soil in response to a potential gradient.

Hydrostatic pressure - the pressure required to stop the movement of water; used as a measure of water potential.

Hypnoid mosses - mosses resembling those in the genus Hypnum, mostly used to indicate a variety of pleurocarpous mosses in peatlands not dominated by Sphagnum.

Lagg - the nutrient-enriched zone at the margin of a raised bog, receiving water from the surrounding mineral ground and from the bog itself.

Limnogenous peatland - a type of minerotrophic peatland developing along a lake or slow-moving stream.

Marsh - a wet area, periodically inundated with standing or slow-moving water, that has a grassy or herbaceous vegetation and often little peat accumulation; the water may be salt, brackish or fresh.

Medifibrist - an organic soil great group belonging to the fibrist suborder, and distinguished from the sphagnofibrists by a surface layer that contains less Sphagnum fiber or is less thick.

Mesotrophic - having moderate levels of nutrients; referring to a habitat intermediate in richness between eutrophic and oligotrophic.

Meteoric water - atmospheric water, i.e. precipitation.

Minerotrophic - areas influenced by water that has been in contact with soil or bedrock, and is richer in mineral-nutrient elements than rainwater.

Mire - a general term for a variety of peatlands ranging from ombrotrophic bogs to fens and swamps.

Mud-bottom - a flat depression or hollow in a bog, with a sparse cover of vascular plants and covered mostly by liverworts or with exposed peat.

Obligate associates - species which always occur together.

Obligate commensals - a pair of species in which one species requires the other to survive, but in which the other species is not reduced in fitness.

Oligotrophic - poor to extremely poor in nutrients; referring to a habitat less nutrient-rich than eutrophic or mesotrophic.

Ombrogenous peatland - a type of peatland in which development is controlled by precipitation; ombrogenous peatlands are primarily ombrotrophic but contain minerotrophic sites, mostly near their margins.

Ombrotrophic - rain-fed; used mostly to indicate peatlands or portions of peatlands which receive water only from precipitation.

Paludification - swamping of dry land by the rise of a water table in adjacent peatlands.

Pattern - a repetitive micro-physiographic arrangement in a peatland; used mostly to refer to the pattern of strings and pools.

Peat - the partially-decayed remains of plant material accumulating on wet sites because of water-logging.

Peatland - a wet area in which peat has accumulated.

Perched water table - a water table held above the regional level by an impermeable or slowly permeable layer.

Plant community - an assemblage of plants interacting with one another and occupying, and often modifying, a habitat.

Plateau bog - a type of raised ombrotrophic peatland characterized by a pronounced slope rising to an almost flat central plain; in the northeastern United States, this type of bog is restricted to the northeast coast of Maine (Figures 1 and 2).

Quaking bog - a bog with a surface that quakes or yields under foot, and that rises and falls with water level changes, e.g., the mat of a floating bog.

Raised bog - a type of ombrogenous peatland, with the ombrotrophic center raised above the minerotrophic bog border or lagg; this includes plateau and convex domed bogs.

Saprist - a suborder of organic soils (Histosols) characterized by a subsurface layer dominated by muck, a black organic material composed of less than one-third identifiable fibers; more decomposed and more nutrient-rich than fibrists or hemists.

Sapropel - a form of strongly reduced, biologically active, limnic peat.

Sclerophyllous - having thick, leathery, and usually wintergreen leaves.

Sedges - plant species in the sedge family (Cyperaceae), especially species of the genus Carex.

Seepage - lateral water flow through the soil; it represents an important mineral-soil water input into many peatlands.

Slope fen - a type of soligenous peatland that develops on slopes; it can occur far south of the zone of aapa mires if the supply of seepage water is abundant.

Soligenous peatland - a type of minerotrophic peatland depending on a reliable source of seepage water; water seeps through or over the surface peat.

Sphagnofibrist: an organic soil great group belonging to the fibrist suborder, and having a surface layer that consists of 75% or more of material derived from Sphagnum mosses, and being either 90 cm or more thick, or rests on rock or mineral soil.

Stratigraphy - the vertical sequence of layers of peat and other materials as deposited by vegetation in situ; this sequence records the history of the depositional environment and may be used to trace the development of the peatland.

String - narrow, elevated ridges oriented with their long axes across the slope and alternating with elongated pools.

Swamp - a wet minerotrophic peatland in which standing or gently flowing water occurs seasonally or persists for long periods, e.g., wooded swamps and shrub swamps.

Telluric water - terrestrial water; water that has been in contact with the mineral soil or bedrock.

Topogenous peatland - a type of minerotrophic peatland developing in topographical positions where water accumulates; generally maintained by a permanent ground water table.

Wooded heath - an ericaceous dwarf-shrub bog with some tree cover; heath and wooded heath are used in this sense only in Maine.

Wooded swamp - a wet minerotrophic peatland with sparse to dense tree cover; the trees are rooted below mean water level and can tolerate large water-level fluctuations.

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The publication reviews the ecological information available for peat bogs in the glaciated Northeastern United States, a region extending from the Canadian border to the Pocono Mountain area of Pennsylvania. Peat bogs depend on acidic, nutrient-poor water for development and usually occur in areas underlain by sand, gravel, or glacial till. The hydrologic characteristics and chemical composition of bogs influences both nutrient cycling and plant community development within bogs. This publication describes peat bogs, their distribution in the area under consideration, the physical settings in which they exist, and the types of bogs generally recognized. Hydrology, water chemistry, and the cycling of nutrients and other elements in peat bogs are discussed. This discussion leads into two chapters describing the vegetation and animal communities of peat bogs. The final chapters discuss anthropogenic influences on peat bogs and recommend studies to fill the gaps in our present understanding of the ecology of the peat bogs.


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