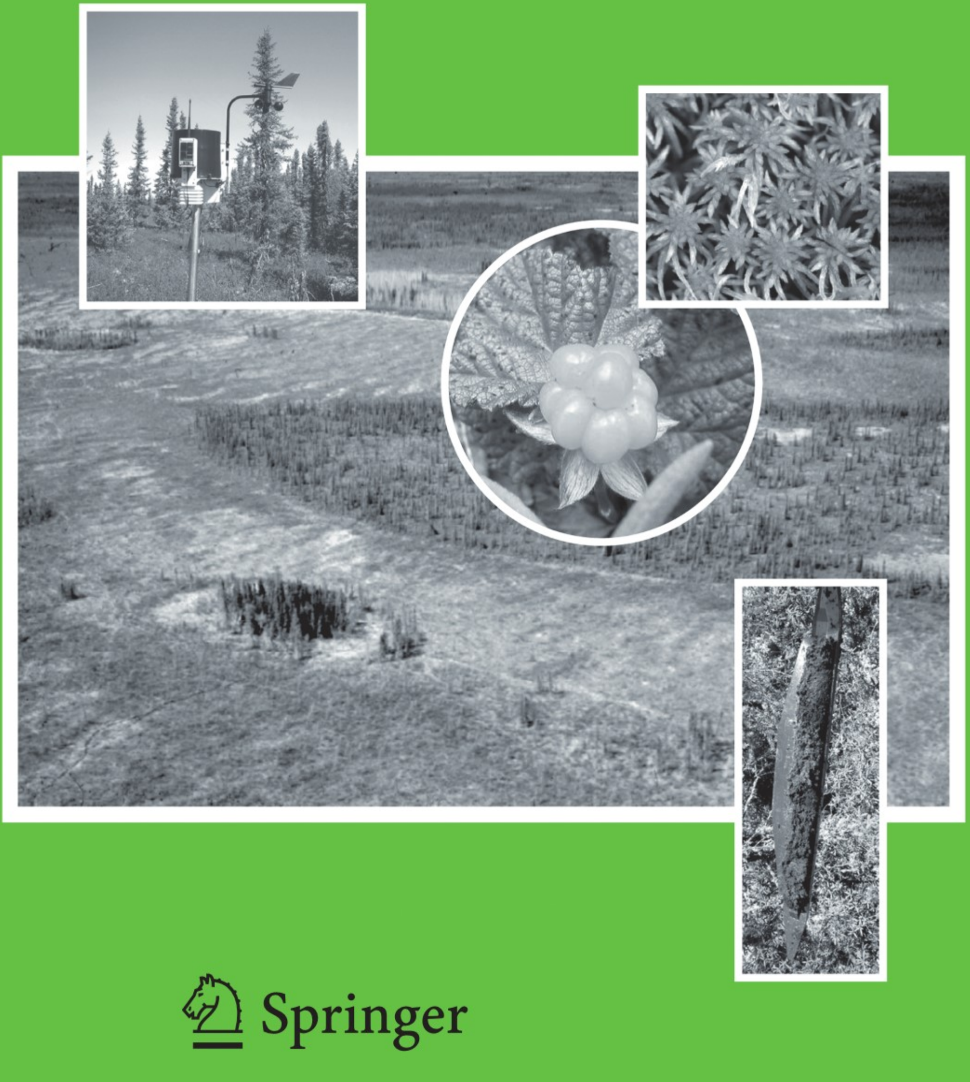
Ecological Studies 188

R. K. Wieder D. H. Vitt (Eds.)

Boreal Peatland Ecosystems



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R.K. Wieder D.H. Vitt (Eds.)

Boreal Peatland Ecosystems

With 73 Figures, 6 in Color, and 22 Tables

Springer

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Cover illustration: Boreal peatlands at Thickwood Hills, northeastern Alberta, Canada. Large wooded bog island with open internal lawns caused by localized permafrost melt. Paludified upland island (foreground left) surrounded by patterned rich fen (left and background) and bordered by aspen-dominated upland ridges (sand dunes) in center background. Photo taken May 23, 1982 by Dale H. Vitt. Insets: (top left to bottom right) Weather station in continental bog (Canada) [photo taken by Kimberli Scott; *Rubus chamaemorus* (Canada) [photo taken by Bin Xu]; *Sphagnum riparium* (Canada) [photo taken by Dale Vitt]; peat core with Macaulay corer (Canada) [photo taken by Rose Boise].

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Preface

Boreal peatland ecosystems – bogs and fens – cover only about 3 % of the earth's land surface, but their overall ecological and societal importance is proportionately much greater than their area might suggest. Most of these ecosystems are located in the northern hemisphere in areas that were completely covered with ice 10,000–25,000 years ago. In the relatively short period of time since deglaciation, peatlands have become widely established in northern boreal regions. Peatlands are characterized, of course, by accumulations of incompletely decomposed organic matter, or peat, that is often deep. Globally, peatlands contain about 30% of the world's terrestrial soil carbon, such that their carbon storage is much greater than their land surface area would suggest. The fate of this carbon, and indeed of boreal peatland ecosystems, in the face of ongoing climate change remains uncertain.

Peatlands also are the basis for a variety of human activities, including harvest for the horticultural industry, harvest for fuel, and forestry, the last especially in Scandinavian countries. Peatlands provide habitat for a unique suite of animal species. Several peatland plant species produce fruits that are consumed, directly or indirectly by humans (cranberries and cloudberries being prime examples). Many of the world's peatlands receive atmospherically deposited pollutants, including nitrogen, sulfur, and heavy metals, whose local and regional deposition patterns have changed in the past and will continue to change in the coming decades. With organic soils that are aerobic near the surface, and anaerobic below the water table, the behavior of these anthropogenically deposited materials differs considerably from the behavior in other terrestrial ecosystems.

Especially over the past 2 decades, boreal peatlands have received considerable attention from researchers in various parts of the world. In preparing this volume of *Ecological Studies*, our goal was to produce a current synthesis of the considerable research on boreal peatland ecosystems in which an *ecosystem perspective* is maintained throughout. At the heart of ecosystem science are the fundamental processes of nutrient cycling and energy flow. To understand these fundamental processes for a particular ecosystem, it is necessary to quantify nutrient pools and fluxes, as well as the biotic and abiotic controls on fluxes. Key processes include net primary production, decomposition, and secondary production through fauna, with important controls that include climate and hydrology, along with their anthropogenic influences. In putting together the new volume, we have asked chapter authors to do their best at synthesizing available information from peatlands around the world. We also have encouraged chapter authors to keep an ecosystem perspective in mind in preparing their chapters. Our overall goal was to produce the first truly ecosystem-oriented peatland volume, with global, rather than local or regional, relevance.

Villanova, PA, March 2006 *R. Kelman Wieder* and *Dale H. Vitt*

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1 Peatlands and the Boreal Forest

R. Kelman Wieder, Dale H. Vitt, and Brian W. Benscoter

> "Eos shared love's bed with Astraeus
> and bore him the mighty-spirited winds,
> bright Zephyrus and gusty **Boreas** and Notus."
>
> From the poet Hesiod, *Theogony*

Peatland ecosystems, in the simplest definition, are terrestrial environments where over the long term, on an areal basis, net primary production exceeds organic matter decomposition, leading to the substantial accumulation of a deposit rich in incompletely decomposed organic matter, or peat. Under this very broad definition, peatland ecosystems can be found in arctic, boreal, temperate, or tropical climates (Gore 1983; Immirzi et al. 1992; Gignac and Vitt 1994; Lappalainen 1996; Charman 2002), although 80 % of the world's peatlands are found in the boreal region (Joosten and Clarke 2002). We have chosen to focus this book on boreal peatlands.

The word boreal derives from Boreas (Βορεας), Greek god of the north wind, one of the four children of Eos, goddess of the dawn, whom Aphrodite had cursed with nymphomania, and the Titan Astraeus, god of the night sky and father of the stars. Boreas's siblings, Eurus, Zephyrus, and Notus, gods of the east, west, and south winds, respectively, generally were portrayed as gentler than Boreas. Boreas was envisioned as a bearded, curly-haired, and winged god who wore boots and a tunic to protect him against the cold. In some portrayals, Boreas held a spiral conch shell that he could blow to herald the advent of the winds under his command. Boreas was a powerful god of blustery temperament. Boreas's daughter was Chione, the goddess of snow. Boreal regions, however defined, are characterized by cold climates.

One of the most straightforward climatically based definitions of the boreal zone was provided by Walter (1973), who divided the world into nine zonobiomes, of which the eighth was the "zonobiome of the cold-

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temperate boreal climate." According to Walter (Breckle 2002), "the true boreal zone commences at the point where the climate becomes too unfavorable for the hardwood deciduous species, i.e, when summers become too short and winters too long." Walter defined the southern limit of the boreal zone climatically, as occurring where the duration of the period with a mean daily temperature of more than 10 °C drops below 120 days and the cold season lasts longer than 6 months. The northern limit of the boreal zone, above which arctic tundra prevails, occurs where the duration of the period with a mean daily temperature of more than 10 °C drops below approximately 30 days and the cold season lasts longer than 8 months. The terms boreal forest and taiga are often used interchangeably, although taiga is sometimes reserved for Russian and/or European regions. Taiga is commonly referred to as having subarctic climate, a term that is synonymous with boreal climate. According to the Köppen–Trewartha system (Köppen 1931; Trewartha and Horn 1980), boreal/subarctic climate gives way to polar climates to the north when the mean monthly temperature for the coldest month drops below 10 °C, and gives way to temperate climates to the south when the average temperature exceeds 10 °C for more than 4 months.

Holdridge (1947) introduced an objective system to differentiate "the vegetation of dry land areas of the world into 100 closely equivalent formations separated by temperature, precipitation, and evaporation lines of equal value." According to the Holdridge life zone classification system, cold or boreal regions of the earth can be found where the mean annual biotemperature (mean annual temperature calculated with all temperatures less than 0 °C set to 0 °C) is between 3 and 6 °C (Fig. 1.1). On the basis of Gignac and Vitt's (1994) superimposition of the distribution of the world's peatlands onto the Holdridge life zone diagram (Fig. 1.1a), boreal peatlands can be found where mean annual precipitation is between 500 and 3,000 mm, where the potential evapotranspiration ratio is between 0.125 and about 0.800, and where mean annual biotemperatures are between 3 and 6 °C (Fig. 1.1b). The spatial distribution of these conditions across the northern hemisphere provides a climatically based view of where boreal peatland ecosystems potentially could be found (Fig. 1.2; data from Leemans and Cramer 1990).

The boreal region has also been defined by its characteristic vegetation (Fig. 1.3), rather than by climate, as consisting of extensive conifer-dominated forest – the boreal forest or taiga. "The flora of boreal regions is impoverished, and the dominant arboreal element is particularly poor in genera and species" (Hare and Ritchie 1972). At its northern limits, the boreal forest gives way to treeless tundra, yet the boundary to the south is defined by the replacement of conifer-dominated forests with deciduous broadleaf forest, parkland, or grassland, depending on the prevailing regional climate (Larsen 1980).

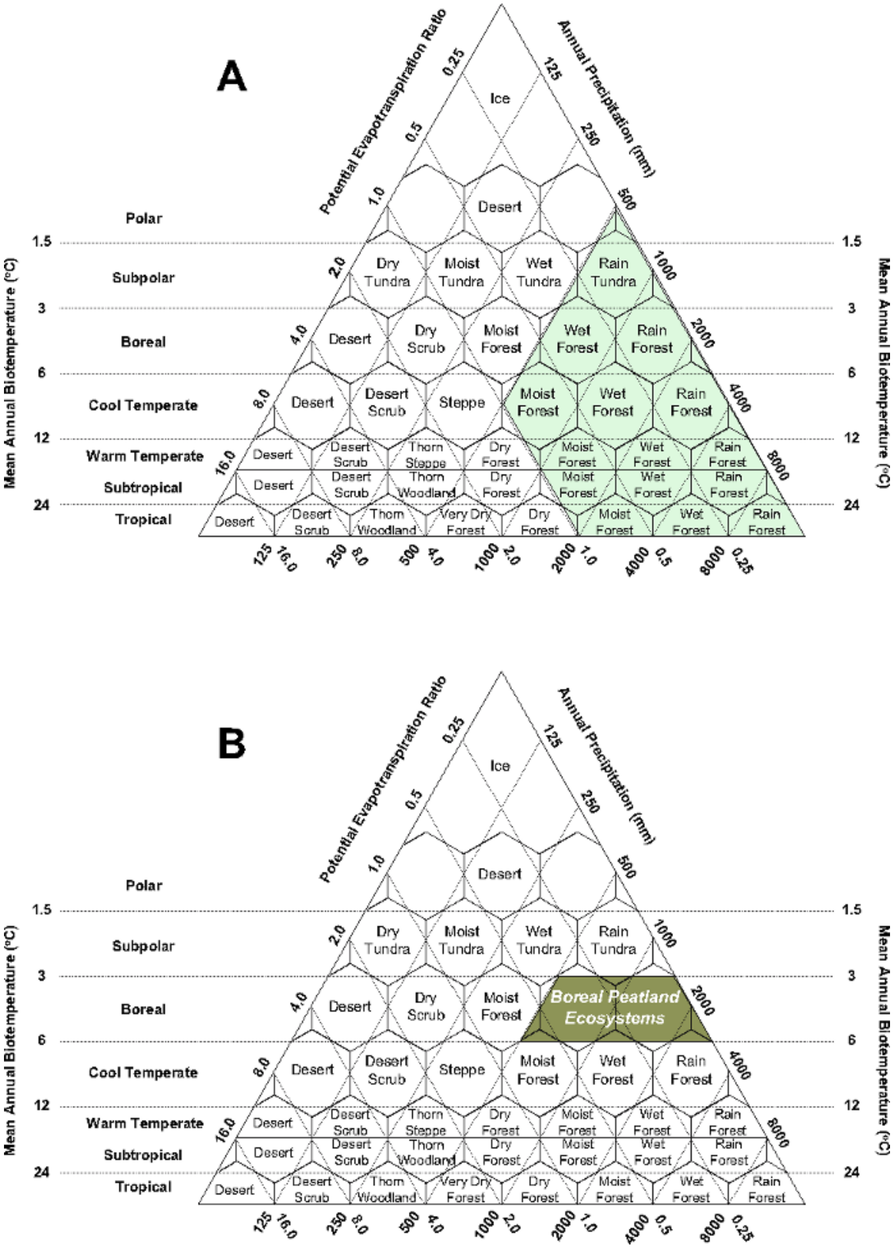

Fig. 1.1. A The Holdridge life zone approach (adapted from Hartshorn 1988) to delineating the global climatic distribution of peatland ecosystems and **B** the climatic distribution of boreal peatland ecosystems (**a** adapted from Gignac and Vitt 1994)

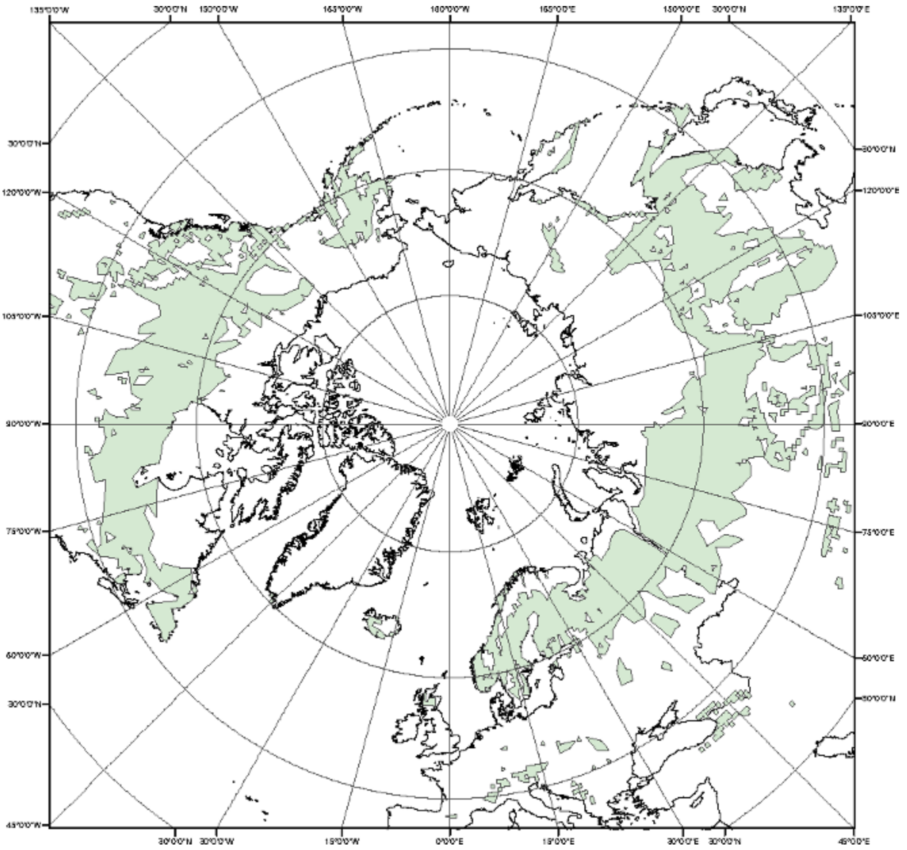

Fig. 1.2. Distribution of the earth's land surfaces where boreal peatlands potentially can be found based on the Holdridge life zone system (Fig. 1.1b)

More recently, interest in biodiversity has led to an effort to map the ecoregions of the world on the basis of floristic, faunistic, and vegetation information (Olson and Dinerstein 1998). Within this scheme, biome is a broad term that refers to ecoregions with similar climate, vegetation structure, biodiversity patterns, flora and fauna with similar guild structures and life histories, similar thresholds for maintaining biodiversity, and similar sensitivities to human disturbance. Boreal forests/taiga (Fig. 1.4) is one of 14 recognized biomes in this scheme.

All of these schemes for classifying boreal environments (Figs. 1.1–1.4) produce similar global distributions of the boreal zone, reflecting the strong relationship between climate and vegetation. Boreal forests cover 1.4 × 10^9 ha, or one third of the global forested areas (IPCC 2000). However, it is important to note that while most of the boreal forest is occupied by upland forests underlain by mineral soils, about 24 % of the boreal for-

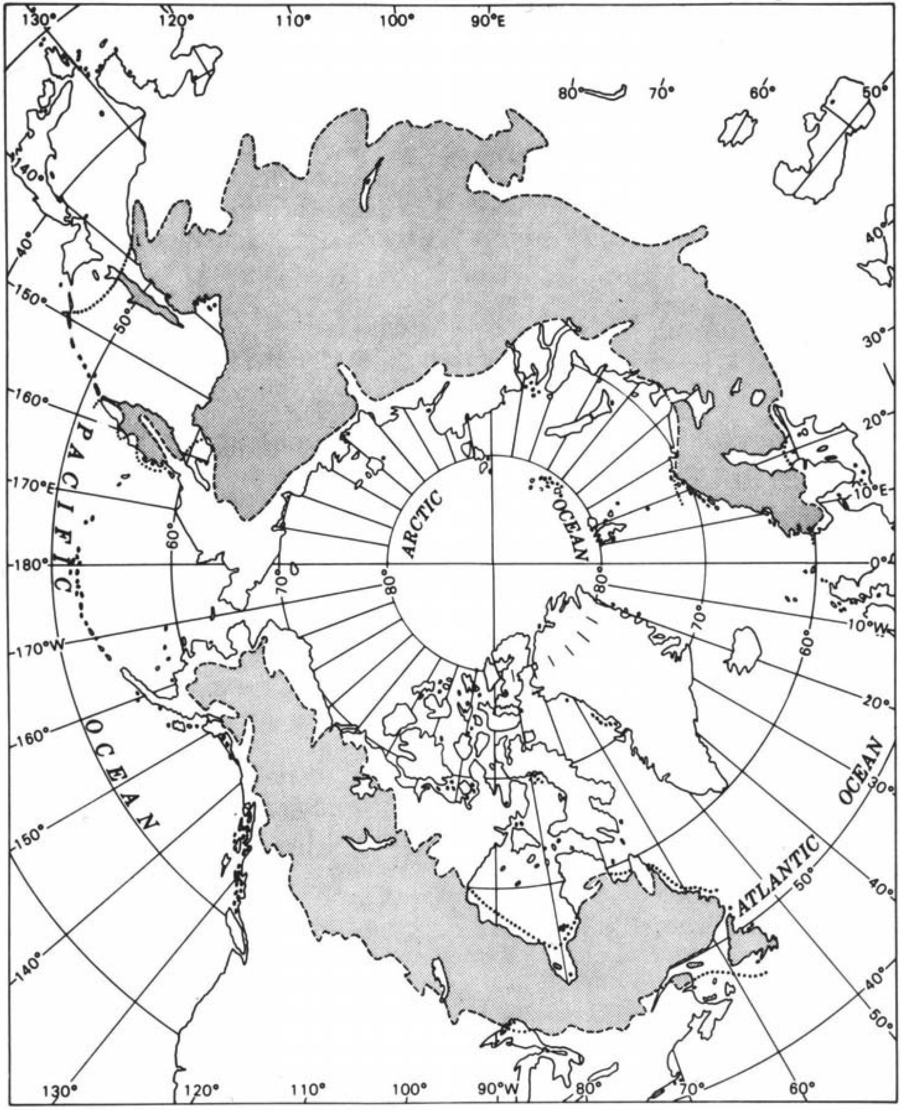

Fig. 1.3. Geographical distribution of the boreal forest in the northern hemisphere (from Hare and Ritchie 1972, adapted from Sjörs 1963)

est region is occupied by peatlands (the percentage was calculated from peatland areas for Norway, Sweden, Finland, Russia, and Canada given in Joosten and Clarke 2002 and for Alaska given in Immirzi et al. 1992, which collectively represent 330 × 10^6 ha).

Boreal and peatland ecosystems cover only about 2–3 % of the earth's land surface, but their overall ecological and societal importance is pro-

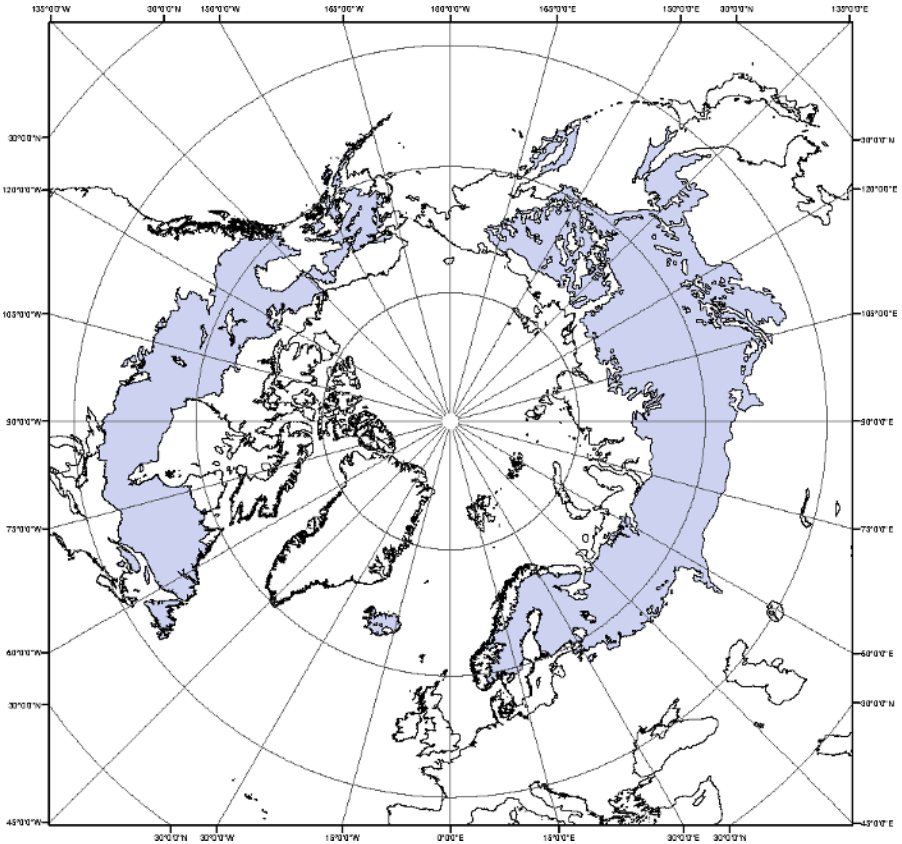

Fig. 1.4. Distribution of the boreal biome of the northern hemisphere (*light blue*), as defined by Olson and Dinerstein (1998) and Olson et al. (2001). GIS data downloaded from the World Wildlife Fund database (http://www.worldwildlife.org/science/data/terreco.cfm)

portionately much greater than their area might suggest. Most of these ecosystems are located in the northern hemisphere in areas that were completely covered with ice 10,000–25,000 years ago. In the relatively short period of time since deglaciation, peatlands have become widely established in northern boreal regions. Globally, peatlands contain about 30 % of the world's terrestrial soil carbon (Gorham 1991), such that their carbon storage is much greater than their land surface area would suggest. The fate of this carbon under scenarios of future climate change, however, remains uncertain.

Peatlands are also the basis for a variety of human activities, including peat harvest for the horticultural industry, fuel, and forestry; the last of these being especially important in Scandinavian countries. Peatlands provide habitat for a unique suite of animal species. Several peatland plant species produce fruits that are consumed, directly or indirectly, by humans (cranberries and cloudberries being prime examples).

Many of the world's peatlands receive atmospherically deposited pollutants (including nitrogen, sulfur, and heavy metals) whose local and regional deposition patterns have changed in the past and will continue to change in the coming decades. With organic soils that are aerobic near the surface, and anaerobic below the water table, the behavior of these anthropogenically deposited materials differs considerably from their behavior in other terrestrial ecosystems.

Our goal in this book is to produce a current synthesis of the considerable research on boreal peatlands in which an *ecosystem perspective* is maintained throughout. Authors of chapters will have occasion to cite research conducted on sub-boreal or temperate peatlands, especially the rather substantial literature on such *Sphagnum*-dominated peatlands in North America, Great Britain, and Europe, especially when such information provides insight into the functioning of boreal peatlands.

References

Breckle S-W (2002) Walter's vegetation of the earth – the ecological systems of the geo-biosphere, 4th edn. Springer, Berlin Heidelberg New York

Charman D (2002) Peatlands and environmental change. Wiley, Chichester

Gignac LD, Vitt DH (1994) Responses of northern peatlands to climate change: effects on bryophytes. J Hattori Bot Lab 75:119–132

Gore AJP (ed) (1983) Ecosystems of the world 4A. Mires: swamp, bog, fen and moor. General studies. Elsevier, Amsterdam

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195

Hare FK, Ritchie JC (1972) The boreal paleoclimates. Geogr Rev 62:334–365

Hartshorn GS (1988) Tropical and subtropical vegetation of Meso-America. In: Barbour MG, Billings WD (eds) North American terrestrial vegetation. Cambridge University Press, Cambridge, pp 365–390

Holdridge LR (1947) Determination of world plant formations from simple climatic data. Science 105:367–368

Immirzi CP, Maltby E, Clymo RS (1992) The global status of peatlands and their role in carbon cycling. Friends of the Earth, London

IPCC (2000) Land use, land use change and forestry. In: Watson RT, Noble IR, Bolin B, Ravindranath NH, Verardo DJ, Dokken DJ (eds). Intergovernmental panel on climate change. Cambridge University Press, Cambridge

Joosten H, Clarke D (2002) Wise use of peatlands – background and principles including a framework for decision-making. International Mire Conservation Group and the International Peat Society, Jyväskylä

Köppen W (1931) Grundriss der Klimakunde. de Gruyter, Berlin

Lappalainen E (ed) (1996) Global peat resources. International Peat Society, Jyväskylä

Larsen JA (1980) The boreal ecosystem. Academic, New York

Leemans R, Cramer WP (1990) The IIASA mean monthly temperature, precipitation and cloudiness on an global terrestrial grid. WP-90-41, Biosphere Dynamics Project, International Institute for Applied System Analysis IIASA, A-2361 Laxenburg, Australia

Olson DM, Dinerstein E (1998) The global 200: a representation to conserving the earth's most biologically valuable ecoregions. Conserv Biol 12:502–515

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedeo P, Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51:933–938

Sjörs H (1963) Amphi-Atlantic zonation, Nemoral to Arctic. In: Löve Á, Löve D (eds) North American biota and their history. Oxford University Press, London, pp 109–125

Trewartha GT, Horn LH (1980) An introduction to climate, 5th edn. McGraw-Hill, New York

Walter H (1973) Vegetation of the earth, first English edition. Springer, Berlin Heidelberg New York

2 Functional Characteristics and Indicators of Boreal Peatlands

Dale H. Vitt

2.1 Introduction

Globally, peatlands occupy about 4×10^6 km^2 (Gorham 1991; Joosten and Clarke 2002), with the boreal and subarctic peatland area estimated to be approximately 3.46×10^6 km^2, or about 87 % of the world's peatlands. Six countries have greater than 50,000 km^2 of peatland and these account for 93 % of the world's peatlands – five of these countries are predominantly boreal. Russia contains 1.42×10^6 km^2, Canada 1.24×10^6 km^2, the USA 625,000 km^2, Finland 96,000 km^2, and Sweden 70,000 km^2; in addition, Indonesia has an estimated 270,000 km^2 (Joosten and Clarke 2002).

The term *peatland*, commonly used in the North American literature, is used interchangeably in this chapter with the European term *mire*. Although recently Joosten and Clarke (2002) have given slightly different meanings for these two terms, here I consider the terms to be synonymous. Peatlands are ecosystems in which net primary production (NPP) has exceeded decomposition over thousands of years, and as a result organic matter, rich in carbon, has accumulated over time, and peat is formed. Although peat-forming plant communities occur in most of the world's nine zonobiomes (Walter 1979), they are most prevalent in zonobiome VIII (cold-temperate boreal climate), or more commonly termed the boreal forest. Zonobiome VIII is characterized by short summers and long winters, coniferous, evergreen vegetation, and podzolic upland soils (Chap. 1). Precipitation is variable, ranging from annual total precipitation of 2,000 to about 250 mm; however, because of short cool frost-free seasons even when precipitation is quite low it exceeds potential evapotranspiration.

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2.2 Peatland Initiation

Across the boreal zone, peatlands originate by four processes (Chap. 3). The most common appears to by paludification (or swamping) wherein peat forms on previously drier, vegetated habitats over inorganic soils and in the absence of a body of water, generally owing to a regional water table rise and associated climatic moderation. Additionally, local site factors may have strong influences on paludification (Almquist-Jacobson and Foster 1995; Anderson et al. 2003). Secondly, peat may form directly on fresh, moist, nonvegetated mineral soils. This primary peat formation occurred directly after glacial retreat or on former inundated land that has risen owing to isostatic rebound. Thirdly, shallow bodies of water may gradually be filled in by vegetation that develops floating or grounded mats – these mats filling in, or terrestrializing, the former aquatic habitat. Both lake water chemistry and morphometry, as well as species of plants in the local area, influence the rates and pathways of vegetation succession (Kratz and DeWitt 1986; Vitt and Slack 1975; Wilcox and Simonin 1988). Fourthly, peat may form and be deposited on shallow basins once occupied by early Holocene lakes. These former lake basins, lined with vegetated impervious lake clays, provide hydrologically suitable sites for subsequent peat development. Although the last process has not been recognized previously, I discuss it briefly as it may be common in glaciated areas on flat terrain.

2.3 Critical Factors for Peatland Diversification

Beginning in the early 1900s, many authors have described peatlands and discussed the factors that they perceived as of primary importance to peatland development and persistence. Many of these early studies included boreal peatlands or peatlands just south of the boreal zone. Fundamental classic papers include those by Cajander (1913) in Finland, Weber (1911) in Germany, Clements (1916) in the USA, Lewis and Dowding (1926) in Canada, von Post and Granlund (1926) in Sweden, Katz (1930) in Russia, and Tansley (1939) in Great Britain. Later in that century, studies by DuReitz (1949), Sjörs (1950), Ivanov (1957), Ruuhijärvi (1960), Eurola (1962), and Heinselman (1963) had international importance. These papers (and many others) have provided much of the basis for our understanding of peatland function and diversity. Here I attempt to review these primary factors within the framework of the boreal zone.

Five factors appear to have great significance on how peatlands function– hydrology, climate, chemistry, substrate, and vegetation/flora. All of these have been used to varying degrees to develop classifications of peatlands and to explain how peatlands are distributed.

2.3.1 Hydrology

Peatland persistence depends on a constant, long-term water supply, and the origin of this water influences the form and function of peatlands. Following the ideas of Weber (1911), von Post and Granlund (1926), and Sjörs (1948), water arriving at a peatland can be derived from a variety of sources. Diagrams and useful discussions of these hydrological types can be found in Damman (1986) and Mitsch and Gosselink (2000). Some peatlands are influenced only by waters derived from rain and snow (*ombrogenous*), whereas other peatlands are dominated by ground and surface waters (*geogenous*). Geogenous waters can be of three types depending on the movement and source: (1) stagnant water –generally soil water, but stagnant bodies of water are included here as well (*topogenous*); (2) flowing water – especially sheet flow on gentle slopes, including seepages and springs (*soligenous*); (3) flood water – especially from water courses that result in lateral flow away from the direction of stream flow (*limnogenous*).

Geogenous waters of all three types contain dissolved cations and anions ("minerals") and this minerotrophy (DuReitz 1954) exerts a strong influence on the vegetation, flora, and function of peatlands, and forms the ecological basis for the term fen. Ombrogenous waters have lower concentrations of dissolved cations and anions and provide the ombrotrophic conditions suitable for the development of a bog. Thus, from a hydrological perspective, fens are geogenous and bogs are ombrogenous. From an ecosystem point of view, fens are minerotrophic, while bogs are ombrotrophic. In addition to the fundamental role played by hydrology (Chap. 13), both bogs and fens are also strongly influenced by local climate, regional substrate and geomorphology, prevalent regional vegetation and flora, and water chemistry, and as a result occur on the landscape in a number of different types. These individual peatland types often occur together and form large peatland complexes containing a wide variety of peatland types (Vitt et al. 2003).

2.3.2 Climate

Ruuhijärvi (1960) and Eurola (1962) for Finland, Damman (1979) for eastern North America, Botch and Masing (1979a, b) for Russia, Sjörs (1983) for Sweden, and Vitt et al. (2000) for western Canada have provided maps or diagrams for the broad geographical distribution patterns of the major peatland complexes in the boreal zone. Detailed reviews of these regional peatland complexes are in Gore (1983) and Keddy and Fraser (2005). In Russia, the Vasyugan peatland complex covers about 5.27 × 10^6 ha (Inisheva and Golovatskaya 2002) and is the largest continuous peatland system in the world (Botch and Masing 1983). In Canada, two large areas of peatlands are present: the Hudson Bay Lowlands, with extensively paludified fens, and the MacKenzie River Basin peatland complex in northwestern Canada, with permafrost bogs to the north and fen complexes to the south. In Fennoscandia, extensive aapamire complexes dominate the boreal zone.

At the regional scale, peatland complexes vary with climate. Across the boreal and subarctic zonobiome, the principal peatland complexes are generally correlated with climatic gradients of precipitation and temperature (Fig. 2.1). Climate varies from relatively cool and moist conditions in the south to climates with cold, relatively dry regimes in the north. In relatively cool, moist climates, ombrogenous plateau bogs and soligenous blanket fens dominate. These peatland complexes are abundant in coastal Norway, extreme southern Finland, Scotland, and coastal British Columbia and Newfoundland, Canada, as well as coastal Maine and southwestern Alaska, USA. Generally northward and inland, these coastal zones are followed by a zone of patterned bogs, with regional dominance of concentric and eccentric raised bogs (or basin bogs) especially dominant in more southern, subcontinental boreal areas such as southern Sweden and Finland, Atlantic Canada, Maine, and western (European) Russia. The patterned bogs are treeless or nearly so, dominated by species of *Sphagnum* (*S. tenellum*, *S. capillifolium*, *S. austinii*, and/or *S. cuspidatum*) that are more or less restricted to oceanic/subcontinental climates, and that are generally associated with wet, minerotrophic laggs (or moats) and surrounding wooded fens. As climate becomes more continental, trees and/or shrubs become more abundant and water becomes less available at the bog surface; thus patterns are decreased. Some scattered trees (at least in North America and Siberia), the presence of scattered pools of water, and a lack of hydrological patterning characterize these subcontinental bogs. Glaser and Janssens (1986) proposed a model of peatland development that attempted to place these regional peatland types into a broad successional framework. As with the more oceanic peatland complexes, marginal wooded fens (Canada) and wooded swamps (the Sogua in Siberia; E. Lapshina, personal communication) may be extensively developed around subcontinental bogs. Across the midboreal and southern boreal zones where continentality is further increased, bogs and fens characteristically occupy isolated basins or form peatland complexes containing mixtures of fens and bogs. Continental bogs lack pools of water, are extensively wooded (at least in North America but less so in Siberia), and lack dominance by the more oceanic/subcontinental species of *Sphagnum*. Domi-

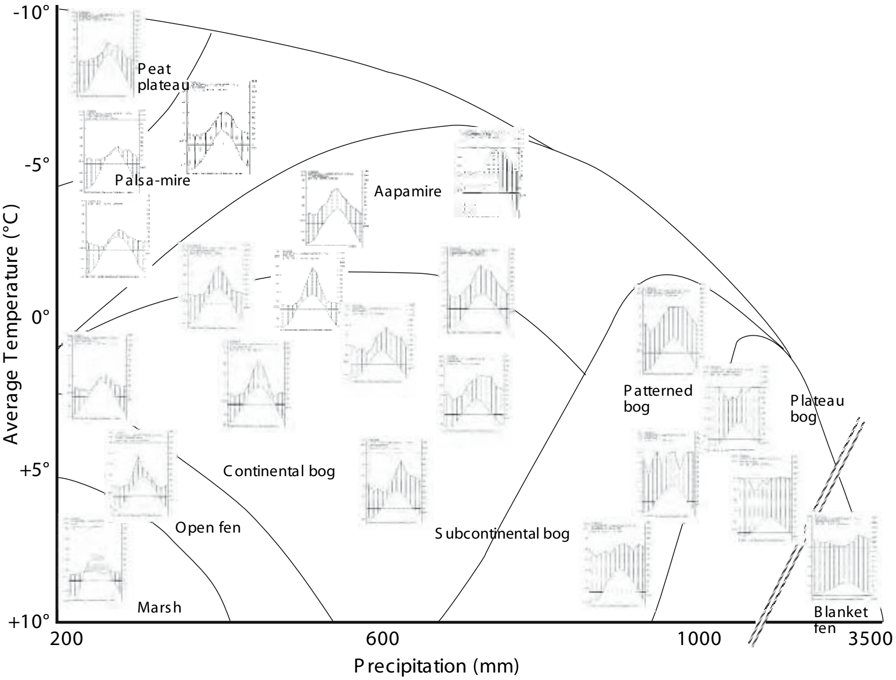

Fig. 2.1. Relationship between climate (temperature and precipitation) and major peatland complexes of the boreal forest (derived from patterns presented by Sjörs 1983, Ruuhjärvi 1983, Botch and Masing 1983, Vitt et al. 2003, Damman 1977, and Zoltai and Pollett 1983; climate diagrams from Lieth 1999)

nating in the midboreal and extending into the northern boreal forest is the aapamire zone. In the broad sense, aapamires are minerotrophic, wet peatland complexes. Aapamire complexes may have patterned fens (flark aapamires), fen lawns (lawn aapamires), and/or small bogs (Laitinen et al. 2005). These large patterned or unpatterned fen complexes always contain mire expanse vegetation (Sjörs 1948) at their centers (Laitinen et al. 2005) and are extremely variable in chemistry and vegetation depending on local substrate conditions (see later). The aapamire zone is extensively developed in central Fennoscandia and northwestern Siberia, as well as to a lesser degree across Alaska and Canada. In continental Canada, extensive aapamire complexes contain open, patterned or unpatterned, fens along with associated densely wooded bog islands and peninsulas. At the northern and most continental end of the climatic gradient are two regional peatland complex types influenced by permafrost. Peat mounds and ridges with permafrost cores contained within an extensive matrix of unfrozen minerotrophic fen characterize palsa mires. Patterned palsa mires with parallel ridges, each with an ice core and alternating with unfrozen pools of water usually filled with carpets of *Sphagnum*, may dominate the landscape. Palsa mires appear to be associated with areas where surface water is abundant. Peatland complexes having peat plateaus or large solitary permafrost peat islands, often within a minerotrophic fen matrix, replace palsa mires in areas where surface water is less abundant and permafrost more extensive. In the subarctic forest-tundra, these permafrost islands coalesce to form extensive frozen landscapes containing only small residual pockets of unfrozen peat (collapse scars; Horton et al. 1979). The latter are common in central Canada and northwestern Siberia, whereas the former are distributed widely in northern Fennoscandia, Russia, Alaska, and Canada. Finally, whereas western Siberia (east of the Ural Mountains) west of the Yensiei River has abundant peatlands, the area east of the Yenisei River is rather mountainous and peatland cover is less (E. Lapshina, personal communication)

2.3.3 Vegetation and Flora

In the 1940s, DuReitz (1954) described minerotrophic, acidophilous, *Sphagnum*-dominated plant communities that are relatively poor in species, and he termed peatlands having these communities "poor fens." He also recognized that there exist minerotrophic plant communities having species with little tolerance for acidity. These "rich fen" communities contain quite a few species with high fidelity to circumneutral or calcareous conditions and are relatively rich in species. He termed these circumneutral fens "moderate rich fens" and the calcareous fens as "extreme rich fens" (DuReitz 1954). Rich fens for the most part lack a significant cover of *Sphagnum*; thus, the peat mosses dominate only in ombrotrophic bogs and minerotrophic poor fens (but see later). Rich fens, on the other hand, have ground layers dominated by a number of true mosses that owing to their reddish-brown coloration have been called brown mosses. This division in ground-layer type as a critical difference between bogs and poor fens, compared with rich fens, has been emphasized by several authors recently (Gorham and Janssens 1992; Vitt 2000; Wheeler and Proctor 2002) and all of these authors have suggested that the fundamental differences in the flora between *Sphagnum*-dominated and brown-moss-dominated peatlands should provide the basic criterion for our classification of peatlands. However, it has long been noted that some circumneutral rich fens can have some abundance of mesotrophic *Sphagnum* species and it may be that *Sphagnum*-dominated rich fens may also deserve special recognition.

Since most species of the ground layer (bryophytes and lichens) have disjunct, rather broad distributions, especially in the boreal region, they allow direct comparisons of peatlands between Asia, Europe, and North

America. As far as I know, all species of peatland bryophytes occur in at least two of these three boreal regions. In contrast, many of the abundant vascular plants occur in only one (or sometimes two) of these geographical areas. Tree species that dominate peatlands in North America (*Picea mariana* in bogs and fens and *Larix laricina* in fens) do not occur in Eurasia. *Pinus sylvestris* and *Picea abies* are restricted to Europe and western Asia, whereas *Larix gmelinii, Larix sibirica, Pinus obovata*, and *Pinus sibirica* are known only from Asia. Species of *Betula* are largely different between the three geographical regions; for example, *Betula pubescens* is characteristic of fens in Siberia, while *B. glandulosa* and *B. glandulifera* are characteristic in North America. The dwarf shrubs have important differences, including *Ledum groenlandicum* (endemic to North America) and *Calluna vulgaris* and *Erica tetralix* [endemic to Eurasia (*Calluna vulgaris* is also known from Newfoundland)]. Additionally, many of the field layer species are restricted to either North America or Eurasia, and few of the *Carex* species are disjunct between North America and Eurasia. However, despite these floristic differences in the vascular plants, several critical species do occur in both Eurasia and North America, including *Chamaedaphne calyculata*, *Ledum palustre*, several species of *Vaccinium*, including *V. oxycoccos* and *V. vitis idaea*, and *Rubus chamaemorus.*

2.3.4 Vegetation Comparisons

Although ombrotrophic bogs are characteristically uniform throughout the boreal zone, several key geographical differences do occur. In boreal North America, *Picea mariana* dominates the tree layer; thus, all continental boreal bogs have a dense canopy beneath which *Ledum groenlandicum* normally dominates. As continentality decreases, *Picea mariana* decreases in cover until North American oceanic bogs become treeless, or have scattered individuals of *Thuja plicata* on the west coast (Vitt et al. 1990). In contrast, in eastern Asia, species of *Larix (*e.g., *L. gmelinii* and *L. sibirica)* dominate in bogs and fens, while in boreal Europe and western Asia, bogs are treeless or have only scattered individuals of *Pinus sylvestris*, with tree cover increasing with continentality. In continental Siberia dwarf *Pinus sylvestris* covers the bogs. Across the boreal zone, fens vary from completely treeless (open) to shrub-dominated (mostly *Betula* and/or *Salix* species) to wooded (with open canopy); however, the occurrence of *Larix laricina* only in North America allows most boreal fens on the continent to have significant tree cover, whereas in Eurasia, fens are either open or dominated by a series of different flowering plant species. None of these tree species, except *Larix laricina*, has the ability to tolerate the high water levels present in aapamires; as a result, patterned aapamires in North America typically have a greater abundance of trees than they do in Eurasia. Also, abundant in Europe and western Russia are wooded swamps (Sogua or black alder swamps), while in western Siberia wooded swamps are highly variable, but have high species richness, especially in the field and ground layers.

In summary, in terms of vegetation, North American bogs and fens, especially throughout the continental boreal areas, are characterized by a higher abundance of trees, while Eurasian peatlands are far more often open or only have scattered individuals present. Comparisons between continents are hampered by intercontinental floristic differences in the vascular plants, especially the lack of several key indicators on one or the other continents (e.g., *Calluna vulgaris*, *Erica tetralix*, *Ledum groenlandicum*). Intercontinental similarities in bryophyte floras, coupled with their highly specific habitat requirements (Gignac et al. 1991), make these ground-layer species highly suitable as peatland indicators.

2.3.5 Floristic Indicators

Perhaps the best integrators of long-term variability in minerotrophy and ombrotrophy are the plants that exist at individual peatland sites. Lists of typical indicator species for bogs and/or fen types are available in Ruuhijärvi (1960) and Eurola (1962) for Finland, Sjörs (1983) for Sweden, and Chee and Vitt (1989) for western Canada. Whereas the flora and vegetation of peatlands have been well studied (Dierssen and Dierssen 2001) and are not dealt with in detail here, the fungi (Chap. 6) and fauna (Chap. 5) are less well understood and are treated in more detail. Integration of indicators from these lists produces a short list of critical indicators of peatland types of the boreal region that largely span North America, Europe, and Asia (Fig. 2.3). Especially noteworthy are the following: for ombrotrophy, *Rubus chamaemorus*, *Sphagnum fuscum*, and *Calluna vulgaris* (Eurasia only) are usually reliable. *Warnstorfia fluitans* is characteristic of bog pools. For minerotrophy, *Betula glandulosa* (North America only), *Sphagnum riparium*, and numerous regional *Carex* species, including *C. lasiocarpa*, *C. limosa*, and *C. rostrata*, are indicated. Especially noteworthy as critical indicators are species of the moss family Amblystegiaceae, particularly species that historically have been placed in the genus *Drepanocladus* (*sensu lato*). Currently these are usually distributed among several genera: *Warnstorfia fluitans* (bogs); *W. exannulatus* (poor fens); *Drepanocladus aduncus* (eutrophic habitats – marshes); *Scorpidium cossonii* (extreme rich fens); *Hamatocaulis vernicosus* and *H. lapponicus* (moderate rich fens).

2.3.6 Substrate

Whereas bogs are hydrologically separated from influences of local groundwater, fens are seasonally in contact with surface water (lake, stream, spring runoff over frozen ground) and/or groundwater. The surrounding bedrock and soil chemistry determine the chemistry of the water flowing into the fen. For example, the highly impervious, granitic and metamorphic bedrock of eastern Canada, Fennoscandia, and the glaciated, alluvial sediments of western Siberia provide inputs poor in minerals and relatively rich in hydrogen ions, whereas the carbonate-rich sedimentary bedrock of Alaska, western Canada, southwestern Siberia, and western Europe provides inputs rich in calcium, magnesium, and carbonates (alkalinity), but poor in hydrogen ions. Thus, brown-moss-dominated fens dominate in carbonate-rich areas, while bogs and poor fens dominate in areas with acidic substrates.

2.3.7 Chemistry

Here fertility refers only to the dissolved inorganic forms of the nutrients nitrogen (NO_3^-, NH_4^+) and phosphorus (ortho-P). Across the boreal zone, it seems that most pristine peatlands are nitrogen-limited. Only some very wet, rich fens or fens associated with lakes may be phosphorus-limited (Chap. 11). Nitrogen and phosphorus concentrations of upper pore waters of bogs are not significantly different from those of fens (Vitt et al. 1995), as would be expected for such nutrient-limited systems. However, greater water flow in fens may result in greater seasonal nutrient input. Thus, bogs and some fens (owing to either minimal flow or nutrient-poor surrounding substrates) can be termed oligotrophic. Fens influenced by more nutrient-rich inflows and higher flow rates can have a mesotrophic nutrient status. Communities with eutrophic nutrient status are restricted to non-peat-forming wetlands (marshes and southern swamps).

This oligotrophic–eutrophic nutrient gradient is independent of the “mineral” gradient composed of pH, base cations (Na^+, K^+, Ca^{2+}, Mg^{2+}), and associated anions (HCO_3^-, CO_3^{2-}, SO_4^{2-}, Cl^-) (Vitt and Chee 1990). The formation of peat and the differentiation of various bog and fen types occurs along this mineral gradient (see Fig. 10.1 in Vitt 2002). Along the peatland gradient, pH varies from 3.0 to 9.0, while concentrations of total base cations vary from nearly zero to more than 1,000 mg L^{-1}. This mineral gradient, especially pH, has been used by many as the fundamental basis for the differentiation and comparison of peatlands (Sjörs 1950; Nakamura et al. 2002; Tahvanainen 2004). However, this pH gradient is compromised through additional minerals that covary and may be influenced by pH itself; thus, as hydrogen ions decrease, base cations increase. Alkalinity and the form in which carbon is dissolved in the water are a function of pH (Wetzel 1983), with bicarbonate (alkalinity) increasing from zero at or below pH 5.5 to about150–200 mg L^{-1} HCO_3^- + CO_3^{2-} at pH 8.0. The complete absence of bicarbonate alkalinity below pH 5.5 is a fundamental dividing point in the habitat limits of many peatland species. Fens with surface waters having pH values less than 5.5 and little or no alkalinity are dominated by oligotrophic species of *Sphagnum*, and minerotrophic poor fens can be defined utilizing both chemical and floristic features. In fens with pH above 5.5 and the presence of alkalinity, *Sphagnum* abundance decreases and true mosses mostly dominate the ground layer.

In summary, boreal peatlands develop and persist owing to a complex set of regional and local factors. In particular, hydrology, climate, chemistry, substrate, and flora/vegetation all contribute to the type of peatland that develops at a site and to the functioning of individual peatlands over time. What follows is an outline of functional criteria for both wetlands and for the dominant peatland types of the boreal forest. Grades are functional levels of organization that may be achieved through unrelated and varied processes. Here, the term grade, long used in systematics, is applied to peatlands in order to allow a more functional (ecosystem) view of peat-

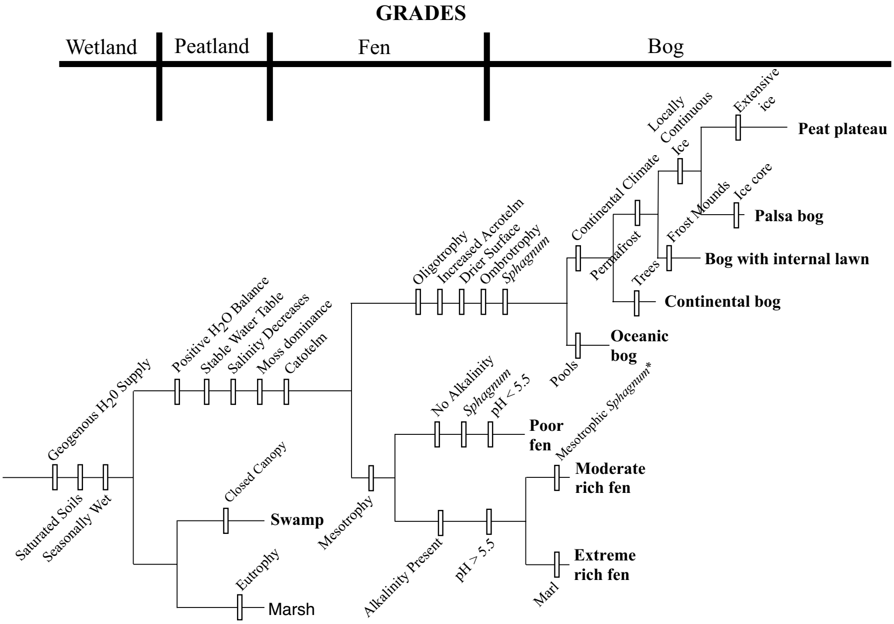

Fig. 2.2. Grades (functional levels of organization) and criteria (*bars*) that define the major boreal wetland types. *Open bars* define attributes for all units placed above the branch

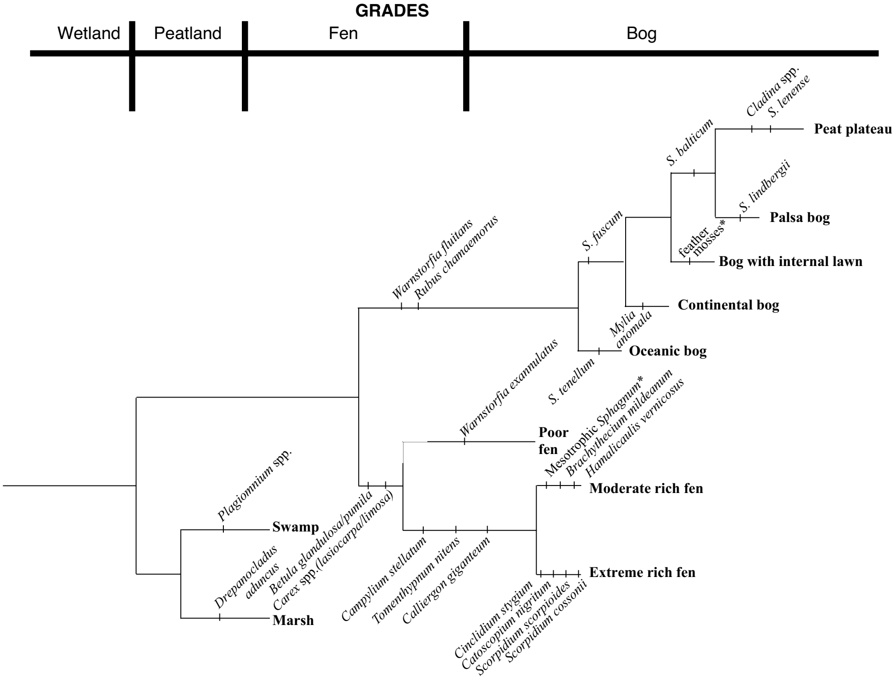

Fig. 2.3. Some floristic indicators for the boreal wetland grades. Species are based on my experience mainly in North America, but in most cases will be appropriate for Eurasia. Feather mosses are *Pleurozium schreberi* and *Hylocomium splendens*. Mesotrophic sphagnums are *S. subsecundum*, *S. warnstorfii*, *S. teres*, *S. subnitens*, and *S. contortum*

land organization. Specific criteria identify each grade in Fig. 2.2, while the apparent floristic indicators for these criteria are provided in Fig. 2.3. This approach attempts to tie individual floristic indicators to appropriate criteria for each functional wetland/peatland grade.

2.4 The Functional Grades of Boreal Wetlands

2.4.1 The Wetland Grade

In the boreal zone, wetlands form when soils are saturated throughout the year or are seasonally wet over much or all of the growing season. Waters that influence the wetland have been in contact with nonwetland soils and thus are enriched with a variety of minerals and nutrients. The local wetland area is influenced by recharge hydrology. These conditions allow organic matter to accumulate to a variable degree, but variable water tables, high nutrient inputs, and wetland plant species allow carbon and nitrogen to be mineralized at rates that prevent development of the anaerobic portion of the peat column (catotelm) and the buildup of peat. When these conditions are present, wetlands of two types may form – swamps and marshes. Wetland ecosystems are characterized by the development of complex woody canopies (deciduous swamps) or by a dense field layer of herbaceous species (marshes) as is characteristic of the southern ecotones of the boreal forest. Indicators of boreal deciduous swamps include woody vegetation dominated by a variety of small trees (e.g., *Acer*, *Alnus*, *Ilex*, *Myrica*, *Nemopanthus*, *Rhus*, *Salix*), an understory rich in herbs, and the lack of an abundant ground layer of bryophytes. Boreal evergreen swamps have closed canopies of *Thuja occidentalis* or *Picea mariana* (in North America), *Pinus sylvestris* (in Fennoscandia), or *Pinus sibirica*, *Pinus obovata*, *Pinus sylvestris*, or *Larix sibirica* (in Russia) as well as abundant herbaceous vegetation and high diversity of bryophytes. Swamps sometimes possess shallow, woody peat layers. Marshes lack tall, woody vegetation and are characterized by species of broad-leafed *Carex*, *Calamagrostis*, *Phragmites*, *Scirpus*, and *Typha*. Ground vegetation is poorly developed.

2.4.2 The Peatland Grade

The formation of extensive, peat-forming ecosystems of the boreal zone is associated with several features. Climatically, there is a regionally positive water balance at least during the growing season; this allows local water tables to stabilize. Young landscapes may be rich in Na^+ ion and flushing of the landscape over time may decrease Na^+ ion concentrations in favor of Ca^{2+} ion. Decreases in Na^+ and stabilization of water tables allow bryophyte colonization and persistence that in turn create conditions suitable for catotelm development.

2.4.3 The Fen Grade

The presence of geogenous water defines fens; however, a well-developed ground layer that functions to sequester nutrients and decreases open water evaporation, as well as development of an anaerobic peat column (catotelm), leads to decreases in wetland nutrient status (mesotrophy). Watershed substrates that contribute high amounts of base cations, the presence of alkalinity, and low hydrogen ion concentrations from inflowing waters lead to the development of rich fens dominated by true mosses. Substrates with few base cations, little or no alkalinity, and high concentrations of hydrogen ion lead to the development of poor fens dominated by peat mosses. Abundant soligenous waters (especially flowing over frozen surface peats in the spring) contribute to the formation of patterning (aapamires).

2.4.4 The Bog Grade

Achievement of ombrotrophy is associated with increased oligotrophy, increased aerobic peat column (acrotelm), drier surface conditions, dominance of oligotrophic *Sphagnum* species, and, at least in boreal North America, with the presence of an open canopy of trees. Autogenic factors become more important relative to allogenic ones (Bauer and Vitt 2003). Pools of open water are characteristic of oceanic bogs, whereas these are not present in continental climatic conditions. Bogs may be influenced by permafrost owing to the insulative properties of *Sphagnum* and the relatively thick acrotelm. In regions with little free water, isolated frost mounds occur in wooded bogs that when melted produce internal lawns (Vitt et al. 1994). Farther north, extensive ice allows peat plateaus to develop. In areas with more available water, palsas form.

2.5 Conclusions

Zonobiome VIII is a mosaic of lakes, upland evergreen and deciduous forest, and peatlands. Most of the world's peat-forming ecosystems occur in the boreal zone where they play important roles in carbon sequestration, erosional control, and landscape filtration. Peatlands are uniquely unbalanced ecosystems that are sensitive to the influences of hydrology, climate, and surrounding substrate. Peat-forming wetlands form two functional levels of organization: fens and bogs. Both of these grades develop deep deposits of peat and stabilize the landscape for long periods of time. Both are characterized by well-developed catotelms and ground layers dominated by bryophytes.

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References

Almquist-Jacobson H, Foster DR (1995) Toward an integrated model for raised-bog development: theory and field evidence. Ecology 76:2503–2516

Anderson R, Foster DR, Motzkin G (2003) Integrating lateral expansion into models of peatland development in temperate New England. J Ecol 91:68–76

Bauer IE, Vitt DH (2003) Autogenic succession and its importance for the peatlands of Canada's western boreal forest. In: Bauerochse A, Haßmann H (eds) Peatlands, archaeological sites – archives of nature – nature conservation – wise use. Proceedings of the peatland conference 2002, Hanover, Germany, pp 179–187

Botch MS, Masing VV (1979a) Regionality in mire typology in the USSR. In: Classification of mires and peats. Proceedings of the international symposium, Hyytiala, Finland, pp 1–11

Botch MS, Masing VV (1979b) Ekosistemy bolot SSSR. Nauka, St Petersburg

Botch MS, Masing VV (1983) Mire ecosystems in the U.S.S.R. In: Gore AJP (ed) Ecosystems of the world 4B. Mires: swamp, bog, fen and moor. Regional studies. Elsevier, Amsterdam, pp 95–152

Cajander AK (1913) Studien über die Moore finnlands. Acta For Fenn 1:1–175

Chee W-L, Vitt DH (1989) The vegetation, surface water chemistry, and peat chemistry of moderate-rich fens in central Alberta, Canada. Wetlands 9:227–262

Clements F (1916) Plant succession: an analysis of the development of vegetation. The Carnegie Institute of Washington, Washington, DC

Damman AWH (1977) Geographical changes in the vegetation pattern of raised bogs in the Bay of Fundy region of Maine and New Brunswick. Vegetatio 35:137–151

Damman AWH (1979) Geographic patterns in peatland development in eastern North America. In: Proceedings of the international symposium on classification of peat and peatlands. International Peat Society, Helsinki, pp 42–57

Damman AWH (1986) Hydrology, development, and biogeochemistry of ombrogenous peat bogs with special reference to nutrient relocation in a western Newfoundland bog. Can J Bot 64:384–394

Dierssen K, Dierssen B (2001) Moore (Ekosysteme Mitteleuropas aus geobotanischer Sicht). Ulmer, Stuttgart

DuRietz GE (1949) Huvudenheter och huvudgränser i svensk myrvegetation. Sven Bot Tidskr 48:274–309

DuRietz GE (1954) Die Mineralbodenwasserzeigergrenze als Grundlage einer natürlichen Zweigliederung der nord- und mitteleuropäischen Moore. Vegetatio 5–6:274–309

Eurola S (1962) Über die regionale Einteilung der südfinnischen Moore. Ann Bot Soc Vanamo 33:1–243

Gignac LD, Vitt DH, Zoltai SC, Bayley SE (1991) Bryophyte response surfaces along climatic, chemical and physical gradients in peatlands of western Canada. Nova Hedwigia 53:27–71

Glaser PH, Janssens JA (1986) Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. Can J Bot 64:395–415

Gore AJP (ed) (1983) Ecosystems of the world 4B. Mires: swamp, bog, fen and moor. Regional studies. Elsevier, Amsterdam

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195

Gorham E, Janssens J (1992) Concepts of fen and bog reexamined in relation to bryophyte cover and the acidity of surface waters. Acta Soc Bot Pol 61:7–20

Heinselman M (1963) Forest sites, bog processes, and peatland types in the Glacial Lake Agassiz Region, Minnesota. Ecol Monogr 33:328–374

Horton DG, Vitt DH, Slack NG (1979) Habitats of circumboreal-subarctic Sphagna. I. A quantitative analysis and review of species in the Caribou Mountains, northern Alberta. Can J Bot 57:2283–2317

Inisheva LI, Golovatskaya EA (2002) Elements of carbon balance in oligotrophic bogs. Russ J Ecol 33:242–248

Ivanov KE (1957) Osnovy gidrologii bolot lesnoi zony. Gidrometizdat, St Petersburg

Joosten H, Clarke D (2002) Wise use of mires and peatlands – Background and principles including a framework for decision-making. International Mire conservation Group and International Peat Society, Finland, http://www.mirewiseuse.com

Katz NY (1930) Zur Kenntnis der Moore Nordosteuropa. Beih Bot Centrabl 2:287–394

Keddy PA, Fraser LH (2005) The world's largest wetlands: ecology and conservation. Cambridge University Press, Cambridge

Kratz TK, DeWitt CB (1986) Internal factors controlling peatland-lake ecosystem development. Ecology 67:100–107

Laitinen J, Rehell S, Huttunen A (2005) Vegetation-related hydrotopographic and hydrologic classification for aapa mires (Hirvisuo, Finland). Ann Bot Fenn 42:107–121

Lewis FJ, Dowding ES (1926) The vegetation and retrogressive changes of peat areas ("muskegs") in central Alberta. J Ecol 14:317–341

Lieth H (ed) (1999) Climate diagram world atlas. Backhuys, Leiden

Mitsch WJ, Gosselink JG (2000) Wetlands, 3rd edn. Wiley, New York

Nakamura T, Uemura S, Yabe K (2002) Hydrochemical regime of fen and bog in north Japanese mires as an influence on habitat and above-ground biomass of *Carex* species. J Ecol 90:1017–1023

Ruuhijärvi R (1960) Über die regionale Einteilung der nordfinnischen Moore. Ann Bot Soc Vanamo 31:1–360

Sjörs H (1948) Myrvegetation i Bergslagen (Mire vegetation in Bergslagen, Sweden). Acta Phytogeogr Suec 21:1-299

Sjörs H (1950) Regional studies in north Swedish mire vegetation. Bot Not 1950:173–222

Sjörs H (1983) Mires of Sweden. In: Gore AJP (ed) Ecosystems of the world 4B. Mires: swamp, bog, fen and moor. Regional studies. Elsevier, Amsterdam, pp 69–94

Tahvanainen T (2004) Water chemistry of mires in relation to the poor-rich vegetation gradient and contrasting geochemical zones of the northeastern Fennoscandian Shield. Folia Geobot 39:353–369

Tansley AG (1939) The British Islands and their vegetation. Cambridge University Press, Cambridge

Vitt DH (2000) Peatlands: ecosystems dominated by bryophytes. In: Shaw AJ, Goffinet B (eds) Bryophyte biology. Cambridge University Press, Cambridge, pp 312–343

Vitt DH, Chee W-L (1990) The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio 89:87–106

Vitt DH, Slack NG (1975) An analysis of the vegetation of *Sphagnum*-dominated kettle-hole bogs in relation to environmental gradients. Can J Bot 53:332–359

Vitt DH, Horton DG, Slack NG, Malmer N (1990) *Sphagnum*-dominated peatlands of the hyperoceanic British Columbia coast: patterns in surface water chemistry and vegetation. Can J For Res 20:696–711

Vitt DH, Halsey LA, Zoltai SC (1994) The bog landforms of continental western Canada relative to climate and permafrost patterns. Arct Alp Res 26:1–13

Vitt DH, Bayley SE, Jin T-L (1995) Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Can J Fish Aquat Sci 52:587–606

Vitt DH, Halsey LA, Bauer IE, Campbell C (2000) Spatial and temporal trends of carbon sequestration in peatlands of continental western Canada through the Holocene. Can J Earth Sci 37:683–693

Vitt DH, Halsey LA, Bray J, Kinser A (2003) Patterns of bryophyte richness in a complex boreal landscape: Identifying key habitats at McClelland Lake wetland. Bryologist 106:372–382

Von Post L, Granlund E (1926) Södra Sveriges torvtillgångar I. Sver Geol Unders Ser C 335:127

Walter H (1979) Vegetation of the earth and ecological systems of the geo-biosphere, 2nd edn. Springer, Berlin Heidelberg New York

Weber C (1911) Das Moore. Hannoversche Geschichsbl 14:255–270

Wetzel RG (1983) Limnology, 2nd edn. Saunders, Philadelphia

Wheeler BD, Proctor MCF (2002) Ecological gradients, subdivisions and terminology of north-west European mires. J Ecol 88:187–203

Wieder RK, Lang GE (1983) Net primary production of the dominant bryophytes in a *Sphagnum*-dominated wetland in West Virginia. Bryologist 86:280–286

Wilcox DA, Simonin HA (1988) The stratigraphy and development of a floating peatland, Pinhook Bog, Indiana. Wetlands 8:75–91

Zoltai SC, Pollett FC (1983) Wetlands in Canada: their classification, distribution, and use. In: Gore AJP (ed) Ecosystems of the world 4B. Mires: swamp, bog, fen and moor. Regional studies. Elsevier, Amsterdam, pp 245–268

3 The Postglacial Development of Boreal and Subarctic Peatlands

Peter Kuhry and Jukka Turunen

3.1 Introduction

The modern distributional areas of boreal peatlands in the North American and Eurasian continents were mostly covered by large ice sheets or dry types of vegetation during the last glacial maximum. In North America, the Laurentide ice sheet covered most of Canada with the exception of an ice-free area in the Yukon (Dyke and Prest 1987). Unglaciated terrain was also present in much of Alaska. The largely treeless tundra conditions in the Yukon and central Alaska at this time were suitable for the occurrence of brown mosses and *Sphagnum* (Halsey et al. 2000). In northern Eurasia, the Fennoscandian ice sheet covered Norway, Sweden, Finland, and parts of western Russia. A debate still rages about the extent of the ice sheet over East European Russia and western Siberia, but it was likely very limited (Mangerud et al. 1999). Only smaller ice sheets and mountain glaciations were likely present in Siberia and the Far East. Unglaciated terrain was occupied by dry continental types of vegetation such as polar desert, tundra-steppe, and forest-steppe (Grichuk 1984). Peatland development was most probably very restricted under those conditions. Hence, the vast expanses of boreal and subarctic peatlands that at present occupy the North American and Eurasian landmasses developed almost exclusively since the last glacial maximum.

This review primarily focuses on boreal peatland development in the North American and Eurasian continents. Subarctic peatlands are included because they mostly originated under "boreal" conditions during the Holocene Hypsithermal (Ritchie 1976; Kremenetski et al. 1998). The aim is to show regional patterns in peatland development related to allogenic (e.g., climate, fire, permafrost) and autogenic (e.g., peat accumulation, acidification) factors.

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3.2 Study Area

On a global scale, the occurrence of peatlands is strongly related to topography and climate, with the greatest abundance found on flat land areas of cool and moist climates (Sjörs 1959; Walter 1977; Botch and Masing 1983; Ovenden 1990; Riley 1994; Botch et al. 1995). In this review we discuss the developmental history of peatlands in four lowland regions of the North American and Eurasian continents that are characterized by extensive peatland coverage.

The west-central Canadian and western Siberian lowlands (largely below 500 m above present sea level, apsl) extend from the prairie/steppes in the south to the tundra in the north. The continental climate in these regions is favorable for more widespread permafrost in peatlands and for the occurrence of peat fires. In Quebec and Finland most of the lands are also below 500 m apsl, but at places low hills and mountains exceed this elevation and the climate is more oceanic. Under these conditions, permafrost in peatlands is more limited and peat fires are generally rare. Differences in peatland development along south-to-north transects (primarily temperature gradient) and between continental and oceanic regions (primarily precipitation gradient) are discussed.

3.3 Methods

Peatlands are special ecosystems in the sense that they "write" their own history. The accumulated layers of peat can be "read" as pages in a book. The peat deposit consists of organic material that can be readily dated by radiocarbon analysis. Nilsson et al. (2001) suggested that moss remains, particularly *Sphagnum*, provide the most reliable dates in meso-oligotrophic peatland ecosystems. However, brown mosses from rich fen and aquatic habitats can provide erroneously old dates owing to the hardwater effect (MacDonald et al. 1987). In the latter cases, terrestrial macrofossils derived from adjacent upland areas are best used.

Peat contains only partly decomposed remains of the organisms that once lived on the peatland surface. The remains can be identified under a stereo binocular and light microscope. Microfossil analyses (pollen, spores, etc.) provide a reconstruction of both the regional and local vegetation history (Charman 2002). The sequence of plant macrofossil assemblages reveals the succession of peatland communities at the site where the peat deposits are collected (Charman 2002). Bryophytes are excellent indicators for surface water level and acidity, which permit quantitative assessments of past environmental change in peatland ecosystems

(Janssens 1983; Kuhry et al. 1993). Several other plant and animal taxa are also good indicators. For instance, testate amoebae assemblages closely reflect surface moisture in peatlands (Tolonen 1966; Warner and Charman 1994). Isotopic analysis and geochemical markers ($^{16}O/^{18}O$, ^{13}C, deuterium-to hydrogen ratio, carbon-to-nitrogen ratio, etc.) can contribute to the understanding of environmental changes at the peat surface (Jasinski et al. 1998). However, these methods have not been widely applied yet in boreal and subarctic regions with the possible exception of carbon-to-nitrogen ratios (Kuhry and Vitt 1996; Vardy et al. 2000). As is the case for other paleoenvironmental studies, multiproxy analyses that combine several paleoecological and geochemical techniques provide the most comprehensive reconstructions of peatland developmental history. Peat accumulation rates can be derived from relatively simple physicochemical analyses (dry bulk density, and loss-on-ignition or carbon contents) in combination with radiocarbon dating.

Paleoecological and geochemical analyses are quite straightforward (although often time-consuming) in terms of elucidating the development of a peatland over time at the site where the peat deposit is sampled. However, general assessments about regional peatland history are much more difficult. There are two main reasons for this. Firstly, the development of a peatland area depends on a whole range of climatic, edaphic, and autogenic factors (temperature, precipitation, evapotranspiration, topography, bedrock and surficial geology, groundwater flow and chemistry, peat fires, permafrost, peat accumulation, acidification, etc.). All these factors can have a significant effect on the inception, expansion, and vegetation succession in peatlands. Discrimination between individual factors is often very difficult. Secondly, the peatland itself is often characterized by a mosaic of landforms (e.g., hummocks and hollows of raised bogs, strings and flarks of aapa mires, peat plateaus and thermokarst ponds), and each site can have its own specific developmental history.

Therefore, large numbers of peatlands (if possible, each with numerous coring sites) are needed to study regional patterns in peatland development. Unfortunately, systematic studies with equidistant (or random) coring in peatland complexes are rare. Paleoecologists tend to focus on the deepest parts of peat areas to obtain the longest possible records; collection sites are often near communication arteries such as (rail-) roads or rivers and not in the central parts of vast peatland complexes; detailed inventories for peat mining, available especially from Russia, avoid the shallower marginal areas of peatland complexes, which are not considered economically significant.

3.4 Regional Patterns in Peatland Development

3.4.1 Peat Inception and Cessation Dates

An extensive database is available of peatland inception, defined as the oldest reported date within a specific peatland area. This includes many peatlands for which only a single date is available. Notwithstanding, the database is quite robust because paleoecologists tend to collect the longest profiles possible. An exception is permafrost peatlands, where frozen deposits preclude extensive probing of peat depths before profile collection.

Basal dates from peat deposits show regional differences in the period of peatland initiation related to glacial, glacio-isostatic, and climatic history. Relatively young inception dates can be found in southern Nunavut because of late deglaciation (Zoltai 1995). Boreal peatlands in west-central Canada to the south of a latitude of approximately 54° 30′ N are younger than 7,000 calibrated years before the present (cal. BP) (Fig. 3.1), which is ascribed to warm and dry climatic conditions in the early to middle Holocene Hypsithermal (Zoltai and Vitt 1990). Kremenetski et al. (2003) also indicated a scarcity of peatland initiation to the south of latitude approximately 58° N in western Siberia due to warm and dry conditions during this period. Exceptions are foothill areas of the southern Canadian Rockies and the central Asian mountains where, owing to higher orographic precipitation, peatlands may have much older basal dates (Kubiw et al. 1989; P'yavchenko 1985). In contrast, the inception of southern boreal peatlands in the more oceanic areas of Finland and Quebec was never limited by precipitation. Basal dates relate to deglaciation history and/or glacio-isostatic emergence (Korhola 1994; Payette 2001a). Young basal peat dates are found in coastal regions that only gradually emerged from the sea owing to ongoing isostatic rebound. Examples are peatlands in the Hudson Bay Lowlands (Kuhry 1998) and in western Finland (Korhola 1996).

Many subarctic peatlands first developed under "boreal" conditions prevailing during the early to middle Holocene Hypsithermal. Climatic cooling has limited peat accumulation in subarctic areas since the mid-Holocene. This is particularly the case in those northern peatlands affected by permafrost aggradation that resulted in the formation of palsas and peat plateaus. Numerous "old" radiocarbon dates are reported for the upper deposits in these permafrost-affected peatlands. Salmi (1968, 1972) reported ages of 3,600 and 4,700 cal. BP for fen deposits at the surface of palsas in Finnish Lapland. Old dates are also reported from Quebec. For instance, Lavoie and Payette (1995) provided an age of 1,900 cal. BP for the surface deposit of a subarctic palsa. Good reviews for

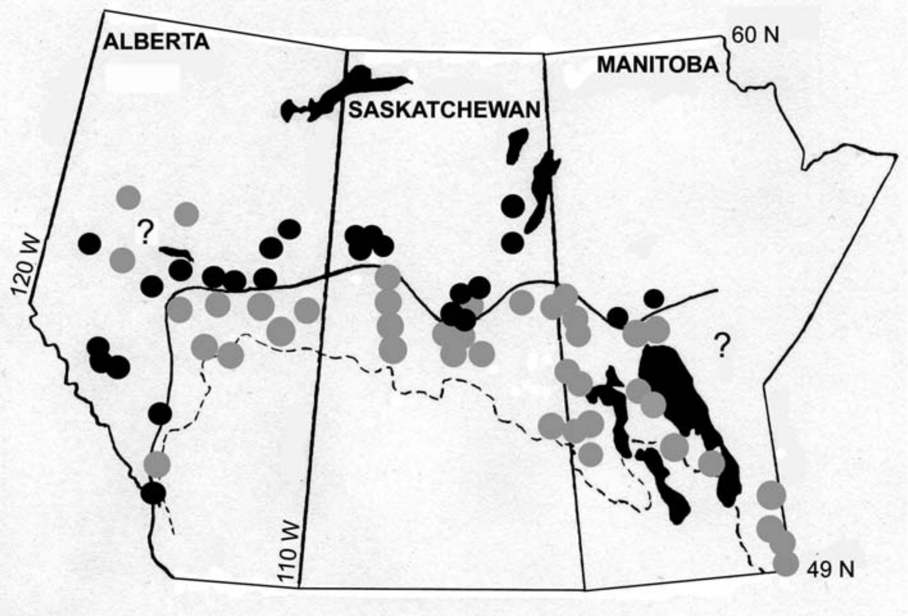

Fig. 3.1. Basal fen peat dates over mineral, limnic, or telmatic contacts to the south of latitude 57° N in west-central Canada. *Light-grey circles* represent dates younger than 7,000 calibrated years before the present (*cal. BP*); *black circles* represent dates older than 7,000 cal. BP. The *dashed line* is the present-day southern limit of fens; the *solid line* is the southern limit of fens at 7,000 cal. BP. (Adapted from Zoltai and Vitt 1990, copyright 1990, with permission from Elsevier, *Quaternary Research*)

"old" radiocarbon dates of upper peat deposits in the northern regions of west-central Canada and western Siberia have been provided by Zoltai (1995) and Peteet et al. (1998), respectively. Zoltai (1995) provided ages of up to 3,650 cal. BP for near-surface peat deposits in polygonal peat plateaus. Peteet et al. (1998) reported ages going back as far as 5,650 cal. BP for an upper palsa deposit in the northern taiga. These dates do not necessarily indicate the time at which local peat accumulation stopped as younger deposits may have been removed by later erosion. Also subrecent dates have been reported from the near-surface deposits of subarctic palsas and peat plateaus (Kershaw and Gill 1979; Zoltai 1995; Vardy et al. 2000).

3.4.2 Peatland Lateral Expansion Rates

Very few studies exist that have investigated in detail the lateral expansion of individual boreal and subarctic peatland complexes through the Holocene (Neustadt 1984; Nicholson and Vitt 1990; Korhola 1994, 1995, 1996; Mäkilä 1997; Bauer et al. 2003). The main reason for this is that extensive fieldwork in inaccessible terrain is difficult and the required radiocarbon dating of multiple basal peat samples expensive. Studies indicate that both slow and rapid phases of lateral growth have occurred depending mainly on the topography of the mineral substrate (Korhola 1994; Mäkilä 1997). The fastest expansion rates are usually associated with peatlands having confining layers such as clays, whereas slow expansion is typical for peatlands on more permeable soils (Foster et al. 1988; Korhola 1994, 1996; Turunen and Turunen 2003). However, more constant lateral expansion rates have also been recorded (Foster and Jacobson 1990; Foster and Wright 1990).

Attempts to relate lateral expansion rates at regional scales to Holocene climatic changes are difficult. Firstly, expansion rates also depend on a whole suite of local factors (topography, drainage, surficial geology, vertical peat accumulation, etc.). A change in climate can have opposite effects on lateral expansion depending on the type of peatland formation. For instance, paludification is likely inhibited under dry climatic conditions (Korhola 1995; Campbell et al. 2000). At the same time, a climate change towards drier conditions may promote terrestrialization by causing low lake levels (Svensson 1988; Nicholson and Vitt 1994; Korhola 1996). Secondly, the extensive database of basal peat dates (including all basal dates available from each individual peatland complex) is most likely biased towards older sites. Long-term trends in peatland expansion throughout the Holocene should be considered with care. Notwithstanding, it should be possible to attribute clusters of basal peat dates to specific Holocene climatic episodes.

Korhola (1994) investigated the lateral expansion in five raised bogs of southern boreal Finland by precise leveling along a network of transects and a total of 71 basal peat dates. The peatlands displayed periods of rapid lateral expansion but these were not synchronous. Peatland expansion was mostly related to the topography of the mineral substrate. A period of overall slow paludification is recorded between 7,000 and 4,500 cal. BP (Fig. 3.2), ascribed to drier climatic conditions prevailing in the region at the time. The peatlands also expanded slowly over the last two to three millennia owing to a steepening of the bottom gradient in the margins of the raised bogs. Campbell et al. (2000) proposed that distinct clusters in calibrated basal peat dates from 71 paludified sites in west-central Canada coincide with wet climatic episodes reflecting an approximately 1,450-year climatic periodicity superimposed on the longer-term orbitally induced northern insolation changes (Yu et al. 2003a). Very few young dates (less than 3,000 cal. BP) have been reported, explained at least partially by sampling bias.

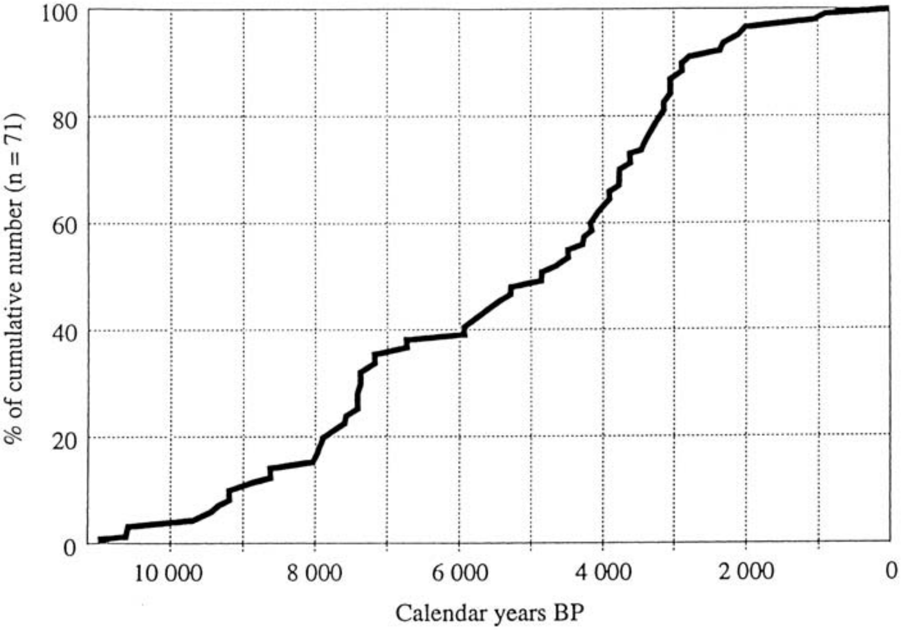

Fig. 3.2. Cumulative frequency of basal peat dates from paludified sites in southern Finland (reprinted from Korhola 1995, copyright 1995, with permission from Edward Arnold Publishers Ltd., *The Holocene*)

3.5 Developmental Pathways in Peatlands

3.5.1 Primary Peatland Formation, Paludification, and Terrestrialization

Primary peatland formation is the process in which peat has accumulated directly on moist mineral ground immediately after deglaciation or as it emerged from beneath the waters (Sjörs 1983). Paludification refers to the formation of peatland ecosystems over previously forested land, grassland, or long-exposed bare land. In terrestrialization, peatlands are formed via the gradual in-filling of water bodies (Chap. 2).

A survey of basal dates[1] in west-central Canada indicates that a majority of 109 recorded sites were formed through paludification (71 %). Terrestrialization is also common (28 %). Primary peatland formation is very rare because there is a significant time-lag between deglaciation and

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[1] Based on Nicholls (1967); Kubiw et al. (1989); Zoltai and Vitt (1990); Kuhry et al. (1992, 1993); Zoltai (1993, 1995); Kuhry (1994, 1998, unpublished results); Vitt et al. (2000)

peatland inception. A probable exception is the Hudson Bay Lowlands, where peat expansion took place rapidly after glacio-isostatic emergence (Kuhry 1998). According to Korhola and Tolonen (1996), most peatlands in Finland originated by primary peatland formation or paludification, although they caution that the percentage of terrestrialization (10 % or less) might be a significant underestimate. Paludification is also probably more widespread than terrestrialization in the boreal zone of western Siberia and in Quebec, (Walter 1977; Payette 2001b). Numerous charcoal layers at the peat–mineral contact indicate that forest fires promote the process of paludification (Ikonen 1993; Korhola 1996; Bauer 2002), as deforestation reduces canopy interception of precipitation and plant evapotranspiration, resulting in ground surface moistening.

3.5.2 Vegetation Succession and Pattern Development

Hydroseral succession is the most frequent and typical form of autogenic development in peatlands (Charman 2002). The open water to fen transition observed at terrestrialized sites is the result of the gradual in-filling of the basin with mineral and organic materials. The subsequent succession from fen to bog is the result of local peat accumulation that gradually lifts the surface of the peatland above the influence of the groundwater. The latter process can be observed both at terrestrialized and at paludified sites. The vegetation now depends (almost) entirely on precipitation for water and nutrient supply, and ombrotrophic conditions develop. Under oligotrophic and ombrotrophic conditions, *Sphagnum* mosses often become dominant, further acidifying their local environment. An example of hydroseral succession in a boreal peatland of west-central Canada is given in Fig. 3.3. A pond surrounded by a marsh is replaced by a rich fen community, followed by a poor fen community and, finally, a bog community.

While hydroseral succession is a very widespread and common phenomenon in peatland development, the rate of change varies greatly from place to place depending on climatic, edaphic, and other factors. At places, rich fen communities can persist for thousands of years because of the strong control exerted by groundwater chemistry (Kubiw et al. 1989). The process of ombrotrophication can be clearly a time-transgressive feature. For example, in Finland the earliest transition to an ombrotrophic bog has been dated to ca. 8,500 cal. BP in southern Finland, ca. 3,000 cal. BP in central Finland, and ca. 2,000 cal. BP in northern Finland (Korhola and Tolonen 1996).

The general pathways of hydroseral (and fen to bog) succession can be reverted as a result of strong or abrupt allogenic influences such as cli-

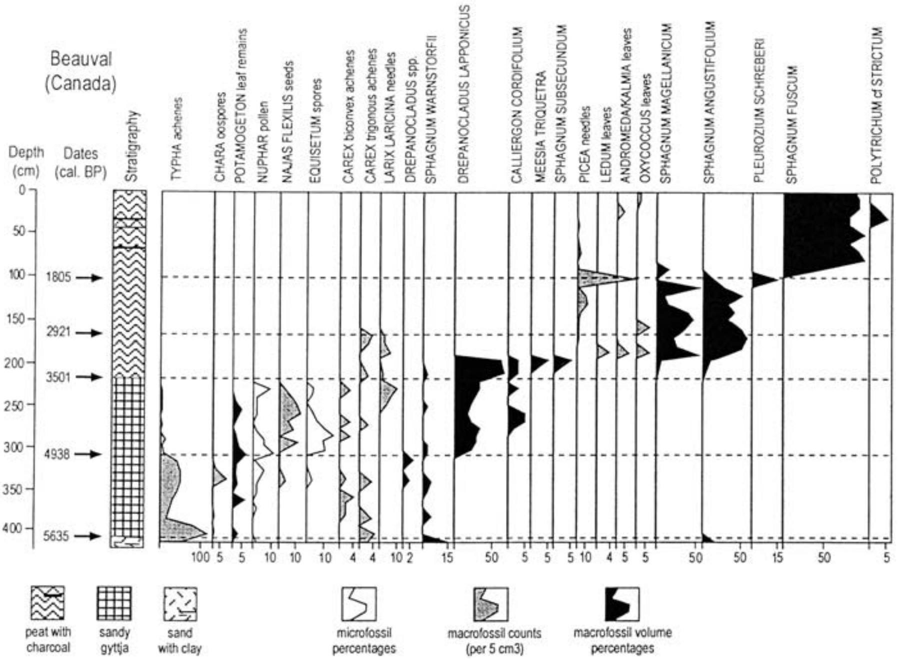

Fig. 3.3. Hydroseral succession in a boreal peatland near Beauval (west-central Canada) (adapted from Kuhry 1997, copyright 1997, with permission from National Research Council Research Press, *Canadian Journal of Botany*)

mate change and flooding. Also (largely) autogenic processes can be responsible, especially pattern development (Foster et al. 1983; Seppälä and Koutaniemi 1985; Glaser 1998). The development of peatland microtopography in raised bogs and aapa mires is secondary and is attributable to biotic factors that can be amplified by physical mechanisms. For instance, hollows and pools probably result from small differences in the rate of peat accumulation. They can coalesce into larger "maturing" ponds where the original peat actively degrades leaving no traceable history. A special situation arises in permafrost peatlands. Here, the physical process of frost heave can raise the surface of the peatlands within years, resulting in abrupt local changes in hydrology and biochemistry. As a result, peatland complexes can develop as isolated palsas surrounded by permafrost-free areas, or as extensive peat plateaus. The subsequent degradation of palsas and peat plateaus as a result of autogenic processes (Seppälä 1988), peat fires (Zoltai 1993), or climatic changes (Halsey et al. 1995) can further diversify local habitats through the formation of internal lawns, collapse scars, and thermokarst ponds. Internal lawns and collapse scars are often characterized by quick regeneration and high rates of peat accumulation. Thermokarst ponds show similar degradation processes as in mature ponds of raised bogs and aapa mires: the original peat deposit quickly decays leaving no traceable history except thin gyttja deposits or sedimentary gaps.

3.6 The Effects of Fire and Permafrost

3.6.1 Peat Fires

Relatively few studies exist that have investigated in detail the influence of fires on boreal and subarctic peatland development. Local fires that burn the peat surface can be recognized by macroscopic charcoal layers in the peat deposits. Such layers are generally more abundant in peatlands developed under the dry continental climate of west-central Canada (Nichols 1967; Kuhry 1994) and western Siberia (Turunen et al. 2001) than in more oceanic areas, although peat fires have also been reported from Finland (Pitkänen et al. 1999) and Quebec (Couillard and Payette 1985).

Peat fires affect both fen and bog ecosystems (Chap. 16). Pitkänen et al. (1999) reported numerous charcoal layers in early to middle Holocene fen deposits at Patvinsuo, eastern Finland. The permeable sandy substrates in the Patvinsuo peatland complex and likely the strong groundwater fluctuations due to the more continental type of climate prevailing at the time enabled the high frequency of local fires. Fires can radically change the vegetation in fens, with many sites showing *Sphagnum* displacing sedges immediately after the fire (Tolonen 1967; Ikonen 1993). On the other hand, *Sphagnum*-dominated bog ecosystems are more resilient. Local vegetation changes following fire, if any, are generally short-lived (Tolonen 1985; Kuhry 1994). Figure 3.4 shows an example of a postfire succession in a boreal peatland of west-central Canada. Charred remains indicate the effects of a local fire that affected the surface of the *S. fuscum* bog. Other mosses and ericaceous taxa become temporarily more abundant but the original community quickly reappears. Clymo and Ducket (1986) demonstrated experimentally the capability of *Sphagnum* to regenerate from deeper layers.

Detailed studies from peat deposits in west-central Canada (Kuhry 1994), western Siberia (Turunen et al. 2001), and eastern Finland (Pitkänen et al. 1999) show increased peat fire frequencies during the early to middle Holocene Hypsithermal. However, in eastern Canada only the earliest part of the Holocene is characterized by a high fire incidence and a major change to lower fire frequencies occurred after 9,000 cal. BP. The mid-Holocene was dominated by wet summers owing to stability of the Atlantic air mass over eastern Canada (Carcaillet and Richard 2000).

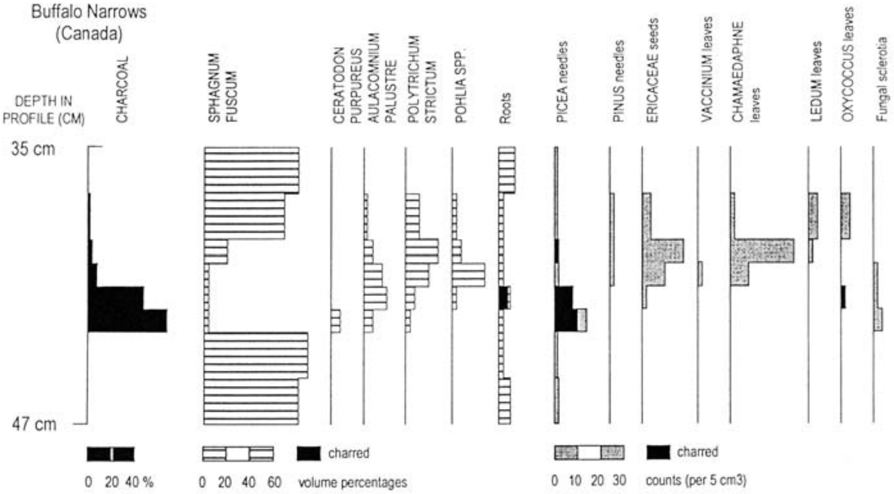

Fig. 3.4. Postfire vegetation succession in a boreal peatland near Buffalo Narrows (west-central Canada) (reprinted from Kuhry 1994, copyright 1994, with permission from Blackwell Publishing Ltd., *Journal of Ecology*)

3.6.2 Permafrost Dynamics

Typical landforms for permafrost peatlands in boreal and subarctic regions are palsas and peat plateaus (Sonesson 1968; National Wetlands Working Group 1988; Seppälä 1988; Botch et al. 1995). Permafrost expands southwards to the middle boreal (taiga) forest regions in peatlands of west-central Canada and western Siberia, owing to the cold and relatively dry (thin snow cover) winters. In northern Fennoscandia and Quebec, permafrost landforms appear in the northern taiga and only become more abundant in the forest-tundra ecotone and the tundra region.

It is not only climate that influences permafrost occurrence and dynamics in peatlands. Classical palsa formation is described as frost heave of fen surfaces on places of thin snow cover, with the uplifted surfaces invaded by lichens and the mosses *Dicranum* and *Polytrichum* (Seppälä 1988). Autogenic successions from fens to densely wooded bogs or *Sphagnum*-dominated hummocks can also create favorable conditions for the aggradation of permafrost. On rare occasions, permafrost seems to have developed directly under wet surface conditions (Zoltai 1995; Oksanen et al. 2001). Peat fires can play a significant role in permafrost dynamics (Couillard and Payette 1985; Zoltai 1993), by removing the surface insolation, increasing ground temperatures, and deepening the active layer (Brown 1983). The slowly progressing thawing of permafrost with depth means that there can be a significant time-lag in the response of permafrost peatlands to climatic warming (Halsey et al. 1995).

There is no simple method to determine the historical timing of permafrost aggradation in peatlands. Gross-stratigraphic approaches can provide meaningful results at regional scales (Zoltai 1995; Oksanen 2002). Only detailed plant macrofossil analysis of peat deposits is able to trace the highly dynamic nature of permafrost in peatlands. Zoltai (1993) inferred repeated permafrost aggradation followed by collapse in a boreal peatland of west-central Canada from the succession of *Sphagnum fuscum*, sylvic peat, charcoal, *S. riparium*, *S. angustifolium*, and back to *S. fuscum*, which he ascribed to the effect of peat fires. Highly dynamic permafrost conditions, however, are not restricted to peatlands affected by local fires (Oksanen et al. 2001). An example of classic palsa uplift followed by collapse and renewed permafrost aggradation in a subarctic peat plateau of the European Russian Arctic is shown in Fig. 3.5. A wet community characterized by sedges and detritus was replaced by a xerophytic community with *Polytrichum*. The permafrost almost immediately degraded, as indicated by the presence of the typical collapse scar species

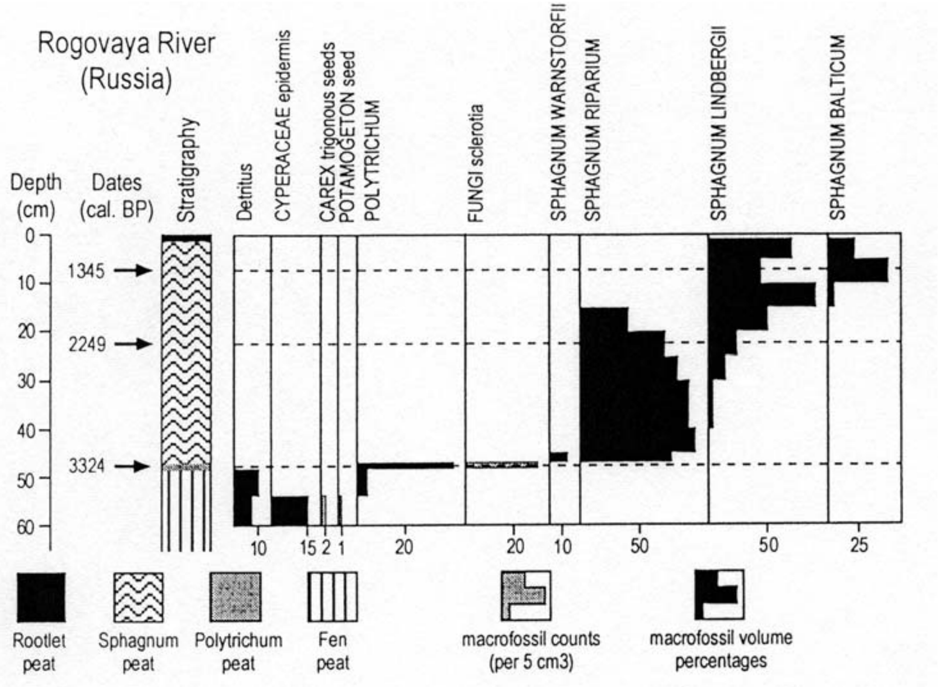

Fig. 3.5. Permafrost aggradation and subsequent dynamics in the Rogovaya River peat plateau (European Russian Arctic) (adapted from Oksanen et al. 2001, copyright 2001, with permission from Edward Arnold Publishers Ltd., *The Holocene*)

S. riparium. Subsequently, *S. lindbergii* and *S. balticum* became dominant. The present peat plateau surface is covered by lichens.

Permafrost aggradation dates in boreal and subarctic peatlands based on gross-stratigraphic or plant macrofosssil evidence can be related to climatic cooling in the second half of the Holocene (P'yavchenko 1955; Richard 1981; Couillard and Payette 1985; Zoltai 1993, 1995; Lavoie and Payette 1995; Jasinski et al. 1998; Peteet et al. 1998; Blyakharchuk and Sulerzhitsky 1999; Oksanen et al. 2001, 2003; Payette 2001a; Oksanen 2002, 2006; Oksanen and Kuhry 2003; Väliranta et al. 2003; Arlen-Pouliot and Bhiry 2005).

3.7 Peat Accumulation Rates

3.7.1 Concepts

In a natural state, peatlands generally accumulate peat since the rate of biomass production is greater than the rate of decomposition. The accumulation of peat involves an interaction between net primary productivity and losses through the process of aerobic and anaerobic decay, leaching, peat fires, wind abrasion, thermokarst erosion (in permafrost peatlands), and deposition of organic material into the mineral soil beneath peat layers.

Most peat-forming systems consist of two layers: an upper aerobic layer of high hydraulic conductivity, the acrotelm, in which the rate of decay is normally high; and the much thicker, predominantly anaerobic underlying layer, the catotelm, of low hydraulic conductivity with a lower rate of decay (Ingram 1978; Clymo 1984). The boundary between these layers is approximately at the mean depth of the minimum water table in summer, about 10–50 cm below the surface (Ivanov 1981; Clymo 1984), depending on peatland type and the microtopography in peatland areas. Organic material is added to the surface through net primary production. About 5–10 % of this biomass is incorporated in the form of peat to the catotelm (Clymo 1984; Gorham 1991; Warner et al. 1993). In the catotelm, slow anaerobic decomposition of the peat results in additional loss of organic material. As pointed out by Vardy et al. (2000), anaerobic decay in deeper layers is probably largely halted when the peat deposits are perennially frozen.

Models of peat accumulation based on a constant rate of input of peat from the acrotelm to the catotelm suggest a concave shape of the cumulative peat mass vs. depth curve as organic matter is progressively decomposed in the catotelm (Clymo 1984). While many peatlands display this kind of concave-shaped curve (Clymo et al. 1998), several studies point to a convex shape (Ikonen 1993; Kuhry and Vitt 1996; Lavoie and Richard 2000a, b; Vardy et al. 2000; Yu et al. 2003b; Klarqvist 2001; Turunen et al. 2001; Muller et al. 2003.). The latter is explained by a decline in net primary productivity and/or mass input to the catotelm over time (Chap. 14).

3.7.2 Regional Patterns

In Quebec and Finland, the thickest peat deposits are generally encountered in the southern boreal/taiga ecoregions (Ovenden 1990; Lappalainen 1996). In west-central Canada, the greatest depths are found slightly farther to the north as peat depths decrease rapidly towards the prairie ecotone (Ovenden 1990). Shallow peat depths are also indicated for the *Carex-Phragmites* swamps in the Eurasian forest-steppe ecotone in western Siberia (Walter 1985; Kremenetski et al. 2003). Exceptions are the foothill areas of the southern Canadian Rockies and the central Asian mountains, where, owing to higher "orographic" precipitation, thick peat deposits are found (Kubiw et al. 1989; Kremenetski et al. 2003). Long-term (apparent) rates of carbon accumulation (LORCA) are a function of the total mass accumulated and the age of the deposits.

Tolonen and Turunen (1996) provided a summary of long-term accumulation rates for Finland and west-central Canada. Bogs show on average higher rates than fens (Fig. 3.6a, c). The main reason for the higher accumulation in bogs is that *Sphagnum* species are more resistant to decay than *Carex* species (Johnson et al. 1990; Johnson and Damman 1991; Malmer 1992; Malmer and Wallén 1993; Szumigalski and Bayley 1996; Clymo et al. 1998; Scheffer et al. 2001). Southern/boreal peatlands have higher rates than northern/subarctic peatlands (Fig. 3.6b, d). These regional differences in accumulation rates are mainly related to degree-days above zero and mean annual temperatures (Clymo et al. 1998). There is no clear difference between the Finnish and Canadian datasets, except that best-fit curves seem to suggest rapider accumulation during the early Holocene followed by slow accumulation during the mid-Holocene in the Canadian datasets. Long-term accumulation rates are higher in western (oceanic) Finland than in eastern (continental) Finland (Tolonen and Turunen 1996).

These regional estimates include peatlands affected by fire and permafrost. Peat fires slow accumulation (Turetsky et al. 2000, 2002), with individual fires creating losses of up to 1.5–4.0 kg C m^{-2} (Kuhry 1994; Pitkänen et al. 1999; Robinson and Moore 2000). Some studies report no significant effects (Turunen et al. 2001). The influence of permafrost seems to be more complicated. Under stable permafrost conditions, accumulation often slows, ceases, or even becomes negative owing to wind

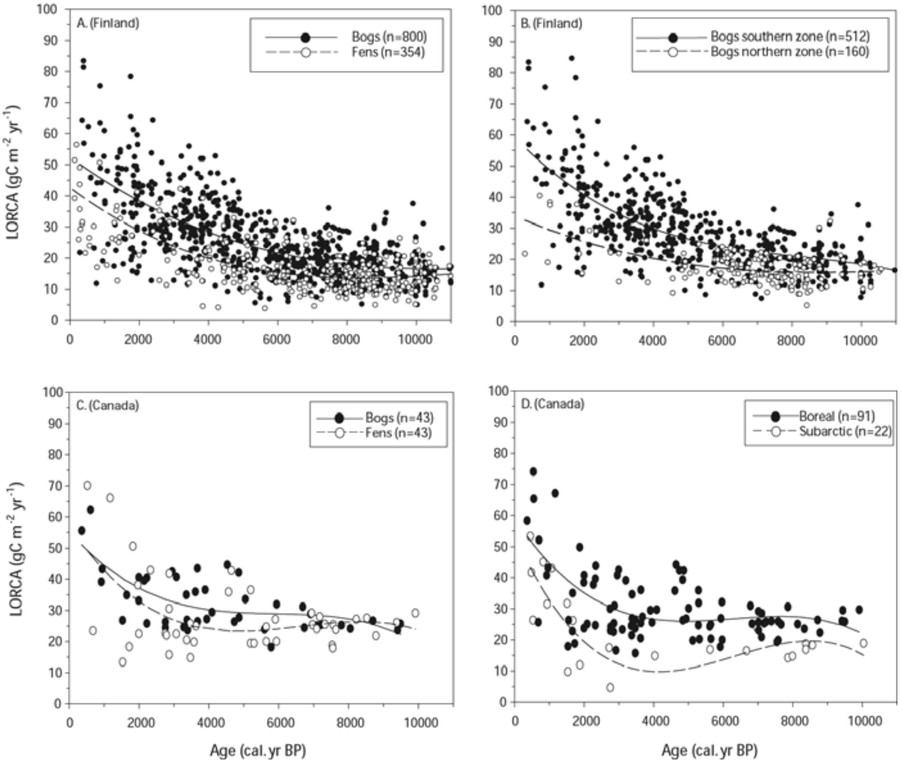

Fig. 3.6. Long-term (apparent) rate of carbon accumulation (*LORCA*) in Finnish (**A**, **B**) and Canadian (**C**, **D**) peatlands. **A** and **B** have been updated with additional sites. Boreal data in **D** include four sites from Maine, USA. (Adapted from Tolonen and Turunen 1996, copyright 1996, with permission from Edward Arnold Publishers Ltd, *The Holocene*)

abrasion or thermokarst erosion (Zoltai 1995; Peteet et al. 1998; Blyakharchuk and Sulerzhitsky 1999). Highly dynamic permafrost conditions in peatlands can result in rather normal or even high accumulation rates (Zoltai 1993; Oksanen et al. 2003).

A recent analysis of 1,302 dated peat cores from Finland gave a LORCA of 18.5 g C m^{-2} $year^{-1}$ for the entire Finnish undrained peatland area (Turunen et al. 2002). In western Sweden, Russian Karelia, western Siberia, and west-central Canada, the LORCA for the whole Holocene is estimated at 13–20 g C m^{-2} $year^{-1}$ (Elina et al. 1984; Robinson and Moore 1999, 2000; Vitt et al. 2000; Klarqvist 2001; Turunen et al. 2001). These new estimates are lower than earlier estimates of 26–30 g C m^{-2} $year^{-1}$ for boreal regions (Gorham 1991; Botch et al. 1995; Tolonen and Turunen 1996; Clymo et al. 1998). However, Borren et al. (2004) reported LORCA values from 19 to 69 g C m^{-2} $year^{-1}$ for the peatlands of the southern taiga zones of western

Siberia. A significant source of error in the calculation of accumulation rates may have been the overestimation of dry peat bulk density (Gorham 1991). This is simply because of the small number of representative samples in previous studies. Also, the shallow peatlands and mire margins have been underrepresented in previous studies as most of the profiles are from deep basins. Furthermore, the age of the peat column is an important predictor of carbon accumulation and has to be taken into account when comparing results (Tolonen and Turunen 1996; Turunen et al. 2002). In arctic and subarctic regions, the LORCA normally ranges from 1.2 to 16.5 g C m^{-2} $year^{-1}$ as summarized by Vardy et al. (2000).

Depending on peatland type and decay rate, the recent accumulation in boreal regions can range from 10 to 300 g C m^{-2} $year^{-1}$ (Tolonen et al. 1988; Wieder et al. 1994; Tolonen and Turunen 1996; Pitkänen et al. 1999; Turetsky et al. 2000). Generally, recent rates are strikingly higher than long-term rates. However, it is logical that the average net accumulation rate of carbon decreases with time because older peatlands have experienced more carbon losses by decay, peat fires, leaching, and deposition of carbon into the mineral soil beneath the peat. The actual (net) rate of carbon accumulation (ARCA) takes into account the cumulative losses by anaerobic decay in the catotelm. Both site-specific calculations (Kuhry and Vitt 1996), modeled results for an entire peatland area (Korhola et al. 1996) and regional estimates (Vitt et al. 2000) suggest that undrained boreal peatlands have continued to represent a carbon sink over the last 1,000–2,000 years (Chap. 10).

3.8 Conclusions

Peatland development is controlled by both autogenic and allogenic factors. The processes of peat (sediment) accumulation and acidification by *Sphagnum* result in hydroseral successions towards drier and more oligotrophic conditions. Secondary pattern development is also largely initiated by local biotic factors, with the exception of permafrost landforms. Within boreal and subarctic peatland development, however, regional patterns arise from the influence of temperature and precipitation. Peat accumulation rates are higher in southern/boreal than in northern/subarctic peatlands. The incidence of fire and permafrost is more important in continental than oceanic areas. The increased use of remote sensing techniques is diminishing uncertainties related to total peatland surface area in boreal and subarctic regions, but regional assessments of peatland development and peat accumulation are still hindered by limited and biased sampling, especially in the more remote areas of the northern hemisphere (e.g., subarctic Canada and western Siberia).

References

Arlen-Pouliot Y, Bhiry N (2005) Palaeoecology of a palsa and a filled thermokarst pond in a permafrost peatland, subarctic Québec, Canada. Holocene 15:408–419

Bauer IE (2002) Internal and external controls over Holocene peatland development in boreal western Canada. PhD thesis, University of Alberta, Edmonton

Bauer IE, Gignac LD, Vitt DH (2003) Development of a peatland complex in boreal western Canada: lateral site expansion and local variability in vegetation succession and long-term peat accumulation. Can J Bot 81:833–847

Blyakharchuk TA, Sulerzhitsky LD (1999) Holocene vegetational and climatic changes in the forest zone of western Siberia according to pollen records from the extrazonal palsa bog Bugristoye. Holocene 9:621–628

Borren W, Bleuten W, Lapshina ED (2004) Holocene peat and carbon accumulation rates in the southern taiga of western Siberia. Quat Res 61:42–51

Botch MS, Masing VV (1983) Peatland ecosystems in the U.S.S.R. In: Gore AJP (ed) Ecosystems of the world 4B. Mires: swamp, bog, fen and moor. Regional studies. Elsevier, Amsterdam, pp 95–152

Botch MS, Kobak KI, Vinson TS, Kolchugina TP (1995) Carbon pools and accumulation in peatlands of the former Soviet Union. Global Biogeochem Cycles 9:37–46

Brown RJE (1983) Effects of fire on the permafrost ground thermal regime. In: Wein RW, Maclean DA (eds) The role of fire in northern circumpolar ecosystems. Wiley, Chichester, pp 97–110

Campbell ID, Campbell C, Yu Z, Vitt DH, Apps MJ (2000) Millennial scale rhythms in peatlands in the western interior of Canada and in the global carbon cycle. Quat Res 54:155–158

Carcaillet C, Richard PJH (2000) Holocene changes in seasonal precipitation highlighted by fire incidence in eastern Canada. Clim Dyn 16:549–559

Charman DJ (2002) Peatlands and environmental change. Wiley, Chichester

Clymo RS (1984) The limits to peat growth. Philos Trans R Soc Lond Ser B 303:605–654

Clymo RS, Duckett JG (1986) Regeneration of *Sphagnum*. New Phytol 102:589–614

Clymo RS, Turunen J, Tolonen K (1998) Carbon accumulation in peatlands. Oikos 81:368–388

Couillard L, Payette S (1985) Évolution holocène d'une tourbière à pergélisol (Québec nordique). Can J Bot 63:1104–1121

Dyke AS, Prest VK (1987) Late Wisconsinan and Holocene history of the Laurentide ice sheet. Geogr Phys Quat 41:237–263

Elina GA, Kuznecov OL, Maksimov AI (1984) Strukturnofunktsional'naja organizatsija i dinamika bolotnyh ekosistem Karelii. Nauka, St Petersburg

Foster DR, Jacobson HA (1990) The comparative development of bogs and fens in central Sweden: Evaluating the role of climate change and ecosystem development. Aquilo Ser Bot 28:15–26

Foster DR, Wright HE Jr (1990) Role of ecosystem development and climate change in bog formation in central Sweden. J Ecol 71:450–463

Foster DR, King GA, Glaser PH, Wright HE Jr (1983) Origin of string patterns in boreal peatlands. Nature 306:256–258

Foster DR, Wright HE Jr, Thelaus M, King GA (1988) Bog development and landform dynamics in central Sweden and south-eastern Labrador, Canada. J Ecol 76:1164–1185

Glaser PH (1998) The distribution and origin of mire pools. In: Standen V, Tallis JH, Meade R (eds) Patterned mires and mire pools. British Ecological Society, London, pp 4–25

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195

Grichuk VP (1984) Late Pleistocene vegetation history. In: Velichko AA (ed) Late quaternary environments of the Soviet Union. University of Minnesota Press, Minneapolis, pp 155–178

Halsey LA, Vitt DH, Zoltai SC (1995) Disequilibrium response of permafrost in boreal continental western Canada to climate change. Clim Change 30:57–73

Halsey LA, Vitt DH, Gignac LD (2000) *Sphagnum*-dominated peatlands in North America since the Last Glacial Maximum: their occurrence and extent. Bryologist 103:334–352

Ikonen L (1993) Holocene development and peat growth of the raised bog Pesänsuo in southwestern Finland. Geol Surv Finl Bull 370

Ingram HAP (1978) Soil layers in mires: function and terminology. J Soil Sci 29:224–227

Ivanov KE (1981) Water movement in mirelands. Translated by Thomson A, Ingram HAP from Ivanov KE (1975) Vodoobmen v bolotnykn landshafter. Academic, London

Janssens JA (1983) Fossil bryophytes and paleoenvironmental reconstruction of peatlands. In: Glime JM (ed) Methods in bryology. Proceedings of the bryological methods workshop, Mainz. The Hattori Botanical Laboratory, Nichinan, Japan, pp 299–306

Jasinski JPP, Warner BG, Andreev AA, Aravena R, Gilbert SE, Zeeb BA, Smol JP, Velichko AA (1998) Holocene environmental history of a peatland in the Lena River valley, Siberia. Can J Earth Sci 35:637–648

Johnson LC, Damman AWH (1991) Species-controlled *Sphagnum* decay on a south Swedish raised bog. Oikos 61:234–242

Johnson LC, Damman AWH, Malmer N (1990) *Sphagnum* macrostructure as an indicator of decay and compaction in peat cores from an ombrotrophic south Swedish peat-bog. J Ecol 78:633–647

Kershaw GP, Gill D (1979) Growth and decay of palsas and peat plateaus in the Macmillan Pass-Tsichu River area, Northwest Territories, Canada. Can J Earth Sci 16:1362–1374

Klarqvist M (2001) Peat growth and carbon accumulation rates during the Holocene in boreal mires. Acta Univ Agric Suec Silvestria 203

Korhola A (1994) Radiocarbon evidence for rates of lateral expansion in raised peatlands in southern Finland. Quat Res 42:299–307

Korhola A (1995) Holocene climatic variations in southern Finland reconstructed from peat-initiation data. Holocene 5:43–58

Korhola A (1996) Initiation of a sloping mire complex in southwestern Finland: Autogenic versus allogenic controls. Écoscience 3:216–222

Korhola A, Tolonen K (1996) The natural history of mires in Finland and the rate of peat accumulation. In: Vasander H (ed) Peatlands in Finland. Finnish Peatland Society, Helsinki pp. 20–26

Korhola A, Alm J, Tolonen K, Turunen J, Jungner H (1996) Three-dimensional reconstruction of carbon accumulation and CH_4 emission during nine millennia in a raised peatland. J Quat Sci 11:161–165

Kremenetski KV, Sulerzhitsky LD, Hantemirov R (1998) Holocene history of the northern range limit of some trees and shrubs in Russia. Arct Alp Res 30:317–333

Kremenetski KV, Velichko AA, Borisova OK, MacDonald GM, Smith LC, Frey KE, Orlova LA (2003) Peatlands of the Western Siberian lowlands: current knowledge on zonation, carbon content and Late Quaternary history. Quat Sci Rev 22:703–723

Kubiw H, Hickman M, Vitt DH (1989) The developmental history of peatlands at Muskiki and Marguerite lakes, Alberta. Can J Bot 67:3534–3544

Kuhry P (1994) The role of fire in the development of *Sphagnum*-dominated peatlands in western Boreal Canada. J Ecol 82:899–910

Kuhry P (1997) The paleoecology of a treed bog in western boreal Canada: a study based on microfossils, macrofossils and physico-chemical properties. Rev Palaeobot Palynol 96:183–224

Kuhry P (1998) Late Holocene permafrost dynamics in two subarctic peatlands of the Hudson Bay Lowlands (Manitoba, Canada). Eurasian Soil Sci 31:529–534

Kuhry P, Vitt DH (1996) Fossil carbon/nitrogen ratios as a measure of peat decomposition. Ecology 77:271–275

Kuhry P, Halsey LA, Bayley SE, Vitt DH (1992) Peatland development in relation to Holocene climatic change in Manitoba and Saskatchewan (Canada). Can J Earth Sci 29:1070–1090

Kuhry P, Nicholson BJ, Gignac LD, Vitt DH, Bayley SE (1993) Development of *Sphagnum*-dominated peatlands in boreal continental Canada. Can J Bot 71:10–22

Lappalainen E (1996) Mires of Finland and their use. In: Lappalainen E (ed) Global peat resources. International Peat Society, Saarijärvi, pp 69–74

Lavoie C, Payette S (1995) Analyse macrofossile d’une palse subarctique (Québec nordique). Can J Bot 78:668–684

Lavoie M, Richard PJH (2000a) The role of climate on the developmental history of Frontenac Peatland, southern Québec. Can J Bot 78:668–684

Lavoie M, Richard PJH (2000b) Paléoécologie de la tourbière du lac Malbaie, dans le massif des Laurentides (Québec): évaluation du rôle du climat sur l’accumulation de la tourbe. Geogr Phys Quat 54:169–185

MacDonald GM, Beukens RP, Kieser WE, Vitt DH (1987) Comparative radiocarbon dating of terrestrial plant macrofossils and aquatic moss from the ice-free corridor of western Canada. Geology 15:837–840

Malmer N (1992) Peat accumulation and the global carbon cycle. Catena Suppl 22:97–110

Malmer N, Wallén B (1993) Accumulation and release of organic matter in ombrotrophic bog hummocks – processes and regional variation. Ecography 16:193–211

Mangerud J, Svendsen JI, Astakhov VI (1999) Age and extent of the Barents and Kara ice sheets in northern Russia. Boreas 28:46–80

Muller SD, Richard PJH, Larouche AC (2003) Holocene development of a peatland (southern Québec): a spatio-temporal reconstruction based on pachymetry, sedimentology, microfossils and macrofossils. Holocene 13: 649–665

Mäkilä M (1997) Holocene lateral expansion, peat growth and carbon accumulation on Haukkasuo, a raised bog in southeastern Finland. Boreas 26:1–14

National Wetlands Working Group (1988) Wetlands of Canada. Ecological land classification series, 24. Environment Canada, Ottawa and Polyscience Publications, Montreal, QC

Neustadt MI (1984) Holocene peatland development. In: Velichko AA (ed) Late Quaternary environments of the Soviet Union. University of Minnesota Press, Minneapolis, pp 201–206

Nichols HN (1967) The post-glacial history of vegetation and climate at Ennadai Lake, Keewatin, and Lynn Lake, Manitoba (Canada). Eiszeitalter Geg 18:176–197

Nicholson BJ, Vitt DH (1990) The paleoecology of a peatland complex in continental western Canada. Can J Bot 68:121–138

Nicholson BJ, Vitt DH (1994) Wetland development at Elk Island National Park, Alberta, Canada. J Paleolimnol 12:19–34

Nilsson M, Klarqvist M, Bohlin E, Possnert G (2001) Variation in ^{14}C age of macrofossils and different fractions of minute peat samples dated by AMS. Holocene 11:579–586

Oksanen PO (2002) Holocene permafrost dynamics in palsa and peat plateau mires of continental Europe. Licentiate thesis, University of Oulu

Oksanen PO (2006) Holocene development of the Vaisjeäggi palsa mire, Finnish Lapland. Boreas (in press)

Oksanen PO, Kuhry P (2003) Permafrost induced changes in the hydrology and carbon balance of mires. In: Järvet E, Lode E (eds) Ecohydrological processes in northern wetlands. Tartu University Press, Tartu, pp 92–98

Oksanen PO, Kuhry P, Alekseeva RN (2001) Holocene development of the Rogovaya River peat plateau, European Russian Arctic. Holocene 11:25-40

Oksanen PO, Kuhry P, Alekseeva RN (2003) Holocene development and permafrost history of the Usinsk mire, northeast European Russia. Geogr Phys Quat 57:169–187

Ovenden L (1990) Peat accumulation in northern wetlands. Quat Res 33:377–386

Payette S (2001a) La stratigraphie. In: Payette S, Rochefort L(eds) Ecologie des tourbières du Québec-Labrador. Les Presses de l'Université Laval, Sainte-Foy, pp 345–370

Payette S (2001b) Les principaux types de tourbières. In: Payette S, Rochefort L(eds) Ecologie des tourbières du Québec-Labrador. Les Presses de l'Université Laval, Sainte-Foy, pp 39–89

Peteet D, Andree A, Bardeen W, Mistretta F (1998) Long-term Arctic peatland dynamics, vegetation and climate history of the Pur-Taz region, western Siberia. Boreas 27:115–126

Pitkänen A, Turunen J, Tolonen K (1999) The role of fire in the carbon dynamics of a peatland, eastern Finland. Holocene 9:453–462

P'yavchenko NI (1955) Permafrost peatlands. Academy of Sciences of the USSR, Moscow (in Russian)

P'yavchenko NI (1985) On the age of peatbogs and sequences of vegetation in the south of West-Siberia. Bull Comm Quat Stud 52:164–170 (in Russian)

Richard PJH (1981) Paléophytogéographie postglaciaire en Ungava par l'analyse pollinique. Paléo-Québec 13. University of Quebec at Montreal,, Montreal

Riley JL (1994) Peat and peatland resources of Northeastern Ontario. Ont Geol Surv Misc Pap 153:1–155

Ritchie J (1976) The late Quaternary vegetational history of the western interior of Canada. Can J Bot 54:1793–1818

Robinson SD, Moore TR (1999) Carbon and peat accumulation over the past 1200 years in a landscape with discontinuous permafrost, northwestern Canada. Global Biogeochem Cycles 13:591–601

Robinson SD, Moore TR (2000) The influence of permafrost and fire upon carbon accumulation in high boreal peatlands, Northwest Territories, Canada. Arct Antarct Alp Res 32:155–166

Salmi M (1968) Development of palsas in Finnish Lapland. Proceedings of the 3rd international peat congress, Quebec, pp 182–189

Salmi M (1972) Present developmental stages of palsas in Finland. The proceedings of the 4th international peat congress, vol 1, Otaniemi, pp 121–141

Scheffer RA, van Logtestijn RSP, Verhoeven JTA (2001) Decomposition of *Carex* and *Sphagnum* litter in two mesotrophic fens differing in dominant plant species. Oikos 92:44–54

Seppälä M (1988) Palsas and related forms. In: Clark MJ (ed) Advances in periglacial geomorphology. Wiley, Chichester, pp 247–278

Seppälä M, Koutaniemi L (1985) Formation of a string and pool topography as expressed by morphology, stratigraphy and current processes on a peatland in Kuusamo, Finland. Boreas 14:287–309

Sjörs, H (1959) Bogs and fens in the Hudson Bay lowlands. J Arct Inst North Am 12:1–19

Sjörs, H (1983) Mires of Sweden. In: Gore AJP (ed) Ecosystems of the world 4B. Mires: swamp, bog, fen and moor. Regional studies. Elsevier, Amsterdam, pp 69–94

Sonesson M (1968) Pollen zones at Abisko, Torne Lappmark, Sweden. Bot Not 121:491–500

Svensson G (1988) Bog development and environmental conditions as shown by the stratigraphy of Store Mosse mire in southern Sweden. Boreas 17:89–111

Szumigalski AR, Bayley SE (1996) Decomposition along a bog to rich fen gradient in central Alberta, Canada. Can J Bot 74:573–581

Tolonen K (1966) Stratigraphic and rhizopod analyses on an old raised bog, Varransuo, in Hollola, South Finland. Ann Bot Fenn 3:147–166

Tolonen K (1967) Über die Entwicklung der Moore im finnischen Nord-Karelien. Ann Bot Fenn 4:219–416

Tolonen K, Turunen J (1996) Accumulation rates of carbon in peatlands in Finland and implications for climate change. Holocene 6:171–178

Tolonen K, Davis RB, Widoff L (1988) Peat accumulation rates in selected Maine peat deposits. Maine Geol Surv Dep Conserv Bull 33:1–99

Tolonen M (1985) Paleoecological record of local fire history from a peat deposit in SW Finland. Ann Bot Fenn 22:15–29

Turetsky MR, Wieder RK, Williams CJ, Vitt DH (2000) Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta. Écoscience 7:379–392

Turetsky MR, Wieder RK, Halsey L, Vitt DH (2002) Current disturbance and the diminishing peatland carbon sink. Geophys Res Lett 29. DOI 10.1029/2001GL014000

Turunen C, Turunen J (2003) Development history and carbon accumulation of a slope bog in oceanic British Columbia, Canada. Holocene 13:225–238

Turunen J, Tahvanainen T, Tolonen K, Pitkänen A (2001) Carbon accumulation in West Siberian peatlands, Russia. Global Biogeochem Cycles 15:285–296

Turunen J, Tomppo E, Tolonen K, Reinikainen A (2002) Estimating carbon accumulation rates of undrained peatlands in Finland: application to boreal and subarctic regions. Holocene 12:69–80

Väliranta M, Kaakinen A, Kuhry P (2003) Holocene climate and landscape evolution east of the Pechora Delta, east-European Russian Arctic. Quat Res 59:335–344

Vardy SR, Warner BG, Turunen J, Aravena R (2000) Carbon accumulation in permafrost peatlands in the Northwestern Territories and Nunavut, Canada. Holocene 10:273–280

Vitt DA, Halsey, LA, Bauer, IE, Campbell, C (2000) Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. Can J Earth Sci 37:683–693

Walter H (1977) The oligotrophic peatlands of western Siberia – the largest peinohelobiome in the world. Vegetatio 34 167–178

Walter H (1985) Vegetation of the earth and ecological systems of the geo-biosphere, 3rd edn. Springer, Berlin Heidelberg New York

Warner BG, Charman DJ (1994) Holocene changes on a peatland in northwestern Ontario interpreted from testate amebas (Protozoa) analysis. Boreas 23:270–279

Warner BG, Clymo RS, Tolonen K (1993) Implications of peat accumulation at Point Escuminac, New Brunswick. Quat Res 39:245–248

Wieder RK, Novak M, Schell WR, Rhodes T (1994) Rates of peat accumulation over the past 200 years in five *Sphagnum*-dominated peatlands in the United States. J Paleolimnol 12:35–47

Yu ZC, Campbell ID, Campbell C, Vitt DH, Bond GC, Apps MJ (2003a) Carbon sequestration in western Canadian peat highly sensitive to Holocene wet-dry climate cycles at millenial timescales. Holocene 13:801–808

Yu ZC, Vitt DH, Campbell ID, Apps MJ (2003b) Understanding Holocene peat accumulation pattern of continental fens in western Canada. Can J Bot 81:267–282

Zoltai SC (1993) Cyclic development of permafrost in the peatlands of northwestern Alberta, Canada. Arct Alp Res 25:240–246

Zoltai SC (1995) Permafrost distribution in peatlands of west-central Canada during the Holocene warm period 6000 years BP. Geogr Phys Quat 49:37–43

Zoltai SC, Vitt DH (1990) Holocene climatic change and the distribution of peatlands in western interior Canada. Quat Res 33:231–240

4 The Role of *Sphagnum* in Peatland Development and Persistence

HÅKAN RYDIN, URBAN GUNNARSSON, and SEBASTIAN SUNDBERG

4.1 Introduction

Since a large proportion of the boreal peatlands is dominated by *Sphagnum*, there might be as much as 1.5×10^6 km^2 of *Sphagnum* cover in these habitats. Functionally, these mosses are even more dominant, and the development from minerotrophic fens to ombrotrophic raised bogs is unthinkable without *Sphagnum*. Key features of *Sphagnum* that shape the habitat and drive peatland dynamics are (1) they create an environment that is acidic, nutrient poor, wet, and anoxic, (2) they tolerate and require low concentrations of nutrients and minerals, (3) they are resistant to decay, and (4) there are a number of species that specialize in different parts of mire gradients (e.g., water level, pH, and shading).

Important mechanisms behind the formation and maintenance of mire structures such as hummocks, hollows, and pools are the differential growth and decay rates among *Sphagnum* species in different microhabitats – notably the position above the water table. This section shows how morphology and physiology can help to explain why different *Sphagnum* species occupy different niches along the water level gradient. In niche theory one often uses the term fundamental niche to describe the environmental conditions in which the species can live (physiological tolerance), whereas realized niche is the narrower conditions to which the species is restricted in the presence of competitors. But we must remember that *Sphagnum* mosses are not only simply "adapted" or "tolerant" to a certain habitat – they create the habitat themselves. To apply traditional niche theory is therefore somewhat problematic.

The formation of microtopography is central for peatland dynamics in the whole boreal zone. Hummocks are commonly formed by species of the section Acutifolia (e.g., *S. capillifolium*, *S. rubellum*, *S. fuscum*) and a number of dwarf shrub species that are restricted to the high positions since

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Table 4.1. Features of bog hummocks and hollows, and of *Sphagnum* species inhabiting these habitats. Hummock and hollows are used here in a rather unspecific sense to indicate the upper and lower parts of the bog microtopography. Note that these are rather broad generalizations and trends, and not every hollow–hummock or species comparison will fit perfectly with every statement. Footnotes a and h refer to review papers that summarize the older literature

Hollow–hummock comparison
• Hollow species have a capacity for a higher photosynthetic or growth rate than hummock species[a,d,h,j,l,n,q]
• Most species grow in hollows as well as, or better, than in hummocks[h,j,n–p,r,s]
• Hollow species are unable to grow much higher than their natural habitat[h]
• Hummock species have better capillary water transport ability than hollow species[h,n]
• Hollow species are more often and more severely desiccated than are hummock species[h,n]
• There are no general differences in photosynthetic response to reduced water content between hummock and hollow species[h,n]
• There are no general differences in desiccation tolerance (survival, recovery) between hummock and hollow species[a,m]
• Well above the water table, shoots of hollow species benefit from being surrounded by shoots of hummock species[h,n]
• Within several species, shoot density is higher in hummock populations[c,i]
• Hummock species have a higher cation-exchange capacity than hollow species[a]
• Within a species cation-exchange capacity is higher in hummock populations[a]
• Hummock species have higher decay resistance than hollow species[e–g,k,t]

[a] Clymo and Hayward (1982)
[b] Bartsch and Moore (1985)
[c] Luken (1985)
[d] Moore (1989)
[e] Rochefort et al. (1990)
[f] Johnson and Damman (1991)
[g] Hogg (1993)
[h] Rydin (1993b)
[i] Rydin (1995)
[j] Gerdol (1995)
[k] Belyea (1996)
[l] Grosvernier et al. (1997)
[m] Schipperges and Rydin (1998)
[n] Bien (1999)
[o] Såstad et al. (1999)
[p] Stokes et al. (1999)
[q] Rice (2000)
[r] Mulligan and Gignac (2001)
[s] Weltzin et al. (2001)
[t] Limpens and Berendse (2003)

they lack aerenchyma. Below the hummock the mire surface is often dominated by *Sphagnum* species of section Cuspidata (e.g., *S. balticum*, *S. cuspidatum*, *S. fallax*, *S. majus*, *S. tenellum*). The highest species richness of *Sphagnum* is often at rather low levels along the vertical gradient, and there may be ten species of *Sphagnum* in a floating soft carpet community even with little variation in topography (Vitt and Slack 1975), and up to five species in a 4-cm-diameter plot (Rydin 1986).

Over the years evidence has accumulated for a number of rather general features of bog hummocks and hollows and of *Sphagnum* species inhabiting these habitats (Table 4.1). The parts that are below the hummocks are often subdivided into several structures (lawns, carpets, etc), but we here use "hollow" as a general term for the lower parts of the bog microtopography. The mechanisms involved were reviewed by Rydin (1993b) and here we only briefly discuss the relevant features of the *Sphagnum* mosses behind the patterns and processes.

4.2 Morphology and Water Relations

In *Sphagnum* the peculiar leaf anatomy with biologically active chlorophyllous cells and dead hyaline cells that store water is important for the ecology, but even more important is the gross morphology and its effect on capillarity. Mosses are poikilohydric, and water lost by evaporation must be replaced by rain or by a capillary uptake from below. In *Sphagnum*, a capillary network is formed by spaces between the leaves, and between the stem and the branches. A *Sphagnum* carpet is typically formed by vertically growing shoots with a density of two to seven shoots per square centimeter depending on the species. Light penetrates only a few centimeters into the carpet (Clymo and Hayward 1982) and in a dense hummock perhaps only 1 cm (Rydin and McDonald 1985), so photosynthesis is almost restricted to the capitulum (the shoot apex with branches not fully developed). This makes the competition for space two dimensional, where superior individuals can only increase their area cover, not grow taller than their neighbours. Lower parts may still be alive, as witnessed by the ability to create a side shoot that can replace the apex if it is damaged.

In *Sphagnum* there is a good relationship between water content and photosynthetic rate, and the water content in the capitula is decisive for the growth. The influence of water content on photosynthesis, survival, or recovery does not appear to differ between hummock and hollow species in any general way, so it is more important that species with good capillarity avoid desiccation and hence are able to grow high up on the hummock (Table 4.1). To a great extent capillarity is probably linked with the arrangement of the pendant branches: in some hummock species the stem is tightly covered by branches and the whole shoot is an effective wick (Rydin 1993b, and references therein). Another factor here is that *Sphagnum* populations on the hummock are very dense, and the collective surface area exposed for evaporation is rather small. In the wettest part species like *S. cuspidatum* and *S. majus* tend to grow horizontally rather than vertically. Their carpets are much looser, and fall apart as the water table drops. Compared with hummocks, each shoot is much more exposed to wind and desiccation. In Table 4.1 we note that the capacity for growth (i.e., under conditions optimal for growth) is generally higher in hollow species (reviewed in Gunnarsson 2005). The growth of hollow-inhabiting *Sphagnum* is, especially in continental areas, often limited by desiccation in the summer, but this happens much more rarely in hummock species, which can explain why the actual growth under field conditions has in some studies been higher in hummocks (Bartsch and Moore 1985; Moore 1989; Rochefort et al. 1990; Gerdol 1995).

Experiments show that some hollow species can grow rather high up on the hummock, but only as individual shoots surrounded by hummock species. As an example, it has been shown that when such individual shoots of the hollow species *S. balticum* are completely surrounded by the hummock species *S. fuscum*, they receive water by lateral transport from the *S. fuscum* shoots. These *S. balticum* shoots may be somewhat drier than the surrounding *S. fuscum* carpet, but wetter than the continuous *S. balticum* carpet growing closer to the water table (Rydin 1985). This could be viewed as a commensalism, i.e., a positive effect on *S. balticum* that is neutral for *S. fuscum*. The hollow species cannot expand since it would then lose the positive interspecific contact. With the commensalistic example, it appears that a hollow species can actually expand and grow outside the part of the gradient that defines its fundamental niche.

In addition to capillary water transport ability, the unique capacity to store water leads to anoxic conditions and gives *Sphagnum* a key role for ecosystem development.

4.3 *Sphagnum* Chemistry: Nutrition, Acidification, and Decay

By its peculiar chemistry *Sphagnum* has the ability to acidify is substrate, to survive in extremely nutrient-poor habitats, and to resist decay (Verhoeven and Liefveld 1997). As the *Sphagnum* plant grows it continuously creates cation-exchange sites. The active substance on these sites is uronic acid (galacturonic acid and 5-keto-D-mannuronic acid, 5KMA). The uronic acids appear in the cell wall as a pectin-like polymer, sometimes referred to as sphagnan (Børsheim et al. 2001). These acids release hydrogen ions and instead cations in the mire water are taken up at the carboxyl group. According to Clymo and Hayward (1982), 10–30 % of the dry mass of *Sphagnum* is uronic acids, and their concentration is higher in typical hummock species, and is also higher in shoots growing higher up from the water table. Experiments (Table 4.1) suggest that hummock species are more resistant to decay than hollow species. The higher resistance to decomposition could help these species to build hummocks, and may also help to maintain the capillary network to a greater depth than in the hollows.

Sphagnum also contains a number of phenolic compounds (the term "sphagnol" represents a mixture of these). The most common phenolic substance is sphagnum acid (*p*-hydroxy-*β*-carboxymethyl-cinnamic acid). Verhoeven and Liefveld (1997) argue that several of them may contribute to acidification and decay resistance in *Sphagnum* plants and peat.

Ecologists have often focused on the anoxic conditions as being responsible for the preservation of peat and of objects preserved in peat, but Børsheim et al. (2001) stressed the importance of 5KMA. Both in the living *Sphagnum* and in its dead remains, sphagnan in the cell wall binds ammonia and makes it unavailable for microorganisms (Painter 1998). Sphagnan therefore prevents microbial attacks on both living and dead *Sphagnum*. Possibly, this could explain the somewhat paradoxical situation that the interior of hummocks is rather well aerated, but still the shoots remain intact and the hummocks do not collapse. Over millennia sphagnan with its 5KMA is released from the dead *Sphagnum* into the mire water, where it reacts with ammonia and amino acids to form an aquatic humus. It reacts with proteins in hair, fur, skin, muscles, etc. of buried organisms. Skin is converted to leather by tanning and bodies are preserved as if they were smoked (Painter 1998).

4.4 Interactions Between *Sphagnum* and Vascular Plants

The formation of mire structures may in many cases be dependent on the interactions between *Sphagnum* and vascular plants. Several important aspects can be related to this. The structural support of vascular plants reinforces *Sphagnum*, asymmetric competition between vascular plants and *Sphagnum* for both light and nitrogen, germination and seedling growth in *Sphagnum*, and chemical interactions between vascular plants and *Sphagnum*.

Malmer et al. (1994) stressed the importance of the growth form of vascular plants for the formation of hummocks, lawns, and carpets. The hummock-growing vascular plants (dwarf shrubs) generally provide a three-dimensional reinforcement to the hummock-forming *Sphagnum* species, while the lawn- and carpet-growing vascular plant only provide a two-dimensional support (rhizoid and lateral growing sedges), not allowing hummock formation. At the same time the dwarf shrubs confined to the hummocks cannot grow under anoxic conditions that occur in lawns and carpets, which makes it a self-regulating system.

In a study of the interactions between *Drosera rotundifolia* and *S. fuscum*, Svensson (1995) found that *D. rotundifolia* had access to nitrogen only when added to the root zone below the *Sphagnum* surface and not when sprayed on the top of the *Sphagnum* mosses. Vascular plants have access to the nitrogen only after mineralization of the mosses unless nitrogen deposition levels are high. This is a case of asymmetric competition for nitrogen, and the same seems to apply for phosphorus (Malmer et al. 2003). Vascular plants have an obvious advantage over *Sphagnum* by being able to grow tall and shadow out the lower mosses, and the competition for light is advantageous for vascular plants. As long as the conditions for vascular plant growth are poor, i.e., low nutrient supply or with a high water table, the vascular plant will not be able to dominate. Whenever the environment changes in favor of vascular plants, the increased shading and litter cover will further disfavor *Sphagnum* and the dense peat-forming *Sphagnum* carpet may be at risk (Berendse et al. 2001; Limpens et al. 2003a).

Sphagnum has been shown to be an excellent substrate for tree seed germination (Ohlson and Zackrisson 1992; Gunnarsson and Rydin 1998), providing a moist and light environment. However, the conditions for survival of small seedlings in *Sphagnum*-dominated habitats are harsh. The seedlings need to grow faster in length than the *Sphagnum* shoots so as not to be overtopped and buried in the *Sphagnum* peat. This increment can be too much for small seedlings in a nutrient-poor environment. The few individuals that survive may, after they have grown to a certain size, have a deleterious effect on the *Sphagnum* carpet and may be beneficial for typical forest-floor bryophytes (Ohlson et al. 2001). Once the transition from *Sphagnum* to forest-floor bryophytes has occurred, the peat production will be reduced. What triggers this switch is unknown but it contributes to changing the mire from a peat-producing system to a treed peatland with little or no peat accumulation.

4.5 Dispersal, Colonization, and Expansion

It would be difficult to imagine the success of *Sphagnum* in boreal peatlands unless there is effective dispersal. Many species are virtually omnipresent in mires throughout the boreal region. That dispersal is a continuous force in *Sphagnum* is highlighted by the fact that severely disturbed mires and newly formed oligotrophic habitats are relatively quickly and spontaneously colonized by species not found nearby.

Peat pits, in which block-cut peat extraction stopped 50 years ago, often show an impressive *Sphagnum* diversity, including species from forested wetlands, poor fens (also in bog pits), and species having their nearest natural occurrences tens of kilometers away (Sjörs 1949; Soro et al. 1999). In eight sites with ombrotrophic peat pits in east-central Sweden, between 11 and 16 *Sphagnum* species were found, as compared with a maximum of nine species found in undisturbed bogs in the region (Soro et al. 1999).

Islands in the Baltic archipelago off Stockholm, continuously rising up from the sea (current rate approximately 5 mm $year^{-1}$) after the last glaciation, which lasted until about 12,000 BP, are seemingly quickly colonized by sphagna in rock pools. A total of 19 *Sphagnum* species were found in a survey of 17 islands up to 41 km from the nearest mainland (Sundberg et al. 2006). Notably, the most widespread species on the islands, *S. fimbriatum*, *S. palustre*, *S. squarrosum*, and *S. russowii*, are all typical of swamp forests and relatively frequently produce spore capsules on the mainland. The absence of spore capsules in most species on the islands (only in *S. fimbriatum* were 8 % of the patches fruiting) indicates that the colonies originated from spores dispersed from the mainland. The success of these species to establish in periodically dry rock pools (usually exposed, without tree cover) could be explained by their tolerance to summer droughts (their usual habitat is on soils with shallow peat). Conversely, species mostly associated with open mires having deep peat were surprisingly rare. *S. squarrosum* occurred nearest to the shore.

Sphagnum has various modes of reproduction (reviewed in Cronberg 1993): (1) asexual (vegetative) reproduction through dichotomous branching of the main stem (which is the main mode of expansion of an established clone) or innovations from the stem, (2) asexual reproduction by detached fragments (branches or stems, but not leaves), and (3) sexual reproduction through spores.

Mean radial growth of solitary *Sphagnum* patches has been reported at 3.6 cm $year^{-1}$ (range 0.4–12.9 cm), with the highest expansion rates in large species such as *S. palustre* and *S. squarrosum* (Högström 1997). Within a closed *Sphagnum* mat, a clonal front may expand at a rate of 1 cm $year^{-1}$ (Rydin 1993a). In restoration trials of severely damaged peatlands, fragments have been widely used (reviewed in Rochefort 2000; Chap. 17), in which the uppermost 6 cm of the *Sphagnum* shoots generally establish themselves best (Rochefort et al. 2003), but Clymo and Duckett (1986) reported occasional shoot formation of seemingly dead *Sphagnum* in peat cores from depths down to 42 cm or up to 60 years old. Little is known about the dispersal capacity and the relative role dispersal and establishment of fragments plays, but they may be important in harsh environments, such as tundra and alpine areas, where spore capsules are rare or absent. McDaniel and Miller (2000) recorded 13 fragments of *Sphagnum* (among more than 1,000 other bryophyte fragments) in seven 0.25-m^2 samples of surface snow collected from two mountain peaks in the Adirondack Mountains in northeastern USA. In an experiment with *S. angermanicum*, a low establishment frequency (approximately 0.1 %) was found for small capitulum fragments (approximately 0.02 mg) over a

9-month period, while whole capitula and shoots showed much higher establishment (20 and 70 %, respectively) (Gunnarsson 2002).

Sphagnum spores have been questioned as a reliable method of dispersal since they do not develop into new plants in mire water, mainly because of phosphorus deficiency (Boatman and Lark 1971). However, they will develop in the presence of decaying vascular plant litter or animal feces that provide the necessary nutrients (Sundberg and Rydin 2002). This indicates that spores are important for establishment in disturbed and newly formed wetlands, but their role in closed mire vegetation remains unknown.

Most *Sphagnum* species regularly produce spore capsules, at least in boreal regions (Maass and Harvey 1973; Cronberg 1993; Sundberg 2002), where bisexual (potentially selfing) species generally have a higher density of spore capsules. Notably, some regionally common species surprisingly rarely produce capsules, e.g., *S. pulchrum* (reviewed in Cronberg 1993). Interspecific variation in spore capsule density seems partly dependent on the distribution and ratio of male, female, and sterile shoots in unisexual species, and also on the frequency of bisexual shoots in bisexual species (Pujos 1994). At least in section Acutifolia, there seems to be a continuum in the degree of bisexuality, ranging from the highly bisexual (51 % of the shoots) and extremely sporulating *S. fimbriatum*, via *S. capillifolium* (12 % bisexual shoots) to the traditionally viewed unisexual *S. fuscum* (approximately 1 % bisexual shoots; J Pujos, personal communication), to *S. girgensohnii*, and *S. russowii* with occasional bisexual shoots (Pujos 1994; cf. Cronberg 1993). Male gamete dispersal in *Sphagnum* is limited to a few centimeters (McQueen 1985), but might be enhanced in running water (Cronberg 1993).

Spore capsule production varies widely among years, at least in dry summer regions, where ample spore capsules occur the year after a wet summer. Gametangium formation seems to be hampered by summer droughts. In permanently wet habitats, such as floating mats, spore capsule production is more stable but seems to be positively related to the amount of precipitation in spring (probably because this enhances fertilization distances). Spore capsule production seems otherwise to be stabler in hummock species than in hollow species, probably because hummock species are more resistant to drying out. Northern boreal sphagna disperse their spores in July and August, where hollow species (sections Cuspidata and Subsecunda) are early, while hummock species (sections Sphagnum and Acutifolia) are late (Sundberg 2002).

Sphagnum spores are tetrahedral and range in mean diameter from 22 to 45 µm among species (Cao and Vitt 1986). Spores with a functional diameter less than about 50 µm are predicted to persist suspended in the atmosphere to a high degree (Gregory 1973). Among species, the number of spores per capsule ranges from 18,500 in *S. tenellum* to 240,000 in

S. squarrosum (Sundberg and Rydin 1998). Around 15 × 10^6 *Sphagnum* spores per square meter of mire surface were produced annually at two Swedish mires (Sundberg 2002).

In a field experiment with transplanted spore-capsule-bearing colonies of six *Sphagnum* species of a great range of spore and spore capsule sizes, spore deposition per unit area showed a strong negative relationship to distance and was fitted well by the inverse power law (i.e., a linear relationship was acquired by log-transforming spore density and distance). Nevertheless, the majority of the dispersed spores (56–90 %) traveled beyond the sampled distance of 3.2 m. In four of the species, the empirical deposition models did not account for all spores dispersed, even when extended to infinity, and thus underestimated the tail of the dispersal curve. Capsule size had the most obvious positive effect on spore dispersal, while the role of spore size (negative relationship) seemed to increase with distance from the patches. The observations indicate that a single patch has a great impact on spore deposition at close range, but for colonization of more isolated sites, spores produced further away play an increasingly important role. The inverse power law of deposition warrants that *Sphagnum* spores are effectively dispersed, but future investigations and modeling will hopefully reveal how far, how much, and how often (Sundberg 2005).

Effective spore dispersal is also indicated by the high genetic variation found within populations of many studied *Sphagnum* species and the relatively low level of genetic differentiation among *Sphagnum* populations (Daniels 1982, 1985; Shaw and Srodon 1995; Cronberg 1996, 1998; Stenøien and Såstad 1999; Thingsgaard 2001; Gunnarsson et al. 2005). In contrast, the asexual *S. troendelagicum* shows high differentiation among populations (Stenøien and Flatberg 2000).

Sphagna not only seem to have effective spore dispersal in space, but also in time by the ability to form a persistent spore bank (Clymo and Duckett 1986) with a half-life of approximately 1–6 years in acrotelm peat, where light-colored spores are more long-lived than dark ones (Sundberg and Rydin 2000). The long-lived spores are probably an adaptive response to disturbance and unpredictable conditions at colonized sites.

4.6 Dynamics and Persistence in *Sphagnum* Assemblages

Interspecific dynamics in *Sphagnum* can be studied at three time scales. First, we have experiments and permanent plots followed by an individual researcher. This rarely goes beyond a decade in duration, and the scale of interest has often been square centimeters to square decimeters since changes at square-meter scale in peatlands are rarely thought to be measurable within so short a time. Second, retrospective studies using old air photographs or previous detailed investigations can reveal changes over several decades. Such studies are mostly concerned with population and vegetation changes at the community scale. Third, for the century–millennium time scale we resort to stratigraphic data.

4.6.1 Fine-Scale Dynamics over 1–10 years

Since the *Sphagnum* clone can expand over the mire surface by lateral growth and vegetative reproduction rates on the order of centimeters per year (see before), there is potential for complete species turnover at the square-decimeter scale within a decade.

A number of transplant experiment and permanently marked *Sphagnum* patches were followed for several years, in some cases as long as 11 years in Sweden (Rydin 1986, 1993a). The experiments contained several dominant bog species in the following order of occurrence from hollow to hummock: *S. cuspidatum*, *S. tenellum*, *S. balticum*, *S. rubellum*, and *S. fuscum*. As predicted from their inability to stay wet, the hollow species transplanted as single-species patches to high hummock positions died because they dried out. Lower positions along the gradient appear to be within the fundamental niches of both hollow and hummock species, and transplants of all species survived well; thus, competition could at least potentially be important here in the hollows. Early results also indicated a decrease in cover of hummock species (Rydin 1986), but later follow-up studies showed that this trend did not continue (Rydin 1993a). Over the years changes instead appeared to be rather erratic, both in transplants and in permanent plots. Only in one year was there a directional change – *S. tenellum* expanded at the cost of *S. balticum* – but this was counteracted by fluctuations in cover of the species in the other years. Most interesting was perhaps that no cases of competitive exclusion were observed despite the fact that the *Sphagnum* patches were only 6–8 cm in diameter. Even when conditions were controlled (growth chamber), there were no cases of competitive exclusion among *Sphagnum* species (Rydin 1997). Directional changes were observed in an experiment with increased temperature (open-top chambers): patches of *S. papillosum* transplanted from hummocks were able to increase up to 40 % in area over 4 years in a *S. balticum* dominated lawn community (Gunnarsson et al. 2004). This indicates that there may be differences among species in their response to climate change. After 9 years of nitrogen treatment (in the same experiment) the *Sphagnum* lawn had more or less collapsed from 100 % cover during the period of 1995–1998, to 63 % cover in 2003, and to 20 % cover in the combined nitrogen and temperature treatment (Wiedermann et al. 2005).

In southern Norway, Nordbakken (2001) analyzed almost 7,000 plots of 4 cm x 4 cm in 1991 and again after 5 years. All *Sphagnum* species (*S. cuspidatum*, *S. tenellum*, *S. balticum*, *S. rubellum*, *S. fuscum*) decreased in plot frequency. In quite a few instances *S. tenellum* gained area from *S. fuscum* and *S. rubellum*, and the area with naked peat increased from 1.3 to 6.5 %, while that covered by plant litter increased from 7.1 to 13.3 %. The study was made in a well-developed raised bog where directional change is somewhat unexpected. Nordbakken suggested that climatic fluctuations rather than nitrogen deposition caused the changes.

Another indication that directional changes in certain periods may level out over time was given by Bien (1999), who followed within-season dynamics of *S. pulchrum* (hollow species, section Cuspidata) and *S. flavicomans* (hummock species, section Acutifolia) in New Jersey. In this area a pronounced drop in water table occurs during the summer, and during that period *S. flavicomans* expanded in the zone of coexistence. Apparently it benefited from a better capillarity, but in the autumn the higher growth potential of *S. pulchrum* allowed it to regain area. Even if *S. pulchrum* in many instances had the higher growth rate, the very highest length growth was in *S. flavicomans* transplanted into the *S. pulchrum* hollow. As in previous studies (Clymo and Reddaway 1971; Rydin 1993a) the difficulty is to explain why the hummock species cannot establish and maintain itself closer to the water table. Bien suggested that growth habit is more important than growth rate. With increasing wetness *S. flavicomans* grows taller and at the same time laxer and slenderer (cf. Hayward and Clymo 1983). Eventually it falls over and is overgrown by *S. pulchrum*.

4.6.2 Dynamics over Several Decades

In retrospective studies of mire development over several decades it is possible to follow changes in *Sphagnum* dominance and cover together with changes in the environment and in the cover of vascular plants. There are only a few studies on this time scale in undisturbed mires (Backéus 1972; Chapman and Rose 1991; Frankl and Schmeidl 2000; Gunnarsson et al. 2000, 2002) but more studies have been done in disturbed peatlands after, for example, drainage (van Diggelen et al. 1996). On this time scale it is possible to follow long time-trends or vegetation succession (important information for the evaluation of experiments). However, by the nature of retrospective studies it is seldom possible to be sure about the causes of the observed changes.

Over these time scales some mire types show an extreme stability in species composition, while other show large changes. Backéus (1972) found only small vegetation changes after 60 years in a poor fen and ombrotrophic bog site at Skagershultamossen (central Sweden). In 1945, Sjörs (1948) analyzed the *Sphagnum* species composition along a 40-m-long and 2-dm-wide transect across a series of hummock strings on Skattlösbergs Stormosse, central Sweden. We reanalyzed this transect after 50 years (Fig. 4.1) and found an almost identical species composition along the transect, with *S. fuscum* on the high elevated hummocks and *S. cuspidatum* in the hollows. *S. rubellum*, *S. balticum*, and *S. tenellum* inhabited intermediate positions. *S. majus*, found in the deepest hollow in 1945, had disappeared by 1995 from a position along the transect (around 30 m) where the surface elevation above the ground water level had increased. Other small shifts in the transitions between hummocks and hollows were found at 12 and 19 m (Fig. 4.1), but the shifts were generally less than 1 dm in the horizontal direction.

In the richer parts of Skattlösbergs Stormosse, a drop in pH was found along with a change in species composition from rich fen bryophytes to *Sphagnum* species (Gunnarsson et al. 2000). This drop in pH was particu-

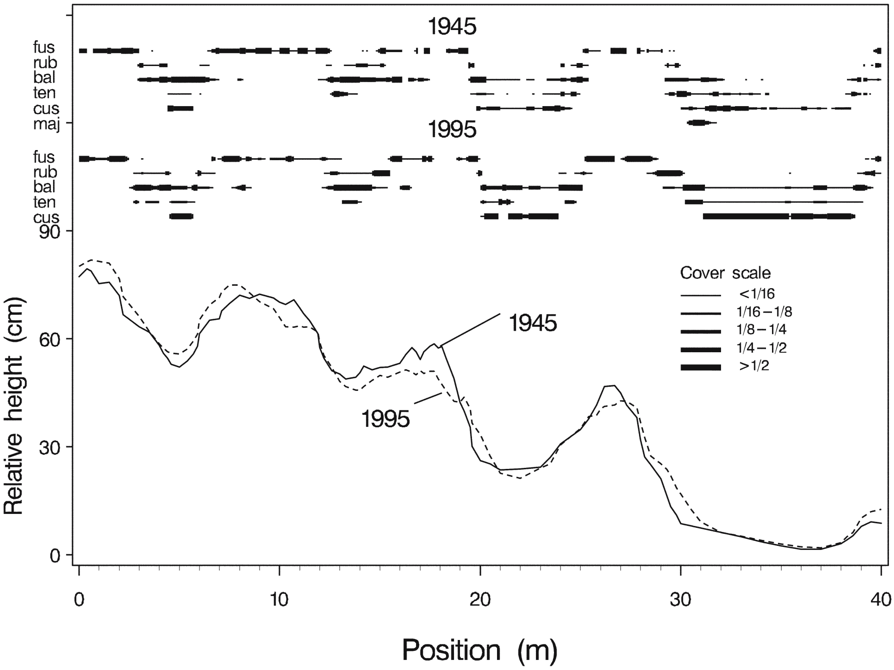

Fig. 4.1. Occurrence of *Sphagnum* species along a 2-dm-wide transect across a series of hummock strings and hollows at Skattlösbergs Stormosse in 1945 and 1995. The *upper part* shows the abundance of six *Sphagnum* species on a logarithmic cover scale. The *lower part* shows the relative height of the moss surface above the lowest hollow. *fus*, *S. fuscum*; *rub*, *S. rubellum*; *bal*, *S. balticum*; *ten*, *S. tenellum*; *cus S. cuspidatum*; *maj*, *S. majus*. (The 1945 data are from Fig. 18 in Sjörs 1948)

larly pronounced in the interval 5.2–5.8. Mire water pH in this interval is very poorly buffered (Gorham 1956) and coincides with the shift from brown mosses to *Sphagnum* (Gunnarsson et al. 2000). In this shift, *S. subsecundum* is the first *Sphagnum* species to establish itself (Kuhry et al. 1993). Once established, it starts to facilitate establishment of other sphagna by autogenic acidification and *S. subsecundum* will soon be replaced by other species, such as *S. fallax* or *S. papillosum*. Also on the mire Åkhultmyren (southern Sweden) pH dropped in the areas with high pH from 1954 to 1997 (Gunnarsson et al. 2002). This coincided with an increase in the areal extension of ombrotrophic and poor fen *Sphagnum* species such as *S. balticum*, *S. tenellum*, *S. fuscum*, *S. cuspidatum*, *S. majus*, and *S. pulchrum*. With decreasing pH the areas suitable for bryophytes typical of rich and intermediate fens decreased, and consequently *S. subsecundum* and *S. subnitens* decreased both at Åkhultmyren and at Skatlösbergs Stormosse (where *S. warnstorfii* had also decreased).

An example of shifts in relative amounts of *Sphagnum* species is described from Germany and The Netherlands where *S. fallax* has increased relative to other sphagna, and has replaced *S. subnitens* in somewhat eutrophic mires in the Netherlands (Kooijman and Kanne 1993). Twenhöven (1992) suggested that increased nitrogen deposition has competitively favored *S. fallax* over *S. magellanicum*, but later experiments indicate that competitive replacement of *S. papillosum* and *S. palustre* by *S. fallax* also requires adequate supplies of water and phosphorus (Limpens et al. 2003b). In addition, it was shown earlier that *S. fallax* is relatively tolerant to SO_2 (Ferguson and Lee 1983).

Other retrospective studies have shown increased tree cover (Frankl and Schmeidl 2000; Gunnarsson et al. 2002), which in turn has altered the understory vegetation to dominance of forest-floor mosses (Gunnarsson et al. 2002).

4.6.3 Long-Term Dynamics and Coexistence Among *Sphagnum* Species

In palaeoecology, peat cores have been used to reveal postglacial vegetation history (by pollen analysis) and climate. Since the species differ in their affinity to differently wet habitats, the *Sphagnum* assemblage is used as a proxy for the climate. Large-scale trends can be verified; the most well-known is the strong decrease in *S. imbricatum sensu lato* (*S. austinii* according to recent taxonomy) in England and Scotland from 1400 to1800, which is considered an indication of a wetter climate (Mauquoy and Barber 1999).

Studies based on coring with the Hiller or Russian corer are difficult to interpret in terms of species interactions since the small diameter makes changes (species appearances and disappearances) somewhat erratic.

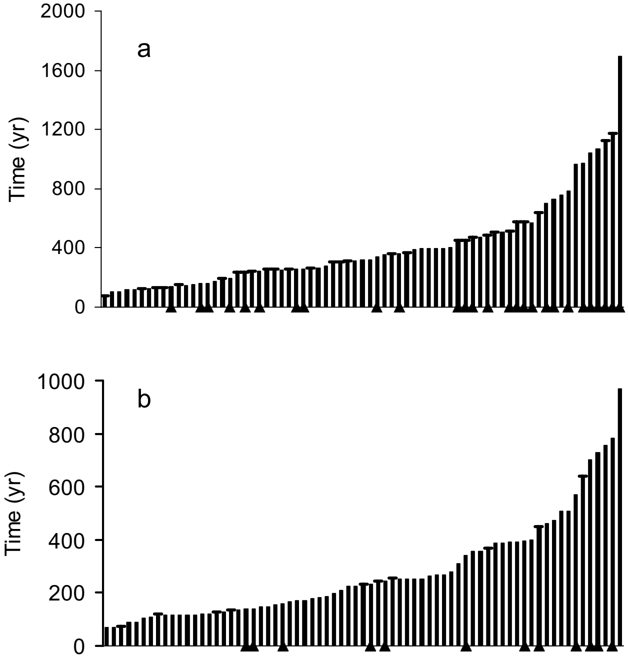

Fig. 4.2. The duration of monospecific *Sphagnum* occurrences (**a**) and two-species coexistences (**b**) in 10-cm x 10-cm peat profiles in northern England. The ceiling on top of some of the *bars* indicates that these *Sphagnum* patches and coexistences persisted to the very top of the profiles, i.e., they were interrupted by the sampling. The *triangles* at the bases indicate that they went all the way to the bottom of the profile investigated. Mean duration was 408 years (**a**) and 278 years (**b**). (Based on data from Barber 1981; cf. Rydin and Barber 2001)

However, Rydin and Barber (2001) made use of stratigraphic data from 10-cm x 10-cm excavated profiles from England where there was also ^{14}C-dating that could be used to establish a good depth–time relationship. Even at this square-decimeter scale some turnover is haphazard, but apart from climatically driven directional changes, the most salient result was that a *Sphagnum* clone can persist within the plot for thousands of years, and species can coexist for many hundreds of years, and even 1,000 years (Fig. 4.2). On one hand, this reinforces the picture from short-term studies that competitive exclusion is not a major force, and that small shifts in advantage between species level out over the years. On the other hand, it makes the directional changes observed by Nordbakken over 5 years more interesting: Are such changes early indications of climatic shift, increased nitrogen deposition, or other human impacts, or do they simply reflect a series of unusual years?

4.7 Conclusions

Sphagnum mosses not only dominate large areas of the boreal peatlands, but they have also formed these habitats by their growth and production of decay-resistant litter. As they invade, they can quickly transform a high-pH fen with little peat accumulation to a bog where large amounts of carbon is stored. They are also responsible for the many types of surface patterns observed in peatlands. Their ability to shape and transform mires can to a large extent be understood from the peculiar anatomy and biochemistry, a fact which makes the links between species' traits and ecosystem functions in peatlands very strong.

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References

Backéus I (1972) Bog vegetation re-mapped after sixty years. Studies on Skagershultamossen, central Sweden. Oikos 23:384–393

Barber KE (1981) Peat stratigraphy and climatic change: A paleoecological test of the theory of cyclic peat bog regeneration. Balkema, Rotterdam

Bartsch I, Moore TR (1985) A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. Can J Bot 63:1241–1248

Belyea LR (1996) Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. Oikos 77:529–539

Berendse F, van Breemen N, Rydin H, Buttler A, Heijmans M, Hoosbeek MR, Lee JA, Mitchell E, Saarinen T, Vasander H, Wallén B (2001) Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. Global Change Biol 7:591–598

Bien WF (1999) Ecological factors influencing spatial patterns in *Sphagnum flavicomans* and *Sphagnum pulchrum* from the New Jersey Pine Barrens, PhD thesis, Drexel University, Philadelphia

Boatman DJ, Lark PM (1971) Inorganic nutrition of the protonemata of *Sphagnum papillosum* Lindb., *S. magellanicum* Brid. and *S. cuspidatum* Ehrh. New Phytol 70:1053–1059

Børsheim KY, Christensen BE, Painter TJ (2001) Preservation of fish embedment in *Sphagnum* moss, peat or holocellulose: experimental proof of the oxopolysaccharidic nature of the preservative substance and of its antimicrobial and tanning action. Innovative Food Sci Emerging Technol 2:63–74

Cao T, Vitt DH (1986) Spore surface structure of *Sphagnum*. Nova Hedwigia 43:191–220

Chapman SB, Rose RJ (1991) Changes in the vegetation at Coom Rigg Moss National Nature Reserve within the period 1958-86. J Appl Ecol 28:140–153

Clymo RS, Duckett JG (1986) Regeneration of *Sphagnum*. New Phytol 102:589–614

Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. In: Smith AJE (ed) Bryophyte ecology. Chapman and Hall, London, pp 229–289

Clymo RS, Reddaway EJF (1971) A tentative dry matter balance sheet for the wet blanket bog on Burnt Hill Moor House NNR. Moor House Occas Pap 3:1–15

Cronberg N (1993) Reproductive biology of *Sphagnum*. Lindbergia 17:69–82

Cronberg N (1996) Clonal structure and fertility in a sympatric population of the peat mosses *Sphagnum rubellum* and *S. capillifolium*. Can J Bot 74:1375–1385

Cronberg N (1998) Population structure and interspecific differentiation of the peat moss sister species *Sphagnum rubellum* and *S. capillifolium* (*Sphagnaceae*) in northern Europe. Plant Syst Evol 209:139–158

Daniels RE (1982) Isozyme variation in British populations of *Sphagnum pulchrum* (Braithw.) Warnst. J Bryol 12:65–76

Daniels RE (1985) Isozyme variation in populations of *Sphagnum recurvum* var. *mucronatum* from Britain and Finland. J Bryol 13:563–570

Ferguson P, Lee JA (1983) The growth of *Sphagnum* species in the southern Pennines. J Bryol 12:579–586

Frankl R, Schmeidl H (2000). Vegetation change in a south German raised bog: ecosystem engineering by plant species, vegetation switch or ecosystem level feedback mechanisms? Flora 195:267–276

Gerdol R (1995) The growth dynamics of *Sphagnum* based on field measurements in a temperate bog and on laboratory cultures. J Ecol 83:431–437

Gorham E (1956) The ionic composition of some bog and fen waters in the English Lake District. J Ecol 44:142–152

Gregory PH (1973) The microbiology of the atmosphere, 2nd edn. Hill, Aylesbury

Grosvernier P, Matthey Y, Buttler A (1997) Growth potential of three *Sphagnum* species in relation to water table level and peat properties with implications for their restoration in cut-over bogs. J Appl Ecol 34:471–483

Gunnarsson U (2002) Swedish populations of *Sphagnum angermanicum* – genetic structure and establishment. In: Såstad SM, Rydin H (eds) 3rd international symposium on the biology of *Sphagnum*, Uppsala – Trondheim August 2002: schedule and abstracts. NTNU Vitenskapsmuseet Rapp Bot Ser 2002–2003:15

Gunnarsson U (2005) Global patterns of *Sphagnum* productivity. J Bryol 27:267–277

Gunnarsson U, Rydin H (1998) Demography and recruitment of Scots pine on raised bogs in eastern Sweden and relationships to microhabitat differentiation. Wetlands 18:133–141

Gunnarsson U, Sjörs H, Rydin H (2000) Diversity and pH changes after 50 years on the boreal mire Skattlösbergs Stormosse, Central Sweden. J Veg Sci 11:277–286

Gunnarsson U, Malmer N, Rydin H (2002) Dynamics or constancy in *Sphagnum* dominated mire ecosystems? A 40-year study. Ecography 25:685–704

Gunnarsson U, Granberg G, Nilsson M (2004) Growth, production and interspecific competition in *Sphagnum*: effects of temperature, nitrogen and sulphur treatments on a boreal mire. New Phytol 163:349–359

Gunnarsson U, Hassel K, Söderström L (2005) Genetic structure of the endangered peat moss *Sphagnum angermanicum* in Sweden: a result of historic or contemporary processes? Bryologist 108:194–203

Sundberg S, Hansson J, Rydinnnnn H (2006) Colonization of *Sphagnum* on land uplift islands in the Baltic Sea: time, area, distance and life history. J. Biogeogr, in press

Hayward PM, Clymo RS (1983) The growth of *Sphagnum*: Experiments on, and simulation of, some effects of light flux and water-table depth. J Ecol 71:845–863

Hogg EH (1993) Decay potential of hummock and hollow *Sphagnum* peats at different depths in a Swedish raised bog. Oikos 66:269–278

Högström S (1997) Habitats and increase of *Sphagnum* in the Baltic Sea island Gotland, Sweden. Lindbergia 22:69–74

Johnson LC, Damman AWH (1991) Species-controlled *Sphagnum* decay on a south Swedish raised bog. Oikos 61:234–242

Kooijman AM, Kanne DM (1993) Effects of water chemistry, nutrient supply and interspecific interactions on the replacement of *Sphagnum subnitens* by *S. fallax* in fens. J Bryol 17:431–438

Kuhry P, Nicholson BJ, Gignac LD, Vitt DH, Bayley SE (1993) Development of *Sphagnum* dominated peatlands in boreal continental Canada. Can J Bot 71:10–22

Limpens J, Berendse F (2003) How litter quality affects mass loss and N loss from decomposing *Sphagnum*. Oikos 103:537–547

Limpens J, Berendse F, Klees H (2003a) N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. New Phytol 157:339–347

Limpens J, Tomassen HBM, Berendse F (2003b) Expansion of *Sphagnum fallax* in bogs: striking the balance between N and P availability. J Bryol 25:83–90

Luken JO (1985) Zonation of *Sphagnum* mosses: interactions among shoot growth, growth form, and water balance. Bryologist 88:374–379

Maass WSG, Harvey MJ (1973) Studies on the taxonomy and distribution of *Sphagnum* VII. Chromosome numbers in *Sphagnum*. Nova Hedwigia 24:193–205

Malmer N, Svensson BM, Wallén B (1994) Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. Folia Geobot Phytotax 29:483–496

Malmer N, Albinsson C, Svensson BM, Wallén B (2003) Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. Oikos 100:469–482

Mauquoy D, Barber K (1999) Evidence for climatic deteriorations associated with the decline of *Sphagnum imbricatum* Hornsch. ex Russ. in six ombrotrophic mires from northern England and the Scottish Borders. Holocene 9:423–437

McDaniel SF, Miller NG (2000) Winter dispersal of bryophyte fragments in the Adirondack Mountains, New York. Bryologist 103:592–600

McQueen CB (1985) Spatial pattern and gene flow distances in *Sphagnum subtile*. Bryologist 88:333–336

Moore TR (1989) Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. Can J Bot 67:1203–1207

Mulligan RC, Gignac LD (2001) Bryophyte community structure in a boreal poor fen: reciprocal transplants. Can J Bot 79:404–411

Nordbakken J-F (2001) Fine-scale five-year vegetation change in boreal bog vegetation. J Veg Sci 12:771–778

Ohlson M, Zackrisson O (1992) Tree establishment and microhabitat relationships in north Swedish peatlands. Can J For Res 22:1869–1877

Ohlson M, Økland RH, Nordbakken JF, Dahlberg B (2001) Fatal interactions between Scots pine and *Sphagnum* mosses in bog ecosystems. Oikos 94:425–432

Painter TJ (1998) Carbohydrate polymers in food preservation: an integrated view of the Maillard reaction with special reference to discoveries of preserved foods in *Sphagnum*-dominated peat bogs. Carbohydr Polym 36:335–347

Pujos J (1994) Systèmes de croisement et fécondité chez le *Sphagnum*. Can J Bot 72:1528–1534

Rice SK (2000) Variation in carbon isotope discrimination within and among *Sphagnum* species in a temperate wetland. Oecologia 123:1–8

Rochefort L (2000) *Sphagnum* – a keystone genus in habitat restoration. Bryologist 103:503–508

Rochefort L, Vitt DH, Bayley SE (1990) Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology 71:1986–2000

Rochefort L, Quinty F, Campeau S, Johnson K, Malterer T (2003) North American approach to the restoration of *Sphagnum* dominated peatlands. Wetlands Ecol Manage 11:3–20

Rydin H (1985) Effect of water level on desiccation of *Sphagnum* in relation to surrounding Sphagna. Oikos 45:374–379

Rydin H (1986) Competition and niche separation in *Sphagnum*. Can J Bot 64:1817–1824

Rydin H (1993a) Interspecific competition among *Sphagnum* mosses on a raised bog. Oikos 66:413–423

Rydin H (1993b) Mechanisms of interactions among *Sphagnum* species along water-level gradients. Adv Bryol 5:153–185

Rydin H (1995) Effects of density and water level on recruitment, mortality and shoot size in *Sphagnum* populations. J Bryol 18:439–453

Rydin H (1997) Competition between *Sphagnum* species under controlled conditions. Bryologist 100:302–307

Rydin H, Barber KE (2001) Long-term and fine-scale co-existence of closely related species. Folia Geobot 36:53–62

Rydin H, McDonald AJS (1985) Tolerance of *Sphagnum* to water level. J Bryol 13:571–578

Såstad SM, Pedersen B, Digre K (1999) Habitat-specific genetic effects on growth rate and morphology across pH and water-level gradients within a population of the moss *Sphagnum angustifolium* (Sphagnaceae). Am J Bot 86:1687–1698

Schipperges B, Rydin H (1998) Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytol 140:677–684

Shaw AJ, Srodon M (1995) Clonal diversity in *Sphagnum rubellum* Wils. Bryologist 98:261–264

Sjörs H (1948) Myrvegetation i Bergslagen (Mire vegetation in Bergslagen, Sweden). Acta Phytogeogr Suec 21:1–299

Sjörs H (1949) Om *Sphagnum Lindbergii* i södra delen av Sverige (On *Sphagnum lindbergii* in the south part of Sweden). Sven Bot Tidskr 43:568–585

Soro A, Sundberg S, Rydin H (1999) Species diversity, niche metrics and species associations in harvested and undisturbed bogs. J Veg Sci 10:549–560

Stenøien HK, Flatberg KI (2000) Genetic variability in the rare Norwegian peat moss *Sphagnum troendelagicum*. Bryologist 103:794–801

Stenøien HK, Såstad SM (1999) Genetic structure in three haploid peat mosses (*Sphagnum*). Heredity 82:391–400

Stokes JR, Alspach PA, Stanley CJ (1999) Effect of water table on growth of three New Zealand *Sphagnum* species: implications for *S. cristatum* management. J Bryol 21:25–29

Sundberg S (2002) Sporophyte production and spore dispersal phenology in *Sphagnum*: the importance of summer moisture and patch characteristics. Can J Bot 80:543–556

Sundberg S (2005) Larger capsules enhance short-range spore dispersal in *Sphagnum*, but what happens further away? Oikos 108: 115–124

Sundberg S, Rydin H (1998) Spore number in *Sphagnum* and its dependence on spore and capsule size. J Bryol 20:1–16

Sundberg S, Rydin H (2000) Experimental evidence for a persistent spore bank in *Sphagnum*. New Phytol 148:105–116

Sundberg S, Rydin H (2002) Habitat requirements for establishment of *Sphagnum* from spores. J Ecol 90:268–278

Svensson BM (1995) Competition between *Sphagnum fuscum* and *Drosera rotundifolia*: a case of ecosystem engineering. Oikos 74:205–212

Thingsgaard K (2001) Population structure and genetic diversity of the amphiatlantic haploid peatmoss *Sphagnum affine* (Sphagnopsida). Heredity 87:485–496

Twenhöven FL (1992) Competition between two *Sphagnum* species under different deposition levels. J Bryol 17:71–80

van Diggelen R, Molenaar WJ, Kooijman AM (1996) Vegetation succession in a floating mire in relation to management and hydrology. J Veg Sci 7:809–820

Verhoeven JTA, Liefveld WM (1997) The ecological significance of organochemical compounds in *Sphagnum*. Acta Bot Neerl 46:117–130

Vitt DH, Slack, NG (1975) An analysis of the vegetation of *Sphagnum*-dominated kettle-hole bogs in relation to environmental gradients. Can J Bot 53:332–359

Weltzin JF, Harth C, Bridgham SD, Pastor J, Vonderharr M (2001) Production and microtopography of bog bryophytes: response to warming and water-table manipulations. Oecologia 128:557–565

Wiedermann MM, Nordin A, Nilsson MB, Gunnarsson U, Ericson L (2005) Global change and trophic interactions on a boreal mire. Paper presented at the XVIIth international botanical congress, Vienna, Austria

5 Peatland Fauna

André Desrochers and Gert-Jan van Duinen

5.1 Introduction

Peatlands (especially bogs) are among the last large undisturbed ecosystems in the world, and are home to substantial numbers of animals; however, bogs have almost completely disappeared from certain areas in western Europe (Joosten and Clarke 2002) and temperate North America (Poulin and Pellerin 2001) and basic information on the fauna of bogs is often lacking. The first descriptions of the invertebrate fauna of European peatlands were compiled in the first decades of the twentieth century (Dampf 1924a, b; Harnisch 1925; Goffart 1928; Peus 1932). From the point of view of vertebrate animals, peatlands remain one of the least studied terrestrial habitats. Perhaps one of the reasons for the modest interest in the vertebrate fauna of peatlands is that no vertebrate species is known to occur only in peatlands, even though certain species are found mostly on peatlands (see later). In contrast, a large number of invertebrate species have been reported almost exclusively from peatlands, at least in the southern part of the distribution area of these species (Peus 1932; Petersen 1954; Krogerus 1960; Spitzer and Jaroš 1993). Among vertebrates, birds have been well studied in Fennoscandinavian peatlands since Hakala (1971), and more recently in eastern Canada (Calmé et al. 2002, and references therein). Peatland mammals and other vertebrates have been less well studied.

Peatlands cover vast areas of the northern regions, but they are also found to a lesser extent in populated, southern regions. Peatlands are thus an increasingly fragmented and distinct habitat as one goes from north to south and toward populated areas (Fig. 5.1). Not only do boreal peatlands change in size and isolation in north–south gradients, but they also change in character (Moore and Bellamy 1974; Pakarinen 1995) and may differ in terms of predator–prey relationships (Berg et al. 1992). For example, pools are less frequent in southern peatlands than in more northern ones, at least in eastern North America (Couillard and Grondin 1986).

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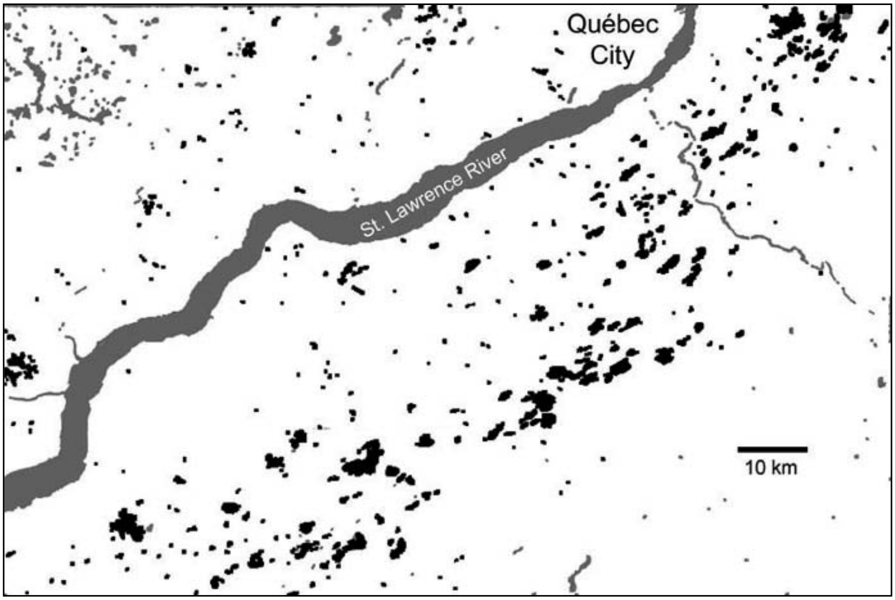

Fig. 5.1. Boreal peatlands (in black) are fragmented habitats in the southern end of their distribution. An example from southern Quebec, Canada

Besides purely latitudinal and climatic effects (Järvinen et al. 1987), the study of peatland fauna must take into account this fragmentation gradient, whereby peatlands form the main matrix of entire landscapes to a set of small, isolated pockets toward the south. Furthermore, the extent of degradation of peatlands due to human activities (drainage, agriculture, forestry, peat extraction, and atmospheric pollution) increases from north to south (Poulin and Pellerin 2001).

In this chapter, we review diversity and distribution patterns of peatland fauna, concentrating on *Sphagnum*-dominated raised bogs. Although there are reports on the wildlife of peatlands in most of the Holarctic region, the focus of this chapter will be northwestern Europe and North America, where our research on peatlands has been conducted. Our focus is birds and aquatic invertebrates – a reflection of our research interests, but partly also of the scientific literature on peatland wildlife. We review both recent and early literature on invertebrates and vertebrates, with an emphasis on conservation. More specifically, we present an overview of species diversity, followed by a more detailed discussion of distribution patterns of particular species or groups in relation to environmental key factors. We close with a presentation of conservation and restoration issues specific to peatland fauna.

5.2 Not One, but Many Wildlife Habitats

Bogs are often regarded as species-poor relative to other habitats, in regard to both vertebrates and invertebrates, either in Europe (Harnisch 1925; Peus 1932; Bölscher 1988) or in North America (Desrochers 2001; Mazerolle et al. 2001). Because of their acidity, extremely low nutrient availability, and wetness, bogs are generally regarded as hostile habitats for many species and some complete taxonomic groups. Chemical deficiencies almost entirely exclude, for example, lumbricid worms, isopods, and snails from acidic bogs (Harnisch 1925; Peus 1932; Speight and Blackith 1983), and low nutrient availability may exclude animal species that have high nutrient demands. Those claims of species poorness may be correct for several taxonomic and functional groups of animals or when these peatlands are compared with heterogeneous upland habitats such as mixed forests. However, the variation in wetness (from open water to relatively dry) and the structural diversity of bog vegetation sometimes makes them more diverse than surrounding habitats (Peus 1932; Stockwell 1994; Schikora 2002a).

While peatlands are often easy to distinguish and delimit from other landscape units, their internal diversity is great and provides a wealth of habitats for a large number of animal species. For example, different bird assemblages are found depending on the amount of forest cover (Kouki et al. 1992), and large open areas of peatlands are typically home to water birds, pipits, and some sparrows, while more generalist species are encountered along peatland edges. Furthermore, factors such as the nutrient availability and acidity – fens vs. bogs (Smits et al. 2002), presence of pools (Poulin et al. 1999), and soil drainage (Mazerolle et al. 2001) have marked effects on amphibians, reptiles, birds, and arthropods alike. On a smaller scale, arthropod communities differ considerably between dry hummocks and wet hollows in raised bogs (Göttlich 1980) or even on a smaller scale in the case of, for example, testate amoebae (Mitchell et al. 2000a, b). This internal diversity of bogs, as well as gradients to the surrounding landscape, provides a suitable environment for species that need different sites to complete their lifecycle, such as carabid beetles inhabiting the open bog plateau, which stay in the top of dry hummocks in winter and in damp *Sphagnum* lawns in summer (Främbs 1994), and golden plover (*Pluvialis apricaria*) and black grouse (*Tetrao tetrix*) breeding in the central raised bog, but foraging in the more nutrient-rich edges of the bog landscape (Niewold 1993, 1996; Heckenroth 1994).

As with other systems, the diversity of microhabitats in a peatland generally increases with its size. This pattern was well illustrated in eastern North America (Fig. 5.2). Because of this, larger peatlands will tend to be more species-rich, as reported in Fennoscandinavia (Hakala 1971; Nilsson

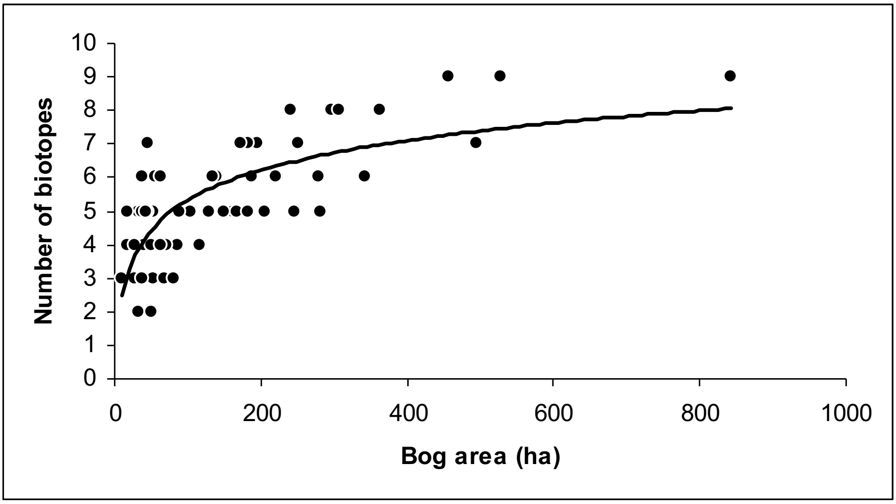

Fig. 5.2. Large eastern North American bogs have more microhabitats (biotopes) than smaller ones (adapted from Calmé and Desrochers 2000)

1986), Maine (Stockwell 1994), and Quebec (Calmé and Desrochers 2000). However, patterns of species diversity vary greatly among taxonomic groups, each of which responds to a particular set of environmental gradients.

5.3 Species Diversity and Distribution

As with other habitats, species diversity patterns in peatlands are shaped by or result from a combination of intrinsic and extrinsic abiotic and biotic factors. The importance of the various factors differs between taxonomic and functional groups of animals, but among the most important intrinsic factors availability of nutrients, vegetation structure, peatland size (see before), and the presence of pools can be regarded as key. However, subtler factors also influence species distributions. Among these are plant species composition (at least the part of it independent from vegetation structure), interspecific relationships like predation and competition, and, finally, intraspecific spacing or attraction.

Additionally, peatland species diversity would be impossible to understand without accounting for landscapes in which peatlands are embedded, especially in more southern regions. In this section, we describe species diversity of peatlands in light of known and likely influences of intrinsic and extrinsic ecological factors.

5.3.1 Invertebrates

5.3.1.1 Species Richness

Although raised bogs are often regarded as species-poor systems, Maavara (1955) found about 800 insect species in Estonian raised bogs and Valk (1988) gave 1,200 insect species, of which 49 are only found in bogs in Estonia. In the study of Maavara (1955) the most species rich taxonomic groups were Coleoptera (244 species found), Lepidoptera (250 species), Diptera (150 species), Rhynchota (103 species), and Hymenoptera (70 species). Continued research will have added many species to these numbers. In the Wagner Natural Area, a boreal spring fen in central Alberta, 2,181 species of arthropods were found, of which 1,410 were Hymenoptera (Finnamore 1994). From the number of parasitoid wasps this fen area is estimated to contain about 6,000 species of arthropods, of which Lepidoptera, Diptera, and Hymenoptera are the most species rich groups. Krogerus (1960) took samples from 38 Fennoscandinavian peatlands – including bogs, poor fens, rich fens, and peaty woods – and found 4,020 insect species and 296 other arthropod species. To these numbers many species from other arthropod and nonarthropod groups, like Cladocerans, Rotifers, and unicellular Rhizopods and Ciliates, can be added. The latter figures largely depend on the taxonomic focus, sampling methods used in the study, and of course on the characteristics of the areas studied, especially their heterogeneity.

According to Maavara (1955) the proportion of characteristic species in raised bogs is quite high, compared with that in other biotopes, showing the high level of specialization of bog fauna, because of the special environmental conditions in raised bogs. On the other hand, most of the species living in bogs, including a number of abundant species, can also live outside bogs (Maavara 1955) or can be characterized as generalists (Danks and Rosenberg 1987; Runtz and Peck 1994). For example, New England bogs and adjacent forests have 22 ant species in common. Two ant species were only found in bogs and 15 species were only collected from forests. In these bogs the ant community is dominated by the generalist species *Dolichoderus pustulatus*, occurring in a variety of open habitats, and the specialist *Myrmica dobifrons*, occurring in boreal bogs and other humid microsites (Gotelli and Ellison 2002). For spiders in northern and central European bogs, 80 % of the species (including the four most dominant species) can be regarded as eurytopic[1] species (Schikora 2002a).

Still, generalist or eurytopic species, even those blown into the bog from the surrounding landscape, are part of the bog community and

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[1] Eurytopic species are species occurring in various types of biotopes.

foodweb (Reynolds 1990). A number of the so called eurytopic species might depend on the combination of the bog *and* the surrounding biotopes to complete their life cycle or for persistence of the population. Valk (1988), for instance, mentions insects coming to raised bogs from outside when plants, especially heather, are flowering. Some of these insects, like the fly *Tephritis* sp., stay for a longer time in the bog, even to hibernate. Other species may depend on the specific conditions in the lagg zone that exist as a result of both the adjacent bog plateau and the adjacent minerotrophic landscape. To understand the importance of peatlands for animal species and the role of the species in the functioning of peatland ecosystems, the functions of the distinguished elements of the peatland ecosystem in the species' lifecycles and relations with (a)biotic processes should be analyzed. The lack of these analyses is mainly due to the large number of species and taxonomic groups, the different stages in the lifecycle, the use of different parts of the landscape by mobile animals, and the complex ecological relations, like foodweb relations and competition (Esselink 2002).

5.3.1.2 Latitudinal Variation and Temperature

When analyzing the effects of environmental factors on peatland fauna communities, factors operating at different scales should be taken into account, as well as the biological traits of the species. At both larger and smaller geographic scales species assemblages of peatlands change from north to south. Koponen (1994, 2002) and Koponen et al. (2001) studied spider assemblages along a geographic gradient in northern Europe and northern America from the arctic or hemiarctic to the hemiboreal or temperate zone and found that about half of the species occur along the whole gradient, few were only found in more northern peatlands, and a larger number of species were only found in more southern peatlands. Also along a shorter gradient in New England, within the relatively small range of 45–42° N, bog ant species richness declines with increasing latitude (Gotelli and Ellison 2002).

An important factor determining the occurrence of species along this north–south gradient is undoubtedly the climate. A species has to be able to grow during summer and survive in winter. Schäfer and Lundström (2001) found a clear pattern in the occurrence of mosquito species in forested wetlands from northern to southern Sweden that could be related to the lifecycles and life stage in wintertime of the respective species. Almost all mosquito species present above the Arctic circle have overwintering eggs and one generation per year (univoltine). In mid and southern Sweden species with more than one generation per year (multivoltine) and species with overwintering larvae or females were abundant. Most probably, only eggs can survive the harsh, long winters in the north and because of short summers not more than one generation can develop. The survival costs of the winter period may explain why the waterstrider *Aquarius najas* is wingless in northern Europe while frequently winged in central and southern Europe. This trend also exists between southern and central Finland (60–62° N). Overwinter survival in laboratory conditions was found to be higher in wingless individuals (Ahlroth et al. 1999).

In the southern range of raised bogs a considerable number of species only occur in raised bogs, whereas they can be regarded as generalist of eurytopic species in the northern range of their distribution area. These species are regarded as glacial relicts in the temperate zone. The temperature regime in raised bogs differs from that in surrounding landscape types by both lower-temperature and higher-temperature extremes, a higher chance of ground frost in summer nights, and a lower mean temperature (Peus 1932; Eggelsman 1980). This is due to the efficient absorption and radiation of long-wavelength radiation by the bog surface, as well as the high water content (Moore and Bellamy 1974). Furthermore, owing to the humic substances the bog water is brownish (dystrophic) and tends to warm up relatively fast, compared with clear water. Relatively high maxima are reached, especially between floating *Sphagnum* (Schmidt 1964). These characteristics make bog pools warm "islands" in a colder environment (Sternberg 1993). This could explain the aberrant habitat preference of the dragonfly species *Anax imperator* in Estonia, the northern range of its distribution area. In Estonia, *Anax imperator* is a thermophilous species, occupying smaller, dystrophic water bodies in raised bogs, presumably as these waters warm up fast (Kalkman et al. 2002).

Temperatures on the surface of hummocks in raised bogs can also reach relatively high temperatures (Norgaard 1951; Schikora 2002a). Norgaard (1951) has shown that two lycosid spider species living in *Sphagnum* bogs differ in their temperature tolerance and found a clear relation between the respective tolerance ranges and the activity of the spiders on, respectively, between the *Sphagnum* capituli as well as the basking behavior. Species occupying raised bogs have to cope with, and can benefit from, both low and high temperatures, either by being in a resistant life stage or by moving to suitable parts in or outside the bog during unsuitable periods of time.

5.3.1.3 Environmental Factors

To identify the most important environmental factors in aquatic invertebrate assemblages within pristine raised bog systems, Smits et al. (2002) compared macroinvertebrate assemblages between the various types of water bodies in the Nigula raised bog system (southwestern Estonia).

Within this bog system, species assemblages were most different between the lagg, on the one hand, and the transitional mires and the more ombrotrophic central bog, on the other hand. This is not surprising, of course, as these elements of the bog system clearly differ in environmental conditions, such as pH, nutrient availability, and vegetation composition and structure. Minerotrophic primary bog lakes also generally differ from more ombrotrophic water bodies. Within the transitional mires, variation in macroinvertebrate assemblages was found, related to variation in the proportions of minerotrophic surface or subsoil water and ombrotrophic water. Water bodies that are only slightly influenced by minerotrophic water resemble the species assemblages of the pools and hollows in the central raised bog. Some species were, however, only found in the transitional mires and were absent from the central bog, like the damselfly species *Coenagrion johanssoni* and the dragonflies *Somatochlora arctica* and *Somatochlora flavomaculata*.

Within the Nigula bog, a complex pattern of water flow is present, and as a consequence so is variation in aquatic macroinvertebrate assemblages. In the bog, springs of acidic water are present, giving rise to a water flow through small brooks and a series of pools are influenced by this flow, each to a different extent. The water bodies that are, at least for some part of the year, connected to the bog brooklets or the more diffuse water flow, being a continuation of the brook, have several species in common with the most ombrotrophic sites. They are, however, also inhabited by some species mainly occurring in more minerotrophic or nutrient-rich water bodies, as in transitional mires or outside raised bog systems. Some of the central bog pools are not connected to this water flow, but still show similarity in species assemblage with the connected ones. This is probably due to the presence of subsurface water flows or the presence of fen peat at the pool bottom, resulting in a higher decomposition of the peat, a higher nutrient availability, and probably a higher microbial activity. A higher availability of nutrients in the flowing brooklet and some connected pools was apparent from the presence of filamentous algae in spring. Apart from the lagg, herbivorous water beetles in the central raised bog were only found in these water bodies with algae. The mayfly species *Leptophlebia vespertina* was observed emerging in highest numbers from the bog pools with slightly higher nutrient availability and only in these pools were the phytophagous larvae of the cranefly species *Phalacrocera replicata* (Cylindrotomidae) found (Smits et al. 2002).

Apart from availability of food in a proper quality and quantity, vegetation structure, volume of open water, and permanence are important factors in the occurrence of aquatic macroinvertebrate species (Macan 1954; Crisp and Heal 1996; Smits et al. 2002; van Duinen et al. 2004a). Several species, for example, the water beetle *Laccophilus poecilus* and the bug *Cymatia bonsdorffi*, were found only in central bog pools with open water, whereas other species, like the typical nonbiting midge *Lasiodiamesa* sp., were only found between fairly dense *Sphagnum* percolated by slightly minerotrophic water.

For most terrestrial invertebrate groups the species assemblage differs between the bog plateau and the lagg zone, as just described for aquatic invertebrates. Väisänen (1992) found the highest species richness of diurnal Lepidoptera in the lagg zone of a Finnish raised bog. For these herbivores the availability of host plants having a sufficient nutritional value is an important factor for both larvae and adults. Also for the (semi)terrestrial species in the bog system nutrient availability, acidity, and vegetation structure are important factors. According to Schikora (2002a) light situation and vegetation structure are the most important factors in the spatial distribution of spiders in bog complexes and moisture can be of general importance. For the carnivorous carabid beetles the availability of prey (e.g., springtails) and the presence of dry hummocks for overwintering are important, according to Främbs (1994). The presence of dry overwintering sites is important for all (semi)terrestrial invertebrates living in peatlands with a fluctuating water table, unless they have a resistant life stage in wintertime.

To understand causal relations behind the observed patterns in species assemblages and how species cope with the conditions in raised bogs, research has to be focussed on the "match" between, on the one hand, species traits, like locomotion, home range, growth rate, and feeding guilds, and on the other hand traits of their environment, including structures and processes, like decomposition and bioproduction (Verberk et al. 2005). This research should also take into account the effects of competition and predation. An unknown number of the characteristic aquatic and terrestrial bog invertebrates are potentially able to live outside bogs, as well, but might be excluded from other types of landscapes, because they are poor competitors. For these species the absence, low abundance, or poor performance of competitor and predator species in bogs will be an important factor.

5.3.2 Amphibians and Reptiles

Owing to their acidity, raised bogs are not normally the first habitat to come to mind when one thinks about an amphibian habitat. Indeed, amphibians are highly vulnerable to the biogeochemistry of their habitat because of the osmotic exchanges through their skin, and acidity is often considered as harmful to their development (Pough 1976; Leuven et al. 1986). However, in recent years, there has been growing evidence of amphibians not only occurring in peatlands, but also occasionally breeding in associated pools, as evidenced by tadpoles (Mazerolle and Cormier 2003).

Species commonly found in boreal peatlands of North America include generalists such as the wood frog (*Rana sylvatica*), American toad (*Bufo americanus*), northern spring peeper (*Pseudacris crucifer*), green frog (*R. clamitans*), leopard frog (*R. pipiens*), and red-backed salamander (*Plethodon cinereus*). Less common North American species include eastern gray tree frog (*Hyla versicolor*), western chorus frog (*Pseudacris triseriata*), and mink frog (*R. septentrionalis*). Four-toed salamanders (*Hemidactylium scutatum*) are reputed to occur in peatlands, for they are closely associated with mosses, particularly *Sphagnum* (Wood 1955); however, intensive surveys done recently in bogs in their eastern North American range have resulted in no reports of the species (Mazerolle 2003), despite their regional occurrence (Bider and Matte 1994).

Amphibians have complex life cycles (Wilbur 1980), which may lead them to use peatlands as part of larger sets of habitats during their lifetime (Mazerolle 2001). It has been hypothesized that amphibians retreat to peatlands as summers advance, because other wetlands may disappear following desiccation. However, one study based on capture rates across drift fences on peatland edges found no evidence of net movement toward or from peatlands (Mazerolle, personal communication). Within a peatland, pools are clearly an important asset for amphibians. Despite their low pH, peatland pools harbor a rich invertebrate life (see before) and may thus provide an important feeding habitat for frogs (e.g., mosquito and mayfly larvae) and salamanders, at least in certain periods of their life cycle. Pool size and proximity to areas cut over by the peat industry do influence the probability of occurrence of species such as the green frog (Mazerolle and Cormier 2003).

Unlike amphibians, reptiles are seldom encountered in boreal peatlands. In northern Europe, the common lizard (*Lacerta vivipara*) and common viper (*Vipera berus*) are frequently seen in peatlands, and are able to survive and reproduce, according to sightings of pregnant females and juveniles (H. Strijbosch, unpublished data). However, frogs and toads are rarely observed in Estonian raised bogs. Our surveys in eastern Canadian peatlands have on a few occasions produced garter and green snakes (Rochefort, personal communication). However, we are aware of no quantitative data on bog reptiles.

5.3.3 Birds

Detailed knowledge of peatland birds in North America is a recent phenomenon. However, Fennoscandinavia has been the stage for quantitative work on peatland birds since as early as the 1950s (reviewed in Desrochers 2001). In North America, most of the information on peatland birds comes from Minnesota, Maine, Michigan, and eastern Canada, leaving much to be learned about birds of northern peatland landscapes. The pioneering work by Erskine (1977) provides a notable exception.

5.3.3.1 Avian Diversity Patterns

No bird species are found exclusively in peatlands, either North American or Eurasian ones. Peatlands are home to well over 100 bird species and several families of birds in western Europe and North America. Yet, only mallard and northern harrier (for scientific names not mentioned in the main text, see Table 5.1) are commonly found both in North American and Fennoscandinavian peatlands (Table 5.1). Surveys of breeding birds by Desrochers and colleagues in 120 eastern Canadian bogs from 1993 to 2002 yielded 10,575 birds in point counts, the majority of which belonged to four species. Those species are (in decreasing order) common yellowthroat, white-throated sparrow, Lincoln's sparrow, and savannah sparrow.

As in other habitats, some bird species are very abundant, while most species are only found there occasionally. Certain peatlands in the south can harbor a large avian diversity, for example, 81 species reported by Stockwell (1994) in Maine. It would be tempting to explain the increase of avian diversity in peatlands from north to south (Boström and Nilsson 1983; Desrochers 2001) by the location of the northern limit of species ranges in latitudes where peatlands are found. However, this applies only to a few species and therefore the latitudinal gradient begs another explanation. Besides diversity, species composition varies greatly among regions, with land birds predominant in North American peatlands, and water birds predominant in Eurasian peatlands (Fig. 5.3). The most likely explanations for such contrast are the presence of a latitudinal gradient in the abundance of pools (larger in the north), as well as the greater inputs from surrounding habitats in the south, where peatlands tend to be smaller and more isolated. Despite the north–south gradient of bird diversity, enough species are retained in this latitudinal gradient to confer a contrasting, boreal fauna relative to that found in surrounding landscapes (Calmé et al. 2002). As a result, peatlands are often the most southern locations for certain species, such as palm warbler (Stockwell 1994).

Outside the breeding season, however, avian diversity patterns change drastically. In both North America and Europe (and undoubtedly Asia), peatlands often represent important staging areas for migrants, mostly shorebirds such as snipes and pectoral sandpipers (*Calidris melanotos*), but also ducks and geese that use the pools as staging stops. In winter, a very small number of birds can be found in peatlands, with grouse, for example, sharp-tailed grouse (*Tympanuchus phasianellus*) in North America, red grouse (*Lagopus scoticus*) in the UK, and black grouse in

Table 5.1. Bird species commonly found in North American peatlands have little in common with those found Fennoscandinavian peatlands

Species	Quebec	Michigan	Finland	Sweden	Germany	Western Russia
Horned grebe (*Podiceps auritus*)						x
Red-throated loon (*Gavia stellata*)				x		x
Bean goose (*Anser fabalis*)						x
Eurasian wigeon (*Anas penelope*)						x
Common teal (*Anas crecca*)				x	x	x
Mallard (*Anas platyrhynchos*)		x	x	x	x	x
Black duck (*Anas rubripes*)	x					x
Pintail (*Anas acuta*)						x
Northern shoveler (*Anas clypeata*)						x
Tufted duck (*Aythya fuligula*)					x	x
Common goldeneye (*Bucephala clangula*)				x		x
Osprey (*Pandion haliaeetus*)				x		
Northern harrier (*Circus cyaneus*)	x	x	x			
Peregrine falcon (*Falco peregrinus*)			x			x
Willow ptarmigan (*Lagopus lagopus*)			x			
Common crane (*Grus grus*)			x	x		x
Common snipe (*Gallinago gallinago*)				x	x	
Wilson's snipe (*Gallinago delicata*)			x			
European jacksnipe (*Lymnocryptes minimus*)			x			
Black-tailed godwit (*Limosa limosa*)					x	
Whimbrel (*Numenius phaeopus*)			x	x		x
Eurasian curlew (*N. arquata*)			x	x	x	x
Common redshank (*Tringa totanus*)				x	x	
Common greenshank (*Tringa nebularia*)			x			x
Green sandpiper (*Tringa ochropus*)				x		
Wood sandpiper (*Tringa glareola*)			x	x		x
Broad-billed sandpiper (*Limicola falcinellus*)			x			
Eurasian golden plover (*Pluvialis apricaria*)			x	x	x	x
Northern lapwing (*Vanellus vanellus*)			x	x	x	x

Common gull (*Larus canus*)			x	x	x	
Herring gull (*Larus argentatus*)			x			x
Lesser black-backed gull (*Larus fuscus*)						x
Black-headed gull (*Larus ridibundus*)			x	x		x
Common tern (*Sterna hirundo*)						x
Mourning dove (*Zenaida macroura*)		x				
Common cuckoo (*Cuculus canorus*)				x	x	
Short-eared owl (*Asio flammeus*)			x			
Whip-poor-will (*Caprimulgus vociferus*)		x				
Ruby-throated hummingbird (*Archilochus colubris*)		x				
Northern flicker (*Colaptes auratus*)		x				
Alder flycatcher (*Empidonax alnorum*)[a]	x	x				
Eastern kingbird (*Tyrannus tyrannus*)	x					
Red-backed shrike (*Lanius collurio*)				x		
Northern shrike (*Lanius excubitor*)			x	x		
Blue jay (*Cyanocitta cristata*)	x					
American crow (*Corvus brachyrhynchos*)	x					
Cedar waxwing (*Bombycilla cedrorum*)	x	x				
Eastern bluebird (*Sialia sialis*)		x				
Veery (*Catharus fuscescens*)		x				
Hermit thrush (*Catharus guttatus*)	x					
American robin (*Turdus migratorius*)	x	x				
Whinchat (*Saxicola rubetra*)			x	x	x	
Stonechat (*Saxicola torquata*)					x	
Gray catbird (*Dumetella carolinensis*)		x				
Brown thrasher (*Toxostoma rufum*)		x				
Black-capped chickadee (*Poecile atricapillus*)		x				
Tree swallow (*Tachycineta bicolor*)		x				
Ruby-crowned kinglet (*Regulus calendula*)[a]	x					
Grasshopper warbler (*Locustella naevia*)					x	
Yellow warbler (*Dendroica petechia*)		x				
Skylark (*Alauda arvensis*)			x	x	x	x

Table 5.1. (*Continued*)

Species	Quebec	Michigan	Finland	Sweden	Germany	Western Russia
Pied wagtail (*Motacilla alba*)			x	x		
Yellow wagtail (*Motacilla flava*)			x	x	x	
Tree pipit (*Anthus trivialis*)			x		x	
Meadow pipit (*Anthus pratensis*)			x	x	x	
American goldfinch (*Carduelis tristis*)	x	x				
Linnet (*Carduelis cannabina*)					x	
Purple finch (*Carpodacus purpureus*)[a]						
Yellowhammer (*Emberiza citrinella*)			x			
Reed bunting (*Emberiza schoeniclus*)			x	x	x	
Song sparrow (*Melospiza melodia*)	x	x				
Lincoln's sparrow (*Melospiza lincolnii*)[a]	x					
Swamp sparrow (*Melospiza georgiana*)	x					
White-throated sparrow (*Zonotrichia albicollis*)[a]	x					
Savannah sparrow (*Passerculus sandwichensis*)[a]	x					
Field sparrow (*Spizella pusilla*)		x				
Eastern towhee (*Pipilo erythrophthalmus*)		x				
Tennessee warbler (*Vermivora peregrina*)	x					
Nashville warbler (*Vermivora ruficapilla*)	x	x				
Magnolia warbler (*Dendroica magnolia*)[a]	x					
Yellow-rumped warbler (*Dendroica coronata*)[a]	x					
Palm warbler (*Dendroica palmarum*)[a]	x					
Common yellowthroat (*Geothlypis trichas*)	x	x				
Northern cardinal (*Cardinalis cardinalis*)		x				
Common grackle (*Quiscalus quiscula*)	x					
Brown-headed cowbird (*Molothrus ater*)	x	x				

Data for Quebec from Calmé et al. (2002), for Michigan from Brewer (1967), for Finland from Hakala (1971) and Järvinen and Sammalisto (1976), for Sweden from Boström and Nilsson (1983), for Germany from Bölscher (1995), and for western Russia from Häyrinen (1986). Species sorted according to Monroe and Sibley (1993)

Crosses denote species found in the majority of years or field sites.

[a] Species marked with an *asterisk* are of high conservation concern in Canada (Dunn et al. 1999).

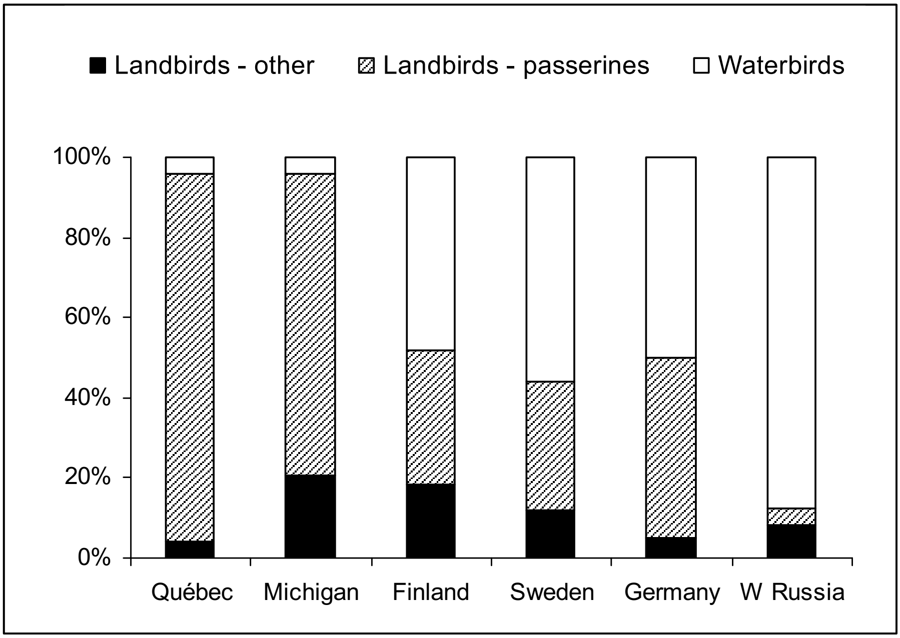

Fig. 5.3. Avian species groups in peatlands of six geographic regions (see Table 5.1 for data sources)

Fennoscandinavia, being among the most notable species. Snow buntings can also be seen in most northern peatlands in winter. In regions under milder winter conditions, such as the UK, geese also widely use peatland pools.

Avian diversity is somewhat greater in North American peatlands than in Fennoscandinavian ones. On the basis of the published literature, the main contrast between Eurasian and North American peatlands in regard to birds would appear to be the preeminence of shorebirds in Eurasian peatlands (Hakala 1971; Väisänen and Järvinen 1977), as opposed to North American peatlands, in which songbirds usually dominate (Calmé et al. 2002). While most species of shorebirds of western Europe are commonly found in peatlands, the only shorebirds to be found regularly in southern peatlands of North America are Wilson's snipe (*Gallinago delicata*) and upland sandpiper (*Bartramia longicauda*). However, peatlands of northern North America do have a more complete assemblage of shorebirds (Morneau 1995), and it is likely that most differences in peatland bird communities between western Europe and North America come about from a purely latitudinal effect, with water birds dominant north of 60° N and songbirds to the south.

5.3.3.2 The Role of Vegetation Structure

While vegetation structure in open peatlands of both continents is somewhat similar, i.e., large expanses of ericaceous shrubs with clumps of conifers, important differences exist, particularly in composition of tree species. In North America, black spruce and tamarack are the main tree species, as opposed to pine *Pinus sylvestris* in Fennoscandinavian peatlands (Chap. 2).

As with other wildlife groups, birds are highly responsive to vegetation structure. From large open areas found deep inside large peatlands to forested areas in their periphery, bird assemblages change almost completely, and it is the wetter and more open areas of peatlands that harbor most peatland specialists. Interestingly, Niemi (1985) found evidence for evolutionary convergence between North American (Minnesota) and Finnish granivorous and insectivorous birds of peatlands. For example, birds found in shrubby habitats are relatively small, with long legs and small flight muscles, compared with species more typically found in forested peatlands.

Vegetation patterns may explain why distributions of bird species in peatlands are nested subsets, i.e., most of the time, all species in a species-poor peatland will be found in peatlands with a larger number of species. In their southern Quebec study area, Calmé and Desrochers (1999) showed that in 67 peatlands whose bird assemblages were measured intensively five bird species were found exclusively in peatlands in the upper 30th percentile range of sizes. Those species were Wilson's snipe, upland sandpiper, American bittern (*Botaurus lentiginosus*), clay-colored sparrow (*Spizella pallida*), and field sparrow. Those species were not typical of peatlands, but rather of large open or biologically-productive areas, such as fen laggs that appear more frequent in Quebec's larger peatlands (Calmé and Desrochers 1999). Nested subsets are not unique to peatlands, but pertain to a wide variety of systems (Glenn and Nudds 1989; Blake 1991; Cutler 1991; Patterson and Brown 1991; McCoy and Mushinsky 1994; Bert 2001; Fernández-Juricic 2002).

5.3.3.3 Landscape and Spatial Issues

While small-scale differences in vegetation patterns may explain distribution patterns of peatland species, larger-scale (landscape) factors also play an important role. In southern Quebec, Calmé and others (Calmé and Haddad 1996; Calmé and Desrochers 2000) demonstrated the importance of peatland area and isolation in explaining species occurrence patterns. Isolation per se may appear as an unlikely cause for bird distribution patterns, given the high vagility of these organisms. However, despite their ability to migrate over large distances, birds are apparently inhibited in their movements during the dispersal periods by small intervening gaps between their habitat patches (Desrochers and Hannon 1997).

Landscape and spatial issues are further complicated by the fact that bird territory sizes can easily vary by 1 or 2 orders of magnitude (0.1–10.0 ha), with obvious consequences for their space needs. Furthermore, recent work on conspecific attraction (Etterson 2003; Green and Ostling 2003; Wagner and Danchin 2003) suggests that species "real-estate" needs may be much larger than expected solely from the size of individual territories. Work by Hokkanen (2004) in the Siikaneva peatland, Finland, supports the conspecific attraction hypothesis (Fig. 5.4).

Vegetation structure generally follows predictable trends from the edge toward the center, especially in large peatlands (Poulin et al. 1999). Thus, because of their association with vegetation structure (see before), bird assemblages are expected to change predictably along the same gradient. The latter prediction has been supported with Finnish peatlands, with yellow wagtails and whinchats associated with peatland edges, in contrast to meadow pipits and wood sandpipers (Sammalisto 1957; Hakala 1971). In

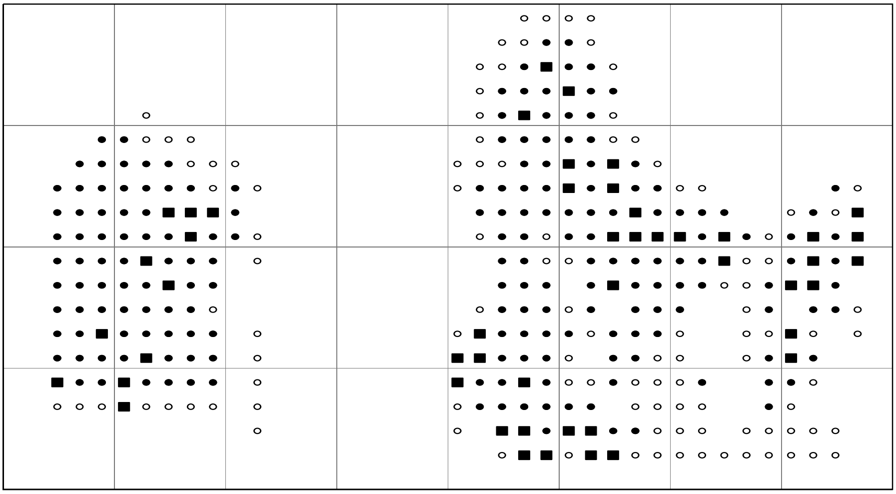

Fig. 5.4. Clumped distribution of meadow pipits and their habitat in Siikaneva Peatland, Finland. *Open circles* peatland outside vegetation parameters suitable for pipits, *closed circles* peatland with suitable vegetation for pipits, *squares* areas used by pipits. Spatial autocorrelation of occurrence within habitat, measured by Moran's I, was significantly positive with distance lags less than 200 m. Grid squares = 1 km × 1 km. (Data courtesy of Reijo Hokkanen, University of Helsinki)

Table 5.2. Population densities of breeding songbirds in eastern Canadian bogs (adapted from Delage et al. 2000)

	Interior		Edge	
Song sparrow	0.45	(0.45)	0.76	(0.55)
White-throated sparrow	0.74	(0.42)	2.39	(1.21)
Lincoln's sparrow	3.99[a]	(1.27)	2.94	(0.93)
Savannah sparrow	3.66[a]	(1.4)	1.30	(0.65)
Hermit thrush	1.26	(1.07)	0.99	(0.68)
Yellow-rumped warbler	0.00	–	0.45	(0.45)
Palm warbler	2.27	(0.88)	4.32[a]	(1.40)
Nashville warbler	0.00	–	0.86	(0.59)
Common yellowthroat	3.88	(1.42)	12.44[a]	(2.69)
Magnolia warbler	0.00	–	0.39	(0.28)

The numbers are pairs per 10 ha, followed by standard errors of the mean (n=20 peatlands).
[a] Associations

eastern Canada, savannah and Lincoln's sparrows are associated with the interior of large peatlands, whereas palm warblers and common yellowthroats are found disproportionately along peatland–forest edges (Table 5.2). Hakala (1971) noted that the degree to which species were associated with edges was itself associated with species' propensity to use pools or isolated trees. Besides vegetation structure, potentially lower exposure to upland predators may lead some species of birds to breed in wet and open, central parts of bogs (Berg et al. 1992).

5.3.4 Mammals

North American boreal peatlands are home to a variety of rodents, such as lemmings (*Synaptomys* sp.), shrews (*Sorex* sp.), and voles (*Clethrionomys* sp., *Microtus* sp.), as well as moose (*Alces alces*), lynx (*Lynx* sp.), black bear (*Ursus americanus*), and (in winter) deer (*Odocoileus virginianus*). In Europe, peatlands are used frequently by elk (*Cervus elaphus*), wolf (*Canis lupus*), fox (*Vulpes vulpes*), beaver (*Castor fiber*), river otter (*Lutra lutra*), muskrat (*Ondatra zibethica*), raccoon dog (*Nyctereutes procyonoides*), badger (*Meles meles*), pine marten (*Martes martes*), polecat (*Mustela putorius*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*). Most of the latter species are absent from central ombrotrophic parts of peatlands. In fact, beaver, otter, muskrat, raccoon dog, badger, marten, and wild boar likely occur only on the edges of bogs.

While large mammals are sometimes found in peatlands, the bulk of species and populations are composed of small species. Mazerolle et al. (2001) found that five species accounted for 91 % of all captures of small mammals made in eastern Canadian bogs: masked shrew (*Sorex cinereus*), meadow jumping mouse (*Sorex cinereus*), meadow vole (*Microtus pennsylvanicus*), pygmy shrew (*Sorex minutus*), and Arctic shrew (*Sorex arcticus*). Remarkably, the latter set of species include only one species known as bog specialists (Arctic shrew). Other bog specialists such as northern bog lemming (*Synaptomys borealis*) and southern bog lemming (*Synaptomys cooper*; Banfield 1977; Nordquist 1992) were not found in the surveys made by Mazerolle et al. (2001), despite the large sampling effort. The use of peatlands by small mammals appears highly dependent on soil moisture (Mazerolle et al. 2001). Drier sites seem to host more species than wet sites, and mostly generalists are also abundant in surrounding areas. Thus, peatland edges are expected to have a richer mammalian fauna than areas located well inside peatlands. However, the interior of peatlands may be of greater relative importance to peatland specialists such as the masked shrew, but that remains unsupported by data. Of 15 small-mammal species encountered in eastern Canadian bogs, only two are known to exhibit a preference for bogs: the Arctic shrew and the southern bog lemming (Mazerolle et al. 2001)

5.4 Conservation Issues

Our knowledge of population trends of most faunal taxa, let alone their demographic dependency on peatlands, is little. Birds are arguably the best monitored faunal taxon in that respect. From the North American Breeding Bird Survey (Sauer et al. 2003), we know that among the 20 most common bird species found in eastern North American peatlands, none have experienced severe declines since the early 1960s. However, nine common peatland birds have their geographic range primarily in peatland-rich Canada (Dunn et al. 1999; flagged species in Table 5.1). Peatlands in northern Canada may be essential to maintain large numbers of the latter nine species. Further south, peatlands may help maintain regionally uncommon species such as upland sandpiper and palm warbler in North America, or golden plover, common crane, black grouse and several dragonfly and butterfly species in parts of western Europe. For many of these species the conservation of only the central ombrotrophic parts of peatlands will not suffice to maintain or restore their populations, as they need gradients to the more minerotrophic parts of the bog landscape as well at least in part of their lifecycle (Heckenroth 1994).

The conservation of peatland fauna is probably not a pressing issue yet as far as global populations are concerned. However, peatland fauna is under pressure at the regional and local levels, particularly in populated areas, and there is associated pressure on land for urban sprawl, agriculture, forestry, or peat-extraction purposes. In fact, the majority of peatlands have disappeared in most of Europe as a result of these activities, while sizeable portions of this habitat remain untouched in North America (Joosten and Clarke 2002). Nutrient enrichment of originally nutrient-poor peatlands, owing to increased atmospheric nitrogen deposition, has affected plant and animal communities (Limpens et al. 2003, Chap. 10; Tomassen et al. 2004; van Duinen et al. 2004b, 2006a).

5.4.1 Urban Sprawl

Urbanization generally has an irreversible impact on peatlands, bringing profound and lasting changes in wildlife communities. From the standpoints of habitat and species conservation, the conversion of peatlands by urban sprawl is clearly a net loss and does not require much ecological analysis, apart from the fact that those losses are particularly important for southern temperate areas, because of their proximity to towns. The loss of peatlands through urban sprawl therefore adds to the vulnerability of species dependent on wetlands which reach their northern range limit in the southernmost peatland regions. If we take into account the high species diversity of vertebrates and, especially, invertebrates in peatlands (see previous sections), there is clearly a case for conservation of peatlands near populated areas, as part of larger wetland conservation strategies. Additionally, most states of North America and western Europe do have plans for conserving regional biodiversity and wetlands in particular (e.g., Ramsar convention).

5.4.2 Agriculture and Forestry

Peatland losses through agriculture and forestry, especially in western Europe, have clearly contributed to endangering peatland species (Chap. 16). It can be argued that replacement habitats such as pastures and crops in Europe have been hosting wildlife communities for decades, if not centuries. However, today, the role of agricultural land as viable replacement habitats is increasingly questionable because of recent changes in agricultural practices, fueled by subsidies that have simplified those ecosystems and led to the decline of flagship bird species such as skylark and barn swallow (*Hirundo rustica*; Gregory et al. 2003).

Converting peatlands into agricultural land generally has irreversible effects on the land, its vegetation, and its associated fauna (Poulin and Pellerin 2001). In continental Europe, and to some extent in the UK, agriculture has been responsible for large peatland losses (Joosten and Clarke 2002; Gregory et al. 2003). Forestry practices also have implications for peatland fauna. The most important of those is drainage of forested peatlands, which owes its existence to the fact that water-logged soils of forests on peat are improper for tree growth (Päivänen 1999). To what extent forest drainage per se affects birds and medium-to-large mammals is unclear, and remains little studied to date. Clearly, vegetation changes through drainage will affect the nesting habitat for birds, especially those nesting on the ground, such as most game species. Drainage may also change food (browse) availability for large mammals. Unlike most birds and medium-to-large mammals, small mammals and amphibians should be significantly affected by forest drainage (Mazerolle 2001). Unlike agricultural practices, changes to peatlands brought by forestry drainage may have the potential to be reversed in part, by restoring a high water table if drainage channels are blocked, although we know of no studies demonstrating such a reversal.

One major northern forestry practice, clear cutting, has an additional, intriguing impact on wildlife. Clear cutting is obviously not designed to create a wildlife habitat, but ironically, by raising the water table and opening the vegetation cover, it has the potential to attract animal species typical of peatlands. For example, in eastern North America, birds such as Lincoln's sparrow and palm warbler will often invade clear-cuts during the period in which vegetation structure is open. But, whether clear-cuts constitute high-quality or suboptimal habitats remain unknown, because of the lack of data on reproduction.

5.4.3 Nutrient Enrichment

Owing to agriculture and industry, the atmospheric deposition of nitrogen, sulfur, and phosphorus has increased in the southern range of originally extremely nutrient poor bogs. In northwestern European raised bogs the increased nutrient deposition has resulted in the invasion of birch (*Betula* spp.) and purple moor grass (*Molinia caerulea*). These effects have been reported from several European countries (Risager 1998; Limpens et al. 2003; Tomassen et al. 2004). These changes in the vegetation composition and its structure affect the faunal species assemblages, for example, ground-breeding birds, because of their frequent reliance on ground vegetation for nest-site selection (Larison et al. 2001). The increased nutrient availability has resulted in an increase of the nutrient content of plant material. This will have consequences for the herbivorous and detritivorous invertebrates that eat this material, but also species at higher trophic levels, such as carnivorous aquatic beetles (Dytiscidae), are affected (van Duinen et al. 2004b).

A comparative study on aquatic oligochaetes, dragonflies, chironomids, bugs, and beetles between pristine raised bogs in Estonia (low deposition level) and degraded and rewetted raised bog remnants in the Netherlands (high deposition level) showed clear differences in the species assemblages. Compared with pristine ombrotrophic sites (central raised bog), the relative abundance of species preferring ombrotrophic conditions is generally low in both the degraded and the rewetted bog sites in the Netherlands (Fig. 5.5). The species assemblages in Dutch bogs are dominated by species that in Estonian bogs prefer the transitional mire or lagg that naturally have

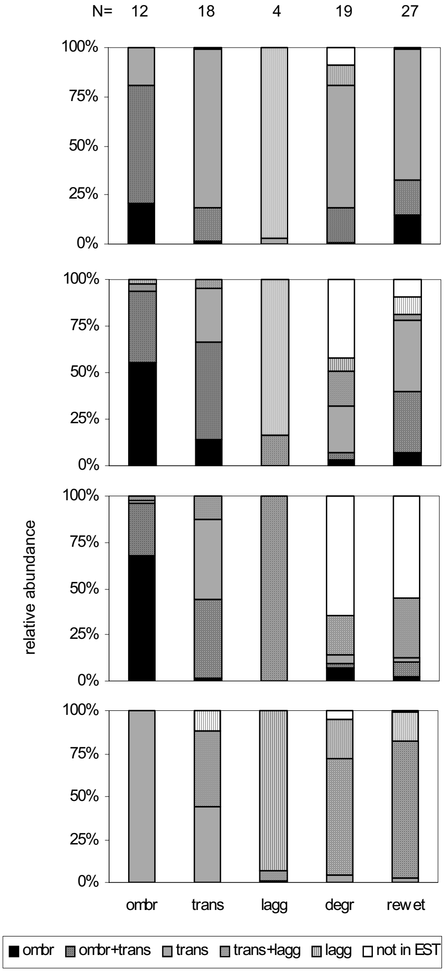

Fig. 5.5. Relative abundance of six groups of (from *top* to *bottom*) Chironomidae, Coleoptera, Hemiptera, and Oligochaeta species. The species are attributed to these groups based on their preference for the ombrotrophic bog, transitional mire, and lagg in the pristine Estonian bogs. Sampling sites are grouped into ombrotrophic water bodies, water bodies in transitional mires, and laggs in pristine raised bogs and water bodies in degraded and rewetted bogs. (From van Duinen et al. 2004b)

higher nutrient availability (van Duinen et al. 2004b). Regarding the oligochaetes, in the Estonian ombrotrophic water bodies only the enchytraeid *Cognettia sphagnetorum* was found. In both degraded and rewetted sites in the Netherlands *Cognettia sphagnetorum* is always accompanied by *Nais variabilis*, whose occurrence in Estonian bogs is limited to the lagg and transitional mire (van Duinen et al. 2006a). For dragonflies the same type of changes in species assemblage was found. In Estonian bogs, *Leucorrhinia dubia* is the most abundant dragonfly larva in spring in the ombrotrophic sites, whereas larvae of *Leucorrhinia rubicunda* are only found in transitional mires. In the Netherlands, however, *Leucorrhinia rubicunda* is the most abundant species found in spring in both degraded and rewetted sites, whereas *Leucorrhinia dubia* is fairly rare. These shifts in species dominance were found for bugs, beetles, and chironomids as well (van Duinen et al. 2004b). To understand the mechanisms behind these shifts, differences in species traits and demands have to be elucidated. Structural aspects of the biotopes might be involved, but many of these shifts are likely related to nutritional requirements of the species involved. Species ability to build up biomass using decomposing organic matter, bacteria, fungi, algae, or microinvertebrates with a low nutrient content (Elser et al. 2000) will play an important role in the species composition of the macroinvertebrate assemblage.

5.4.4 Peat Harvest

The effects of peat harvesting on peatland fauna depend on the manner in which the peat is extracted. In western Europe, the first peat harvesting activities were small scale and started in small peatlands and on the edges of larger peatlands. Large-scale industrial peat harvesting leaves hardly any room for animals. As a consequence of the disappearance of the various habitats of pristine peatlands (first laggs and edges of bogs, later more central bog ecotopes) a number of characteristic faunal species have declined or disappeared. In degraded bogs, characteristic species can still be present, but the species dominant in natural bogs have declined and other species have increased, as has been shown for spiders (Koponen 1979), carabid beetles (Främbs 1990), and aquatic macroinvertebrates (van Duinen et al. 2003b, 2004b), for example. Human activities have also resulted in new habitats within the mire landscape. Dehydration and mineralization of peat and the inlet of minerotrophic or nutrient-rich water have changed water and soil qualities (Lamers 2001), water tables, and vegetation composition and structure. As a result, species that do not occur under ombrotrophic (i.e., acidic, nutrient-poor) conditions were able to establish themselves in bog remnants (Göttlich 1980; Wheeler and Shaw 1995; Irmler et al. 1998). For some of these species, the original habitats have been degraded or have disappeared as a result of cultivation, making remaining peatland areas nowadays a refugium for species that were originally not dependent on peatlands (Akkermann 1982). Changes within peatlands may also translate into intraspecific patterns. Mazerolle (2001) found that near drainage for peat mining, leopard frogs were larger than individuals occurring in undisturbed peatlands. He suggested that this size difference resulted from the higher resistance of larger animals to desiccation, although he could not rule out the possibility that growth near drained areas was promoted by a greater abundance of food.

Certain bird species seem particularly affected by peat harvesting. Palm warblers have never been observed in sites previously harvested, either by block cutting or vacuum, even after 15 years. By contrast, generalist bird species do invade postharvest peatlands, such as mourning dove, American goldfinch and killdeer (*Charadrius vociferus*), in North America. However, a study by Haddad et al. (2000) suggested that nest predation is much greater in remaining natural parts of five harvested peatlands, compared with nine unharvested peatlands of Quebec (63 vs. 8 % of nests). However, nest predation risk was not associated with actual proximity of harvest operations, nor with distance to peatland edge. The results by Haddad et al. (2000) are in accordance with those of Berg et al. (1992) in Swedish peatlands. The latter two studies were based on artificial nests with quail (*Coturnix* sp.) eggs and may only provide a coarse assessment of true nest predation (Faaborg 2004).

5.4.5 Peatland Restoration

The effects of peat extraction may be reversed at least in part through ecological restoration. Peatland restoration has proven successful at reestablishing a cover of *Sphagnum* mosses in several cases in Canada (Lavoie and Rochefort 1996) and Europe (Smolders et al. 2003; Chap. 17). The return of associated fauna remains uncertain, both for invertebrates (Mossakowski and Främbs 2003; van Duinen et al. 2003b) and for birds (Bölscher 1995; Desrochers et al. 1998). As opposed to vacuum-harvested sites, peatlands exploited through labor-intensive cutting of peat blocks tend to be recolonized rapidly (less than 20 years) by plant (Smart et al. 1989) and bird (Desrochers et al. 1998) species typical of untouched peatlands. However, for aquatic macroinvertebrates, like midges, beetles, and caddisflies, large-scale rewetting projects in bog remnants with either abandoned hand peat cuttings or industrial harvested peat fields all resulted in a fairly similar species assemblage (van Duinen et al. 2003b), including only a part of the species spectrum of a pristine raised bog (van Duinen et al. 2002). Compared with rewetted bog remnants, water bodies in bog remnants that had not been rewetted, like water-filled hand peat

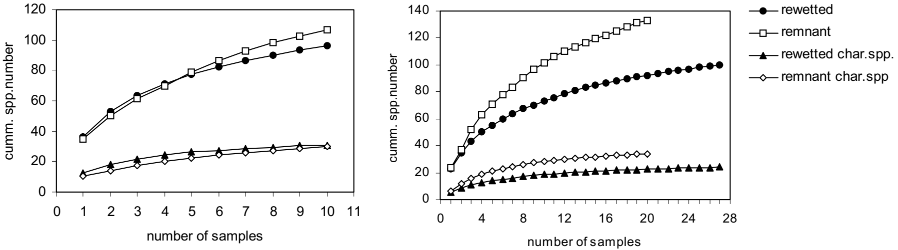

Fig. 5.6. Cumulative species richness curves for all species and for characteristic species of microinvertebrates (*left*) and macroinvertebrates (*right*) in rewetted and not rewetted remnant sites in Dutch bog reserves. The *curves* are composed of averages of 250 random sorts of the sampling sites. (From van Duinen et al. 2003b and van Duinen et al. 2006b)

cuttings and trenches, have a relatively high cumulative species richness, including a considerable number of characteristic macroinvertebrate species, that are not found in rewetted sites (Fig. 5.6). No relation was found between the success of restoration in terms of vegetation development and the number of characteristic macroinvertebrate species. So far, rewetting measures in Dutch raised bog remnants have resulted in a habitat for a limited number of faunal species, including only part of the characteristic raised bog species. Currently, a considerable number of characteristic and rare species are still dependent on bog remnants that have not been rewetted and that have been degraded by small-scale block peat cutting for their survival in raised bog areas, and in the Netherlands as a whole (van Duinen et al. 2003b).

It is unclear whether the return of animal species in restored areas will be complete in the long term. A prerequisite for the establishment of a more complete species spectrum is the conservation and restoration of the heterogeneity in environmental conditions, because different animal species have different demands and many species need a combination of conditions (Verberk et al. 2006), as described in previous paragraphs. Furthermore, species should be able to reach the restored sites. Dispersal ability of the species as well as the proximity of source populations (in remaining, unharvested, peatlands) play important roles in recolonization. On the time scale of 30 years, the total number of characteristic aquatic macroinvertebrate species per site tend to increase with the time elapsed after rewetting, but this increase is slow (van Duinen et al. 2003b). Wheeler and Shaw (1995) assumed that a conservationally worthwhile, more or less balanced invertebrate community could reassemble in rewetted peat works within 50–70 years, depending on the proximity of potentially recolonizing species. Biggs et al. (2001) found that the restoration of the river Cole (UK) was successful because its upper reaches and stagnant water bodies along the river harbored many species that were able to recolonize the river after restoration. Likewise, Schikora (2002b) explained the rapid colonization by hygrophilous spider species of a rewetted bog by the vicinity of a vital population, next to the ability of dispersal by “ballooning.” This stresses the importance of the conservation of current refugia in both relatively untouched and degraded bog remnants until rewetted sites have been recolonized by the species in question. Measures to conserve the current refugia, including rewetting, have to be taken with great care, including monitoring, in order to prevent decline of relict populations of rare and characteristic species (Verberk et al. 2001; van Duinen et al. 2003b).

Aquatic microinvertebrates (Rotifera, Copepoda, and Cladocera) however, seem to recover quickly after rewetting (van Duinen et al. 2003a, 2006b). The difference in cumulative species richness and the number of characteristic species between rewetted and remnant sites found for aquatic macroinvertebrates was not found for microinvertebrates (Fig. 5.6). Likewise, Buttler et al. (1996) showed that the testate amoebae fauna of raised bogs can recover rapidly and fully, regardless of the initial condition of the cutover surface. As microinvertebrates like Rotifera and Cladocera are easily spread by wind or animal vectors (Cáceres and Soluk 2002; Cohen and Shurin 2003), have a short life cycle, and have parthenogenetic reproduction (Nogrady et al. 1993) they can colonize water bodies quickly after rewetting measures are taken. Probably, the first microinvertebrate species colonizing the newly created water bodies have a higher chance to successfully establish a population, as local biotic interactions (like competition and predation) may play a dominant role in structuring the plankton species assemblage by preventing invasion of new species once the community is saturated (Cohen and Shurin 2003). The local or regional species pool probably has an important influence on the final composition of the aquatic microinvertebrate community of rewetted bog remnants (van Duinen et al. 2006b). Thus, the effects of restoration measures on microinvertebrates might be different from that on macroinvertebrates, which disperse less easily or might even be unable to fly, have a more complex life cycle, and make higher demands on their environment.

To set targets for conservation and restoration of raised bogs and to provide knowledge about how to reach those targets, reference data on intact bogs are necessary. Most of the reports on the intact raised bog fauna (compiled in the first decades of the twentieth century; Harnisch 1925; Peus 1932) do not give detailed information about the environmental conditions under which species and species assemblages were found. Moreover, at that time, many bogs were already to some extent degraded. However, knowledge about the environmental factors structuring faunal species assemblages is necessary to understand why species can or cannot establish themselves and survive in raised bogs under restoration and to give useful recommendations for restoration management. In this respect, palaeoecological research can provide useful information (Lavoie et al. 1997; Whitehouse 2004), although research on the actual occurrence and habitat demands of species is necessary, as well.

5.5 Conclusions

Like this chapter, most peatland wildlife studies to date have focused on species occurrence patterns, with little to say about the productivity, let alone the viability, of populations and only limited, correlative information about the environmental factors that limit or facilitate the occurrence of species. Besides this, the function of animal species in peatland systems is hardly known. The impact of beavers' activities on peatland hydrology, the effects of selective grazing by large herbivores, and the indispensability of insects in the survival of carnivorous plants can be easily imagined. However, also, for example, microscopic rotifers in *Sphagnum* mats seem to be important in bog ecosystems, as components in the phosphorus and nitrogen cycles (Bledzki and Ellison 1998, 2002). We would like to end by reiterating a message that is increasingly voiced in reviews such as this one, i.e., the need to move forward by favoring long-term and process studies over short-term and pattern studies. Of course, pattern studies exploring the distribution of species are an essential first step in our understanding of the role of peatlands for their associated fauna. However, they are of little use when it comes to teasing out minor roles that peatlands may play, such as staging areas, movement corridors, and complementary feeding grounds, from major roles such as population refugia and reproductive habitat. There will always be room for further ecological studies of fauna, and the study of peatlands is no exception. But better knowledge of the "functional ecology" of peatland fauna is needed here, particularly reproductive activity, dispersal, and nutritional ecology – three key factors for invertebrates and vertebrates alike. With such information, not only will we be more effective with "decision makers" and practitioners in conservation and restoration management, but, perhaps more importantly, we may help the greater public appreciate how fascinating peatlands are.

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References

Ahlroth P, Alatalo RV, Hyvärinen E, Suhonen J (1999) Geographical variation in wing polymorphism of the waterstrider *Aquarius najas* (Heteroptera, Gerridae). J Evol Biol 12:156–160

Akkermann R (1982) Möglichkeiten und Zielsetzungen für eine Regeneration von Hochmooren – zoologisch betrachtet. In: Akkermann R (ed) Regeneration von Hochmooren Informationen zu Naturschutz und Landschaftspflege in Nordwestdeutschland, Band 3. BSH, Wardenburg, pp 151–163

Banfield AWF (1977) Les mammifères du Canada, 2nd edn. Musées nationaux du Canada, Ottawa

Berg Å, Nilsson SG, Boström U (1992) Predation on artificial wader nests on large and small bogs along a South-North gradient. Ornis Scand 23:13–16

Bert DG (2001) A multiscale analysis of nested species subsets of forest birds in agricultural landscapes near Ottawa, Canada. Thesis, Carleton University, Ottawa

Bider R, Matte S (1994) Atlas des amphibiens et des reptiles du Québec. Société d'histoire naturelle de la vallée du Saint-Laurent & Gouvernement du Québec, Ministère de l'environnement et de la faune, Direction de la faune et des habitats, Sainte-Anne-de-Bellevue

Biggs J, Fox G, Whitfield M, Williams P, Sear D, Bray S (2001) River restoration – Is it worth it? Freshwater Biol Assoc Newsl 14:1–3

Blake JG (1991) Nested subsets and the distribution of birds on isolated woodlots. Conserv Biol 5:58–66

Bledzki LA, Ellison AM (1998) Population growth and production of Habrotrocha rosa Donner (Rotifera: Bdelloidea) and its contribution to the nutrient supply of its host, the northern pitcher plant, *Sarracenia purpurea* L. (Sarraceniaceae). Hydrobiologia 385:193–200

Bledzki LA, Ellison AM (2002) Nutrients regeneration by rotifers in New England (USA) bogs. Verh Int Ver Theor Angew Limnol 28:1328–1331

Bölscher B (1995) Niche requirements of birds in raised bogs: habitat attributes in relation to bog restoration. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) Restoration of temperate wetlands. Wiley, New York, pp 359–378

Bölscher B (1988) On habitat selection of bird species in northwest German raised bogs – a contribution to landscape evaluation (in German). Braunschw Naturkd Schr 3:29–119

Boström U, Nilsson SG (1983) Latitudinal gradients and local variations in species richness and structure of bird communities on raised peat-bogs in Sweden. Ornis Scand 14:213–226

Brewer R (1967) Bird populations of bogs. Wilson Bull 79:371–396

Buttler A, Warner BG, Grosvernier P, Matthey Y (1996) Vertical patterns of testate amoebae (Protozoa: Rhizopoda) and peat-forming vegetation on cutover bogs in the Jura, Switzerland. New Phytol 134:371–382

Cáceres CE, Soluk DA (2002) Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131:402–408

Calmé S, Desrochers A (1999) Nested bird and micro-habitat assemblages in a peatland archipelago. Oecologia 118:361–370

Calmé S, Desrochers A (2000) Biogeographic aspects of the distribution of bird species breeding in Québec's peatlands. J Biogeogr 27:725–732

Calmé S, Haddad S (1996) Peatlands: a new habitat for the upland sandpiper, *Bartramia longicauda*, in eastern Canada. Can Field-Nat 110:326–330

Calmé S, Desrochers A, Savard J-PL (2002) Regional significance of peatlands for avifaunal diversity in southern Québec. Biol Conserv 107:273–281

Cohen GM, Shurin JB (2003) Scale-dependence and mechanisms of dispersal in freshwater zooplankton. Oikos 103:603–617

Couillard L, Grondin P (1986) La végétation des milieux humides du Québec. Gouvernement du Québec, Quebec

Crisp DT, Heal OW (1996) Diversity and distribution of aquatic meso- and microfauna in mires. In: Standen V, Tallis JH, Meade R (eds) Patterned mires and mire pools – Origin and development; flora and fauna – proceedings. University of Durham, Durham, pp 163–168

Cutler A (1991) Nested faunas and extinctions in fragmented habitats. Conserv Biol 5:496–505

Dampf A (1924a) Zur Kenntnis der estländischen Hochmoorfauna 1 (in German). Beitr Kund Estlands 10:33–49

Dampf A (1924b) Zur Kenntnis der estländischen Hochmoorfauna 2 (in German). LUSi aruanded 31:17–71

Danks HV, Rosenberg DM (1987) Aquatic insects of peatlands and marshes in Canada: synthesis of information and identification of needs for research. Mem Entomol Soc Can 140:163–174

Delage V, Fortin M-J, Desrochers A (2000) Effets de lisière et d'isolement des habitats d'oiseaux chanteurs dans les tourbières exploitées. Écoscience 7:149–156

Desrochers A (2001) Les oiseaux: diversité et répartition. In: Payette S, Rochefort L (eds) Écologie des tourbières du Québec-Labrador. Les Presses de l'Université Laval, Sainte-Foy, pp 159–173

Desrochers A, Hannon SJ (1997) Gap crossing decisions by dispersing forest songbirds. Conserv Biol 11:1204–1210

Desrochers A, Rochefort L, Savard J-PL (1998) Avian recolonization of eastern Canadian bogs after peat mining. Can J Zool 76:989–997

Dunn EH, Hussell DJT, Welsh DA (1999) Priority-setting tool applied to Canada's landbirds based on concern and responsibility for species. Conserv Biol 13:1404–1415

Eggelsman R (1980) Mikroklima der Moore (in German). In: Göttlich K (ed) Moor- und Torfkunde. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp 224–230

Elser JJ, Fagan WF, Denno RF, Dobberfuhl DR, Folarin A, Huberty A, Interlandi S, Kilham SS, McCauley E, Sculz KL, Sieman EH, Sterner RW (2000) Nutritional constraints in terrestrial and freshwater food webs. Nature 408:578–580

Erskine AJ (1977) Birds in boreal Canada: communications, densities, and adaptations. Canadian Wildlife Service report series no 41. Canadian Wildlife Service, Ottawa

Esselink H (2002) Fauna in intact hoogveen en hoogveenrestanten (in Dutch). In: Schouwenaars JM, Esselink H, Lamers LPM, van der Molen PC (eds) Ontwikkeling en herstel van hoogveensystemen. Expertisecentrum LNV, Ede/Wageningen, pp 87–113

Etterson MA (2003) Conspecific attraction in loggerhead shrikes: implications for habitat conservation and reintroduction. Biol Conserv 114:199–205

Faaborg J (2004) Truly artificial nest studies. Conserv Biol 18:369–370

Fernández-Juricic E (2002) Nested patterns of species distribution and winter flock occurrence of insectivorous birds in a fragmented landscape. Écoscience 9:450–458

Finnamore AT (1994) Hymenoptera of the Wagner natural area, a boreal spring fen in central Alberta. Mem Entomol Soc Can 169:181–220

Främbs H (1990) Changes in carabid beetle populations on a regenerationg, excavated peat bog in northwest Germany. In: Stork NE (ed) The role of ground beetles in ecological and environmental studies. Intercept, Andover, pp 157–169

Främbs H (1994) The importance of habitat structure and food supply for carabid beetles (Coleoptera, Carabidae) in peat bogs. Mem Entomol Soc Can 169:145–159

Glenn SM, Nudds TD (1989) Insular biogeography of mammals in Canadian parks. J Biogeogr 16:261–268

Goffart H (1928) Beitrag zur Kenntnis der Fauna westfälischer Hochmoore (in German). Beitr Naturdenkmalpflege 12:137–285

Gotelli NJ, Ellison AM (2002) Biogeography at a regional scale: determinants of ants species density in New England bogs and forests. Ecology 83:1604–1609

Göttlich K (1980) Moor- und Torfkunde (in German). E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart

Green JL, Ostling A (2003) Endemics-area relationships: the influence of species dominance and spatial aggregation. Ecology 84:3090–3097

Gregory RD, Eaton MA, Noble DG, Robinson JA, Parsons M, Baker H, Austin G, Hilton GM (2003) The state of the UK's birds 2002. Royal Society for the Protection of Birds, British Trust for Ornithology, Wildfowl and Wetlands Trust, Joint Nature Conservation Committee, Sandy, UK

Haddad S, Desrochers A, Savard J-PL (2000) Artificial nest predation in bogs: does peat harvest increase risk? Écoscience 7:32–37

Hakala A (1971) A quantitative study of the bird fauna of some open peatlands in Finland. Ornis Fenn 48:1–11

Harnisch O (1925) Studien zur Ökologie und Tiergeographie der Moore (in German). Zool Jahrb 51:1-166

Häyrinen U, Järvinen O, Kouki J (1986) The bird sanctuary of Kesonsuo, a raised bog in North Karelia: its breeding bird assemblages, summer visitors and spring migrants. Ornis Fenn 63:97–111

Heckenroth H (1994) Zur Fauna der Hochmoore (Kurzfassung) (in German). NNA Ber 7:48

Hokkanen R (2004) Bird habitats and conspecific relations at Siikaneva mire. Thesis, University of Helsinki, Helsinki

Irmler U, Müller K, Eigner J (1998) Das Dosenmoor – Ökologie eines regenerierenden Hochmoores (in German). Faunistisch-ökologische Arbeitsgemeinschaft, Kiel

Järvinen O, Sammalisto L (1976) Regional trends in the avifauna of finnish peatland bogs. Ann Zool Fenn 13:31–43

Järvinen O, Kouki J, Häyrinen U (1987) Reversed latitudinal gradients in total density and species richness of birds breeding on Finnish mires. Ornis Fenn 64:67–73

Joosten H, Clarke D (2002) Wise use of mires and peatlands – Background and principles indluding a framework for decision-making. International Mire Conservation Group, International Peat Society, Greifswald

Kalkman VJ, van Duinen GA, Esselink H, Kuper JT (2002) New records of Odonata from Estonia, with notes on breeding in the Baltic sea and on species assemblages of raised bog systems. Notul Odonatol 5:120–152

Koponen S (1979) Differences of spider fauna in natural and man-made habitats in a raised bog. In: Hytteborn H (ed) The use of ecological variables in environmental monitoring, report PM 1151. The National Swedish Environment Protection Board,, Stockholm, pp 104–108

Koponen S (1994) Ground-living spiders, opilionods, and pseudoscorpions of peatlands in Québec. Mem Entomol Soc Can 169:41–60

Koponen S (2002) Ground-living spiders in bogs in northern Europe. J Arachnol 30:262–267

Koponen S, Relys V, Dapkus D (2001) Changes in structure of ground-living spider (Araneae) communities on peatbogs along a transect from Lithuania to Lapland. Norw J Entomol 48:167–174

Kouki J, Niemi GJ, Rajasärkkä A (1992) Habitat associations of breeding peatland passerine species in eastern Finland. Ornis Fenn 69:126–140

Krogerus R (1960) Ökologische Studien über nordische Moorarthropoden (in German). Commentat Biol 21:1-238

Lamers LPM (2001) Tackling biogeochemical questions in peatlands. Thesis, University of Nijmegen, Nijmegen

Larison B, Laymon SA, Williams PL, Smith TB (2001) Avian responses to restoration: nest-site selection and reproductive success in song sparrows. Auk 118:432–442

Lavoie C, Rochefort L (1996) The natural revegetation of a harvested peatland in southern Québec: a spatial and dendroecological analysis. Écoscience 3:101–111

Lavoie C, Elias SA, Filion L (1997) A 7000-year record of insect communities from a peatland environment, southern Québec. Écoscience 4:394–403

Leuven RSEW, den Hartog C, Christiaans MMC, Heijligers WHC (1986) Effects of water acidification on the ditribution pattern and the reproductive success of amphibians. Experienta 42:495–503

Limpens J, Berendse F, Klees H (2003) N deposition affects N availability in interstitial water, growth of Sphagnum and invasion of vascular plants in bog vegetation. New Phytol 157:339–347

Maavara V (1955) The Entomofauna of Estonian bogs and its changes in response to human activity (in Estonian). Thesis, University of Tartu, Tartu

Macan TT (1954) A contribution to the study of the ecology of Corixidae (Hemiptera). J Anim Ecol 23:115–141

Mazerolle MJ (2001) Amphibian activity, movement patterns, and body size in fragmented peat bogs. J Herpetol 35:13–20

Mazerolle MJ (2003) Detrimental effects of peat mining on amphibian abundance and species richness in bogs. Biol Conserv 113:215–223

Mazerolle MJ, Cormier M (2003) Effects of peat mining intensity on green frog (*Rana clamitans*) occurrence in bog ponds. Wetlands 23:709–716

Mazerolle MJ, Drolet B, Desrochers A (2001) Small-mammal responses to peat mining of southeastern Canadian bogs. Can J Zool 79:296–302

McCoy ED, Mushinsky HR (1994) Effects of fragmentation on the richness of vertebrates in the Florida scrub habitat. Ecology 75:446–457

Mitchell EAD, Borcard D, Buttler AJ, Grosvernier P, Gilbert D, Gobat J-M (2000a) Horizontal distribution patterns of testate amoebae (Protozoa) in a *Sphagnum magellanicum* carpet. Microb Ecol 39:290–300

Mitchell EAD, Buttler A, Grosvernier P, Rydin H, Albinsson C, Greenup AL, Heijmans MMPD, Hoosbeek MR, Saarinen T (2000b) Relationships among testate amoebae (Protozoa), vegetation and water chemistry in five Sphagnum-dominated peatlands in Europe. New Phytol 145:95–106

Monroe BL, Jr., Sibley CG (1993) A World checklist of birds. Yale University Press, New Haven, CT

Moore PD, Bellamy DJ (1974) Peatlands. Elek, London

Morneau F (1995) Les oiseaux des tourbières. In: Gauthier J, Aubry Y (eds) Les oiseaux nicheurs du Québec: atlas des oiseaux nicheurs du Québec méridional. Association québécoise des groupes d'ornithologues, Société québécoise de protection des oiseaux, Service canadien de la faune, Environnement Canada (région du Québec), Montreal, p 1206

Mossakowski D, Främbs H (2003) Arthropoden intakter Hochmoore und regenerierender Abtorfungsflächen (in German). In: Aschemeier C (ed) Naturschutz in Moor und Heide. Biologische Station Zwillbrock, Vreden, pp 35–41

Niemi GJ (1985) Patterns of morphological evolution in bird genera of New World and Old World peatlands. Ecology 66:1215–1228

Niewold FJJ (1993) Raamplan voor behoud en herstel van de leefgebieden van Korhoenders (*Tetrao tetrix*) in Midden-Brabant (in Dutch). Instituut voor Bos- en Natuuronderzoek, Wageningen

Niewold FJJ (1996) Das Birkhuhn in den Niederlanden und die problematik des Wiederaufbaus der Population. NNA Ber 1:11–20

Nilsson SG (1986) Are bird communities in small biotope patches random samples from communities in large patches? Biol Conserv 38:179–204

Nogrady T, Wallace R, Snell T (eds) (1993) Rotifera – biology, ecology and systematics. SPB, The Hague

Nordquist GE (1992) Small mammals. In: Wright HE Jr, Coffin B, Aaseng NE (eds) The patterned peatlands of Minnesota. University of Minnesota Press, Minneapolis, MN, pp 85–110

Norgaard E (1951) On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish sphagnum bog. Oikos 3:1–21

Päivänen J (1999) Tree stand structure on pristine peatlands and its change after forest drainage. Int Peat J 9:66–72

Pakarinen P (1995) Classification of boreal mires in Finland and Scandinavia: a review. Vegetatio 118:29–38

Patterson BD, Brown JH (1991) Regionally nested patterns of species composition in granivorous rodent assemblages. J Biogeogr 18:395–402

Petersen B (1954) Some trends of speciation in the cold-adapted holarctic fauna. Zool Bidr Uppsala 30:233–314

Peus F (1932) Die Tierwelt der Moore. Handbuch der Moorkunde III (in German). Bornträger Verlag, Berlin

Pough FH (1976) Acid precipitation and embryonic mortality of spotted salamanders, *Ambystoma maculatum*. Science 192:68–70

Poulin M, Pellerin S (2001) La conservation. In: Payette S, Rochefort L (eds) Écologie des tourbières du Québec-Labrador. Les Presses de l'Université Laval, Sainte-Foy, pp 505–518

Poulin M, Rochefort L, Desrochers A (1999) Conservation of bog plant species assemblages: assessing the role of natural remnants in mined sites. Appl Veg Sci 2:169–180

Reynolds JD (1990) Ecological relationships of peatland invertebrates. Ecology and conservation of Irish peatlands. In: Doyle GJ (ed). Royal Irish Academy, Dublin, pp 135–143

Risager M (1998) Impact of nitrogen on *Sphagnum* dominated bogs. Thesis, University of Copenhagen, Copenhagen

Runtz MWP, Peck SB (1994) The beetle fauna of a mature Spruce-*Sphagnum* bog, Algonquin Park, Ontario; ecological implications of the species composition. Mem Entomol Soc Can 169:161–171

Sammalisto L (1957) The effect of the woodland – open peatland edge on some peatland birds in south Finland. Ornis Fenn 34:81–89

Sauer JR, Hines JE, Fallon J (2003) The North American Breeding Bird Survey, eesults and analysis 1966–2002. USGS Patuxent Wildlife Research Center, Laurel

Schäfer M, Lundström JO (2001) Comparison of mosquito (Diptera: Culicidae) fauna characteristics of forested wetlands in Sweden. Ann Entomol Soc Am 94:576–582

Schikora H-B (2002a) Spinnen (Arachnida, Araneae) nord- und mitteleuropäischer Regenwassermoore entlang ökologischer und geographischer Gradienten (in German). Thesis, University of Bremen, Bremen

Schikora H-B (2002b) Bodenlebende Spinnen als Element der Effizienzkontrolle bei Revitalisierungsvorhaben: Beispiel Rehberger Sattelmoor (Harz, Niedersachsen) (in German). Telma 32:175–190

Schmidt E (1964) Biologisch-ökologische Untersuchungen an Hochmoorlibellen (Odonata) (in German). Z Wiss Zool 169:313–386

Smart PJ, Wheeler BD, Willis AJ (1989) Revegetation of peat excavation in a derelict raised bog. New Phytol 111:733–748

Smits MJA, van Druinen GA, Bosman JG, Brock AMT, Javois J, Kuper JT, Peeters TMJ, Peeters MAJ, Esselink H (2002) Species richness in a species poor system: Aquatic macroinvertebrates of *Nigula raba*, an intact raised bog system in Estonia. In: Schmilewski G, Rochefort L (eds) Proceedings of the international peat symposium. International Peat Society Commission V: peatland restoration, Pärnu, Estonia, pp 283–291

Smolders AJP, Tomassen HBM, van Mullekom M, Lamers LPM, Roelofs JGM (2003) Mechanisms involved in the re-establishment of *Sphagnum*-dominated vegetation in rewetted bog remnants. Wetlands Ecol Manage 11:403–418

Speight MCD, Blackith RE (1983) The animals. In: Gore AJP (ed) Ecosystems of the world 4A. Mires: swamp, bog, fen and moor. Elsevier, Amsterdam pp 349–365

Spitzer K, Jaroš J (1993) Lepidoptera associated with the Cevené Blato bog (Central Europe): conservation implications. Eur J Entomol 90:323–336

Sternberg K (1993) Hochmoorschlenken als warme Habitatinseln im kalten Lebensraum Hochmoor. Telma 23:125–146

Stockwell SS (1994) Habitat selection and community organization of birds in eight peatlands of Maine, Thesis, University of Maine, Orono

Tomassen HBM, Smolders AJP, Limpens J, Lamers LPM, Roelofs JGM (2004) Expansion of invasive species on ombrotrophic bogs: desiccation or high N deposition? J Appl Ecol 41:139–150

Väisänen R (1992) Distribution and abundance of diurnal Lepidoptera on a raised bog in southern Finland. Ann Zool Fenn 29:75–92

Väisänen RA, Järvinen O (1977) Structure and fluctuation of the breeding bird fauna of a north Finnish peatland area. Ornis Fenn 54:143–153

Valk KU (1988) Estonian peatlands (in Estonian). Valgus, Tallinn

van Duinen GA, Brock AMT, Kuper JT, Peeters TMJ, Smits MJA, Verberk WCEP, Esselink H (2002) Important keys to successful restoration of characteristic aquatic macroinvertebrate fauna of raised bogs. In: Schmilewski G, Rochefort L (eds) Proceedings of the international peat symposium. International Peat Society Commission V: peatland restoration, Pärnu, Estonia, pp 292–302

van Duinen GA, Brock AMT, Kuper JT, Peeters TMJ, Verberk WCEP, Zhuge Y, Esselink H (2003a) Restoration of degraded raised bogs: do aquatic invertebrates tell a different story? In: Järvet A, Lode E (eds) Ecohydrological processes in northern wetlands. Selected papers of the international conference & educational workshop, Tallinn, Estonia, pp 255–261 van Duinen GA, Brock AMT, Kuper JT, Leuven RSEW, Peeters TMJ, Roelofs JGM, van der Velde G, Verberk WCEP, Esselink H. (2003b) Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates. Wetlands Ecol Manage 11:447–459

van Duinen GA, Dees AJ, Esselink H (2004a) Importance of permanent and temporary water bodies for aquatic beetles in the raised bog remnant Wierdense Veld. Proc Exp Appl Entomol (NEV) 15:15–20

van Duinen GA, Brock AMT, Kuper JT, Peeters TMJ, Esselink H (2004b) Do raised bog restoration measures rehabilitate aquatic fauna diversity? A comparative study between pristine, degraded, and rewetted raised bogs. In: Päivänen J (ed) Wise use of peatlands. Proceedings of the 12th international peat congress, Tampere, Finland, 6–11 June 2004, pp 399–405

van Duinen GA, Timm T, Smolders AJP, Brock AMT, Verberk WCEP, Esselink H (2006a) Differential response of aquatic oligochaete species to increased nutrient availability – a comparative study between Estonian and Dutch raised bogs. Hydrobiologia (in press)

van Duinen GA, Zhuge Y, Verberk WCEP, Brock AMT, van Kleef HH, Leuven RSEW, van der Velde G, Esselink H (2006b) Effects of rewetting measures in Dutch raised bog remnats on assemblages of aquatic Rotifera and microcrustaceans. Hydrobiologia 565:187–200

Verberk WCEP, van Duinen GA, Peeters TMJ, Esselink H (2001) Importance of variation in water-types for water beetle fauna (Coleoptera) in Korenburgerveen, a bog remnant in the Netherlands. Proc Exper Appl Entomol (NEV) 12:121–128

Verberk WCEP, van Kleef HH, Dijkman M, van Hoek P, Spierenburg P, Esselink H (2005) Seasonal changes on two different spatial scales: response of aquatic invertebrates to water body and microhabitat. Insect Science 12:263–280

Verberk WCEP, van Duinen GA, Brock AMT, Leuven RSEW, Siepel H, Verdonschot PFM, van der Velde G, Esselink H (2006) Importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bog landscapes. Journal of Nature Conservation (in press)

Wagner RH, Danchin E (2003) Conspecific copying: a general mechanism of social aggregation. Anim Behav 65:405–408

Wheeler BD, Shaw SC (1995) Restoration of damaged peatlands. HMSO, London

Whitehouse NJ (2004) Mire ontogeny, environmental and climatic change inferred from fossil beetle successions from Hatfield Moors, eastern England. Holocene 14:79–93

Wilbur HM (1980) Complex life cycles. Ann Rev Ecol Syst 11:67–93

Wood JT (1955) The nesting of the Four-toed Salamander, *Hemidactylium scutatum* (Schlegel), in Virginia. Am Midl Nat 53:381–389

6 The Role of Fungi in Boreal Peatlands

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6.1 Introduction

Wetlands cover about 4 % of the world's landscape and 14 % of the landscape in Canada (National Wetlands Working Group 1988). Peatlands accumulate peat, a heterogeneous assemblage of partially decomposed plant materials (about 45–50 % C; Clymo 1984; Clymo et al. 1998). Gorham (1991) estimated that northern peatlands store between 180 and 277 Gt C, which represents about 10–16 % of the total global terrestrial detrital C, emphasizing their importance to the global C cycle. Peat accumulates because of an imbalance between plant production and organic matter decomposition (Clymo 1965; Malmer 1986). Despite the prevalence of peatlands in the northern hemisphere and their importance to the global C cycle, relatively little is known about the microbial diversity and roles in these ecosystems, specifically as they pertain to decomposition dynamics. It has long been suggested that fungi are the principal decomposer microbes in many acidic ecosystems, such as many peatlands, and assume a more dominant role than bacteria (Kox 1954; Latter et al. 1967; Williams and Crawford 1983). The objectives of this chapter are to (1) summarize the current knowledge of fungal species richness in peatlands, (2) examine the ability of common saprobes, mycorrhizal fungi, and other root endophytes in peatlands to decompose organic matter, (3) address the significance of litter quality on fungal communities, (4) describe how *Sphagnum* is decomposed by fungi, and (5) indicate gaps in our understanding of fungal communities and their influence on decomposition dynamics in peatlands.

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6.2 Decomposition of Organic Matter

Decomposition is a complex process that includes nearly all changes in organic matter that has undergone senescence or death (Brinson et al. 1981). Leaching of soluble organic matter precedes losses due to assimilation by microorganisms or removal by animals. Decomposition is completed with the loss of the physical structure and changes in the chemical constituents of the remaining organic matter. Numerous studies have measured decomposition rates of vascular and nonvascular plants in boreal peatlands (Chap. 7). Some of the more common taxa include the vascular plant species *Carex*, *Salix*, *Typha*, and *Betula*, and the bryophyte genera *Sphagnum*, *Drepanocladus*, and *Tomenthypnum*. The rate of litter decomposition is affected by moisture, oxygen availability, temperature, acidity, and the nutrient status of ecosystems (primarily N- and P-related surface water chemistry variables). In addition, litter quality [total N (TN), total P (TP), and total C (TC) tissue concentrations, TC-to-TN quotients] also affects the rate of decomposition (Bartsch and Moore 1985; Farrish and Grigal 1988; Gorham 1991; Bridgham and Richardson 1992; Szumigalski and Bayley 1996; Thormann and Bayley 1997; Thormann et al. 2001a). From a mycological perspective, changes in litter quality, the water potential of the litter, temperature, and pH have been shown to affect fungal communities of various substrata (Pugh 1958; Christensen and Whittingham 1965; Pugh and Mulder 1971; Dix 1985; Nilsson et al. 1992; Lumley et al. 2001; Thormann et al. 2003).

6.2.1 Role of Fungi in Decomposition Dynamics

6.2.1.1 Fungal Species Richness in Peatlands

Microfungal communities of hummocks and hollows of bogs, fens, swamps, moors, muskeg, anthropogenically altered wetlands, and individual wetland plants have been examined in Europe, Asia, and North and South America. From a taxonomic perspective, in excess of 860 individual records of microfungi from peatlands have been reported, representing 656 different species. These were 408 anamorphic species with putative ascomycete affinities (reproduce asexually only), 22 teleomorphic ascomycetes (reproduce sexually), 25 basidiomycetes, 67 zygomycetes, 28 chytridiomycetes, and 106 taxa with unknown taxonomic affinities, yeasts, and sterile isolates (Table 6.1).

Anamorphic ascomycetes were by far the largest group of fungi isolated from peatlands (408 species, or 62 % of all species; Table 6.1). Species of *Penicillium* and *Acremonium* dominated this group (89 and 27 different species, respectively), with *P. frequentans* Westl., *P. purpurogenum* Stoll, *P. spinulosum* Thom, *P. thomii* Maire, and *A. kiliense* Grütz being the dominant species. Zygomycetes were also very frequently isolated from peat (67 different species, or 10 % of all species; Table 6.1). In this group, species of *Mortierella* [*M. alpina* Peyronel, *M. isabellina* Oudem. & Koning, *M. minutissima* van Tieghem, *M. ramanniana* (Möller) Linnem., *M. vinacea* Dixon-Stewart] and *Mucor* (*M. hiemalis* Wehmer) comprise 80 % of all isolates from peat. Several specific surveys for chytridiomycetes yielded 28 species (4 % of all species; Table 6.1), with *Rhizophydium*, *Phlyctochytrium*, and *Septosperma* being the dominant genera (61 % of all chytridiomycete species). Teleomorphic ascomycetes (22 species, or 3 % of all species) and basidiomycetes (25 species, or 4 % of all species) were rarely isolated from peat. Among the former group, species of *Chaetomium*, *Gelasinospora*, *Sordaria*, and *Thielavia* predominated (68 % of all ascomycete species), while basidiomyceteous yeasts predominated the latter group (*Cryptococcus* and *Rhodotorula* spp., 36 % of all basidiomycete species). Lastly, 106 records of fungi from peatlands remained unidentified (sterile and otherwise unidentified – 77 taxa, yeasts – 12 taxa, pycnidial – seven taxa) or belonged to taxa with unknown taxonomic affinities (ten taxa; Table 6.1).

It is interesting to note that the majority of microfungi isolated from peat and peatland plants are prolific sporulators with fast growth rates, particularly species of *Penicillium*, *Trichoderma*, *Aspergillus*, *Verticillium*, *Cladosporium*, *Mortierella*, and *Mucor* (Table 6.2). These taxa are easily cultured on most standard media and under most growth conditions. This explains their preponderance in almost all studies, irrespective of location and substrate, and undoubtedly skews the species list towards that group of fungi at the expense of slower-growing and less prolific sporulators. Several groups of fungi are underrepresented in almost all studies, includ-

Table 6.1. Taxonomic profile of fungi from peatlands

Fungal group	No. of records	Different taxa	Unidentified taxa
Anamorphic ascomycetes	566	408	170
Teleomorphic ascomycetes	23	22	6
Basidiomycetes	25	25	12
Chytridiomycetes	30	28	7
Zygomycetes	118	67	15
Unidentified taxa	106	–	106
Total	868	550[a]	316

[a] Excludes unidentified taxa

Table 6.2. Dominant fungal taxa from peatlands

Fungal group	Fungal taxa	No. of taxa
Anamorphic ascomycetes	*Penicillium* spp.	89
	Acremonium spp.	27
	Verticillium spp.	16
	Aspergillus spp.	15
	Trichoderma spp.	15
	Fusarium spp.	14
	Cladosporium spp.	11
	Oidiodendron spp.	7
Teleomorphic ascomycetes	*Chaetomium* spp.	6
	Gelasinospora spp.	3
	Sordaria spp.	3
	Thielavia spp.	3
Basidiomycetes	*Cryptococcus* spp.	5
	Rhodotorula spp.	4
Chytridiomycetes	*Rhizophydium* spp.	9
	Phlyctochytrium spp.	5
	Septosperma spp.	3
Zygomycetes	*Mortierella* spp.	34
	Mucor spp.	19
Unidentified taxa	*Mycelia sterilia*	46
	Yeast species	12
	Unknown affinities	10

ing yeasts, chytridiomycetes, basidiomycetes, and teleomorphic ascomycetes (Table 6.2). Taxa in these groups are characterized by slower growth rates and, in some cases, the prerequisite for specialized growth media and conditions. While yeasts were frequently isolated, few studies have identified them to either genus or species. Only three surveys for chytridiomycetes have been conducted in peatlands to my knowledge (Sparrow and Lange 1977; Zattau 1981; Czeczuga 1993), and virtually all records of chytridiomycetes from peatlands are novel. There may be a large diversity of these mostly parasitic and saprobic fungal taxa that has received little attention so far. Surprising also is the underrepresentation of basidiomycetes. Most basidiomycetes on record are yeasts and originated from a single study in Russia (13 of 25 taxa; Polyakova et al. 2001), with 11 of the remaining 12 records originating from a second study in Canada, most of which were not identified to genus or species (nine of 11; Thormann et al. 2001b, 2003). Clearly, there is the potential to gain a much better understanding of microfungi in peatlands with additional studies focusing on these underrepresented groups of fungi.

6.2.1.2 Saprobes

Fungi play fundamental roles in the decomposition processes of organic matter in all ecosystems and may be more important than bacteria in wetlands from a functional perspective (Kox 1954; Latter et al. 1967; Williams and Crawford 1983), because of their extensive hyphal growth habit, faster growth rates, and ability to translocate nutrients through their hyphal networks. Five major "behavioral groupings" of decomposer fungi have been recognized (Deacon 1997). Group 1 – fungi, pathogens, and weak parasites – can tolerate host defense mechanisms but are generally poor competitors in dead organic matter and include species of *Cladosporium*, *Aureobasidium*, *Botrytis*, and *Alternaria*. These fungi rely on simple sugars and other storage compounds that leach out of plant tissues. Following the senescence and death of plants, all organic matter is sequentially colonized by pioneer saprobes (group 2 – mostly zygomycetes, e.g., species of *Mucor* and *Mortierella*), followed by simple polymer-degrading fungi (group 3 – includes species of *Fusarium*, *Chaetomium*, *Trichoderma*, and *Penicillium*), and finally degraders of recalcitrant polymers (group 4 – includes species of basidiomycetes and select groups of ascomycetes). Secondary, or opportunistic, saprobes (group 5 – includes species of *Pythium*, *Mortierella*, and others) are common throughout the entire process of decomposition (Deacon 1997). Hence, from the point of senescence to complete decomposition, all organic matter is colonized by a suite of saprobes with specific enzymatic profiles and preferences for specific (non)structural C compounds. This succession has previously been shown in a variety of litters, including leaves, roots, cones, seeds, dung, and wood, in a variety of ecosystems, including forests, wetlands, and grasslands (Wicklow and Yokum 1981; Heilman-Clausen 2001; Lumley et al. 2001; Thormann et al. 2003).

Fungi from all five "behavioral groups" of saprobes have previously been isolated from peatlands; however, group 4 fungi are rarely reported. This is significant, since it is this group of fungi that has most often been linked to the degradation of the most complex structural polymers, including lignin, tannins, and other polyphenolics, which can comprise up to 50 % of the chemical constituents of peat (Turetsky et al. 2000). There are two reasons why this group is underrepresented in previous studies. First, it is possible that these fungi are naturally rare in peatlands, which is contradicted by the preponderance of conspicuous epigeous basidiomycete fruiting bodies in these ecosystems; however, the majority of these basidiomycetes may be ectomycorrhizal species of *Picea*, *Larix*, and *Salix*. While these fungi can grow in vitro, they appear to have limited abilities to degrade complex polymers (Hutchison 1990). The rarity of this group of fungi may partially explain why organic matter is not fully decomposed and accumulates in peatlands. Second, group 4 fungi may be abundant in peatlands, but previous isolation protocols may have been inadequate. The dilution plating technique, predominantly used in the infancy of surveys of soil fungi, selects those organisms that produce large quantities of propagules. In contrast, the particle plating technique, which has been used more extensively in recent studies, largely avoids that bias; however, other methodological biases are introduced, such as the selection of primary isolation media and culture conditions.

6.2.1.3 Mycorrhizas and Other Root Endophytes

Mycorrhizas are mostly mutualistic associations between fungi and the roots of higher plants, in which the fungi form consistently recognizable and physically distinct associations without causing any perceivable negative effect (Fernando 1995). It is thought that in excess of 90 % of all land plants are mycorrhizal; irrelevant of climate, ecosystem, soil type, vegetation communities, and environmental conditions (Read 1991). Detailed information on the different types of mycorrhizas and their roles as nutrient scavengers is provided elsewhere (Smith and Read 1997). Although not generally considered to be important players during the decomposition of organic matter, many mycorrhizal fungi, particularly ericoid and ectomycorrhizal fungi, also produce a suite of extracellular enzymes that allow them to access nutrients and C from organic matter.

Ericoid Mycorrhizal Fungi

Fungal strains belonging to the *Rhizoscyphus ericae* (Read) Zhuang & Korf–*Scytalidium vaccinii* Dalpé, Litten & Sigler complex, species of *Oidiodendron*, most notably *O. maius* Barron and *O. griseum* Robak, and *Meliniomyces variabilis* Hambleton & Sigler have been implicated as being mycorrhizal fungi of members of the Ericaceae (Read 1991; Hambleton and Currah 1997; Hambleton et al. 1999; Monreal et al. 1999). Various additional taxa, including *Phialocephala fortinii* Wang & Wilcox, have frequently been isolated from roots of ericaceous plants as well (Hambleton and Currah 1997); however, their functions remain speculative.

While ericoid mycorrhizal fungi are abundant in peatlands, their roles in the decomposition of organic matter have received limited attention (Domsch 1960; Bending and Read 1997; Rice and Currah 2001; Piercey et al. 2002). Rice and Currah (2001) developed physiological profiles of 22 strains of *O. maius*, isolated primarily from ericaceous plants. They found that most of their strains had the ability to decompose lignin, cellulose, chitin, starch, pectin, and gelatin. Lipids were not used by any of their strains. Domsch (1960) showed that *O. griseum* is able to degrade cellulose and starch, and Bending and Read (1997) showed the production of peroxidases and polyphenol oxidases (PPO), a suite of enzymes required for tannic acid and lignin degradation. A more limited enzymatic profile was shown by *R. ericae* (as *Hymenoscyphus ericae* (Read) Korf & Kernan; Leake and Read 1989, 1990). Currah and Tsuneda (1993) showed that *P. fortinii* is lignolytic and laccase positive, suggesting its ability to decompose complex polyphenolic polymers. Hence, ericoid mycorrhizal fungi appear to have the potential to degrade a wide variety of structural polymers common in peat (reviewed in Read et al. 2004).

While previous studies most often used specific media, more recent studies have used mass loss of standard organic matter to assess the saprobic abilities of selected fungi in vitro (Piercey et al. 2002; Thormann et al. 2002). For example, Piercey et al. (2002) showed that *O. maius* caused the greatest mass loss of *S. fuscum* compared with *R. ericae* (as *H. ericae*) and *M. variabilis* (as variable white taxon, VWT) (11.2 vs. 8.6 and 6.7 %, respectively) after 70 days. From their data, there appears to be a positive relationship between enzymatic diversity and the ability to cause mass loss of organic matter, i.e., ericoid mycorrhizal fungi with broad enzymatic profiles (e.g., *O. maius*) may be better adapted to decompose organic matter than those with more limited enzymatic profiles (e.g., *R. ericae*). The presence of ericoid mycorrhizal fungi in peatlands not only enables ericoid plants to thrive in harsh, nutrient-poor, acidic ecosystems (Hambleton and Currah 2000), but these fungi may also cause the formation of high molecular weight recalcitrant organic acid polymers via a series of complex biogeochemical pathways. Hence, ericoid mycorrhizal fungi also contribute to the accumulation of complex organic acids in peatlands (Bending and Read 1997). Therefore, these fungi play significant roles as mycorrhizas and as saprobes (Kox 1954).

Ectomycorrhizal Fungi

Previous surveys of conspicuous epigeous fruiting bodies revealed a great diversity of ectomycorrhizal fungi in peatlands (Salo 1993; Dhillion 1994). Species of *Lactarius*, *Hebeloma*, *Laccaria*, *Russula*, *Tomentella*, and *Cortinarius* are most frequently collected and are associated with the roots of species of *Picea*, *Larix*, *Salix*, and *Betula*. Several studies have investigated the abilities of ectomycorrhizal taxa to degrade organic matter (reviewed in Read et al. 2004), producing variable results. Durall et al. (1994) showed that hemicellulose and cellulose were readily degraded by four ectomycorrhizal fungi of *Pseudotsuga menziesii* (Mirb.) Franco, while more complex polymers, including humic substances and needles, were more decay resistant. In support, Hutchison (1990) and Bending and Read (1997) showed that ectomycorrhizal fungi (mostly species of *Lactarius*, *Hebeloma*, *Laccaria*, *Russula*, *Tomentella*, *Cortinarius*, *Suillus*, *Amanita*, *Boletus*, *Rhizopogon*, and *Tricholoma*) had limited abilities to use a variety of complex organic compounds, including polyphenolic polymers, such as tannic acid and lignin, cellulose, and pectin. Simpler structural carbohydrates, including starch, gelatin, and urea, were more frequently used, but utilization patterns were genus-specific, for example, species of *Laccaria* were able to degrade urea but not starch (Hutchison 1990). Conversely, other studies showed that ectomycorrhizal fungi could synthesize PPOs (reviewed in Read et al. 2004).

On the basis of these variable results, the role of ectomycorrhizal fungi in organic matter decomposition in peatlands is uncertain. It has been suggested that many ectomycorrhizal fungi may be able to survive as saprobes; however, this notion appears to be based on circumstantial evidence and resulted from either misidentified specimens or incorrect interpretation of the colonized substrate, according to Hutchison (1990). The generally reported low enzymatic activities of ectomycorrhizal fungi may be an adaptation to a symbiotic life, where the fungus must avoid eliciting host defense responses, which may be caused by extracellular enzymes (Ramstedt and Söderhäll 1983). As it stands, most ectomycorrhizal fungi appear to have limited saprobic capabilities, sufficient to colonize the roots of their hosts, and tend to require their plant hosts for the acquisition of C. However, owing to the preponderance of ectomycorrhizal fungi in peatlands, their combined effects on organic matter decomposition at the ecosystem level may be significant (Bending and Read 1997; Read et al. 2004).

Mycelium radicis atrovirens

In addition to the aforementioned widespread mycorrhizal fungi, a diverse assemblage of fungi frequently occurs in and on the roots of most plant species, including peatland plants. Recent studies designated some species of *Leptodontidium* (*L. orchidicola* Sigler & Currah), *Phialocephala* (*P. fortinii*, *P. dimorphospora* Kendrick), and *Phialophora* (*P. finlandia* Wang & Wilcox) as *Mycelium radicis atrovirens* (MRA), in addition to some isolates of pezizalean and entirely unknown affinities (Currah et al. 1988; Currah and Tsuneda 1993; Fernando and Currah 1995; Caldwell et al. 2000). The hyphae of these unidentified taxa can be melanized, hyaline, septate, aseptate, with and without clamp connections, some of them forming microsclerotia and others sclerotial plaques attached to the surfaces of plant roots (Jumpponen and Trappe 1998; Thormann et al. 1999). Extracellular hyphae terminate in appressoria (swollen hyphal structures used for attachment in the early stages of infection) on root surfaces, while others grow intracellularly. These fungi are rarely identified and may belong to the MRA complex (Melin 1922), which partially or entirely overlaps with the dark septate endophyte (DSE) complex of fungi (Jumpponen and Trappe 1998; Caldwell et al. 2000). MRA and DSE taxa occur frequently in roots of herbaceous (Currah et al. 1987; Stoyke and Currah 1991) and woody (Summerbell 1987; Danielson and Visser 1990; Hennon et al. 1990) plants in temperate, alpine, and arctic habitats, including wetlands.

The ecological significance of MRA taxa remains uncertain (Jumpponen and Trappe 1998). Previous work showed that *Phialocephal fortinii* and *Phialophora finlandia* are able to degrade cellulose, laminarin, starch, and xylan, but lignolytic enzymes were not detected (Caldwell et al. 2000); however, PPOs and laccases were reported by Currah and Tsuneda (1993) and Fernando and Currah (1995). On the basis of these enzymatic profiles, Caldwell et al. (1996) suggested that MRA (and DSE) fungi are able to access common detrital C and P polymers. While it is still uncertain if these fungi actually decompose organic matter in situ (Jumpponen and Trappe 1998), they have the potential to play significant roles in decomposition dynamics in peatlands, where they are common (Thormann et al. 1999).

6.2.2 Litter Quality

6.2.2.1 Microfungal Community Analyses

Macromolecules of plant origin comprise the primary substrate available for fungal decomposers in terrestrial ecosystems (Kjøller and Struwe 1992). Lignin, holocellulose, and cellulose are the dominant structural polymers in plant tissues (more than 80 % of all C polymers; Swift et al. 1979). The decomposition of these macromolecules by fungi is accomplished via the synthesis of a diverse suite of extracellular enzymes, including cellulase, PPO, pectinase, and amylase (Deacon 1997). Many fungi have the ability to degrade simple molecules, including starch; however, their ability to degrade complex structural polymers (lignins, tannins, and their derivatives) is limited (Domsch et al. 1980) and has most often been ascribed to basidiomycetes and select groups of ascomycetes, for example, members of the *Xylariaceae*, some of which have wood-decay capabilities and/or are known plant pathogens. As organic matter decomposes, desirable nutrients, such as N, P, amino acids, and simple sugars, become scarce, while more complex structural polymers, such as lignin and lignocellulose, increase proportionally in the litter (Deacon 1997). This generally results in a succession of fungi, both taxonomically and functionally, as plant litters decompose.

Taxonomic succession of fungi during the process of decomposition has been observed in a variety of plant species in terrestrial (Frankland 1966; Saitô 1966; Kasai et al. 1995; Lumley et al. 2001) and wetland (Pugh

1958; Pugh and Mulder 1971; Apinis et al. 1972; Fell and Hunter 1979; Tanaka 1991; Tokumasu 1994; Thormann et al. 2003) ecosystems. This succession of saprobic fungi results in the decomposition of the substrate and may be due to the process of facilitation, where species of a particular behavioral group alter the substrate sufficiently to allow other species to become established and form a subsequent community (Lumley et al. 2001). In wetlands, the majority of fungal community succession studies have been conducted on plants from marshes and swamps, which generally accumulate little or no peat. Species examined include the emergent macrophytes *Juncus roemaerianus* Scheele, *Carex paniculata* L., *Typha latifolia* L., and *Phragmites communis* Trin. (Pugh 1958; Pugh and Mulder 1971; Apinis et al. 1972; Fell and Hunter 1979; Tanaka 1991; Tokumasu 1994). Newly emerged, senesced, and decomposed leaves were examined in these studies; however, neither precise stages of decomposition nor specific litter quality variables were correlated with the fungal communities. In most cases, temperature and moisture content of the litter were cited as environmental variables most significantly affecting the microfungal communities. This is not surprising, since these macrophytes often begin to decompose in the standing position, where they desiccate prior to falling into the water column, where they then continue to decompose. However, most peatland plants do not decompose in this manner; instead, their leaves abscise and moisture is rarely a limiting factor during their decomposition process.

In one of the very few studies that directly linked litter quality changes of specific litters to their microfungal community throughout the process of decomposition in peatlands, Thormann et al. (2003) found that distinct patterns of microfungal succession occurred in two of their five litters [*S. fuscum* (Schimp.) Klinggr. (plants) and *Carex aquatilis* Wahlenb. (leaves)], with litter quality variables correlating most frequently with the respective fungal communities (TP, TN, and TC tissue concentrations as well as litter TC-to-TN quotients; Fig. 6.1). In *S. fuscum* tissues for example, elevated TP tissue concentrations figured prominently during the latter stages of decomposition (365–730 days). In contrast, surface water chemistry variables were of less consequence and of the 13 variables they measured, only the pH and TP in the surface water correlated positively with the microfungal communities of this decomposing bryophyte. A similar trend was observed in the decomposing *C. aquatilis* leaf litter, where TN and TP tissue concentration significantly affected microfungal communities (Fig. 6.1).

Contrary to expectations, a clear succession pattern of functional groups of fungi, previously demonstrated in other substrates (Wicklow and Yokum 1981; Heilman-Clausen 2001; Lumley et al. 2001), was not observed in any of the five litters by Thormann et al. (2003), i.e., cellulose degraders did not precede lignin and polyphenolic polymer degraders.

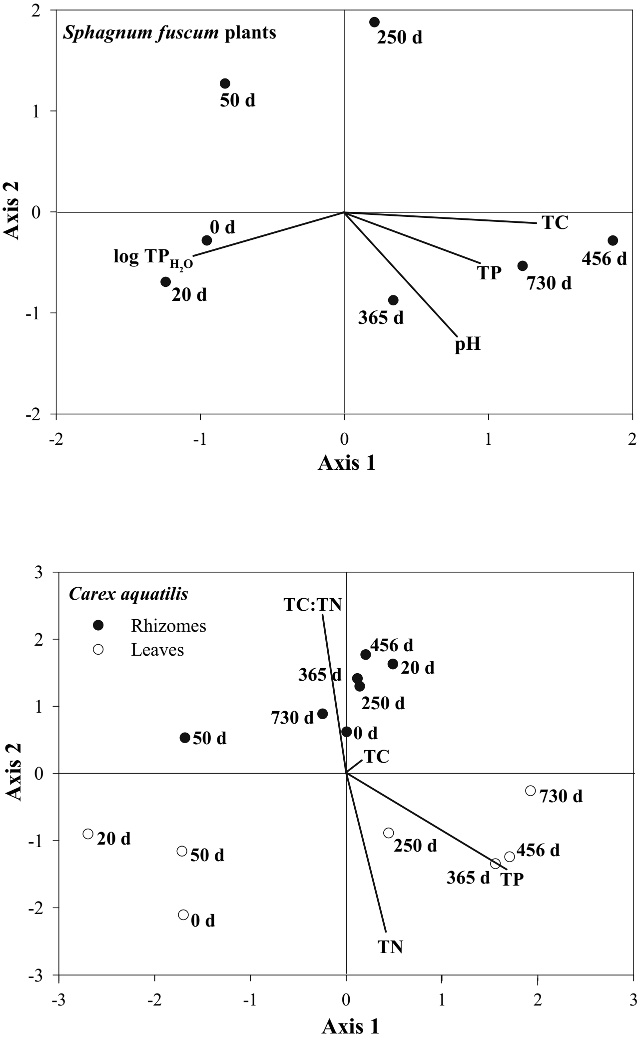

Fig. 6.1. Canonical correspondence analyses of microfungus assemblages isolated from decomposing *Sphagnum fuscum* plants from a bog (eigenvalues for *axes 1* and *2* are 0.367 and 0.255, respectively) and *Carex aquatilis* leaves and rhizomes from a sedge fen (eigenvalues for *axes 1* and *2* are 0.619 and 0.597, respectively) after 0, 20, 50, 250, 365, 456, and 730 days. *TC* total C, *TN* total N, *TP* total P. (Thormann et al. 2003)

Instead, microfungi with broad enzymatic profiles coexisted and simultaneously degraded their litters (Thormann et al. 2003). For example, they determined that species of *Mortierella* (*M. verticillata* Linnem., *M. horticola* Linnem.), *Aspergillus* [*A. niger* van Tieghem, *A. versicolor* (Vuill.) Tiraboschi] and *Trichoderma* [*T. harzianum* Rifai, *T. polysporum* (Link ex Pers.) Rifai] were among those isolated exclusively from early-stage decomposing *S. fuscum*, while *Oidiodendron scytaloides* Gams & Söderström, the *Sporothrix* state of *Ophiostoma stenoceras* (Robak) Melin & Nannf., *Sporothrix* sp. 1, *M. isabellina*, and species of *Acremonium* [*A. chrysogenum* (Thisum. & Sukop.) W. Gams, *A. strictum* W. Gams]

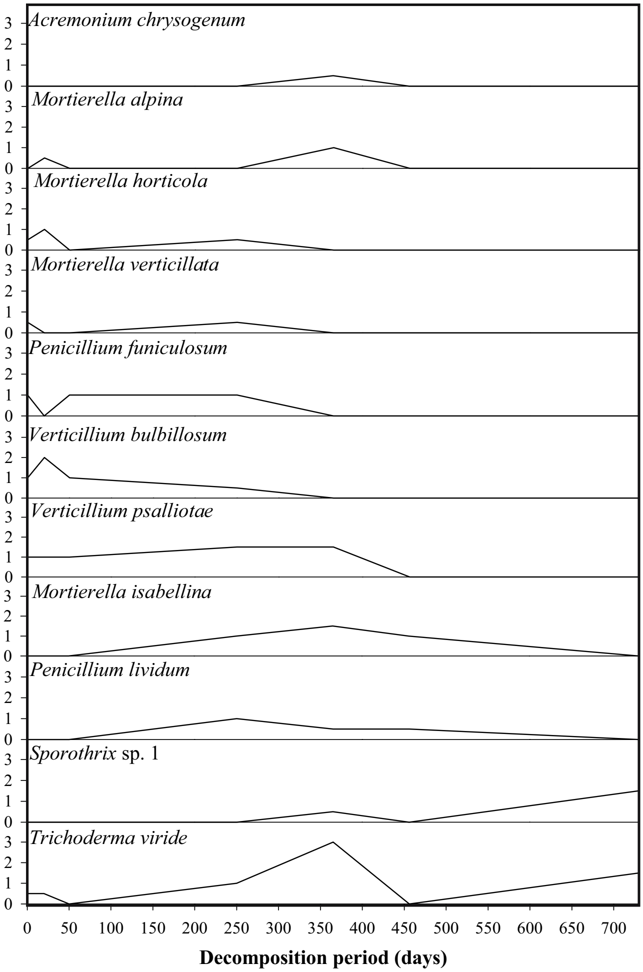

Fig. 6.2. Isolation frequencies of selected microfungi isolated during the 2-year decomposition period of *S. fuscum* in a bog in southern boreal Alberta, Canada. These fungi were selected because of their preponderance during the early to mid (0–365 days) or mid to late (365–730 days) stages of decomposition. Fungi not shown did not show clear isolation patterns during the process of decomposition. (Thormann et al. 2003)

appeared only in well-decomposed *S. fuscum* (Thormann et al. 2003, 2004a; Fig. 6.2). These taxa do not reflect taxonomic or functional patterns of succession.

6.2.2.2 Enzymatic Profiles of Microfungi

Enzymatic profiles of numerous fungi have been developed (Domsch et al. 1980) in order to gain a better understanding of their roles in ecosystems; however, it is difficult to ascertain the relationship between in vitro and in situ enzymatic abilities of fungi, because in vitro analyses present individual fungi with optimal, but highly artificial, growth conditions, for example, ample nutrients for growth and no competition with other organisms. Nonetheless, a positive test result indicates the potential of that fungus to synthesize the specific enzyme(s) under investigation. Enzymatic profiles have been developed for a wide variety of fungi (Domsch et al. 1980). Those from decomposing *S. fuscum* are summarized in Thormann et al. (2001b) and show that of 55 identified/isolated taxa, only 13 (24 %) have the ability to degrade polyphenolic polymers. These included species of *Oidiodendron*, seven anamorphic taxa with putative ascomycete affinities, four of ten sterile taxa, and three basidiomycetes. The degradation of polyphenolic polymers requires the synthesis of a suite of different enzymes owing to the complex arrangement of the basic building blocks of these polymers, including PPOs, laccase, and peroxidases. In contrast, 29 taxa (53 %) degraded cellulose and 31 degraded starch (56 %). Cellulose and starch degraders included species of *Acremonium*, *Penicillium*, *Trichoderma*, *Verticillium*, *Mortierella*, and several sterile taxa (Thormann et al. 2001b). Cellulase and amylase are required for the degradation of these polymers. Pectin, gelatin, chitin, fats, and various other carbohydrates were degraded to variable degrees (7–33 %).

More recent approaches used sterilized natural substrates to assess the role of specific fungal taxa in the decomposition of organic matter. Thormann et al. (2002) examined the ability of nine frequently isolated fungi from *S. fuscum* to cause mass losses of sterilized spruce wood chips and *S. fuscum* plant tissues. They showed that mass losses of the wood ships generally exceeded those of the bryophyte tissues. After 8 weeks, a basidiomycete [*Bjerkandera adusta* (Willd. Fr.) Karst.] and an ascomycete [*Sordaria fimicola* (Rob.) Ces. & de Not.] caused the greatest mass losses of the wood chips (10.2 %) and *S. fuscum* plant tissues (5.1 %) (Table 6.3). The decay of organic matter is controlled by different microfungal communities, likely using different approaches to access C and nutrients from the organic matter (see later; Tsuneda et al. 2001b). There was no relationship between their natural substrate mass losses and in vitro enzymatic profiles of tannic acid, cellulose, and starch degradation (Thormann et al. 2002). This suggests that physiological profiles obtained from calorimetric tests may have a limited use as an indicator of the ability of specific fungi to decompose organic matter. In fact, such relationships have never been shown previously (Harper 1985; Bowen and Harper 1990).

Many fungi previously isolated from peatlands possess broad enzymatic profiles (e.g., species of *Trichoderma*, *Verticillium*, and *Penicillium*) and are able to degrade many structural and storage polymers of peat and peatland plants. Hence, they play crucial roles in the mineralization of plant tissues and peat; however, it appears that the most commonly isolated fungi have a limited ability to degrade the most complex polymers (Thormann et al. 2001b, 2002), which subsequently accumulate in peatlands and increase in proportion with increasing depth in the peat profile

Table 6.3. Mass losses of spruce wood chips and *Sphagnum fuscum* by nine fungal taxa from living and decomposing *S. fuscum* from a bog in southern boreal Alberta. *n*=3 per treatment

Fungal taxa	Substrata	Mass Loss (% ± SE) 4 weeks	 8 weeks
cf. *Bjerkandera adusta*	Spruce wood chips	4.8 (0.3) *a1*	10.2 (1.1) *b1*
	S. fuscum[a]	1.6 (0.6) *a2*	1.7 (0.7) *a2*
Mucor hiemalis	Spruce wood chips	4.3 (0.2) *a1*	4.9 (0.2) *b1*
	S. fuscum	0.3 (0.0) *a2*	0.1 (0.0) *a2*
Oidiodendron maius	Spruce wood chips	4.4 (0.2) *a1*	4.6 (0.2) *a1*
	S. fuscum	1.5 (0.4) *a2*	2.5 (0.5) *a2*
O. scytaloides	Spruce wood chips	3.3 (0.1) *a1*	3.4 (0.5) *a1*
	S. fuscum	3.2 (0.3) *a1*	3.6 (1.2) *a1*
Penicillium thomii	Spruce wood chips	4.2 (0.3) *a1*	5.1 (0.3) *b1*
	S. fuscum	0.5 (0.1) *a2*	1.8 (0.2) *b2*
Pochonia bulbillosa[b]	Spruce wood chips	4.5 (0.6) *a1*	4.6 (0.1) *a1*
	S. fuscum	3.3 (0.4) *a1*	3.9 (0.8) *a1*
Sordaria fimicola	Spruce wood chips	5.2 (0.3) *a1*	5.2 (0.6) *a1*
	S. fuscum	4.2 (1.2) *a1*	5.1 (0.7) *a1*
Sporormiella intermedia	Spruce wood chips	3.5 (0.3) *a1*	5.1 (0.3) *b1*
	S. fuscum	3.4 (0.4) *a1*	3.2 (0.3) *a2*
Trichoderma viride	Spruce wood chips	4.3 (0.1) *a1*	5.6 (0.2) *b1*
	S. fuscum	0.4 (0.0) *a2*	0.5 (0.0) *a2*

Italic letters indicate significant differences in mass losses between decomposition periods for each substratum, while *italic numbers* indicate significant differences in mass losses between the substrata at each decomposition period for each fungal taxon.

[a] In situ mass losses of *S. fuscum* were 14 and 17 % after 4 and 8 weeks, respectively (Thormann et al. 2001a).

[b] Previously reported as *Acremonium* cf. *curvulum* (Thormann et al. 2001b, 2003).

(Turetsky et al. 2000). Whether these polymers are not degraded owing to environmental constraints, such as low temperature or low oxygen concentrations, or physiological constraints of the prevalent microfungal community remains unclear.

6.2.3 Process of *Sphagnum* Decomposition

Bryophytes are the dominant plant in nearly all boreal peatlands, yet remarkably little is known about their fungal communities and how they decompose. In an effort to summarize information on fungi growing on bryophytes, Felix (1988) compiled the first extensive host index for bryophytes. For example, he listed 20 different fungi growing on species of

Sphagnum and only one specifically on *S. fuscum*, the dominant bryophyte in western boreal bogs in Canada. More recently, Thormann et al. (2001b) expanded this list by 55 taxa (28 anamorphic taxa with putative ascomycete affinities, 11 zygomycetes, three ascomycetes, three basidiomycetes, and ten unidentified sterile taxa). Most of the fungi known from *S. fuscum* are cosmopolitan and are not restricted to this bryophyte. In fact, very few fungi are known to colonize exclusively species of *Sphagnum*. Examples include the basidiomycete *Lyophyllum palustre* (Pk.) Singer, the ascomycete *Discinella schimperi* (Naw.) Redhead & Spicer, and the anamorphic taxon *Scleroconidioma sphagnicola* Tsuneda, Currah & Thormann that cause necrosis and death of *S. fallax* (Klinggr.) Klinggr. (Untiedt and Müller 1985), *S. squarrosum* Crome (Redhead and Spicer 1981), and *S. fuscum* (Schimp.) Klinggr. (Tsuneda et al. 2001a, b), respectively.

These parasites, as well as saprobes, produce specific enzymes that degrade plant tissues in a characteristic sequence (Redhead 1981; Untiedt and Müller 1985; Tsuneda et al. 2001a, b). *Oidiodendron maius*, common in peatlands, an ericoid mycorrhizal fungus (see before), and able to degrade tannic acid, cellulose, and starch in vitro (Thormann et al. 2002), degrades all cell wall components of *S. fuscum* simultaneously, resulting in voids. In contrast, *Pochonia bulbillosa* (W. Gams and Malla) Zare & W. Gams (identified as *Acremonium* cf. *curvulum*), reported only once from peatlands (Thormann et al. 2004a) and able to degrade cellulose and starch in vitro (Thormann et al. 2002), sequentially first fragments and removes the outer amorphous cell wall layer, then attacks the central and inner cell wall layers, before finally decomposing the microfibrils of the central cell wall layer, eventually producing localized voids in leaf tissues. A third approach to decompose *S. fuscum* leaf tissues is shown by *Scleroconidioma sphagnicola* (Tsuneda et al. 2001a). This microfungus penetrates into chlorophyllous cells and causes the subsequent degeneration of chloroplasts, causing chlorosis and death of leaf tissues. In addition, its hyphae penetrate into adjacent leaf cells, causing first cavitation and then voids in leaves. This attack mirrors that of *L. palustre* (Redhead 1981; Untiedt and Müller 1985). Hence, modes of decomposition of *Sphagnum* tissues differ among fungi, possibly as a response to pressures from competition and specialized life history strategies. Leaf tissue cell death frequently occurs in advance of fungal hyphae, because the enzymatic activity of fungi is extracellular in nature and secreted enzymes diffuse into plant tissues in advance of the growing hyphae. Untiedt and Müller (1985) described the formation of secondary cell walls in attacked living cells of *S. fallax*, which they ascribed to an increased metabolism in response to the fungal attack. This is unusual and has not been described in similar subsequent ultrastructural microscopy studies of decomposing *Sphagnum* tissues (Tsuneda et al. 2001a, b). However, such defense mechanisms have been shown in elms infected with *Ceratocystis ulmi* (Buisman) C. Moreau (Ouellette 1981). In any event, the defense mechanism is unsuccessful in *Sphagnum*, since infected plants quickly succumb to the fungal attack.

Traditionally, it has been suggested that the inhibitory phenolic compound "sphagnol" (Czapek 1899) and an unusual form of lignin containing *p*-hydroxyphenol units (Lindberg and Theander 1952) retard the decomposition of *Sphagnum* tissues; however, more recent research indicated that *Sphagnum* does not contain any lignin owing to the absence of typical *β*-*O*-4- and phenylcoumaran ^{13}C NMR signals (Nimz and Tutschek 1977) and the lack of methyl-substituted phenolics in the oxidation products of *Sphagnum* tissues (Williams et al. 1998). Instead, two unique polyphenolic polymers, sphagnum acid and butenolide, and *p*-hydroxybenzoic acid appear to be the principal components of *Sphagnum* cell walls that retard microbial attack and subsequent decomposition (Nimz and Tutschek 1977; Rasmussen et al. 1995). These polymers constitute part of the amorphous surface layer of *Sphagnum* cell walls and provide a physical barrier for microorganisms and their extracellular enzymes, particularly cellulases. Hence, the ability to degrade polyphenolic polymers may be a prerequisite for microorganisms to decompose *Sphagnum* tissues in the aerobic zone (Tsuneda et al. 2001b). Consequently, peat, in part, accumulates owing to the apparent scarcity of polyphenolic polymer-degrading fungi in peatlands. Additionally, Freeman et al. (2001) showed that phenol oxidases do not work under anaerobic conditions, i.e., in the catotelm.

6.3 Conclusions

Our understanding of peatland microbial community composition and dynamics and their roles has expanded in recent years; however, how these communities respond to natural and anthropogenic disturbances remains uncertain and needs to be investigated in the near future (Table 6.4). This uncertainty is troublesome in light of a changing climate and associated disturbance regimes, including permafrost degradation and wildfire frequency (Chap. 16), which may have potentially significant impacts on the global C cycle owing to altered mineralization rates of organic matter, especially in peatlands with their significant C stocks.

Table 6.4. Knowledge gaps and future research needs

Disturbances	Issues
Litter quality changes	Elevated atmospheric CO_2 concentrations have the potential to alter leaf litter chemistry and hence decomposition dynamics, possibly altering rates of C and N cycling in ecosystems (O'Neill and Norby 1996; Randlett et al. 1996). Although several studies have examined decomposition rates of leaf litters grown at ambient and elevated CO_2 concentrations, the results were variable and mainly depended on the experimental design, the litter used, and the length of the experiment (Melillo 1983; Rastetter et al. 1992; Randlett et al. 1996; Hirschel et al. 1997). How fungal communities respond to litter quality changes remains largely unknown
Temperature	Temperature has been recognized as an important factor influencing rates of decomposition; however, its effects on microbial populations are rarely examined and only recently have received some attention (Kandeler et al. 1998; Bardgett et al. 1999; Thormann et al. 2004b)
Permafrost degradation	Permafrost in peatlands has recently begun to degrade and continues to degrade at the southern limit of the discontinuous permafrost zone in Canada with no evidence of regeneration (Halsey et al. 1995; Beilman et al. 2001). How microbial communities respond to changes in the local hydrology, insolation, plant community composition, landscape topography, and biogeochemical processes (Beilman 2001; Turetsky et al. 2002) is unknown
Fire	Fire frequency, although highly variable on an annual basis, has increased in the second half of the twentieth century in Canada (Amiro et al. 2001). Many peatlands, particularly bogs, burn regularly, and substantial quantities of peat, and hence C, can be burned off (Turetsky and Wieder 2001). Regardless of the intensity of the fire, fungal communities, which are most prevalent in the fire-prone acrotelm, are affected as well; however, how fungal communities, i.e., colonization dynamics, community structure, and physiological profiles, respond to fire is uncertain

Table 6.4. (*Continued*)

Disturbances	Issues
Polyphenolic polymer-degrading fungi	Few fungi with the ability to degrade complex polyphenolic polymers, primarily basidiomycetes, have been isolated from peat, which is surprising given the widespread occurrence of this group of fungi in adjacent upland ecosystems. Colonization of peatlands by upland basidiomycete taxa is undoubtedly occurring via spores and fruiting body fragments; however, their colonization rates and success in acidic, nutrient-poor peatlands are unknown
Saprobic abilities of specific fungal groups	Mycorrhizal fungi and other root endophytes are prevalent in peatlands and may play significant roles as saprobes, yet their physiological responses to changing environmental conditions are uncertain. This applies to zygomycetes as well, which are frequently isolated from peat, yet their specific roles in peatlands remain largely unknown
Fungal vs. bacterial decomposition dynamics	The relative contribution of fungi and bacteria to organic matter decomposition needs to be clarified. To date, only Thormann et al. (2004b) have compared decomposition dynamics of the most frequently isolated bacteria and fungi from a very limited number of peatland plants. Their data show that these microbial groups respond differently to increasing temperatures in vitro, as determined by altered decomposition dynamics, and hence C dynamics, of peatland plant litters

References

Amiro BD, Stocks BJ, Alexander ME, Flanigan MD, Wotton BM (2001) Fire, climate, carbon and fuel management in the Canadian boreal forest. Int J Wildland Fire 10:405–413

Apinis AE, Chester CGC, Taligoola HK (1972) Colonisation of *Phragmites communis* leaves by fungi. Nova Hedwigia 23:113–124

Bardgett RD, Kandeler E, Tscherko D, Hobbs PJ, Bezemer TM, Jones TH, Thompson LJ (1999) Below-ground microbial community development in a high temperature world. Oikos 85:193–203

Bartsch I, Moore TR (1985) A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Quebec. Can J Bot 63:1241–1248

Beilman DW (2001) Plant community and diversity changes due to localized permafrost dynamics in bogs of western Canada. Can J Bot 79:983–993

Beilman DW, Vitt DH, Halsey LA (2001) Localized permafrost peatlands in western Canada: definition, distributions, and degradation. Arct Antarct Alp Res 33:70–77

Bending GD, Read DJ (1997) Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. Mycol Res 101:1348–1354

Bowen RM, Harper SHT (1990) Decomposition of wheat straw and related compounds by fungi isolated from straw in arable soils. Soil Biol Biochem 22:393–399

Bridgham SD, Richardson CJ (1992) Mechanisms controlling soil respiration (CO_2 and CH_4) in southern peatlands. Soil Biochem 24:1089–1099

Brinson MM, Lugo AE, Brown S (1981) Primary productivity, decomposition and consumer activity in freshwater wetlands. Annu Rev Ecol Syst 12:123–161

Caldwell BA, Trappe JM, Jumpponen A (1996) Physiological characters of dark-septate root endophytes. In: Szaro TM, Bruns TD (eds) 1st international conference on mycorrhizae, 4–9 August 1996.University of California, Berkeley, p 19

Caldwell BA, Jumpponen A, Trappe JM (2000) Utilization of major detrital substrates by dark-septate, root endophytes. Mycologia 92:230–232

Christensen M, Whittingham WF (1965) The soil microfungi in open bogs and conifer swamps in Wisconsin. Mycologia 57:882–889

Clymo RS (1965) Experiments on breakdown of *Sphagnum* in two bogs. J Ecol 53:747–757

Clymo RS (1984) The limits to peat bog growth. Philos Trans R Soc Lond Biol Sci 303:605–654

Clymo RS, Turunen J, Tolonen K (1998) Carbon accumulation in peatlands. Oikos 81:368–388

Currah RS, Tsuneda A (1993) Vegetative and reproductive morphology of *Phialocephala fortinii* (Hyphomycetes, *Mycelium radicis atrovirens*) in culture. Trans Mycol Soc Jpn 34:345–356

Currah RS, Sigler L, Hambleton S (1987) New records and new taxa of fungi from the mycorrhizae of terrestrial orchids of Alberta. Can J Bot 65:2473–2482

Currah RS, Hambleton S, Smreciu A (1988) Mycorrhizae and mycorrhizal fungi of *Calypso bulbosa*. Am J Bot 75:739–752

Czapek F (1899) Zur Chemie der Zellmembranen bei den Laub- und Lebermoosen. Flora (Jena) 86:361–381

Czeczuga B (1993) Aquatic fungi of the Gorbacz and Ostrówski peatbogs. Acta Mycol 28:69–75

Danielson RM, Visser S (1990) The mycorrhizal and nodulation status of container-grown trees and shrubs reared in commercial nurseries. Can J For Res 20:609–614

Deacon JW (1997) Modern mycology, 3rd edn. Blackwell, Boston

Dhillion SS (1994) Ectomycorrhizae, arbuscular mycorrhizae, and *Rhizoctonia* sp. of alpine and boreal *Salix* spp. in Norway. Arct Alp Res 26:304–307

Dix NJ (1985) Changes in relationship between water content and water potential after decay and its significance for fungal successions. Trans Br Mycol Soc 85:649–653

Domsch KH (1960) Das Pilzspektrum einer Bodenprobe. 3. Nachweis der Einzelpilze. Arch Mikrobiol 35:310–339

Domsch KH, Gams W, Anderson T-H (1980) Compendium of soil fungi, vols 1 and 2. Academic, London

Durall DM, Todd AW, Trappe JM (1994) Decomposition of ^{14}C-labelled substrates by ectomycorrhizal fungi in association with Douglas-fir. New Phytol 127:725–729

Farrish KW, Grigal DF (1988) Decomposition in an ombrotrophic bog and a minerotrophic fen in Minnesota. Soil Sci 145:353–358

Felix H (1988) Fungi on bryophytes, a review. Bot Helv 98:239–269

Fell JW, Hunter IL (1979) Fungi associated with the decomposition of the black rush, *Juncus roemerianus*, in south Florida. Mycologia 71:322–342

Fernando AA (1995) *Leptodontidium orchidicola* (*Mycelium radicis atrovirens* complex, Fungi Imperfecti): conidiogenesis and interaction with some subalpine plants in culture. Thesis, University of Alberta, Edmonton

Fernando AA, Currah RS (1995) *Leptodontidium orchidicola* (*Mycelium radicis atrovirens* complex): aspects of its conidiogenesis and ecology. Mycotaxon 54:287–294

Frankland JC (1966) Succession of fungi on decaying petioles of *Pteridium aquilium*. J Ecol 54:41–63

Freeman C, Ostle J, Kang H (2001) An enzymic latch on a global carbon store. Nature 409:149

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195

Halsey LA, Vitt DH, Zoltai SC (1995) Disequilibrium response of permafrost in boreal continental western Canada to climate change. Clim Change 30:57–73

Hambleton S, Currah RS (1997) Fungal endophytes from the roots of alpine and boreal Ericaceae. Can J Bot 75:1570–1581

Hambleton S, Currah RS (2000) Molecular characterization of the mycorrhizas of woody plants. In: Jain SM, Minocha SC (eds) Molecular biology of woody plants. Kluwer, Dordrecht, pp 351–373

Hambleton S, Huhtinen S, Currah RS (1999) *Hymenoscyphus ericae*: a new record from western Canada. Mycol Res 103:1391–1397

Harper SHT (1985) Colonization and decomposition of straw by fungi. Trans Br Mycol Soc 85:655–661

Heilman-Clausen J (2001) A gradient analyses of communities of macrofungi and slime molds on decaying beech logs. Mycol Res 195:575–596

Hennon PE, Shaw CJ, Hansen EM (1990) Symptoms and fungal associations of declining *Chamaecyparis nootkatensis* in southeast Alaska. Plant Dis 74:267–273

Hirschel G, Körner C, Arnone III JA (1997) Will rising atmospheric CO_2 affect leaf litter quality and *in situ* decomposition rates in native plant communities. Oecologia 110:387–392

Hutchison LJ (1990) Studies on the systematic of ectomycorrhizal fungi in axenic culture. II. The enzymatic degradation of selected carbon and nitrogen compounds. Can J Bot 68:1522–1530

Jumpponen A, Trappe JM (1998) Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi. New Phytol 140:295–310

Kandeler E, Tscherko D, Bardgett RD, Hobbs PJ, Kampichler C, Jones TH (1998) The response of soil microorganisms and roots to elevated CO_2 and temperature in a terrestrial model ecosystem. Plant Soil 202:251–262

Kasai K, Morinaga T, Horikoshi T (1995) Fungal succession in the early decomposition process of pine cones on the floor of *Pinus densiflora* forests. Mycoscience 36:325–334

Kjøller A, Struwe S (1992) Functional groups of microfungi in decomposition. In: Carrol GC, Wicklow DT (eds) The fungal community: its organization and role in the ecosystem, 2nd edn. Dekker, New York, pp 631–652

Kox E (1954) Der durch Pilze und aerobe Bakterien veranlaßte Pectin- und Cellulose-Abbau im Hochmoor unter besonderer Berücksichtigung des *Sphagnum*-Abbaus. Arch Mikrobiol 20:111–140

Latter PM, Cragg JB, Heal OW (1967) Comparative studies on the microbiology of four moorland soils in the northern Pennines. J Ecol 55:445–464

Leake JR, Read DJ (1989) Biology of mycorrhiza in the Ericaceae. XIII. Some characteristics of the extracellular proteinase activity of the ericoid endophyte *Hymenoscyphus ericea*. New Phytol 112:69–76

Leake JR, Read DJ (1990) Chitin as a nitrogen source for mycorrhizal fungi. Mycol Res 94:993–995

Lindberg B, Theander O (1952) Studies on *Sphagnum* peat. II. Lignin in *Sphagnum*. Acta Chem Scand 6:311–312

Lumley TC, Gignac LD, Currah RS (2001) Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixedwood region of Alberta. Can J Bot 79:76–92

Malmer N (1986) Vegetation gradients in relation to environmental conditions in northwestern European mires. Can J Bot 64:375–38

Melillo JM (1983) Will increases in atmospheric CO_2 concentrations affect litter decay rates? In: The ecosystem center annual report. Woods Hole Oceanographic Institution, Marine Biological Laboratory, Woods Hole, pp 10–11

Melin E (1922) On the mycorrhizas of *Pinus sylvestris* L. and *Picea abies* Karst. A preliminary note. J Ecol 9:254–257

Monreal M, Berch SM, Berbee M (1999) Molecular diversity of ericoid mycorrhizal fungi. Can J Bot 77:1580–1594

National Wetlands Working Group (1988) Wetlands of Canada. Ecological land classification series, no 24. Sustainable Development Branch, Environment Canada, Ottawa, and Poly Science, Montreal

Nilsson M, Bååth E, Söderström B (1992) The microfungal communities of a mixed mire in northern Sweden. Can J Bot 70:272–276

Nimz MH, Tutschek R (1977) Kohlenstoff-13-NMR-Spektren von Ligninen, 7. Zur Frage des Ligningehalts von Moosen (*Sphagnum magellanicum* Brid.). Holzforschung 31:101–106

O'Neill EG, Norby RJ (1996) Litter quality and decomposition rates of foliar litter produced under CO_2 enrichment. In: Koch GW, Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic, San Diego, pp 87–103

Ouellette GB (1981) Ultrastructural cell wall modifications in secondary xylem of American elm surviving the acute stage of Dutch elm disease. Can J Bot 59:2425–2438

Piercey MM, Thormann MN, Currah RS (2002) Mycorrhizal and saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of *Rhododendron groenlandicum* and *Picea mariana* in culture. Mycorrhiza 12:175–180

Polyakova AV, Chernov IY, Panikov NS (2001) Yeast diversity in hydromorphic soils with reference to a grass-*Sphagnum* wetland in western Siberia and a hummocky tundra region at Cape Barrow (Alaska). Microbiol 70:617–622

Pugh GJF (1958) Leaf litter fungi found on *Carex paniculata* L. Trans Br Mycol Soc 41:185–195

Pugh GJF, Mulder JL (1971) Mycoflora associated with *Typha latifolia*. Trans Br Mycol Soc 57:273–282

Ramstedt M, Söderhäll K (1983) Protease, phenoloxidase and pectinase activities in mycorrhizal fungi. Trans Br Mycol Soc 81:157–161

Randlett DL, Zak DR, Pregitzer KS, Curtis PS (1996) Elevated atmospheric carbon dioxide and leaf litter chemistry: influences on microbial respiration and net nitrogen mineralization. Soil Sci Soc Am J 60:1571–1577

Rasmussen S, Wolff C, Rudolph H (1995) Compartmentalization of phenolic constituents in *Sphagnum*. Phytochem 38:35–39

Rastetter EB, McKane RB, Shaver GR, Melillo JM (1992) Changes in C storage by terrestrial ecosystems: how C-N interactions restrict responses to CO_2 and temperature. Water Air Soil Pollut 64:327–344

Read DJ (1991) Mycorrhizas in ecosystems. Experientia 47:376–391

Read DJ, Leake JR, Perez-Moreno J (2004) Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Can J Bot 82:1243–1263

Redhead SA (1981) Parasitism of bryophytes by agarics. Can J Bot 59:63–67

Redhead SA, Spicer KW (1981) *Discinella schimperi*, a circumpolar parasite of *Sphagnum squarrosum*, and notes on *Bryophytomyces sphagni*. Mycologia 73:904–913

Rice AV, Currah RS (2001) Physiological and morphological variation in *Oidiodendron maius*. Mycotaxon 74:383–396

Saitô T (1966) Sequential pattern of decomposition of beech litter with special reference to microbial succession. Ecol Rev 16:245–254

Salo K (1993) The composition and structure of macrofungus communities in boreal upland type forests and peatlands in North Karelia, Finland. Karstenia 33:61–99

Smith SE, Read DJ (1997) Mycorrhizal symbiosis, 2nd edn. Academic, New York

Sparrow FK, Lange L (1977) Some bog chytrids. Can J Bot 55:1879–1890

Stoyke G, Currah RS (1991) Endophytic fungi from the mycorrhizae of alpine ericoid plants. Can J Bot 69:347–352

Summerbell R (1987) Microfungi associated with the mycorrhizal mantle and adjacent microhabitats within the rhizosphere of black spruce. Can J Bot 67:1085–1095

Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. Blackwell, Oxford

Szumigalski AR, Bayley SE (1996) Decomposition along a bog-fen gradient in central Alberta, Canada. Can J Bot 74:573–581

Tanaka Y (1991) Microbial decomposition of reed (*Phragmites communis*) leaves in a saline lake. Hydrobiol 220:119–129

Thormann MN, Bayley SE (1997) Decomposition along a moderate-rich fen–marsh peatland gradient in boreal Alberta, Canada. Wetlands 17:123–137

Thormann MN, Currah RS, Bayley SE (1999) The mycorrhizal status of the dominant vegetation along a peatland gradient in southern boreal Alberta, Canada. Wetlands 19:438–450

Thormann MN, Bayley SE, Currah RS (2001a) Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. Can J Bot 79:9–22

Thormann M, Currah RS, Bayley SE (2001b) Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta, Canada. Bryologist 104:548–559

Thormann MN, Currah RS, Bayley SE (2002) The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon sources. Can J Microbiol 48:204–211

Thormann MN, Currah RS, Bayley SE (2003) Succession of microfungal assemblages in decomposing peatland plants. Plant Soil 250:323–333

Thormann MN, Currah RS, Bayley SE (2004a) Patterns of distribution of microfungi in decomposing bog and fen plants. Can J Bot 82:710–720

Thormann MN, Bayley SE, Currah RS (2004b) Microcosm tests of the effects of temperature and microbial species number on the decomposition of sedge and bryophyte litter from southern boreal peatlands. Can J Microbiol 50:793–802

Tokumasu S (1994) Trophodynamic structure of a swampy bog at the climax stage of limnological succession III. Filamentous fungi associated with the standing leaves of *Typha latifolia*. Water Air Soil Pollut 76:491–499

Tsuneda A, Chen MH, Currah RS (2001a) Characteristics of a disease of *Sphagnum fuscum* caused by *Scleroconidioma sphagnicola*. Can J Bot 79:1217–1224

Tsuneda A, Thormann MN, Currah RS (2001b) Modes of cell-wall degradation of *Sphagnum fuscum* by *Acremonium* cf. *curvulum* and *Oidiodendron maius*. Can J Bot 79:93–100

Turetsky MR, Wieder RK (2001) A direct approach to quantifying organic matter lost as a result of peatland wildfire. Can J For Res 31:363–366

Turetsky MR, Wieder RK, Williams CJ, Vitt DH (2000) Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta. Écoscience 7:379–392

Turetsky MR, Wieder RK, Vitt DH (2002) Boreal peatland C fluxes under varying permafrost regimes. Soil Biol Biochem 34:907–912

Untiedt E, Müller K (1985) Colonization of *Sphagnum* cells by *Lyophyllum palustre*. Can J Bot 63:757–761

Wicklow DT, Yokum DH (1981) Fungal species numbers and decomposition of rabbit feces. Trans Br Mycol Soc 76:29–32

Williams CJ, Yavitt JB, Wieder RK, Cleavitt NL (1998) Cupric oxide oxidation products of northern peat and peat forming plants. Can J Bot 76:51–62

Williams RT, Crawford RL (1983) Microbial diversity of Minnesota peatlands. Microb Ecol 9:201–214

Zattau WC (1981) Topographic features of chytrids collected from a *Sphagnum* bog. Mycologia 73:1189–1194

7 Decomposition in Boreal Peatlands

Tim Moore and Nate Basiliko

7.1 Introduction

Peatlands are characterized by substantial amounts of organic matter, with stocks commonly 50–150 kg C m^{-2} and accumulation rates between 10 and 30 g C m^{-2} $year^{-1}$ (Gorham 1991; Turunen et al. 2001). These accumulations represent an imbalance between input of C from plant production and its export from the peatland as CO_2, CH_4, or dissolved organic carbon, which are the products of the decomposition of plant tissues and organic matter in the soil. Rates of net primary production in peatlands are generally small (Campbell et al. 2000; Moore et al. 2002; Chap. 8), as are rates of net ecosystem exchange of CO_2 and soil respiration (Frolking et al. 1998; Chap. 9). Thus, the accumulation of organic matter in peatlands is generally ascribed to slow rates of decomposition associated with cool temperatures, anoxic conditions, functionally limited decomposer communities, and litter and organic matter substrates that are naturally slow to decompose. Many studies have measured the rates of litter and organic matter decomposition in peatlands and the controls on these rates. In this chapter, we review their major findings and present some new results. Although the change from plant tissues to peat is part of a continuum, the techniques used to determine rates of litter and peat decomposition are different and thus we treat them separately.

7.2 Litter Decomposition

A common method of determining rates of litter or plant tissue decomposition in soils is to enclose the material in mesh bags, place the bags in the soil profile at the position in which the litter would normally decompose, and then retrieve subsets of the initially placed bags over a number of years and establish the residual mass in the bag and associated changes in

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chemistry, such as C, N, and P contents. This litter-bag method has been criticized because monospecific litters are usually employed, the bags may either exclude soil organisms if the mesh is small or allow litter particles to fall through if the mesh is large and separation of original litter from incorporated soil humus becomes difficult in the late stages of decomposition. Furthermore, there are concerns that the bags may create their own environment in terms of chemistry, water content, and temperature distinct from the environment of the bulk soil. Nevertheless, the method is relatively inexpensive and easily allows comparisons to be made of decomposition rates of distinct litter types at different locations or at different depths in the soil profile. Decomposition rates are fast in warm, well-drained soils with rich litters, but rates are slow in peatlands, so most peatland litter-bag studies lasting for 2 or 3 years show that only a small proportion of the mass has been decomposed, thus tracing only a small proportion of the continuum from litter to peat.

Results may be reported as the proportion of original litter mass remaining after a defined period and/or by assuming a mathematical relationship between the mass and time. A simple exponential decay pattern is assumed in most cases, providing a regression with a constant term (a, the mass at time zero) and a decay constant, frequently given the symbol k, usually on a per year basis (mass remaining equals ae^{kt}). Litter-bag experiments have rarely been run for long enough to evaluate whether a simple exponential decay model adequately explains the longer-term decomposition rate. The exception is a study by Latter et al. (1998), in which four litters (*Rubus* leaves, *Eriophorum* leaves, and *Calluna* stems and shoots) were placed in mesh bags, hair nets, or left unenclosed and retrieved for up to 23 years. Mass loss after 5 years ranged from 70 % (*Rubus* leaves) to 24–55 % for the other tissues. The use of a double exponential decay regression for the 23-year data resulted in an improvement in the proportion of variance explained by 1.5 % (*Calluna* stems), 10.0 % (*Calluna* shoots), to 29.2 % (*Eriophorum*), and an asymptotic model provided the best fit. Nevertheless, a single exponential model commonly fits data from short-term studies of mass loss and facilitates comparison between litter types and environments.

Typical short-term (6 years) decomposition rates of litter in northern peatlands (bog, fen, and swamp) are illustrated in Fig. 7.1. In general, the simple exponential decay model works well, with k values ranging from -0.01 to -0.45 year^{-1} and high coefficients of determination ($r^2>0.8$) when litter decays rapidly. Coefficients of determination, however, can be small ($r^2<0.2$) when decomposition rates are slow, such as in wood blocks or *Sphagnum fuscum*. The intercept value (a) of the regression of mass remaining against time relates to the early mass loss, such as water-soluble material and other labile material within the tissues (Trofymow et al. 2002). Simple exponential decay constants (k) for peatlands collated by lit-

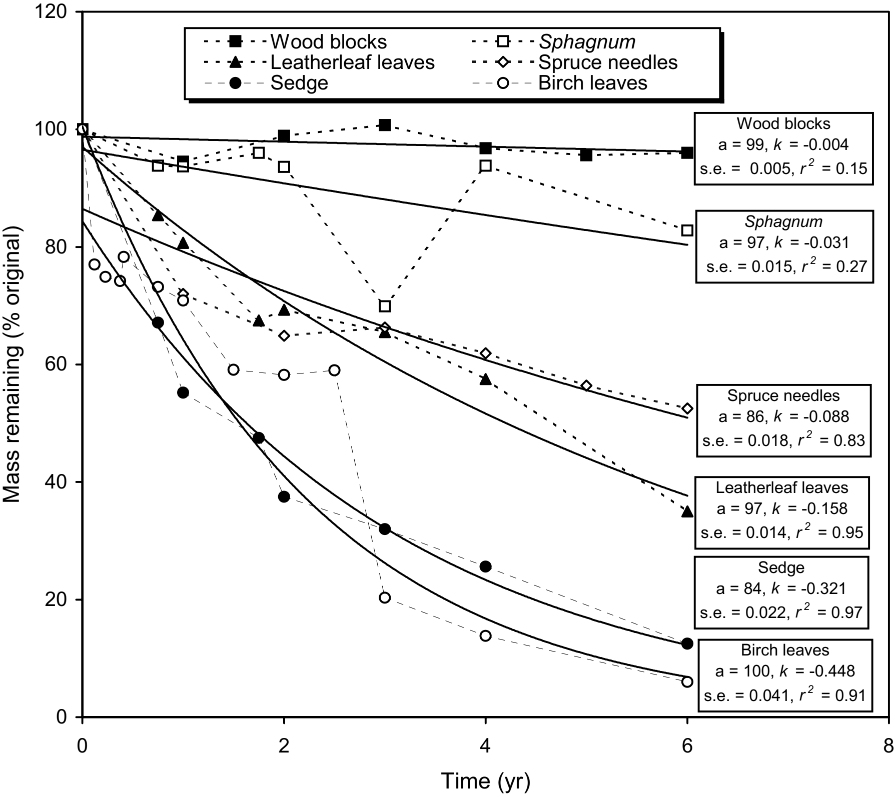

Fig. 7.1. Decomposition rates of litters in representative Canadian peatlands. Western hemlock (*Tsuga heterophylla*) wood blocks and spruce needles (*Picea mariana*) decomposed at a bog near Nelson House, Manitoba (Moore et al. 2006); *Sphagnum* (*S. fuscum*) and sedge (*Carex rostrata*) decomposed at a poor fen near Schefferville, Quebec; leatherleaf leaves (*Chamaedaphne calyculata*) decomposed in a bog near Sept-Îles, Quebec; and yellow birch leaves (*Betula alleghaniensis*) decomposed at a swamp, Mont St. Hilaire, Quebec (Moore, unpublished data). Each value represents the mean of three to four replicate bags collected at each date. The *curved lines* represent the exponential decay regression for each litter type: mass remaining (% original) = ae^{kt}, with t in years. The values for a and k (year^{-1}) are indicated for each tissue, along with the standard error (*s.e.*) of k and the coefficient of determination (r^2)

ter type based on studies at several Canadian peatlands in which mass loss has been measured for 6 years are presented in Table 7.1. In general, the *k* values follow the sequence of decomposition from slowest to fastest of woody material<hummock *Sphagnum*<hollow/lawn *Sphagnum*<tree needles<tree leaves<shrub leaves<sedge. Within the trees and shrubs, evergreen material decomposes at a slower rate than deciduous material. These results are similar to those collated by Aerts et al. (1999), based on *k*

Table 7.1. Exponential decay constants (*k*) for different litter types in northern peatlands, based on studies lasting 6 years (Moore et al. 2005; Moore unpublished data)

Litter type	*k* value Range	Mean	Locations
Wood blocks[a]	−0.00 to −0.01	−0.01	Boreal bogs, central Canada
Tree foliage			
Needles	−0.08 to −0.23	−0.15	Bogs and swamp
Needles[a]	−0.04 to −0.12	−0.09	Bogs and pothole peatland
Leaves	−0.07 to −0.38	−0.22	Bogs and swamp
Leaves[a]	−0.09 to −0.12	−0.11	Bogs and pothole peatland
Shrub stems	−0.23 to −0.27	−0.21	Temperate bog
Shrub leaves			
Evergreen	−0.12 to −0.19	−0.15	Bogs and swamp
Deciduous	−0.19 to −0.23	−0.21	Bogs and swamp
Sedges	−0.16 to −0.44	−0.28	Subarctic fens and boreal bogs
Sphagnum moss			
Hummock species (e.g., *S. fuscum*, *S. rubellum*, *S. capillifolium*)	−0.01 to −0.03	−0.02	Subarctic, boreal, and cool temperate bogs and fens
Hollows/lawn species (e.g., *S. angustifolium*, *S. lindbergii*)	−0.07 to −0.15	−0.08	
Lichen	–	−0.08	Boreal bog

Most results were obtained with litter bags with openings of 1 mm × 2 mm.

[a] Part of the Canadian Intersite Decomposition Experiment in which litter bags with 0.25-mm × 0.50-mm openings were used at sites in central Canada

values calculated for the first year of study. Although there is a general correlation between first-year *k* values and those found after 6 years, differences in decomposition rate develop as the tissues decompose.

7.2.1 Controls on Litter Decomposition

The main controls on litter decomposition in peatlands can be identified as macroclimate and microclimate, position within the peat profile, and litter and peat chemistry. The influence of macroclimate on decomposition rates in forest litters has been well established, showing that decomposition slows as temperatures decrease and becomes faster with increasing precipitation (Meentemeyer 1978; Moore et al. 1999; Trofymow et al. 2002). There have been few litter transplant experiments in peatlands, so this pattern has not been clearly established in peatlands. In a study of leaf litter decomposition rates in Canadian forests, an increase in mean annual temperature from 0 to 10 °C resulted in an average increase in decomposition rates, shown by 6-year *k* values changing from −0.13 to −0.23 year^{-1}, and a decrease from 50 to 22 % of the original mass (Trofymow et al. 2002). At three peatland sites in central Canada, Moore et al. (2005) showed that the overall rate of decomposition of 12 litter types decreased as the mean annual temperature declined, although this pattern was confounded by microclimatic and other effects.

It is often assumed that rates of litter decomposition are slower in upland, well-drained forests than in adjacent peatlands. This pattern is variable. There was a slower decomposition (as shown by less negative *k* values) over 6 years of three tree leaf types in a temperate swamp than in an adjacent deciduous forest (Fig. 7.2). In central Canada, however, the pattern was variable among 12 litters decomposing over 6 years between three pairs of upland and peatland sites (Fig. 7.3). Strong differences between upland and peatland decomposition rates may only develop in

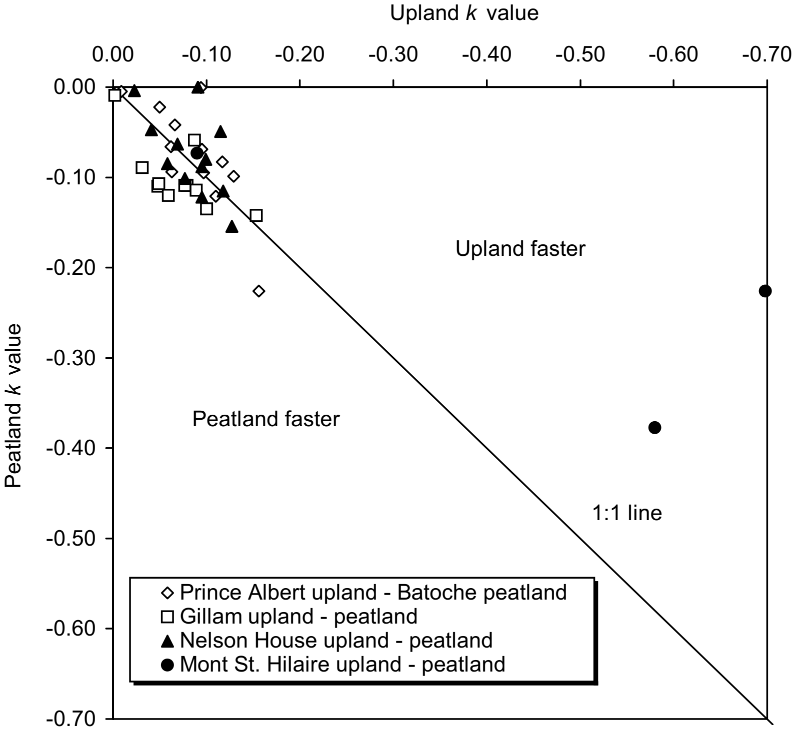

Fig. 7.2. Comparison of exponential decay *k* values for plant tissues decomposing at three peatland and nearby upland forest sites, Canada. Data for the swamp–deciduous forest were obtained at Mont St. Hilaire, southern Quebec (Moore, unpublished data) and for the CIDET sites in central Canada from Moore et al. (2005)

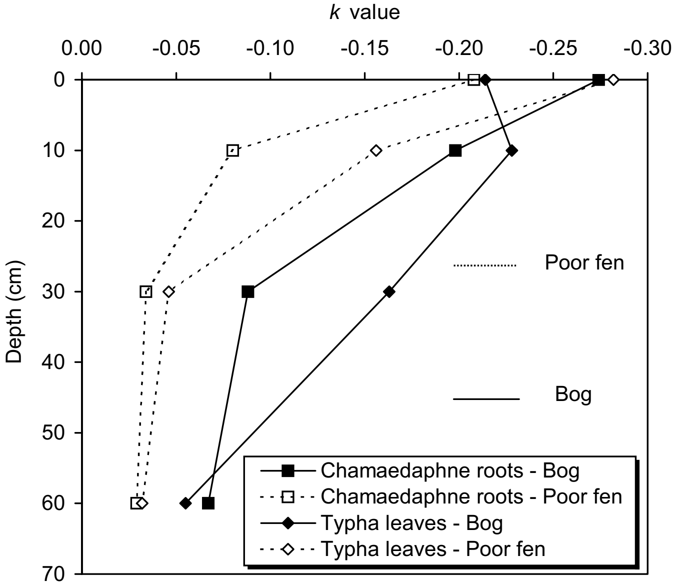

Fig. 7.3. Exponential decay *k* values for *Chamaedaphne calyculata* roots (2–5-mm diameter) and *Typha latifolia* leaves placed in litter bags from the peat surface to 60 cm at a cool temperate bog and poor fen, Mer Bleue, eastern Ontario, calculated over 6 years (Moore, unpublished data). The *horizontal lines* represent the average summer water table position at the two sites. Standard errors of the estimate of the *k* values are not shown, but average 0.02

the later stages of decomposition. The effect of flooding on litter decomposition rates has been examined in several studies with variable results, depending on duration, litter type, and influence of water chemistry (Day 1983, Wylie 1987, Lockaby et al. 1996, Baker et al. 2001). Short periods of flooding may stimulate decomposition, while prolonged flooding may slow rates. Thus, the effect of drainage class on litter decomposition in peatlands may become important after several years for slowly decomposing litter or when the litter is inundated for long periods.

Position within the peat profile can have a profound influence on the rates of litter decomposition, as the lower sections of the peat profile are both cooler and exposed to more frequent anoxic conditions than the surface layers (Clymo 1965). At an ombrotrophic bog and poor fen in eastern Canada, the exponential decay *k* value showed a pronounced change from –0.2 to –0.3 year^{-1} for *Typha latifolia* leaves and *Chamaedaphne calyculata* roots (2–5-mm diameter) placed on the peat surface to –0.05 to –0.10 year^{-1} at depths of 10, 30, and 60 cm (Fig. 7.3). The greatest change was observed in the poor fen, where the water table was closer to the peat surface, keeping the 30- and 60-cm depths waterlogged for nearly all the year, whereas the water table dropped beneath 30 cm for most of the summer at the bog site. In a Swedish bog, Johnson and Damman (1991) also observed a decrease in decomposition rate (mass loss over 22 months) of *Sphagnum* samples placed in oxic or anoxic zones in a hummock. Although much of plant production in peatlands occurs belowground, studies of decomposition of root and rhizomes lag behind those of aboveground components. Thormann et al. (2000) observed rapid decomposition of sedge rhizomes and willow roots placed 3–10 cm beneath the surface of boreal peatlands, and collated data on belowground 1-year mass losses ranging from 15 to 60 % in temperate and boreal peatlands. At a temperate bog, sedge and shrub roots lost between 16 and 52 % and 18 and 66 %, respectively, of their original mass over 5 years, the larger losses occurring at a depth of 10 cm and the smaller losses at 30 or 60 cm in the peat profile (Moore, unpublished data).

Litter chemistry plays an important role in controlling rates of decomposition in peatlands. From studies of upland forests, the lignin and N concentration of litter has been found to exert an important influence on decomposition rate (Meentemeyer, 1978; Trofymow et al. 2002). At three peatland sites in central Canada, the decomposition rate (expressed as the k value over 6 years) of ten upland foliar litters was significantly correlated with the lignin-to-N ratio of the initial litter (Fig. 7.4). This relationship, however, breaks down when nonvascular litters, such as lichen and *Sphagnum* mosses, are included, because of their specific organic composition.

The cause of the very slow decomposition rates of *Sphagnum* (Table 7.1) has been linked to specific organic compounds within the plant tissue, as well as to low concentrations of nutrients such as N and P. Verhoeven and Liefveld (1997) reviewed organochemical compounds produced by *Sphagnum*, noting the production of phenolics and uronic acids as well as "sphagnol" and "sphagnum acid," which negatively affect vascular plant growth and aid in the preservation of bodies (Painter 1991). These compounds also slow down the rate of decomposition of plant tissues, through acidification and the inhibition of microbial decay of litter. The latter is supported by the inhibition of Gram-positive bacteria by *Sphagnum* extracts (Banerjee and Sen 1979) and the slowed rates of decomposition of sedge and moss tissues in laboratory experiments when homogenized *Sphagnum* capitula were added (Verhoeven and Toth 1995). There are variations in the rate at which *Sphagnum* mosses decompose: hummock mosses decompose at slower rates than those found in hollows, even though the decay environment is less favorable in the hollows (Johnson and Damman 1993). Johnson and Damman (1993) suggested that rates of *Sphagnum* decay could be negatively correlated to the concentration of polyuronic acid and positively to the nonstructural carbohydrate content,

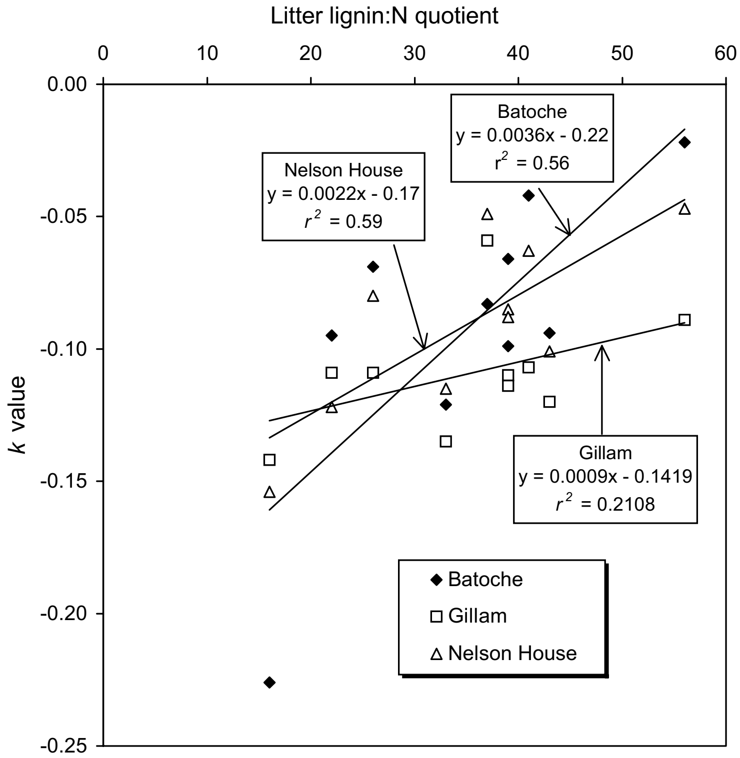

Fig. 7.4. Relationship between lignin-to-N quotient and exponential decay *k* value for ten leaf litters over 6 years placed on the peat surface at three peatland sites in central Canada. The litters comprised aspen, beech, and birch leaves; western red cedar, Douglas fir, jack pine, black spruce, and tamarack needles; and grass and bracken fern. The regression between the quotient and *k* value is shown. (Moore et al. 2005)

and Limpens and Berendse (2003) also suggested that N concentration is important, although P concentration may also play a role.

7.2.2 Peat Decomposition

Plant litter becomes peat through partial decomposition. Peat mineralization is constrained by many of the same factors as litter mineralization; however, because rates are slower and particle sizes can be too small for containment within mesh bags, in vitro incubations and measurement of gaseous mineral products have more commonly been used to investigate controls. Although many of the specific microbial mechanisms involved in both partial decomposition of plant litter resulting in peat formation and subsequent peat mineralization are still not fully understood, a great deal of work has been done investigating broad controls on peat mineralization.

Lignin and other polymeric phenolic molecules, including sphagnum acid, originally derived from woody tissues and *Sphagnum*, are degraded to monomeric phenolics only under aerobic conditions by various microbial oxidase enzymes (Freeman et al. 2001); however, decomposition proceeds slowly even under aerobic conditions owing to pH constraints of these enzymes (Williams et al. 2000). As a result, mineralization is rapider under aerobic than anaerobic conditions (Moore and Dalva 1993; Yavitt et al. 1997; Glatzel et al. 2004), a key factor in peat accumulation. Although the anoxic separation of polymeric phenolic molecules either cannot occur or has not yet been characterized, anaerobic metabolic pathways leading to and including methanogenesis still contribute to production of organic decomposition products and partial mineralization of peat. In the 1920s, Waksman and Stevens (1929) described *Sphagnum*-derived peat soils as a mixture of partially decomposed plant residue and secondary microbial products. Owing to analytical constraints, since the 1920s our understanding of molecular structures of microbially formed peat has not improved greatly, especially for high molecular weight polymeric molecules.

The partial decomposition of phenolic molecules through anaerobic fermentations produces, in part, several short-chain fatty acids that provide a C substrate for other microbial activities and ultimately a suitable redox potential and a C substrate for methanogenesis (Bräuer et al. 2004; Chap. 9). In the presence of more energetically profitable electron acceptors, particularly oxidized inorganic N, Fe, or S, methanogens, especially when they utilize the aceticlastic pathway, cannot compete well for fatty acids. Rates of microbial denitrification are usually low and do not contribute largely to C turnover, as incoming inorganic oxidized N in unpolluted to moderately polluted sites is largely retained by vegetation (Li and Vitt 1997; Williams et al. 1999; Chap. 10). Microbial Fe reduction has not been demonstrated to contribute substantially to C turnover, and total Fe concentrations are low particularly in northern bogs (Robert et al. 1999; Basiliko and Yavitt 2001). Despite relatively low inputs of S to most northern peatlands, microbial S reduction can contribute to the anaerobic mineralization of C (Vile et al. 2003a, b; Chap. 12). Sulfate reduction potentials measured in the laboratory are often high, despite low inputs of oxidized S (Blodau and Moore 2003). This probably indicates internal recycling between oxidized and reduced S species (Wieder and Lang 1988; Wieder et al. 1990) either by the temporary presence of O_2, perhaps as delivered by vascular roots as demonstrated in other ecosystems (Wind and Conrad 1997), or there may be a yet-unidentified organic electron acceptor that could reoxidize reduced S (Blodau et al. 2002).

Many studies have quantified production of CO_2 and CH_4 as a proxy for peat decomposition (Chap. 9). Measuring gaseous release of mineral C is both rapid and a relevant measure of microbial activity to C and greenhouse gas budgets of peatlands, but it is important to note that these are only terminal decomposition products. Although controls on mineralization rates of peat to CO_2 and CH_4 often are assumed to correlate with controls on bulk decomposition, it must be recognized that mineralization of peat is a final step of a much more detailed, and poorly understood, set of processes.

Microbial CO_2 production cannot be measured directly in situ because living *Sphagnum* and vascular roots throughout peat also produce CO_2. In vitro incubation of peat in the absence of plant respiration has commonly been used to investigate controls on relative rates of decomposition between sites, throughout depths or under different laboratory conditions (Moore and Dalva 1997; Yavitt et al. 1997; Scanlon and Moore 2000; Basiliko and Yavitt 2001; Blodau et al. 2004; Glatzel et al. 2004). Advantages to using in vitro incubation techniques include utilizing peat of any age as opposed to fresh plant litter with mesh bags, rapidity, and the ability to capture the effects of nutrient and chemical changes in recently formed plant litter and peat arising; for example, from increased nutrient deposition. On the other hand, incubation techniques inevitably involve severe sample disturbance, introduce artificial environmental conditions, and estimate decomposition rates over very short periods of time. At best, these techniques may indicate relative rates of peat decomposition, and because they are carried out under controlled and often idealized conditions they are often described as potential CO_2 production measurements.

We suggest that potential CO_2 production rates likely occur as a function of in situ substrate, nutrient, and microbial biomass potential to mineralize peat. For example, aerobic CO_2 production potentials determined in 416 samples from a wide range of sites in eastern Canadian peatlands revealed positive correlations with extractable organic N and P and microbial biomass C and N (Figs. 7.5, 7.6). Within more constrained sets of samples, for example indicated with closed circles in Figs. 7.5 and 7.6, correlations with single potentially controlling factors were stronger, similar to patterns reported by Turetsky (2004) across peatlands in the boreal discontinuous permafrost region of central Canada. The size of the microbial biomass, which presumably results from substrate and nutrient availability and suitable environmental conditions and relates to decomposition and mineralization rates, may be similar to that of forest soils. On average, our 416 peat samples from eastern Canadian sites had biomass values similar to those reported for organic layers of southern Canadian conifer forests, and both organic portions of forest soils and peats had much smaller biomass than mineral agricultural soils when normalized for soil organic C (Table 7.2). Our samples were biased toward less humified peat

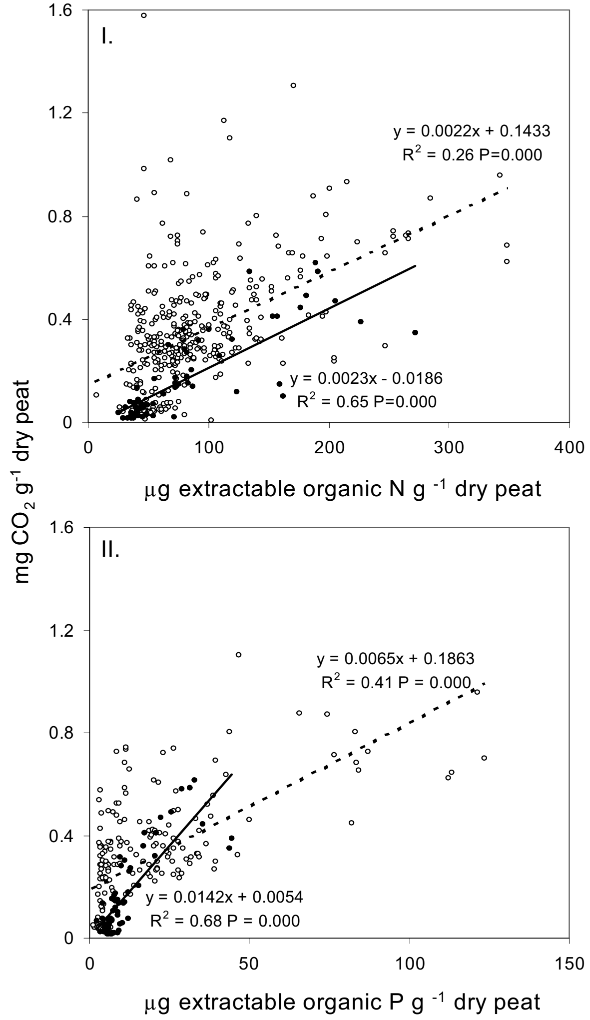

Fig. 7.5. Relationships between K_2SO_4-extractable organic N (*I*) and P (*II*) and aerobic CO_2 production potential in peat from nine eastern Canadian peatlands in pristine condition or undergoing commercial harvesting or nutrient fertilization taken at different times of year and throughout depth (Basiliko and Moore, unpublished data). *Data points* and regressions in *closed circles* represent peat collected on one sampling date at sites from one region near Shippagan, New Brunswick

from the upper 0.5 m of the peat deposit, whereas highly humified peat had much less biomass than forest soils, and it may be this highly recalcitrant fraction that supports small biomass and is responsible for the larger C storage functions in peatlands relative to forests (Table 7.2). Owing to both different measurement techniques and differential C extraction efficiencies among soils, comparisons of microbial biomass must be interpreted with caution.

Potential CO_2 production has been used in many previous studies to determine controls on peat decomposition. Rates generally depend on peat temperature, availability of oxygen, vascular plant activity, environmental fluctuations, and chemical characteristics (Moore and Dalva 1993;

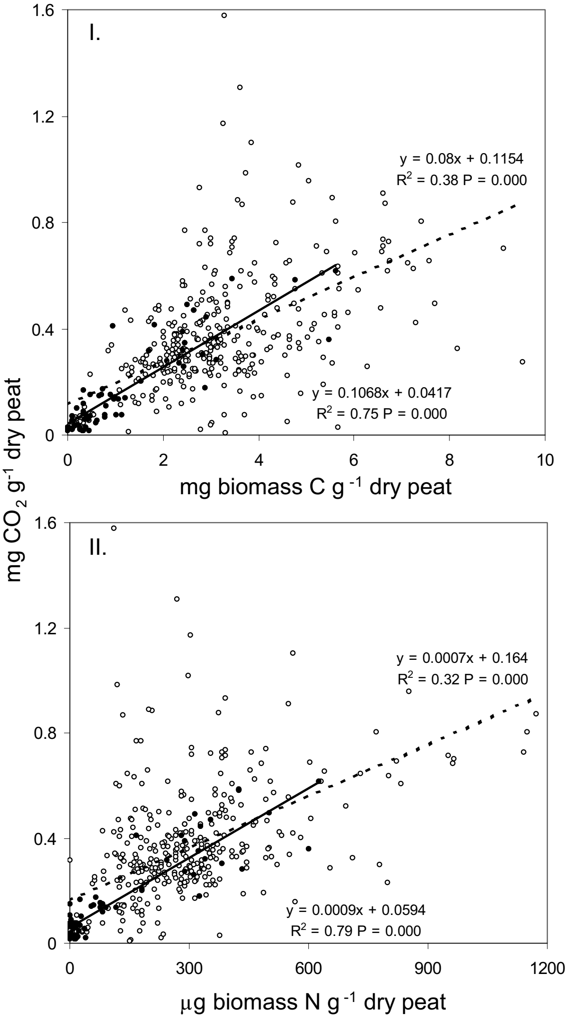

Fig. 7.6. Relationships between microbial biomass C (*I*) and N (*II*), determined with $CHCl_3$ fumigation–extraction and CO_2 production potential in peat from nine eastern Canadian peatlands in pristine condition or undergoing commercial harvesting or nutrient fertilization taken at different times of year and throughout depth (Basiliko and Moore, unpublished data). *Data points* and regressions in *closed circles* represent peat collected on one sampling date at sites from one region near Shippagan, New Brunswick

Thomas et al. 1996; Yavitt et al. 1997). Potential CO_2 production responds to a 10 °C change in temperature, within the 2–23 °C range, by a factor of approximately 2.2–2.4 (Moore and Dalva 1993; Yavitt et al. 1997), although smaller, and site- and depth-specific, responses to changing temperatures have also been reported (Scanlon and Moore 2000). Potential CO_2 production in aerobic incubations is greater than in anaerobic incubations, but the pattern is very variable, varying by a factor of 1.2 (Yavitt et al. 1997) to 200 (Hogg 1993), although factors of 2–6 are more common (Moore and Dalva 1997; Glatzel et al. 2004) The activity of vascular plants (Thomas et al. 1996) and *Sphagnum* mosses (Fenner et al. 2004) in releasing photosynthates to the peat profile also apparently provides a labile C source that

Table 7.2. Microbial biomass C in Canadian mineral agricultural soils under various crops (Arshad et al. 2004), organic soils in mixed conifer stands (Leckie et al. 2004), and nine eastern peatlands (Basiliko and Moore, unpublished data) expressed per gram of dry soil and per gram of soil organic C (*SOC*). Humified peat samples were from commercially harvested sites, where harvesting exposed deep, old peat to the surface. Organic C content of forest humus and peat was assumed to be 50 %

Soil type	Microbial biomass mg microbial C g^{-1} soil	mg microbial C g^{-1} SOC
Mineral soils with crops		
Smooth brome	1.08	25.0
Red fescue	1.16	25.9
Continuous wheat	0.93	23.7
Wheat–canola rotation	0.86	21.4
Wheat–pea rotation	0.86	23.1
Wheat–fallow rotation	0.87	23.5
Forest soils		
Cedar–hemlock, forest floor	4.27	8.5
Cedar–hemlock, upper humus	2.88	5.8
Cedar–hemlock, lower humus	1.84	3.7
Hemlock–amibilis fir, forest floor	3.75	7.5
Hemlock–amibilis fir, upper humus	2.77	5.5
Hemlock–amibilis fir, forest floor	1.49	3.0
Peatlands		
All peat samples (*n*=416)	2.80	5.6
Humified peat (*n*=60)	0.31	0.6

contributes to microbial CO_2 production (however, Thomas et al. 1996 and Fenner et al. 2004 used isotope tracer techniques and not CO_2 production potential assays). Labile trigger molecules may enhance decomposition of bulk peat (Basiliko et al., unpublished data). Water table fluctuations leading to drying and wetting of peat, or freeze–thaw cycles, may also increase decomposition rates (Wynn-Williams 1982; Freeman et al. 1997).

Peat chemical characteristics play a large role in decomposition and mineralization rates (Updegraff et al. 1996; Yavitt et al. 1997; Turetsky 2004); however, Yavitt et al. (1997) has suggested that among *Sphagnum*-dominated sites, very subtle chemical differences may be responsible for variability in mineralization rates. Chemical fractionation or proximate analyses as well as total and extractable nutrient concentrations have been used to characterize the chemical nature of peat (Waksman and Stevens 1928; Yavitt et al. 1997; Turetsky 2004). Although these methods do not illustrate exact molecular composition, they group molecules and compounds into classes that may relate to bioavailability. Fractionation methods traditionally rely, at least in part, on high-temperature oxidation in strong acids and extractions. N and P concentrations or quality have the potential to influence decomposition rates (Turetsky 2004; Fig. 7.5); however, traditional measures, such as lignin-to-N or acid insoluble material-to-N quotients that can predict organic matter mineralization rates across other terrestrial ecosystems, are apparently only successful across some (Turetsky 2004), but not all, *Sphagnum*-derived peats (Yavitt et al. 1997).

Methanogenesis, an important terminal anaerobic decomposition step, is carried out in peatlands by a group of strictly anaerobic euryarchaeota that utilize nine 1-C or 2-C organic acids or H_2 (Zinder 1993), and it is unclear if and when aceticlastic or hydrogenitrophic methanogenesis is the more common methanogenic pathway in peatlands (Hornibrook et al. 1997; Duddleston et al. 2002; Chap. 9). Similar to microbial CO_2 production, many studies utilize laboratory incubations to examine controls on CH_4 production. Methanogens rely on substrates produced by fermentative bacteria, and peat organic matter quality has been related to rates of CH_4 production (Updegraff et al. 1996; Yavitt et al. 1997). Substrates otherwise available for methanogenesis may be more readily utilized by sulfate reducers in the presence of oxidized S, through inferior thermodynamic competition (Nedwell and Watson 1995). Alternatively, buildup of moderate to large concentrations of acetate inhibits CH_4 production (Bräuer et al. 2004). Methanogens are strict anaerobes, and following flooding and initiation of anoxia, CH_4 production is usually characterized by a lag period until rapid rates are achieved (Basiliko and Yavitt 2001). Methane production is also dependent on temperature and pH (Dunfield et al. 1993; Moore and Dalva 1993), and response to temperature is greater than for potential CO_2 production with Q_{10} factors of about 4 (Segers 1998). Micronutrients that are not limiting for many other organisms may limit methanogenesis (Basiliko and Yavitt 2001). Simultaneous anaerobic CH_4 and CO_2 production potential measurements have shown that more CO_2 than CH_4 (molar basis) is produced, although CH_4 and CO_2 production potentials often correlate, indicating that similar controlling factors may exist (Moore and Dalva 1997; Glatzel et al. 2004). In peat from North American peatlands, anaerobic CH_4 production potential over 30 days ranged from 3 to 21 % of CO_2 produced (Basiliko and Yavitt 2001).

Some estimate of relative decomposition rates, compared with rates for fresh litter, can be made. Scanlon and Moore (2000) incubated undisturbed cores from the upper part of peat profiles in a temperate bog under varying temperature and oxic/anoxic conditions. From these results, and thermal and water table regimes at the site, they estimated that *k* values ranged from -0.05 year^{-1} at a depth of 10–20 cm to -0.002 to -0.02 year^{-1} at a depth of 40–50 cm. Using transplants of peat, Belyea (1996) estimated rates of -0.01 to -0.08 year^{-1} from beneath the water table to close to the surface in a Scottish peatland. Wieder (2001) used ^{210}Pb-dating of the surface layers of three bogs in Alberta to estimate *k* values ranging from 0 to -0.12 year^{-1}, with average values over the top 30 cm of -0.02 to -0.03 year^{-1}. Analyzing profiles of bogs, Clymo et al. (1998) estimated that decay rates in the catotelm of bog profiles ranged from -1×10^{-4} to -1×10^{-8} year^{-1}, showing an increase with mean annual temperature. Thus, there is consistency in boreal peatland decomposition *k* values ranging from -0.03 to -0.30 year^{-1} in fresh plant tissues (from mosses to nutrient-rich leaves) to -0.02 to -0.0001 year^{-1} in the upper and lower parts of the profile.

Many boreal and cool temperate peatlands have been harvested for their peat, especially for horticultural peat moss. Global production of peat amounted to 28×10^6 t in 2000 (Jasinski 2001). Most of the harvested peat decomposes in an aerobic environment, mixed with mineral soil or other substrates or fertilizer and exposed to a wider range of soil fauna than in a bog. There are few studies of the rates of peat decomposition when added to well-drained soils, but the results of Aendekerk (1997) and Murayama et al. (1990) suggest that decomposition rates are much accelerated, with first-year mass losses of between 5 and 25 % when placed in mineral aerobic soils. Cleary et al. (2005) have shown that for the peat extraction industry in Canada, this poorly understood rate of decomposition of the harvested peat dominates the C cycle, and deserves further attention.

7.3 Conclusions

The slow rates of decomposition of plant tissues and peat are critical to the accumulation of large amounts of organic matter in boreal peatlands. This slowness is a combination of the poor nutrient content and high refractory content of most peatland plants and the underlying peat, the generally cool and frequently anoxic conditions in which the plant tissues and peat decompose, and small microbial populations, when normalized to soil organic C content. Although several studies have identified and quantified the influence of these controls of decomposition rates for individual peatlands, we still lack a coherence, compared with forest or grassland systems, in the application of this knowledge to the broad range of peatlands that occur with boreal environments under both natural and disturbed (such as drained, harvested, or flooded) conditions or under climate-change scenarios.

References

Aendekerk TGL (1997) Decomposition of peat substances in relation to physical properties and growth of chamaecyparis. Acta horticulturae 450:191–198

Aerts R, Verhoeven JTA, Whigham DF (1999) Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology 80:2170–2181

Arshad MA, Franzluebbers AJ, Azooz RH (2004) Surface-soil structural properties under grass and cereal production on a Mollic Cyroboralf in Canada. Soil Tillage Res 77:15–23

Baker TT, Lockaby BG, Conner WH, Meier CE, Stanturf JA, Burke MK (2001) Leaf litter decomposition and nutrient dynamics in four southern forested floodplain communities. Soil Sci Soc Am J 65:1334–1347

Banerjee RD, Sen SP (1979) Antibiotic activity of bryophytes. Bryologist 82:141–153

Basiliko N, Yavitt JB (2001) Influence of Ni, Co, Fe, and Na additions on methane production in *Sphagnum*-dominated northern American peatlands. Biogeochemistry 52:133–153

Belyea LR (1996) Separating the effects of litter quality and macroenvironment on decomposition rates in a patterned peatland. Oikos 77:529–539

Blodau C, Moore TR (2003) Micro-scale CO_2 and CH_4 dynamics in a peat soil during a water fluctuation and sulfate pulse. Soil Biol Biochem 35:535–547

Blodau C, Roehm CL, Moore TR (2002) Iron, sulfur, and dissolved carbon dynamics in a northern peatland. Achiv Hydrobiol 154:561–583

Blodau C, Basiliko N, Moore TR (2004) Carbon turnover in peatland mesocosms exposed to different water table levels. Biogeochemistry 67:331–351

Bräuer SL, Yavitt JB, Zinder SH (2004) Methanogenesis in McLean Bog, an acidic peat bog in upstate New York: stimulation by H_2/CO_2in presence of rifampicin, or by low concentrations of acetate. Geomicrobiol J 21:433–443

Campbell C, Vitt DH, Halsey LA, Campbell ID, Thormann MN, Bayley SE (2000) Net primary production and standing biomass in northern continental wetlands. Canadian Forestry Service information report NOR-X-369. Canadian Forestry Service, Edmonton

Cleary J, Roulet NT, Moore TR (2005). Greenhouse gas emissions from Canadian peat extraction, 1990-2000: a life-cycle analysis. Ambio 34:456–461

Clymo RS (1965) Experiments on breakdown of *Sphagnum* in two bogs. J Ecol 53:737–757

Clymo RS, Turunen J, Tolonen K (1998) Carbon accumulation in peatland. Oikos 81:368–388

Day FP (1983) Effects of flooding on leaf litter decomposition in microcosms. Oecologia 56:180–184

Dunfield P, Knowles R, Dumont RT, Moore TR (1993) Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. Soil Biol Biochem 25:321–326

Duddleston KN, Kinney MA, Kiene RP, Hines ME (2002) Anaerobic microbial biogeochemistry in a northern bog: acetate as a dominant metabolic end product. Global Biogeochem Cycles 16. DOI 10.1029/2001GB001402

Fenner N, Ostle N, Freeman C, Sleep D, Reynolds B (2004) Peatland carbon efflux partitioning reveals that *Sphagnum* photosynthate contributes to the DOC pool. Plant Soil 259:345–354

Freeman C, Liska G, Ostle NJ, Lock MA, Hughes S, Reynolds B, Hudson J (1997) Enzymes and biogeochemical cycling in wetlands during a simulated drought. Biogeochemistry 39:177–187

Freeman C, Ostle N, Kang H (2001) An enzymatic ‘latch’ on global carbon store. Nature 409:149

Frolking S, Bubier JL, Moore TR, Ball T, Bellisario LM, Bhardwaj A, Carroll P, Crill PM, Lafleur PM, McCaughey JH, Roulet NT, Suyker AE, Verma SB, Waddington JM, Whiting GJ (1998) The relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. Global Biogeochem Cycles 12:115–126

Glatzel SN, Basiliko N, Moore TR (2004) Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, eastern Québec, Canada. Wetlands 24:261–267

Gorham E (1991) Northern Peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195

Hogg HE (1993) Decay potential of hummock and hollow *Sphagnum* peats at different depths in a Swedish raised mire. Oikos 66:269–278

Hornibrook ERC, Longstaff FJ, Frye WS (1997) Spatial distribution of microbial methane production pathways in temperate zone wetland soils: stable carbon and hydrogen isotope evidence. Geochim Cosmochim Acta 61:745–753

Jasinski SM (2001) Peat. Mineral Commodity Summaries, January, 2001. US Department of the Interior: US Geological Survey, Washington, DC

Johnson LC, Damman AWH (1991) Species controlled *Sphagnum* decay on a south Swedish raised bog. Oikos 61:234–242

Johnson LC, Damman AWH (1993) Decay and its regulation in *Sphagnum* peatlands. Adv Bryol 5:249–296

Latter PM, Howson G, Howard DM, Scott WA (1998) Long-term study of litter decomposition on a Pennine peat bog: which regression? Oecologia 113:94–103

Leckie SE, Prescott CE, Grayston SJ, Neufeld JD, Mohn WW (2004) Characterization of humus microbial communities in adjacent forest types that differ in nitrogen availability. Microbial Ecol 48:29–40

Li Y, Vitt DH (1997) Patterns of retention and utilization of aerially deposited nitrogen in boreal peatlands. Écoscience 4:106–116

Limpens J, Berendse F (2003) How litter quality affects mass loss and N loss from decomposing *Sphagnum*. Oikos 103:537–547

Lockaby BG, Wheat RS, Clawson RG (1996) Influence of hydroperiod on litter conversion to soil organic matter in a floodplain forest. Soil Sci Soc Am J 60:1989–-1993

Meentemeyer V (1978) Macroclimate and lignin control of litter decomposition rates. Ecology 59:465–472

Moore TR, Dalva M (1993) The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatlands soil. J Soil Sci 44:651–664

Moore TR, Dalva M (1997) Methane and carbon dioxide exchange potentials of peat in aerobic and anaerobic laboratory incubations. Soil Biol Biochem 29:1157–1164

Moore TR, Bubier JL, Frolking SE, Lafleur PM, Roulet NT (2002) Plant biomass and production and CO_2 exchange in an ombrotrophic bog. J Ecol 90:25–36

Moore TR, Trofymow JA, Taylor B, Prescott C, Camiré C, Duschene L, Fyles J, Kozak L, Kranabetter M, Morrison I, Siltanen M, Smith S, Titus B, Visser S, Wein R, Zoltai S (1999) Litter decomposition rates in Canadian forests. Global Change Biol 5:75–82

Moore TR, Trofymow JA, Siltanen M, Prescott C, CIDET Working Group (2005) Patterns of decomposition and carbon, nitrogen and phosphorus dynamics of litter in upland forest and peatland sites, central Canada. Can J For Res 35:133–142

Moore TR, Trofymow JA, Prescott CE, Fyles J, Titus BD, CIDET Working Group (2006) Patterns of carbon, nitrogen and phosphorus dynamics in decomposing foliar litter in Canadian forests. Ecosystems (in press)

Murayama S, Asakawa Y, Ohno Y (1990) Chemical properties of subsurface peats and their decomposition kinetics under field conditions. Soil Sci Plant Nutr 36:129–140

Nedwell D, Watson A (1995) CH_4 production, oxidation and emissions in a UK ombrotrophic peat bog: influence of SO_4^{2-} from acid rain. Soil Biol Biochem 27:893–903

Painter TJ (1991) Lindow Man, Tollund Man and other peat-bog bodies: the preservative and antimicrobial action of Sphanan, a reactive glycurnoglycan with tanning and sequestering properties. Carbohydr Polym 15:123–142

Robert EC, Rochefort L, Garneau M (1999) Natural revegetation of two block-cut mined peatlands in eastern Canada. Can J Bot 77:447–459

Scanlon D, Moore TR (2000) Carbon dioxide production from peatland soil profiles: the influence of temperature, oxic/anoxic conditions and substrate. Soil Sci 165:153–160

Segers R (1998) Methane production and methane consumption: a review of processes underlying wetland methane fluxes. Biogeochemistry 41:23–51

Thomas KL, Benstead J, Davies KL, Lloyd D (1996) Role of wetland plants in the diurnal control of CH_4 and CO_2 fluxes in peat. Soil Biol Biochem 28:17–23

Thormann MN, Bayley SE, Currah RS (2000) Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta. Can J Bot 79:9–22

Trofymow JA, Moore TR, Titus B, Prescott C, Morrison I, Siltanen M, Smith S, Fyles J, Wein R, Camiré C, Duschene L, Kozak L, Kranabetter M, Visser S (2002) Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can J For Res 32:789–804

Turetskey MR (2004) Decomposition and organic matter quality in continental peatland: the ghost of permafrost past. Ecosystems 7:740–750

Turunen J, Pitkänen A, Tahvanainen T, Tolonen K (2001) Carbon accumulation in West Siberian mires, Russia. Global Biogeochem Cycles 15:285–296

Updegraff K, Pastor J, Bridgham SD, Johnston CA (1996) Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecol Appl 5:151–163

Verhoeven JTA, Liefveld WM (1997) The ecological significance of organochemical compounds in *Sphagnum*. Acta Bot Neerl 46:117–130

Verhoeven JTA, Toth E (1995) Decomposition of *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibition by living tissue homogenates. Soil Biol Biochem 27:271–275

Vile MA, Bridgham SD, Wieder RK, Novak M (2003a) Atmospheric sulfur deposition alters pathways of gaseous carbon production in peatlands. Global Biogeochem Cycles 17:1058. DOI 10.1029/2002GB001966

Vile MA, Bridgham SD, Wieder RK (2003b) Response of anaerobic carbon mineralization rates to sulfate amendments in a boreal peatland. Ecol Appl 13:720–734

Waksman SA, Stevens KR (1928) Contribution to the chemical composition of peat I. Chemical nature of organic complexes in peat and methods of analysis. Soil Sci 26:113–137

Waksman SA, Stevens KR (1929) Contribution to the chemical contribution of peat. II. The role of microorganisms in peat formation. Soil Sci 28:315–340

Wieder RK (2001) Past, present and future carbon balance – an empirical model based on ^{210}Pb-dated cores. Ecol Appl 11:321–336

Wieder RK, Lang GE (1988) Cycling of inorganic and organic sulfur in peat from Big Run Bog, West Virginia. Biogeochemistry 5:221–242

Wieder RK, Yavitt JB, Lang GE (1990) Methane production and sulfate reduction in 2 Appalachian peatlands. Biogeochemistry 10:81–104

Williams B, Silcock D, Young M (1999) Seasonal dynamics of N in two *Sphagnum* moss species and the underlying peat treated with $^{15}NH_4{}^{15}NO_3$. Biogeochemistry 45:285–302

Williams CJ, Shingara EA, Yavitt JB (2000) Phenol oxidase activity in peatlands in New York state: response to summer drought and peat type. Wetlands 20:416–421

Wind T, Conrad R (1997) Localization of sulfate reduction in planted and unplanted rice field soil. Biogeochemistry 37:253–278

Wylie GD (1987) Decomposition and nutrient dynamics of litter of *Quercus palustris* and *Nelumbo lutea* in a wetland complex of Southeast Missouri, U.S.A. Arch Hydrobiol 111:95–106

Wynn-Williams DD (1982) Simulation of seasonal changes in microbial activity of maritime Antarctic peat. Soil Biol Biochem 14:1–12

Yavitt JB, Williams CJ, Wieder RK (1997) Production of methane and carbon dioxide in peatland ecosystems across North America: effects of temperature, aeration, and organic chemistry of peat. Geomicrobiol J 14:299–316

Zinder SH (1993) Physiological ecology of methanogens. In: Ferry JG (ed) Methanogenesis: ecology, physiology, biochemistry, and genetics. Chapman and Hall, New York, pp 128–206

8 Primary Production in Boreal Peatlands

R. Kelman Wieder

8.1 Introduction

Primary production is arguably the most important ecological function of peatland ecosystems, as long-term and substantial peat accumulation, the hallmark of peatlands, depends on inputs of new plant organic matter, viz., net primary production. Moore and Bellamy (1974) state that "Peatlands are, by definition, unbalanced systems in which the rate of production of organic material by living organisms exceeds the rate at which these compounds are respired and degraded." Similarly, Crum (1992) notes that "It is only when plant growth exceeds decomposition that organic matter accumulates as sodden peat." Such claims, while seemingly self-evident, are overstatements that reveal a decided peatland bias. Indeed, the accumulation of organic matter in soils, as a result of an excess of production over decomposition over long periods of time, is essentially universal across terrestrial ecosystems. Even in systems with tiny soil organic matter stores compared with peatlands, these stores represent the integrated long-term excess of net primary production over decomposition.

What makes peatlands unique then is the *magnitude* of the long-term imbalance between net primary production and decomposition that has led to the impressive and massive quantities of organic matter presently stored in these ecosystems worldwide. In boreal peatlands, the huge quantities of peat are especially impressive given that the accumulation has occurred over such a short period of time, 5,000–7,000 years, during the Holocene. Commonly, peat accumulation in boreal environments is ascribed to the slow rates of decomposition in the cold, anoxic, sometimes acidic and sometimes nutrient-deficient catotelm layer (deeper, permanently water-saturated peat layer) of the peat deposit (Clymo 1984; Chap. 7). Clymo (1984) gives an overall estimate of the exponential decay rate for the catotelm of 0.00014 year^{-1} (equivalent to a residence time of nearly 7,150 years), which provides a quantitative measure of the exceptionally slow turnover of organic matter in the catotelm. However, peat

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accumulation in the acrotelm (surface peat, above the catotelm) is very sensitive to even small changes in both net primary production and decomposition (Wieder 2001). The fate of net primary production in the acrotelm determines the quantity and quality of organic matter that is eventuallytransferred into the catotelm (Clymo 1984). Thus, it is rather futile to attribute peat accumulation primarily to net primary production *or* decomposition throughout the entire peat column; it is the *balance* between these two functions that is important.

To understand factors that can influence past, present, and future peat accumulation, it is critical that we understand factors that can influence past, present, and future peatland net primary production. This chapter reviews net primary production in boreal peatland ecosystems by vegetation type, with a focus on what is known about the factors that influence net primary production. For the most part, studies that have reported growth responses in metrics that are not useful for estimating net primary production (e.g., growth in length of *Sphagnum* or other mosses, growth in leader length or basal area for trees) have not been incorporated into this synthesis.

8.2 *Sphagnum* Production

Understandably, most research on peatland production has centered on *Sphagnum* species. Of the vascular and nonvascular plant species that contribute to peat accumulation, *Sphagnum* is the most important, at least for bogs and poor fens (Chap. 2). Clymo and Hayward (1982) note that the genus *Sphagnum* probably stores more carbon in its recognizable plant remains as peat than any other plant genus worldwide. Methods for measuring *Sphagnum* production are well established (Clymo 1970). Recent reviews have compiled data on *Sphagnum* production for Canadian peatlands (Campbell et al. 2000) and globally (Gunnarsson 2005). Gunnarsson (2005) reports that globally, *Sphagnum* production of individual species at individual sites ranges from 8 to 1,450 g m^{-2} $year^{-1}$, with an overall mean of 259 g m^{-2} $year^{-1}$ (±206 standard deviation; 68 sites), with most of the sites from boreal and subboreal peatlands in the northern hemisphere. In light of these recent reviews, this section will focus on a synthesis of the factors that influence peatland *Sphagnum* growth and production.

8.2.1 Nitrogen

Although *Sphagnum* production in boreal peatlands has generally been thought to be nitrogen-limited (Chap. 10), early studies in the UK suggested that elevated atmospheric nitrogen deposition could alter competitive interactions among *Sphagnum* species, as well as inhibit the growth of some *Sphagnum* species, ultimately leading to the loss of these species from UK peatlands (Press and Lee 1982; Woodin et al. 1985; Press et al. 1986; Chap. 10). More recent studies have revealed that although boreal *Sphagnum*-dominated ombrotrophic bogs in pristine regions in general are nitrogen-deficient, the response of the *Sphagnum* layer to enhanced atmospheric nitrogen deposition is triphasic. With increasing atmospheric nitrogen deposition (1) nitrogen limits *Sphagnum* production such that increased nitrogen deposition leads to increased moss growth/production, (2) nitrogen is no longer limiting, but increases in nitrogen deposition are transferred to increases in the organic nitrogen concentration in living *Sphagnum* tissues, and (3) the living *Sphagnum* layer becomes nitrogen-saturated such that inorganic nitrogen bypasses the living *Sphagnum* layer and is transferred downward (Lamers et al. 2000; Berendse et al. 2001; Limpens and Berendse 2003; Limpens et al. 2003a; Bragazza et al. 2004). For *Sphagnum fuscum*, phase 1 may span nitrogen deposition values up to 16 kg ha^{-1} $year^{-1}$, with higher nitrogen deposition leading to diminished production (Vitt et al. 2002).

Field nitrogen fertilization studies have produced mixed results, in part attributable to variation in preexisting background nitrogen deposition levels. Fertilization studies conducted where background nitrogen deposition was low (western Canada, northern Minnesota, and northern Sweden) have generally shown enhanced nitrogen uptake and attendant increased *Sphagnum* growth/production (Bayley et al. 1987; Rochefort et al. 1990; Aerts et al. 1992; Li and Vitt 1997; Chapin et al. 2004), although one study in northern Sweden found no effect of nitrogen fertilization on *Sphagnum* production (Aerts et al. 2001). Where background nitrogen deposition is high, nitrogen fertilization has produced either no effect or repression of *Sphagnum* production (Austin and Wieder 1987; Aerts et al. 1992, 2001; Gunnarsson and Rydin 2000), suggestive of either phase 2 or phase 3 of the triphasic response.

8.2.2 Other Nutrient Effects on Production

8.2.2.1 Sulfur

Tallis (1964) suggested that acid rain (elevated deposition of acidity and nitrogen- and sulfur-containing compounds) across the UK could be causally related to an observed demise of peatland *Sphagnum* species. Subsequent research demonstrated that atmospheric sulfur compounds (SO_2, HSO_3^-, SO_4^{2-}) indeed could exert inhibitory influences on the photosynthesis, growth, and survival of *Sphagnum* species (Ferguson et al. 1978;

Ferguson and Lee 1979, 1980, 1983). Although the dominant form of sulfur in atmospheric deposition, SO_4^{2-}, appears to have little or no inhibitory influence on *Sphagnum* growth/production (Ferguson et al. 1978; Austin and Wieder 1987; Gunnarsson et al. 2004), sulfate deposition can influence other ecosystem-level processes in boreal peatlands (Chap. 12).

8.2.2.2 Phosphorus and Potassium

Under conditions of high nitrogen deposition, nitrogen limitation of the *Sphagnum* layer in peatlands may shift to phosphorus limitation (Aerts et al. 1992; Chap. 11). A field fertilization study (Limpens et al. 2004) confirmed that at moderate and high nitrogen deposition sites *Sphagnum* growth (height growth and net primary production) is phosphorus-limited, and also showed that when phosphorus is added to the *Sphagnum* layer, *Sphagnum* can take up some of the excess atmospherically deposited nitrogen that otherwise would be transported downward below the growing moss layer. However, in a fertilization and liming experiment in subboreal northern Minnesota (Chapin et al. 2004), phosphorus addition did not ameliorate the negative effects of the high nitrogen fertilization on *Sphagnum fuscum/capillifolium* production. Under conditions of elevated nitrogen deposition and elevated atmospheric CO_2, nitrogen and phosphorus concentrations of *Sphagnum* species were unaffected, while potassium concentrations decreased, suggesting a shift to potassium limitation of growth (Hoosbeek et al. 2002). A synoptic study of *Sphagnum* nitrogen-to-phosphorus and nitrogen-to-potassium ratios also suggested a shift to phosphorus and/or potassium limitation under conditions of high atmospheric nitrogen deposition (Bragazza et al. 2004). High nitrogen deposition, coupled with enhanced phosphorus availability, may alter competitive interactions between *Sphagnum* species, leading to increased dominance by relatively minerotrophic species, such as *Sphagnum fallax* (Limpens et al. 2003b).

8.2.3 Carbon Dioxide

With increasing interest in the effects of elevated atmospheric CO_2 levels on terrestrial ecosystems (Norby et al. 1999), some research has focused on photosynthetic responses of peatland *Sphagnum* to elevated CO_2 (Silvola 1990; Jauhiainen and Silvola 1999). Laboratory studies of peatland *Sphagnum* growth responses to elevated CO_2 and elevated nitrogen deposition (Jauhiainen et al. 1994, 1999; van der Heijden et al. 2000) have produced somewhat ambiguous results, contributed in part by both interspecies and intraspecies variability in *Sphagnum* responses. All of this work has focused on European locations. The European Bog Ecosystem Research Initiative (BERI) represents the only field CO_2 enhancement experiment in boreal peatlands, implemented using free-air CO_2 enrichment (FACE) technology. After 3 years of exposure to elevated CO_2, *Sphagnum* (mainly *S. magellanicum*, *S. balticum*, *S. papillosum*, and *S. fallax*; Hoosbeek et al. 2002) net primary production was unaffected at all four BERI sites (Hoosbeek et al. 2001). It remains uncertain whether increasing atmospheric CO_2 concentration, in and of itself, will have any substantial effect on *Sphagnum* net primary production in boreal peatlands.

8.2.4 Climate and Moisture

The distribution of mosses, and in particular of *Sphagnum* species, has been shown to be closely related to climatic factors, such as mean annual precipitation and mean annual temperature (Gignac et al. 1998). In light of the wide distribution of *Sphagnum* mosses, attempts have been made to relate *Sphagnum* production to broad climatic gradients (Damman 1979; Wieder and Lang 1983; Moore 1989; Rochefort et al. 1990; Vitt 1990). The most geographically comprehensive effort in this regard is that of Gunnarsson (2005), who compiled literature data to assess patterns in *Sphagnum* production in relation to taxonomic sections (Cuspidata>Acutifolia), field microhabitat (hummock, lawn, carpet; about 200, 260, and 370 g m^{-2} $year^{-1}$, respectively), geographic factors (latitude, altitude, distance to the sea), and broad climatological factors. Mean annual temperature and mean annual precipitation explained over 30 % of the total variation in production across all *Sphagnum* species (Gunnarsson 2005).

On a more local scale, moisture availability appears to influence *Sphagnum* production. *Sphagnum* plants appear to grow best during the cool and humid conditions that characterize spring and autumn, with slower growth during hotter, drier summer months (Brock and Bregman 1989; Lindholm 1990). For poor fens in northern Quebec, production of hummock sphagna (58–73 g m^{-2} $year^{-1}$) was greater than lawn sphagna (9–19 g m^{-2} $year^{-1}$) (Bartsch and Moore 1985) and in an poor fen in Ontario (Canada), production of *Sphagnum* species was greater on hummocks than on either hollows or on “midhummocks” (Rochefort et al. 1990). In both of these studies, differences in *Sphagnum* net primary production could be attributed both to differences in the relative abundance of *Sphagnum* species along these microtopographic gradients and to differences in the production of individual *Sphagnum* species depending on microtopographic location (Vitt 1990). Gunnarsson’s (2005) broad geographic synthesis revealed that *Sphagnum* production was greater on carpets than on lawns or on hummocks, attributable in part to peatland microtopographic moisture gradients.

8.3 True Moss Production

There is a paucity of data on production of true mosses in boreal peatlands. In a nonpermafrost bog in Manitoba, Reader and Stewart (1972) reported production of *Aulacomnium palustre* and *Polytrichum juniperinum* as 5.4 and 35 g m^{-2} $year^{-1}$, respectively. Across two boreal and three montane rich fens in Alberta, Canada, Vitt (1990) reported production values for *Tomenthypnum nitens*, *Campylium stellatum*, *Drepanocladus revolvens*, and *Scorpidium scorpioides* of 55–131, 58–78, 65–109, and 60–170 g m^{-2} $year^{-1}$, respectively. Thormann and Bayley (1997) reported production for *Aulacomnium palustre* and *Drepanocladus aduncus* in an Albertan moderate rich fen in two different years of 136–405 and 27–121 g m^{-2} $year^{-1}$, respectively. In another moderate rich fen in Alberta, Busby et al. (1978) reported production of *Hylocomium splendens* and *Tomenthyphum nitens* of 79 and 190 g m^{-2} $year^{-1}$.

Vitt (1990) examined microtopographic effects on overall moss (natural communities consisting predominantly of *Sphagnum fuscum*, *Sphagnum magellanicum*, *Sphagnum angustifolium*, *Tomenthypnum nitens*, *Campylium stellatum*, *Drepanocladus revolvens*, and *Scorpidium scorpioides*) production in bogs, poor fens, boreal rich fens, and montane rich fens of Alberta, Canada. Across all peatland types, production was higher in carpets than in lawns. For bogs, production was lower in hummocks than in lawns, but in poor fens and rich fens, production in hummocks was greater than or equal to production in lawns.

Responses of boreal peatland-dwelling true mosses to broad climatic gradients has received little attention. The distribution and abundance of several boreal peatland true mosses have been successfully modeled using mean annual temperature and mean annual precipitation (Gignac et al. 1991a, b; Gignac 1992). Vitt (1990) examined annual growth increments of *H. splendens* and *Polytrichum strictum* from herbarium specimens collected from locations across nonarctic North America. Growth of the drought-tolerant, ectohydric *H. splendens* was highly variable across its boreal range, but was correlated with both precipitation and continentality. In contrast, growth of the less drought tolerant, endohydric, *Polytrichum strictum* was more constant and could not be related to climatic variability. Despite these efforts, the net primary production response of true mosses to broad climatic gradients is not well understood.

Little effort has been made to examine nutrient effects on true moss production, although there is some evidence that *Tomenthypnum nitens* production may be limited by nitrogen (Bayley et al. 1987; Rochefort and Vitt 1988), at least in geographical locations where ambient atmospheric nitrogen deposition is low. In a cutover bog in the Swiss Jura Mountains (Mitchell et al. 2002), *Polytrichum strictum* production over a 3-year period was stimulated by elevated nitrogen levels (535 and 931 g m^{-2}, respectively, in control and elevated nitrogen treatments, difference significant), but was similar in control and elevated CO_2 treatments (525 and 629 g m^{-2}, respectively, difference not significant).

While Gunnarsson's (2005) synthesis suggested that true moss production in boreal peatlands was generally lower than *Sphagnum* production for western Canadian peatlands, Vitt (1990) concluded that *Sphagnum* species and brown mosses had similar production values. In rich fen ecosystems dominated by true mosses, *Sphagnum* mosses may be a relatively minor contributor to overall moss production. Our understanding of the chemical and climatic factors that influence true moss production in boreal peatlands is deficient.

8.4 Herbaceous Species and Field Layer Production

Herbaceous species are much more abundant in minerotrophic fens than in ombrotrophic bogs although production data for total herbaceous species in either boreal bogs or boreal fens are sparse. Total herb production at an Albertan bog, measured in three different years, was 8.5, 14.5, and 34 g m^{-2} $year^{-1}$, and was contributed by *Rubus chamaemorus*, *Smilacina trifolia,* and *Eriophorum vaginatum* (Szumigalski 1995; Thormann 1995). Grigal et al. (1985) reported total herb production for a raised and a perched bog in Minnesota of 14 and 22 g m^{-2} $year^{-1}$, respectively. Ranges for total herb production for an extremely rich fen (mainly from *Scirpus cyperinus*, *Muhlenbergia glomeratum*, *Triglochin* spp., and *Juncus* spp.), moderately rich fens (mainly from *Carex* spp., *Menyanthes trifoliata*, *Potentilla palustris*, and *Smilacina trifolia*), and a poor fen (mainly from *Carex* spp., *Menyanthes trifoliata*, and *Smilacina trifolia*) in Alberta were 81.4–96.9, 52.3–302.0, and 51.6–55.3 g m^{-2} $year^{-1}$, respectively (Szumigalski 1995; Thormann 1995). No data have been reported for belowground herbaceous species production in boreal bogs.

In a fertilization and liming experiment in two subboreal peatlands in northern Minnesota (Chapin et al. 2004), bog graminoid (*Carex oligosperma* and *E. spissum*) aboveground production was unaffected by any treatment and fen graminoid (mainly *Carex exilis*, with smaller contributions from *Rhynchospora alba*, *Scheuchzeria palustris*, *Rhynchospora fusca*, and *Carex lasiocarpa*) aboveground production was elevated only by the high nitrogen and high phosphorus fertilization with lime in the third year of the study.

Carex rostrata is an indicator of minerotrophy in peatlands, and as such is found in fens, but not bogs (Chap. 2). Aboveground production of *Carex rostrata* has been reported as 90, 116, and 176±15 (standard error) g m^{-2} $year^{-1}$ at a moderately rich fen in Quebec (Bartsch and Moore 1985), a shrubby peatland in Manitoba (Reader and Stewart 1972), and a mesotrophic fen in southern Finland (Saarinen 1996), respectively. At the last site, *Carex rostrata* rhizomes, coarse root, and fine root production was 113±32, 82±22, and 1,053±135 g m^{-2} $year^{-1}$, such that aboveground production was only 12% of total production (Saarinen 1996). At the moderately rich fen in Quebec (Bartsch and Moore 1985), *Carex aquatilis* production was 164 g m^{-2} $year^{-1}$.

There is a paucity of recent research on the factors that influence herbaceous species production in boreal peatlands. In contrast, some of the earliest research on nutrient limitation in peatland ecosystems focused on the responses of herbaceous species. These early studies (Tamm 1954; Gore 1961 a, b; Goodman and Perkins 1968 a, b) found no consistent influence of nitrogen, phosphorus, potassium, calcium, or magnesium on growth (data were not presented as net primary production) for peatland species including the herbaceous species *E. vaginatum*, *Molinea caerulea*, and *Dactylis glomerata.* More recently, however, enhanced atmospheric nitrogen deposition and associated increased nitrogen availability in European bogs has been implicated as a possible cause of increased invasion of the grass *Molinea caerulea*, as well as the small tree *Betula pubescens* (Limpens et al. 2003a), although a shift to phosphorus limitation may limit vascular plant success (Tomassen et al. 2004). Herbaceous production in boreal peatlands and the factors that influence it remain poorly understood.

8.5 Shrub Production

Although shrubs, especially in the Ericaceae, can be a dominant feature of many peatland types, production data for the total shrub layer in either boreal bogs or boreal fens are sparse. Total shrub production at a bog in Alberta, measured in three different years, was 77, 97, and 117 g m^{-2} $year^{-1}$, and was contributed mainly by *Ledum groenlandicum*, *Vaccinium vitis-idaea*, *Andromeda polifolia*, *Chamadeaphne calyculata*, and *Oxycoccos quadripetalus* (Szumigalski 1995; Thormann 1995). Reader and Stewart (1972) reported total shrub production for a Manitoba bog of 316 g m^{-2} $year^{-1}$, contributed mainly by *Chamaedaphne calyculata*, *Ledum groenlandicum*, *V. vitis-idaea*, *O. quadripetalus*, and *Kalmia polifolia*. Grigal et al. (1985) reported total shrub production for a raised and a perched bog in Minnesota of 200 and 43 g m^{-2} $year^{-1}$, respectively, contributed mainly by *Ledum groenlandicum* and *Chamaedaphne calyculata*. Ranges for total shrub production for a wooded moderately rich fen (mainly from *Andromeda polifolia,* *B. pumila*, and *Salix pedicularis*), a shrubby moderately rich fen (mainly from *Andromeda polifolia* and *Salix pedicularis*), and a shrubby poor fen (mainly from *B. pumila*, *Salix pedicularis*, and *Andromeda polifolia*) in Alberta were 96–120, 7–52, and 112–157 g m^{-2} $year^{-1}$, respectively (Szumigalski 1995; Thormann 1995). No data have been reported for belowground shrub production in boreal peatlands. *Myrica gale*, with root-associated nitrogen fixers, can form dense stands in peatlands of North America and Europe (Skene et al. 2000). At a temperate-zone peatland in central Massachusetts, USA, aboveground and belowground production of *Myrica gale* was reported as 392 and 157 g m^{-2} $year^{-1}$, respectively, with nitrogen fixation providing 43 % of the nitrogen supporting this production (Schwintzer 1983).

Little research has focused on the factors that influence shrub production in boreal peatlands. Fertilization (phosphorus and potassium) and drainage of a bog in southern Finland dramatically increased aboveground production of the shrub layer (defined by the author as comprising small *Pinus sylvestris*, *B. pendula*, and *B. pubescens*) from 2.4 to 12.5 g m^{-2} $year^{-1}$, as well as belowground production of the shrub layer from 0.7 to 3.1 g m^{-2} $year^{-1}$ (Vasander 1982). Fertilization with nitrogen, phosphorus, and potassium increased production of *Chamaedaphne calyculata* from 31 to 115 and from 55 to 198 g m^{-2} $year^{-1}$ in the first and second years of treatment at Caribou Bog in Maine, USA, but did not influence production at a nearby weakly minerotrophic poor fen (average production in control and fertilized sites over 2 years of 294 g m^{-2} $year^{-1}$; Bartsch and Schwintzer 1994). Lack of a response at the fen site appears to have been related to an inherently higher nutrient availability. To examine aboveground net primary production responses, a subboreal bog and a poor fen in northern Minnesota were fertilized with two levels of nitrogen and phosphorus, with or without lime additions (Chapin et al. 2004). For the bog, *Chamaedaphne calyculata* production was enhanced by phosphorus, but not nitrogen, addition, although this effect disappeared with liming. The bog shrub *Ledum groenlandicum* exhibited a complex fertilization and liming interaction, while the bog shrubs *V. oxycoccus* and *K. polifolia* and the fen shrub *Andromeda glaucophylla* had no clear responses to fertilization or liming. Overall, for either the bog or the fen, total shrub layer production in any of the treatments, however, did not differ from control shrub layer production (Chapin et al. 2004). As with herbaceous production, shrub production in boreal peatlands and the factors that influence it remain poorly understood.

8.6 Tree Production

Production of tree species on boreal peatlands has received little attention, and data on belowground production are especially sparse. Because there are only a few dominant tree species in boreal peatlands worldwide, the information that exists can be easily addressed by species.

Black spruce, *Picea mariana*, is a dominant tree species in ombrotrophic peatlands (bogs) of North America, and it also occurs as a major species in poor fens (Chap. 2). *Picea mariana* is widely distributed across boreal Canada, growing not only in peatlands, but also on a wide variety of nonpeatland soil types (Viereck and Johnston 1990; Montague and Givnish 1996). Because *Picea mariana* is a very important pulpwood species in eastern North America, some research has focused on factors affecting its growth. Height-growth patterns for *Picea mariana* differ between peatland and upland stands in Ontario (Payandeh 1978, 1989), and probably across Canada more generally. In upland sites, soil moisture and aeration influence growth (Jeglum 1974; Lieffers and Rothwell 1986; Dang and Lieffers 1989; Hillman et al. 1990; MacDonald and Yin 1999; Roy et al. 1999), while water chemistry as reflective of the ombrotrophic–minerotrophic status of peatlands has a major influence on *Picea mariana* growth (Heinselman 1970). *Picea mariana* growth can be enhanced by fertilization with nitrogen and phosphorus in upland (van Nostrand 1979) as well as peatland (Alban and Watt 1981; Payandeh 1989; Wells 1993) sites.

Tamarack, *Larix laricina*, is a dominant tree species in treed fens of boreal North America and can be found across a wide range along the ombrotrophic–minerotrophic gradient (Heinselman 1970; Sims et al. 1979; Montague and Givnish 1996; Chap. 2). *Larix laricina* is widely distributed across boreal Canada. Although *Larix laricina* grows on a variety of soil types, because of its tolerance for high soil moisture, acidity, and low soil temperature, *Larix laricina* tends to be more abundant in peatlands than in surrounding uplands (Johnston 1990). Growth sensitivity to soil moisture has been demonstrated as postdrainage growth release (MacDonald and Yin 1999). *Larix laricina* is an important pulpwood species, and its growth depends on both soil moisture/aeration and nutrient status (Glerum and Pierpoint 1968; Tilton 1977; Johnston 1990).

Scots pine, *Pinus sylvestris*, is the world's most widely distributed pine species, although it is native to Europe and Asia and was introduced in North America (Skilling 1990). Although *Pinus sylvestris* grows on a variety of soil types in upland areas, it also grows as a dominant tree species in boreal peatlands of Europe and Asia (Chap. 2), where its growth is generally stunted (Steven and Carlisle 1959), probably because of unfavorable soil moisture/aeration conditions (Seppälä 1969). The sensitivity of peatland *Pinus sylvestris* to growing season temperature and precipitation suggested that this species might provide sensitive historical climate reconstructions through dendrochronological analyses, but observed temporal patterns were more pronounced for upland than peatland trees (Linderholm et al. 2002). *Pinus sylvestris* root biomass increases with drainage (Heikurainen 1955; Paavilainen 1966, cited in Finér 1991). Drainage of Finnish pine bogs may result in small increases in carbon mineralization in peat, but the resulting carbon losses are outstripped by stimulated aboveground net primary production (increased litterfall) and fine root production of *Pinus sylvestris* (Minkkinen and Laine 1998). *Pinus sylvestris* seedling root biomass and length were enhanced by NPK and PK fertilization (Paavilainen 1967, 1968, cited in Finér 1991), although no root growth response to NPK or PK fertilization was found for a stand with 85-year-old trees (Finér 1991).

Although forestry-motivated research has examined factors that influence *Picea mariana*, *Larix laricina*, and *Pinus sylvestris* growth, such research has focused more on upland stands that tend to be more productive than peatlands. In addition, such research has focused on aboveground growth only and has not made an effort to convert forestry-relevant growth information to ecologically relevant net primary production data. Data on peatland tree production are sparse.

Aboveground net primary production data for *Picea mariana* have been reported for a permafrost bog in northern Alaska (77 g m^{-2} year^{-1}; Billings 1987) and for permafrost plateaus in northern Manitoba (32–140 g m^{-2} year^{-1}; Camill et al. 2001) where production increased as the mean annual temperature increased from –5 to –1 °C. Production has been estimated for nonpermafrost bogs in northern Alberta (27 and 54 g m^{-2} year^{-1}; Szumigalski and Bayley 1996 and Szumigalski 1995, respectively) and in southeastern Manitoba (58 and 302 g m^{-2} year^{-1} in the bog forest and muskeg zones, respectively, of a single peatland; Reader and Stewart 1972). *Picea mariana* production has been reported for a few subboreal peatlands, viz., for a raised and a perched bog in subboreal northern Minnesota (100 and 310 g m^{-2} year^{-1}; Grigal et al. 1985) and for Waterloo Black Spruce Bog in southeastern Michigan (176 g m^{-2} year^{-1}; Ulrich 1980). Aboveground *Picea mariana* production estimates for fens are limited to a single moderately rich fen in northern Alberta (5.6 g m^{-2} year^{-1}; Szumigalski 1995).

Even sparser than the data for aboveground production of trees in boreal peatlands are data for belowground production. Using the root ingrowth approach at an Albertan peatland dominated by *Picea mariana* and *Larix laricina*, Conlin and Lieffers (1993) demonstrated that root growth for both species began in July and continued through mid-September for *Larix laricina* and mid-October for *Picea mariana*. The data were not expressed as production, but are roughly equivalent to 200 and 340 g m^{-2} year^{-1} for *Larix laricina* and *Picea mariana*, respectively (Conlin

Table 8.1. Production data for *Pinus sylvestris* (tree species not mentioned in Vasander 1982; assumed to be *P. sylvestris*)

Site location	Peatland description	Production (g m^{-2} year^{-1})		Reference
		Above-ground	Below-ground	
Laaviosuo, Finland	Virgin bog	22.5	14.6	Vasander (1982)
	Drained and fertilized bog	173.9	22.8	
	Drained bog	93.8	14.9	
Vasjuganiya, Russia	*Sphagnum fuscum* raised bog, 100 years old	34.9	5.1	Bazilevich (1967)[a]
Russian Karelia	Oligotrophic "pine-dwarf shrub-*Sphagnum*" bog, 120 years old	20.4	2.6	Kozlovskaya et al. (1978)[a]
Vilppula, Finland	Unfertilized dwarf pine shrub bog drained in 1909	469.3	172.7	Paavilainen (1980)[a]
Lyly, Finland	Oligotrophic sedge fen drained and fertilized in 1938	202.0	54.0	Ouni (1977)[a]
Russian Karelia	Mesotrophic pine-herb-*Sphagnum* mire, drained 40 years ago, age 118 years	639.0	93.0	Kozlovskaya et al. (1978)[a]

[a] Cited in Vasander (1982)

and Lieffers 1993). These values are considerably larger than those estimated for a permafrost bog in northern Alaska (32 g m^{-2} $year^{-1}$; Billings 1987). In a detailed study of root dynamics at three Finnish peatlands, Finér and Laine (1998) reported *Pinus sylvestris* root production in the top 20 cm of a meso-oligotrophic tall sedge fen, an oligotrophic tall sedge pine fen, and an ombrotrophic dwarf-shrub pine bog to be 63, 64, and 112 g m^{-2} $year^{-1}$, respectively, and 221, 261, and 310 g m^{-2} $year^{-1}$, respectively, using sequential root harvesting techniques and two different methods of calculation. These values for *Pinus sylvestris* are larger than those obtained by Backéus (1990) for an ombrotrophic Swedish bog (51 and 86 g m^{-2} $year^{-1}$ in hummocks and lawns, respectively), and smaller than those obtained for a Finnish tall sedge fen using a pulsed-labeling of ^{14}C (1,100 g m^{-2} $year^{-1}$; Saarinen 1996).

Pinus sylvestris is the only major peatland tree species for which several studies have estimated both aboveground and belowground production at the same sites over the same time period, with most of these results being compiled by Vasander (1982). Both aboveground and belowground production values vary considerably, with aboveground production exceeding belowground production by factors of 1.5–7.8 (Table 8.1).

8.7 Conclusions

Most of the research on net primary production in boreal peatlands has focused on *Sphagnum* mosses, whose production seems to be related broadly to coarse climatic factors (mean annual temperature and mean annual precipitation) as well as to atmospheric nitrogen deposition. Much less effort has focused on production of true mosses, even though these species may dominate some peatlands, notably rich fen ecosystems. Few data are available for production of herbaceous or shrub species in boreal peatlands and even less is known about the factors that control their growth/production. Although considerable research has focused on net primary production of boreal peatland tree species, much of this has been directed toward understanding growth on drained and/or fertilized sites in relation to forestry practices. The extent to which these findings have relevance to tree growth/production in unmanaged settings remains uncertain. Probably because of methodological difficulties and constraints (Finér and Laine 2000; Hansen et al. 2000), measurements of belowground production of vascular plants in boreal peatlands are few. Our understanding of the factors that influence belowground production and root turnover is meager and represents a major knowledge gap given that root-related processes may play an important major role in peatland carbon balance (Silvola et al. 1996; Crow and Wieder 2005).

Few studies have quantified net primary production for all vegetation layers at a single site. Total aboveground net primary production for North American boreal and subboreal bogs averaged 462 g m^{-2} $year^{-1}$ (range 280–755 g m^{-2} $year^{-1}$; five sites), and for fens averaged 319 g m^{-2} $year^{-1}$ (range 114–710 g m^{-2} $year^{-1}$; ten sites) (data compiled and presented in Thormann and Bayley 1997). However, none of these studies measured belowground production. The only study of which I am aware in which all components, aboveground and belowground, of net primary production were quantified is that of Vasander (1982). For a virgin bog, a drained bog, and drained and fertilized bogs in southern Finland, total aboveground net primary production was 238, 136, and 354 g m^{-2} $year^{-1}$, respectively, and total belowground production was 139, 78, and 266 g m^{-2} $year^{-1}$, respectively (Vasander 1982).

Over the past 50 years, considerable effort has been devoted to quantifying peatland net primary production and to understanding the biotic and abiotic factors that influence this key ecosystem functional property. Most of the research has focused on *Sphagnum* mosses, to the extent that it has become possible to synthesize global patterns in *Sphagnum* production (Gunnarsson 2005). For other species or groups of species, however, limited data make this sort of synthesis premature. Because so few studies have tried to quantify whole ecosystem net primary production, we seem a long way from uncovering consistent patterns within or across different boreal peatland types with regard to the relative contribution of mosses, herbs, shrubs, and trees to either aboveground or total net primary production, or with regard to the relative importance of aboveground versus belowground contributions to total net primary production. Although ombrotrophic bogs, minerotrophic poor fens, and minerotrophic rich fens, each with their own unique plant community composition, occur across the boreal region, within the boreal region, climatic gradients in temperature and precipitation exist, along with anthropogenically influenced gradients in nitrogen deposition. A complete view of how these broad gradients influence whole ecosystem net primary production in different peatland types remains elusive.

Clearly, the fate of the huge quantity of carbon stored in the boreal peatlands of the northern hemisphere will hinge on how the offsetting processes of net primary production and decomposition are influenced by future climatic conditions. As models of peatland carbon cycling and accumulation continue to be developed (Hilbert et al. 2000; Frolking et al. 2001; LaFleur et al. 2003; Belyea and Malmer 2004), a more comprehensive view of peatland net primary production will be needed. Despite over a half a century of interest and research on net primary production in boreal peatlands, considerable additional effort will be needed to develop an overarching understanding of this key ecosystem process, in terms of both rates and controlling factors.

References

Aerts R, Wallén B, Malmer N (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. J Ecol 80:131–140

Aerts R, Wallén B, Malmer N, de Caluwe H (2001) Nutritional constraints on *Sphagnum*-growth and potential decay in northern peatlands. J Ecol 89:292–299

Alban DH, Watt RF (1981) Fertilization of black spruce on poor site peatland in Minnesota. USDA Forest Service, research paper NC-210. North Central Forest Experiment Station, St Paul

Austin, KA, Wieder RK (1987) Effects of elevated H^+, SO_4^{2-}, NO_3^-, and NH_4^+ in simulated acid precipitation on the growth and chlorophyll concentration of 3 North American *Sphagnum* species. Bryologist 90:221–229

Backéus I (1990) Production and depth distribution of fine roots in a boreal open bog. Ann Bot Fenn 27:261–265

Bartsch I, Moore TR (1985) A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. Can J Bot 69:1241–1248

Bartsch I, Schwintzer CR (1994) Growth of *Chamaedaphne calyculata* at two peatland sites in relation to nutrient availability. Wetlands 14:147–158

Bayley SE, Vitt DH, Newbury RW, Beaty KG, Bent R, Miller C (1987) Experimental acidification of a *Sphagnum*-dominated peatland: first year results. Can J Fish Aquat Sci 44:194–205

Bazilevich NI (1967) Productivnost' I biologicheskii krugovorot v mohovyh bolotah yuzhnogo Vacjuganiya. Rastit Resursy 3:567–588

Belyea LR, Malmer N (2004) Carbon sequestration in peatland: patterns and mechanisms of response to climate change. Global Change Biol 10:1043–1052

Berendse F, van Breemen N, Rydin H, Buttler A, Heijmans MMPD, Hoosbeek MR, Lee JA, Mitchell E, Saarinen T, Vasander H, Wallén B (2001) Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. Global Change Biol 7:591–598

Billings WD (1987) Carbon balance of Alaskan tundra and taiga ecosystems: past, present, and future. Quat Sci Rev 6:165–177

Bragazza L, Tahvanainen T, Kutnar L, Rydin H, Limpens J, Hájek M, Grosvernier P, Hájek T, Hajkova P, Hansen I, Iacumin P, Gerdol R (2004) Nutritional constraints in ombrotrophic *Sphagnum* plants under increasing atmospheric nitrogen deposition in Europe. New Phytol 163:609–616

Brock TCM, Bregman R (1989) Periodicity on growth, productivity, nutrient content and decomposition of *Sphagnum recurvum* var. *mucronatum* in a fen woodland. Oecologia 80:44–52.

Busby JR, Bliss LC, Hamilton CD (1978). Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. Ecol Monogr 48:95–110

Camill P, Lynch JA, Clark JS, Adams JB, Jordan B (2001) Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. Ecosystems 4:461–478

Campbell C, Vitt DH, Halsey LA, Campbell ID, Thormann MN, Bayley SE (2000). Net primary production and standing biomass in northern continental wetlands. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta. Information report NOR-X-369

Chapin CT, Bridgham SD, Pastor J (2004) pH and nutrient effects on above-ground net primary production in a Minnesota, USA bog and fen. Wetlands 24:186–201

Clymo RS (1970) The growth of *Sphagnum*: Methods of measurement. J Ecol 58:13–19

Clymo RS (1984) *Sphagnum*-dominated peat bog: A naturally acid ecosystem. Philos Trans R Soc Lond Ser B 305:487–499

Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. In: Smith AJE (ed) Bryophyte ecology. Chapman and Hall, London, pp 229–289

Conlin TS, Lieffers VJ (1993) Seasonal growth of black spruce and tamarack roots in an Alberta peatland. Can J Bot 71:359–360

Crow SE, Wieder RK (2005) Sources of CO_2 emission from a northern peatland: the role of root respiration, root exudates, and organic matter. Ecology 86:1825–1834

Crum H (1992) A focus on peatlands and peat mosses. University of Michigan Press, Ann Arbor, MI

Damman AWH (1979) Geographic patterns in peatland development in eastern North America. Proceedings of the international symposium on classification of peat and peatlands, Hyytialä, Finland. International Peat Society, Jyväskylä

Dang QL, Lieffers VJ (1989) Assessment of patterns of tree ring growth of black spruce following peatland drainage. Can J For Res 19:924–929

Ferguson P, Lee JA (1979) The effects of bisulphite and sulphate on photosynthesis in *Sphagnum*. New Phytol 82:703–712

Ferguson P, Lee JA (1980) Some effects of bisulphite and sulphate on the growth of *Sphagnum* in the field. Environ Pollut 21:58–71

Ferguson P, Lee JA (1983) The growth of *Sphagnum* species in the southern Pennines. J Bryol 12:579–586

Ferguson P, Lee JA, Bell JNB (1978) Effects of sulfur pollution on the growth of *Sphagnum* species. Environ Pollut 16:151–162

Finér L (1991) Root biomass on an ombrotrophic pine bog and the effects of PK and NPK fertilization. Silva Fenn 25:1–12

Finér L, Laine J (1998) Root dynamics at drained peatland sites of different fertility in southern Finland. Plant Soil 201:27–36

Finér L, Laine J (2000) The ingrowth bag method in measuring root production on peatland sites. Scand J For Res 15:75–80

Frolking S, Roulet NT, Moore TR, Richard JPH, Lavoie M (2001) Modeling northern peatland decomposition and peat accumulation. Ecosystems 4:479–498

Gignac LD (1992) Niche structure, resource partitioning and species interactions of mire bryophytes relative to climatic and ecological gradients in western Canada. Bryologist 95:406–418

Gignac LD, Vitt DH, Bayley SE (1991a) Bryophyte response surfaces along ecological and climatic gradients. Vegetatio 93:29–45

Gignac LD, Vitt DH, Zoltai SC, Bayley SE (1991b) Bryophyte response surfaces along climatic, continental and physical gradients in peatlands of western Canada. Nova Hedwigia 53:27–71

Gignac LD, Nicholson BJ, Bayley SE (1998) The utilization of bryophytes in bioclimatic modelling: Predicted northward migration of peatlands in the Mackenzie River Basin, Canada as a result of global warming. Bryologist 101:572–587

Glerum C, Pierpoint G (1968) The influence of soil moisture deficits on seedling growth of three coniferous species. For Chron 44:26–29

Goodman GT, Perkins DF (1968a) The role of mineral nutrients in *Eriophorum* communities. III. Growth response to added inorganic elements in two *E. vaginatum* communities. J Ecol 56:667–683

Goodman GT, Perkins DF (1968b) The role of mineral nutrients in *Eriophorum* communities. IV. Potassium supply as a limiting factor in an *E. vaginatum* community. J Ecol 56:685–696

Gore AJP (1961a) Factors limiting plant growth on high-level blanket peat. I. Calcium and phosphate. J Ecol 49:399–402

Gore AJP (1961b) Factors limiting plant growth on high-level blanket peat. II. Nitrogen and phosphate in the first year of growth. J Ecol 49:605–616

Grigal DF, Buttleman CG, Kernik LK (1985) Biomass and productivity of the woody strata of forested bogs in northern Minnesota. Can J Bot 63:1204–1207

Gunnarsson U (2005) Global patterns of *Sphagnum* productivity. J Bryol 27:269–279

Gunnarsson U, Rydin H (2000) Nitrogen fertilization reduces *Sphagnum* production in bog communities. New Phytol 147:527–537

Gunnarsson U, Granberg G, Nilsson M (2004) Growth, production and interspecific competition in *Sphagnum*: Effects of temperature, nitrogen and sulphur treatments on a boreal mire. New Phytol 163:349–359

Hansen PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48:115–146

Heikurainen L (1955) Rämemännikön juuriston rakenne ja kuivatuksen vaikutus siiben. Referat: Der Wurzelaufbau der Kiefernbeständen auf Reisermoorböden und seine Beflussung durch die Entwässerung. Acta For Fenn 65:1–86

Heinselman ML (1970) Landscape evolution, peatland types, and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. Ecol Monogr 40:235–261

Hilbert DW, Roulet NT, Moore TR (2000) Modelling and analysis of peatlands as dynamic systems. J Ecol 88:241–256

Hillman GR, Johnson JD, Takyi SK (1990) The Canada Alberta Wetlands Drainage and Improvement for Forestry Program. Forestry Canada/Alberta Forestry, Lands and Wildlife, project no 141301417086, Edmonton, Canada

Hoosbeek MR, van Breemen N, Berendse F, Grosvernier P, Vasander H, Wallén B (2001) Limited effect of increased atmospheric CO_2 concentration on ombrotrophic bog vegetation. New Phytol 150:459–463

Hoosbeek MR, van Breemen N, Vasander H, Buttler A, Berendse F (2002) Potassium limits potential growth of bog vegetation under elevated atmospheric CO_2 and N deposition. Global Change Biol 8:1130–1138

Jauhiainen J, Silvola J (1999) Photosynthesis of *Sphagnum fuscum* at long-term raised CO_2 concentrations. Ann Bot Fenn 36:11–19

Jauhiainen J, Vasander H, Silvola J (1994) Response of *Sphagnum fuscum* to N deposition and increased CO_2. J Bryol 18:183–195

Jauhiainen J, Silvola J, Vasander H (1999) The effects of increased nitrogen deposition and CO_2 on *Sphagnum angustifolium* and *S. warnstorfii*. Ann Bot Fenn 35:247–256

Jeglum JK (1974) Relative influence of moisture-aeration and nutrients on vegetation and black spruce growth in northern Ontario. Can J For Res 4:114–126

Johnston WF (1990). Tamarack. In: Burns RM, Honkala BH (eds) Silvics of North America. Agriculture handbook 654, vol 1. (Conifers). US Department of Agriculture, Washington, DC, pp 141–151

Kozlovskaya LS, Medvedeva VM, P'yavchenko NI (1978) Dinamika organicheskogo vechestva v prochesse torfoobrazovanuiya (The dynamics of organic matter development in the process of peat formation). Nauka, St Petersburg

LaFleur PM, Roulet NT, Bubier JL, Frolking S, Moore TR (2003) Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. Global Biogeochem Cycles 17:1036. DOI 1029/2002GB001983

Lamers LPM, Bobbink R, Roelofs JGM (2000) Natural nitrogen filter fails in raised bogs. Global Change Biol 6:583–586

Li Y, Vitt DH (1997) Patterns of retention and utilization of aerially deposited nitrogen in boreal peatlands. Écoscience 4:106–116

Lieffers VJ, Rothwell RL (1986) Effects of water table and substrate temperature on root and top growth of *Picea mariana* and *Larix laricina* seedlings. Can J For Res 16:1201–1206

Limpens J, Berendse F (2003) Growth reduction of *Sphagnum magellanicum* subjected to high nitrogen deposition: The role of amino acid nitrogen concentration. Oecologia 135:339–345

Limpens J, Berendse F, Klees H (2003a) N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. New Phytol 157:339–347

Limpens J, Tomassen HBM, Berendse F (2003b) Expansion of *S. fallax* in bogs: Striking the balance between N and P availability. J Bryol 25:83–90

Limpens J, Berendse F, Klees H (2004) How phosphorus availability affects the impact of nitrogen deposition on *Sphagnum* and vascular plants in bogs. Ecosystems 7:793–804

Linderholm HW, Moberg A, Gould H (2002) Peatland pines as indicators? A regional comparison of the climatic influence of Scots pine growth in Sweden. Can J For Res 32:1400–1410

Lindholm T (1990) Growth dynamics of the peat moss *Sphagnum fuscum* on hummocks on a raised bog in southern Finland. Ann Bot Fenn 27:67–78

MacDonald SE, Yin F (1999) Factors influencing size inequality in peatland black spruce and tamarack: Evidence from post-drainage release growth. J Ecol 87:404–412

Minkkinen K, Laine J (1998) Long-term effect of forest drainage on the peat carbon stores of pine mires in Finland. Can J For Res 28:1267–1275

Mitchell EAD, Buttler A, Grosvernier P, Rydin H, Siegenthaler A, Gobat J-M (2002) Contrasted effects of increased N and CO_2 supply on two keystone species in peatland restoration and implications for global change. J Ecol 90:529–533

Montague TG, Givnish TJ (1996) Distribution of black spruce versus eastern larch along peatland gradients: relationship to relative stature, growth rate, and shade tolerance. Can J Bot 74:1514–1532

Moore TR (1989) Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. Can J Bot 67:1203–1207

Moore PD, Bellamy DJ (1974) Peatlands. Elek, London

Norby RJ, Kobayashi K, Kimball BA (1999) Commentary – Rising CO_2 – future ecosystems. New Phytol 150:215–221

Ouni K (1977) Kasvibiomassen ja sen vuotuisen tuotoksen määrä ja jakaantuminen luonnontilaisella ja ojitetulla varsinaisella saranevalla. MSc thesis, University of Helsinki, Department of Silviculture, Helsinki

Paavilainen E (1966) Maan vestialouden järjestelyn vaikutuksesta rämemännikön juuristosuhteisiin. Summary: on the effect of drainage on root systems of Scots pine on peat soils. Comm Inst For Fenn 61:1–110

Paavilainen E (1967) Lannoituksen vaikutus rämemännikön juurisuhteisiin. Summary: The effect of fertilization on the root systems of swamp pine stands. Folia For 31:9

Paavilainen E (1968) Juuristotukimuksia Kivisuon metsänlannoituskoekentällä. Summary: root studies at the Kivisuo forest fertilization area. Commun Inst For Fenn 66:1–31

Paavilainen E (1980) Effect of fertilization on plant biomass and nutrient cycle on a drained dwarf shrub pine swamp. Commun Inst For Fenn 98:1–71

Payandeh B (1978) A site index formula for peatland black spruce in Ontario. For Chron 54:39–41

Payandeh B (1989) Growth of black spruce trees following fertilization on drained peatland. For Chron 65:102–106

Press MC, Lee JA (1982) Nitrate reductase activity of *Sphagnum* species in the south Pennines. New Phytol 92:487–492

Press MC, Woodin SJ, Lee JA (1986) The potential importance of an increased atmospheric nitrogen supply to the growth of ombrotrophic *Sphagnum* species. New Phytol 103:45–55

Reader RJ, Stewart JM (1972) The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. Ecology 53:1024–1037

Rochefort L, Vitt DH (1988) Effects of simulated acid rain on *Tomenthypnum nitens* and *Scorpidium scorpioides* in a rich fen. Bryologist 91:121–129

Rochefort L, Vitt DH, Bayley SE (1990) Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology 71:1986–2000

Roy V, Bernier PY, Plamondon AP, Ruel JC (1999) Effect of drainage and microtopography in forested wetlands on the microenvironment and growth of planted black spruce seedlings. Can J For Res 29:563–574

Saarinen T (1996) Biomass and production of two vascular plants in a boreal mesotrophic fen. Can J Bot 74:934–938

Schwintzer CR (1983) Primary productivity and nitrogen, carbon, and biomass distribution in a dense *Myrica gale* stand. Can J Bot 61:2943–2948

Seppälä K (1969) Postdrainage growth or Norway spruce and Scots pine on peat. Acta For Fenn 93:1–89

Silvola J (1990) Combined effect of varying water content and CO_2 concentration on photosynthesis in *Sphagnum fuscum*. Holarct Ecol 13:224–228

Silvola J, Alm J, Ahlholm U, Nykanen H, Martikainen PJ (1996) The contribution of plant roots to CO_2 fluxes from organic soils. Biol Fert Soils 23:126–131

Sims RA, Riley JL, Jeglum JK (1979) Vegetation, flora and vegetational ecology of the Hudson Bay Lowland: a literature review and annotated bibliography. Canadian Forestry Service, report O-X-297. Sault Ste. Marie, Canada

Skene KR, Sprent JI, Raven JA, Herdman L (2000) *Myrica gale* L. J Ecol 88:1079–1094

Skilling DD (1990) Scotch pine. In: Burns RM, Honkala BH (eds) Silvics of North America. Agriculture handbook 654, vol 1. (Conifers). US Department of Agriculture, Washington, DC, pp 489–496

Steven HM, Carlisle A (1959) The native pinewoods of Scotland. Oliver and Boyd, Edinburgh

Szumigalski AR (1995) Production and decomposition of vegetation along a wetland gradient in central Alberta. MSc thesis, University of Alberta, Edmonton

Szumigalski AR, Bayley SE (1996) Net above-ground primary production along a bog-rich fen gradient in central Alberta, Canada. Wetlands 16:467–476

Tallis JH (1964) Studies of southern Pennine peats. III. The behaviour of *Sphagnum*. J Ecol 52:345–353

Tamm CO (1954) Some observations on the nutrient turn-over in a bog community dominated by *Eriophorum vaginatum* L. Oikos 5:189–194

Thormann MN (1995) Primary production and decomposition in fens and marshes in the boreal region of Alberta, Canada. MSc thesis, University of Alberta, Edmonton

Thormann MN, Bayley SE (1997) Aboveground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada. Écoscience 4:374–384

Tilton DL (1977) Seasonal growth and foliar nutrients of *Larix laricina* in three wetland ecosystems. Can J Bot 55:1291–1298

Tomassen HBM, Smolders AJP, Limpens J, Lamers LPM, Roelofs JGN (2004) Expansion of invasive species on ombrotrophic bogs: Desiccation or high N deposition. J Ecol 41:139–150

Ulrich K (1980) Net primary productivity of a mature southern Michigan bog. Mich Acad 12:289–295

van der Heijden E, Verbeek SK, Kuiper PJC (2000) Elevated atmospheric CO_2 and increased nitrogen deposition: effects on C and N metabolism and growth of the peat moss *Sphagnum recurvum* P. Beauv. var. *mucronatum* (Russ.) Warnst. Global Change Biol 6:201–212

van Nostrand RS (1979) Growth response of black spruce in Newfoundland to N, P and K fertilization. For Chron 55:189–193

Vasander H (1982) Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Ann Bot Fenn 19:103–125

Viereck LA, Johnston WF (1990) Black spruce. In: Burns RM, Honkala BH (eds) Silvics of North America. Agriculture handbook 654, vol 1. (Conifers). US Department of Agriculture, Washington, DC, pp 227–237

Vitt DH (1990) Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients. Bot J Linn Soc 104:35–59

Vitt DH, Wieder K, Halsey LA, Turetsky M (2002) Response of *Sphagnum fuscum* to nitrogen deposition: A case study of ombrogenous peatlands in Alberta, Canada. Bryologist 106:235–245

Wells ED (1993) Effects of planting spacing and refertilization on growth and nutrition of black spruce (*Picea mariana* (Mill.) B.S.P.) planted on a minerotrophic peatland in Newfoundland, Canada. Can J For Res 24:1302–1311

Wieder RK (2001) Past, present and future peatland carbon balance – an empirical model based on ^{210}Pb-dated cores. Ecol Appl 11:321–342

Wieder RK, Lang GE (1983) Net primary production of the dominant bryophytes in a *Sphagnum*-dominated wetland in West Virginia. Bryologist 86:280–286

Woodin SJ, Press MC, Lee JA (1985) Nitrate reductase activity in *Sphagnum fuscum* in relation to wet deposition of nitrate from the atmosphere. New Phytol 99:381–388

9 Carbon in Boreal Peatlands

Harri Vasander and Anu Kettunen

9.1 Introduction

Although peatlands have been developing on Earth since wetland plants first existed, the great majority of present-day peatlands have originated during the last 11,000 years (Gajewski et al. 2001; Chap. 3). Owing to different definitions of wetland ecosystems the global coverage estimates of peatlands differ considerably. The estimates of the total area of peatlands in the world have changed from 1×10^6 to 5×10^6 km^2 during the last 100 years as more inventory results have become available (Kivinen and Pakarinen 1981). One reason for the differences is the required minimum peat thickness (see Joosten and Clarke 2002 for a thorough discussion). While not going deeper into that discussion, it is interesting to note that if a geological definition with a minimum peat thickness of 30 cm is compared with the biological definition (Laine and Vasander 1996) that requires only potentially peat-forming vegetation, the ratio between geological and biological peatlands is approximately 0.7 for Finland and Sweden (Lappalainen 1996; Vasander et al. 2003) as well as for the European part of the former USSR (calculated from the data of Tjuremnov 1949). Joosten and Clarke (2002) and Charman (2002) estimate that the area of boreal and subarctic peatlands with more than 30 cm of peat is approximately 3.5×10^6 km^2.

Also, estimates of the C pool in peatlands have varied by over an order of magnitude from 41.5 Pg (Buringh 1984) to 489 Pg (Schlesinger 1977) owing to differences in estimates of average peat depth and bulk density. The moderate estimate of 300 Pg (Sjörs 1981) represents about 13 % of the terrestrial C in the biosphere and is in line with later studies that estimate 270–370 Pg for northern mires (Turunen et al. 2002), 249 Pg for boreal and subarctic mires (Armentago and Menges 1986), and 234–252 Pg for boreal mires (Lappalainen 1996). The often cited figure by Gorham (1991; 455 Pg) was calculated by using a total area of pristine boreal and subarctic

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peatlands of 3.42×10^6 km^2, a mean depth of the peat layers of 2.3 m, a bulk density of 0.122 g cm^{-3}, and a C content of 51.7 %. With a lower mean bulk density of 0.091 g cm^{-3} (Mäkilä 1994; Turunen 2003) and a mean depth of 1.7 m for all boreal and subarctic mires (Turunen 2003), the C pool of northern mires would be 274 Pg, which is in accordance with most of the aforementioned values. The large range in the C storage estimate mainly reflects uncertainty in the depth of global peat deposits (Gorham 1991, Botch et al. 1995, Clymo et al. 1998). A more accurate characterization of the age–depth distributions of mires, especially from North America and Russia, is needed (Bauer et al. 2003, Yu et al. 2003, Borren et al 2004, Sheng et al. 2004).

9.2 Carbon Cycle in Peatlands

Atmospheric CO_2 is fixed by plants via photosynthesis during the growing season and subsequently is deposited as litter both on and in the soil. Net primary production (NPP) in boreal peatlands is lower than in many other ecosystems (Ruimy et al. 1996; Frolking et al. 1998; Bubier et al. 1999; Chap. 8). Decay rates are also low as the water table lies near the soil surface, leading to anoxic conditions. Peat accumulates whenever the rate of organic matter production exceeds the rate of decay. While the NPP and peat accumulation values in different kinds of peatlands differ widely, the "efficiency" of peatlands, i.e., the ratio between peat accumulation and NPP, varies between 1 and 20 % (Tolonen 1979; Tolonen et al. 1992; Warner et al. 1993; Francez and Vasander 1995; Moore et al. 2002; Feng 2002). The peat accumulation rate has been related to peatland geographical location (south greater than north), age (young greater than old), and type (Korhola et al. 1995).

Part of the photosynthesized C is returned to the atmosphere as CO_2 in the maintenance and growth respiration of aboveground and belowground plant parts, and in the respiration of consumers such as soil animals and heterotrophic microbial communities. By measuring the total flux of CO_2 it is impossible to distinguish these from each other, but by other means it has been found that autotrophic and heterotrophic respiration comprise about one third of the CO_2 uptake via photosynthesis during the intensive growth period (Bubier et al. 1998; Heikkinen et al. 2002). The rate of autotrophic respiration is regulated by photosynthesis, temperature, and water and nutrient availability, while heterotrophic respiration is controlled largely by soil temperature, oxic peat layer volume, nutrients and soil pH, and the quality and quantity of decomposable material (Chapman and Thurlow 1998; Chapin et al. 2002). Root-associated respiration follows the vegetation phenology and may account for

10–45 % of the total soil CO_2 release, originating mainly from the turnover of fine roots and from root exudates (Silvola et al. 1996a).

The remaining C is transformed into plant structures, especially into the belowground parts of plants where the majority of the plant biomass is located (Metsävainio 1931; Vasander 1982; Wallén 1986, 1992; Sjörs 1991; Saarinen 1996). Finally it is deposited as dead plant matter (litter) on and in the soil (Fig. 9.1). Mosses grow upward, die gradually, and regulate the vertical growth rate of peatlands. Besides adding stem, rhizome, and root matter to the peat, vascular plants provide physical support for the upward growth of mosses (Malmer et al. 1994). In the oxic surface parts of the peat (acrotelm), litter initially is decomposed primarily by aerobic bacteria, leading to the release of CO_2, but eventually litter becomes covered by the gradually rising water table (Reader and Stewart 1972; Clymo 1984, 1992; Bartsch and Moore 1985; Laine et al. 1996; Scanlon and Moore 2000). In the water-saturated anaerobic part of the peat (catotelm), decomposition is slow and a large portion of the total mineralized C is released to the atmosphere as CH_4.

C also flows in and out of the peatland in dissolved form (dissolved organic C, DOC) (Urban et al. 1989; Sallantaus 1992; Schiff et al. 1998; Moore 2003). As peatlands have very high C densities, the DOC output from them usually exceeds the DOC input to them with water inflow. The C leaching rate and loss as DOC from peatlands depend especially on hydrologic throughflow rates and on peatland NPP (DeVito and LaZerte 1989; Sallantaus 1992; Moore 2003). C leaching and DOC losses from peatlands may be increasing owing to warming climate (Freeman et al. 2001). Also, the significance of episodic factors like fires causing C loss from peatland ecosystems (Pitkänen et al. 1999; Turetsky et al. 2002, 2004) may increase in the future (Robinson and Moore 2000).

C leaches downward in the peat profile (Charman et al. 1994; Domisch et al. 1998) and can reach the underlying mineral soil (Turunen et al. 1999) especially during the early developmental phase of a peatland. Long-term average C accumulation rates beneath Lakkasuo mire in central Finland were 19 g m^{-2} $year^{-1}$ at sites younger than 500 years and 1 g m^{-2} $year^{-1}$ at sites older than 500 years (Turunen and Moore 2003), while the average estimates throughout the Holocene were 17–19, 20, and 24 g C m^{-2} $year^{-1}$ in Finland, Russia, and Canada, respectively (Turunen et al. 2001, 2002; Vitt et al. 2000; Turetsky et al. 2002).

Fig. 9.1. a *Sphagnum*-dominated bogs and poor fens may be considered to have a diplotelmic acrotelm–catotelm structure. Mosses add new organic matter to the surface. Most of the decay takes place in the upper oxic surface peat layer. Below this is the anoxic catotelm layer with stagnant water where the decomposition of organic matter is much slower. The lowest water level is the main regulator of the oxic acrotelm layer and only a small amount of new photosynthetic organic matter is transported to the anoxic catotelm layer for the methanogens. **b** In sedge fens the diplotelmic structure with a horizontal limit between acrotelm and catotelm does

9.3 Carbon Dioxide Uptake and Release

Photosynthesis is a light-controlled process in which CO_2 is the C source and light is used as energy (Fig. 9.2). Other controlling factors of photosynthesis are CO_2 concentration, temperature, and water and nutrient availability, as well as the leaf area (Mooney 1986). To tackle the spatial and temporal variation in gas fluxes from boreal peatlands that partly results from the considerable spatial variability in microtopography (Figs. 9.1, 9.2), several approaches such as the chamber technique (Crill 1991; Carroll and Crill 1997) and eddy covariance (EC; Baldocchi 2003) have been used. While the chamber technique is applicable for microscale flux measurements, the EC technique can be applied to landscape-scale measurements of net CO_2 flux and energy balance (Lafleur et al. 1997, 2001; Aurela et al. 1998; Soegaard and Nordstroem 1999; Vourlitis and Oechel 1999; Hargreaves et al. 2001; Frolking et al. 2002). Chamber and EC techniques have yielded quite similar C fluxes (Norman et al. 1997).

The difference between the gross uptake of CO_2 in photosynthesis (P_{GP}) and both autotrophic and heterotrophic respiration (R_a and R_h, respectively; the sum of which is the total ecosystem respiration, or R_{tot}) is called net ecosystem production (P_{NE}) (Curtis et al. 2002). P_{NE} can be directly measured with chamber and EC techniques, while the same is not true for P_{GP}. However, as P_{NE} is small compared with P_{GP} and R_{tot}, accurate measurements are needed to determine its rate. Ecologists and other soil-related researchers consider P_{NE} positive when the system acquires more CO_2 from the atmosphere than is released back to it. When P_{NE} is negative, there is a net flow of CO_2 to the atmosphere. Meteorologists and other atmosphere-related researchers consider flows to and from the atmosphere in the opposite way in terms of the positive or negative signs to the fluxes.

As photosynthesis is highly dependent on the amount of light, P_{NE} is usually determined under different light conditions with artificial shad-

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not exist. Roots of sedges grow deep into anoxic peat, releasing root exudates and producing easily degradable root litter directly in the anoxic layer where methanogenic processes occur. These new photosynthates enable high methane production. Also oxygen is transported deep into the peat by the aerenchymous tissues of sedges forming oxic "pockets" to the anoxic peat layer. Also new organic matter is produced on the surface as well as in the deeper peat layers. Vascular plants possessing aerenchymous tissues facilitate the transport of methane from anoxic layers to the atmosphere. Increased root exudation in combination with transport of methane in the intercellular space of sedges explains the higher methane emissions in oligotrophic sedge fens in comparison with ombrotrophic bogs and mesotrophic fens. (Photographs by Harri Vasander from Russian Karelia)

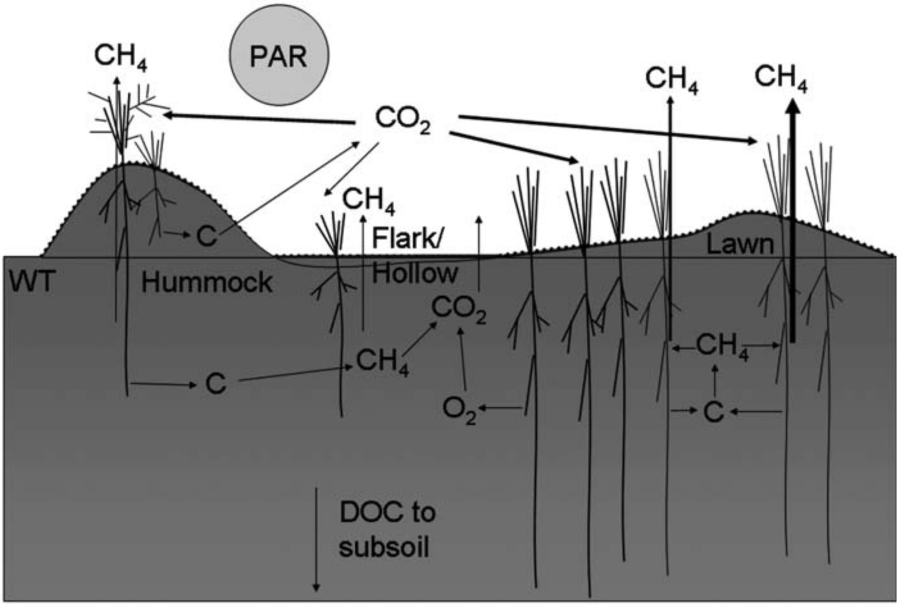

Fig. 9.2. The key interactions in carbon cycling dynamics in different microsites of a boreal peatland. Plants bind atmospheric carbon dioxide in photosynthesis (function of plant community, temperature, water level, photosynthetically active radiation, *PAR*) and supply part of the carbon to the peat matrix (function of litter quality, temperature, water level). In a hollow/flark with scarce field layer vegetation the carbon supply is lower. In high hummocks, the carbon is mainly supplied to the unsaturated layers where it is aerobically degraded. In lawn surfaces, low sedge abundance results in low methane flux owing to the lack of substrate and, further on, methane flux increases with an increase in sedge cover until at some point the increased oxygen supply to the peat profile starts to decrease the methane flux. Plants also supply the peat matrix with oxygen, which enhances methane oxidation and inhibits methane production. Methane is transported upward by plants and diffusion. Also ebullition occurs, especially in undefeated surfaces. Oxygen concentrations determine the proportion of substrate to aerobic decomposition and methane production. Aerobic decomposition (function of plant community, temperature, water level, peat chemistry) consumes oxygen. The amount of substrate available for methanogenesis also depends on the substrate production rate (function of photosynthesis, root profile in peat) and substrate consumption rate (function of methanogens, substrate concentrations). The methane oxidation rate increases with increasing population of methane oxidizers and increasing methane and oxygen concentrations. The population dynamics, i.e., biomass gain and dying of methane producers and methane oxidizers, plays an important role when the water table (*WT*) shows short-tem and long-term fluctuations. Carbon is also transported as dissolved organic carbon (*DOC*; function of plant community, temperature, water level, hydrology). The possible flow of $CaCO_3$ in the case of rheotrophic mires and from soil layers beneath the peat in ombrotrophic mires (Lamers et al. 1999) is not considered here. (Modified from Kettunen 2002 with the permission of Helsinki University of Technology)

ing. Photosynthetically active radiation (PAR) is measured as photosynthetic photon flux density (PPFD, micromoles per square meter per second). R_{tot} can be measured in total darkness by blocking the light entering the chamber. P_{GP} can then be calculated by adding P_{NE} and R_{tot}, assuming that plant photorespiration equals plant respiration under dark conditions. Over the past decade, many measurements have been made to determine the relationships between PPFD and P_{NE} in different kinds of boreal peatland ecosystems in Canada, Russia, Scandinavia, and the USA (see review tables in Blodau 2002; Heikkinen 2003). Most of the measurements have been made during the growing season.; however, more measurements are now being made during other seasons when R_{tot} continues even under snow, but photosynthesis has ceased. Dark measurements during the summer show that R_{tot} varies from –1 to –7 μmol CO_2 m^{-2} s^{-1} (–1.0 to –7.3 g CO_2-C m^{-2} day^{-1}) (Martikainen et al. 1995; Alm et al. 1997; Frolking et al. 1998; Ikkonen et al. 2001; Moore 2001; Moore 2002; Saarnio et al. 2003; Tatarinov et al. 2003). Respiration is quite similar in different kinds of peatlands (poor – rich) and depends mostly on temperature and water table variation (Updegraff et al. 2001; Moore et al. 2002; Chimner and Cooper 2003).

When PAR increases to about 200 μmol m^{-2} s^{-1} P_{GP} equals R_{tot} (P_{NE}=0); with increasing PAR, peatlands become net CO_2 sinks. Average maximum summer P_{GP} values are 5 μmol CO_2 m^{-2} s^{-1} with 1,000–1,500 μmol m^{-2} s^{-1} PAR on minerotrophic peatlands and 2 μmol CO_2 m^{-2} s^{-1} on ombrotrophic peatlands (Frolking et al. 1998; Moore 2001). Based on the hourly values of measured P_{NE}, seasonal net exchange may be modeled (Alm et al. 1997; Carroll and Crill 1997; Bellisario et al. 1998; Saarnio et al. 2003; Tuittila et al. 2004). Growing season P_{NE} estimates vary considerably, but may reach values as high as 200 g CO_2-C m^{-2} (Moore 2001).

PAR has a clear diurnal cycle (Oechel et al. 1995). Diurnal rhythm was also measured for CO_2 exchange on all microsites of a boreal bog (Kettunen 2000), acting as net C sinks during the day when the photosynthesis rate exceeded respiration and as net C sources during the night when photosynthesis ceased, but respiration continued. Dry sites were found to fix more C during the daytime than wet sites, which parallels reported differences in CO_2 exchange across hydrological and vegetation gradients (Bubier et al. 1998, 1999; Frolking et al. 1998; Christensen et al. 2000). Respiration rates remained relatively low as the water table stayed close to the peat surface (Silvola et al. 1996b) and, consequently, daily CO_2 exchange was clearly positive for all microsites for most of the season. The results of Kettunen (2000) emphasized that CO_2 exchange is extremely sensitive to variation in environmental factors on short-term time scales and, consequently, annual C exchange estimates are also affected by short-term variation (Bubier et al. 1998, 1999; Griffis et al. 2000; Soegaard et al. 2000).

In boreal peatlands, seasons other than the growing season are important contributors to annual CO_2 exchange. In spring, peatlands usually function as a small source of CO_2 to the atmosphere, at least until plants are released from under the snow cover and photosynthesis begins. Hummocks are released first and they become the first microsites to turn into sinks of CO_2 with the bright sunny days in spring (Bubier et al. 1998). Because of the decreases in vascular plant leaf area and in the capacity of vascular plant leaves to photosynthesize, during late autumn only bryophytes photosynthesize (Silvola and Hanski 1979).

Significant proportions (10–40 %) of CO_2 fixed during the growing season are released from arctic, subarctic, alpine tundra, and boreal peats during the winter (Sommerfeld et al. 1993, 1996; Zimov et al. 1993; Brooks et al. 1997; Oechel et al. 1997; Mast et al. 1998; Alm et al. 1999a; Fahnestock et al. 1999; Panikov and Dedysh 2000; Aurela et al. 2001, 2002; Lafleur et al. 2001; Heikkinen et al. 2002; Roehm and Roulet 2003). Soil biological activity partly controls the soil CO_2 production rate during the winter, while vertical gas transport is controlled by snowpack characteristics such as porosity, tortuosity, and depth (Sommerfeld et al. 1993; Mast et al. 1998). Brooks et al. (1997) suggested that for an alpine tundra site the majority of CO_2 flux during the winter originated from the thin organic layer at the soil surface. The total as well as proportional winter CO_2 emissions depend on the duration and timing of snow accumulation (Brooks et al. 1997; Aurela et al. 2004,).

Lafleur et al. (2001) obtained an annual CO_2 uptake of 248 g CO_2 m^{-2} $year^{-1}$ (equivalent to 68 g C m^{-2} $year^{-1}$) at a boreal bog in central Canada (growing season 200 days), while the corresponding uptake in a subarctic fen in northern Finland (growing season 70 days) was 68 g CO_2 m^{-2} $year^{-1}$ (equivalent to 19 g C m^{-2} $year^{-1}$; Aurela et al. 2002). The maximum daily net uptake at the subarctic site with no night was slightly higher than that of the Canadian bog with clear diurnal light rhythm (9.3 and 8.3 g CO_2 m^{-2} day^{-1}; Aurela et al. 2002 and Lafleur et al. 2001, respectively). Typical winter CO_2 efflux for the subarctic fen was 0.5 g m^{-2} day^{-1}, leading to a seasonal winter efflux of 110 g CO_2 m^{-2}, which was greater than the total annual sink term (Aurela et al. 2002). Fluxes at this fen in northern Finland have been measured continuously for 6 years (1997–2002) and the annual CO_2 balance has consistently been positive (15–192 g CO_2 m^{-2} $year^{-1}$ equivalent to 4–53 g C m^{-2} $year^{-1}$) (Aurela et al. 2004).

9.4 The Methane Cycle in Wet Ecosystems

9.4.1 Substrate Supply

Even though peat itself represents a large reservoir of C, the C in the peat matrix is very resistant to decomposition in the anaerobic conditions that prevail in the peat profile and, therefore, peat C can provide only a limited substrate for methanogenesis (Kuder and Kruge 2001). Even though it has long been known that recent C bound by vegetation can promote methanogenesis by providing root exudates and easily decomposable litter (Rovira 1969), the full importance of plants to CH_4 fluxes has been realized only recently. Supported by experimental evidence, CH_4 flux was suggested to increase with the photosynthetic activity of plants in a variety of wetland types (Whiting et al. 1991; Whiting and Chanton 1992, 1993). The significantly lower CH_4 fluxes from unvegetated compared with vegetated surfaces and studies where clipping of vascular plants decreased CH_4 flux provided indirect evidence for the importance of plants (Chanton et al. 1992a; Torn and Chapin 1993; Kelker and Chanton 1997; King et al. 1998; Verville et al. 1998; Frenzel and Karofeld 2000; Christensen et al. 2003). Furthermore, CH_4 fluxes were found to be correlated to sedge cover both across microsites within a single mire (Bubier et al. 1995a, b; Schimel 1995; Bellisario et al. 1999; Tuittila et al. 2000; Nykänen et al. 2002) and across different mires (Nilsson and Bohlin 1993; Bubier 1995; Granberg et al. 2001; Nilsson et al. 2001). Positive correlations between CO_2 fixation and CH_4 flux at sites covered by sedge vegetation have been reported (Waddington et al. 1996; Friborg et al. 2000; Strack et al. 2004). Also pore water CH_4 concentrations were found to increase from unvegetated to vegetated surfaces (Whiting and Chanton 1992).

Use of stable and radioisotopes of C have supported the link between vascular plant root exudates and the methanogenic food chain. Having found that ^{14}C-dated CH_4 collected directly from peat was 2,000 years younger than adjacent peat, Charman et al. (1994) suggested that at least part of the C in CH_4 originates from DOC in mire water and that root exudates are one potential source of DOC. In some studies using C isotopes, recent photosynthetic C was found to be the predominant substrate for methanogenesis (van den Pol-van Dasselaar and Oenema 1999; Chasar et al. 2000), while in others this contribution was considered to be much lower (King and Reeburgh 2002; King et al. 2002; Christensen et al. 2003). The variation is understandable as allocation of C to aboveground and belowground parts of the plants and to exudation is known to be affected by plant species, plant age, tillering stage, root damage, light intensity, soil temperature, soil water stress, nutrient availability/deficiency, and soil microorganisms (Rovira 1969; Shaver and Cutler 1979; Kummerow and

Ellis 1984). Root exudation has been shown to increase the availability of the uptake of many nutrients, for example phosphate (Hoffland 1992), iron (Römheld 1991), manganese, and copper (Mench and Martin 1991), through formation of complexes with nutrient ions. Exudation can also promote the mineralization of nutrients by enhancing microbial activity in the rhizosphere (Darrah 1993). Root exudation of *Eriophorum angustifolium* grown in ombrotrophic and oligotrophic mire conditions was found to increase with decreasing availability of nutrients, suggesting that high root exudation might be a compensative mechanism to deal with low concentration of cations and low pH in mire ecosystems (Saarinen 1999). On average, about 15 % of the photosynthetically fixed C is estimated to be released from the roots, mainly in microbial and plant respiration (Saarnio et al. 1998; Saarnio and Silvola 1999).

Even if the proportion of root exudates is usually very small in comparison to the net photosynthesis, this fraction of C consisting of, for example, soluble sugars (glucose, fructose, sucrose, and other mono- and oligosaccharides) and organic acids is readily available for microbes (Rovira 1969; Russell 1977; Ström et al 2003). Methanogenic Archaea, in general, rely on other anaerobic bacteria for the initial breakdown of complex organic structures into simpler molecules (Svensson and Sundh 1992). Besides soluble sugar exudates, plant roots release secretions, sloughed cells, and material from root turnover into the soil, and these compounds can be exploited by microorganisms for biosynthesis and energy production (van Veen et al. 1989).

9.4.2 Acetate and Hydrogen Pathways

In freshwater systems, CH_4 is formed either from acetate dissimilation (acetate pathway) or bicarbonate reduction (hydrogen pathway) (Kelley et al. 1992; Westermann 1993) (Fig. 9.3), which differ in relation to temperature dependence and substrate availability (Ferguson and Mah 1983; Svensson 1984; Westermann 1993). At low temperatures (between 10 and 15 °C), the acetate pathway was found to contribute 85–90 % of the CH_4 produced; the contribution of the hydrogen pathway increased with increasing temperature (Avery et al. 1999; Fey and Conrad 2000). In addition to temperature control, vegetation affects the pathways, so in vegetated sites where fresh organic matter is available owing to high plant productivity, the acetate pathway dominates, while in unvegetated sites the hydrogen pathway becomes important (Bellisario et al. 1999; Popp et al. 1999; Chasar et al. 2000; Ström et al. 2003). Recent studies using C isotope methods (Chanton et al. 1995; Avery et al. 1999; Bellisario et al. 1999; Popp et al. 1999; Chasar et al. 2000) have shown that the acetate pathway clearly dominates in northern peatlands during summer. Also, the acetate path-

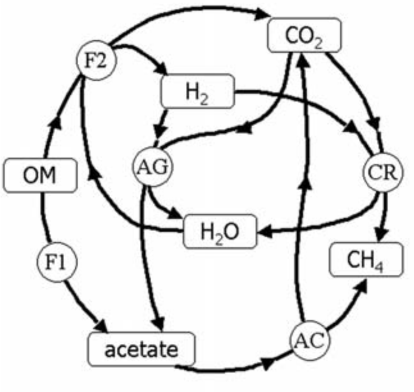

Fig. 9.3. The internal cycles of methane and carbon dioxide in peatlands showing the major microbial acetogenic and methanogenic processes. High molecular weight organic matter (*OM*) is decomposed by two different fermentation reactions (*F1*, *F2*) into acetate ($2CH_2O \rightarrow CH_3COO^- + H^+$), hydrogen and carbon dioxide ($CH_2 + H_2O \rightarrow CO_2 + 2H_2$): Aceticlastic reactions (*AC*) allow further splitting of acetate to produce methane and carbon dioxide ($CH_3COO^- + H^+ \rightarrow CH_4 + CO_2$). Hydrogen and carbon dioxide can recombine to form methane by CO_2 reduction (*CR*: $CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$) or again form acetate by acetogenesis (*AG*: $2CO_2 + 4H_2 \rightarrow CH_3COOH + 2H_2O$). Not explicitly shown are processes such as the production of bacterial biomass, the initial decay of plant material, and the generation of high molecular weight DOC. (Adapted from Eilrich and Steinmann 2003 with the permission of E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart)

way is favored in the shallow subsurface peat, while the hydrogen pathway becomes more dominant in older, less reactive deeper peat (Hornibrook et al. 1997). The analysis of methanogenic communities from boreal mires supported the idea that upper peat layers that receive fresh organic matter harbor acetoclastic methanogens, while hydrogen-utilizing methanogens prevail in deeper layers (Galand et al. 2002, 2003).

9.4.3 Methane Production

CH_4 is formed as a terminal step of a very complicated anaerobic degradation chain (Cicerone and Oremland 1988) by methanogenic Archaea (Garcia et al. 2000). In wetlands, changes in substrate availability and redox conditions are suggested to control the CH_4 production rate and the growth and death of methanogens (Conrad 1989, 1996; Morrissey and Livingston 1992; Valentine et al. 1994). In addition, in principle, CH_4 production is enhanced by an increase in temperature, but under in situ conditions, substrate availability strongly affects the temperature response (Dunfield et al. 1993; Valentine et al. 1994; Bergman et al. 1998). Deeper in peat, oxygen concentrations are lower, but the fresh organic C is supplied mainly to the uppermost layers where plant roots survive (Svensson and

Sundh 1992; Schimel 1995). Maximal CH_4 production has been observed at about 20 cm below the water table (Sundh et al. 1994). Addition of monovalent and divalent cations as well as acetate has been found to increase CH_4 production in peat cores (Thomas and Pearce 2004).

9.4.4 Methane Oxidation

In wetlands, CH_4 oxidation is carried out by low-affinity CH_4 oxidizers and oxidation rates depend on CH_4 and oxygen availability, which are connected to peat moisture conditions, temperature, and the activity of CH_4-oxidizing bacteria in the peat matrix. Populations of CH_4 oxidizers develop where CH_4 and oxygen profiles overlap in the peat profile (Conrad 1989, 1996; Sundh et al. 1995; Segers and Kengen 1998). Changes in CH_4 and oxygen concentrations during the growing season affect the population dynamics of methanotrophic bacteria (Svensson and Rosswall 1984; Whiting and Chanton, 1993) that are reflected in the net flux of CH_4. On the basis of the microbial 16S ribosomal DNA similarities of near-surface (20 cm) and deeper (6 m) peat layers, Steinmann et al. (P. Steinmann, S. Huon, P. Rossi, B. Eilrich, S. Casati, unpublished results) have speculated about the possibility of the presence of methanotrophs in the deepest anoxic peat layers. A possible oxidizing agent could be solid or colloidal trivalent iron. Temperature control has been suggested to be less important for CH_4 oxidation than for CH_4 production (Dunfield et al. 1993). Estimates of the CH_4 fraction that becomes reoxidized before reaching the atmosphere vary from 0 to 100 % (Yavitt et al. 1988, 1990; Moosavi and Crill 1998; Frenzel and Karofeld 2000; Popp et al. 2000; Pearce and Clymo 2001).

9.4.5 Methane Transport

CH_4 is liberated from peat via three routes: diffusion, ebullition, and passage through plants (Conrad 1989; Chanton et al. 1992b; Joabsson et al. 1999). In unvegetated surfaces, ebullition mainly dominates (van der Nat and Middelburg 1998; van der Nat et al. 1998). In vegetated surfaces, bubble flux may become important during wintertime when plant biomass is low (van der Nat and Middelburg 1998). Also, individual CH_4 bubbles can be formed in normal pore water concentrations by "scavenging" CH_4 from surrounding pore water (Baird et al. 2004). However, whenever vascular plants are present, bubbling is rare and flux via plants tends to dominate the diffusive flux (Sebacher et al. 1985; Morrissey and Livingston 1992; Whiting and Chanton 1992; Schimel 1995; van der Nat et al. 1998; Joabsson et al. 1999; Frenzel and Karofeld 2000). Nevertheless, abrupt and high ebullition fluxes of “old” CH_4 from the catotelm may represent a large source for CH_4 emissions from northern peatlands (Christensen et al. 2003; Glaser et al. 2004).

Some plants, like *Phragmites* and *Typha*, show active gas transport based on pressure differences, while others, like *Carex* spp., have only passive diffusion (Koncalová et al. 1988; Chanton et al. 1992a, 1993; van der Nat and Middelburg 1998; van der Nat et al. 1998; Popp et al. 1999). Active gas transport leads to a strong diurnal pattern in CH_4 flux and, consequently, if no diurnal pattern is observed, plants that use active gas transport are not present (Morrissey et al. 1993; van der Nat and Middelburg 1998; van der Nat et al. 1998). The within-plant diffusion rate has been found to be higher for *Eriophorum angustifolium* than for *Carex aquatilis* (Schimel 1995). Also, temperature has been shown to have an effect on the within-plant diffusion rate (Thomas et al. 1996). In spite of many examples for a plant-associated CH_4 oxidation (Frenzel 2000; Heilman and Carlton 2001), there is growing evidence that a few plants, including *Eriophorum* sp., do not support CH_4 oxidation (King et al. 1990; Chanton et al. 1992b; Kelker and Chanton 1997; Frenzel and Rudolph 1998), possibly owing to differences in the quality and type of root exudates between those plant species that support plant-associated CH_4 oxidation and those that do not (Frenzel and Rudolph 1998).

Kettunen et al. (1996) noticed that diurnal fluctuations in CH_4 emissions tended to occur when the difference between the air temperature and the peat temperature was large, i.e., during the warm days in the early season when deep peat layers had not warmed up. The large diurnal variations in peat temperatures apparently were related to the diffusion rate of CH_4 in peat (Jähne et al. 1987) and possibly also to CH_4 production (Dunfield et al. 1993; Westerman 1993) causing diurnal variations in CH_4 flux. The result that diurnal fluctuation in the microsites, where they occurred, could be correlated to peat surface temperatures only for short time periods indicates that the control mechanisms for CH_4 fluxes may change over the growing season.

9.4.6 Relations Between Environmental Factors and Methane Flux

The CH_4 fluxes from wetlands, which are controlled by the dynamic balance between CH_4 production and oxidation rates in peat profiles and the transport rate from peat to the atmosphere (Conrad 1989, 1996; Bubier and Moore 1994), show high spatial and temporal variation (Moore et al. 1990; Whalen and Reeburgh 1988, 1992; Dise 1993; Kettunen 2003). The spatial variation is due to the fact that the basic processes are affected by site-specific factors, such as average hydrological conditions (Svensson and Rosswall 1984; Sebacher et al. 1986; Roulet et al. 1992, 1993; Moore et al. 1994; Fiedler and Sommer 2000; Bosse and Frenzel 2001; Christensen et al. 2004), soil nutrient contents (Svensson and Rosswall, 1984; Dise, 1993), substrate concentration and quality (Morrissey and Livingston 1992; Whiting and Chanton 1992; Valentine et al. 1994; Fiedler and Sommer 2000), and vegetation type (Torn and Chapin 1993; Shannon and White 1994; Bubier 1995; Bubier et al. 1995a, b). The connection between CH_4 flux and hydrology and vegetation at the microsite scale has been established in numerous studies (Roulet et al. 1992, 1993; Bubier et al. 1993a, b, 1995a, b; Christensen 1993; Torn and Chapin 1993; Vourlitis et al. 1993; Moore et al. 1994; Shannon and White 1994; Bubier 1995; Schimel 1995; Bellisario et al. 1999; van den Pol-van Dasselaar et al. 1999; Tuittila et al. 2000; Granberg et al. 2001; Nilsson et al. 2001; Heikkinen et al. 2002; Nykänen et al. 2003; Christensen et al. 2004). Interannual variation (Mattson and Likens 1990; Whalen and Reeburgh 1992; Frolking and Crill 1994; Shurpali and Verma 1998; Nykänen et al. 2003), seasonal variation (Dise et al. 1993; Shurpali et al. 1993; Frolking and Crill 1994; Alm et al. 1999a; Mast et al. 1998; Panikov and Dedysh 2000; Silvola et al. 2003), diurnal cycles (Chanton et al. 1993; Mikkelä et al. 1995; Thomas et al. 1996; van der Nat et al. 1998), and episodic fluxes (Mattson and Likens 1990; Windsor et al. 1992; Christensen 1993; Frolking and Crill 1994; Grant and Roulet 2002; Christensen et al. 2003) have been related to effects of temporally changing environmental factors, like weather conditions, on the basic processes that affect CH_4 fluxes (Conrad 1989). Segers et al. (2001), Walter et al. (2001a, b), Kettunen (2003), and Zhuang et al.(2004) have modeled the CH_4 fluxes from peatlands. The model of Kettunen (2003) connects CH_4 fluxes to microsite vegetation cover and water level throughout the growing season.

The efflux of CH_4-C corresponds to less than 1 to more than 100 % of the annual total C efflux from boreal peatland ecosystems (Svensson et al. 1975; Svensson and Rosswall 1984; Crill et al. 1988; Nykänen et al. 1998; Heikkinen et al. 2002). The values exceeding 100 % also include "old" CH_4 released from pools, mud-bottoms, and other wet or sparsely vegetated sites that can lose C in many ways (Karofeld 2004). The logarithmic relationship between water level and CH_4 flux has been shown in many studies (Moore 2001; Heikkinen et al. 2003), while Nykänen et al. (1998) showed this relationship to differ between ombrotrophic, minerotrophic, and drained peatlands. As with CO_2, an important part of the annual CH_4 flux (up to 40 %) from boreal peatlands also occurs during winter (Windsor et al. 1992; Dise 1993; Melloh and Crill 1996; Alm et al. 1999a). The proportion of winter flux increases toward drier site types (summer dryness) and toward the north (long winters).

Kettunen et al. (1999) noticed that when the water level showed a downward shift, CH_4 production and oxidation potentials in the layers that no longer were water-saturated very slowly decreased toward rates more characteristic of permanently unsaturated layers. The decrease was faster in wet microsites, where a 2-week period of unsaturation eliminated the potentials, while in dry microsites, significant CH_4 production and oxidation potentials were found after 6 weeks of unsaturation. These findings imply that methanogens and methanotrophs are well adapted to natural conditions where the water table shows both a seasonal cycle and short-term fluctuation (von Fischer and Hedin 2002). Under laboratory conditions, both methanogenic Archaea (Huser et al. 1982) and methanotrophic bacteria (Roslev and King 1994) have been shown to retain their viability during periods of unsaturation and nutritional starvation. The results of Kettunen et al. (1999) also indicate that methanogens and methanotrophs are attached to peat particles and are not transported by vertical water movements (van den Pol-van Dasselaar and Oenema 1999). The reactivation of potentials in Kettunen et al. (1999) and simulated CH_4 flux in Kettunen (2003) depended on the length of the period of unsaturation, being slow after a rise in water level if the populations of CH_4-producing and CH_4-oxidizing bacteria had considerably decreased during the period of unsaturation (Freeman et al. 2002).

In addition to the direct effect on moisture and oxygen concentrations in the peat profile, changes in water level may affect substrate levels. After a decrease in water table position, increased aerobic degradation in the unsaturated layers consumes the C compounds that in anoxic conditions could promote CH_4 production. The reduction in substrate then decreases the CH_4 production potential. The CH_4 oxidation potential may also be reduced by a decrease in CH_4 concentration in the unsaturated peat layers. On the other hand, a temporary rise followed by a downward shift in water level may liberate CH_4 in deep layers (Moore and Roulet 1993), so CH_4 oxidation may be reactivated by the substrate peak (Kettunen et al. 1999).

Pore water CH_4 concentration builds up only gradually and causes a lag before the CH_4 formed in the peat is released to the atmosphere (Christensen 1993; Shurpali et al. 1993). The result in Kettunen et al. (1996) that CH_4 fluxes did not correlate with a differentiated temperature series during the early season strengthens the hypothesis that during the early season substrate availability is a dominant control for CH_4 fluxes. Later during the season, the correlation between a differentiated temperature series and CH_4 fluxes in Kettunen et al. (1996) and the higher production potentials toward late summer in Kettunen et al. (1999) suggest that the higher photosynthetic activity of plants had supplied methanogenesis with substrates, so temperature effects became more evident. The methanogenic activity that is found to be strongly temperature dependent (Dunfield et al. 1993; Segers and Kengen 1998) is argued to decrease at low autumn temperature, so excess substrate may accumulate in peat (Saarnio et al. 1997). In the laboratory, the CH_4 production potential measured at a temperature higher than the in situ temperature activated the CH_4-producing bacteria, resulting in a high CH_4 production potential (Yavitt et al. 1988; Valentine et al. 1994). The population dynamics of methanogenic population in response to substrate supply may also contribute to the observed increase in CH_4 production potentials late in the growing season (Svensson and Rosswall 1984; Dunfield et al. 1993; Westerman 1993; Whiting and Chanton 1993; Valentine et al. 1994; Kettunen et al. 1999).

9.5 Conclusions

Northern peatlands play an important role in the global C cycle. Furthermore, the CO_2 and CH_4 exchange rates between peatlands and the atmosphere show large variation (see review tables in Crill et al. 2000; Blodau 2002; Heikkinen 2003). Consequently, C cycling of northern peatlands is crucial to global C cycle dynamics under both current and future conditions. Although peatlands have shown positive long-term average net ecosystem exchange sequestration of large amounts of atmospheric C during the past few thousand years, the actual present-day C sequestration may be positive during a wet year and negative during a subsequent dry one (Alm et al. 1999a, b; Griffis et al. 2000; Waddington and Roulet 2000; Heikkinen et al. 2002; Bubier et al. 2003a; Lafleur et al. 2003). This variability suggests that the peatland C cycle is susceptible to environmental change (Moore et al. 1998; Malmer and Wallén 2004) and in the short term, the C exchange in mires depends on the rates of photosynthesis and respiration, each of which is affected by short-term variation in environmental factors (Bubier et al. 2003b).

Even though peatlands on average have acted as C sinks, they simultaneously are the most important single CH_4 source, globally. High-latitude northern peatlands, most of which lie within the boreal zone, are suggested to contribute 34–60 % of the global wetland CH_4 emissions (Matthews and Fung 1987; Cicerone and Oremland 1988; Aselman and Crutzen 1989; Bartlett and Harriss 1993). Because CH_4 has a global warming potential (GWP) factor of 23 in relation to CO_2 over a 100-year time horizon (IPCC 2001), boreal peatlands may have a considerable warming influence over a 100-year time horizon. Over a longer (e.g., 500-year) time horizon, with a GWP of 7 for CH_4, the same peatlands may act predominantly as net sinks owing to the dominance of long-lived CO_2 molecules. Thus, in the long term, the development of peatlands contributes as a mediator of or even as a positive feedback for atmospheric trace gas concentrations (Prinn 1994; Gajewski et al. 2001; Whiting and Chanton 2001; Friborg et al. 2003). Considering human-induced climate change, ecohydrological changes may be considered to be the primary driving force in the changes of the peatland C cycle (Gorham 1991; Roulet et al. 1992; Laine et al. 1996; Moore 2002; Turetsky et al. 2002; Belyea and Malmer 2004; Christensen et al. 2004; Malmer and Wallén 2004; Shurpali et al. 2004; Strack et al. 2004; Fig. 9.2).

References

Alm J, Talanov A, Saarnio S, Silvola J, Ikkonen E, Aaltonen H, Nykänen H, Martikainen PJ (1997) Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. Oecologia 110:423–431

Alm J, Saarnio S, Nykänen H, Silvola J, Martikainen PJ (1999a) Winter CO_2, CH_4 and N_2O fluxes on some natural and drained boreal peatlands. Biogeochemistry 44:163–186

Alm J, Schulman, L, Walden, J, Nykänen H, Martikainen PJ, Silvola J (1999b) Carbon balance of a boreal bog during a year with an exceptionally dry summer. Ecology 80:161–177

Armentano TV, Menges ES (1986) Patterns of change in the carbon balance of organic-soil wetlands of the temperate zone. J Ecol 74:755–774

Aselmann I, Crutzen PJ (1989) Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. J Atmos Chem 8:307–358.

Aurela M, Tuovinen J-P, Laurila T (1998) Carbon dioxide exchange in a subarctic peatland ecosystem in northern Europe measured by eddy covariance technique. J Geophys Res 103:11289–11301

Aurela M, Laurila T, Tuovinen J-P (2001) Seasonal CO_2 balances of a subarctic mire. J Geophys Res 106:1623–1637

Aurela M, Laurila T, Tuovinen J-P (2002) Annual CO_2 balance of a subarctic fen in northern Europe: importance of the wintertime efflux. J Geophys Res 107. DOI 10.1029/2002JD002055

Aurela M, Laurila T, Tuovinen J-P (2004) The timing of snow melt controls the annual CO_2 balance in a subarctic fen. Geophys Res Lett 31:L16119. DOI 10.1029/2004GL020315

Avery GB Jr, Shannon RD, White JR, Martens CS, Alperin MJ (1999) Effect of seasonal change in the pathway of methanogenesis on the $\delta^{13}C$ values of pore water methane in a Michigan peatland. Global Biogeochem. Cycles 6:271–291

Baird A, Beckwith CW, Waldron, S, Waddington JM (2004) Ebullition of methane-containing gas bubbles from near-surface *Sphagnum* peat. Geophys Res Lett 31:L21505. DOI 10.1029/2004GL021157

Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Global Change Biol 9:479–492

Bartlett KB, Harriss RC (1993) Review and assessment of methane emissions from wetlands. Chemosphere 26:261–320

Bartsch I, Moore TR (1985) A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. Can J Bot 63:1241–1248

Bauer IE, Gignac D, Vitt DH (2003) Development of a peatland complex in boreal western Canada: lateral site expansion and local variability in vegetation succession and long-term peat accumulation. Can J Bot 81:833–847

Bellisario L, Moore TM, Bubier JL (1998) Net ecosystem exchange in a boreal peatland, northern Manitoba. Écoscience 5:534–541

Bellisario LM, Bubier JL, Moore TR, Chanton JP (1999). Controls on CH_4 emissions from a northern peatland. Global Biogeochem Cycles 9:455–470

Belyea, LR Malmer N (2004) Carbon sequestration in peatland: patterns and mechanisms of response to climate change. Global Change Biol 10:1043–1052

Bergman I, Svensson BH, Nilsson M (1998) Regulation of methane production in a Swedish acid mire by pH, temperature and substrate. Soil Biol Biochem 30:729–741

Blodau C (2002) Carbon cycling in peatlands – a review of processes and controls. Environ Rev 10:111–134

Borren W, Bleuten W, Lapshina ED (2004) Holocene peat and carbon accumulation rates in the southern taiga of Western Siberia. Quat Res 61:42–51

Bosse U, Frenzel P (2001) CH_4 emissions from a West Siberian mire. Suo 52:99–114

Botch M, Kobak KI, Vinson TS, Kolchugina TP (1995) Carbon pools and accumulation in peatlands of the former Soviet Union. Global Biochem Cycles 9:37–46

Brooks PD, Schmidt SK, Williams MW (1997) Winter production of CO_2 and N_2O from alpine tundra: environmental controls and relationships to inter-system C and N fluxes. Oecologia 110:403–413

Bubier JL (1995) The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. J Ecol 83:403–420

Bubier JL, Moore TR (1994) An ecological perspective on methane emissions from northern wetlands. Trends Ecol Evol 9:460–464

Bubier JL, Costello LA, Moore TR, Roulet NT, Savage K (1993a) Microtopography and methane flux in boreal peatlands, northern Ontario, Canada. Can J Bot 71:1056–1063

Bubier JL, Moore TR, Roulet NT (1993b) Methane emissions from wetlands in the midboreal region of northern Ontario, Canada. Ecology 74:2240–2254

Bubier JL, Moore TR, Bellisario L, Corner NT, Crill PM (1995a) Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada. Global Biogeochem Cycles 9:455–470

Bubier JL, Moore TR, Juggins S (1995b) Predicting methane emission from bryophyte distribution in northern Canadian peatlands. Ecology 76:677–693

Bubier JL, Crill PM, Moore TR, Savage K, Varner R (1998) Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex. Global Biogeochem Cycles 12:703–714

Bubier JL, Frolking S. Crill PM, Linder E (1999) Net ecosystem productivity and its uncertainty in a diverse boreal peatland. J Geophys Res 104:27683–27692

Bubier JL, Bhatia G, Moore TR, Roulet NT, Lafleur PM (2003a) Between year and site variability in growing season net ecosystem CO_2 exchange at a large peatland, Ontario, Canada. Ecosystems 6:353–367

Bubier J, Crill P, Mosedale A, Frolking S (2003b) Peatland responses to varying interannual moisture conditions as measured by automatic CO_2 chambers. Global Biogeochem Cycles 17:1066. DOI 10.1029/2002GB001946

Buringh P (1984) Organic carbon in soils of the world. In: Woodwell GM (ed) The role of terrestrial vegetation in the global carbon cycle, SCOPE 23. Wiley, New York, pp 91–109

Carroll P, Crill PM (1997) Carbon balance of a temperate poor fen. Global Biogeochem Cycles 11:349–356

Chanton JP, Whiting GJ, Showers WJ, Crill PM (1992a) Methane flux from *Peltandra virginica*: stable isotope tracing and chamber effects. Global Biogeochem Cycles 6:15–31

Chanton JP, Martens CS, Kelley CA, Crill PM, Showers WJ (1992b) Methane transport mechanisms and isotopic fractionation in emergent macrophytes of an Alaskan tundra lake. J Geophys Res 97:16681–16888

Chanton JP, Whiting GJ, Happell JD, Gerard G (1993) Contrasting rates and diurnal patterns of methane emissions from emergent aquatic macrophytes. Aquat Bot 46:111–128

Chanton JP, Bauer J, Glaser P, Tyler SC, Ramonowitz E, Siegel D, Kelley C, Lazrus A (1995) Radiocarbon evidence for the substrates supporting methane formation within northern Minnesota peatland. Geochim Cosmochim Acta 59:3773–3668

Chapin FS III, Matson PA, Mooney H (2002) Principles of terrestrial ecosystem ecology. Springer, Berlin Heidelberg New York

Chapman SJ, Thurlow M (1998) Peat respiration at low temperatures. Soil Biol Biochem 30:1013–1021

Charman D (2002) Peatlands and environmental change. Wiley, Chichester

Charman D, Aravena R, Warner BD (1994) Carbon dynamics in a forested peatland in north-eastern Ontario, Canada. J Ecol 82:55–62

Chasar LS, Chanton JP, Glaser PH, Siegel DI, Rivers JS (2000) Radiocarbon and stable carbon isotopic evidence for transport and transformation of dissolved organic carbon, dissolved inorganic carbon, and CH_4 in a northern Minnesota peatland. Global Biogeochem Cycles 14:1095–1108

Chimner RA, Cooper DJ (2003) Influence of water table levels on CO_2 emissions in a Colorado subalpine fen: an in situ microcosm study. Soil Biol Biochem 35:435–351

Christensen TR (1993) Methane emission from Arctic tundra. Biogeochemistry 21:117–139

Christensen TR, Friborg T, Sommerkorn M, Kaplan J, Illeris L, Soegaard H, Nordstroem C, Jonasson S (2000) Trace gas exchange in a high-arctic valley, 1. Variations in CO_2 and CH_4 flux between tundra vegetation types. Global Biogeochem Cycles 14:701–714

Christensen TR, Panikov N, Mastepanov M, Joabsson A, Stewart A, Öquist M, Sommerkorn M, Reynaud S, Svensson B (2003) Biotic controls on CO_2 and CH_4 exchange in wetlands – a closed environment study. Biogeochemistry 64:337–354

Christensen TR, Friborg T, Åkerman HP, Mastepanov M (2004) Thawing sub-arctic permafrost: effects on vegetation and methane emissions. Geophys Res Lett 31:L04501. DOI 10.1029/2003GL018680

Cicerone RJ, Oremland RS (1988) Biogeochemical aspects of atmospheric methane. Global Biogeochem Cycles 2:299–327

Clymo RS (1984) The limits to peat growth. Philos Trans R Soc,Lond Ser B 303:605–654

Clymo RS (1992) Models of peat growth. Suo 43:173–182

Clymo RS, Turunen J, Tolonen K (1998) Carbon accumulation in peatland. Oikos 81:368–388

Conrad R (1989) Control of methane production in terrestrial ecosystems. In: Andreae, MO, Schimel, DS (eds) Exchange of trace gases between terrestrial ecosystems and the atmosphere. Wiley, New York, pp 39–58

Conrad R (1996) Soil microorganisms as controllers of atmospheric trace gases (H_2, CO, CH_4, OCS, N_2O and NO). Microbiol Rev 60:609–640

Crill P (1991) Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil. Global Biogeochem Cycles 5:319–334

Crill PM, Bartlett KB, Harriss RC, Gorham E, Verry ES, Sebacher DL, Madzar L, Sanner W (1988) Methane flux from Minnesota peatlands. Global Biogeochem Cycles 2:371–384

Crill P, Hargreaves K, Korhola A (2000) The role of peat in Finnish greenhouse gas balances. Ministry of Trade and Industry, studies and reports 10/2000, Helsinki, Finland

Curtis PS, Hanson PJ, Bolstad P, Barford C, Randolph JC, Schmid HP, Wilson KB (2002) Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. Agric For Meteorol 113:3–19

Darrah PR (1993) The rhizosphere and plant nutrition: a quantitative approach. Plant Soil 155/156:1–20

DeVito KJ, LaZerte BD (1989) Phosphorus and nitrogen retention in five Precambrian shield wetlands. Biogeochemistry 8:185–204

Dise NB (1993) Methane emission from Minnesota peatlands: spatial and seasonal variability. Global Biogeochem Cycles 7:123–142

Dise NB, Gorham E, Verry ES (1993) Environmental factors controlling methane emissions from peatlands in northern Minnesota. J Geophys Res 98:10583–10594

Domisch T, Finér L, Karsisto M, Laiho R, Laine J (1998) Relocation of carbon from decaying litter in drained peat soils. Soil Biol Biochem 30:1529–1536

Dunfield P, Knowles R, Dumont R, Moore TR (1993) Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. Soil Biol Biochem 25:321–326

Eilrich B, Steinmann P (2003) Acetate in deep peat bog environments – Seasonal variation and implications for methanogenesis: investigation of an ombrotrophic peat bog in the Jura Mountains, Switzerland. Z Dtsch Geol Ges 153:145–157

Fahnestock JT, Jones MH, Welker JM (1999) Wintertime CO_2 efflux from arctic soils: implications for annual carbon budgets. Global Biogeochem Cycles 13:775–779

Feng X (2002) A theoretical analysis of carbon isotope evolution of decomposing plant litters and soil organic matter. Global Biogeochem Cycles 16:1119. DOI 10.1029/2002GB001867

Ferguson TJ, Mah RA (1983) Effect of H_2-CO_2 on methanogenesis from acetate or methanol in *Methanosarcina* spp. Appl Environ Microbiol 46:348–355

Fey A, Conrad R (2000) Effect of temperature on carbon and electron flow and on the archaeal community in methanogenic rice field soil. Appl Environ Microbiol 66:4790–4797

Fiedler S, Sommer M (2000) Methane emissions, groundwater levels and redox potentials of common wetland soils in a temperate-humid climate. Global Biogeochem Cycles 14:1081–1093

Francez A-J, Vasander H (1995) Peat accumulation and peat decomposition after human disturbance in French and Finnish mires. Acta Oecol 16:599–608

Freeman C, Evans CD, Monteith DT, Reynolds B, Fenner N (2001) Export of organic carbon from peat soils. Nature 412:785

Freeman C, Nevison GB, Kang H, Hughes S, Reynolds B, Hudson JA (2002) Contrasted effects of simulated drought on the production and oxidation of methane in a mid-Wales wetland. Soil Biol Biochem 34:61–67

Frenzel P (2000) Plant associated methane oxidation in ricelands and wetlands. Adv Microb Ecol 16:85–114

Frenzel P, Karofeld E (2000) CH_4 emission from a hollow-ridge complex in a raised bog: the role of CH_4 production and oxidation. Biogeochemistry 51:91–112

Frenzel P, Rudolph J (1998) Methane emission from a wetland plant: the role of CH_4 oxidation in *Eriophorum*. Plant Soil 202:27–32

Friborg T, Christensen TR, Hansen BU, Nordstroem C, Soegaard H (2000) Trace gas exchange in a high-arctic valley 2. Landscape CH_4 fluxes measured and modeled using eddy correlation data. Global Biogeochem Cycles 14:715–723

Friborg T, Soegaard H, Christensen TR, Lloyd CR, Panikov, NS (2003) Siberian wetlands: where a sink is a source. Geophys Res Lett 30:2129. DOI 10.1029/2003 GL017797

Frolking S, Crill P (1994) Climate controls on temporal variability of methane flux from a poor fen in southeastern New Hampshire: measurement and modeling. Global Biogeochem Cycles 8:385–397

Frolking SE, Bubier JL, Moore TR, Ball T, Bellisario LM, Bhardwaj A, Carroll P, Crill PM, Lafleur PM, McCaughey JH, Roulet NT, Suyker AE, Verma SB, Waddington JM, Whiting PJ (1998) Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. Global Biogeochem Cycles 12:115–126

Frolking S, Roulet NT, Moore TR, Lafleur PM, Bubier JL, Crill PM (2002) Modeling seasonal to annual carbon balance of Mer Bleu Bog, Ontario, Canada. Global Biogeochem Cycles 16. DOI 10.1029/2001GB001457

Gajewski K, Viau A, Sawada M, Atkinson D, Wilson S (2001) *Sphagnum* peatland distribution in North America and Eurasia during the past 21000 years. Global Biogeochem Cycles 15:297–310

Galand PE, Saarnio S, Fritze H, Yrjälä K (2002) Depth related diversity of methanogen Archaea in Finnish oligotrophic fen. FEMS Microbiol Ecol 42:441–449

Galand PE, Fritze H, Yrjälä K (2003) Microsite-dependent changes in methanogenic populations in a boreal oligotrophic fen. Environ Microbiol 5:1133–1143

Garcia J-L, Patel BKC, Ollivier B (2000) Taxonomic, phylogenetic and ecological diversity of methanogenic *Archaea*. Anaerobe 6:205–226

Glaser PH, Chanton JP, Morin P, Rosenberry DO, Siegel DI, Ruud O, Chasar LI, Reeve AS (2004) Surface deformations as indicators of deep ebullition fluxes in a large northern peatland. Global Biogeochem Cycles 18:GB1003. DOI 10.1029/2003 GB002069

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable response to climatic warming. Ecol Appl 1:182–195

Granberg G, Sundh I, Svensson BH, Nilsson M (2001) Effects of increased temperature, nitrogen, and sulphur deposition on methane emission from a mixed mire in northern Sweden: a three year factorial designed field experiment. Ecology 82:1982–1998

Grant RF, Roulet, NT (2002) Methane efflux from boreal wetlands: theory and testing of the ecosystem model Ecosys with chamber and tower flux measurements. Global Biogeochem Cycles 16:1054. DOI 10.1029/2001GB001702

Griffis TJ, Rouse WR, Waddington JM (2000) Interannual variability of net ecosystem CO_2 exchange at a subarctic fen. Global Biogeochem Cycles 14:1109–1122

Hargreaves KJ, Fowler D, Pitcairn CER, Aurela M (2001) Annual methane emission from Finnish mires estimated from eddy covariance campaign measurements. Theor Appl Climatol 70:203–213

Heilman MA, Carlton RG (2001) Methane oxidation associated with submersed vascular macrophytes and its impact on plant diffusive methane flux. Biogeochemistry 52:207–224

Heikkinen JEP (2003) Carbon balance of the arctic wetlands in Europe. Doctoral dissertation, Kuopio University Publications C. Natural and Environmental Sciences 153, Kuopio, Finland

Heikkinen JEP, Elsakov V, Martikainen, PJ (2002) Carbon dioxide and methane dynamics and annual carbon balance in tundra wetland in NE Europe, Russia. Global Biogeochem Cycles 16:1115. DOI 10.1029/2002GB001930

Hoffland E (1992) Quantitative evaluation of the role of organic acid exudation in the mobilization of rock phosphate by rape. Plant Soil 140:279–289

Hornibrook ERC, Longstaffe FJ, Fyfe WS (1997) Spatial distribution of microbial methane production pathways in temperate zone wetland soils: stable carbon and hydrogen biotope evidence. Geochim Cosmochim Acta 61:745–753

Huser BA, Wuhrmann K, Zehnder JB (1982) *Methanothrix soehgenii gen. nov. sp. nov.*, a new acetotrophic non-hydrogen-oxidizing methane bacterium. Arch Microbiol 132:1–9

Ikkonen EN, Kurets VK, Grabovik SI, Drozdov SN (2001) The rate of carbon dioxide emission into the atmosphere from a southern Karelian mesooligotrophic bog. Russ J Ecol 32:382–385

IPCC (2001) Climate change 2001: impacts, adaptation and vulnerability, summary for policymakers, 3rd assessment report of the inter intergovernmental panel on climate change. Cambridge University Press, Cambridge

Jähne B, Heinz G, Dietrich W (1987) Measurement of the diffusion coefficients of sparingly soluble gases in water. J Geophys Res 92:10767–10776

Joabsson A, Christensen TR, Wallén B (1999) Vascular plant controls on methane emissions from northern peatforming wetlands. Trends Ecol Evol 14:385–388

Joosten H, Clarke D (2002) Wise use of mires and peatlands – background and principles including a framework for decision-making. International Mire Conservation Group and International Peat Society, Jyväskylä, Finland

Karofeld E (2004) Mud-bottom hollows: exceptional features in carbon-accumulating bogs? Holocene 14:119–124

Kelker D, Chanton J (1997) The effect of clipping on methane emissions from *Carex*. Biogeochemistry 39:37–44

Kelley CA, Dise NB, Martens CS (1992) Temporal variations in the stable carbon isotopic composition of methane emitted from Minnesota peatlands. Global Biogeochem Cycles 6:263–269

Kettunen A (2000) Short term carbon dioxide exchange and environmental factors in a boreal fen. Verh Int Ver Limnol 27:1–5

Kettunen A (2002) Modeling of microscale variations in methane fluxes. Doctoral dissertation, Helsinki University of Technology, Systems Analysis Laboratory Research Reports A83, Helsinki, Finland

Kettunen A (2003) Connecting methane fluxes to vegetation cover and water table fluctuations at microsite level: a modelling study. Global Biogeochem Cycles 17:1051. DOI 10.1029/2002GB001958

Kettunen A, Kaitala V, Alm J, Silvola J, Nykänen H, Martikainen PJ (1996) Cross-correlation analysis of the dynamics of methane emissions from boreal peatlands. Global Biogeochem Cycles 10:457–471

Kettunen A, Kaitala V, Lehtinen A, Lohila A, Alm J, Silvola J, Martikainen PJ (1999) Methane production and oxidation potentials in relation to water table fluctuations in two boreal mires. Soil Biol Biochem 31:1741–1749

King JY, Reeburgh WS (2002) A pulse-labeling experiment to determine the contribution of recent plant photosynthates to net methane emission in arctic wet sedge tundra. Soil Biol Biochem 34:173–180

King GM, Roslev P, Skovgaard H (1990) Distribution and rate of methane oxidation in sediments of the Florida Everglades. Appl Environ Microbiol 56:2902–2911

King JY, Reeburgh WS, Regli SK (1998) Methane emission and transport by arctic sedges in Alaska: results of a vegetation removal experiment. J Geophys Res 103:29083–29092

King JY, Reeburgh WS, Thieler KK, Kling GW, Loya WM, Johnson LC, Nadelhoffer KJ (2002) Pulse-labeling studies of carbon cycling in Arctic tundra ecosystems: the contribution of photosynthates to methane emission. Global Biogeochem Cycles 16:1062. DOI 10.1029/2001GB001456

Kivinen E, Pakarinen P (1981) Geographical distribution of peat resources and major peatland complex types in the world. Ann Acad Sci Fenn Ser A III Geol Geogr 132:1–28

Koncalová H, Pokorny J, Kvêt J (1988) Root ventilation in *Carex gracilis* Curt.: diffusion or mass flow? Aquat Bot 30:149–155

Korhola A, Tolonen K, Turunen J, Jungner H (1995) Estimating long-term carbon accumulation rates in boreal peatlands by radiocarbon dating. Radiocarbon 37:575–584

Kuder, T, Kruge MA (2001) Carbon dynamics in peat bogs: insights from substrate macromolar chemistry. Global Biogeochem Cycles 115:721–727

Kummerow J, Ellis BA (1984) Temperature effect on biomass production and root/shoot biomass ratios in two arctic sedges under controlled environmental conditions. Can J Bot 62:2150–2153

Lafleur PM, McCaughey JH, Joiner DW, Bartlett PA, Jelinski DE (1997) Seasonal trends in energy, water, and carbon dioxide fluxes at a northern boreal wetland. J Geophys Res 102:29009–29020

Lafleur PM, Roulet NT, Admiral SW (2001) Annual cycle of CO_2 exchange at a bog peatland. J Geophys Res 106:3071–3081

Lafleur PM, Roulet NT, Bubier JL, Frolking S, Moore TR (2003) Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. Global Biogeochem Cycles 17:1036. DOI 10.1029/2002GB001983

Laine J, Vasander H (1996) Ecology and vegetation gradients of peatlands. In: Vasander H (ed) Peatlands in Finland. Finnish Peatland Society, Helsinki, Finland, pp 10–19

Laine J, Silvola J, Tolonen K, Alm J, Nykänen H, Vasander H, Sallantaus T, Sinisalo J, Martikainen PJ (1996) Effect of water-level drawdown on global climatic warming: northern peatlands. Ambio 25:179–184

Lamers LPM, Farhoush C, van Groenendael JM, Roelofs JGM (1999) Calcareous groundwater raised bogs: the concept of ombrotrophy revisited. J Ecol 87:639–648

Lappalainen E (ed) (1996) Global peat resources. International Peat Society and Geological Survey of Finland, Jyväskylä, Finland

Mäkilä M (1994) Calculation of the energy content of mires on the basis of peat properties (in Finnish with English summary). Geological Survey of Finland, report of investigations 121. Espoo, Finland

Malmer N, Wallén B (2004) Input rates, decay losses and accumulation rates of carbon in bogs during the last millennium: internal processes and environmental changes. Holocene 14:11–117

Malmer N, Svensson BM, Wallén B (1994) Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. Folia Geobot Phytotaxon 29:483–496

Martikainen PJ, Nykänen H, Alm J, Silvola J (1995) Changes in fluxes of carbon dioxide, methane and nitrous oxide due to forest drainage of mire sites with different trophy. Plant Soil 168-169:571–577

Mast MA, Wickland KP, Striegel T, Clow DW (1998) Winter fluxes of CO_2 and CH_4 from subalpine soils in Rocky Mountain National Park, Colorado. Global Biogeochem Cycles 12:607–620

Matthews E, Fung I (1987) Methane emission from natural wetlands: global distribution, area, and environmental characteristics of sources. Global Biogeochem Cycles 1:61–86

Mattson MD, Likens GE (1990) Air pressure and methane fluxes. Nature 347:718–719

Melloh RA, Crill PM (1996) Winter methane dynamics in a temperate peatland. Global Biogeochem Cycles 10:247–254

Mench M, Martin E (1991) Mobilization of cadmium and other metals from two soils by roots exudates of *Zea mays* L., *Nicotiana tabacum* L. and *Nicotiana rustica* L. Plant Soil 132:187–196

Metsävainio K (1931) Untersuchungen über das Wurzelsystem der Moorpflanzen. Ann Bot Soc Zool-Bot Fenn Vanamo 1:1–422

Mikkelä C, Sundh I, Svensson BH, Nilsson M (1995) Diurnal variation in methane emission in relation to the water table, soil temperature, climate and vegetation cover in a Swedish mire. Biogeochemistry 28:93–114

Mooney HA (1986) Photosynthesis. In: Crawley MJ (ed) Plant ecology. Blackwell, Oxford, pp 345–373

Moore PD (2002) The future of cool temperate bogs. Environ Conserv 29:3–20

Moore TR (2001) Les processus biogéochimiques lies au carbone. In: Payette S, Rochefort L (eds) Écologie des tourbières du Québec-Labrador. Les Presses de l'Université Laval, Sainte-Foy, pp 183–197

Moore TR (2003) Dissolved organic carbon in a northern boreal landscape. Global Biogeochem Cycles 17:1109. DOI 10.1029/2003GB002050

Moore TR, Roulet NT (1993) Methane flux: water table position relations in northern peatlands. Geophys Res Lett 20:587–590

Moore T, Roulet N, Knowles R (1990) Spatial and temporal variations of methane flux from subarctic/northern boreal fens. Global Biogeochem Cycles 4:29–46

Moore TR, Heyes A, Roulet NT (1994) Methane emissions from wetlands, southern Hudson Bay lowland. J Geophys Res 99:1455–1467

Moore TR, Roulet NT, Waddington JM (1998) Uncertainty in predicting the effect of climatic change on the carbon cycle of Canadian peatlands. Clim Change 40:229–245

Moore TR, Bubier JL, Frolking SE, Lafleur PM, Roulet NT (2002) Plant biomass and production and CO_2 exchange in an ombrotrophic bog. J Ecol 90:25–36

Moosavi SC, Crill PM (1998) CH_4 oxidation by tundra wetlands as measured by a selective inhibitor technique. J Geophys Res 103:29093–29106

Morrissey LA, Livingston GP (1992) Methane emission from Alaska arctic tundra: an assessment of local scale variability. J Geophys Res 97:16661–16670

Morrissey LA, Zobel DB, Livingston GP (1993) Significance of stomatal control on methane release from *Carex* dominated wetlands. Chemosphere 26:339–355

Nilsson M, Bohlin E (1993) Methane and carbon dioxide concentrations in bogs and fens with special reference to the effects of the botanical composition of peat. J Ecol 81:615–625

Nilsson M, Mikkelä C, Sundh I, Granberg G, Svensson BH, Ranneby B (2001) Methane emission from Swedish mires: national and regional budgets and dependence on mire vegetation. J Geophys Res 106:20847–20860

Norman JM, Kucharik CJ, Gower ST, Baldocchi DD, Crill PM, Rayment M, Savage K, Striegl RG (1997) A comparison of six methods for measuring soil-surface carbon dioxide fluxes. J Geophys Res 102:28771–28777

Nykänen H, Alm J, Silvola J, Tolonen K, Martikainen PJ (1998) Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. Global Biogeochem Cycles 12:53–69

Nykänen H, Vasander H, Huttunen JT, Martikainen PJ (2002) Effect of experimental nitrogen load on methane and nitrous oxide fluxes on ombrotrophic boreal peatland. Plant Soil 242:147–155

Nykänen H, Heikkinen JEP, Pirinen L, Tiilikainen K, Martikainen PJ (2003) Annual CO_2 exchange and CH_4 fluxes on a subarctic palsa mire during climatically different years. Global Biogeochem Cycles 17:1018. DOI 10.1029/2002GB001861

Oechel WC, Vourlitis GL, Hastings SJ, Bochkarev SA (1995) Change in arctic CO_2 flux over two decades: effects of climate change at Barrow, Alaska. Ecol Appl 5:846-855

Oechel WC, Vourlitis G, Hastings SJ (1997) Cold season CO_2 emission from arctic soils. Global Biogeochem Cycles 11:163–172

Panikov NS, Dedysh SN (2000) Cold season CH_4 and CO_2 emission from boreal peat bogs (West Siberia): winter fluxes and thaw activation dynamics. Global Biogeochem Cycles 14:1071–1080

Pearce DME, Clymo RS (2001) Methane oxidation in a peatland core. Global Biogeochem Cycles 15:709–720

Pitkänen A, Turunen J, Tolonen K (1999) The role of fire in the carbon dynamics of a mire, eastern Finland. Holocene 9:453–462

Popp TJ, Chanton JP, Whiting GJ, Grant N (1999) Methane stable isotope distribution at a *Carex* dominated fen in north central Alberta. Global Biogeochem Cycles 13:1063–1077

Popp TJ, Chanton JP, Whiting GJ, Grant N (2000) Evaluation of methane oxidation in the rhizosphere of a *Carex* dominated fen in north central Alberta, Canada. Biogeochemistry 51:259–281

Prinn PR (1994) The interactive atmosphere: global atmospheric-biospheric chemistry. Ambio 23:50–61

Reader RJ, Stewart JM (1972) The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. Ecology 53:1024–1037

Robinson SD, Moore TR (2000) The influence of permafrost and fire upon carbon accumulation in high boreal peatlands, Northwest Territories, Canada. Arct Antarct Alp Res 32:155–166

Roehm CL, Roulet NT (2003) Seasonal contribution of CO_2 fluxes in the annual C budget of a northern bog. Global Biogeochem Cycles 17:1029. DOI 10.1029/2002GB001889

Römheld V (1991) The role of phytosiderophores in acquisition of iron and other micronutrients in graminaceous species: an ecological approach. Plant Soil 130:127–134

Roslev P, King GM (1994) Survival and recovery of methanotrophic bacteria starved under oxic and anoxic conditions. Appl Environ Microbiol 60:2602–2608

Roulet NT, Moore T, Bubier JL, Lafleur PM (1992) Northern fens: methane flux and climatic change. Tellus B 44:100–105

Roulet NT, Ash R, Quinton W, Moore T (1993) Methane flux from drained northern peatlands: effect of persisting water table lowering on flux. Global Biogeochem Cycles 7:749–769

Rovira AD (1969) Plant root exudates. Bot Rev 35:35–57

Ruimy AP, Jarvis D, Baldocchi D, Saugier B (1996) CO_2 fluxes over plant canopies and solar radiation: a review. Adv Ecol Res 26:1–68

Russell RS (1977) Plant root systems: their function and interaction with the soil. McGraw-Hill, London

Saarinen T (1996) Biomass and production of two vascular plants in a boreal mesotrophic fen. Can J Bot 74:934–938

Saarinen T (1999) Vascular plants as input of carbon in boreal sedge fens: control of production and partitioning of biomass. Publications in Botany, University of Helsinki 28, Yliopistopaino, Finland

Saarnio S, Silvola J (1999) Effects of increased CO_2 and N on CH_4 efflux from a boreal mire: a growth chamber experiment. Oecologia 119:349–356

Saarnio S, Alm J, Silvola J, Lohila A, Nykänen H, Martikainen PJ (1997) Seasonal variation in CH_4 emissions and production and oxidation potentials at microsites on an oligotrophic pine fen. Oecologia 110:414–422

Saarnio S, Alm J, Martikainen PJ, Silvola J (1998) Effects of raised CO_2 on potential CH_4 production and oxidation in, and CH_4 emission from, a boreal mire. J Ecol 86:261–268

Saarnio S, Järviö S, Saarinen T, Vasander H, Silvola J (2003) Minor changes in vegetation and carbon gas balance in a boreal mire under a raised CO_2 or NH_4NO_3 supply. Ecosystems 6:46–60

Sallantaus T (1992) Leaching in the material balance of peatlands – preliminary results. Suo 43:253–258

Scanlon D, Moore T (2000) CO_2 production from peatland soil profiles: the influence of temperature, oxic/anoxic conditions and substrate. Soil Sci 165:153–160

Schiff S, Aravena R, Mewhinney E, Elgood R, Warner BG, Dillon P, Trumbore S (1998) Precambrian shield wetlands – hydrologic control of the sources and export of dissolved organic matter. Clim Change 40:167–188

Schimel JP (1995) Plant transport and methane production as controls on methane flux from arctic wet meadow tundra. Biogeochemistry 28:183–200

Schlesinger WH (1977) Carbon balance in terrestrial detritus. Annu Rev Ecol Syst 8:51–81

Sebacher DI, Harriss RC, Bartlett KB (1985) Methane emissions to the atmosphere through aquatic plants. J Environ Qual 14:40–46

Sebacher DI, Harriss RC, Bartlett KB, Sebacher SM, Grice SS (1986) Atmospheric methane sources: Alaskan tundra bogs, an alpine fen, and a subarctic boreal marsh. Tellus 38:1–10

Segers R, Kengen SWM (1998) Soil methane production as a function of anaerobic carbon mineralisation: a process model. Soil Biol Biochem 30:1107–1117

Segers R, Rappoldt C, Leffelaar PA (2001) Modeling methane fluxes in wetlands with gas-transporting plants 2. Soil layer scale. J Geophys Res 106:3529–3540

Shannon RD, White JR (1994) A three-year study of controls on methane emissions from two Michigan peatlands. Biogeochemistry 27:35–60

Shaver GR, Cutler JC (1979) The vertical distribution of live vascular phytomass in cottongrass tussock tundra. Arct Alp Res 11:335–342

Sheng Y, Smith LC, MacDonald GM, Kremenetski KV, Frey KE, Velichko AA, Lee M, Beilman DW, Dubinin P (2004) A high-resolution GIS-based inventory of the west Siberian peat carbon pool. Global Biogeochem Cycles 18:GB3004. DOI 10.1029/2003GB002190

Shurpali NJ, Verma SB (1998) Micrometeorological measurements of methane flux in a Minnesota peatland during two growing seasons. Biogeochemistry 40:1–15

Shurpali NJ, Verma SB, Clement RJ, Billesbach DP (1993) Seasonal distribution of methane flux in a Minnesota peatland measured by eddy correlation. J Geophys Res 98:20649–20655

Shurpali N, Saarnio S Alm, J (2004) Modelling land use impacts of annual emissions of CO_2, CH_4 and N_2O from peatlands in Finland. In: Päivänen J (ed) Wise use of peatlands. Proceedings of the 12th international peat congress, vol. 1, pp 170–177

Silvola J, Hanski I (1979) Carbon accumulation in a raised bog. Oecologia 37:285–295

Silvola J, Alm J, Ahlholm U, Nykänen H, Martikainen PJ (1996a) The contribution of plant roots to CO_2 fluxes from organic soils. Biol Fert Soils 23:126–131

Silvola J, Alm J, Ahlholm U, Nykänen H, Martikainen PJ (1996b) CO_2 fluxes from boreal mires under varying temperature and moisture conditions. J Ecol 84:219–228

Silvola J, Saarnio S, Foot J, Sundh I, Greenup A, Heijmans M, Ekberg A, Mitchell E, van Breemen N (2003) Effects of elevated CO_2 and N deposition on CH_4 emissions from European mires. Global Biogeochem Cycles 17:GB1068. DOI 10.1029/2002GB001886

Sjörs H (1981) Peat on earth: multiple use or conservation? Ambio 9:303–308

Sjörs H (1991) Phyto- and necromass above and below ground in a fen. Holarctic Ecol 14:208–218

Soegaard H, Nordstroem C (1999) Carbon dioxide exchange in a high-arctic fen estimated by eddy covariance measurements and modeling. Global Change Biol 5:547–562

Soegaard H, Nordstroem C, Friborg T, Hansen BU, Christensen TR, Bay C (2000) Trace gas exchange in a high-arctic valley, 3. Integrating and scaling CO_2 fluxes from canopy to landscape using flux data, footprint modeling, and remote sensing. Global Biogeochem Cycles 14:725–744

Sommerfeld RA, Mosier AR, Musselman RC (1993) CO_2, CH_4 and N_2O flux through a Wyoming snowpack and implications for global budgets. Nature 361:140–142

Sommerfeld RA, Massman WJ, Musselman RC, Mosier AR (1996) Diffusional flux of CO_2 through snow: spatial and temporal variability among alpine-subalpine sites. Global Biogeochem Cycles 10:473–482

Strack M, Waddington JM, Tuittila E-S (2004) Effect of water table drawdown on northern peatland methane dynamics: implications for climate change. Global Biogeochem Cycles 18:GB4003. DOI 10.1029/2003GB002209

Ström L, Ekberg A, Mastepanov M, Christensen TR (2003) The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Global Change Biol 9:1185–1192

Sundh I, Nilsson M, Granberg G, Svensson BH (1994) Depth distribution of microbial production and oxidation of methane in northern boreal peatlands. Microb Ecol 27:253–265

Sundh I, Mikkelä C, Nilsson M, Svensson BH (1995) Potential aerobic methane oxidation in a *Sphagnum* dominated peatland – controlling factors and relation to methane emission. Soil Biol Biochem 27:829–837

Svensson BH (1984) Different temperature optima for methane formation when enrichments from acid peat are supplemented with acetate or hydrogen. Appl Environ Microbiol 48:389–394

Svensson BH, Rosswall T (1984) *In situ* methane production from acid peat in plant communities with different moisture regimes in a subarctic mire. Oikos 43:341–350

Svensson BH, Sundh I (1992) Factors affecting methane production in peat soils. Suo 43:183–190

Svensson BH, Veum AK, Kjelvik S (1975) Carbon losses from tundra soils. In: Wielgolaski FE (ed) Fennoscandian tundra ecosystems 1, plants and microorganisms. Springer, Berlin Heidelberg New York, pp 279–286

Tatarinov F, Kurbatova J, Molchanov A, Minaeva T, Orlov T (2003) Measuring of components of peat and ground vegetation CO_2 balance in a southern taiga peat bog. In: Järvet A, Lode E (eds) Ecohydrological processes in northern wetlands. Tartu University Press, Tartu, pp 215–220

Thomas KL, Benstead J, Davies KL, Lloyd D (1996) Role of wetland plants in the diurnal control of CH_4 and CO_2 fluxes in peat. Soil Biol Biochem 28:17–23

Thomas PA, Pearce DME (2004) Role of cation exchange in preventing the decay of anoxic deep bog peat. Soil Biol Biochem 36:23–32

Tjuremnov SN (1949) Torfjanie mestorochdenija. 2 izd. Nedra, Moscow

Tolonen K (1979) Peat as a renewable resource: long-term accumulation rates in northeuropean mires. In: Kivinen E, Heikurainen L, Pakarinen P (eds) Classification of peat and peatlands. International Peat Society, Helsinki, Finland, pp 282–296

Tolonen K, Vasander H, Damman AWH, Clymo RS (1992) Preliminary estimate of long-term carbon accumulation and loss in 25 boreal peatlands. Suo 43:277–280

Torn MS, Chapin FS III (1993) Environmental and biotic controls over methane flux from Arctic tundra. Chemosphere 26:357–368

Tuittila E-S, Komulainen V-M, Vasander H, Nykänen H, Martikainen PJ, Laine J (2000) Methane dynamics of a restored cut-away peatland. Global Change Biol 6:569–581

Tuittila E-S, Vasander H, Laine J (2004) Sensitivity of C sequestration in reintroduced *Sphagnum* to water level variation in a cut-away peatland. Restor Ecol 12:483–493

Turetsky MR, Wieder RK, Vitt DH (2002) Boreal peatland C fluxes under varying permafrost regimes. Soil Biol Biochem 34:907–912

Turetsky MR, Amiro BD, Bosch E, Bhatti JS (2004) Historical burn area in western Canadian peatlands and its relationship to fire weather indices. Global Biogeochem Cycles 18:GB4014. DOI 10.1029/2004GB002222

Turunen J. (2003) Past and present carbon accumulation in undisturbed boreal and subarctic mires: a review. Suo 54:15–28

Turunen J, Moore TR (2003) Controls of carbon accumulation and storage in the mineral subsoil beneath peat in Lakkasuo mire, central Finland. Eur J Soil Sci 54:279–286

Turunen J, Tolonen K, Tolvanen S, Remes M, Ronkainen J, Jungner H (1999) Carbon accumulation in the mineral subsoil of boreal mires. Global Biogeochem Cycles 13:71–79

Turunen J, Tahvanainen T, Tolonen K, Pitkänen A (2001) Carbon accumulation in West Siberian mires, Russia. Global Biogeochem Cycles 15:285–296

Turunen J, Tomppo E, Tolonen K, Reinikainen A (2002) Estimating carbon accumulation rates of undrained mires in Finland – application to boreal and subarctic regions. Holocene 12:69–80

Updegraff K, Bridgham SD, Pastor J, Weishampel P, Harth C (2001) Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulations. Ecol Appl 11:311–326

Urban NR, Bayley SE, Eisenreich SJ (1989) Export of dissolved organic carbon and acidity from peatlands. Water Resour Res 25:1619–1628

Valentine DW, Holland EA, Schimel DS (1994) Ecosystem and physiological controls over methane production in northern wetlands. J Geophys Res 99:1563–1571

van den Pol-van Dasselaar A, Oenema O (1999) Methane production and carbon mineralisation of size and density fractions of peat soil. Soil Biol Biochem 31:877–886

van den Pol-van Dasselaar A, van Beusichem ML, Oenema O (1999) Determinants of spatial variability of methane emissions from wet grasslands on peat soil. Biogeochemistry 44:221–237

van der Nat F-J, Middelburg JJ (1998) Effects of two common macrophytes on methane dynamics in freshwater systems. Biogeochemistry 43:70–104

van der Nat F-JWA, Middelburg JJ, van Meteren D, Wielemakers A (1998) Diel methane emission patterns from *Scirpus lacustris* and *Phragmites australis*. Biogeochemistry 41:1–22

van Veen JA, Merckx R, van de Geijn SC (1989) Plant- and soil-related controls of the flow of carbon from roots through the soil microbial biomass. Plant Soil 115:179–188

Vasander H (1982) Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Ann Bot Fenn 19:103–125

Vasander H, Tuittila E-S, Lode E, Lundin L, Ilomets M, Sallantaus T, Heikkilä R, Pitkänen M-L, Laine J (2003) Status and restoration of peatlands in northern Europe. Wetlands Ecol Manage 11:51–53

Verville JH, Hobbie SE, Chapin FS, Hooper DU (1998) Response of CH_4 and CO_2 flux to manipulation of temperature and vegetation. Biogeochemistry 41:215–235

Vitt DH, Halsey LA, Bauer IE, Campbell C (2000) Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. Can J Earth Sci 37:683–693

von Fischer JC, Hedin LO (2002) Separating methane production and consumption with a field-based isotope pool dilution technique. Global Biogeochem Cycles 16:1034. DOI 10.1029/2001GB001448

Vourlitis GL, Oechel WC (1999) Eddy covariance measurements of CO_2 and energy fluxes of an Alaskan tussock tundra ecosystem. Ecology 80:686–701

Vourlitis GL, Oechel WC, Hastings SJ, Jenkins MA (1993) The effect of soil moisture and thaw depth on CH_4 flux from wet coastal tundra ecosystems on the north slope of Alaska. Chemosphere 26:329–337

Waddington JM, Roulet NT (2000) Carbon balance of a boreal patterned peatland. Global Change Biol 6:87–97

Waddington JM, Roulet NT, Swanson RV (1996) Water table control of CH_4 emission enhancement by vascular plants in boreal peatlands. J Geophys Res 101:22775–22785

Wallén B (1986) Above and below ground dry mass of the three main vascular plants on hummocks on a subarctic peat bog. Oikos 46:51–56

Wallén B (1992) Methods for studying below-ground production in mire ecosystems. Suo 43:155–162

Walter BP, Heimann M, Matthews E (2001a) Modeling modern methane emissions from natural wetlands, 1. Model description and results. J Geophys Res 106: 34189–34206

Walter BP, Heimann M, Matthews E (2001b) Modeling modern methane emissions from natural wetlands, 2. Interannual variations 1982-1993. J Geophys Res 106:34207–34219

Warner BG, Clymo RS, Tolonen K (1993) Implications of peat accumulation at Point Escuminac, New Brunswick. Quat Res 39:245–248

Westermann P (1993) Temperature regulation of methanogenesis in wetlands. Chemosphere 26:321–328

Whalen SC, Reeburgh WS (1988) A methane flux time series for tundra environments. Global Biogeochem Cycles 2:399–409

Whalen SC, Reeburgh WS (1992) Interannual variations in tundra methane emisison: a four year time series at fixed sites. Global Biogeochem Cycles 6:139–159

Whiting GJ, Chanton JP (1992) Plant-dependent CH_4 emission in a subarctic Canadian fen. Global Biogeochem Cycles 6:225–231

Whiting GJ, Chanton JP (1993) Primary production control of methane emission from wetlands. Nature 364:794–795

Whiting GJ, Chanton JP (2001) Greenhouse carbon balance of wetlands: methane emission versus carbon sequestration. Tellus B 53:521–528

Whiting GJ, Chanton JR, Bartlett DS, Happell JD (1991) Relationship between CH_4 emission biomass and CO_2 exchange in a subtropical grassland. J Geophys Res 96:13067–13071

Windsor J, Moore TR, Roulet NT (1992) Episodic fluxes of methane from subarctic fens. Can J Soil Sci 72:441–452

Yavitt JB, Lang GE, Downey GE (1988) Potential methane production and methane oxidation rates in peatland ecosystems of the Appalachian mountains, United States. Global Biogeochem Cycles 2:253–268

Yavitt JA, Downey DM, Lancaster E, Lang GE (1990) Methane consumption in decomposing *Sphagnum*-derived peat. Soil Biol Biochem 22:441–447

Yu Z, Vitt DH, Campbell ID, Apps MJ (2003) Understanding Holocene peat accumulation pattern of continental fens in western Canada. Can J Bot 81:267–282

Zhuang Q, Melillo JM, Kicklighter DW, Prinn RG, McGuire AD, Steudler PA, Felzer BS, Hu S (2004) Methane fluxes between terrestrial ecosystems and the atmosphere at northern high latitudes during the past century: a retrospective analysis with a process-based biogeochemistry model. Global Biogeochem Cycles 18:GB3010. DOI 10.1029/2004GB002239

Zimov SA, Zimova GM, Daviodov, SP, Daviodova AI, Voropaev YV, Voropaeva ZV, Zemiletov IP, Zemiletova IV (1993) Winter biotic and production of CO_2 in Siberia soils: a factor in the greenhouse effect. J Geophys Res 98:5017–5023

10 The Nitrogen Cycle in Boreal Peatlands

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10.1 Introduction

It is nearly impossible to describe the relative importance of the inputs and outputs of nitrogen (N) to peatlands without first distinguishing among peatland types. As discussed in Vitt (Chap. 2), one way to classify peatlands is to group them according to their main nutrient sources; bogs mainly depend on the atmosphere as a nutrient source (ombrotrophic), whereas fens are fed mainly by surface water or groundwater (minerotrophic). At the local scale, the division between minerotrophy and ombrotrophy is fairly easy to make. At the landscape level, however, the distinction becomes increasingly difficult, as exemplified by the so-called mixed mires or patterned peatlands that may be composed of both minerotrophic and ombrotrophic elements. Another complicating factor relevant to describing the N cycle for peatlands is the influence of humans. The N dynamics in drained peatlands or in peatlands subject to elevated N deposition may be very different from that of undisturbed ecosystems. We have focused this chapter primarily on the N dynamics of undisturbed peatlands that are mainly ombrotrophic, with at most a few minerotrophic elements, such as a lagg zone. After a concise review of the main N inputs, N outputs, N pools, and within-ecosystem N flows, we will elaborate in our discussion on the human influence on the N cycle in peatlands, paying special attention to the disruptive effects of N deposition.

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10.2 The Peatland Nitrogen Cycle

10.2.1 Inputs

The main inputs to peatlands are N deposition from the atmosphere, N_2 fixation by bacteria or algae, and N inflow through upland runoff or discharge (Table 10.1).

10.2.1.1 Nitrogen Deposition

In ombrotrophic peatlands, atmospheric deposition of N is regarded as the main external source of N, providing 13–80 % of the nutrient requirements of plants (Damman 1988; Urban and Eisenreich 1988). Total N deposition is usually divided into a wet and a dry component, and includes deposition of inorganic inputs of NO_x and NH_y as well as organic

Table 10.1. N input in peatlands

N input	Organisms/specifics	Type of peatland, location	Reference
Fixation			
1.00	Aerobic surface peat	Bog, USA Massachusetts	Chapman and Hemond (1982)
0.07	Aerobic heterotrophs	Bogs, Germany, S	Waughman and Bellamy (1980)
0.53	Aerobic heterotrophs	Poor fens, Germany, S	Waughman and Bellamy (1980)
0.05–0.07	Aerobic heterotrophs	Bogs, USA, Minnesota, and Ontario	Urban et al. (1988)
0.03–0.15	Anaerobic bacteria	Bog, Sweden, N	Granhall and Selander (1973)
0.16–11.5	Blue-green algae	Fen, Sweden, N	Granhall and Selander (1973)
1.00–6.40	Blue-green algae	Fen, Sweden, N	Basilier et al. (1978)
0.12–0.38	Bacteria	Tundra, Canada, NW	Stutz and Bliss (1975)
0.05–3.20	Bacteria	Bog, UK, Pennines	Martin and Holding (1978)
0.20	Organisms	Bog, Sweden, NN	Rosswall and Granhall (1980)
0.07–0.10	Organisms	Tundra, Canada, NW	Henry and Svoboda (1986)

inputs, such as the N in pollen (Lee et al. 1996), amino acids, and organic nitrates (Neff et al. 2002). The combustion of fossil fuels is the main source of NO_x in the atmosphere, whereas the emission of NH_y is related mainly to intensive agriculture (Asman et al. 1998). As a consequence, there often exists a gradient from low N deposition in remote areas toward a relatively high N deposition in more inhabited regions, with peak deposition downwind of major emission sources (Fenn et al. 2003). For Scandinavia, the total N deposition gradient runs roughly from north to south, ranging

Table 10.1. (*Continued*)

N input	Organisms/specifics	Type of peatland, location	Reference
Deposition			
0.80–1.00	Bulk deposition	Peatlands, Germany, NE	Lütt (1992)
0.40–0.60	Bulk deposition	Peatlands, USA, N	Malmer and Wallén (1993)
0.20–0.40	Bulk deposition	Peatlands, Scandinavia, N	Malmer and Wallén 1993
0.50–1.10	Bulk deposition	Peatlands, Scotland and Scandinavia, S	Malmer and Wallén (1993)
0.70	Bulk deposition	Bog, Finland, S	Williams et al. (1999b)
0.80	Bulk deposition	Bog, Estonia	Williams et al. (1999b)
0.10–0.30	Total deposition	Bogs, Canada	Vitt at al. (2003)
0.70–1.40	Bulk deposition	Peatland, Sweden, S	Malmer et al. (2003)
0.10–0.70	Bulkdeposition	Bogs, Finland	Vuorenmaa (2004)
Pollen			
0.03–0.05		Forest, Canada, Manitoba	Lee et al. (1996)
Inflow			
1.28	Surface runoff	Lagg-zone USA, Minnesota,	Timmons et al. (1977)
1.36	Surface runoff	Bog and lagg, USA, Minnesota	Timmons et al. (1977)
0.09–0.23	Interflow	Lagg zone, USA, Minnesota	Verry (1975); Verry and Timmons (1982)
0.12–2.20	Interflow	Bog and lagg, USA, Minnesota	Verry (1975); Verry and Timmons (1982)

Values are in grams per square meter per year.
N north, *NN* high north, *S* south, *E* east, *W* west, referring to locations within countries

from less than 0.1 to 1.0 g N m^{-2} $year^{-1}$ through bulk deposition (Fig. 10.1, Table 10.1). A similar range in wet inorganic N deposition can be found for the USA from west to east (NADP 2004). For northern peatlands in Canada and in the former Soviet Union, total N deposition remains well below 0.5 g N m^{-2} $year^{-1}$ (Penner et al. 1991; Ro and Vet 2002). Whereas the N input via wet deposition is relatively easy to measure, the input through dry deposition is more difficult to quantify. The latter is affected by wind speed (Sutton et al. 1993), wetness and acidity of the deposition surface (Adema et al. 1986; Flechard et al. 1999), and the leaf area index (LAI) of the vegetation (van Breemen et al. 1982; Heil et al. 1988; Matzner 1989). To complicate things further, plant and moss species may absorb gasses and aerosols of NO_x and NH_y directly (Hosker and Lindberg 1982; Pearson et al. 2000). The deposition of aerosols is usually referred to as occult deposition, and may be important in upland ecosystems that are frequently shrouded in clouds or mist (Woodin and Lee 1987; Proctor and Maltby 1998). It has been estimated that dry deposition on open bogs is equal to (Urban and Eisenreich 1988; Sutton et al. 1992) or 1.5 times greater than (Rosswall and Granhall 1980) bulk deposition, the latter being only a fraction higher than wet deposition. (Bulk deposition is usually measured with open-air funnels. Since the surface of these funnels is smooth, they catch mainly wet deposition, with a small amount of dry deposition. As a consequence, bulk deposition is equal to or slightly higher than wet deposition. The latter is measured with special, closed funnels that open only

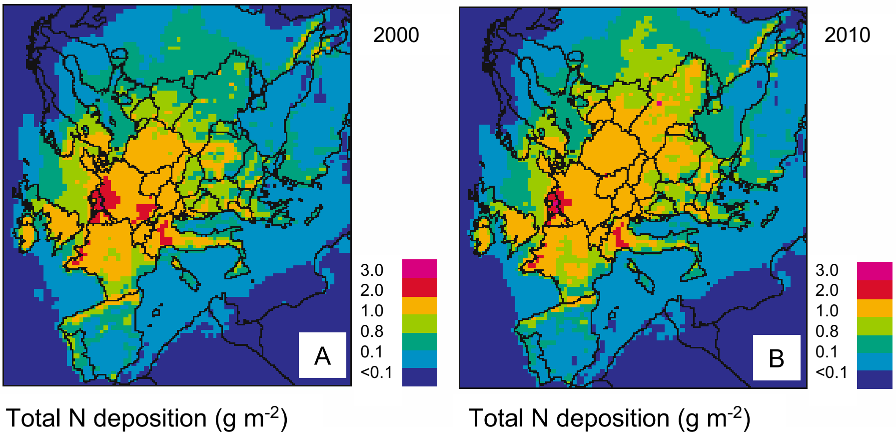

Fig. 10.1 Modeled total N deposition in Europe for 2002 (**A**) and projected total N deposition in Europe for 2010 (**B**). The data refer to the total of dry and wet N deposition on an average vegetation surface. Different colors refer to different deposition levels. The figure illustrates that an increasing number of bogs will face an increase in atmospheric N supply in the near future. (Source EMEP; Tarrason et al. 2003)

during precipitation events.) The estimates of dry deposition have been supported by actual measurements in *Calluna* heathland (Bobbink et al. 1992) and for bog vegetation dominated by *Erica tetralix* (Limpens et al. 2004) in the Netherlands. For sedge-dominated fens and wooded bogs, which tend to have a higher total leaf area, this ratio may well be higher.

10.2.1.2 Nitrogen Fixation

N fixation in peatlands remains difficult to quantify as a result of its high spatio-temporal variability (Rosswall and Granhall 1980; Waughman and Bellamy 1980; Urban and Eisenreich 1988). Rates of N fixation have been positively correlated with peat moisture availability (Davey and Marchant 1983), temperature, redox potential, pH, and K concentration, and negatively with peat Ca concentration (Waugham and Bellamy 1980). In peatlands, the ability to fix atmospheric N_2 into organic compounds has been demonstrated for cyanobacteria, symbiotic actinomycetes, and free-living bacteria (Dickinson 1983). Although all these N fixers seem to prefer minerotrophic conditions or, for the symbionts, hosts that occur in these habitats, most of the species can occur in more ombrotrophic and acidic conditions.

Cyanobacteria seem to prefer wet, minerotrophic, and neutral-to-alkaline habitats (Steward 1974), but also can be found in wet depressions or pools in bogs, the conspicuous globular colonies of *Nostoc muscorum* being a good example of the latter. In addition, free-living algae in symbiotic associations with moss species, such as *Drepanocladus* spp. and *Sphagnum* spp. (Granhall and Lid-Torsvik 1975; Sheridan 1991), and lichens (Millbank 1985; Gunther 1989) have been described. Like their free-living brethren, the endophytic algae are most abundant at a pH above 4.0 (Granhall 1970; Dooley and Houghton 1973). Genera of cyanobacteria living as epiphytes and/or intracellular in mosses have been shown to fix as much as 9.4 g N m^{-2} $year^{-1}$ (Granhall and Selander 1973).

Symbiotic actinomycetes, mainly members of the genus *Frankia*, occur in specialized root nodules of some vascular plants, such as alder (*Alnus glutinosa*) and bog myrtle (*Myrica gale*). The N-fixing potential of these organisms may be considerable, as has been shown by Akkermans (1971), who reported N-fixation rates of 5.6–13.0 g N m^{-2} $year^{-1}$ for alder woodland on acidic peat in the Netherlands.

N_2 also is utilized by a wide range of bacteria, including aerobes, facultative anaerobes, and strict anaerobes (Dickinson 1983). Despite aerobic N-fixers being generally restricted to alkaline and neutral soils, it has been found that N fixation in acidic, ombrotrophic mires is mediated mainly by this group of bacteria (Granhall and Selander 1973; Granhall and Lid-

Torsvik 1975). pH does not seem to be the main factor limiting nitrogenase activity in peat soils (Waughman and Bellamy 1980). Nevertheless, the highest rates of N fixation have been reported from rich fen peats at lower latitudes, amounting to 6 g N m^{-2} $year^{-1}$ (Waughman and Bellamy 1980), whereas the lowest rates, 0.03–0.15 g N m^{-2} $year^{-1}$, have been measured in the surface peat of a subarctic mire in Sweden (Granhall and Selander 1973).

10.2.1.3 Nitrogen Inflow

Inflow of N through upland runoff is usually associated with fens, especially sloping fens, or the lagg zone of bogs (Urban and Eisenreich 1988), but these N inputs may gain importance in bogs with a thin peat layer, such as blanket bogs. Data on N input through upland runoff are scarce, and data on input through groundwater discharge are even nonexistent. To our knowledge, Marcell Bog in Minnesota (USA) is the only bog where N input via upland runoff was measured for several years (Verry and Timmons 1982).

Upland runoff is usually separated into two components: surface runoff and interflow (Timmons et al. 1977; Chap. 13). The first flows through the organic (O) horizon of the upland soil and is confined mainly to the period of snowmelt, whereas the latter is restricted to the deeper A, B, and A2 horizons and may take place year-round. The N carried with both water flows is mainly organic, peaks during snowmelt, and increases with the relative size of the catchment area. The magnitude of runoff, and thus N input, is highly variable, being determined by the interactions between the amount and timing of snowfall, the degree to which the upland soil is saturated with water, and the rate of snowmelt (Timmons et al. 1977). Estimates for Marcell Bog indicate input through surface runoff to be about 1.4 g N m^{-2} $year^{-1}$ and through interflow to range between 0.12 and 0.22 g N m^{-2} $year^{-1}$ (Verry 1975; Verry and Timmons 1982).

10.2.2 Outputs

For undisturbed peatlands, N exports via runoff or streamflow and denitrification are considered the main losses from the ecosystem; volatilization of NH_3 (Hemond 1983) is regarded as an almost negligible component of the N budget (Table 10.2).

Table 10.2. N output from peatlands

N output	Type of peatland, location	Reference
Denitrification		
0.1	Bog, UK, Pennines	Martin and Holding (1978)
0–0.4	Bog, USA, Massachusetts	Hemond (1980, 1983)
0.18	Natural forested bog, USA, Minnesota	Urban and Eisenreich (1988)
Runoff		
0.30	Eroding moorland, UK, Pennines	Crisp (1966)
0.30	Bog, USA, Massachusetts	Hemond (1980, 1983)
0.63	Forested bog, USA, Minnesota	Verry and Timmons (1982)
0.32	Bog, USA, North Carolina	Richardson (1983)
0.15	Minerotrophic part bog, Finland, S	Sallantaus and Kaipainen (1995)
Runoff and erosion		
1.50	Eroding moorland, UK, Pennines	Crisp (1966)
1.40	Natural forested bog, USA, Minnesota	Urban and Eisenreich (1988)
1.30	Natural forested peatland, Finland	Kortelainen and Saukkonen (1994)
1.07–1.50	Cutover peatlands, Finland	Kløve (2001)
Volatilization		
0.09	Bog, USA, Massachusetts	Hemond (1983)

Values are in grams per square meter per year.
S south, referring to location within countries

10.2.2.1 Runoff

Undisturbed peatlands, especially bogs, are parsimonious in their use of plant nutrients, and as a result, inorganic nutrient concentrations in the interstitial water are usually very low (Verhoeven et al. 1996; Bragazza et al. 2003). Consequently, the N lost with runoff is relatively small and mainly takes place in organic forms (Urban et al. 1988; Koerselman and Verhoeven 1992). Total export of N seems to be more a function of the total volume of runoff than of the flow rate. Since the volume of runoff peaks during snowmelt, the accuracy of the export estimate strongly depends on samples taken during this period. Urban et al. (1988) showed for a bog in Minnesota that 50–65 % of the total N export took place before June. Annual export of N via runoff was estimated at 0.15–0.63 g N m^{-2} for undisturbed peatlands (Verry and Timmons 1982; Sallantaus and Kaipainen 1995) and 1.1–1.5 g N m^{-2} for eroding peatlands (Kløve 2001; Table 10.2).

10.2.2.2 Denitrification

Denitrification refers to the microbial reduction of NO_3^- to N_2O and N_2. Denitrification takes place under anaerobic conditions. When NO_3^- is present, it can proceed rapidly and can be further enhanced by temperature and pH (Sikora et al. 1983). However, in peatlands, particularly in ombrotrophic acidic peat, the supply of NO_3^- is generally very low. In these peatlands, NO_3^- may be supplied by nitrification of NH_4^+, by atmospheric deposition, or by N fixation. Nitrification is notoriously slow in acidic peatlands because of the unfavorable anaerobic, acidic, and cold environment. Additionally, other microorganisms, *Sphagnum* and other mosses, and vascular plants may take up the NO_3^- supplied by deposition or nitrification before it reaches the anaerobic zones or microsites where denitrification takes place (Woodin and Lee 1987; Urban et al. 1988). As a result, denitrification in ombrotrophic bogs is generally regarded as quantitatively unimportant, with rates ranging from 0 to 0.4 g N m^{-2} $year^{-1}$ (Hemond 1983, Table 10.2).

In mixed mires or fens, where the supply of inorganic N is greater (Bragazza et al. 2003) and the higher pH does not inhibit nitrification of NH_4^+, the amount of N lost through denitrification may well be higher. Likewise, water table drawdown may enhance nitrification and subsequent denitrification by stimulating N mineralization (Freeman et al. 1993; Martikainen et al. 1993). This effect is most pronounced in nutrient-rich fen peat, and was illustrated by Regina et al. (1999), who reported a threefold increase in the N_2O efflux from tall sedge peat after a 25-cm decrease in the water table, whereas the N_2O efflux from nutrient-poor low-sedge peat remained largely unaffected.

10.2.2.3 Volatilization

Volatilization of NH_3 in natural ecosystems may occur as a result of a number of microbial processes. NH_3 may be released under aerobic as well as anaerobic conditions. In the presence of O_2, NH_3 is released as a byproduct of bacteria that break down amino acids, a process not uncommon to peat (Dickinson 1983). In the near absence of O_2, nitrate can be used as an electron acceptor by a number of bacteria instead and, as a result, NH_3 is released as an end product of the oxidation of organic matter, iron, or sulfur (Dickinson 1983). Both denitrification and nitrate ammonification (reduction of nitrate to ammonium) may occur simultaneously in soils, as has been shown for marine sediments (Bonin et al. 1998).

Hemond (1983) found a trace NH_3 efflux of about 0.09 g N m^{-2} $year^{-1}$ from Thoreau's Bog. As the concentrations measured just above the bog surface decreased in cold weather and could not be ascribed to some sort of chemical equilibrium, the author assumed that a biological process, such as that described before, must be involved in the NH_3 efflux.

10.2.3 Storage

Ombrogenous peatlands are generally are regarded as effective N sinks. This view may slightly change, however, if the N balance is calculated for an entire ecosystem, including more minerotrophic elements, such as lagg zones. Urban and Eisenreich (1988) estimated that about 65 % of the annual N input was retained in the ombrotrophic part of the mire they investigated, whereas retention decreased to 46 % when the lagg zone was included. The latter corresponds with our own value for N retention (Fig. 10.2).

The main pool of N in peatlands resides in dead organic matter; a minor part is stored in living organisms. In order of magnitude, vascular plants, the living moss layer, microbes, and pore water represent the other main pools (Table 10.3).

10.2.3.1 Peat

In ombrotrophic bogs, the peat layer is usually divided into two functional layers: the acrotelm and the catotelm. The first is usually 30–40-cm thick and mainly aerobic, whereas the latter may extend over meters and is mainly anaerobic (Chap. 2). The main losses of N occur in the biologically active upper layer and peak in the first few years after the N is initially deposited (Damman 1988). After approximately 290 years (Rosswall and Granhall 1980), the N enters the catotelm. Because decay in this layer is regarded as negligible (Clymo 1983) and the first deposition of organic matter in the catotelm may date back to the last ice age, the N turnover time in this layer must be on the order of thousands of years. As such, N storage in the catotelm is regarded as semipermanent.

As a result of the long-term accumulation of peat, a considerable amount of N historically has been locked in the anaerobic layers of a peat column. If we assume that the average C-to-N ratio of peat is 30–55 (Damman 1988; Urban and Eisenreich 1988; Malmer and Wallén 1993, 2004; Kuhry and Vitt 1996; Bridgham et al. 1998,; Heijmans, unpublished

Table 10.3. Main N pools in peatlands

N pool	Type of peatland, location	Reference
Trees		
36.6	Natural forested bog, USA, Minnesota	Grigal (1985); Grigal et al. (1985)
Shrubs		
1.4	Bog, Sweden, NN	Rosswall et al. (1975), and unpublished refs therein
1.4	Natural forested bog, USA, Minnesota	Grigal (1985); Grigal et al. (1985)
Herbs		
0.4	Bog, Sweden, NN	Rosswall et al. (1975)
0.6	Natural forested bog, USA, Minnesota	Grigal (1985); Grigal et al. (1985)
Graminoids		
0.1	Bog, Sweden, NN	Rosswall et al (1975); Wielgolaski et al. (1975)
Vascular plant roots (excl trees)		
4.0	Bog, Sweden, NN	Rosswall et al. (1975); Wielgolaski et al. (1975)
Bryophytes		
4.4	Bog, Sweden, NN	Sonesson (1973)
5.4	Natural forested bog, USA, Minnesota	Grigal (1985);Grigal et al. (1985)
Acrotelm (<30 cm)		
189	Bog, UK	Heijmans (unpublished data)
157	Bog, Denmark	Heijmans (unpublished data)
66	Bogs, USA, N, and Scandinavia	Damman (1988)
200	Natural forested bog, USA, Minnesota	Urban and Eisenreich (1988)
Catotelm (>30 cm) per 10-cm slice		
160	Inferred from N concentration and peat bulkdensity	See comments in Fig. 10.2

Values are given in grams per square meter.
N north, NN high north, referring to location within countries

data), and that about 450 Pg of C is stored in peat worldwide (Gorham 1991; O'Neill 2000), then the corresponding amount of N stored in peat-layers would be around 8–15 Pg of N. If we further assume that the global soil organic N pool equals 95 Pg (Schlesinger 1991), then peat accounts for about 9–16 % of this N.

Estimates of the N accumulation rates in the catotelm of boreal peatlands range from 0.19 to 0.48 g N m^{-2} $year^{-1}$ (Table 10.3), with an average of 0.42 g N m^{-2} $year^{-1}$. We have to realize, however, that these estimates are derived from the analyses of peat profiles, and thus mainly reflect the average accumulation rate over the past 1,000 years or so.

10.2.3.2 Plants

The quantity of N stored in vascular plants depends on vascular plant cover and the dominant growth form: a wooded bog is likely to store more N in vascular plants than a bog dominated by shrubs. In turn, the latter would store more N than a bog dominated by herbs or graminoids. This was illustrated by Reader and Stewart (1972), who quantified dry matter accumulation along a gradient across four peatland types: lagg, bog, muskeg, and bog forest in southeastern Manitoba. The authors estimated the aerial vascular biomass at 1.5, 0.1, 0.6, and 4 kg m^{-2}, respectively. Because the dominant growth forms were either dwarf shrubs or trees, and thus should have had rather similar tissue N concentrations, it seems reasonable to assume that the amount of stored N would reflect the relative differences in aboveground biomass.

The belowground biomass of vascular plants, let alone how much N is stored in belowground components, largely remains a matter of debate. The few who have attempted to determine the belowground biomass of vascular plants in peatlands reported extremely high root-to-shoot ratios that varied widely among species. Wallén (1986) reported root-to-shoot ratios of 13 (*Empetrum hermaphroditicum*) and 48–54 (*Rubus chamaemorus* and *Andromeda polifolia*) for a subarctic peat bog, and ratios between 0.55 and 1 (*Calluna vulgaris*) for an ombrotrophic bog in southern Sweden (Wallén 1987). When later comparing the total belowground-to-aboveground ratios of the same bogs, ratios of 19 and 13 were estimated (Wallén 1992). These high values were mainly the result of including the fine-root fraction (less than 0.5 mm), which is usually lost when roots are manually removed from the peat (Wallén 1992). Furthermore, which parts of plants must be assigned to the belowground versus aboveground biomass may significantly affect the results. Thus, the ratios of the aforementioned bogs decreased from 19 and 13 to 6 and 2, respectively, when the biomass within the uppermost 2.5 cm of *Sphagnum*, mainly comprising overgrown stem parts, was counted as aboveground biomass (Wallén 1992).

10.2.3.3 Moss

For open bogs with a sparse tree cover, the amount of N that resides in the living moss layer exceeds that in vascular plants. The estimates for undisturbed bogs with a closed *Sphagnum* cover are more or less in agreement; averages range from 4.4 (Sonesson 1973) to 5.4 g N m^{-2} (Grigal 1985; Grigal et al. 1985).

In time, an increase in the atmospheric N supply may result in enhanced *Sphagnum* growth (Aerts et al. 1992; Vitt et al. 2003) along with higher tissue N concentrations, resulting in higher storage. The latter will either increase until *Sphagnum* becomes saturated with N (Malmer 1990; Lamers et al. 2000; Berendse et al. 2001) or until the N excess depresses *Sphagnum* production (Gunnarsson and Rydin 2000; Limpens and Berendse 2003a).

10.2.3.4 Microbes

The microbial biomass in peatlands, which mainly consists of heterotrophic organisms (Mitchell et al. 2003), is subject to considerable temporal variability as a result of the disruptive influence of the seasonal water table fluctuations on the aeration of the soil (Williams and Silcock 2000). As a consequence, the amount of N stored in the microbial biomass shows a similar variability and ranges between 1.5 and 3.7 g N m^{-2} for the upper (5–25-cm) peat layer (Williams and Wheatley 1989; Williams and Silcock 2000).

10.2.3.5 Water

The pore water, particularly in the rhizosphere, is the most transient pool of N in all wetlands, and as such is difficult to quantify. Concentrations, and thus contents, fluctuate in time, with the highest values usually measured in winter, when uptake rates are lowest (Proctor 1994; Limpens et al. 2003a; Tomassen et al. 2003). In addition, concentrations depend strongly on depth, with a steep increase below 25 cm (Tomassen, unpublished data).

Most studies focus on inorganic N, of which ammonium is the most common form in bogs. In bogs, nitrate concentrations rarely reach the detection limit (0.01 mg L^{-1}) of most elemental analyzers (Gerdol 1990; Proctor 1994). Although dissolved organic N (DON) is likely the most important form of N in the pore water, and can be taken up by vascular plants as well as bryophytes (Kielland 1994, 1997; Lipson and Näsholm 2001), data on concentrations are scarce and the ratio between dissolved inorganic N (DIN) and total DON varies with the sampled microsite. From Williams and Silcock (1997) and Williams et al. (1999a), we can deduce a ratio of DIN to DON of 1:5 for pore water, which is similar to that reported by Urban (1983) for Marcell Bog. Water samples taken from small bodies of free-standing water across a wide range of European bogs show a ratio of 1:3 (Bragazza and Limpens 2004), whereas Kalbitz and Geyer (2002) reported the most conservative ratio of 1:1.4 for water extracted from peat soils.

10.3 Within-Ecosystem Nitrogen Cycling

In undisturbed ombrotrophic peatlands, the balance between *Sphagnum* and vascular plants is maintained by their use of different sources of mineral nutrients. *Sphagnum* uses nutrients derived from atmospheric deposition and efficiently relocates nutrients from older tissue, whereas vascular plants depend more on nutrients released during decomposition of organic material (Malmer et al. 1994, 2003). The very presence of *Sphagnum* restricts the nutrient supply to vascular plants by intercepting deposited nutrients, and by slowing down decomposition through its recalcitrant litter (van Breemen 1995, Malmer et al. 2003). As long as the input of deposited nutrients, such as N, does not exceed the capacity of *Sphagnum* to retain them, nutrient availability to vascular plants is kept low. Once *Sphagnum* is no longer able to sufficiently restrict nutrient availability in the rhizosphere, the competitive balance may shift toward vascular plants, which may ultimately outcompete *Sphagnum* (Malmer et al. 1994; Lamers et al. 2000; Berendse et al. 2001; Chap. 4).

In the following paragraphs we will cover the three most important N flows: N retention in *Sphagnum*, N retranslocation, and N mineralization. We are aware this leaves out a number of other flows such as total N uptake by *Sphagnum* and vascular plants (Table 10.4) and DON production from acrotelm peat. When constructing our conceptual N budget (Fig. 10.2) we did take these flows into account.

10.3.1 Nitrogen Retention in *Sphagnum*

Generally, N retention is defined as the percentage of deposited N that the living *Sphagnum* layer is able to retain in its tissue, or as Lamers et al. (2000) put it, the degree to which *Sphagnum* acts as a filter for atmos-

Table 10.4. Internal N cycling in peatlands

N flow	Organism or specifics	Type of peatland, location	Reference
Uptake			
0.33	Trees	Natural forested bog, USA, Minnesota	Grigal (1985); Grigal et al. (1985)
0.37	Shrubs	Natural forested bog, USA, Minnesota	Grigal (1985); Grigal et al. (1985)
0.60	Herbs	Natural forested bog, USA, Minnesota	Grigal (1985); Grigal et al. (1985)
3.80	Vegetation (no trees)	Bog, USA, Massachusetts	Hemond (1983)
0.67	Vegetation (no trees)	Bog, Sweden, NN	Rosswall and Granhall (1980)
3.95	*Sphagnum*	Forested bog, USA, Minnesota	Grigal (1985); Grigal et al. (1985)
0.36	*Sphagnum*	Bog, Sweden, NN	Rosswall and Granhall (1980)
3.60	*Sphagnum*	Bog, Sweden, N	Malmer and Nihlgård (1980)
2.28	*Sphagnum*	Bog, USA, Maine	Aldous (2002b)
Mineralization (inorganic N only)			
0.80–7.70	Peat	Peatlands, USA, Minnesota,	Grigal and Homann (1994)
0.10–1.10	Peat	Peatland, USA, Minnesota,	Chapin et al. (2001)
0.70–0.80	Peat	Bog, Sweden, NN	Rosswall and Granhall (1980)
4.30–5.90	Peat	Natural forested bog, USA, Minnesota	Urban and Eisenreich (1988)
0.80–2.80	Peat	Fens, The Netherlands	Koerselman and Verhoeven (1992)
1.40–2.90	Peat	Bogs, The Netherlands	Koerselman and Verhoeven (1992)
2.10	Peat	Bog, USA, Massachusetts	Hemond (1983)
Retention (expressed as % N applied to moss surface)			
50–90	*Sphagnum*	Bogs, USA, Maine	Aldous (2002a)
11–100	*Sphagnum*	Bogs, Europe	Williams et al. (1999a)
98–99	*Sphagnum*	Bog, Canada, Alberta	Li and Vitt (1997)
79	*Sphagnum*	Bog, The Netherlands	Heijmans et al. (2002)
Retention (expressed as capitulum N content per square meter)/(N deposition)			
1,000–9,500	*Sphagnum*	Bogs, Europe	Bragazza et al. (2004a)

Table 10.4. (*Continued*)

N flow	Organism or specifics	Type of peatland, location	Reference
Relocation (% N in stem that becomes relocated to capitulum)			
11–80	*Sphagnum*	Bogs, USA, Maine	Aldous (2002b)
10–55	*Sphagnum*	Bogs, Europe	Bragazza et al. (2004a)

Values are grams per square meter per year, unless stated otherwise.
NN high north, referring to location within countries

pheric N. The efficiency with which *Sphagnum* seems to retain N seems subject to considerable variation, ranging from 11 to almost 100% (Table 10.4).

An increase in atmospheric N input seems to have a negative effect on the retention efficiency of *Sphagnum*. This has been demonstrated by Bragazza et al. (2004a), who calculated N retention efficiency from the ratio between the capitulum N content and bulk deposition for bogs along a N deposition gradient across Europe. These data showed that N retention efficiency decreased exponentially with N deposition, with the biggest decrease found between bulk deposition values of 0.25 and 0.50 g N m^{-2} $year^{-1}$.

Apart from N deposition, other factors such as water table (Williams et al. 1999b, Aldous 2002a), metabolic activity (Aldous 2002a), and *Sphagnum* species (Jauhiainen et al. 1998a) have been shown to affect N retention efficiency. Aldous (2002a) compared two low-deposition sites with two intermediate-deposition sites in northeastern USA and found that *Sphagnum* from the low-deposition site retained N more efficiently than *Sphagnum* from the intermediate-deposition site in the first year, but not in the second year of the study. Furthermore, retention efficiency of the capitulum differed between seasons, with higher efficiencies in summer than in spring. She contributed the differences between the years to a shortage of water due to drought for the low-deposition sites, and the difference in seasons to reduced metabolic activity during the cold spring. Williams et al. (1999b) also reported a negative relationship between N retention and water table depth. In Petri dish experiments with isolated capitula of different species, Twenhöven (1992) and Jauhianen et al. (1998a) showed that N uptake from an aqueous solution differed between *Sphagnum* species, and these differences were correlated with their preferred position above the water table; hummock species may be more efficient in retaining N than lawn species. This pattern is further supported

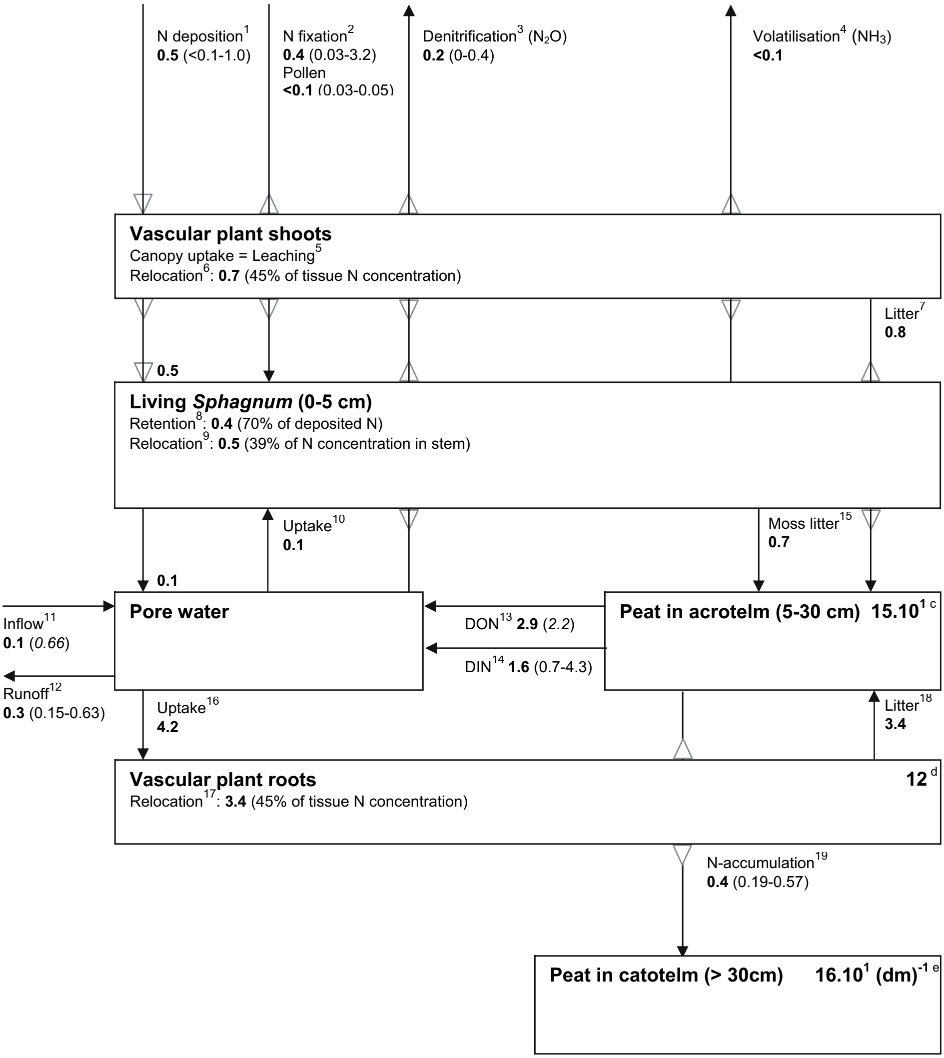

Fig. 10.2. Conceptual N budget for a bog in the boreal zone. N flows are given in grams per square meter per year and N pools in grams of N per square meter. The minimum and maximum values from the literature or the average for the number given in *italics* are reported in *parentheses*. Details on assumptions and references are given in a separate *textbox* and are indicated by superscript numbers and letters. Comments indicated by numbers refer to N flows and comments indicated by letters to N pools. *DIN* dissolved inorganic nitrogen, *DON* dissolved organic nitrogen.

Comments referring to N flows in the conceptual N budget given in Fig. 10.2

1. Median of EMEP data & literature (Fig. 10.1, Table 10.1): we used EMEP data of latitudes of 58° N and higher. The data refer to modeled values of total N deposition on an average vegetated surface.
2. Average from data Table 10.1, maximum value for fens 16.4 g N m^{-2} $year^{-1}$.

3. Average from data Table 10.2.
4. Trace flux, omitted from flow calculations.
5. Assumed canopy uptake and leaching 10 % deposition (0.05 g N m^{-2} $year^{-1}$).
6. Relocation of N from aboveground senescent tissue of 45 % (Aerts and Chapin 2000). Assumed tissue N concentration of 8.0 mg g^{-1} (average based on Malmer and Nihlgård 1980; Waughman 1980; Bartsch and Moore 1985; Michelsen et al. 1996) and production of 185 g m^{-2} $year^{-1}$ (average based on Forrest 1971; Reader and Stewart 1972; Doyle 1973; Wein and Bliss 1974; Yelina 1974; Forrest and Smith 1975; Rosswall et al. 1975; Smith and Forrest 1978; Svensson and Rosswall 1980; Rosswall and Granhall 1980; Vasander 1981; Botch and Masing 1983; Bartsch and Moore 1985; Backéus 1985; Van Wijk et al. 2003).
7. We assumed that the N loss through litter input equals the amount of N needed to sustain the aboveground plant parts minus relocation. Values from the literature range from 0.33 to3.8 g N m^{-2} $year^{-1}$ (Table 10.4).
8. Retention 70 % (Table 10.4) of input via deposition.
9. Relocation of N from senescent tissue of 39 % (Table 10.4). Assumed tissue N concentration of 7.8 mg g^{-1} (average based on data Kivinen 1933; Malmer and Sjörs 1955; Sonesson 1973; Pakarinen & Tolonen 1977; Coulson and Butterfield 1978; Damman 1978; Bartsch and Moore 1985; Lütt 1992; Malmer and Wallén 1993; Bragazza et al. 2003; Malmer et al. 2003), production assumed of 150 g m^{-2} $year^{-1}$ (average based on Overbeck and Happach 1957; Reader and Stewart 1972; Wein and Bliss 1974; Forrest and Smith 1975; Botch and Masing 1983; Bartsch and Moore 1985; Gunnarsson and Rydin 2000; Aldous 2002)
10. We divided N uptake from interstitial water into evaporation-driven water flow and active uptake. The first turned out to be negligible, with 1 mg m^{-2} $year^{-1}$. We assumed an equilibrium between N uptake and N loss, an evaporation of 3 L m^{-2} day^{-1} for 50 day $year^{-1}$ (Overbeck and Happach 1957; Heijmans et al. 2001b), a N concentration of 5 mg N L^{-1} in interstitial water (Bragazza et al. 2003, Limpens, unpublished data), *Sphagnum* production of 150 g m^{-2} $year^{-1}$, and a tissue N concentration of 8 mg g^{-1} (see comment 9).
11. The given value was needed for a closed N budget. Average from the literature (Table 10.1) in parentheses.
12. Average from data Table 10.2.
13. The given value was needed for a closed N budget for the acrotelm. The value inferred from the literature is in parentheses, assumptions made for the latter are that the DON flux is a function of DIN (McFarland et al. 2002), that the input ratio of DIN and DON reflects the concentration ratio of 1:1.4 in interstitial water (Kalbitz and Geyer 2002), and that DIN and DON are taken up in equal quantities by the biota.
14. Average from mineralization data (Table 10.4). Minimum and maximum values in parentheses.
15. We assumed that the N loss via litter equals the N requirements for growth minus relocation. Values from the literature range from 0.36 to 4.0 g N m^{-2} $year^{-1}$ (Table 10.4).
16. We assumed that N uptake from the environment equals the amount of N needed to sustain the production of both aboveground and belowground plant parts minus relocation. For aboveground parts we assumed a relocation of 45 %, a tissue N concentration of 7.96 mg g^{-1}, and a production of 185 g m^{-2} $year^{-1}$ (see comment 6). For belowground parts we assumed a relocation of 45 %, a tissue N concentration of 8 mg g^{-1} (Limpens, unpublished data), and a production of 770 g m^{-2} yr^{--1} (average from Wallén 1992 and a value derived from aboveground production data, assuming a ratio of 1:4 between aboveground and belowground production).

17. We assumed that relocation of N from belowground senescent tissue would equal that of aboveground tissue. In addition we assumed a tissue N concentration of 8 mg g^{-1} and a production of 770 g m^{-2} $year^{-1}$ (see comment 16).
18. We assumed that the N loss through litter input equals the amount of N needed to sustain the belowground plant parts minus relocation.
19. The value is an average based on the literature (Rosswall and Granhall 1980; Sallantaus and Kaipainen 1995; Heijmans, unpublished data) and calculations based on the average carbon accumulation in the acrotelm (Gorham 1991; Botch et al.1995; Damman 1995; Clymo et al. 1998; Belyea and Warner 1996; Vardy et al. 2000; Turunen et al. 2001, 2002; Anderson 2002; Gorham et al. 2003), the peat C-to-N quotient (Damman 1988; Urban and Eisenreich 1988; Malmer and Wallén 1993; Kuhry and Vitt 1996; Bridgham et al. 1998,; Malmer and Wallén 2004, Heijmans, unpublished data), and the assumption that N is retained in the peat profile (Damman 1988).
    a. We assumed a tissue N concentration of 8 mg g^{-1}, a production of 185 g m^{-2} $year^{-1}$ (see comment 6), and a ratio of 1:2 between production and standing crop (Backéus 1985). For literature values see Table 10.3.
    b. The value is an average of literature values (Table 10.3) and a calculated value based on the following assumptions: a bulk density of 20 g dm^{-3} for the upper 5-cm layer (Sonesson 1973; Grigal 1985; Grigal et al. 1985; Damman 1988; Mauquoy et al. 2004) and a corresponding tissue N concentration of 5 mg g^{-1} (Damman 1988).
    c. The value is an average of literature values (Table 10.3) and a calculated value based on the following assumptions: a bulk density of 40 g dm^{-3} for the 5–30-cm layer (Mauquoy et al. 2004) and a corresponding peat N concentration of 11 mg g^{-1} (Sonesson 1973; Waughman and Bellamy 1980; Koerselman and Verhoeven 1992; Malmer and Wallén 1993; Verhoeven et al. 1996; Bragazza et al. 2003; Chapin et al. 2001).
    d. We assumed a tissue N concentration of 8 mg g^{-1}, a production of 770 g m^{-2} $year^{-1}$ (see comment 16) and a ratio of 1:2 between production and standing crop (see comment a). For literature values see Table 10.3.
    e. We assumed a bulk density of 100 g dm^{-3} (Damman 1988, Malmer & Wallén 1993) throughout the whole catotelm and a corresponding peat N concentration of 16 mg N g^{-1} (Malmer & Wallén 1993).

by the relatively high vulnerability of *Sphagnum fuscum* to an elevation in N supply (Jauhiainen et al. 1994); despite a severe N-induced growth depression, this species continued to take up N.

10.3.2 Retranslocation

Retranslocation or resorption of nutrients from senescent tissues to metabolically active plant parts is a common mechanism for reducing nutrient losses in vascular plants (Berendse and Aerts 1987; Aerts and Chapin 2000). Generally 30–60 % of the tissue N concentration is retranslocated before senescence; for evergreen species, which often dominate nutrient-poor environments, the median N retranslocation is around 45 % (Aerts and Chapin 2000).

Despite its lack of vascular conducting tissues, *Sphagnum* also retranslocates nutrients from its decaying tissue to the capitulum; with relocation efficiencies ranging from 11 to more than 80 % (Table 10.4). Retranslocation may occur extracellularly with the substantial capillary water flow capacity of *Sphagnum* mosses (Overbeck and Happach 1957; Hayward and Clymo 1982) or intracellularly via a network of plasmodesmata in the parenchyma cells of individual *Sphagnum* plants (Ligrone and Duckett 1998). Rydin and Clymo (1989) documented the latter, internal, pathway for the transport of C and P. Retranslocation of N seems to be a function of water availability, suggesting the importance of capillary water flow for N transport (Aldous 2002b). If we assume that at least part of the N transport takes place via the active, internal pathway, it seems reasonable that there must also be some feedback mechanism linked to the N demand of the growing tissues. As a consequence, one would expect that when N supply increases, the retranslocation of N would decrease. Aldous (2002b) indeed documented this expected N deposition effect in the first year of her study, but the effect disappeared in the second year, supposedly as a result of the shortage of water that was mentioned earlier. Some additional, albeit indirect, evidence of a N deposition effect on retranslocation may be found in the difference in N concentrations between the capitulum and the stem. Usually, the N concentration in the capitulum exceeds that in the stem (Gunnarsson and Rydin 2000; van der Heijden et al. 2000). However, when *Sphagnum* is subject to a chronically elevated N supply, the difference in concentrations between stem and capitulum gradually diminishes (Limpens and Berendse 2003a), suggesting decreased retranslocation to the capitulum. This is further supported by Bragazza et al. (2004a), who showed that this difference decreased exponentially along a deposition gradient across Europe.

10.3.3 Mineralization

Decomposition and mineralization are key processes in the cycles of nutrients in terrestrial ecosystems and wetlands (Vitousek 1982; van Vuuren and Berendse 1993). This is particularly true for ombrotrophic peatlands where accumulation of organic matter, and thus sequestration of N, is controlled by slow decomposition rates rather than by high productivity (Clymo 1983; Chap. 7). Litter decomposition rates in peatlands are controlled by environmental conditions, such as pH, redox potential, and temperature, and by the chemical composition of the litter itself; decomposition is restricted mainly to the biologically active, upper 30–40-cm peat layer called the acrotelm (Chap. 7). Considering that more than

50 % of the original N contained in litter enters semipermanent storage in the catotelm (Nordbakken et al. 2003), and that most of this N is contained in *Sphagnum* litter, the disproportional importance of this genus in N storage becomes apparent. On account of this, we will further expand on the N mineralization of *Sphagnum* litter.

The decrease in aboveground productivity from minerotrophic to ombrotrophic conditions suggests a concomitant decrease in mineralization rate and nutrient availability (Bridgham et al. 1996). Contrary to this expectation, however, N mineralization rates in bogs (1.4–2.9 g N m^{-2} $year^{-1}$) seem to exceed those in fens (0.8–2.8 g N m^{-2} $year^{-1}$– Koerselman and Verhoeven 1992, Bridgham et al. 1998), resulting in an overall higher N (and P) availability in bogs than in fens (Waughman 1980; Koerselman et al. 1993; Chap. 11). Consequently, the differences in aboveground productivity between these ecosystems can hardly be explained by a shortage of available nutrients. Problems with nutrient uptake in bogs, as suggested by Waughman (1980), could be an alternative explanation.

Generally, mineralization of nutrients contained in litter is distinguished by three successive stages: (1) nutrients in soluble form are leached from the litter; then (2), nutrient immobilization by microorganisms occurs; and, finally (3), when the N-to-C ratio of the litter exceeds the ratio required for the growth of microorganisms, net N mineralization from the litter takes place (Aerts and Chapin 2000). Considering this, the relatively low N-to-C ratios of *Sphagnum* litter and peat seem in disagreement with the relatively fast N turnover, for in bogs, the litter N-to-C ratio is lower than the N-to-C ratio of the microorganisms, suggesting net immobilization instead of mineralization. As an explanation, Damman (1988) suggested that P rather than N or C may limit microbial respiration. Later work showed that although C mineralization was indeed associated with soil P content (Koerselman and Verhoeven 1992; Verhoeven et al. 1996; Smolders et al. 2002), N mineralization was explained better by overall nutrient concentration (N, P, as well as K) in the interstitial water (Verhoeven et al. 1996). As an alternative, Verhoeven et al. (1988) and Koerselman and Verhoeven (1992) proposed that the organic material in bogs, predominantly composed of litter and peat formed by *Sphagnum* (Zoltai et al. 2000), can be subdivided into two chemically different components: a labile cell protoplasm component with a high N-to-C ratio and a recalcitrant cell wall component with a very low N-to-C ratio. As a result, the former fraction would have a high decay rate, resulting in a fast nutrient release, whereas the latter fraction would have a slow decay rate and a concomitantly slow nutrient release. This hypothesis is supported by results from Bridgham et al. (1998). They found that N mineralization in the acrotelm could be best described by a double-exponential model, earlier used by Updegraff et al. (1995), describing mineralization kinetics for a small labile N pool and a large recalcitrant pool. The size of the labile pool turned out to be generally less than 10 % of the total pool size, with a 50 % turnover time of 3 months or less; the 50 % turnover time of the recalcitrant pool ranged from 6 to more than 1,300 years.

Environmental changes seem to particularly affect the labile N pool; Updegraff et al. (1995) showed that the kinetics of this pool was more sensitive to changes in temperature and aeration than that of the larger recalcitrant pool. Likewise, an increase in atmospheric N deposition presumably would affect the labile N pool first. This presumed influence of atmospherically deposited N is supported by a number of fertilization experiments. In general, adding N results in an increase in the concentrations of easily degradable compounds in *Sphagnum* and vascular plants, such as chlorophyll (Rudolph and Voigt 1986; van der Heijden et al. 2000), and N-rich free amino acids (Baxter et al. 1992; Näsholm et al. 1994; Nordin and Gunnarsson 2000; Limpens and Berendse 2003a). Additionally, N release from decomposing *Sphagnum* litter after a 1-year incubation period turned out to be a function of the initial N concentration (Limpens and Berendse 2003b).

10.4 Discussion

10.4.1 Nitrogen Budgets of Boreal Peatlands

10.4.1.1 Conceptual Nitrogen Budget

From our review of N inputs, outputs, and flows within the ecosystem, we constructed a N budget for boreal peatlands (Fig. 10.2). Most flow rates and pools were directly based on, or deduced from, literature sources for boreal peatlands (Tables 10.1–10.4). When data for boreal peatlands were nonexistent or scarce, however, additional data for temperate peatlands were used. For our deductions, we often had to make a number of assumptions. For example, we used literature data on moss and vascular plant production in combination with N concentrations to estimate N uptake, and set N losses due to litter production equal to N uptake so that the plant N pools would be in equilibrium (see legend of Fig. 10.2 for details). We used two flow rates, about which very little is known, to close the N budget. DON production from acrotelm peat was used to close the N balance for the acrotelm and N inflow from upland runoff was used to close the N balance of the whole ecosystem. Overall, there is large uncertainty with respect to most of the flows. It is, for example, difficult to determine N fixation and denitrification on an annual basis, owing to inherently large spatial and temporal variation. These are relatively small flows. Also, the large flow of N uptake by vascular plants is based on crude calculations. In addition, there is of course large variation among peatlands in the size of the different N pools and N flows, so the values given should not be taken too strictly. For example, N fixation and denitrification may be larger in more minerotrophic peatlands, while they may be virtually absent in ombrotrophic peatlands. Furthermore, N inflow from upland runoff and N runoff from the peatland each depend very much on the topographical position of the mire. Despite these uncertainties and variations, this scheme gives an overview of the order of magnitude of the pools and flows and forms the basis of our following discussion.

10.4.1.2 Nitrogen Uptake by *Sphagnum*

Sphagnum acquires N from atmospheric deposition, N fixation, and pore water, whereas vascular plants have the N in their rhizosphere as their sole source of N. The atmospheric sources are most important for *Sphagnum*, but several authors have observed that atmospheric N deposition was not sufficient to meet the N requirements for growth (Damman 1978; Aldous 2002b; Bragazza et al. 2004a). These authors usually used this argument to stress the importance of retranslocation in *Sphagnum*. It must be noted however, that dry deposition often was not taken into account because it is difficult to quantify. As the N input via dry deposition may be larger than wet N deposition (Bobbink et al. 1992; Lovett 1992), and as *Sphagnum* has a large moist leaf surface, the moss may be a very effective absorber of dry N deposition. As a result, *Sphagnum* may have access to more atmospheric N than previously assumed. In addition, deposition and subsequent uptake of organic N compounds has not been well quantified.

When atmospheric sources and retranslocation are not sufficient for sustaining *Sphagnum* growth, then absorption from pore water is necessary to meet the N demand. The latter seems likely enough, given the ability of *Sphagnum* to absorb nutrients over the entire moss surface (Brown 1982) and the dominant upward water flow due to evapotranspiration in dry periods in summer. As long as it is not too dry, the evaporated water is replaced by water transported from below through internal as well as external pathways (Hayward and Clymo 1982). Although the N concentrations in bog water are generally very low, the resulting nutrient flux may still be sufficient to meet the remaining *Sphagnum* N demand as a result of the relatively high evapotranspiration rates in *Sphagnum*-dominated bogs (Bridgham et al. 1999; Heijmans et al. 2001b).

10.4.1.3 Nitrogen Uptake by Vascular Plants and Mineralization

The largest N flows are N uptake and N loss by vascular plants and decomposition/mineralization in the acrotelm peat resulting in DIN and DON production. It is possible that our estimation of litter production from vascular plants, particularly from the belowground plant parts, is too high. That belowground biomass is 4 times as large as aboveground biomass seems a reasonable assumption, but very little is known about the turnover rate of this large pool of N, which is necessary for an estimation of belowground (litter) production. Belowground biomass mainly consists of overgrown stems of ericaceous species, rhizomes of graminoids and herbs, and fine roots. The turnover rate of buried stems is probably very low, but this might be compensated by a relatively fast turnover of fine roots. The measurement of overgrown stem biomass is also difficult, as there is no clear visible distinction between live stems and dead stems (personal observation).

Alternatively, measured rates of N mineralization might be underestimated. It is likely that mineralization rates are highest in the vicinity of vascular plant roots that may exude a considerable amount of easily degradable C compounds (King and Reeburgh 2002). Measurement of N mineralization rates in patches of low vascular plant cover could result in an underestimation of these rates. As a result of large vascular plant litter production and modest mineralization rates, DON production had to be quite high in our scheme in order to close the N budget for acrotelm peat. Nevertheless, it has been shown that DON concentrations in pore water can be considerably higher than DIN concentrations and that many tundra plant species, often also occurring in boreal peatlands, are able to use organic N (Kielland 1994). From this, it seems clear that belowground processes need more study. Perhaps, the use of ^{15}N natural abundances (Nordbakken et al. 2003) and tracer studies with ^{15}N and ^{13}C may shed some light in this black box.

10.4.2 Effects of Atmospheric Nitrogen Deposition

10.4.2.1 Nitrogen Availability

Given that ombrotrophic boreal peatlands mainly depend on atmospheric sources for water and nutrient supply, it is understandable that globally rising N deposition rates have been of concern to peatland ecologists. Apart from some locations where N fixation may be the dominant N source, N deposition is the main input of N to most peatlands. Consequently, an increase in atmospheric N input affects the N budget directly.

Firstly, it increases the availability of N to the mosses, as *Sphagnum* is very efficient in capturing atmospheric N deposition (Woodin and Lee 1987; Williams et al. 1999b; Heijmans et al. 2002). Secondly, as N retention from atmospheric deposition by *Sphagnum* is less than 100 %, rising atmospheric N inputs also increase the N concentrations in pore water. As a result, more N becomes available for absorption by plants, microorganisms, and peat.

The increased capture of N by *Sphagnum* with rising N deposition is confirmed by increases in *Sphagnum* N concentration. This is a very general response to experimental N additions (Jauhiainen et al. 1998b; Aerts et al. 2001; Berendse et al. 2001; Heijmans et al. 2001a; Limpens et al. 2003a) and is also observed when *Sphagna* from sites differing in N deposition are compared (Malmer 1988, 1990; Pitcairn et al. 1995; Lamers et al. 2000; Berendse et al. 2001; Bragazza et al. 2004b). Even when N did clearly not limit growth, the N pools in *Sphagnum* still increased, suggesting that there is limited regulation of N absorption by *Sphagnum*. However, in the long term, *Sphagnum* seems able to adapt to some degree to increasing N deposition by reducing NH_4^+ uptake rate (Press et al. 1986), by reducing nitrate reductase activity (Woodin and Lee 1987), and by reducing retranslocation (Aldous 2002b; Bragazza et al. 2004a).

Increased N concentrations in pore water and peat due to experimental N additions (Limpens et al. 2003a; Nordbakken et al. 2003; Tomassen et al. 2003) and differences in background N deposition (Lamers et al. 2000; Bragazza et al. 2003) have also been observed. Additionally, there is experimental evidence that some vascular plant species may profit from the increase in N availability in their rhizosphere (Heijmans et al. 2002; Limpens et al. 2003a), with shallow rooting species usually responding first (Heijmans et al. 2002; Nordbakken et al. 2003).

10.4.2.2 Productivity

In the previous section it was discussed that rising N deposition rates increased the N availability to *Sphagnum*, almost invariably leading to higher tissue N concentrations. Additionally, the higher N availability may affect *Sphagnum* production (Chap. 8). Adding N sometimes enhanced *Sphagnum* production in areas with very low N deposition, such as north Sweden and parts of North America (Rochefort 1990; Aerts et al.1992; Li and Vitt 1997; Vitt et al. 2003). More often, however, N addition had no effect or even had a negative effect on *Sphagnum* production (Twenhöven 1992; Berendse et al. 2001; Heijmans et al. 2001a; Gunnarsson and Rydin 2000; Limpens et al. 2004). There are several ways in which increased N availability might affect *Sphagnum* production. Direct negative effects have been demonstrated in greenhouse experiments with monocultures of *Sphagnum* (Press et al. 1986; Jauhiainen et al. 1994, 1998b) and in field plots where vascular plants were removed (Aerts et al. 1992). This inhibitory effect might be caused by an accumulation of NH_4^+ in *Sphagnum* cells (Press et al. 1986; Rudolph and Voigt 1986; Limpens and Berendse 2003a), or by the increased metabolic effort *Sphagnum* has to put into the production of N-rich free amino acids to avoid these toxic effects (Baxter 1992; Nordin and Gunnarsson 2000). The latter explanation seems unlikely, however, as no relation between *Sphagnum* growth and amino acid concentration was observed in an experiment using three N supply rates (Limpens and Berendse 2003a). Indirect effects through interactions with other organisms may be more important. For example, it was shown that high N treated *Sphagnum* was susceptible to infection by a fungus and expansion of epiphytic algae, resulting in reduced *Sphagnum* growth rates (Limpens et al. 2003b). In other experiments, effects through competition with vascular plants or taller *Polytrichum* contributed to reduced *Sphagnum* growth (Berendse et al. 2001; Heijmans et al. 2001a; Limpens et al. 2004). All in all, N deposition seems to act as a stress factor, which may add to other stresses like summer drought. However, negative effects of N deposition may be (partly) compensated for by favorable growing conditions, such as by additional P supply (Limpens et al. 2004; Chap. 11). When *Sphagnum* grows vigorously, and thus has a high N demand, it is able to use a large proportion of deposited N, thereby reducing toxic effects due to NH_4^+ accumulation and reducing N availability to other organisms.

In contrast to *Sphagnum*, vascular plant production seems to show an overall positive response to an increase in N availability, with usually only a few species being responsible for the increase in production (Heijmans et al. 2002; Limpens et al. 2003a, 2004). This selective response may be explained by different nutrient limitations among species (Hoosbeek et al. 2002), and by differences in rooting depth, as the enrichment of the pore water by increased atmospheric N supply only slowly penetrates deeper layers (Nordbakken et al. 2003). Again depending on plant species, the increase in production may be expressed as an increase in the turnover, resulting in an increased litter production, or in an increased investment in aerial biomass, leading to a higher cover. Shading may increasingly hamper *Sphagnum* growth either way.

10.4.2.3 Feedbacks and Carbon Accumulation

It has been well established that vascular plants decompose faster than *Sphagnum* (Heal et al. 1978; Hobbie 1996), resulting in an overrepresentation of *Sphagnum* in the peat (Hayward and Clymo 1982). This means that changes in the relative proportion of *Sphagnum* biomass will have strong effects on decomposition and mineralization rates. Changes in the degradability of *Sphagnum* litter itself, for example, by increased tissue N concentrations (Coulson and Butterfield 1978; Limpens and Berendse 2003b), may add to this effect.

Most fertilization experiments, usually lasting for 3–4 years, miss the species feedback effects on nutrient availability as it takes longer before changes in the vegetation and litter quality are reflected in the botanical and chemical composition of the peat (Berendse 1998). Models therefore are necessary to explore potential long-term effects of global changes, like altered N deposition, on peatland ecosystems. However, very few ecosystem models take species composition into account (Berendse 1994; van Oene et al. 1999). If increased N deposition reduces *Sphagnum* production, it may result in a positive feedback loop through increases in mineralization rates and vascular plant production, further reducing *Sphagnum* production. This means that negative N effects may become more pronounced over longer time periods than observed in short-term experiments. To elucidate the potential importance of this feedback loop, we developed a process-based bog ecosystem model, including interactions between species and feedbacks through species effects on nutrient dynamics (Heijmans, unpublished data). Several model runs confirmed the role of *Sphagnum* as an ecosystem engineer (van Breemen 1995; Malmer et al. 2003), controlling nutrient availability to vascular plants and C accumulation rates.

The foregoing discussion implies that the effect of increased N deposition on C accumulation in peatlands depends on how *Sphagnum*, being the main peat former, responds to increases in N supply. In areas with very low N deposition, positive effects are possible (Vitt et al. 2003); however, regarding the rising global rates of N deposition (Fig. 10.1), negative effects seem more likely. On account of this, Malmer and Wallén (2004) partly attributed the recent reductions in apparent C accumulation rate of many boreal peatlands to increased N deposition. Their hypothesis is that as long as nutrient supply to the ecosystem is similar to nutrient removal due to peat formation (i.e., semipermanent storage in the catotelm), nutrient availability is kept low and *Sphagnum* remains the dominant component of the vegetation, resulting in relatively constant C accumulation for long time periods. Increased N deposition as well a drier mire surface (Gunnarsson et al. 2002) as a result of climate warming (Hendon and Charman 2004) may both slow down C accumulation rates by reducing *Sphagnum* production and increasing litter residence times in the acrotelm, where conditions for decay are more favorable. The associated decline in N removal by peat formation leads to increasing nutrient availability, prompting vegetation changes, which, in turn, may feed back on C accumulation.

10.5 Conclusions

Because of the interactions between plant species and nutrient dynamics and the importance of species composition for C accumulation, further developing our understanding of N cycling in peatlands is essential for predicting the future of boreal peatlands, and, potentially, global C budgets. Global warming, drainage, and fires are all likely to increase nutrient availability through increases in biological activity as a result of increased temperature or increased depth of oxygenated peat. Their impact on vegetation composition and C accumulation may therefore be similar to the discussed effects of N deposition. Still, very few studies have addressed the effects of climate change on the vegetation of peatlands (Weltzin et al. 2000, 2003). Other global changes or disturbances that reduce the relative proportion of *Sphagnum* litter or that increase the residence time of peat in the acrotelm will reduce C accumulation rates and slow down N removal.

References

Adema EH, Heeres R, Hulskotte J (1986) On the dry deposition of NH_3, SO_2 and NO_2 on wet surfaces in a small scale wind tunnel. Proceedings of the 7th world clean air congress, Sydney, Australia

Aerts R, Chapin FSI (2000) The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. Adv Ecol Res 30:1–67

Aerts R, Wallén B, Malmer N (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. J Ecol 80:131–140

Aerts R, Wallén B, Malmer N, De Caluwe H (2001) Nutritional constraints on *Sphagnum*-growth and potential decay in northern peatlands. J Ecol 89:292–299

Akkermans A DL (1971) Nitrogen fixation and nodulation of *Alnus* and *Hippophae* under natural conditions. PhD thesis, University of Leiden, The Netherlands

Aldous AR (2002a) Nitrogen retention by *Sphagnum* mosses: responses to atmospheric nitrogen deposition and drought. Can J Bot 80:721–731

Aldous AR (2002b) Nitrogen translocation in *Sphagnum* mosses: effects of atmospheric nitrogen deposition. New Phytol 156:241–253

Anderson DE (2002) Carbon accumulation and C/N ratios of peat bogs in northwest Scotland. Scot Geogr J 118:323-341

Asman WAH, Sutton MA, Schjorring JK (1998). Ammonia: emission, atmospheric transport and deposition. New Phytol 139:27–48

Backéus I (1985) Aboveground production and growth dynamics of vascular bog plants. Thesis, Uppsala University, Uppsala

Bartsch I, Moore TR (1985) A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Quebec. Can J Bot 63:1241–1248

Basilier K, Granhall V, Stenstrøm TA (1978) Nitrogen fixation in wet minerotrophic moss communities of a subarctic mire. Oikos 31:236–246

Baxter R, Emes MJ, Lee DS (1992) Effects of an experimentally applied increase in ammonium on growth and amino-acid metabolism of *Sphagnum cuspidatum* Ehrh. ex. Hoffm. from differently polluted areas. New Phytol 120:265-274

Belyea LR, Warner BG (1996) Temporal scale and the accumulation of peat in a *Sphagnum* bog. Can J Bot 74:366–377

Berendse F (1994) Litter decomposability – a neglected component of plant fitness. J Ecol 82:187–190

Berendse F (1998) Effects of dominant plant species on soils during succession in nutrient-poor ecosystems. Biogeochemistry 42:73–88

Berendse F, Aerts R (1987) Nitrogen-use-efficiency: a biologically meaningful definition? Funct Ecol 1:293–296

Berendse F, Van Breemen N, Rydin H, Buttler A, Heijmans MMPD, Hoosbeek MR, Lee JA, Mitchell E, Saarinen T, Vasander H, Wallén B (2001) Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. Global Change Biol 7:591–598

Bobbink R, Heil GW, Raessen MBAG (1992) Atmospheric deposition and canopy exchange processes in heathland ecosystems. Environ Pollut 75:29–37

Bonin P, Omnes P, Chalamet A (1998) Simultaneous occurrence of denitrification and nitrate ammonification in sediments of the French Mediterranean coast. Hydrobiologia 389:169–182

Botch MS, Masing VV (1983) Mire ecosystems in the USSR. In: Gore AJP (ed) Ecosystems of the world 4A. Mires: swamp, bog, fen and moor. Elsevier, Amsterdam, pp 95–152

Botch M, Kobak K, Kolchugina T, Vinson T (1995) Carbon pools and accumulation in peatlands of the former Soviet Union. Global Biogeochem Cycles 9:37–46

Bragazza L, Limpens J (2004). Dissolved organic nitrogen dominates in European bogs under increasing atmospheric N deposition. Global Biogeochem Cycles 18: GB4018. DOI 10.1029/2004GB002267

Bragazza L, Gerdol R, Rydin H (2003) Effects of mineral and nutrient input on mire bio-geochemistry in two geographical regions. J Ecol 91:417–426

Bragazza L, Limpens J, Gerdol R, Grosvernier P, Hájek M, Hajkova P, Iacumin P, Kutnar L, Rydin H, Tahvanainen T (2004a). Nitrogen concentration and $\delta^{15}N$ signature of ombrotrophic *Sphagnum* mosses at different N deposition levels in Europe. Global Change Biol 11:106–114

Bragazza L, Tahvanainen T, Kutnar L, Rydin H, Limpens J, Hàjek M, Grosvernier P, Hansen I, Iacumin P, Gerdol R (2004b). Nutritional constraints in ombrotrophic *Sphagnum* plants under increasing atmospheric nitrogen depositions in Europe. New Phytol 163:609–116

Bridgham SD, Pastor J, Janssens JA, Chapin C, Malterer TJ (1996) Multiple limiting gradients in peatlands: A call for a new paradigm. Wetlands 16:45–65

Bridgham SD, Updegraff K, Pastor J (1998) Carbon, nitrogen, and phosphorus mineralisation in northern wetlands. Ecology 79:1545–1561

Bridgham SD, Pastor J, Updegraff K, Malterer TJ, Johnson K, Harth C, Chen JQ (1999) Ecosystem control over temperature and energy flux in northern peatlands. Ecol Appl 9:1345–1358

Brown DH (1982) Mineral nutrition. In: Smith AJE (ed) Bryophyte ecology. Chapman and Hall, London, pp 383–444

Chapin CT, Bridgham SD, Pastor J, Updegraff K (2001) Nitrogen, phosphorus and carbon mineralization in response to nutrient and lime additions in peatlands. Soil Sci 168:409

Chapman RR, Hemond HF (1982) Dinitrogen fixation by surface peat and *Sphagnum* in an ombrotrophic bog. Can J Bot 60:5–543

Clymo RS (1983) Peat. In: Gore AJP (ed) Ecosystems of the world 4A. Mires: swamp, bog, fen and moor. Elsevier, Amsterdam, pp 159–224

Clymo RS, Turunen J, Tolonen K (1998) Carbon accumulation in peatland. Oikos 81:368–388

Coulson JC, Butterfield J (1978). An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. J Ecol 66:631–650

Crisp DT (1966) Input and output of minerals for an area of Pennine moorland: the importance of precipitation, drainage, peat erosion and animals. J Appl Ecol 3:327–348

Damman AWH (1978) Distribution and movement of elements in ombotrophic peat bogs. Oikos 30:480–495

Damman AWH (1988). Regulation of nitrogen removal and retention in *Sphagnum* bogs and other peatlands. Oikos 51:291–305

Damman AWH (1995) Boreal peatlands in Norway and eastern North America: a comparison. Gunneria 43–65

Davey A, Marchant HJ (1983) Seasonal variation in nitrogen fixation by *Nostoc commune* at the Vestfold Hills Antarctica. Phycologia 22:377–386

Dickinson CH (1983) Micro-organisms in peatlands. In: Gore AJP (ed) Ecosystems of the world 4A. Mires: swamp, bog, fen and moor. Elsevier, Amsterdam, pp 225–244

Dooley F, Houghton JA (1973) The nitrogen-fixing capacities and occurrence of blue-green algae in peat soils. Bryol Phycol J 8:289–293

Doyle GJ (1973) Primary production estimates of native blanket bog and meadow vegetation growing on reclaimed peat at Glenamoy, Ireland. In: Bliss LC, Wielgolaski FE (eds) Primary production and production processes. Tundra Biome Steering Committee Report, Edmonton, Alberta, Canada, pp 141–151

Fenn ME, Haeuber R, Tonnesen GS, Baron JS, Grossman-Clarke S, Hope D, Jaffe DA, Copeland S, Geiser L, Rueth HM, Sickman JO (2003) Nitrogen emissions, deposition, and monitoring in the western United States. BioScience 53:391–403

Flechard CR, Fowler D, Sutton MA, Cape JN (1999) A dynamic chemical model of bi-directional ammonia exchange between semi-natural vegetation and the atmosphere. Q J R Meteorol Soc 125:2611–2641

Forrest GI (1971) Structure and production of northern Pennine blanket bog vegetation. J Ecol 59:453–479

Forrest GI, Smith RAH (1975) The productivity of a range of blanket bog types in the northern Pennines. J Ecol 63:173–202

Freeman C, Lock MA, Reynolds B (1993) Fluxes of CO_2, CH_4 and N_2O from a Welsh peatland following simulation of WT drawdown: potential feedback to climate change. Biogeochemistry 19:51–60

Gerdol R (1990) Seasonal variations in the element concentrations in mire water and in *Sphagnum* mosses on an ombrotrophic bog in the southern Alps. Lindbergia 16:44–50

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195

Gorham E, Janssens JA, Glaser PH (2003) Rates of peat accumulation during the postglacial period in 32 sites from Alaska to Newfoundland with special emphasis on northern Minnesota. Can J Bot 81:429–438

Granhall U (1970) Acetylene reduction by blue-green algae isolated from Swedish soils. Oikos 21:330–332

Granhall U, Lid-Torsvik V (1975) Nitrogen fixation by bacteria and free-living blue-green algae in tundra sites. In: Wielgolaski FE (ed) Ecological studies 17.

Fennoscandian tundra ecosystems, part II. Animals and systems analysis. Springer, Berlin Heidelberg New York, pp 305–315

Granhall U, Selander H (1973) Nitrogen fixation in a subarctic mire. Oikos 24:8–15

Grigal DF (1985) *Sphagnum* production in forested bogs of northern Minnesota. Can J Bot 63:1204–1207

Grigal DF, Homann PS (1994) Nitrogen mineralisation, groundwater dynamics, and forest growth on a Minnesota outwash landscape. Biogeochemistry 27:171–185

Grigal DF, Buttleman CG, Kernik LK (1985) Biomass and productivity of the woody strata of forested bogs in northern Minnesota. Can J Bot 63:2416–2424

Gunnarsson U, Rydin H (2000) Nitrogen fertilization reduces *Sphagnum* production in bog communities. New Phytol 147:527–537

Gunnarsson U, Malmer N, Rydin H (2002) Dynamics or constancy in *Sphagnum* dominated mire ecosystems? A 40-year study. Ecography 25:685–704

Gunther AJ (1989) Nitrogen fixation by lichens in a subarctic Alaskan watershed (USA). Bryologist 92:202–208

Hayward PM, Clymo RS (1982) Profiles of water content and pore size in *Sphagnum* peat, and their relation to peat bog ecology. Proc R Soc Lond Ser B 215:299–325

Heal OW, Latter PM, Howson G (1978). A study of the rates of decomposition of organic matter. In: Heal OW, Perkins DE (eds) Production ecology of British moors and montane grasslands. Springer, Berlin Heidelberg New York, pp 136–159

Heijmans MMPD, Berendse F, Arp WJ, Masselink AK, Klees H, De Visser W, van Breemen N (2001a) Effects of elevated carbon dioxide and increased nitrogen deposition on bog vegetation in the Netherlands. J Ecol 89:268–279

Heijmans MMPD, Arp WJ, Berendse F (2001b) Effects of elevated CO_2 and vascular plants on evapotranspiration in bog vegetation. Global Change Biol 7:817–827

Heijmans MMPD, Klees H, De Visser W, Berendse F (2002) Effects of increased nitrogen deposition on the distribution of ^{15}N-labeled nitrogen between *Sphagnum* and vascular plants. Ecosystems 5:500–508

Heil GW, Werger MJA, Mol de W, Van Dam D, Heijne B (1988) Capture of atmospheric ammonium by grassland canopies. Science 239:764–765

Hemond HF (1980) Biogeochemistry of Thoreau's Bog, Concord, Massachusetts. Ecol Monogr 50:507–526

Hemond HF (1983) The nitrogen budget of Thoreau's Bog. Ecology 64:99–109

Hendon D, Charman DJ (2004) High-resolution peatland water-table changes for the past 200 years: the influence of climate and implications for management. Holocene 14:125–134

Henry GHR, Svoboda J (1986) Dinitrogen fixation (acetylene reduction) in high arctic sedge meadow communities. Arct Alp Res 18:181–187

Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol Monogr 66:503–522

Hoosbeek MR, van Breemen N, Vasander H, Buttler A, Berendse F (2002) Potassium limits potential growth of bog vegetation under elevated atmospheric CO_2 and N deposition. Global Change Biol 8:1130–1138

Hosker RP, Lindberg SE (1982) Atmospheric deposition and plant assimilation of gases and particles. Atmos Environ 16:889–899

Jauhiainen J, Vasander H, Silvola J (1994) Response of *Sphagnum fuscum* to N deposition and increased CO_2. J Bryol 18:83–95

Jauhiainen J, Silvola J, Vasander H (1998a) The effects of increased nitrogen deposition and CO_2 on *Sphagnum angustifolium* and *S. warnstorfii*. Ann Bot Fenn 35:247–256

Jauhiainen J, Wallén B, Malmer N (1998b) Potential NH_4^+ and NO_3^- uptake in seven *Sphagnum* species. New Phytol 138:287–293

Kalbitz K, Geyer S (2002) Different effects of peat degradation on dissolved organic carbon and nitrogen. Org Geochem 33:319–326

Kielland K (1997) Role of free amino acids in the nitrogen economy of arctic cryptogams. Écoscience 4:75–79

Kielland K (1994) Amino-acid absorption by arctic plants – implications for plant nutrition and nitrogen cycling. Ecology 75:2373–2383

King JY, Reeburgh WS (2002) A pulse-labeling experiment to determine the contribution of recent plant photosynthates to net methane emission in arctic wet sedge tundra. Soil Biol Biochem 34:173–180

Kivinen E (1933) Suokasvien ja niiden kasvualustan kasvinravintoainesuhteista. Acta Agral Fenn 27:1–140

Kløve B (2001) Characteristics of nitrogen and phosphorus loads in peat mining wastewater. Water Res 10:2362

Koerselman W, Verhoeven JTA (1992) Nutrient dynamics in mires of various trophic status: nutrient inputs and outputs and the internal nutrient cycle. In: Verhoeven JTA (ed) Fens and bogs in the Netherlands: vegetation, history, nutrient dynamics and conservation. Kluwer, Dordrecht, pp 397–432

Koerselman W, Van Kerkhoven MB, Verhoeven JTA (1993) Release of inorganic nitrogen, phosphorus and potassium in peat soils: effect of temperature, water chemistry and water level. Biogeochemistry 20:63–81

Kortelainen P, Saukkonen S (1994) Leaching of organic carbon and nitrogen from forested catchments. Academy of Finland. The Finnish research programme on climate change, second progress report 285–290

Kuhry P, Vitt DH (1996) Fossil carbon/nitrogen ratios as a measure of peat decomposition. Ecology 77:271–275

Lamers LPM, Bobbink R, Roelofs JGM (2000) Natural nitrogen filter fails in raised bogs. Global Change Biol 6:583–586

Lee EJ, Kenkel N, Booth T (1996) Atmospheric deposition of macronutreints by pollen in the boreal forest. Écoscience 3:304–309

Li Y, Vitt DH (1997) Patterns of retention and utilisation on aerially deposited nitrogen in boreal peatlands. Écoscience 4:106–116

Ligrone R, Duckett JG (1998) The leafy stems of *Sphagnum* (Bryophyta) contain highly differentiated polarized cells with axial arrays of endoplasmic microtubules. New Phytol 140:567–579

Limpens J, Berendse F (2003a) Growth reduction of *Sphagnum magellanicum* subjected to high nitrogen deposition: the role of amino acid nitrogen concentration. Oecologia 135:339–345

Limpens J, Berendse F (2003b) How litter quality affects mass loss and N loss from decomposing *Sphagnum*. Oikos 103:537–547

Limpens J, Berendse F, Klees H (2003a) N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. New Phytol 157:339–347

Limpens J, Raymakers JTAG, Baar J, Berendse F, Zijlstra JD (2003b) The interactions between epiphytic algae, a parasitic fungus and *Sphagnum* as affected by N and P. Oikos 103:59–68

Limpens J, Berendse F, Klees H (2004) How P affects the impact of N deposition on *Sphagnum* and vascular plants in bogs. Ecosystems 7:793–804

Lipson DA, Näsholm T (2001) The unexpected versatility of plants: organic nitrogen use and availability in terrestrial ecosystems. Oecologia 128:305–316

Lovett GM (1992) Atmospheric deposition and canopy interactions of nitrogen. In: Johnson DW, Lindberg SE (eds) Atmospheric deposition and forest nutrient cycling. Springer, Berlin Heidelberg New York, pp 152–166

Lütt S (1992) Produktionsbiologische Untersuchungen zur Sukzession der Torfstichvegetation in Schleswig-Holstein. Mitteilungen der Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg. PhD thesis, University of Kiel, Germany

Malmer N (1988) Patterns in the growth and the accumulation of inorganic constituents in the *Sphagnum* cover on ombrotrophic bogs in Scandinavia. Oikos 53:105–120

Malmer N (1990) Constant or increasing nitrogen concentrations in *Sphagnum* mosses on mires in Southern Sweden during the last few decades. Aquilo Ser Bot 28:57–65

Malmer N, Nihlgård B (1980) Supply and transport of mineral nutrients in a subarctic mire. Ecol Bull 30:63–95

Malmer N, Sjörs H (1955) Some determinations of elementary constituents in mire plants and peats. Bot Not 108:46–80

Malmer N, Wallén B (1993) Accumulation and release of organic matter in ombotrophic hummocks – processes and regional variation. Ecography 16:193–211

Malmer N, Wallén B (2004) Input rates, decay losses and accumulation rates of carbon in bogs during the last millennium: internal processes and environmental changes. Holocene 14:111–117

Malmer N, Svensson BM, Wallén B (1994) Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. Folia Geobot Phytotaxon 29:483–496

Malmer N, Albinsson C, Svensson BH, Wallén B (2003) Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. Oikos 100:469–482

Martikainen PJ, Nykänen H, Crill PM, Silvola J (1993) Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. Nature 366:51–53

Martin NJ, Holding AJ (1978) Nutrient availability and other factors limiting microbial activity in the blanket peat. In: Heal OW, Perkins DE (eds) Production ecology of British moors and montane grasslands. Springer, Berlin Heidelberg New York, pp 113–135

Matzner E (1989). Acidic precipitation: case study soiling. In: Adriano DC, Havas M (eds) Acidic precipitation, vol I: case studies. Springer, Berlin Heidelberg New York, pp 39–83

Mauquoy D, Van Geel B, Blaauw M, Speranza A, van der Plicht J (2004). Changes in solar activity and Holocene climatic shifts derived from C-14 wiggle-match dated peat deposits. Holocene 14:45–52

McFarland JW, Ruess RW, Kielland K, Doyle AP (2002) Cycling dynamics of $NH4^+$ and amino acid nitrogen in soils of a deciduous boreal forest ecosystem. Ecosystems 5:775–788

Michelsen A, Jonasson S, Sleep D, Havström M, Callaghan TV (1996) Shoot biomass, $d^{13}C$, nitrogen and chlorophyll responses of two arctic dwarf shrubs to in situ shading, nutrient application and warming simulating climate change. Oecologia 105:1–12

Millbank JW (1985) Lichens and plant nutrition. Proc R Soc Edinburgh Sect B 85:253–261

Mitchell CE, Gilbert D, Buttler A, Amblard C, Grosvernier P, Gobat JM (2003) Structure of microbial communities in *Sphagnum* peatlands and effect of atmospheric carbon dioxide enrichment. Microb Ecol 46:187–199

NADP/NTN National Atmospheric Deposition Program (2004). National Atmospheric Deposition Program 2003 Annual Summary. NADP Data report 2004-01. Illinois State Water Survey, Champaign, IL, USA

Näsholm T, Edvast A, Ericsson A, Norden L (1994) Accumulation of amino acids in some boreal forest plants in response to increased nitrogen availability. New Phytol 126:137–143

Neff JC, Holland EA, Dentener FJ, McDowell WH, Russell KM (2002) The origin, composition and rates of organic nitrogen deposition: a missing piece of the nitrogen cycle? Biogeochemistry 57/58:99–136

Nordbakken JF, Ohlson M, Högberg P (2003) Boreal bog plants: nitrogen sources and uptake of recently deposited nitrogen. Environ Pollut 126:191–200

Nordin A, Gunnarsson U (2000) Amino acid accumulation and growth of *Sphagnum* under different levels of N deposition. Écoscience 7:474–480

O'Neill KP (2000) Role of bryophyte-dominated ecosystems in the global carbon budget. In: Shaw AJ, Goffinet B (eds) Bryophyte biology. Cambridge University Press, Cambridge, pp 344–368

Overbeck F, Happach H (1957) Über das Wachstum und den Wasserhaushalt einiger Hochmoorsphagnen. Flora Jena 144:335–402

Pakarinen P, Tolonen K (1977) Nutrient contents of *Sphagnum* mosses in relation to bog water chemistry in northern Finland. Lindbergia 4:27–33

Pearson JD, Wells KJ, Seller A, Bennett A, Soares J, Woodall J, Ingrouille MJ (2000) Traffic exposure increases natural 15N and heavy metal concentrations in mosses. New Phytol 147:317–326

Penner JE, Atherton CS, Dignon J, Ghan SJ, Walton JJ, Hameed S (1991) Tropospheric nitrogen: a three dimensional study of sources, distributions and deposition. J Geophys Res 96:959–990

Pitcairn CER, Fowler D, Grace J (1995) Deposition of fixed atmospheric nitrogen and foliar nitrogen content of bryophytes and *Calluna vulgaris* (L.) Hull. Environ Pollut 88:193–205

Press MC, Woodin S, Lee JA (1986) The potential importance of an increased atmospheric nitrogen supply to the growth of ombrotrophic *Sphagnum* species. New Phytol 103:45–55

Proctor MCF (1994) Seasonal and shorter-term changes in surface-water chemistry on four English ombrogenous bogs. J Ecol 82:597–610

Proctor MCF, Maltby E (1998) Relationships between acid atmospheric deposition and the surface pH of some ombrotrophic bogs in Britain. J Ecol 86:329–340

Reader RJ, Stewart JM (1972) The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. Ecology 53:1024–1037

Regina K, Silvola J, Martikainen PJ (1999) Short-term effects of changing water table on N_2O fluxes from peat monoliths from natural and drained boreal peatlands. Global Change Biol 5:183–189

Richardson CJ (1983) Pocosins: vanishing wastelands or valuable wetlands? BioScience 33:626–633

Ro CvU, Vet RJ (2002) Analyzed data fields from the national Atmospheric Chemistry Database (NAtChem) and Analysis facility. Air Quality Research Branch, Meteorological Service of Canada, Environment Canada. Toronto, ON

Rochefort L, Vitt DH, Bayley SE (1990). Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology 71:1986–2000

Rosswall T, Granhall U (1980) Nitrogen cycling in a subarctic ombrotrophic mire. Ecol Bull 30:209–234

Rosswall T, Veum AK, Kärenlampi L (1975) Plant litter decomposition at Fennoscandian tundra sites. In: Wielgolaski FE (ed) Ecological studies 17. Fennoscandian tundra ecosystems 17, part I. Plants and microorganisms. Springer, Berlin Heidelberg New York, pp 268–278

Rudolph H, Voigt JU (1986) Effects of NH_4^+-N and NO_3^--N on growth and metabolism of *Sphagnum magellanicum*. Physiol Plant 66:339–343

Rydin H, Clymo RS (1989) Transport of carbon and phosphorus compounds about *Sphagnum*. Proc R Soc Lond Ser B 237:63–84

Sallantaus T, Kaipainen H (1995) Water-carried element balances of peatlands. In: Laiho R, Laine J, Vasander H (eds) Northern peatlands in global climatic change. Publications of the Academy of Finland 1/96, Helsinki, pp 197–203

Schlesinger WH (1991) Biogeochemistry: an analysis of global change. Academic, San Diego

Sheridan RP (1991) Nitrogenase activity by *Hapalosiphon flexuosus* associated with *Sphagnum erythrocalyx* mats in the cloud forest on the volcano La Soufriere, Guadeloupe, French West Indies. Biotropica 23:134–140

Sikora LJ, Keeney DR, Gore AJP (1983) Further aspects of soil chemistry under anaerobic conditions. In: Gore AJP (ed) Ecosystems of the world 4A. Mires: swamp, bog, fen and moor. Elsevier, Amsterdam, pp 247–256

Smith RAH, Forrest GI (1978) Field Estimates of Primary Production. In: Heal OW, Perkins DE (eds) Production ecology of British moors and montane grasslands. Springer, Berlin Heidelberg New York, pp 17–37

Smolders AJP, Tomassen HBM, Lamers LPM, Lomans BP, Roelofs JGM (2002) Peat bog restoration by floating raft formation: the effects of groundwater and peat quality. J Appl Ecol 39:391–401

Sonesson M (1973) Some chemical characteristics of the Stordalen mire. In: Sonesson M (ed) Progress Report 1972. IBP Swedish Tundra Biome Project technical report, pp 31–43

Steward JM (1974) Blue-green algae. In: Quispel A (ed) The biology of nitrogen fixation. North Holland, Amsterdam, pp 202–237

Stutz RC, Bliss LC (1975) Nitrogen fixation in soils of Truelove Island, Northwest Territories. Can J Bot 53:1387–1399

Sutton MA, Moncrieff JB, Fowler D (1992) Deposition of atmospheric ammonia to moorlands. Environ Pollut 75:15–24

Sutton MA, Pitcairn CER, Fowler D (1993) The exchange of ammonia between atmosphere and plant communities. Adv Ecol Res 24:301–396

Svensson BH, Rosswall T (1980) Energy flow through the subarctic mire at Stordalen. Ecol Bull 30:283–301

Tarrason L, Jonson JE, Fagerli H, Benedictow A, Wind P, Simpson D, Klein H (2003) Transboundary acidification, eutrofication and ground level ozone in Europe. Part III. Source-receptor relationships. EMEP Status Report 2003. Norwegian Meteorological Institute EMEP/MSC-W

Timmons DR, Verry ES, Burwell RE, Holt RF (1977) Nutrient transport in surface runoff and interflow from an aspen-birch forest. J Environ Qual 6:192

Tomassen HBM, Smolders AJP, Lamers LPM, Roelofs JGM (2003) Stimulated growth of *Betula pubescens and Molinia caerulea* on ombrotrophic bogs: role of high levels of atmospheric nitrogen deposition. J Ecol 91:357–370

Turunen J, Tahvanainen T, Tolonen K, Pitkanen A (2001) Carbon accumulation in West Siberian mires, Russia. Global Biogeochem Cycles 15:285–296

Turunen J, Tomppo E, Tolonen K, Reinikainen A (2002) Estimating carbon accumulation rates of undrained mires in Finland – application to boreal and subarctic regions. Holocene 12:69–80

Twenhöven FL (1992) Competition between two *Sphagnum* species under different deposition levels. J Bryol 17:71–80

Updegraff K, Pastor J, Bridgham SD, Johnston CA (1995) Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecol Appl 5:151–163

Urban NR (1983) The nitrogen cycle in a forested bog watershed in northern Minnesota. PhD thesis University of Minnesota, Minneapolis

Urban NR, Eisenreich SJ (1988) Nitrogen cycling in a forested Minnesota bog. Can J Bot 66:435–449

Urban NR, Eisenreich SJ, Bayley SE (1988) The relative importance of denitrification and nitrate assimilation in midcontinental bogs. Limnol Oceanogr 33:1611–1617

van Breemen N (1995) How *Sphagnum* bogs down other plants. Trends Ecol Evol 10:270–275

van Breemen N, Burrough PA, Velthorst EJ, Van Dobben HF, De Wit T, Ridder TB, Reynders HFR (1982) Soil acidification from atmospheric ammonium sulphate in forest canopy throughfall. Nature 22:548–550

van der Heijden E, Verbeek SK, Kuiper PJC (2000) Elevated atmospheric CO_2 and increased nitrogen deposition: effects on C and N metabolism and growth of peat moss *Sphagnum recurvum* P. Beauv. var. *mucronatum* (Russ.) Warnst. Global Change Biol 6:201–212

van Oene H, Berendse F, De Kovel CGF (1999) Model analysis of the effects of historic CO_2 levels and nitrogen inputs on vegetation succession. Ecol Appl 9:920–935

van Vuuren M, Berendse F (1993) Changes in soil organic matter and net nitrogen mineralization in heathland soils, after removal, addition or replacement of litter from *Erica tetralix* or *Molinia caerulea*. Biol Fertil Soils 15:268–274

van Wijk MT, Williams M, Gough L, Hobbie SE, Shaver GR (2003) Luxury consumption of soil nutrients: a possible competitive strategy in above-ground and below-ground biomass allocation and root morphology for slow-growing arctic vegetation? J Ecol 91:644–676

Vardy SR, Warner BG, Turunen J, Aravena R (2000) Carbon accumulation in permafrost peatlands in the Northwest Territories and Nunavut, Canada. Holocene 10:273–280

Vasander H (1981) Keidäsrameen kasvibiomassaja tuotos. Suo 32:94

Verhoeven JTA, Koerselman W, Beltman B (1988) The vegetation of fens in relation to their hydrology and nutrient dynamics; a case study. In: Symoens JJ (ed) Vegetation of inland waters. Handbook of vegetation science 15. Kluwer, Dordrecht, pp 249–282

Verhoeven JTA, Keuter A, Van Logtestijn R, Van Kerkhoven MB, Wassen M (1996) Control of local nutrient dynamics in mires by regional and climatic factors: a comparison of Dutch and Polish sites. J Ecol 84:647–656

Verry ES (1975) Streamflow chemistry and nutrient yields from upland-peatland watersheds in Minnesota. Ecology 56:1157

Verry ES, Timmons DR (1982) Waterborne nutrientflow through an upland-peatland watershed in Minnesota. Ecology 63:1456–1467

Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. Am Nat 119:553–572

Vitt DH, Wieder RK, Halsey LA, Turetsky MR (2003) Response of *Sphagnum fuscum* to nitrogen deposition: a case study of ombrogenous peatlands in Alberta, Canada. Bryologist 106:235–245

Vuorenmaa J (2004) Long-term changes of acidifying deposition in Finland (1973–2000). Environ Pollut 128:351–362

Wallén B (1986) Above and below ground dry mass of the three main vascular plants on hummocks on a subarctic peat bog. Oikos 46:51–56

Wallén B (1987) Growth pattern and distribution of biomass of *Calluna vulgaris* on an ombrotrophic peat bog. Holarct Ecol 10:73–79

Wallén B (1992) Methods for studying below-ground production in mire ecosystems. Suo 43:155–162

Waughman GJ (1980) Chemical aspects of the ecology of some south German oeatlands. J Ecol 68:1025–1046

Waughman GJ, Bellamy DJ (1980) Nitrogen fixation and the nitrogen balance in peatland ecosystems. Ecology 61:1185–1198

Wein RW, Bliss LC (1974) Primary productivity of alpine meadow communities. Arct Alp Res 6:261–274

Weltzin JF, Pastor J, Harth C, Bridgham SD, Updegraff K, Chapin CT (2000) Response of bog and fen plant communities to warming and water-table manipulations. Ecology 81:3464–3478

Weltzin JF, Bridgham SD, Pastor J, Chen JQ, Harth C (2003) Potential effects of warming and drying on peatland plant community composition. Global Change Biol 9:141–151

Wielgolaski FE, Kjelvik S, Kallio P (1975) Mineral content of tundra and forest tundra plants in Fennoscandia. In: Wielgolaski FE (ed) Ecological studies 17. Fennoscandian tundra ecosystems, part II. Animals and systems analysis. Springer, Berlin Heidelberg New York, pp 316–332

Williams BL, Silcock DJ (1997) Nutrient and microbial changes in the peat profile beneath *Sphagnum magellanicum* in response to additions of ammonium nitrate. J Appl Ecol 34: 961–970

Williams BL, Silcock DJ (2000) Impact of NH_4NO_3 on microbial biomass C and N and extractable DOM in raised bog peat beneath *Sphagnum capillifolium* and *S. recurvum*. Biogeochemistry 49:259–276

Williams BL, Wheatley RE (1989) Nitrogen transformations in poorly-drained reseeded blanket peat under different management systems. Int Peat J 3:97–106

Williams BL, Silcock DJ, Young M (1999a) Seasonal dynamics of N in two *Sphagnum* moss species and underlying peat treated with $^{15}NH_4{}^{15}NO_3$. Biogeochemistry 45:285–302

Williams BL, Buttler A, Grosvernier P, Francez AJ, Gilbert D, Ilomets M, Jauhiainen J, Matthey Y, Silcock DJ, Vasander H (1999b) The fate of NH_4NO_3 added to *Sphagnum magellanicum* carpets at five European mire sites. Biogeochemistry 45:73–93

Woodin S, Lee JA (1987) The fate of some components of acidic deposition in ombrotrophic mires. Environ Pollut 45:61–72

Yelina GA (1974) Biological productivity of Karelian peatlands. Proceedings of the international symposium on forest drainage, Oulu, Jyväskylä, Finland, pp 71–79

Zoltai SC, Siltanen RM, Johnson JD (2000) A wetland database for the western boreal, subarctic and arctic regions of Canada. Natural Resources Canada. Northern Forestry Centre, information report. Report no NOR-X-368, Edmonton, Alberta, Canada

11 Phosphorous in Boreal Peatlands

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11.1 Introduction

Boreal peatlands are one of the most extensive and important wetland types in the world (Chap. 1). They comprise a significant proportion of the boreal landscape of three continents in the northern hemisphere – North America, Europe, and Asia – and are only precluded from a more significant distribution in the southern hemisphere by the small land mass at boreal latitudes.

Because they represent a large pool of stored organic carbon (C) that potentially could be released to the atmosphere under scenarios of future global warming, boreal peatlands play a major role in the global C cycle (Chap. 9). While changes in climate will be the most important drivers of changes in C cycling in boreal peatlands, nutrient availability, particularly the availability of nitrogen (N) and phosphorus (P), may play an important secondary role in determining the future fate of C stored in boreal peatlands. This is due to the potential roles of N and P in controlling the rates of C fixation (i.e., net primary production, NPP) and oxidation (i.e., decomposition) in both aerobic and anaerobic portions of the peat profile. Thus, a general understanding of P cycling in boreal peatlands has implications for understanding the potentially complex responses of these ecosystems to global climate change.

Studies of boreal peatland biogeochemistry in the literature extend back to the mid-twentieth century, nearly to the inception of the "ecosystem" concept itself (Sjörs 1950; DuRietz 1954; Tamm 1954; Malmer 1962, 1963; Holmen 1964). In fact, some of the earliest studies of "ecosystem dynamics" were conducted in peatland ecosystems (i.e., bogs) (Lindemann 1942). Despite this long history of biogeochemical investigations, our current understanding of P cycling is based primarily on inference from studies of arctic tundra (Chapin et al. 1978) and cool temperate peatland (Kellogg and Bridgham 2003) ecosystems. There has been little specific examination of the cycling and availability of P in boreal peatlands.

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In this chapter, we develop a theoretical framework for P cycling and availability in boreal peatlands based on our understanding of P cycling in terrestrial and wetland ecosystems in general, as modified by constraints specific to boreal peatland environments. We then analyze information available in the literature to determine if it corresponds to our theoretical expectations. Finally, we propose suggestions for future research.

11.2 Methods

In a review of literature, we searched for studies containing data on P concentrations and/or pool sizes in plant tissues, surface soils, and pore waters, comparing ratios of total N to total P, to gain some understanding of the relative availability of N and P in boreal peatland ecosystems. We restricted our review to studies conducted specifically in the boreal zone (in Russia, the Baltic Republics, Fennoscandia, Alaska, and Canada), utilizing information from other systems (e.g., arctic tundra; cool temperate wetlands) only when directly relevant to boreal environments. Peatland types (bogs and fens) were categorized as they were defined by the authors. In general, peatland ecosystems were subdivided into two broad types or features: ombrotrophic bogs and minerotrophic fens (mineral nutrients supplied by surface water) (Chap. 2). Bogs are ombrotrophic peat-accumulating systems that typically are acidic (pH less than 4.0), receive water and nutrients solely from precipitation, and are dominated by oligotrophic species of *Sphagnum* mosses. The average water table position in bogs is low and the seasonal fluctuations are wide. Fens are minerotrophic and are influenced by stagnant groundwaters, surface waters, or by associated lakes or ponds, as well as precipitation inputs, and are characterized by a high, but relatively stable water table. Fens are further subdivided into poor fens (also acidic) that are dominated by mesotrophic species of *Sphagnum*, and brown moss-dominated rich fens. Bogs and poor fen waters (pH between 4.0 and 5.5) are low in base cation concentrations and have low conductivities, whereas rich fen waters have pH values greater than 5.5 (in some cases as high as pH 8.5) and have high concentrations of base cations and high conductivity values.

When literature data were presented as bar graphs, N, P, iron (Fe), or aluminum (Al) content in plant tissue, soil, and water chemistry were approximated by extrapolating absolute values from the axis representing nutrient concentration. When studies included a fertilization experiment, only values reported for control plots were used in our analyses. To establish a constant unit of measurement for the nutrient content of plant tissue and peat soils across all datasets, concentrations of N, P, Al, and Fe were converted to a percent mass (per weight of dry sample) value.

11.3. Phosphorus Cycling and Availability in Boreal Peatlands – Theoretical Framework

11.3.1 Weathering, Pedogenesis, and Primary Succession

Apatite minerals (calcium phosphates) are the ultimate source of all available P on Earth (Schlesinger 1997). As primary minerals formed under conditions of temperature and pressure very different from those at the Earth's surface, apatite minerals are transformed to secondary mineral forms at surface conditions. This "weathering" of primary minerals can involve physical, chemical, and biological processes. All primary minerals exposed at the Earth's surface eventually weather to secondary mineral forms. For P, the most common secondary minerals involve associations with Al, Fe, and manganese (Mn) in acidic environments, and calcium (Ca) and magnesium (Mg) in alkaline environments (Lindsay et al. 1989).

In the absence of external inputs, as primary minerals weather, ecosystem stores of P and other sedimentary elements (those without a significant gas phase) slowly decline during the course of soil development (i.e., pedogenesis). The hydrologic cycle drives this decline in most environments. Surface and subsurface water flows remove both dissolved and particulate species, eventually depositing them in coastal estuarine and marine environments (Meybeck 1982, 1993). As a result, both total P pool sizes and P availability generally decline during the course of soil development.

Examining a chronosequence of soils in New Zealand, Walker and Syers (1976) found that primary minerals (i.e., apatite) were the predominant form of soil P during the early stages of soil development. Over time, pool sizes of both apatite and total P declined, while secondary mineral and organic P forms increased in relative abundance. The oldest stages of soil development were characterized by a continued slow decline of total P (terminal steady state), with remaining P occurring primarily in two forms – occluded P (secondary minerals effectively unavailable to plants) and organic P (P_o). In the absence of external P inputs, these changes are irreversible (Vitousek and White 1981). Our first theoretical prediction is that P cycling and availability in boreal peatlands, particularly ombrotrophic bogs, will be similar to P cycling and availability during the oldest stages of soil development, in that both systems are dominated by the cycling and availability of organic P. Given that plant growth on soils developed over older parent materials is commonly considered to be P-limited, the potential for P limitation exists for bogs.

Vitousek and White (1981) compared P cycling and availability over the course of soil development as predicted by the model of Walker and Syers (1976) with similar knowledge for N, developing a theoretical model of changes in N vs. P availability during the course of primary succession. Vitousek and White (1981) proposed that ecosystems developing on freshly exposed parent materials (e.g., substrates exposed by retreating glaciers) would experience maximum P availability (stores of apatite mineral P would be at their highest levels). In contrast, because the atmosphere represents the ultimate source of all available N, N availability would be at a minimum during the earliest stages of primary succession and soil development. Ecosystems developing on these freshly exposed parent materials would be strongly N limited, with N availability controlled by rates of biological N fixation, as supported by the large stores of available P.

In contrast, at the latest stages of soil development, Vitousek and White (1981) hypothesized that NPP would be strongly P limited, soil P stores having declined over time owing to weathering and loss, with soil N stores representing thousands of years of accumulation associated with biological N fixation. While high P availability during the early stages of soil development has the potential to increase N availability by increasing rates of biological N fixation, the comparatively high N availability associated with later stages of soil development offers no similar mechanism for increasing P availability. Thus, soil P availability has the potential to control ecosystem NPP in both relatively young and relatively old soils. More recent analyses of successional chronosequences in a variety of environments worldwide (including boreal systems in both Alaska and Sweden) have, in large part, borne out these predictions (Vitousek et al. 2004; Wardle et al. 2004).

Because they have developed over parent materials exposed following recent glacial episodes (i.e., 5,000–10,000 BP), boreal peatlands are relatively young in terms of soil development. As such, both soils and underlying parent materials should be relatively P rich and N poor. Thus, our second theoretical prediction is: to the extent that nutrient availability limits NPP in these ecosystems, based on parent material age alone, young boreal peatlands becoming established and expanding laterally in pristine environments, particularly ombrotrophic bogs, are likely to be N-limited rather than P-limited.

It is significant to note the apparent contradiction with respect to the proximal limiting nutrient controlling NPP in boreal peatlands outlined in predictions 1 and 2.

11.4 Peatland Development, N–P Balance, and Anthropogenic Effects

As peatlands develop, they become isolated from the underlying influence of the mineral soil and associated parent materials by the accumulation of peat (Chap. 3). In the absence of continued mineral soil influence (i.e., groundwater inputs), available P stores in boreal peatlands (particularly in ombrotrophic bogs) likely represent mineral P previously converted to organic form through biotic uptake (plants and soil microorganisms) that is currently stored in either plant or microbial biomass or peat. Because substantial additional inputs of P are unlikely to occur in pristine peatlands, particularly under ombrotrophic conditions, both biological and pedological P stores in boreal peatlands should be tightly conserved, with plants exhibiting strong resorption efficiencies (cf. Damman 1978; Jonasson and Shaver 1999) and maximum soil P concentrations occurring in the upper portions of the peat profile (i.e., the rooting zone). Despite conservative P cycling, P losses to the lower portions of the peat profile (below the rooting zone) probably are inevitable. At best, for ombrotrophic boreal peatlands, the rate of P loss below the rooting zone would be balanced by a similar low rate of P input from atmospheric sources (i.e., wet and dry deposition). Steady-state P accumulation in boreal peatlands might be modeled as the balance between these two opposing processes. However, as observed for terrestrial ecosystems (Walker and Syers 1976; Chadwick et al. 1999), P losses below the rooting zone in ombrotrophic systems probably exceed atmospheric inputs. This is because atmospheric P inputs are generally small, reabsorption of P by plants, even in strongly P limited environments, is unlikely to be 100% efficient (Walbridge 1991), and losses below the rooting zone associated with percolating water are inevitable. This information can be combined into our third theoretical prediction: at best, for ombrotrophic boreal peatlands, P inputs in precipitation are balanced by P losses below the rooting zone to deeper peats. If, as is likely the case, P losses exceed P inputs, P limitation would become more severe as ombrotrophic systems develop over time. In either case, P cycling should be tightly conserved in boreal peatland ecosystems.

In more minerotrophic peatlands (fens), additional external inputs will affect P accumulation and availability. Unlike the terrestrial ecosystems studied by Walker and Syers (1976), external inputs resulting from hydrologic sources are common in minerotrophic wetlands. Understanding P cycling and availability in boreal fen peatlands will require consideration of these additional potential sources of P. Historic inputs of P from hydrologic sources during the development of ombrotrophic peatlands also must be considered when analyzing the current P stores held in ombrotrophic peatland soils. Different developmental histories could result in different accumulations of P in the ombrotrophic peatland profile. The amount of P held within the boreal peatland ecosystem at the shift from minerotrophic to ombrotrophic conditions, which may vary owing to differences in external inputs during the course of paludification in comparison with rates of P input in precipitation and P loss below the rooting zone, will determine the length of time it takes a peatland to reach the terminal steady state described before, following the inception of ombrotrophic conditions. Thus, we expect that the history of peatland development may be important in determining the initial P stores available at the onset of ombrotrophy.

Given the importance of precipitation as the sole nutrient source in ombrotrophic systems, N and P availability are likely to be closely linked. Elevated anthropogenic N inputs could drive ombrotrophic boreal peatlands toward P limitation. In southern portions of the peatland range in Europe, this condition has been observed (Malmer 1988; Damman 1990; Aerts et al. 1992). Thus, whether limited by N or P, N and P availability in ombrotrophic boreal peatlands are likely to be closely linked; elevated anthropogenic inputs of N could readily drive systems toward P limitation.

Boreal peatlands contain a significant amount of C as peat. This C accumulates in peatlands, in part, because conditions preclude the complete decomposition of organic matter (Chaps. 7, 9). Organic matter accumulates in most ecosystems, but is especially pronounced in peatlands. Some of this organic matter is prevented from decomposing completely owing to the anaerobic and cold soil conditions that are common below the rooting zone in boreal peatlands.

Global climate change has the potential to increase the oxidation (decomposition) rate of this pool of organic C, providing a potential positive feedback to global warming because a proportion of this C would be released to the atmosphere as CO_2 (Chaps. 7, 9). As these organic C pools decompose, associated nutrients (N and P) that are bound to organic C in soil organic matter will be mineralized. Substantial amounts of N and P are known to be associated with the organic matter that accumulates in peat soils (Clymo 1965). Depending on the N-to-P ratio of the underlying peat, release of N and P associated with organic matter decomposition could alter the nutrient balance of peatland ecosystems.

11.5 Biological and Geochemical Control of Phosphorus Cycling in Boreal Peatlands

Because organic forms of P predominate in peat soils, biological processes are likely to control the cycling and availability of P in boreal peatlands, particularly in ombrotrophic bogs. However, as the degree of mineral influence increases along the gradient from bog to poor fen to rich fen, geochemical processes may become more important in controlling ecosystem P dynamics. Because soil minerals are the ultimate source of P for all ecosystems, increasing minerotrophic status should favor increased availability of P vs. N. Thus, in general, fens are likely to be N-limited (rather than P-limited) and more strongly N limited than bogs; however, the extent to which these increased P stores can be used to support increased rates of N fixation could ameliorate N limitation to some extent in fens, and the general view is that both N and P availability are higher in fens than bogs (Moore and Bellamy 1974; Mitsch and Gosselink 2000).

Rates of primary production are known to be higher in fens than in bogs (Brinson et al. 1981), while rates of organic C mineralization (i.e., decomposition) are known to be severely limited in bogs (Clymo 1965; Swift et al. 1979; Damman 1988; Farrish and Grigal 1988; Maltby 1988). Low rates of decomposition in bogs might also limit N and P mineralization rates, adversely affecting plant nutrient supply. Verhoeven et al. (1990) observed the opposite for bogs in the Netherlands, however. Although their method for estimating P mineralization is equivocal, observed rates of N mineralization were higher in bogs than in fens. Given the high levels of atmospheric N deposition in this region, groundwater inputs may represent vectors of both N and P supply to fens in these environments (Verhoeven et al. 1988). In bogs, where precipitation represents the sole external nutrient source, higher nutrient mineralization rates might be required to support plant growth than in fens, where groundwater inputs provide an additional nutrient source, particularly of N. Clearly, rigorous comparative examination of N and P supply in bogs and fens requires consideration and quantification of all potential sources of N and P, rather than mineralization rates alone.

11.6. Stoichiometric Analyses

11.6.1 Plant Tissues

Following the approach of Koerselman and Meuleman (1996) and Bedford et al. (1999), we examined the relative concentrations of N and P in plant tissues of boreal peatlands to assess the potential for N vs. P limitation of plant growth in these ecosystems. Literature data (Table 11.1) were analyzed in three ways: (1) independent of both geographic plant species variations (Fig. 11.1); (2) consideration of geographic variation (Fig. 11.2); and (3) consideration of both geographic variation and differences between *Sphagnum* spp. and herbaceous vegetation (Figs. 11.3, 11.4). We used the approach of Koerselman and Meuleman (1996) to assess whether plants were most likely limited by N ($N/P \leq 14:1$), P ($N/P \geq 16:1$), or co-limited by N and some other element (P, K) ($14:1 < N/P < 16:1$).

Data for ombrotrophic systems (called bogs, ombrotrophic bogs, or ombrotrophic mires in the literature) support our theoretical observation that N and P availability are closely linked in these ecosystems (Fig. 11.1). While the observed range of bog plant N concentrations is fairly narrow (5–10 mg g^{-1}), P concentrations are more variable (0.25–1.5 mg g^{-1}), resulting in a range of N-to-P ratios in plant tissues that suggest both N and P limitation across all sites. These data are consistent with the apparent contradiction of systems developed over relatively young substrates, suggesting N limitation, vs. systems where the majority of P is present in organic form, suggesting P limitation.

Systems identified simply as fens appear to have higher N concentrations in plant tissues than bogs (10–23 mg g^{-1}), with ratios suggesting P limitation. While these systems seem clearly different from bogs, data for poor fens, transitional fens, rich fens, and minerotrophic systems are much more variable. It is hard to distinguish these systems from bogs on the basis of plant tissue N-to-P ratios, and these systems do not appear to be solely N-limited or P-limited. In contrast, sedge fens and marshes are clearly different from most other ecosystems, with higher concentrations of both N and P in plant tissues and consistent N limitation of NPP (Fig. 11.1).

Considering geographic variation helps to explain some of the apparent contradictions previously indicated (Fig. 11.2). Data for both Sweden and Finland show that N-to-P ratios are clearly higher in southern vs. northern bogs. Malmer (1988) measured average N-to-P ratios in *Sphagnum* capitula from northern and southern Sweden of 6 and 34, respectively. These ratios varied geographically more so than by species. All *Sphagnum* species from northern Scandinavia had low N-to-P ratios, while all *Sphagnum* species from southern Scandinavia had high N-to-P

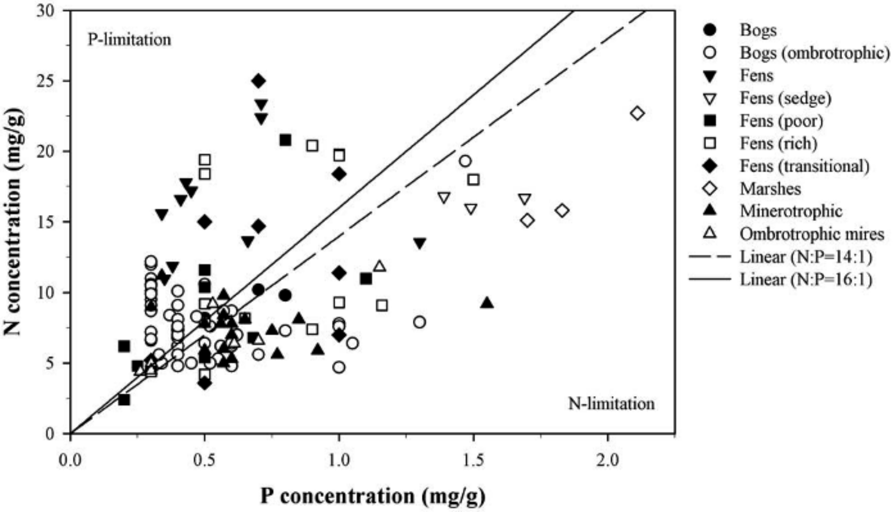

Fig. 11.1. N and P concentrations in plant tissue

ratios. Malmer (1988) suggested that the difference was due to elevated N inputs associated with acidic deposition in southern vs. northern Sweden. On the basis of mass-balance calculations, Rosswall and Granhall (1980) proposed that plant growth in ombrotrophic bogs was N-limited, in particular owing to low rates of atmospheric N deposition (Chaps. 8, 10). Damman (1990) also suggested differences in atmospheric deposition as a principal cause of variation in the fertility of ombrotrophic bogs. Differences in atmospheric deposition are mostly caused by geographic variation in the amount and chemical composition of precipitation and dust fall.

Aerts et al. (1992) examined the effects of increased N supply on the productivity of *Sphagnum*-dominated ombrotrophic bogs in Sweden. At the Åkhult mire in southern Sweden, atmospheric N deposition ranges from 0.7 to 0.9 g N m^{-2} $year^{-1}$, in comparison with atmospheric N deposition at the subarctic Stordalen mire in Swedish Lapland, which ranges from 0.06 to 0.2 g N m^{-2} $year^{-1}$. Aerts et al. (1992) found that *Sphagnum magellanicum* growth at the Åkhult mire responded to P, but not N, fertilization, while *Sphagnum balticum* growth at the subarctic Stordalen mire responded to N, but not P, fertilization. From 1955 to 1983, Malmer (1990) observed an increase in *Sphagnum* N-to-P ratio at the Åkhult mire. In combination, these data suggest that ombrotrophic bogs in southern Sweden have become P-limited in response to increased rates of atmospheric N deposition, while those in nonimpacted northern Sweden remain N-limited. Bayley et al. (1987) observed increases in *Sphagnum* growth in response to N additions to ombrotrophic bogs in Alberta, Canada, but

Table 11.1. N and P concentration in plant tissue of boreal peatlands

Peatland type	Country	Region/ province	% N	% P	N-to-P ratio	% Fe
Vegetation – *Sphagnum* spp.						
Bog (ombrotrophic)	Canada	Manitoba	0.62	0.04	15.6	0.049
			0.87	0.06	15.2	0.028
Mire (ombrotrophic)	Canada	British Columbia	0.44	0.03	16.9	0.009
Mire (ombrotrophic)	Canada	Alberta	0.64	0.06	10.5	0.023
Bog (ombrotrophic)	Finland	Northern	0.64	0.05	12.8	0.020
			0.76	0.05	14.6	0.030
			0.48	0.04	12.0	0.050
			0.84	0.04	22.7	0.040
			0.53	0.06	9.6	0.040
			0.78	0.10	7.8	0.010
			0.76	0.10	7.6	0.020
			0.50	0.05	11.1	0.020
			0.87	0.06	14.5	0.030
			0.70	0.06	11.3	0.030
			0.48	0.06	8.0	0.020
			0.48	0.06	8.0	0.030
			0.62	0.06	10.3	0.040
			0.56	0.07	8.0	0.040
			0.64	0.11	6.1	0.050
			0.50	0.05	9.6	
			0.50	0.03	14.7	
			0.62	0.06	11.1	
			0.56	0.03	17.0	
			0.64	0.06	10.1	
Bog (ombrotrophic)	Finland	Southern	0.68	0.04	16.2	
			0.56	0.04	13.7	
			0.74	0.04	19.0	
			0.81	0.04	19.8	
			0.67	0.03	20.9	
			0.79	0.05	17.2	
			0.66	0.03	21.3	
			0.87	0.03	25.6	
			0.73	0.04	20.3	
			0.73	0.08	9.1	
			0.72	0.03	22.5	
			1.06	0.05	21.6	
			0.67	0.03	20.3	
			1.01	0.04	28.9	
			0.70	0.04	20.0	
			0.83	0.05	17.7	
Bogs (ombrotrophic raised)	Sweden	Northern	0.47	0.10	4.9	
			0.79	0.13	6.2	
Bog	Sweden	Southern	0.98	0.08	11.7	
Bogs	Sweden	Southern	1.20	0.03	34.8	
			1.22	0.03	37.0	
			0.91	0.04	22.2	0.020

% Al	*Sphagnum* species/microsite	Name	Study
0.058	*fuscum*		1
0.029	*fuscum*		1
0.008	*imbricatum, capillifolium, fuscum*		2
0.020	*acutifolia*		2
	balticum	Sodankyla, Jankavuopaja	3
	balticum	Kittila, Ahvenjarvi	3
	balticum	Inari, Ahmajanka	3
	balticum	Inari, Ahmajanka	3
	balticum	Kolari, Juustovuoma	3
	balticum	Kolari, Juustovuoma	3
	balticum	Yli-li, Martimoaapa	3
	balticum	Yli-li, Martimoaapa	3
	balticum	Yli-kiiminki, Hirvisuo	3
	balticum	Pyhanta, Muurainneva	3
	balticum	Pyhanta, Muurainneva	3
	jensenii	Kemijarvi, Seljanaapa	3
	compactum	Puolanka, Poytapuro	3
	lindbergii	Kittila, Pallasjarvi	3
	lindbergii	Enontekio, Pousujarvi	3
	nemoreum	Kemijarvi, Kummunvaara	3
	lindbergii	Sodankyla, Jankavuopaja	3
	majus	Sodankyla, Jankavuopaja	3
	majus	Sodankyla, Vaalajarvi	3
	Various species/hollow (mean)		3, 4
	fuscum/hummock	Kaurastensuo	4
	balticum/hollow	Kaurastensuo	4
	fuscum/hummock	Petkelsuo	4
	balticum/hollow	Petkelsuo	4
	fuscum/hummock	Kananiemensuo	4
	balticum/hollow	Kananiemensuo	4
	fuscum/hummock	Fagelmosse	4
	majus/hollow	Fagelmosse	4
	fuscum/hummock	Klaukkalan Isosuo	4
	balticum/hollow	Klaukkalan Isosuo	4
	fuscum/hummock	Radkila Stormosse	4
	majus/hollow	Radkila Stormosse	4
	fuscum/hummock	Mattmosse	4
	balticum/hollow	Mattmosse	4
	fuscum/hummock (mean)	n=7	4
	(*balticum*, *majus*)/hollow (mean)	n=7	4
	balticum	Stordalen mire	5
	balticum	Stordalen mire	6
0.040	*magellanicum*	Tranerods Mosse	7
	magellanicum	Åkhult mire	5
	magellanicum	Åkhult mire	6
	magellanicum	Åkhult mire	8

Table 11.1. (*Continued*)

Peatland type	Country	Region/ province	% N	% P	N-to-P ratio	% Fe
			0.76	0.04	21.6	0.050
			1.06	0.03	31.3	
			1.01	0.03	36.0	0.090
			0.95	0.03	31.7	0.070
			1.05	0.03	32.8	
			0.99	0.03	38.2	0.090
			0.91	0.03	32.5	0.070
Mire (ombrotrophic) and fen (poor)	Canada	Ontario	0.92	0.05	17.4	0.037
Fen (poor)	Canada	Quebec	0.24	0.02	12.0	
			0.62	0.02	31.0	
			0.54	0.05	10.8	
Fen (poor)	Canada	British Columbia	0.48	0.03	19.2	0.009
Fen (poor)	Canada	Alberta	0.68	0.07	10.0	0.026
Fen (transitional)	Canada	Quebec	0.70	0.10	7.0	
			0.52	0.03	17.3	
			0.36	0.05	7.2	
Fens (moderate and extreme rich)	Canada	Alberta	0.82	0.07	12.6	0.031
Fen (rich)	Canada	Quebec	0.44	0.03	14.7	
Fen (rich)	Canada	Quebec	0.42	0.05	8.4	
Fen	Sweden	Southern	1.19	0.04	31.1	
			1.10	0.04	31.5	
			1.37	0.07	20.7	
Minerotrophic (moderate)	Finland	Northern	0.73	0.08	9.7	
			0.78	0.06	13.9	
			0.90	0.03	30.0	
			1.12	0.03	32.9	
Minerotrophic	Finland	Northern	0.78	0.05	15.6	0.060
			0.53	0.06	8.8	0.080
			0.48	0.03	16.0	0.150
			0.59	0.05	11.8	0.200
			0.60	0.06	10.5	0.030
			0.98	0.06	17.2	0.080
			0.70	0.06	11.7	0.020
			0.59	0.09	6.4	0.050
			0.81	0.07	12.5	0.580
			0.56	0.08	7.3	0.040
			0.78	0.06	13.0	0.040
			0.84	0.06	14.7	0.020
			0.92	0.16	5.9	0.020
			0.50	0.06	8.8	0.020
			0.81	0.09	9.5	0.050

% Al	*Sphagnum* species/microsite	Name	Study
	magellanicum	Åkhult mire	8
	magellanicum	Åkhult mire	8
	magellanicum	Åkhult mire	8
	magellanicum	Åkhult mire	8
	magellanicum	Åkhult mire	8
	magellanicum	Åkhult mire	8
	magellanicum	Åkhult mire	8
0.040	*acutifolia*		2
	lindbergii		9
	(riparium, angustifolium)/lawn		9
	(russowii, angustifolium, warstorfii)/hummock		9
0.008	*imbricatum, capillifolium,fuscum*		2
0.016	*acutifolia*		2
	lindbergii		9
	(riparium, angustifolium)/lawn		9
	(russowii, angustifolium, warstorfii)/hummock		9
0.011	*acutifolia*		2
	(*riparium, angustifolium*)/lawn		9
	(russowii, angustifolium, warstorfii)/hummock		9
	magellanicum, affine, papillosum	Smaland	10
	magellanicum, affine, papillosum	Smaland	10
	magellanicum, affine, papillosum	Smaland	10
	warnstorfii	Rovaniemi, Oinaanvaara	3
	subsecundum	Rovaniemi, Oinaanvaara	3
	subfulvum	Sodankyla, Jankavuopaja	3
	aongstromeii	Kemijarvi, Kummunvaara	3
	balticum	Vaala, Jylhama	3
	balticum	Haapavesi, Hirvineva	3
	lindbergii	Kittila, Ristivuoma-Nuolivuoma	3
	lindbergii	Kittila, Ristivuoma-Nuolivuoma	3
	lindbergii	Inari, Akshujarvi	3
	fallax	Kemijarvi, Seljanaapa	3
	fallax	Kittila, Pallasjarvi	3
	fallax	Kolari, Juustovuoma	3
	fallax	Yli-li, Martimoaapa	3
	fallax	Haapavesi, Hirvineva	3
	fallax	Pyhanta, Muurainneva	3
	riparium	Inari, Ahmajanka	3
	riparium	Inari, Akshujarvi	3
	riparium	Enontekio, Markkina	3
	riparium	Yli-li, Martimoaapa	3

Table 11.1. (*Continued*)

Peatland type	Country	Region/ province	% N	% P	N-to-P ratio	% Fe
Vegetation – Herbaceous species						
Bog (ombrotrophic)	Canada	Alberta	1.93	0.15	13.1	
Mire (ombrotrophic)	Sweden	Northern	1.18	0.12	10.2	0.004
Bog	Sweden	Southern	0.98	0.08	12.3	
			1.02	0.07	14.8	
			0.82	0.05	17.1	
Bog (ombrotrophic)	Sweden	Southern	1.10	0.03	36.7	
Fen (poor)	Canada	Quebec	1.04	0.05	20.8	
			1.10	0.11	10.0	
			1.16	0.05	23.2	
			1.98	0.10	19.8	
			2.08	0.08	26.0	
Fen (transitional)	Canada	Quebec	1.47	0.07	21.0	
			1.14	0.10	11.4	
			1.50	0.05	30.0	
			1.84	0.10	18.4	
Fens (n=4)	Canada	Alberta	1.36	0.13	10.8	
Fens (moderate and rich)	Canada	Alberta	0.91	0.12	7.8	0.032
Fen (rich)	Canada	Quebec	1.84	0.05	36.8	
			0.92	0.05	18.4	
			0.74	0.09	8.2	
			1.80	0.15	12.0	
			1.94	0.05	38.8	
			1.97	0.10	19.7	
			2.04	0.09	22.7	
Fen (extremely rich)	Canada	Quebec	0.93	0.10	9.3	
Fen (floating sedge)	Canada	Alberta	1.68	0.14	12.1	
Fen (lacustrine sedge)	Canada	Alberta	1.60	0.15	10.8	
Fen (riverine sedge)	Canada	Alberta	1.67	0.17	9.9	
Fen (marginal)	Sweden	Aneboda	2.50	0.07	35.7	
Fen	Sweden	Southern	1.78	0.04	41.4	
			1.72	0.05	38.5	
			2.34	0.07	32.8	
			1.56	0.03	46.5	
			1.66	0.04	40.1	
			2.24	0.07	31.7	
Marsh (lacustrine)	Canada	Alberta	1.58	0.18	8.6	
Marsh (riverine)	Canada	Alberta	2.27	0.21	10.7	
Marshes (n=6)	Canada	Alberta	1.51	0.17	9.0	

Study numbers *1* Pakarinen and Gorham (1984), *2* Malmer et al. (1992), *3* Pakarinen and Tolonen (1977), *4* Pakarinen (1978a, b), *5* Aerts et al. (1992), *6* Aerts et al. (2001), *7* Damman (1978), *8* Malmer (1990), *9* Bartsch and Moore (1985), *10* Malmer et al. (2003), *11* Thormann and Bayley (1997), *12* Malmer and Nihlgard (1980), *13* Richardson et al. (1978), *14* Malmer and Sjörs (1955), *15* Bayley and Mewhort (2004)

% Al	*Sphagnum* species/microsite	Name	Study
	Eriophorum vaginatum	Bleak Lake	11
0.002	*Empetrum hermaphroditum*	Stordalen mire	12
	Eriophorum vaginatum	Tranerods Mosse	7
0.010	*Calluna vulgaris*	Tranerods Mosse	7
0.020	*Erica tetralix*	Tranerods Mosse	7
	Rhynchospora sp., *Sphagnum* spp.	Aneboda	13, 14
	Carex limosa	Schefferville	9
	Carex rostrata	Schefferville	9
	Scirpus cespitosus		9
	Betula glandulosa		9
	Salix pedicellaris		9
	Carex limosa	Schefferville	9
	Carex rostrata	Schefferville	9
	Scirpus cespitosus		9
	Betula glandulosa		9
	Carex aquatilis, utriculata, atherodes, lasiocarpa		15
0.033	*Tomenthypnum nitens*		2
	Carex limosa	Schefferville	9
	Carex rostrata	Schefferville	9
	Carex aquatalis		9
	Carex chordorrhiza		9
	Scirpus cespitosus		9
	Betula glandulosa		9
	Salix pedicellaris		9
	Carex aquatalis		9
	Carex lasiocarpa	Perryvale	11
	Carex lasiocarpa	Perryvale	11
	Carex lasiocarpa	Perryvale	11
	Carex sp., *Sphagnum* spp.		13,14
	Narthecium ossifragum	Smaland	10
	Narthecium ossifragum	Smaland	10
	Narthecium ossifragum	Smaland	10
	Narthecium ossifragum	Smaland	10
	Narthecium ossifragum	Smaland	10
	Narthecium ossifragum	Smaland	10
	Carex lasiocarpa	Clyde	11
	Carex lasiocarpa	Perryvale	11
	Carex aquatilis, utriculata, atherodes, lasiocarpa		15

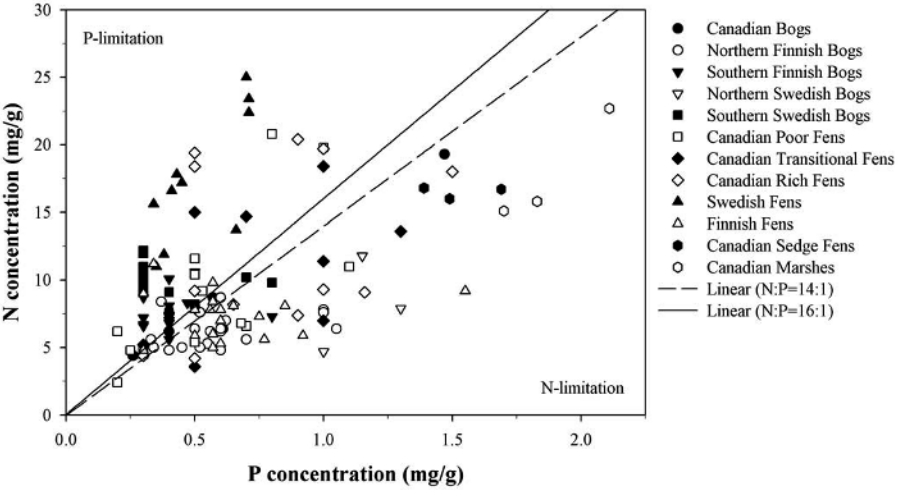

Fig. 11.2. N and P concentrations in plant tissue (all species with geographic differentiation)

Tamm (1954) found that the growth of *Eriophorum vaginatum* in a peat bog in southern Sweden was P-limited. While these data confirm the general tendency toward N limitation in pristine ombrotrophic peatlands in the boreal zone, the fact that increases in N availability quickly lead to P limitation suggests that P is also in relatively short supply (Chaps. 8, 10).

Plant tissue N-to-P ratios suggest that a similar situation occurs in Norway – pristine systems appear to be N-limited, while those impacted by elevated N deposition appear to be P-limited. In contrast, in Canada, where western boreal regions do not experience significantly elevated levels of N deposition, bogs appear N-limited or transitional. For fens, Swedish systems appear P-limited, while both Canadian and Norwegian systems are much more variable. As noted previously, sedge fens and marshes in Canada appear to be clearly N limited (Fig. 11.2). Thus, bogs, in general, appear N-limited, except when anthropogenic N inputs drive these systems toward P limitation. Fens and marshes also tend toward N limitation, but are more variable. Swedish fens appear to be P-limited, which could also be the result of elevated atmospheric N inputs.

When differences between *Sphagnum* spp. and vascular plants are considered, additional trends appear. N concentrations in *Sphagnum* tissues are generally lower and less variable than those of vascular plants (5–10 mg g^{-1} vs. 7.5–23 mg g^{-1}, respectively) (Figs. 11.3, 11.4). On the basis of N and P concentrations in *Sphagnum* tissues, southern Finnish and Swedish bogs are again clearly differentiated from northern ones, and again the majority of Finnish fens appear N-limited, in contrast to the apparently P-limited Swedish fens (Fig. 11.3). Canadian bogs and fens generally fall in the region suggesting closely balanced N and P availability (i.e., co-limitation by N and P or K). One additional difference was observed in comparing vascular and bryophyte N and P concentrations. In Canadian poor and transitional fens, tissue N-to-P ratios suggest that the majority of vascular plants may be P-limited (Fig. 11.4), while the

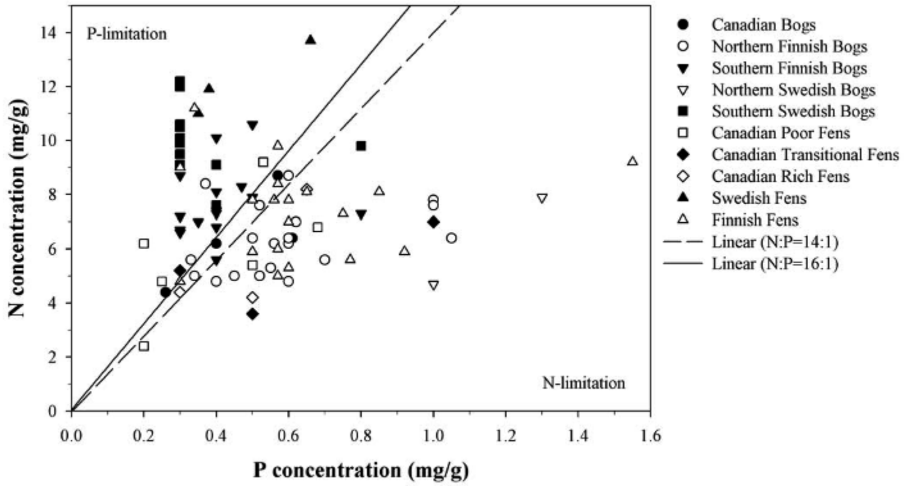

Fig. 11.3. N and P concentrations in plant tissue (*Sphagnum* spp. with geographic differentiation)

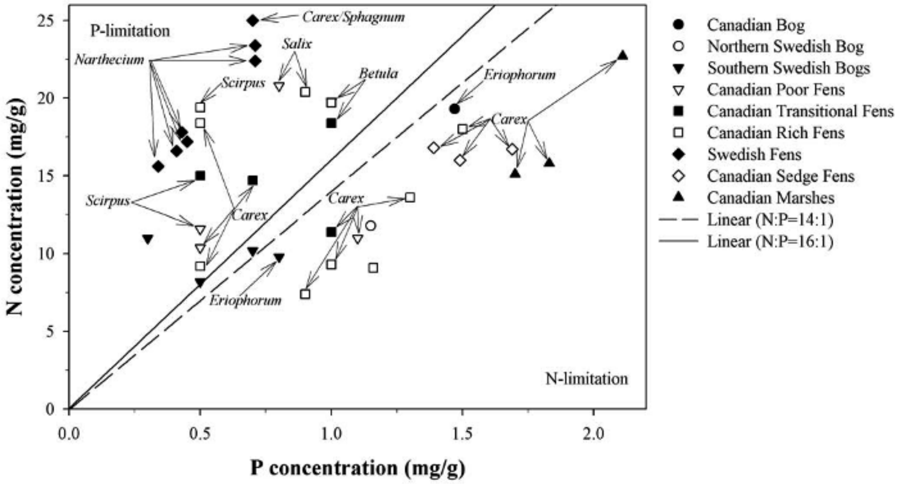

Fig. 11.4. N and P concentrations in plant tissue (vascular species. with geographic differentiation)

majority of *Sphagnum* species may be N-limited (Fig. 11.3). In richer fens, N limitation of vascular plant species seems more common, although with some variability. These observations could reflect different nutrient acquisition strategies of bryophyte vs. vascular plants (Bayley and Mewhort 2004), possibly indicating a general shift from P limitation to N limitation in vascular plants along the poor fen–rich fen gradient in boreal Canadian systems. However, the data of Bartsch and Moore (1985) for *Carex limosa* and *Scirpus cespitosus* suggest the opposite (Fig. 11.4). Some of the additional variability in rich fens observed in Fig. 11.4 appears to be related to species differences.

11.6.2 Surface Soils

Because they integrate processes of nutrient reabsorption and plant uptake across species, surface-soil N-to-P ratios provide an index of N vs. P limitation at the ecosystem scale, and changes in surface-soil N-to-P ratios have been linked to changes in N vs. P availability (Walbridge 1991; Bedford et al. 1999). Only a few studies have reported data on total N and P concentrations in soils of boreal peatlands (Table 11.2). Because of the potential importance of Fe and Al in influencing P availability in these normally acid soils, we also examined soil Fe and Al concentrations. We focused on surface soils (0–30 or 35 cm), because this is the portion of the peat profile where the majority of plant roots are found and where the majority of plant nutrient uptake occurs. Total N and P data were analyzed using methods identical to those for plant tissues (Koerselman and Meuleman 1996; Bedford et al. 1999); however, unlike the plant nutrient data reported in Figs. 11.1–11.4, soil data represent organic matter and nutrient inputs for the ecosystem as a whole, rather than those of individual species. As such, our analyses of surface soils are more comparable to Koerselman and Meuleman's (1996) analysis of N and P in total aboveground biomass.

Although the data set is limited (nine sites), only a single bog (Malmmyran – an oceanic blanket bog in Norway) has surface peat N-to-P ratios that are suggestive of N limitation (Fig. 11.5). The remaining bogs, as well as the Swedish slope forest, all fall within the range suggesting P limitation. In addition to the blanket bog, the other two N-limited sites are fens in Sweden and Canada, respectively. Note that data for the Swedish fen contrast with the plant tissue analyses, suggesting that Swedish fens are P-limited (Figs. 11.2–11.4). Canadian marshes fall within the range, suggesting co-limitation. These data are also in general contrast with plant tissue analyses. Note in particular the shift in position of Canadian marshes and fens in comparison with Figs. 11.2–11.4. Although soil data for northern Swedish bogs are lacking, bogs in southern Sweden appear more strongly

Table 11.2. N and P concentration in soils of boreal peatlands

Peatland type	Country	Region/ province	% N	% P	N-to-P ratio	% Fe	% Al	Depth (cm)	Peatland name	Study
Ombrotrophic bog	Canada	Manitoba	0.50	0.03	15.72	0.067	0.077	0–10		1
		Ontario	0.53	0.03	15.77	0.050	0.477	0–10		1
Ombrotrophic bog	Sweden	Composite	0.95	0.04	27.20	2.390	3.520	Not given	Various	2
		Central south	0.36	0.02	14.70	0.604	0.025	0–30	Store Mosse	3
		Central south	1.03	0.06	17.46			0–30	Store Mosse	3
		Southern	0.88	0.05	16.77	0.148	0.079	0–30	Tranerods Mosse	3
		Aneboda	1.10	0.03	36.67			0–20		4
Ombrotrophic mire peat	Sweden	Southern				0.062	0.068	0–25	Fjallmossen	5
Ombrotrophic blanket bog	Norway	Central	0.35	0.04	8.65	0.027	0.009	0–30	Malmmyran	3
Marginal fen	Sweden	Aneboda	2.50	0.07	35.71			0–20		4
Fens	Canada	Alberta	1.66	0.34	4.88			0–4	Various	6
Marshes	Canada	Alberta	2.45	0.16	15.22			0–4	Various	6
Slope forest	Sweden	Central south (Smaland)	0.90	0.04	22.69	0.128	0.061	0–30	Store Mosse	3
Moraine	Sweden	Southern				0.145	0.020	0–35	Skoggardsangar	5

Study numbers *1* Pakarinen and Gorham (1984), *2* Malmer (1988), *3* Damman (1978), *4* Richardson et al. (1978), *5* Mornsjo (1968), *6* Bayley and Mewhort (2004).

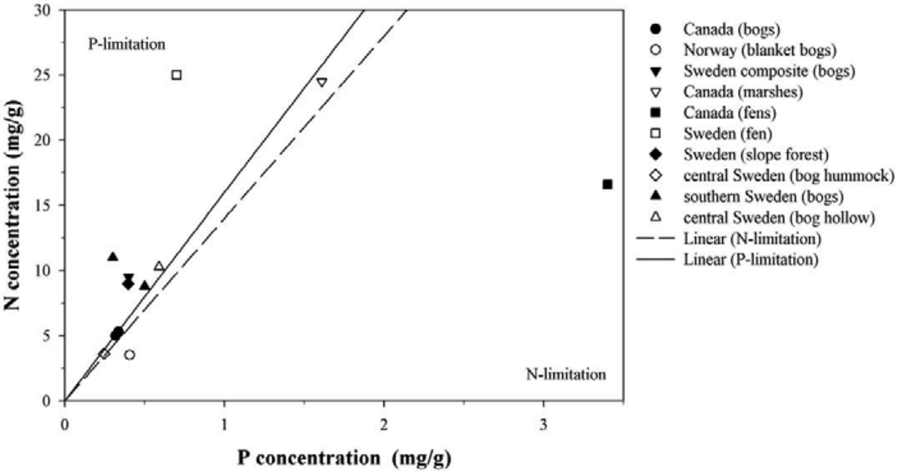

Fig. 11.5. N and P concentrations in boreal surface peats

P limited than those in central Sweden (Fig. 11.5), again agreeing with the findings of Malmer (1988) and Aerts et al. (1992) that atmospheric deposition in southern Sweden has driven ombrotrophic bogs toward P limitation. These data support our hypotheses concerning the fine balance between N vs. P limitation in boreal peatlands and that fens are likely to be more strongly N limited than bogs.

Analysis of Fe and Al concentrations in surface soils has relevance both to understanding processes associated with P availability, as well as providing a potential index of the degree of minerotrophic influence. Although in boreal peatlands the majority of Fe and Al is likely to be organically bound, organically bound Al and Fe have been suggested to play an important role in P cycling in other wetland ecosystems (Darke and Walbridge 2000). The majority of boreal peatlands for which data were available were characterized by low Fe concentrations in surface peats (0.20 %) and variable Al concentrations (0.00–0.23 %) (Fig. 11.6). Canadian fens had the highest Al concentrations, expected given their greater mineral soil influence vs. more ombrotrophic systems. Blanket bogs had the lowest values for both Fe and Al concentrations. Most bogs, and the Swedish slope forest, had Al concentrations in the range 0.05–0.13 %. Higher surface-soil Fe concentrations (0.60–0.13 %) differentiated Store Mosse (in central Sweden) from all other bog soils. Fe concentrations were generally higher in hollows than in hummocks (Fig. 11.6). Overall, as expected, Al and Fe concentrations in bog peats are generally low, suggesting that biological processes predominate in controlling P cycling and availability. Higher Al concentrations suggest increased

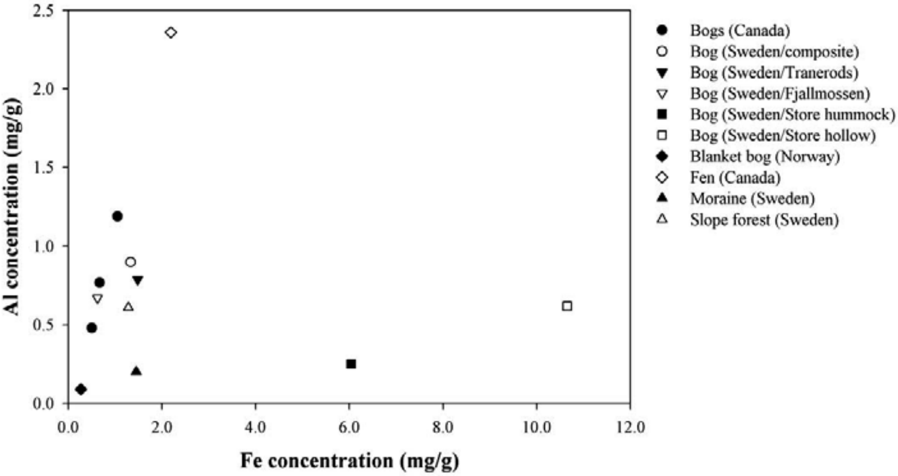

Fig. 11.6. Al and Fe concentrations in boreal surface peats

importance of geochemical processes in Canadian fens, and as evidenced by Store Mosse, some variation can exist among bog sites as well.

11.6.3 Surface Waters

Only four studies reported both total N and P data for boreal peatland surface waters (Table 11.3). The three Finnish studies all reported total N and P; the single Canadian study reported only total dissolved N and P. In general, total dissolved P concentrations clustered around 0.05 mg L^{-1}, while total P concentrations clustered around 0.15 mg L^{-1} (Fig. 11.7). Total dissolved N concentrations ranged from 1 to 3 mg L^{-1}, while with one exception, total N concentrations ranged from 7.5 to 9 mg L^{-1}. The greater importance of particulate N resulted in strikingly higher N-to-P ratios in total vs. total dissolved components. Although scant, these data suggest some intriguing differences in the forms of organic N and P in boreal peatland surface waters. With the exception of a single data point (Canadian marsh), both total and total dissolved N-to-P ratios were higher than the 16:1 metric, suggesting P limitation.

We found only a single study (Blancher and McNicol 1987) that reported data for both Fe and Al concentrations in boreal peatland surface waters (Table 11.3). Both bog and poor fen sites were examined in two areas of central Ontario differing in acid deposition influence – Wanapitei (high deposition) and Ranger (low deposition). Areas differed both in the Fe and Al concentrations observed in surface waters and in the apparent

Table 11.3. N and P concentrations for boreal peatland surface waters

Peatland type	Country	Region/ province	pH	TDN ($\mathrm{mg\ L^{-1}}$)	TDP ($\mathrm{mg\ L^{-1}}$)	TN ($\mathrm{mg\ L^{-1}}$)	TP ($\mathrm{mg\ L^{-1}}$)	N-to-P ratio	Fe ($\mathrm{mg\ L^{-1}}$)	Al ($\mathrm{mg\ L^{-1}}$)	Peatland name	Study
Bog (ombrotrophic)	Canada	Alberta	3.9	1.185	0.059			20.08			Bleak Lake	1
Fen (sedge, lacustrine)	Canada	Alberta	7.0	1.027	0.019			54.05			Perryvale	1
Fen (sedge, floating)	Canada	Alberta	6.2	1.185	0.029			40.86			Perryvale	1
Fen (sedge, riverine)	Canada	Alberta	7.1	1.072	0.039			27.49			Perryvale	1
Marsh (lacustrine)	Canada	Alberta	7.4	2.649	0.207			12.80			Clyde	1
Marsh (riverine)	Canada	Alberta	7.4	1.62	0.059			27.46			Perryvale	1
Bog (ombrotrophic)	Finland	South				2.25	0.08	28.13				2
Mire (ombrotrophic)	Finland		3.8			8.17	0.127	64.33				3
Mire (ombrotrophic)	Finland		3.8			8.17	0.127	64.33				4
Mire (minerotrophic)	Finland		4.3			8.24	0.147	56.05				3
			4.3			8.24	0.147	56.05				4
Hollow (moss)	Finland		3.7			7.78	0.128	60.78			Multiple sites	4
Hollow (*Sphagnum*)	Finland		3.7			7.78	0.128	60.78			Multiple sites	3
Hollow (mud bottom)	Finland		3.7			7.66	0.149	51.41			Multiple sites	3
Hollow (mud bottom)	Finland		3.7			7.66	0.149	51.41			Multiple sites	4
Pool	Finland		4.0			8.72	0.122	71.48			Multiple sites	4
Pool (water)	Finland		4.0			8.72	0.122	71.48			Multiple sites	3
Bog (ombrotrophic)	Canada	Ontario	4.5						0.097	0.0493	Ranger Lake, Sault Ste. Marie	5
			4.2						0.215	0.191	Lake Wanapitei, Sudbury	5
			4.4						0.11	0.127	Ranger Lake, Sault Ste. Marie	5
			4.0						0.48	0.111	Lake Wanapitei, Sudbury	5
Fen (poor)	Canada	Ontario	5.7						0.0945	0.114	Ranger Lake, Sault Ste. Marie	5
			5.4						0.235	0.129	Lake Wanapitei, Sudbury	5
			4.7						0.119	0.0615	Ranger Lake, Sault Ste. Marie	5
			4.5						0.69	0.0825	Lake Wanapitei, Sudbury	5

Study numbers *1* Thormann and Bayley (1997), *2* Pakarinen (1978a, b), *3* Tolonen (1974), *4* Tolonen and Hosiaisluoma (1978), *5* Blancher and McNicol (1987), *TDN* total dissolved N, *TDP* total dissolved P, *TN* total N, *TP* total P

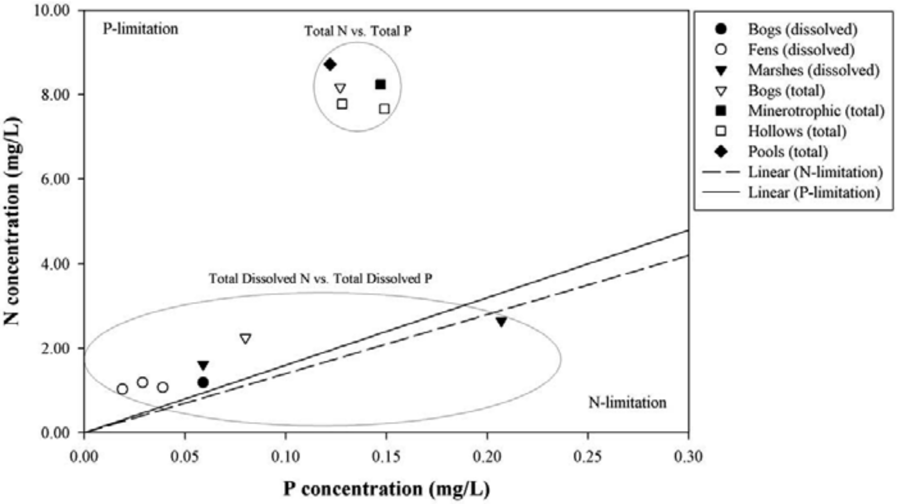

Fig. 11.7. N and P concentrations in surface waters

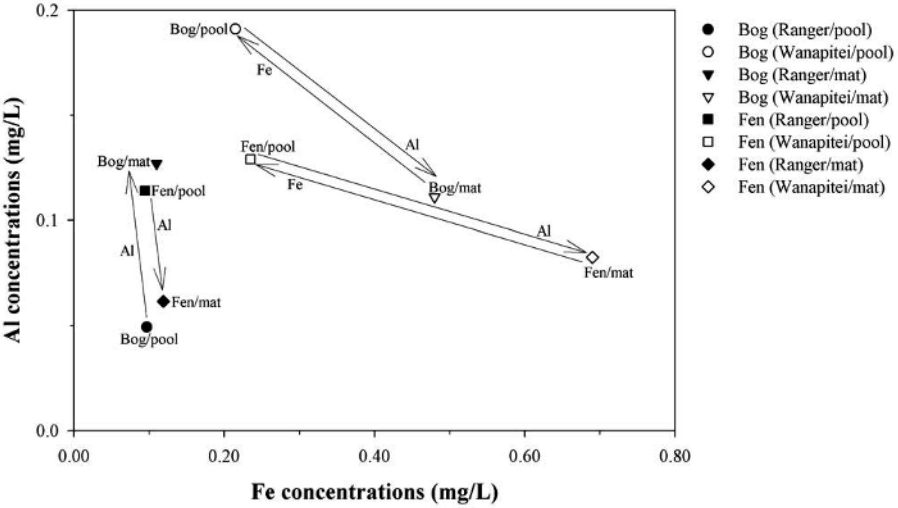

Fig. 11.8. Fe and Al concentrations in surface waters

concentration gradients between pool and mat microsites. Fe concentrations were generally low at the Ranger site (0.1 mg L^{-1}), while Al concentrations differed threefold (from 0.05 to 0.15 mg L^{-1}) (Fig. 11.8). On the basis of concentration differences, mats appear to act as a source of Al to pool environments in nonimpacted bogs, while the reverse is true in poor fens, possibly reflecting the importance of groundwater mineral influence. The high-deposition Wanapitei site exhibited higher concentrations of both Fe (0.25–0.70 mg L^{-1}) and Al (0.13–0.20 mg L^{-1}) than the Ranger site, and in both bog and poor fen environments the concentrations suggested that pool environments were a source of both elements to mat environments. This could be due to direct inputs of particulate Fe and Al (i.e., aerosols) associated with atmospheric deposition, or increased mobilization of these metals from peat owing to the more acidic environment created by the increased deposition. In association with the enhanced N inputs associated with acidic deposition, changes in Fe and Al dynamics in surface waters have the potential to further exacerbate P availability through complexation of dissolved phosphate.

11.7 Suggestions for Future Research

Our examination of the available literature on P concentrations and availability in boreal peatlands leads us to propose three specific areas for future research: (1) detailed examination of the P chemistry of boreal peatland soils; (2) tracer studies to elucidate important pools and pathways of P cycling in these ecosystems; and (3) detailed examination of spatial and temporal variation in N–P balance.

Currently, no data exist that characterize soil P fractions in boreal peatlands, using any of the commonly used fractionation techniques (Hedley et al. 1982; Paludan and Jensen 1995). Similarly, although data do exist for percentages of soil minerals important in controlling P dynamics in boreal peatlands (e.g., Al, Fe), there has been no attempt to quantify organically bound, amorphous, or crystalline fractions of these minerals by either selective dissolution (Darke and Walbridge 2000) or more sophisticated techniques. Adding data of this nature to the boreal peatland literature would greatly enhance our understanding of P cycling in boreal peatlands, and allow comparison with other types of ecosystems for which data are available.

Specific knowledge of P cycling pathways can only be gained through the use of isotopic tracers. For P, two options are available: ^{32}P or ^{33}P. As both are radioisotopes, their use in field studies may be severely limited. Isotope tracer studies have been successfully conducted in other systems (Richardson and Marshall 1986; Walbridge 1991; Kellogg and Bridgham 2003; Olander and Vitousek 2004) and are long overdue for boreal peatlands. It is possible that at some time in the future, techniques may be developed that allow the tracking of P movements using an ^{18}O tag on one or more of the phosphate oxygens; however, the methodological problems associated with this approach are such that these methods are unlikely to be available in the near future.

Our analysis of the current literature suggests potentially important spatial and temporal variation in N vs. P availability that could determine whether N or P limits NPP in boreal peatlands. Significant insights could be gained by a rigorous examination of these variations through well-designed studies using common methods and procedures. Specific lines of investigation could include latitudinal variations in each of the three northern hemisphere continents where peatlands occur (North America, Europe, and Asia). Changes in N-to-P stoichiometry with both peat depth and peat age should also be examined to elucidate how N vs. P availability changes over the course of peatland development. Such knowledge could then be integrated with information on the specific history of development for each site.

11.8 Conclusions

1. Boreal peatlands are an important global C sink. This C is potentially labile under future global warming scenarios. Nutrient (N and P) availability could influence rates of both C fixation and C oxidation under future warming scenarios.
2. N and P availabilities are closely balanced in boreal peatlands, and N and P are likely to be tightly conserved in these ecosystems.
3. Both N and P can limit NPP in boreal peatlands. Either N or P can be limiting, depending of developmental history and current anthropogenic influence.
4. Little is known about P cycling in boreal peatlands. Three specific areas of research are proposed that would greatly improve our understanding in this area.

References

Aerts R, Wallen B, Malmer N (1992) Growth-limiting nutrients *in Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. J Ecol 80:131–400

Aerts R, Wallen B, Malmer N, De Caluwe H (2001) Nutritional constraints on *Sphagnum* and potential decay in northern peatlands. J Ecol 89:292–299

Bartsch I, Moore TR (1985) A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. Can J Bot 63:1241–1248

Bayley SE, Mewhort RL (2004) Plant community structure and functional differences between marshes and fens in the southern boreal region of Alberta, Canada. Wetlands 24:277–294

Bayley SE, Vitt DH, Newbury RW, Beaty KG, Behr R, Millar C (1987) Experimental acidification of a *Sphagnum*-dominated peatland: first year results. Can J Fish Aquat Sci 44:192–204

Bedford BL, Walbridge MR, Aldous A (1999) Patterns of nutrient availability and plant diversity of temperate North American wetlands. Ecology 80:2151–2169

Blancher PJ, McNicol DK (1987) Peatland water chemistry in central Ontario in relations to acid deposition. Water Air Soil Pollut 35:217–232

Brinson MM, Lugo AE, Brown S (1981) Primary productivity, decomposition, and consumer activity in freshwater wetlands. Annu Rev Ecol Syst 12:123–161

Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO (1999) Changing sources of nutrients during four million years of ecosystem development. Nature 397:491–497

Chapin FS, Barsdate RJ, Barèl D (1978) Phosphorus cycling in Alaskan coastal tundra: a hypothesis for the regulation of nutrient cycling. Oikos 31:189–199

Clymo RS (1965) Experiments on the breakdown of *Sphagnum* in two bogs. J Ecol 53:747–758

Damman AWH (1978) Distribution and movement of elements in ombrotrophic peat bogs. Oikos 30:480–495

Damman AWH (1988) Regulation of nitrogen removal and retention in *Sphagnum* and other peatlands. Oikos 51:291–305

Damman AWH (1990) Nutrient status of ombrotrophic peat bogs. Aquilo Ser Bot 28:5–14

Darke AK, Walbridge MR (2000) Al and Fe biogeochemistry in a floodplain forest: implications for P retention. Biogeochemistry 51:1–32

Du Rietz GE (1954) Die Mineralbodenwasserzeigergrenze als Grundlage einer natürlichen Zweigliederung der nord- und mitteleuropäischen Moore. Vegetatio 8:571–585

Farrish KW, Grigal DF (1988) Decomposition in an ombrotrophic bog and a minerotrophic fen in Minnesota. Soil Sci 145:353–358

Hedley MJ, Stewart JWB, Chauhan BS (1982) Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. Soil Sci Soc Am J 46:970–976

Holmen H (1964) Forest ecological studies on drained peat land in the province of Uppland, Sweden. Parts I–III. Stud Forest Suec 16:1–236

Jonasson S, Shaver GR (1999) Within-stand nutrient cycling in arctic and boreal wetlands. Ecology 80:2139–2150

Kellogg LE, Bridgham SD (2003) Phosphorous retention and movement compared across an ombrotrophic-minerotrophic gradient in Michigan. Biogeochemistry 63:299–315

Koerselman W Meuleman ARM (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. J Appl Ecol 33:1441–1450

Lindemann RI. (1942) The trophic-dynamic aspect of ecology. Ecology 23:399–418

Lindsay WL, Vlek PLG, Chien SH (1989) Phosphate minerals. In: Dixon JB, Weed SB (eds) Minerals in soil environments, 2nd edn., Soil Science Society of America, Madison, pp 1089–1130

Malmer N (1962) Studies on mire vegetation in the Archaean area of southwestern Gotaland. I. Vegetation and habitat conditions on the Åkhult mire. Opera Bot 7:1–322

Malmer N (1963) Studies on mire vegetation in the Archaean area of southwestern Gotaland. III. On the relation between specific conductivity and concentrations of ions in the mire water. Bot Not 116:249–256

Malmer N (1988) Patterns in the growth and the accumulation of inorganic constituents in the Sphagnum cover on ombrotrophic bogs in Scandinavia. Oikos 53:105–120

Malmer N (1990) Constant or increasing nitrogen concentrations in *Sphagnum* mosses in mires in Southern Sweden during the last few decades. Aquilo Ser Bot 28:57–65

Malmer N, Nihlgard B (1980) Supply and transport of mineral nutrients in a subarctic mire. Ecol Bull 30:63–95

Malmer N, Sjörs H (1955) Some determinations of elementary constituents in mire plants and peats. Bot Not 108:46–80

Malmer N, Horton DG, Vitt DH (1992) Elemental concentrations in mosses and surface waters of western Canadian mires relative to precipitation chemistry and hydrology. Ecography 15:114–128

Malmer N, Albinsson C, Svensson B, Wallén B (2003) Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. Oikos 100:469–482

Maltby E (1988) Use of cotton strip assay in wetland and upland environments – an international perspective. In: Harrison AF, Latter PM, Walton DWH (eds) Cotton strip assay: an index of decomposition in soils. Institute of Terrestrial Ecology. Grange-over-Sands, pp 140–156

Meybeck M (1982) Carbon, nitrogen, and phosphorus transport by world rivers. Am J Sci 282:401–450

Meybeck M (1993) C, N, P, and S in rivers: from sources to global inputs. In: Wollast R, Mackenzie FT, Chou L (eds) Interactions of C, N, P, and S on biogeochemical cycles and global change. Springer, Berlin Heidelberg New York, pp 163–193

Mitsch WJ, Gosselink JG (2000) Wetlands. 3rd edn. Wiley, New York

Moore PD, Bellamy DJ (1974) Peatlands. Elek, London

Mornsjo T (1968) Stratigraphical and chemical studies on two peatlands in Scania, South Sweden. Bot Not 121:343–360

Olander L, Vitousek PM (2004) Biological and geochemical sinks in soil from a wet tropical forest. Ecosystems 7:404–419

Pakarinen P (1978a) Production and nutrient ecology of three *Sphagnum* species in southern Finnish raised bogs. Ann Bot Fenn 15:15–26

Pakarinen P (1978b) Distribution of heavy metals in the *Sphagnum* layer of bog hummock and hollows. Ann Bot Fenn 15:287–293

Pakarinen P, Gorham E (1984) Mineral element composition of *Sphagnum fuscum* peats collected from Minnesota, Mannitoba and Ontario. In: Spigarelli S (ed). Proceedings of the international peat symposium, October 1983. Bemidji State University, Bemidji, pp 471–479

Pakarinen P, Tolonen K (1977) Nutrient contents of *Sphagnum* mosses in relation to bog water chemistry in northern Finland. Lindbergia 4:27–33

Paludan C, Jensen HS (1995) Sequential extraction of phosphorus in freshwater wetland and lake sediments. Significance of humic acids. Wetlands 15:365–373

Richardson CJ, Marshall PE (1986) Processes controlling the movement, storage, and export of phosphorus in a fen, peatland. Ecol Monogr 56:279–302

Richardson CJ, Tilton DL, Kadlec JA, Chamie JPM, Wentz WA (1978) Nutrient dynamics of northern wetland ecosystems. In: Good RE, Whigham DF, Simpson RL, (eds) Freshwater wetlands: ecological processes and management potential. Academic, New York, pp 217–241

Rosswall T, Granhall U (1980) Nitrogen cycling in a subarctic ombrotrophic mire. Ecol Bull 30:209–234

Schlesinger WH (1997) Biogeochemistry: an analysis of global change. 2nd edn. Academic, New York

Sjörs H (1950) On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2:241–258

Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. Studies in ecology 5. Blackwell, Oxford

Tamm C O (1954) Some observations on the nutrient turn-over in a bog community dominated by *Eriophorum vaginatum*. Oikos 5:189–194

Thormann MN, Bayley SE (1997) Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. Plant Ecol 131:1–16

Tolonen K (1974) On the nutrient content of surface water in ombrotrophic mire complexes in Finland. Suo 25(3–4):41–51

Tolonen K, Hosiaisluoma V (1978) Chemical properties of surface water in Finnish ombrotrophic mire complexes with special reference to algal growth. Ann Bot Fenn 15:55–72

Verhoeven JTA, Kooijman AM, van Wirdum G (1988) Mineralisation of N and P along a trophic gradient in a fresh water mire. Biogeochemistry 6:31–43

Verhoeven JTA, Maltby E Schmitz MB (1990) Nitrogen and phosphorus mineralization in fens and bogs. J Ecol 78:713–726

Vitousek PM, White PS (1981) Process studies in succession. In: West DC, Shugart HH, Botkin DB (eds) Forest succession, concepts and application. Springer, Berlin Heidelberg New York, pp 267–276

Vitousek PM, Ladefoged TN, Kirch PV, Hartshorn AS, Graves MW, Hotchkiss SC, Tuljapurkar S, Chadwick OA (2004) Soils, agriculture, and society in precontact Hawaii. Science 304:1665–1669

Walbridge MR (1991) Phosphorus availability in acid organic soils of the lower North Carolina coastal plain. Ecology 72:2083–2100

Walker TW Syers JK (1976) The fate of phosphorus during pedogenesis. Geoderma 15:1–19

Wardle DA, Walker LA, Bardgett RD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305:509–513

12 Sulfur Cycling in Boreal Peatlands: from Acid Rain to Global Climate Change

MELANIE A. VILE and MARTIN NOVÁK

12.1 Introduction

Beginning in prehistoric times, sulfur (S) was touted as the quintessential substance from use as a medicine by pagan priests 2,000 years before the birth of Christ, to use as an insecticide and sick room purifier by the Romans in 1,000 BC. The discovery of sulfuric acid in the 1700s however, is, when S received its greatest impetus as a valuable mineral resource (Davis and Detro 1992). So valuable is this resource that presently approximately 90 % of current S production in the USA is converted to its acid form, and its manufacturing demand is used as an accurate indicator of the country's business activity (Davis and Detro 1992). Only during the twentieth century, however, that the more deleterious environmental impacts of capitalizing on the many exploits of S considered.

During the pinnacle of the acid rain phenomenon, S pollution occupied a notorious spotlight for its negative impacts on many aspects of ecosystem function (Likens et al. 2002). In North America and Europe, total anthropogenic S deposition increased tenfold between the Industrial Revolution and the late 1960s, peaked in the 1970s and 1980s, and gradually decreased throughout the 1990s, owing to implementation of pollution control devices and important legislation (Brimblecombe et al. 1989). Concomitant with reauthorization of the Clean Air Act in 1990, potential funding sources for acid rain research, at least in the USA, paralleled trends of decreasing S deposition, and the issue of acid rain faded from public consciousness (Abate 1995). Yet, as evidenced by the Seventh International Conference on Acid Deposition, Acid Reign 2005, many questions remain. Despite large SO_2 emission reductions in many parts of the industrialized world, atmospheric S deposition continues to result in acidification of soils, lakes, and streams. Moreover, coal and oil combustion continue to be the major sources of S pollution in large regions of North

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America, Europe, and now in many developing countries in Asia (Bhatti et al. 1992; Badr and Probert 1994; Venkataraman et al. 1999). Between 1980 and 1995, SO_2 emissions decreased by 47 and 31 % in Europe and the USA, respectively, and during this same time period, S deposition more than doubled in Asia (O'Meara 1998). As a result, many regions of the globe will only begin dealing with S-induced acidification, while other regions will continue the battle of acidification reversal well into the twenty-first century.

Over the past 20 years, research driven by S-induced acidification has led to an increased understanding of the biogeochemical cycling of S in terrestrial and aquatic ecosystems and at the interface of the two wetland ecosystems, of which peatlands are one, a dominant type. In this latter category, in particular, there has been considerable interest in understanding the S cycle because high quantities of carbon (C) stored in peatland soils, coupled with aerobic and anaerobic microsites within distinct redox zones (i.e., the acrotelm and catotelm), create conditions whereby S can cycle dynamically, potentially having profound implications for ecosystem function. Among various peatland types (Chap. 2), ombrotrophic bogs are particularly sensitive to acid deposition owing to their already low pH (typically less than 4), and low base cation concentrations (Vitt et al. 1995). Peatlands generally contain large C stores, making them ideal study systems for examining C–S interactions. Peatlands also may act as a storage facility for atmospherically deposited S (Novák and Wieder 1992; Novák et al. 1994). Because peatlands can act as a source, a sink, and as a transformer of C, S, and other pollutants, such as mercury (Hg), they figure prominently in understanding the dynamic cycling of elements/compounds in organic-rich soils with a wide range of redox conditions. A small number of studies, however, have examined the role of S in these unique ecosystems, and even fewer of these studies have focused on boreal regions of the world.

Despite uncertainties in recent estimates of global wetland area, most studies agree that more than half of the earth's wetlands lie between 50 and 70° N latitude, with peatlands comprising 50–95 % of this total, mainly located in the boreal zone (Bridgham et al. 2001; Chap. 1). Boreal peatlands have a circumpolar range primarily spanning Russia, Canada, Alaska, and Fennosscandia, although extensions, or relics, of the boreal forest are known to occur at lower latitudes on high-elevation, mountain ridges in New Jersey, Pennsylvania, West Virginia, and in the southern Appalachians, as well as at sea level in both Maine and Canada in North America (Cameron 1968; McDonald 1982; Gore 1983; Joosten and Clarke 2002).

In Europe, boreal forests historically have been found in Scotland, however, long periods of forest removal for agricultural purposes have resulted in the almost complete disappearance of the boreal forest, and as a result, Scotland is rarely mentioned in current inventories, although significant advances have been made with regard to understanding S and climate interactions in Scottish peats (Gauci et al. 2002), and we will reference these studies later in the chapter. In densely populated central Europe, industrial and agricultural activities have resulted in even fewer relics of the former boreal forest. However, peatlands can be found interspersed within complex mountain systems of spruce forest and mixed broadleaf coniferous plantations throughout central Europe. At the opposite extreme in Russia, expansive, intact boreal forests exist, but only recently have they become subject to study. While our goal is to discuss research in boreal peatlands, we reference studies in the more abundant, former boreal, now subboreal regions throughout the chapter. The paucity of S cycling data from boreal regions is the result of many factors, including, but not limited to, climate, remoteness/accessibility, and a narrow window of opportunity for research owing to short growing seasons. The former Soviet Union had the added political complication of being bound by the Iron Curtain, which made it difficult to estimate peat inventories, and provided little opportunity for international collaborative research. Presently, we are making great strides in filling the gaps of our knowledge of these little studied ecosystems, at a time when ongoing industrialization of developing countries is certain to expand the range of S deposition throughout once pristine boreal regions (Gauci et al. 2004).

As industrialization progresses, coal extraction and combustion will continue to be a major energy source, and as such, vast quantities of C, S, and Hg, will be released into the environment. It is therefore not surprising that coal is linked to the cycles of S, C, and Hg. As with the present-day C cycle, the present-day S and Hg cycles are not in steady state (Schlesinger 1997). Anthropogenic activities are the primary culprit for disequilibrium in all three cycles; however, unlike C and Hg, global pools of S show little change. Rather, owing to the dynamic cycling of S, movement from the more stable, reduced pools to more mobile, oxidized pools alters the proportion of S that is permanently buried, with net movement toward S mobility (Schlesinger 1997), thus compromising storage of reduced S in various ecosystem components, such as in peatlands. The dynamic nature of S cycling can have profound implications for many aspects of ecosystem functioning, and in this chapter, we highlight the role that atmospheric S deposition plays in global climate change dynamics, the fate of current S stores, methylation of Hg, and production of dimethyl sulfide (DMS).

12.2 Sulfur Cycle: Peatlands Function as a Source, Sink, and Transformer of Sulfur

Although S cycling processes have been reviewed extensively in forest soils (Fitzgerald et al. 1984), in salt marshes (Howarth and Teal 1979), and in freshwater wetland ecosystems (Mitsch and Gosselink 2000), the intricacies of dynamic S-cycling processes in peatland ecosystems have not been synthesized (except see Mandernack et al. 2000). Because peatlands have a permanently saturated anaerobic zone (the catotelm), coupled to an overlying layer of aerobic peat (the acrotelm), where water tables fluctuate, redox conditions allow for the persistence of both anaerobic and aerobic zones plus microsites, which contribute to dynamic S cycling (Fig. 12.1).

S occurs in several different redox states (S valences ranging from +6 in SO_4^{2-} to −2 in H_2S, S-containing amino acids, and other compounds) in peatlands, and conversions between these states are the direct result of microbially mediated transformations. In ombrotrophic peatlands, the sole S input is via atmospheric deposition, while in minerotrophic peatlands, atmospheric deposition can be augmented by surface water and/or groundwater inputs, which may contain S derived from weathering of minerals in rock and soil. Regardless of the S source, when S enters a peatland, there are a variety of pathways through which it can cycle (Fig. 12.1). In the aerobic zone, sulfate (SO_4^{2-}) can be adsorbed onto soil particles, or assimilated by both plants and microbes. In the anaerobic zone, sulfate also can be adsorbed onto soil particles, assimilated by plants or microbes, or reduced by sulfate-reducing bacteria through the process of dissimilatory sulfate reduction (Fig. 12.1). Dissimilatory sulfate reduction is a chemoheterotrophic process whereby bacteria in at least 19 different genera oxidize organic matter to meet their energy requirements using sulfate as the terminal electron acceptor (Fauque 1995; King et al. 2000). If sulfate is reduced by sulfate-reducing bacteria, the end product (S^{2-}) can have several different fates. In the anaerobic zone, where S^{2-} is formed, it can react with hydrogen to produce hydrogen sulfide (H_2S) gas, which can diffuse upwardly into or through the acrotelm, where it can be either oxidized to sulfate or lost to the atmosphere (Fig. 12.1). Alternatively, H_2S can react by nucleophilic attack with organic matter to form organic or C-bonded S (CBS; Casagrande 1979). If iron (Fe) is present, S^{2-} can react with Fe to form FeS and FeS_2 (pyrite), which is referred to as reduced inorganic S (RIS) (Wieder and Lang 1988). The RIS pool tends to be unstable in peat and can be reoxidized aerobically with oxygen if the water table falls, or anaerobically, probably using Fe^{3+}as an anaerobic electron acceptor (Wieder and Lang 1988; Vile and Wieder 1994; Fig. 12.1). If Hg is present and combines with S^{2-} to form neutrally charged HgS, then HgS is capable of passive diffusion across cell membranes of bacteria that methylate Hg (Galloway and Branfireun 2004; Fig. 12.1). Alternatively, bacteria can transfer the methoxy groups of naturally occurring compounds, such as syringic acid, to S^{2-}, and form methyl sulfide (MeSH) or DMS, although the exact mechanisms by which this occurs still are unknown (Kiene and Hines 1995; Lomans et al. 1997, 1999; Fig. 12.1).

Sulfate-reducing bacteria exist within complex associations with other microbial populations. They must compete in a predictable manner for electron donors (e.g., organic C) and electron acceptors (e.g., oxygen, nitrate, sulfate), following an energy-driven sequence of reactions, sometimes referred to as the thermodynamic ladder (Hedin et al. 1998; Fig. 12.1). Under anaerobic conditions, individual organic compounds can be oxidized by bacteria to obtain the greatest amount of energy using nitrate (NO_3^-), with successively lower energy yields moving down the ladder toward manganese (Mn^{4+}), ferric Fe (Fe^{3+}), and sulfate; the lowest energy yield results when organic substrates and CO_2 are used as electron acceptors in fermentation reactions (Conrad 1989). From a thermodynamic standpoint, these reactions are well characterized and well understood, and in theory form a basis for predicting how specific nutrient transformation and gaseous losses should vary within and between ecosystems. In practice, however, the considerable spatial and temporal heterogeneity in the physical and chemical properties of peat, along with nonlinearities across different spatial scales, compromise our predictive capabilities in determining the outcome of these competitive interactions. Thermodynamic theory is best applied in homogenized, controlled, or relatively stable environments, and is less applicable in peatland matrices where biogeochemical processes rarely occur under steady-state conditions (Hedin et al. 1998; Blodau and Moore 2003). While thermodynamic theory as well as many empirical studies in nonpeatland systems have suggested that methanogens should be inhibited or outcompeted in the presence of more energetically favorable electron acceptors, such as sulfate (Lovely and Klug 1983), a large number of studies have demonstrated suppression, but usually not complete inhibition, of methanogenesis in the presence of sulfate reducers (Wieder et al. 1990; Nedwell and Watson 1995; Dise and Verry 2001; Gauci et al. 2002; 2004; Vile et al. 2003a, b). We now know that spatial separation of aerobic and anaerobic microsites within peat matrices allows for the persistence of both bacterial groups in close physical proximity. As a result, drawing a strict analogy between the highly variable, intricately linked, microbial interactions in peatlands with spatially and temporally distinct rungs of a thermodynamic ladder falsely simplifies the complexity of C and S cycling in peatland ecosystems. Thermodynamic theory provides a framework, but should be interpreted in light of the real-world complexity of the system.

12.3 The Role of Sulfur in the Carbon Balance of Peatlands

12.3.1 Sulfate Reduction in Peatlands

Peatland ecosystems cover only 3 % of the earth's land surface, yet store approximately 33 % of the global soil C pool (Aselmann and Crutzen 1989; Gorham 1991). Currently, boreal peatlands are widely believed to function as a net sink for atmospheric C (Chap. 8), sequestering an estimated 0.076 Pg of C annually from the atmosphere (Aselmann and Crutzen 1989; Fung et al. 1991; Gorham 1991; Bartlett and Harriss 1993). In contrast, peatlands also function as a net source of atmospheric C in the form of methane (CH_4), annually releasing an estimated 47 Tg to the atmosphere, which is approximately 10 % of the global total (Aselmann and Crutzen 1989; Bartlett and Harriss 1993; Bridgham et al. 1995). Under projected global climate change, elevated temperature is expected to increase rates of microbial processes (Jenkinson et al. 1991; Kirschbaum 1995), potentially resulting in mineralization of sequestered C back to the atmosphere as both CO_2 and CH_4, two of the most important anthropogenic greenhouse gases. The response and magnitude of peatland gaseous C fluxes to both changing climate and to atmospheric S deposition remain uncertain, despite recent advances on both issues (Gauci et al. 2004).

Wieder (Wieder and Lang 1988; Wieder et al. 1990) pioneered initial work investigating the role of atmospheric S deposition on S and C cycling in freshwater peatlands in West Virginia in the late 1980s. Further studies were carried out in the Pine Barrens of New Jersey (Spratt et al. 1987), Michigan (Shannon and White 1996), Minnesota (Dise and Verry 2001), Canada and the Czech Republic (Vile et al. 2003a, b), and the UK (Nedwell and Watson 1995; Watson and Nedwell 1998; Granberg et al. 2001; Gauci et al. 2002, 2004). Prior to the work of Wieder, most wetland-related research on S cycling occurred in salt marsh habitats, where high dissolved SO_4^{2-} concentrations (45 mM) do not limitsulfate reducers (Howarth and Teal 1979; Giblin and Wieder 1992). The importance of dissimilatory sulfate reduction to anaerobic C mineralization, C balance, and energy flow has been demonstrated widely and repeatedly in marine systems (Howarth and Teal 1979, 1980; Howarth and Jorgenson 1984). In freshwater wetlands, however, dissolved SO_4^{2-} concentrations are typically less than 15 μM. Previously it was thought that low SO_4^{2-} concentrations would limit rates of sulfate reduction, diminishing its importance as a terminal C mineralization pathway in freshwater environments. When rates of dissimilatory sulfate reduction were measured in freshwater peat, contrary to what was expected, Wieder et al. (1990) found that sulfate reduction played a substantial role in anaerobic C mineralization. Despite the small SO_4^{2-} pool size, rates of sulfate reduction in freshwater peat overlapped with the lower end of rates typically reported for salt marshes (Spratt et al. 1987; Wieder and Lang 1988; Wieder et al. 1990). The overlap was attributed to RIS comprising a substantial proportion of the end product of sulfate reduction, and to the rapid turnover of S between reduced and oxidized inorganic forms (Wieder and Lang 1988; Nedwell and Watson 1995; Fig. 12.1).

High rates of atmospheric S deposition throughout large regions of the northeastern USA and Europe, coupled with the unexpected importance of sulfate reduction in freshwater peatlands, led Wieder et al. (1990) to suggest a new hypothesis: peatlands receiving low inputs of atmospheric SO_4^{2-} should exhibit a predominance of methanogenesis over sulfate reduction if all other electron acceptors are in low supply. However, if such peatlands become subjected to high rates of S deposition, sulfate reduction could be enhanced as an anaerobic C mineralization pathway, compromising the dominant role of methanogenesis.

Stoichiometrically, every mole of biologically reduced SO_4^{2-} produces two moles of CO_2, which represents greater gaseous C production than oxidation of organic matter with other electron acceptors (NO_3^- Mn^{4+}, Fe^{3+}, CO_2) (Conrad 1989; Fig. 12.1). As a result, a shift in the importance of

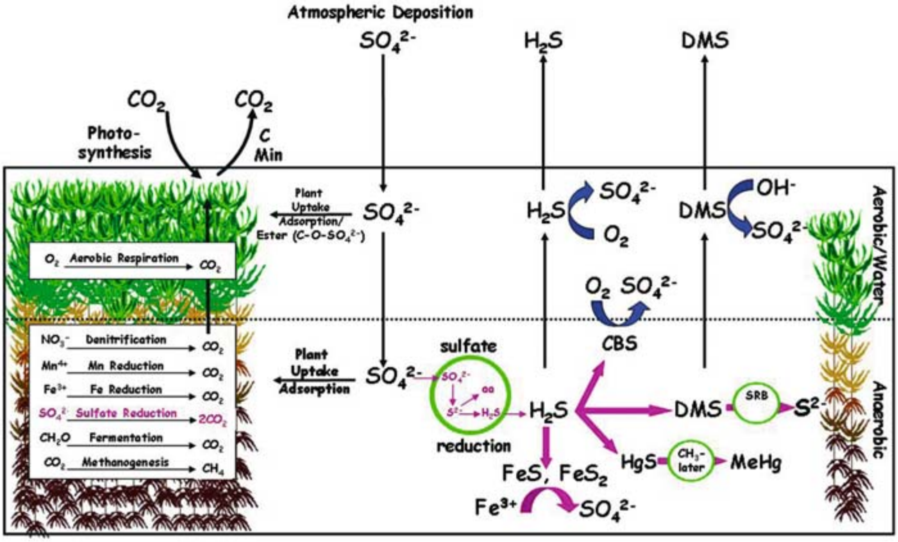

Fig. 12.1. Sulfur cycling in peatlands. The *dotted line* signifies a fluctuating water table, which separates the aerobic zone from the anaerobic zone. Aerobic oxidations are represented by *blue curved arrows*, and anaerobic oxidations are represented by *purple curved arrows*. *Green circles* represent sulfate-reducing bacteria. Thermodynamic carbon mineralization pathways are shown with stoichiometric carbon yields per mole of reduced electron acceptor. *aa* amino acid incorporation during assimilatory sulfate reduction, *DMS* dimethyl sulfide

sulfate reduction as a C mineralization process potentially could lead to greater overall anaerobic C mineralization, a net loss of C from the ecosystem, and large net fluxes of CO_2 to the atmosphere (Wieder et al. 1990; Vile et al. 2003 a, b). Alternatively, greater sulfate reduction may inhibit (Fauque 1995; Watson and Nedwell 1998; Dise and Verry 2001), outcompete (Lovely and Klug 1983), or have no effect (Granberg et al. 2001; Blodau and Moore 2003; Vile et al. 2003a) on methanogenesis. Thus, there is the potential for both positive and negative feedbacks between SO_4^{2-} inputs and climate change in terms of greenhouse gas emissions from peatlands. Only a few recent studies have measured rates of sulfate reduction in freshwater peat, and even fewer have been conducted in boreal sites or where S deposition is substantially different from that in previous studies (i.e., either substantially higher or lower than moderate deposition rates in northeastern North America).

12.3.2 Effect of Atmospheric Sulfur Deposition on Peatland CO_2 Production

By applying the thermodynamic ladder to C metabolism in pristine ombrotrophic bogs where all nutrient input is via atmospheric precipitation and where input of SO_4^{2-} from acid deposition is minimal, methanogenesis should dominate anaerobic C mineralization, using CO_2 or acetate as an electron acceptor (Nedwell 1984; Conrad 1989; Fauque 1995). Under these same conditions, NO_3^-, Mn^{4+}, and Fe^{3+} generally would not contribute substantially to anaerobic C mineralization. The formation of NO_3^- is inhibited by both anaerobic and acidic conditions (Lang et al. 1993), whereas oxidized Mn and Fe are usually present in low concentrations owing to minimal atmospheric inputs (Wieder and Lang 1986). For CO_2, however, plant and microbial respiration serve as abundant sources such that CO_2 is unlikely to be limiting under anaerobic conditions. In ombrotrophic peatlands, new inputs of SO_4^{2-} are supplied exclusively by atmospheric deposition, and thus it seems reasonable to expect a relationship between sulfate reduction rates and atmospheric S deposition.

We tested the hypothesis put forth by Wieder et al. (1990) in a boreal, ombrotrophic peatland in central Alberta, Canada (Vile et al. 2003a, b) where rates of S deposition (less than 0.5 kg S ha^{-1} $year^{-1}$) are near recorded lows for the northern hemisphere. Given this low atmospheric S deposition and our expectation that methanogenesis would dominate C mineralization, we further hypothesized that with S amendments, we could increase the importance of sulfate reduction over methanogenesis.

We amended field plots at Bleak Lake Bog, Alberta, Canada with SO_4^{2-} (application equivalent to an atmospheric deposition of approximately

25 kg S ha^{-1} $year^{-1}$ in multiple doses over the growing season), and retrieved peat cores to measure rates of sulfate reduction, CH_4 production, and CO_2 production under anaerobic conditions in the laboratory. In opposition to our hypotheses, sulfate amendments did not increase rates of CO_2 production (Vile et al. 2003a; Fig. 12.2). Further, despite significant increases in the dissolved SO_4^{2-} pool, dissimilatory sulfate reduction contributed less than 2 % to total anaerobic C mineralization (Fig. 12.3). This finding was in stark contrast to that of Wieder et al. (1990), where between 38 and 64 % of total anaerobic C mineralization in two *Sphagnum*-dominated Appalachian peatlands (annual S deposition of 18 kg ha^{-1} $year^{-1}$) was attributed to sulfate reduction. Why is this? The answer could be due to the nature of the peat and hence the organic C compounds available to support anaerobic microbial metabolism (different *Sphagnum* species in Appalachian versus boreal peat bogs), differences in mean annual temperature between the sites of 1 °C, and/or possibly to different microbial communities. Our Alberta system was an ombrotrophic boreal bog, which is different hydrologically and chemically from the Appalachian peatlands studied by Wieder et al. (1990), both of which are minerotrophic fens. Finally, it is possible that 2 years of S amendments where more than 25–30 kg S ha^{-1} $year^{-1}$ was added to plots over background rates of less

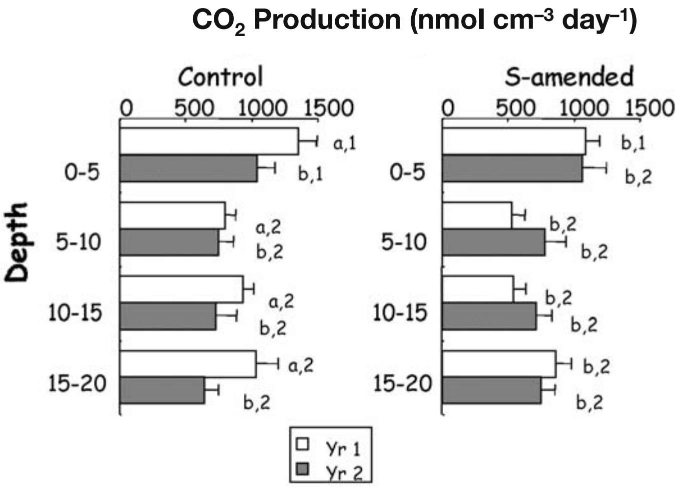

Fig. 12.2. Rates of CO_2 production as a function of depth (centimeters) based on control and S-amended plots for years 1 and 2. Lowercase letters represent the nature of the interaction between treatment and time, and numbers illustrate the depth effect. Each value represents the mean of nine determinations ± the standard error (three core determination x three subreplicates per core). Means with different lowercase letters and numbers represent significant differences. (Adapted from Vile et al. 2003a)

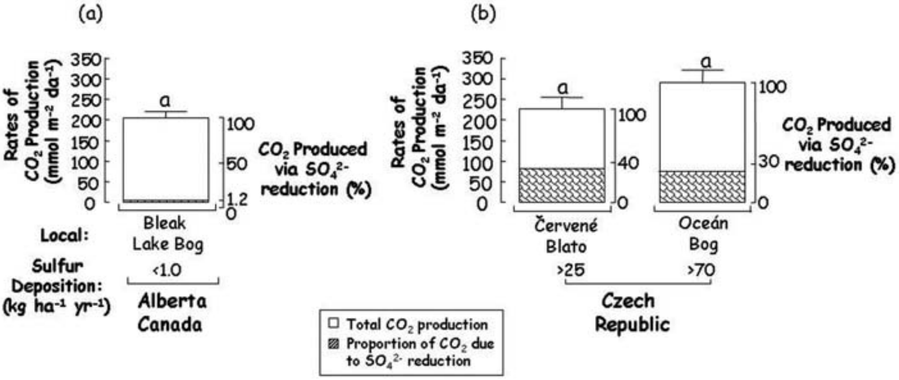

Fig. 12.3. Rates of CO_2 production for **a** Bleak Lake Bog in Alberta, Canada, and **b** Cervené Blato and Oceán bog in the Czech Republic as a function of atmospheric S deposition. The *hatched portion* of each *bar* represents the proportion of total CO_2 production resulting from SO_4^{2-} reduction. Means with different lowercase letters represent significant differences ($p<0.05$, Duncan's multiple range a posteriori comparison)

than 0.5 kg S ha^{-1} year^{-1} might not be long enough to produce the response that we observe in more highly polluted sites.

To examine more closely the effect of time, Vile et al. (2003b) examined rates of sulfate reduction and CO_2 production in two peatlands in the Czech Republic, where high rates of atmospheric S deposition have occurred for at least 45 years. The more polluted site (Oceán) received more than 70 kg S ha^{-1} year^{-1}, and the moderately polluted peatland (Cervené Blato) received 25 kg S ha^{-1} year^{-1}. Interestingly, rates of sulfate reduction were 1 order of magnitude greater – approximately 40 mmol m^{-2} year^{-1} – at both sites in the Czech Republic than at Bleak Lake Bog, in boreal Alberta, Canada (Fig. 12.4), yet CO_2 production was not significantly different among any of the sites (Fig. 12.3). These results are interesting as they suggest that over longer time frames, atmospheric S deposition dramatically increases rates of SO_4^{2-} reduction, yet at the same time has little effect on overall anaerobic C mineralization. When we combine all published studies on SO_4^{2-} reduction in several peatlands in North America and Europe, we see a clear pattern of increasing rates of SO_4^{2-} reduction with higher rates of atmospheric S deposition (Fig. 12.4). Why then do we not see a difference in CO_2 production across this S gradient?

To resolve this confounding issue, we dissected further the relationship between atmospheric S deposition, rates of SO_4^{2-} reduction, and rates of CO_2 production. When we examine the proportion of total CO_2 production resulting from SO_4^{2-} reduction (hatched portions of bars in Fig. 12.3), we find that the amount of C mineralization resulting from SO_4^{2-} reduc-

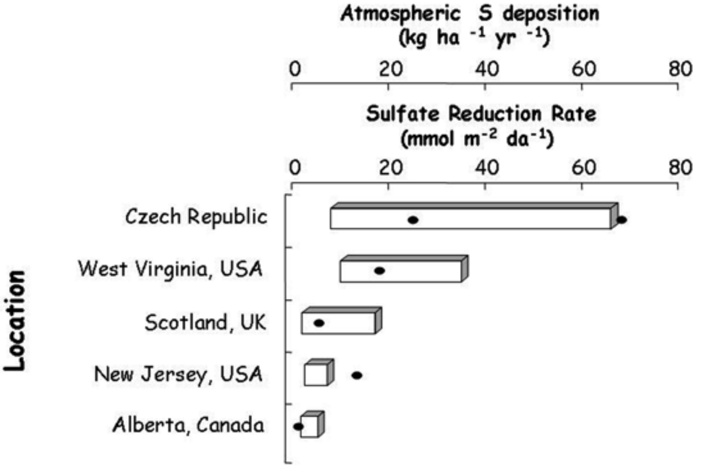

Fig. 12.4. Rates of sulfate reduction for numerous sites in North America and Europe. Each *bar* represents the range in rates. Bleak Lake Bog, Alberta, Canada (Vile et al. 2003a), Scotland, UK (Nedwell and Watson 1995), New Jersey, USA (Spratt et al. 1987), West Virginia, USA (Wieder et al. 1990), Czech Republic (Vile et al. 2003b). Each *black circle* represents the rate of atmospheric S deposition for each site; the Czech Republic had two sites. (Adapted from Vile et al. 2003b)

tion indeed increases along an atmospheric S deposition gradient (1.2 % for Bleak Lake Bog, 35.9 % for Cervené Blato, and 26.7 % for Oceán; Vile et al. 2003b), thereby highlighting the important factor of time. If we go one step further, and compare these data with those of the 2-year S field manipulation study at Bleak Lake Bog, by averaging the data in Fig. 12.2 over years and plotting CO_2 production as a function of SO_4^{2-} reduction rates for each depth, we find a significant relationship for control cores, yet this same relationship disintegrates for the S-amended cores (Fig. 12.5a), suggesting that removal of SO_4^{2-} limitation results in limitation by another factor, and the most likely candidate is organic compounds. Additional evidence to support the role of C as the limiting factor at Bleak Lake Bog is highlighted in Fig. 12.5b, where after a 2-year S-fertilization period, Vile et al. (2003a) found no further increases in rates of SO_4^{2-} reduction with further increases in the SO_4^{2-} pool size, and actually observed a decrease when compared with control cores (Fig. 12.5b). Similarly, Watson and Nedwell (1998) found no further increase in rates of sulfate reduction with SO_4^{2-} additions, and also observed a net decrease in the overall rate.

Collectively, these studies suggest that the relationship between rates of sulfate reduction and SO_4^{2-} concentration or deposition is more complex than we originally thought, and may be influenced by factors such as exposure time to atmospheric S deposition and C limitation. The results in Fig. 12.4 clearly illustrate that rates of sulfate reduction do increase with

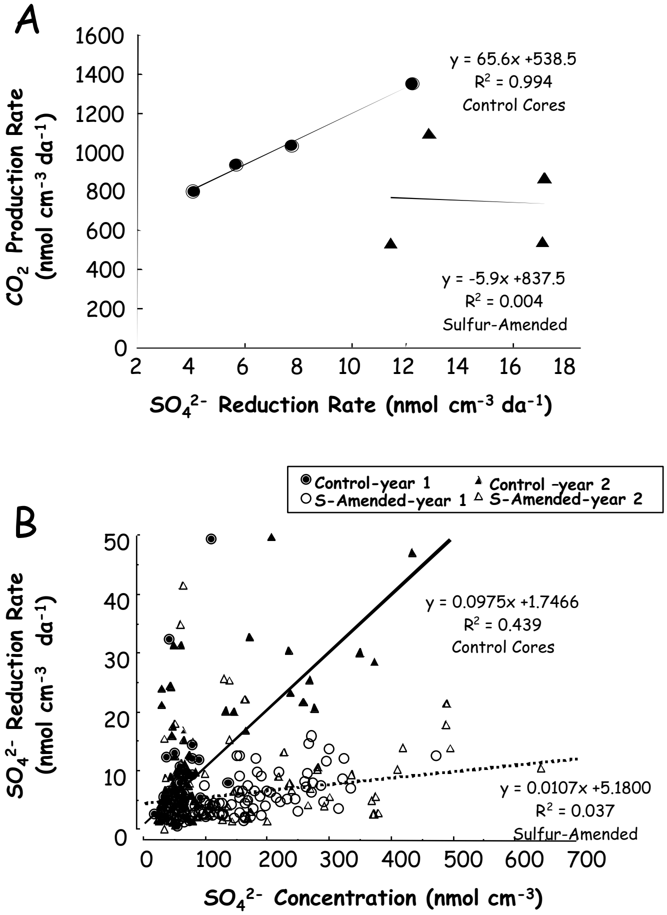

Fig. 12.5. **A** Correlations of CO_2 production rates with SO_4^{2-} reduction rates for control and S-amended plots. The regression lines represent averages over both years. **B** Correlations of sulfate reduction rate with sulfate pool size for control and S-amended plots in years 1 and 2. The regression lines represent the average for each year (n=162). (Adapted from Vile et al. 2003a)

increasing rates of atmospheric S deposition, yet most short-term (i.e., 1–3 years) laboratory and field S-fertilization studies show little augmentation of sulfate reduction rates. While the proportion of C flow through SO_4^{2-} reduction is influenced by atmospheric S deposition, the total amount of CO_2 produced does not change substantially across peatlands with vastly different S inputs (Vile et al. 2003b). Further research might be directed toward understanding the fundamental C quality and microbial community differences between northern boreal peatlands and their more southern counterparts.

12.3.3 Effect of Atmospheric Sulfur Deposition on CH_4 Cycling in Peatlands

Several studies have focused on the impact of atmospheric S deposition on CH_4 emissions from peatlands. Drawing once again upon thermodynamic theory, we would expect that when SO_4^{2-} is abundant, methanogens should be outcompeted. While we do consistently observe lower rates of methanogenesis under elevated levels of atmospheric S deposition, the relationship is certainly not linear, and rarely shows a complete inhibition or suppression. Nedwell and Watson (1995) demonstrated greater C flow through sulfate reduction than through methanogenesis during most of the year, except in summer, when SO_4^{2-} concentrations dipped below 50 μM. Contrastingly, Vile et al. (2003a) consistently observed greater C flow through sulfate reduction than through methanogenesis, even with instantaneous SO_4^{2-} concentrations less than 5 μM. Dise and Verry (2001) published the first field experiment designed to examine the effects of S amendments on CH_4 emission. S was added to a peatland in Minnesota over the course of one growing season, resulting in reduced CH_4 emissions by one third relative to those from control plots. Granberg et al. (2001) conducted a combination field/laboratory study with 2 years of S amendments applied in the field. In the laboratory, Granberg et al. (2001) demonstrated that S additions of 20 kg ha^{-1} $year^{-1}$ to Swedish peats had negative effects on CH_4 emissions at ambient temperatures, but no inhibitory effect at higher temperatures. Contrastingly, Blodau and Moore (2003) found under laboratory conditions that sulfate additions in excess of 500 μM significantly increased CH_4 production in surficial layers of peat, but inhibited CH_4 production in deeper peat layers, suggesting noncompetitive interactions between sulfate reducers and methanogens, with each group of bacteria restricted to spatially distinct zones within the peat.

While there is general agreement that the contribution of methanogenesis to anaerobic C mineralization is highly variable both temporally and spatially (Crill et al. 1995; Shannon and White 1996; Chap. 9) and that CH_4 emission is strongly linked to rates of atmospheric S deposition, there is less agreement about the importance of methanogenesis to overall anaerobic C mineralization. Wieder et al. (1990) found that CH_4 production integrated over the top 30 cm of peat accounted for 5.6 and 23.5 % of total anaerobic C mineralization in two Appalachian peatlands, representing the largest percentages ever measured for peatlands. Contrastingly, Vile et al. (2003b) found no significant contribution (less than 0.1 %) of CH_4 production to anaerobic C mineralization in a boreal bog in Alberta, Canada. Similarly, Bridgham et al. (1998) demonstrated that the contribution of CH_4 production to anaerobic C mineralization was less than 0.5 and 2.0 % in Minnesota bogs and fens, respectively. Again, fundamental differences in the nature of the peat, viz., minerotophic fens in Wieder et al. (1990)

versus pristine ombrotrophic bogs in Bridgham et al. (1998) and Vile et al. (2003a), could cause large disparities in the CH_4 contribution to anaerobic C mineralization. Nonetheless, natural wetlands are believed to be the largest single source of CH_4, with 33 % derived from boreal and northern peatlands. So how can we have peatlands as a major source of CH_4, yet multiple studies showing methanogenesis in peatlands contributing minimally to anaerobic C mineralization?

Dise and Verry (2001) point out that the observed current rate of increase in CH_4 concentrations in the atmosphere (0.5 % $year^{-1}$) is approximately half that observed 20 years ago, for reasons as yet unknown. New evidence suggests that this difference could be related to atmospheric S deposition. Gauci et al. (2004) estimated that current rates of atmospheric S deposition may suppress CH_4 emissions to preindustrial levels, thereby offsetting the effect of greenhouse warming by 26 Tg by 2030 or 15 % of the total global CH_4 source. Gauci et al. (2004) concluded that CH_4 suppression is occurring presently, has been occurring in the past, and is perhaps a contributing reason for the 50 % decrease in the rate of CH_4 growth in the atmosphere. Gauci et al. (2004) further concluded that documented increases in atmospheric CH_4 concentration since the late nineteenth century are most likely due to factors other than the warming of the world's peatlands. More Recently, Keppler et al. (2006) have demonstrated methane production from terrestrial plants under aerobic conditions by processes that yet are not understood fully, but that could change profoundly our current views of the dominant controls, mechanisms, and primary sources of methane to the atmosphere.

12.3.4 Summary and Future Research

Overall, these findings suggest that soil C turnover in peatlands may not be enhanced by increased atmospheric S deposition, at least in the short term. In particular, increased S deposition could mitigate the global greenhouse effect via its inhibition of CH_4 production (Gauci et al. 2004). One question raised is: are peatlands in Alberta, Canada, different from their more southern and eastern counterparts, and if so, why? Why did S amendments at the Alberta bog affect sulfate reduction rates, with no effect on rates of CO_2 production? Could C be limiting? If we were to expose Albertan peat to 50 years of S deposition, would we see the same response in terms of sulfate reduction and CH_4 inhibition that we see in eastern North American and European peatlands? We suspect that sulfate-reducing bacteria are ubiquitous across all peatlands, albeit sometimes acting slowly. However, for our Albertan peatland study, it may be the case that immediately after S fertilization, there was a boom in sulfate-reducing bacteria populations, and hence sulfate-reducing activity, followed by a bust, where rates actually decreased relative to those for control conditions (Fig. 12.3). Had we measured rates of sulfate reduction immediately following fertilization, we might have observed the opposite pattern (Fig. 12.3). Given the paucity of data for sulfate reduction rates in boreal peats, it would be interesting to compare S cycling and S–C interactions between Bleak Lake Bog, Alberta, and boreal peats in parts of Russia, where S deposition has been higher historically, and where many of the confounding variables of temperature and latitude that plague comparisons between boreal peatlands and those of eastern North American and European peatlands are removed.

12.4 The Fate and Stability of Peatland Sulfur

Over the past 10–20 years, atmospheric S deposition in North America and Europe has been decreasing (Likens et al. 2002). As a consequence of S emission reductions, the stability of existing soil S stores has recently become a matter of concern (Mayer et al. 1995a; Alewell and Novák 2001). If a considerable proportion of atmospherically deposited S thought to have been stabilized in soils is instead remobilized, acidification of the environment may continue long after reduction in industrial emissions (Mayer et al. 1995b; Branfireun et al. 1999; Gauci et al. 2004).

Potential effects of changes in atmospheric S deposition are widely challenged and debatable and depend in part on the type of soil, the degree of internal transformations that occur, and the depth/age of the soil profile (Armbruster et al. 2003). Recovery from acidification is usually defined as an increase in alkalinity within streams, lakes, or soils draining a watershed. Using this criterion, most of northern Europe has recovered in response to significant reductions in S deposition owing to the nature of their young, shallow soils, whereas in central Europe, soils tend to be older and deeper, causing a delayed response, or no little response at all to decreased acidification (Ambruster et al. 2003). Within the last 5 years, processes and patterns of S cycling and acidification recovery have been reviewed extensively in boreal forested ecosystems (Pirainen et al. 1998; Alewell et al. 1999; Beier et al. 2003; Aherne et al. 2004; Houle et al. 2004; Novák et al. 2004), but little is known about the fate of current S stores with decreased acidification in boreal peatlands (Lamers et al. 1998; Morth et al. 1999; Vile et al. 2003a). Peatlands will be especially susceptible to delayed acidification reversal as a result of their already low pH, low concentration of base cations, and relatively older (since last glaciation), deep C deposits. Under scenarios of predicted increased climatic warming in northern latitudes, drier peat would allow for greater oxidation of sequestered, reduced S in these systems. However, very few studies have addressed the question of the fate and mobility of peatland S stores.

Sphagnum-dominated peatlands have been identified consistently as net sinks for atmospherically deposited S (Brown 1985; Bayley et al. 1986; Wieder and Lang 1988; Urban et al. 1989; Novák and Wieder 1992; Novák et al. 1994). Several transformation processes can account for either net retention or net mobilization of different S fractions in peat. Possible retention mechanisms include dissimilatory sulfate reduction, which produces RIS and/or CBS that can accumulate in peat under anaerobic conditions. Deposited atmospheric SO_4^{2-} can also be assimilated by soil microbes and *Sphagnum* mosses producing CBS and/or ester SO_4^{2-} ($C–O–SO_3^-$) (Fig. 12.1). Possible mobilization mechanisms include the mineralization of organic S compounds to inorganic forms of S, such as SO_4^{2-} (Fitzgerald et al. 1984). S mineralization usually occurs under aerobic conditions, but can also occur under anaerobic conditions (Johnson and Wood 1993). Mobilization of RIS can occur via aerobic oxidation with O_2, or anaerobic oxidation with Fe^{3+} (Vile and Wieder 1994; Fig. 12.1). In forested soils, two additional mechanisms of S retention and mobilization occur via adsorption and desorption, respectively (Singh 1984). These processes are dependent upon the degree to which the soil has previously adsorbed SO_4^{2-}, the SO_4^{2-} concentration of incoming solutions relative to existing soil SO_4^{2-} concentrations, changes in soil pH, and the reversibility of SO_4^{2-} adsorption (Mayer et al. 1995b). Adsorption/desorption contributes substantially to mobilization/immobilization in forest soils (Alewell et al. 1999; Houle et al. 2001), but is thought to be less important in peatlands, especially in ombrotrophic peatlands, where Al and Fe oxides are in low concentration.

Three approaches exist to evaluate the stability of S stores, each with its associated merits and disadvantages: (1) a mass-balance approach, (2) an evaluation of changes in S pool sizes over time, and (3) use of stable S isotope ratios. A mass-balance approach can determine if a watershed is a source or sink for S, but regards the watershed as a black box, making it difficult to elucidate mechanisms of net retention or net mobilization. Evaluation of changes in different S pools provides more information about transformations within the black box, and if coupled to process measurements can begin to determine mechanisms of S retention or mobilization. In many instances, stable S isotope ratios are the only tool that can elucidate S cycling at the ecosystem level, because ratios can implicate processes that are not detectable by mass balance, changes in pool sizes, or rate determinations alone. Stable S isotope ratios provide insights into S transformations between the atmosphere and the hydrosphere, by reflecting changes in the $\delta^{34}S$ signal between atmospherically deposited SO_4^{2-} and the various S pools in the soil profile (Krouse and Grinenko 1991; Zhang et al. 1998). Only biological processes can result in shifts in $\delta^{34}S$ ratios under natural environmental conditions (Krouse 1986, 1989; Krouse and Grinenko 1991), adding to the utility of $\delta^{34}S$ ratios as an evaluation tool. If S-mineralizing bacteria have a choice between ^{34}S and ^{32}S, they will preferentially break the lighter ^{32}S–C bond during CBS mineralization (Mayer et al. 1995b; Mitchell et al. 1998; Alewell et al. 1999). Similarly, sulfate reducing bacteria preferentially reduce $^{32}SO_4^{2-}$ over $^{34}SO_4^{2-}$, causing a depletion of ^{34}S in the reaction product (i.e., RIS and/or CBS), while enriching the remaining SO_4^{2-} pool (Krouse and Tabatabai 1986). While there is general agreement that abiotic processes (desorption/adsorption) in the soil do not result in isotope fractionation (Fuller et al. 1986; Gebauer et al. 1994; Novák et al. 1994, 1996, 1999, 2001; Mayer et al. 1995b; Driscoll et al. 1998; Zhang et al. 1998), and that biotic processes (dissimilatory reduction of SO_4^{2-} by bacteria and organic S mineralization) do result in isotopic fractionation, evidence for shifts in $\delta^{34}S$ ratios during assimilatory uptake of SO_4^{2-} by plants is inconclusive (van Stempvoort et al. 1992; Mayer et al. 1995a). Most agree that some degree of fractionation occurs with assimilatory SO_4^{2-} uptake (Schoenau and Bettany 1989; Krouse et al. 1991). Recently, Novák et al. (2001) showed that plant assimilation of S was associated with a negative $\delta^{34}S$ shift, as *Sphagnum* mosses preferred the lighter isotope by 2‰ on average.

Research on the response of forested watersheds to long-term changes in atmospheric S deposition is abundant, while for peatlands, few studies exist. If we compare results for boreal forests with those for peatlands, we find very different patterns of S retention, mobility, and cycling. In almost all cases, the mass-balance approach to evaluate S storage in forests reveals a net export of S from the watershed despite decreases in atmospheric S inputs (Alewell et al. 1999; Morth et al. 1999; Eimers and Dillon 2002). One exception was reported by Alewell and Gehre (1999) where a balanced S budget was calculated for the Lehstenbach forested catchment in northeastern Bavaria, Germany. Interestingly, approximately 30 % of this watershed was covered by fens or intermittent seeps. These results suggest that wetlands, and specifically peatlands, behave very differently from upland forests, and could represent a large storage facility for atmospherically deposited S. Moreover, the existence of peatlands could be the single most important defining criterion for having a balanced or unbalanced S budget in any given watershed. The question then becomes: can peatlands continue to function as a long-term sink for atmospherically deposited S in light of long-term changes in atmospheric S deposition?

Vile et al. (unpublished data) examined changes in pool sizes of various S fractions from peat cores that were transplanted from an area in the Czech Republic that received more than 70 kg S ha^{-1} $year^{-1}$ (Oceán) to a peatland that received less than 25 kg S ha^{-1} $year^{-1}$ (Cervené Blato). One year after transplantation, there were no significant decreases in any of the S pools sizes (i.e., total S, CBS, SO_4^{2-}, and RIS), but interestingly in some cases, a significant increase in both CBS and RIS occurred (Table 12.1). Interestingly, these results suggest intensive cycling via dissimilatory sulfate reduction, despite lower rates of atmospheric S deposition, and that these rates are fueled by existing soil S stores. More importantly, total S pools appear to be quite stable, at least in the short term (1–2 years), and the time frame for how long dissimilatory sulfate reduction can continue to sequester S remains to be determined

While few studies have calculated S mass balances in peatlands, it is generally thought that inputs exceed outputs under conditions of high atmospheric S input, and preliminary data suggest that peatlands will continue to store S under scenarios of decreasing atmospheric S deposition (Table 12.1). The difference between forests and peatlands is primarily due to the mode of organic matter formation, which ultimately controls the mechanisms of biological processing. While the CBS pool tends to dominate both in forests (approximately 50–70%) and in peatlands (approximately 90%), the origin of the organic matter is different. For example, Houle et al. (2001) demonstrated that the forest floor accumulates organic S mainly from litterfall and less than 1% of this organic S pool participates in immobilization reactions, indicating that recent deposition of atmospheric SO_4^{2-} is actively cycled within the soil profile, and rapidly reaches steady-state conditions with no net accumulation of S (Houle et al. 2004). In peatlands, organic matter originates from decomposing *Sphagnum* plants, and owing to the waterlogged nature of the system, dead plant remains decompose slowly. In forests, soils tend to be well drained and hence aerobic, with higher rates of organic matter decay. It seems reasonable then to assume that peatland S stores will be most vulnerable if increasing temperatures lower water tables, thereby exposing peat to aerobic conditions and potentially oxidizing S stores. Eimers and Dillon (2002) found strong controls of climate on SO_4^{2-} export from watersheds after drought conditions in south central Ontario owing to oxidation and release of S stored in wetlands. Similarly,

Table 12.1. Mean (n=5) pool size of S fractions integrated over 20 cm of peat expressed on an area basis (millimoles per square meter). Lowercase letters indicate significant differences

Origin	Oceán	
Transplanted to	Cervené Blato	Oceán
Total S	$2{,}586^{a}\pm240$	$2{,}080^{a}\pm374$
C-bonded S	$2{,}316^{a}\pm167$	$1{,}785^{b}\pm366$
SO_4^{2-}	$82^{b}\pm21$	$88^{b}\pm19$
Reduced inorganic sulfur	$309^{a}\pm33$	$221^{b}\pm34$

Morth et al. (1999) found high SO_4^{2-} runoff after a drought coupled with low $\delta^{34}S$ values for SO_4^{2-}. Low $\delta^{34}S$ values indicate oxidation of RIS or CBS originally produced via dissimilatory sulfate reduction which shuttles light $^{32}SO_4^{2-}$ through the reaction. Alewell et al. (1999) also found lower $\delta^{34}S$ values for SO_4^{2-} in stream runoff than in bulk precipitation at the Hubbard Brook Experimental Forest, suggesting intense cycling through the organic pool.

Interestingly, when we compare stable S isotope ratios for the few peatland studies with those of upland forests, we see contrasting patterns (Novák et al. 1996). Alewell and Novák (2001) and Novák et al. (1999) illustrated that organic S concentrations do not differ between surface and deep peat sections in both wetland and upland soils, yet wetlands have an order of magnitude higher S than their upland counterparts (Fig. 12.6a). Alewell and Novák (2001) and Novák et al. (1999) reported increasing $\delta^{34}S$ values with depth in aerated, upland forests (Fig. 12.6b). While we observe a similar trend in peatlands, there are isotopically lighter $\delta^{34}S$ values in both surface and deeper peat as compared with upland forests (Fig. 12.6). In the former case, preferential mineralization of lighter CBS, comprising most of total S, leaves behind isotopically heavier CBS, whereas in the latter case, funneling of isotopically lighter SO_4^{2-} into dissimilatory sulfate reduction produces isotopically lighter CBS. These results indicate that peatland organic S stores are governed more by biological processes (dissimilatory sulfate reduction and mineralization), while S cycling in upland forests tends to be governed more by abiotic processes (adsorption/desorption) and to a lesser extent by S mineralization. However,

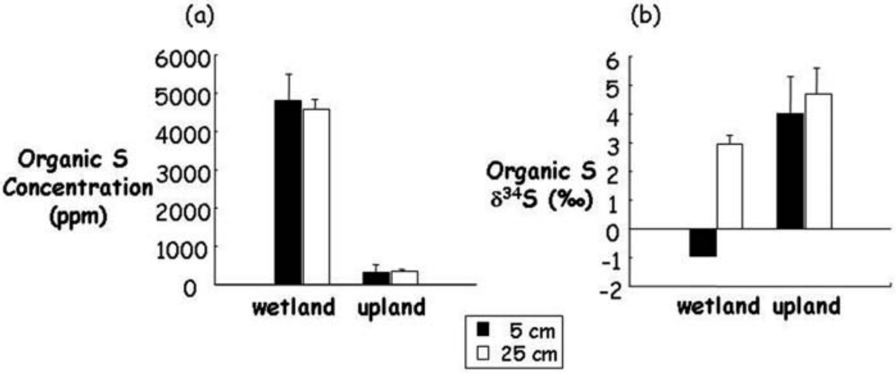

Fig. 12.6. Organic S concentrations and organic S $\delta^{34}S$ ratios for two different depths at a wetland site (Schlöppnerbrunnen) and an upland site (Coulissenhieb) in northeastern Bavaria, Germany. The values shown represent approximations based on the original published figure. (Reproduced and adapted with permission from Alewell and Novák 2001)

Novák et al. (2000) have challenged our traditional views of S cycling in forested catchments by demonstrating that about 50 % of all S discharged in two watersheds in the Czech Republic is organically cycled, suggesting that biotic S cycling in aerated forest soils is much more important than traditionally believed. When considering the fate of peatland S stores, the most important *biotic* factors determining stability will be the degree of internal S cycling of existing S pools via dissimilatory sulfate reduction and CBS remineralization, which we now understand to be quite dynamic. The most important *abiotic* factor determining stability of peatland S stores may be climate-induced oxidation of existing organic S, and perhaps to a lesser extent, fire. Boreal forest fires can have a significant impact on peatland C stores (Turetsky and Wieder 2001), and in areas where substantial S has been deposited after fire, pulses of SO_4^{2-} to the system would not be trivial, and should be taken into consideration. Clearly, owing to the distinct nature of peatlands, the myriad of differences exhibited when compared with upland forests and the intensity of S cycling in even the most S-poor environments compels us to ask more questions concerning the fate of current S peatland stores.

12.5 The Role of Sulfur in Methylating Mercury and Dimethyl Sulfide Formation

Anthropogenic activities, especially coal burning, have increased rates of atmospheric Hg deposition since the Industrial Revolution, and now Hg can be detected even in the remotest regions of the globe, such as Greenland (Swain et al. 1992). We have fairly accurate estimates of the deposition of Hg, which occurs predominantly in inorganic form (Hg^0 or Hg^{2+}). However, it is the methylated form of Hg (CH_3Hg) that is harmful to living organisms. Estimates of atmospherically deposited CH_3Hg are insufficient to account for the amount of CH_3Hg found in living organisms (Branfireun et al. 1998, 2001). Because of this imbalance, we know that a substantial amount of atmospherically derived Hg is methylated subsequent to deposition (Gilmour et al. 1992). Presently, it is fairly well accepted that the methylation of Hg by sulfate-reducing bacteria in wetland ecosystems is the main pathway of Hg introduction to food chains of aquatic environments (Gilmour et al. 1992; King et al. 2000; Branfireun et al. 2001; Skyllberg et al. 2003).

Earlier research suggested a negative feedback between CH_3Hg formation and SO_4^{2-} reduction. Sulfide formation, the end product of SO_4^{2-} reduction, was thought to inhibit methylation of Hg at concentrations higher than 30 µM (Gilmour et al. 1992). Sulfate reduction rates, however, are limited by low concentrations of SO_4^{2-}, and, therefore, maximizing conditions favorable for one process limit rates of the other. In salt marshes and estuarine ecosystems, where a large proportion of C flows through SO_4^{2-} reduction, high sulfide concentrations would not be conducive to Hg methylation. As a result, freshwater wetlands with lower rates of SO_4^{2-} reduction and lower sulfide concentrations (Wieder and Lang 1988; Vile et al. 2003a) are ideal ecosystems for maximizing both processes, and, therefore, have aided our understanding of biogeochemical controls on CH_3Hg (St. Louis et al. 1994, 1996).

The relationship between S and Hg, specifically in boreal peatlands, only recently has been examined (Branfireun et al. 1998, 1999; Branfireun and Roulet 2002). St. Louis et al. (1994, 1996) have demonstrated that boreal watersheds containing peatlands tend to export more CH_3Hg to streams and lakes than those without peatlands. Moreover, Xun et al. (1987, as cited in Branfireun et al. 2001) reported sevenfold greater rates of Hg methylation at pH 4.5 than at pH 8.0. Low pH values in peatlands prevent the formation of charged Hg complexes, thereby allowing Hg to cross the cell membranes of sulfate-reducing bacteria. The combination of low pH, regionally high rates of atmospheric S deposition, and the large aerial extent of boreal peatlands highlights the importance of understanding the biogeochemical controls on Hg methylation in peatlands.

"Rules" for predicting the concentrations of Hg and sulfate in peat porewaters that could maximize Hg methylation rates while at the same time minimize sulfide production are still not well characterized (Heyes et al. 2000). Gilmour et al. (1992) demonstrated CH_3Hg production at sulfate concentrations as low as 30 μM and up to 100–200 μM, while Winfrey and Rudd (1988) found that addition of sulfate to produce concentrations of 1 mM inhibited Hg methylation. More recently, Branfireun et al. (2001) found that S amendments equivalent to acid rain deposition in the 1980s in southern Sweden of 10–20 kg S ha^{-1} $year^{-1}$ increased CH_3Hg concentrations in peat porewater fourfold. Interestingly, King et al. (2000) measured rates of Hg methylation in the presence of 30 mM sulfate and millimolar levels of sulfide in both pure culture and in marine sediments that were well within the range reported for other freshwater sediments. Moreover, King et al. (2000) demonstrated that acetate-utilizing, sulfate-reducing bacteria methylate Hg at higher rates than sulfate-reducing bacteria that do not use acetate. These results suggest profound implications for C–S–Hg cycling dynamics. The collection of studies reported here all took place in boreal and subboreal peatlands in Fennoscandia and North America, where rates of atmospheric S deposition have decreased substantially since 1990. We are aware of only one study that has examined the importance of CH_3Hg formation in Asia. Liu et al. (2003) reported CH_3Hg concentrations for a peatland in northeastern China that are well within the range reported for North America and Europe. The paucity of data for

Asia, a region with steadily increasing rates of S and Hg deposition, underscores the need for further research.

12.6 The Importance of Volatile Sulfur Compounds from Peatlands

H_2S gas has long been known to be the dominant biogenic S-containing gas emitted from freshwater wetlands and anoxic soils (Brown and McQueen 1985; Nriagu et al. 1987), although its emission from peat tends to be quite low. New evidence from Novák et al. (2004) suggests that volatilized H_2S from forested catchments in the Czech Republic may exceed 13 kg ha^{-1} $year^{-1}$, which is more than current rates of atmospheric S deposition in many parts of Europe and North America, but more importantly, this “missing S flux” may explain unbalanced S budgets for many forested catchments (Driscoll et al. 1998).

DMS is the dominant S-containing gas emitted from oceans and other marine systems. Previously it was thought DMS emissions resulted exclusively from plants and oceanic phytoplankton. Recently, however, DMS emissions have been measured in anoxic *Sphagnum* peat (Kiene and Hines 1995), and are the direct result of microbial activity. Further exploration revealed that although in situ DMS production may be substantial in peat, emissions tend to be insignificant as DMS is degraded rapidly by methanogenic and sulfate-reducing bacteria (Chapman et al. 1996; Lomans et al. 1997, 1999).

12.7 Conclusions

Over the last 6 decades, atmospheric S deposition has peaked in some parts of the world, while simultaneously it continues to impact other regions of the globe. During this same time, we have increased considerably our ecosystem-level understanding of the consequences of atmospheric S deposition on aquatic, terrestrial and wetland systems. Biogeochemical cycling of S is highly complex in ecosystems having predominantly anaerobic zones, yet even in well-drained upland forests, we now know that many of the processes thought only to be dominant in wetlands must be considered to accurately evaluate S fluxes and cycling patterns.

In terms of trace-gas emissions, elevated inputs of atmospheric S deposition may cause an increase in rates of sulfate reduction, but may not cause a shift in peatland C stores from that of net C sink to net C source.

The response of peatlands in large parts of Europe and North America, where dramatic decreases in atmospheric S have occurred, may be delayed as the currently large S pools in these peats will continue to provide free SO_4^{2-} for years to come. The net long-term effect then of declining rates of atmospheric S deposition on peatland carbon stores is likely to enhance their potential emissions of CH_4, but not of CO_2. Current increases in the severity of atmospheric S deposition in large parts of Asia, which contain the fourth-largest global peatland area, are a matter of concern. Specifically, we have shown in North America and in Europe that if a considerable proportion of atmospherically deposited S, thought to be immobilized in soils, is remobilized, acidification of the environment has the potential to continue long after industrial emissions have been eliminated.

Despite our advances, presently we have little data on S cycling dynamics in boreal regions with regard to trace-gas emissions, S stores, and S–Hg interactions, and especially for one region in particular, Siberia. Exploration of Siberian peatlands will undoubtedly reaffirm, readjust, and revitalize our scientific understanding on the role of S on future aspects of ecosystem function.

References

Abate T (1995) Swedish scientists take acid rain research to developing nations. Bioscience 45:738–740

Aherne J, Posch M, Dillon PJ, Henriksen A (2004) Critical loads of acidity for surface waters in South Central Ontario, Canada: regional application of the first order acidity balance (FB) model. Water Air Soil Pollut Focus 4:25–36

Alewell C, Gehre M (1999) Patterns of stable S isotopes in a forested catchment as indicators for biological S turnover. Biogeochemistry 47:319–333

Alewell C, Novák M (2001) Spotting zones of dissimilatory sulfate reduction in a forested catchment: the ^{34}S–^{35}S approach. Environ Pollut 112:369–377

Alewell C, Mitchell MJ, Likens GE, Krouse HR (1999) Sources of stream sulfate at the Hubbard Brook Experimental Forest: long-term analyses using stable isotopes. Biogeochemistry 44:281–299

Armbruster M, Mengistu A, Feger KH (2003) The biogeochemistry of two forested catchments in the Black Forest and the eastern Ore Mountains (Germany). Biogeochemistry 65:341–368

Aselmann I, Crutzen PJ (1989) Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. J Atmos Chem 8:307–359

Badr O, Probert SD (1994) Atmospheric sulphur: trends, sources, sinks and environmental impacts. Appl Energy 47:1–67

Bartlett KB, Harriss RC (1993) Review and assessment of methane emissions from wetlands. Chemosphere 26:261–320

Bayley SE, Behr RS, Kelly CA (1986) Retention and release of S from a freshwater wetland. Water Air Soil Pollut 31:101–114

Beier C, Moldan F, Wright RF (2003) Terrestrial ecosystem recovery-modelling the effects of reduced acidic inputs and increased inputs of sea salts induced by global change. Ambio 32:275–282

Bhatti N, Streets DG, Foell WK (1992) Acid rain in Asia. Environ Manage 16:541–562

Blodau C, Moore TR (2003) Micro-scale CO_2 and CH_4 dynamics in a peat soil during a water fluctuation and sulfate pulse. Soil Biol Biochem 35:535–547

Branfireun BA, Roulet NT (2002) Controls on the fate and transport of methylmercury in a boreal headwater catchment, northwestern Ontario, Canada. Hydrol Earth Syst Sci 6:785–794

Branfireun BA, Hilbert D, Roulet NT (1998) Sinks and sources of methylmercury in a boreal catchment. Biogeochemistry 41:277–291

Branfireun BA, Roulet NT, Kelly CA, Rudd JWM (1999) In situ sulphate stimulation of mercury methylation in a boreal peatland: toward a link between acid rain and methylmercury contamination in remote environments. Global Biogeochem Cycles 13:743–750

Branfireun BA, Bishop K, Roulet NT, Granberg G, Nilsson M (2001) Mercury cycling in boreal ecosystems: the long-term effect of acid rain constituents on peatland pore water methylmercury concentrations. Geophys Res Lett 28:1227–1230

Bridgham SD, Johnston CA, Pastor J, Updegraff K (1995) Potential feedbacks of northern wetlands on climate change. Bioscience 45:262–274

Bridgham SD, Updegraff K, Pastor J (1998) Carbon, nitrogen and phosphorus mineralization in northern wetlands. Ecology 79:1545–1561

Bridgham SD, Ping CL, Richardson JL, Updegraff K (2001) Soils of peatlands: histosols and gelisols. In: Richardson JL, Vepraskas MJ (eds) Wetland soils: genesis, hydrology, landscapes, and classification. CRC, Boca Raton, pp 343–370

Brimblecombe P, Hammer C, Rhode H, Ryaboshapko A, Boutron CF (1989) Human influence on the sulphur cycle. In: Brimblecombe P, Leub AY (eds) Evolution of the global biogeochemical sulphur cycle. Wiley, New York, pp 77–121

Brown KA (1985) Sulphur distribution and metabolism in waterlogged peat. Soil Biol Biochem 17:39–45

Brown KA, McQueen JF (1985) Sulphate uptake from surface water by peat. Soil Biol Biochem 17:411–420

Cameron CC (1968) Peat. In: Mineral resources of the Appalachian region. US Geological Survey professional paper 580, US Government Printing Office, Washington, DC

Casagrande DJ, Indowu G, Friedman A, Rickert P, Schlenz D (1979) H_2S incorporation in coal precursors: Origins of sulfur in coal. Nature 282:599–600

Chapman SJ, Ken-ichi K, Tsuruta H, Minami K (1996) Influence of temperature and oxygen availability on the flux of volatile sulphur compounds from wetlands: a comparison of peat and paddy soils. Soil Sci Plant Nutr 42:279–288

Conrad R (1989) Control of methane production in terrestrial ecosystems. In: Andreae MO, Schimel DS (eds) Exchange of trace gases between ecosystems and the atmosphere. Wiley, Chichester, pp 37–58

Crill PM, Butler JH, Cooper DJ, Novelli PC (1995) Standard analytical methods for measuring trace gases in the environment. In: Matson PA, Harriss RC (eds) Biogenic trace gases: measuring emissions from soil and water. Blackwell, Oxford, pp 164–205

Davis DW, Detro RA (1992) Fire and brimstone, the history of melting Louisiana's sulphur. Louisiana Geological Survey, Baton Rouge

Dise N, Verry E (2001) Suppression of peatland methane emission by cumulative sulfate deposition in simulated acid rain. Biogeochemistry 53:143–160

Driscoll CT, Likens GE, Buso D, Church MR (1998) Recovery of soil and surface waters in the northeastern US from decreases in atmospheric deposition of sulfur. Water Air Soil Pollut 105:306–316

Eimers MC, Dillon PJ (2002) Climate effects on sulphate flux from forested catchments in south-central Ontario. Biogeochemistry 61:337–355

Fauque GD (1995) Ecology of sulfate reducing bacteria. In: Barton L (ed) Sulfate reducing bacteria. Plenum, New York, pp 217–235

Fitzgerald JW, Andrew TL, Swank WT (1984) Availability of carbon-bonded sulfur for mineralization in forest soils. Can J For Res 14:839–843

Fuller RD, Mitchell MJ, Krouse HR, Wyskowski BJ, Driscoll CH (1986) Stable sulfur isotope ratios as a tool for interpreting ecosystem sulfur dynamics. Water Air Soil Pollut 28:163–171

Fung I, John J, Lerner J, Matthews E, Prather M, Steele LP, Fraser PJ (1991) Global budgets of atmospheric methane: Results from a three-dimensional global model synthesis. J Geophys Res 96:13033–13065

Galloway ME, Branfireun BA (2004) Mercury dynamics of a temperate forested wetland. Sci Total Environ 325:239–254

Gauci V, Dise N, Fowler D (2002) Controls on suppression of methane flux from a peat bog subjected to simulated acid rain sulfate deposition. Global Biogeochem Cycles 16:1–12

Gauci V, Matthews E, Dise N, Walter B, Koch D, Granberg G, Vile M (2004) Sulfur pollution suppression of the wetland methane source in the 20th and 21st centuries. Proc Natl Acad Sci USA 101:12583–12587

Gebauer G, Giesemann A, Schulze ED, Jäger HJ (1994) Isotope ratios and concentrations of sulfur and nitrogen in needles and soils of *Picea abies* stands as influenced by atmospheric deposition of sulfur and nitrogen compounds. Plant Soil 164:267–281

Giblin AE, Wieder RK (1992) Sulphur cycling in marine and freshwater wetlands. In: Howarth R, Stewart JWB, Ivanov MV (eds) Sulfur cycling on the continents: wetlands, terrestrial ecosystems, and associated water bodies. Wiley, New York, pp 85–124

Gilmour CC, Henry EA, Mitchell R (1992) Sulfate stimulation of mercury methylation in freshwater sediments. Environ Sci Technol 26:2281–2287

Gore AJP (1983) Ecosystems of the world 4A. Mires, swamp, bog, fen and moor. General studies. Elsevier, Amsterdam

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195

Granberg G, Sundh I, Svensson BH, Nilsson M (2001) Effects of temperature, and nitrogen and sulfur deposition on methane emission from a boreal mire. Ecology 82:1982–1998

Hedin LO, von Fischer JC, Ostrom NE, Kennedy BP, Brown MG, Robertson GP (1998) Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil-stream interfaces. Ecology 79:684–703

Heyes A, Moore TR, Rudd JWM, Dugoua JJ (2000) Methyl mercury in pristine and impounded boreal peatlands, Experimental Lakes Area, Ontario. Can J Fish Aquat Sci 57:2211–2222

Houle D, Carignan R, Ouimet R (2001) Soil organic sulfur dynamics in a coniferous forest. Biogeochemistry 53:105–124

Houle D, Carignan R, Roberge J (2004) The transit of $^{35}SO_4^{2-}$ and ^3H_2O added *in situ* to soil in a boreal coniferous forest. Water Air Soil Pollut Focus 4:501–518

Howarth RW, Jorgensen BB (1984) Formation of 35S-labelled elemental sulfur and pyrite in coastal marine sediments (Limfjorden and Kysing Fjord, Denmark) during short term ${}^{35}SO_4{}^{2-}$ reduction measurements. Geochim Cosmochim Acta 48:1807–1818

Howarth R, Teal JM (1979) Nitrification potentials at different pH values in peat samples from various layers of a drained mire. Am Nat 116:862–872

Howarth RW, Teal JM (1980) Energy flow in a salt marsh ecosystem: the role of reduced inorganic sulfur compounds. Am Nat 116:862–872

Jenkinson, DS, Adams, DE, Wild A (1991) Model estimates of CO_2 emissions from soil in response to global warming. Nature 351:304–306

Johnson AC, Wood (1993). Sulphate-reducing bacteria in deep aquifer sediments of the London Basin: their role in anaerobic mineralization of organic matter. J Appl Bacteriol 75: 190–197

Joosten H, Clarke D (2002) Wise use of peatlands, background and principles including a framework for decision-making. International Mire Conservation Group and the International Peat Society, Saarijärvi, Finland

Kiene RP, Hines ME (1995) Microbial formation of dimethyl sulfide in anoxic *Sphagnum* peat. Appl Environ Microbiol 61:2720–2726

King JK, Kostka JE, Frischer ME, Saunders FM (2000) Sulfate-reducing bacteria methylate mercury at variable rates in pure culture and in marine sediments. Appl Environ Microbiol 66:2430–2437

Kirschbaum MUF (1995) The temperature dependence of soil organic matter decomposition, and the effects of global warming on soil organic C storage. Soil Biol Biochem 27:753–760

Krouse HR (1986) Sulfur isotopes in our environment. In: Fritz P, Fontes JC (eds) Handbook of environmental isotope geochemistry. Elsevier, New York, pp 435–471

Krouse HR (1989) Sulfur isotope studies of the pedosphere and biosphere. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecological research. Springer, Berlin Heidelberg New York, pp 424–444

Krouse HR, Grinenko VA (eds) (1991) Stable isotopes: natural and anthropogenic sulphur in the environment, SCOPE 43. Wiley, Chichester

Krouse HR, Tabatabai MA (1986) Stable sulfur isotopes. In: Tabatabai MA, Beaton JD, Fox RL (eds) Agronomy monograph 27. American Society of Agronomy, Crop Science Society of Americas, Soil Science Society of America, Madison, pp 169–205

Krouse HR, Stewart JWB, Grinenko VA. (1991) Pedosphere and biosphere. In: Krouse HR, Grinenko VA (eds) Stable isotopes: natural and anthropogenic sulphur in the environment. Scope 43. Wiley, Chichester, pp 267–306

Lamers LPM, Tomassen HBM, Roelofs JGM (1998) Sulfate-induced eutrophication and phytotoxicity in freshwater wetlands. Environ Sci Technol 32:199–205

Lang K, Lehtonen M, Martikainen P (1993) Nitrification potentials at different pH values in peat samples from various layers of a drained mire. Geomicrobiol J 11:141–147

Likens GE, Driscoll CT, Buso MJ, Mitchell MJ, Lovett GM, Bailey SW, Siccama TG, Reiners WA, Alewell C (2002) The biogeochemistry of sulfur at Hubbard Brook. Biogeochemistry 60:235–316

Liu R, Want Q, Lu X, Fang F, Wang Y (2003) Distribution and speciation of mercury in the peat bog of Xiaoxing'an Mountain, northeastern China. Environ Pollut 124:39–46

Lomans BP, Smolders JP, Intven LM, Pol A, Op den Camp HJM, van der Drift C (1997) Role of dimethyl sulfide and methanethiol in anoxic freshwater sediments. Appl Environ Microbiol 63:4741–4747

Lomans BP, Op den Camp HJM, Pol A, van der Drift C, Vogels GD (1999) Role of methanogens and other bacteria in degradation of dimethyl sulfide and methanethiol in anoxic freshwater sediments. Appl Environ Microbiol 65:2116–2121

Lovely DR, Klug MJ (1983) Sulfate reducers can outcompete methanogens at freshwater sulfate concentrations. Appl Environ Microbiol 45:187–192

Mandernack KW, Lynch L, Krouse HR, Morgan MD (2000). Sulfur cycling in wetland peat of the New Jersey Pinelands and its affect on stream water chemistry. Geochim Cosmochim Acta 64:3949–3964

Mayer B, Fritz P, Prietzel J, Krouse HR (1995a) The use of stable sulfur and oxygen isotope ratios for interpreting the mobility of sulfate in aerobic forest soils. Appl Geochem 10:161–173

Mayer B, Feger KH, Giesemann A, Jager HJ (1995b) Interpretation of sulfur cycling in two catchments in the Black Forest (Germany) using stable sulfur and oxygen isotope data. Biogeochemistry 30:31–58

McDonald BR (1982) Wetlands of West Virginia, location and classification. West Virginia Department of Natural Resources, Elkins

Mitchell MJ, Krouse HR, Mayer B, Stam AC, Zhang YM (1998) Use of stable isotopes in evaluating biogeochemistry of forest ecosystems In: Kendall C, McDonnell JJ (eds) Isosope tracers in catchment hydrology. Elsevier, Amsterdam, pp 489–518

Mitsch WJ, Gosselink JG (2000) Wetlands, 3rd edn. Wiley, New York

Morth C-M, Torssander P, Kusakabe M, Hultberg H (1999) Sulfur isotope values in a forested catchment over four years: evidence for oxidation and reduction processes. Biogeochemistry 44:51–71

Nedwell, DB (1984) The input and mineralisation of organic C in anaerobic aquatic sediments. Adv Microb Ecol 7:93–131

Nedwell DB, Watson A (1995) CH_4 production, oxidation and emission in a UK ombrotrophic peat bog: influence of SO_4^{2-} from acid rain. Soil Biol Biochem 27:893–903

Novák M, Wieder RK (1992) Inorganic and organic sulfur profiles in nine *Sphagnum* peat bogs in the United States and Czechoslovakia. Water Air Soil Pollut 65:353–369

Novák M, Wieder RK, Schell WR (1994). Sulfur during early diagenesis in *Sphagnum* peat: insights from ?δ^{34}S ratio profiles in ^{210}Pb-dated peat cores. Limnol Oceanogr 39:1172–1185

Novák M, Bottrell SH, Fottová D, Bu_ek F, Groscheová H, _ak K (1996) Sulfur isotope signals in forest soils of central Europe along an air pollution gradient. Environ Sci Technol 30:3473–3476

Novák M, Buzek F, Adamová M (1999) Vertical trends in δ^{13}C, δ^{15}N and δ^{34}S ratios in bulk *Sphagnum* peat. Soil Biol Biochem 31:1343–1346

Novák M, Kirchner JW, Groscheová H, Havel M, Cerny J, Krejcí R, Buzek F (2000) Sulfur isotope dynamics in two Central European watersheds affected by high atmospheric deposition of SO_x. Geochim Cosmochim Acta 64:367–383

Novák M, Bottrell SH, Prechová E (2001) Sulfur isotope inventories of atmospheric deposition, spruce forest floor and living *Sphagnum* along a NW-SE transect across Europe. Biogeochemistry 53:23–50

Novák M, Michel RL, Prechová E, _tepánová (2004) The missing flux in a ^{35}S budget for the soils of a small polluted catchment. Water Air Soil Pollut Focus 4:517–529

Nriagu JO, Holdway DA, Coker RD (1987) Biogenic sulfur and the acidity of rainfall in remote areas of Canada. Science 237:1189–1192

O'Meara M (1998) Acid rain threats vary. In: Brown LA, Renner M, Flavin C (eds) Vital signs the environmental trends that are shaping our future. Norton, New York, pp 134–137

Pirainen S, Finer L, Starr M (1998) Canopy and soil retention of nitrogen deposition in a mixed boreal forest in eastern Finland. Water Air Soil Pollut 105:165–174

Schlesinger WH (1997) Biogechemistry-an analysis of global change, 2nd edn. Academic, New York

Schoenau JJ, Bettany JR (1989) ^{34}S natural abundance variations in prairie and boreal forest soils. J Soil Sci 40:397–413

Shannon RD, White JR (1996) The effects of spatial and temporal variations in acetate and sulfate on methane cycling in two Michigan peatlands. Limnol Oceanogr 41:435–443

Singh BR (1984) Sulfate sorption by acid forest soils: 3. Desorption of sulfate from adsorbed surfaces as a function of time, desorbing ion, pH, and amount of adsorption. Soil Sci 138:346–353

Skyllberg U, Qian J, Frech W, Xia K, Bleam WF (2003) Distribution of mercury, methylmercury and organic sulphur species in soil, soil solution and stream of a boreal forest catchment. Biogeochemistry 64:53–76

Spratt HG, Morgan MD, Good RE (1987) Sulfate reduction in peat from a New Jersey pinelands cedar swamp. Appl Environ Microbiol 53:1406–1411

St Louis VL, Rudd JWM, Kelly CA, Beaty KG, Bloom NS, Flett RJ (1994) Importance of wetlands as sources of methylmercury to boreal forest ecosystems. Can J Fish Aquat Sci 51:1065–1076

St Louis VL, Rudd JWM, Kelly CA, Beaty KG, Flett RJ, Roulet NT (1996) Production and loss of methylmercury and loss of total mercury from boreal forest catchments containing different types of wetlands. Environ Sci Technol 30:2719–2729

Swain EB, Engstrom DR, Brigham ME, Henning TA, Brezonik PL (1992) Increasing rates of atmospheric mercury deposition in midcontinental North America. Science 257:784–787

Turetsky MR, Wieder RK (2001) A direct approach for quantifying organic matter lost as a result of peatland wildfire. Can J For Res 31:363–366

Urban NR, Eisenreich SJ, Grigal DF (1989) Sulfur cycling in a forested *Sphagnum* bog in northern Minnesota. Biogeochemistry 7:81–109

van Stempvoort DR, Fritz P, Reardon EJ (1992) Sulfate dynamics in upland forest soils, central and southern Ontario, Canada: stable isotope evidence. Appl Geochem 7:159–175

Venkataraman C, Chandramouli B, Patwardhan C (1999) Anthropogenic sulphate aerosol from India: estimates of burden and direct radiative forcing. Atmos Environ 33:3225–3235

Vile MA, Wieder RK (1994) Alkalinity generation from Iron reduction versus sulfate reduction in wetlands constructed for acid mine drainage treatment. Water Air Soil Pollut Focus 69:425–441

Vile MA, Bridgham S, Wieder RK (2003a) Response of anaerobic carbon mineralization rates to sulfate amendments in a boreal peatland. Ecol Appl 13:720–734

Vile MA, Bridgham S, Wieder RK, Novák M (2003b) Atmospheric sulfur deposition alters pathways of gaseous C production in peatlands Global Biogeochem Cycles 17:1058. DOI 10.1029/2002GB001966

Vitt DH, Bayley SE, Jin TL (1995) Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Can J Fish Aquat Sci 52:587–606

Watson A, Nedwell DB (1998) Methane production and emission from peat: the influence of anions (sulphate, nitrate) from acid rain. Atmos Environ 32:3239–3245

Wieder RK, Lang GE (1986) Fe, Al, Mn, and S chemistry of *Sphagnum* peat in four peatlands with different metal and sulfur input. Water Air Soil Pollut 29:209–320

Wieder RK, Lang GE (1988) Cycling of inorganic and organic sulfur in peat from Big Run Bog, West Virginia. Biogeochemistry 5:221–242

Wieder RK, Yavitt JB, Lang GE (1990) Methane production and sulfate reduction in two Appalachian peatlands. Biogeochemistry 10:81–104
Winfrey MR, Rudd JWM (1990) Environmental factors affecting the formation of methylmercury in low pH lakes. Environ Toxicol Chem 9:853–869
Xun L, Campbell NER, Rudd JWM (1987) Measurements of specific rates of net methyl mercury production in the water column and surface sediments of acidified and circumneutral lakes. Can J Fish Aquat Sci 44:750–757
Zhang Y, Mitchell MJ, Christ M, Likens GE, Krouse HR (1998) Stable sulfur isotopes at Hubbard Brook Experimental Forest, New Hampshire. Biogeochemistry 41:259–275

13 The Hydrology of Peatlands

Donald I. Siegel and Paul Glaser

13.1 Introduction

Almost from the time of its inception, the field of peatland ecology has had a strong hydrological foundation. Early investigators in the British Isles and northern Europe recognized that (1) waterlogged soils retard decomposition, leading to peat formation and (2) water-table elevations influence plant growth, creating the characteristic vegetation patterns of hummocks, hollows, and pools (Gorham 1953; Iversen 1973: Sjörs 1963). Without any formal training in hydrology and only rudimentary chemical data, some of the early workers also recognized that the source of the waters percolating through a peatland is a decisive determinant for ecosystem development (Chap. 2). Dau (1823), for example, recognized three types of peatlands, one of which, the raised bog, obtained all its salts and water from the atmosphere. The absence of "geogenous" waters on these peat mounds was responsible for the abundance of *Sphagnum* and the impoverished acidiphilous flora.

Through the twentieth century ecological investigations on peatlands continued to build on this close link between hydrology and the ecology of the biota. Weber (1902) advanced the concept that the development of a raised bog creates a three-dimensional organic landform with its own hydrological system. This system is fed solely by atmospheric precipitation and is isolated from geogenous waters that apparently discharged at the bog margins, forming fen water-tracks or "rullen." He noted the chemical differences between the dilute acidic bog waters and the waters in adjacent fens that were less acidic and contained higher concentrations of dissolved solids, particularly calcium. His work fostered the competing themes of allogenic (environmental) vs. autogenic (biotic) drivers for peatland development that culminate into a state of stasis under a given climatic regime (Glaser 2002).

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Technological advances in the twentieth century confirmed the exceptionally close relationship of the northern peatland flora to the acidity, dissolved cations, and nutrients of the surface waters. Swedish scientists, for example, demonstrated the exceptionally close relationship of the species assemblages in peatlands to the pH and calcium concentrations of the surface waters, relationships that were successfully applied to peatlands across the circumboreal belt (reviewed in Sjörs 1963, 1983). However, investigations of the physical hydrology of peatlands were largely limited to applications of surface hydrology because of the perception based on laboratory studies that the permeability of deep peat was too low to permit vertical or horizontal flow of water (Ingram 1983). As a result peatlands were assumed to be divided into two compartments: (1) an upper zone of high porosity and low levels of decomposition in which the pore fluids flowed rapidly and (2) a lower, more deeply humified zone with exceptional low permeability and essentially negligible flow. It is therefore not surprising that the field of groundwater hydrology was not applied to peatland science until the 1980s when this methodology provided the first direct confirmation of the concepts of minerotrophy and ombrotrophy in northern peatlands.

Since Ingram's (1983) comprehensive review remains the best overview of the surface hydrology of peatlands, we will instead summarize some subsequent work that shows how groundwater hydrology has expanded our appreciation of the close linkages between hydrology and peatland ecology, while confirming some of the basic assumptions with regard to ombrotrophy and minerotrophy. This review will (1) provide some basic principles of groundwater hydrology, (2) compare analytical vs. groundwater modeling approaches, and (3) show examples of applications to large peatlands.

13.2 Basic Principles

Ground water is defined as subsurface water that flows through any saturated porous media regardless of its composition (mineral or organic), degree of consolidation (rock or sediment), or location (terrestrial or marine). In this context, peat pore waters are considered ground water, although for the sake of clarity we will reserve this latter term for pore waters originating in the mineral substratum.

Several mathematical equations govern groundwater flow through peat and other porous media. All porous media have spaces, called pores, through which fluids can potentially pass under the influence of gravity and differences in pressure. Total porosity is expressed as a mathematical ratio:

$$n_T = V_P / V_T \quad (13.1),$$

where n_T is the total porosity, V_P is the volume of spaces unoccupied by solid material (mineral or plant fibers), and V_T is the total volume of the porous medium.

Total porosity has less effect on groundwater flow than effective porosity, which is the volume of the large-diameter (more than 0.5 mm) connected pores to the total volume of the porous medium. Ground water and other fluids can only move through the connected pore space, leaving the remaining pores as "dead pore space." Since all pores are not connected, the effective porosity will always be less than the total porosity.

Primary porosity develops when a rock or soil is formed. Although the total porosity of any rock or mineral soil is spatially variable, it remains relatively constant over decadal or century time scales. In contrast, the effective porosity of peat continually changes both spatially and temporally because of biological processes. Microbial decomposition, for example, continually breaks down the solid-phase peat skeleton, reducing the size of the pores and increasing the bulk density of the peat. As the pores become smaller the capillary tension between the pore waters and peat walls increases exponentially, thereby restricting the movement of water under the force of gravity or pressure. Although the total porosity may remain unchanged, the effective porosity of the peat will continue to decrease in time without the formation of secondary porosity.

Secondary porosity is produced by fractures or other deformations that increase the effective porosity of a porous medium after it has been deposited or emplaced. Pipe systems that permeate blanket bogs (Gilman and Newsome 1980; Jones 1981; Ingram 1983), raised bogs (Glaser and Janssens 1986), or sloping peatlands (Siegel 1988a) in regions with high rainfall are one of the most striking examples of secondary porosity in peatlands. Less dramatic processes that produce secondary porosity in peatlands are (1) changes in water storage that create small surface deformations (Weber 1902; Hobbs 1986; Nuttle et al. 1990; Price and Schlotzhauer 1999), (2) the production and passage of gas bubbles produced as end products of anaerobic decomposition (Glaser et al. 2004a), and (3) chemical transformations that can raise the bulk hydraulic conductivity in peat by 2–5 times as inorganic cations interact with organic acids to dilate the peat pores (Ours et al. 1997).

Effective porosity is not the only material property that controls the movement of water through peat. Equally important is hydraulic conductivity:

$$K = k\rho g/\mu, \quad (13.2)$$

where K is the hydraulic conductivity (dimensions of length per unit time), ρ is the fluid density, μ is the fluid viscosity, g is the accelaration of gravity, and k is the intrinsic permeability, a constant multiplied by the square of a statistical measure of the pore diameter; $k=cd^2$.

Hydraulic conductivity is best measured in situ with piezometer standpipes (Chason and Siegel 1986). Values for both vertical and horizontal hydraulic conductivity can be obtained with piezometers for any particular depth using "slug and bail" tests designed by Hvorslev (1951). Laboratory determinations based on small samples, in contrast, often yield unrealistically low values because of the scale dependency of the important hydraulic parameters. Beard (1972), for example, has demonstrated that the hydraulic conductivity of any porous medium tends to increase over longer flow paths or greater representative volumes as the probability of intersecting a macropore increases.

The hydraulic conductivity of all porous media usually changes with direction (Freeze and Cherry 1979). Usually the greatest differences in K are observed between axes that are parallel and perpendicular to the original bedding planes. Since these bedding planes are generally oriented parallel to the land surface, the values for vertical (K_v) and horizontal (K_h) hydraulic conductivity are therefore used to express the anisotropy ratio (K_h/K_v) of a medium. This ratio is highly variable within the peat column (Chason and Siegel 1986), but values for K_h are generally 1–2 orders of magnitude greater than K_v in large peatlands (Siegel 1983; Romanowicz et al. 1995; Reeve et al. 2001).

Without the formation of secondary porosity, hydraulic conductivity will decline exponentially with depth as various physical and biological processes reduce the volume of interconnected pore space (Baden and Eggelsman 1963; Boelter 1969; Rycroft et al. 1975; Boelter and Verry 1977; Ivanov 1981). As a result peat profiles are commonly divided into two layers with contrasting hydraulic properties: an uppermost acrotelm with very high values for K and a deeper catotelm, in which the hydraulic conductivity is too low to support water movements (Ingram 1978; Ivanov 1981). However, this trend in many large peatlands is obscured by the formation of macropores (Ours et al 1997; Glaser et al 2004a), variations in peat facies (Chason and Siegel 1986), and past changes in rates of peat accumulation (Glaser and Janssens 1986). For example, field measurements made from the profiles of a bog, fen, and spring fen showed almost no relationship between K and the bulk density or peat type (Chason and Siegel 1986). Moreover, the values for K in these peats were 2–6 times higher than those reported for other peatlands and ranged as high as those found in silty sands (1×10^{-4} cm s^{-1}).

Hydraulic conductivity is the proportionality constant in Darcy's Law, the fundamental equation that governs groundwater flow in porous media. Darcy's Law can be expressed in one dimension as

$$Q=KIA, \tag{13.3}$$

where Q is the rate of groundwater flow (dimensions of length cubed per unit time), K is hydraulic conductivity in the direction of interest (dimensions of length per unit time), I is the unitless hydraulic gradient (dimensions of length per unit length), and A is the cross-sectional area across which ground water moves (dimensions of length squared)

The hydraulic gradient is the difference in hydraulic head between two measuring points divided by the distance between these points. Hydraulic head is the elevation (relative to sea level) that water rises in a monitoring well and is a measure of the potential energy of the water at the point where it enters the well. All water moves from regions of high to low hydraulic head. Monitoring wells installed with screens below the water table are called piezometers. They can easily be constructed from a PVC casing and inserted by hand to any depth in peat (Chason and Siegel 1986). By installing clusters of piezometers at different depths it is possible to determine if groundwater flow is downward (recharge), upward (discharge), or horizontal (lateral) relative to the peat surface (Fig. 13.1).

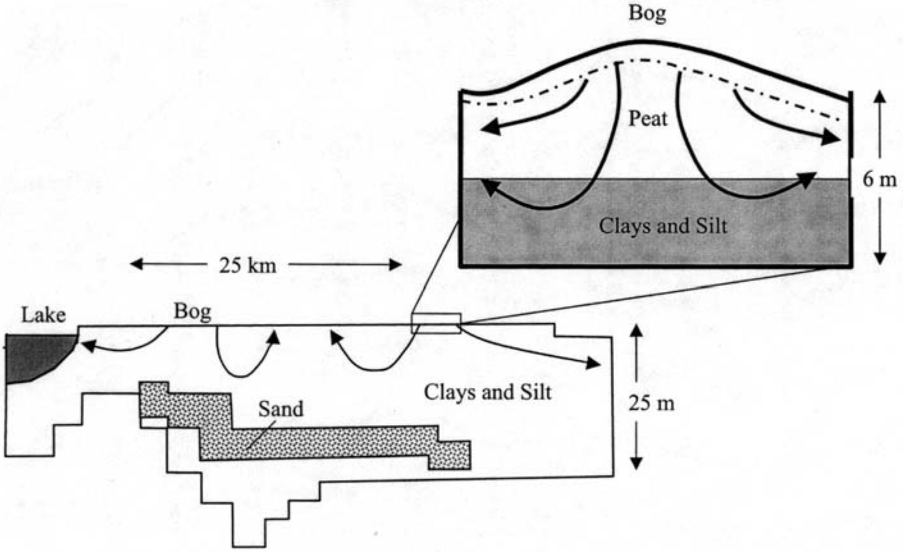

Fig. 13.1. A portion of a regional numerical finite-difference model of theoretical groundwater flow under a large peatland similar to the Glacial Lake Agassiz peatlands of northern Minnesota. The *dash/dot line* in the *inset* is the water table, defining a raised mound under the raised bog. The peat thickness is only 3 m, a veneer on the mineral soils underneath. Note how the theoretical model calculated groundwater flow paths originating at the raised bog and which moved downward through the humified peat and into the mineral soils. These flow paths then move upward toward the bog margins, to discharge at fens. Subsequent hydrological field studies and refined numerical models fundamentally confirm the pervasive influence of raised-bog water-table mounds on the groundwater hydraulics of peatlands. (After Siegel 1983)

Equipotential lines for hydraulic head are often contoured in water-table maps to show horizontal directions for groundwater flow, whereas hydrogeologic cross sections through a porous medium are constructed to show vertical directions of flow.

Darcy's Law can be reconfigured to incorporate effective porosity (n_e) in order to calculate the average velocity (i.e., seepage velocity, v) of ground water between two points:

$$v = KI/n_e. \tag{13.4}$$

Equations 13.3 and 13.4 are included in the more complex differential equations governing how hydraulic potential varies in porous media in space and time. Studies on peatland hydrogeology usually assume steady-state conditions in which the spatial variability of hydraulic head does not vary seasonally (i.e., seasonality can be smoothed out to a general trend as a first approximation). For this case the second-order partial differential equation governing how hydraulic head varies in three-dimensional space (x,y,z) is

$$d^2h/dx^2 + d^2h/dy^2 + d^2h/dz^2 = 0. \tag{13.5}$$

For studies that directly incorporate seasonal changes in hydraulic head, Eq. 13.6 contains terms on the right-hand side for water-storage properties and change in hydraulic head with time.

13.3 Modeling the Hydrodynamics of Groundwater Flow Systems in Peatlands

13.3.1 Analytical Approaches

The first attempts to model the hydrodynamics of peatlands employed a general water balance approach (Wickman 1951; Fig. 13.2) based on the assumptions that (1) water readily moved through the upper layers of undecomposed peat and (2) flow was negligible in the deeper humified peat (Boelter 1969; Boleter and Verry 1977; Ingram 1978; Ivanov 1981). As a result, groundwater flow models incorporating Darcy's Law were only slowly applied to problems in peatland hydrology (Ivanov 1981; Ingram 1982; Siegel 1983). Two different types of mathematical models are employed. Analytical models exactly solve the differential equations governing groundwater flow but require simple geometry, uniform properties, and idealized boundary conditions (Konikow and Bredehoeft 1992).

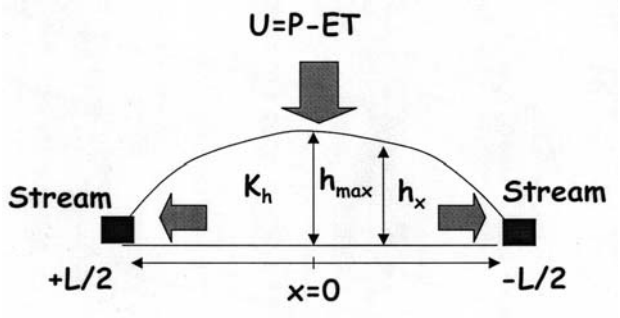

Fig. 13.2. Conceptual model for an analytical solution for groundwater flow driving by a water-table mound and recharge. *U* is net recharge (dimensions of length per unit time), *K* is the horizontal hydraulic conductivity (dimensions of length per unit time), *H* is the water-table elevation above the bottom of the bog, assumed as flat (dimensions of length), *L* is half the width of the bog along the cross section (dimensions of length), and *x* is the distance from a stream toward the center of the bog (dimensions of length)

This type of model is best reserved for theoretical analyses or very simple field conditions. In contrast, numerical models solve the governing equations by successive approximation within a model domain that is divided into a mesh of elements or nodes (Wang and Anderson 1982; Anderson and Woessner 1992). These models relax the simplifications imposed by analytical models and therefore provide a more realistic solution for the hydrodynamics of heterogenous field sites.

The analytical approach was popularized by Ingram's (1982) seminal analysis of the water-table mound in Dun Moss, a small raised bog in Scotland. Ingram's model was based on the Dupuit–Forcheimer approximation for Darcy's Law that assumes (1) vertical flow is negligible, (2) the slope of the water table is equal to the hydraulic gradient, and (3) no seepage face occurs except at the model boundary. Ingram used Childs (1969) solution for Dupuit flow that is expressed as

$$U/K=H^2/(2Lx-x^2), \tag{13.6}$$

where *U* is *P–ET*, net recharge (dimensions of length per unit time), *K* is the horizontal hydraulic conductivity (dimensions of length per unit time), *H* is the water-table elevation above an assumed flat bottom of the bog (dimensions of length), *L* is half the width of the bog along the cross section (dimensions of length), and *x* is the distance from a stream toward the center of the bog (dimensions of length).

Because this model uses single input values for each parameter and requires simple boundary conditions, it is best applied to small symmetric raised bogs like Dun Moss, which are bordered by two parallel streams.

Although the model solutions fit the actual water-table topography observed at Dun Moss, this approach proved less suitable when it was applied to irregularly shaped raised bogs with more complex boundary conditions (Kneale 1987). Armstrong (1995) and Winston (1994) tried to extend the application of this model by adding a systematic decrease in hydraulic conductivity with depth, and peat bioaccumulation and degradation rates. Baird and Gaffney (1994), however, challenged Armstrong's (1995) modifications because the values for hydraulic conductivity did not incorporate secondary porosity.

Despite its limitations, the Ingram model inspired new theoretical approaches for analyzing feedbacks between hydrology and carbon cycling in peatlands. New sets of analytical models were developed that coupled the equation for Dupuit flow and peat growth (Clymo 1984, 1991; Winston 1994; Ivanov 1981; Beleya and Clymo 2001) based on the understanding that water-table elevations (i.e., thickness of the aerobic layer) largely regulate rates of decomposition in peatlands. This basic assumption permits a general application of groundwater models to the peatland ecology. Glaser et al. (2004b, c), for example, used an expanded form of the Dupuit equation (Siegel 1981; Fetter 2000) to investigate interactions between landscape processes and bog development in the Hudson Bay Lowlands. By means of a sensitivity analysis they showed that the growth of water-table mounds in the interfluves between adjacent streams can drive the formation and development of raised bog. They also demonstrated that the Dupuit equation predicts an unrealistically high water-table mound for bogs in interfluves wider than 5–6 km. Above this threshold the surface of a bog is prone to flooding, thus violating a fundamental assumption for Dupuit flow. This modeling result provides an explanation for the observation that bogs larger than 20 km^2 consistently have drains or internal water tracks (Glaser et al. 1981, 2004b; Glaser 1987, 1992). Finally, they used simulations based on the Dupuit formula to show how asymmetric downcutting by the bounding streams will alter the geometry of the bog cupola, producing a shift in the bog crest toward the upgradient bog margin.

The simplifying assumptions that make analytical models so suitable for theoretical-type studies also impose limitations on the degree to which they can be directly tested by field observations. Not only are most peatlands heterogeneous in space and time, but the responses of these ecosystems to transient changes in the environment may be the most interesting and significant aspects of the system. Numerical models are therefore preferred for most field studies because of their greater flexibility and capacity to focus future field investigations.

13.3.2 Numerical Approaches

At the same time that Ingram's (1982) seminal paper appeared, Siegel (1981, 1983) used a numerical two-dimensional groundwater model to simulate flow systems in a large peat basin in northern Minnesota. This type of model, which combines Darcy's Law with the Laplace continuity equation, provides an approximate solution for the water-table topography, directions and magnitude of groundwater flow, and complete water balances for any given area. In a benchmark numerical-modeling experiment, Freeze and Witherspoon (1978) had previously shown how subtle sinusoidal changes in the regional water table can compartmentalize groundwater flow into discrete local flow systems.

Siegel's model showed that water-table mounds form under raised bogs that drive local recharge (downward flow) systems downward through the peat and into underlying glacial deposits. A rise in the water table mound of only 30 cm was sufficient to drive these flow systems downward 30 m into the mineral substratum, whereas a rise in the mound of 60 cm was capable of driving flow down 60 m to the bedrock basement. Upon reaching the bedrock these flow systems curved upward and discharged at the margins of the raised bogs. Although the groundwater fluxes in these simulated flow systems were small, his calculations indicated that the mixing of as little as 10 % ground water from the mineral substratum with 90 % surface water from a raised bog would raise the pH at the surface from 3.6 to 7.6 (Siegel 1983).

These model simulations were first tested in the Lost River peatland where two peat mounds with contrasting vegetation and water chemistry developed in close proximity to each other (Siegel and Glaser 1987; Glaser et at 1990). Field data (e.g., head gradients and pore-water chemistry) indicated that ground water discharges at the surface of one mound, which is a spring fen; whereas ground water recharges downward at the other mound, which is a raised bog. Although this investigation provided the first direct confirmation of the hydrological concept of "ombrotrophy," many unexpected findings at this bog site (e.g., seasonal reversals in hydraulic head at depth, zones of overpressure, and topographic oscillations) were more fully explained by subsequent work in the region (Almendinger et al. 1986; Romanowicz et al. 1993; Siegel et al.1995; Glaser et al. 1997, 2004a; Rosenberry et al. 2003). During the same period, Wilcox et al. (1986) showed that another spring-fen mound, called "Cowles Bog," was also formed by discharging ground water.

These studies together showed that numerical groundwater models are the best approach for modeling all but the simplest peatland ecosystems, but these models still need to be rigorously calibrated, parameterized, and tested by field investigations. Numerical computer models have subsequently been widely applied to peatlands in northern Minnesota and other regions; particularly Canada and the Netherlands. Boldt (1986), for example, showed how the location of discharge zones in large peatlands may be determined by heterogeneities in the geologic substratum, such as buried sand, gravel lenses, and bedrock ridges. Seismic reflection profiling (Miller et al. 1992) in this region later confirmed these buried bedrock ridges under peat landforms where ground water discharges at the land surface.

The role of geologic factors was further explored by a suite of numerical groundwater models applied to large peat basins in northern Minnesota and the Hudson Bay Lowlands. Roulet and McKenzie (1998), for example, showed how major breaks in the regional slope could shape both the regional flow systems and zonation in peatland vegetation. Their model simulated the formation of regional flow systems that recharged on the higher interior plains and discharged downgradient along nick points closer to the coast. In contrast, Reeve et al. (2000, 2001) used coupled groundwater–mass transport models to show that vertical flow systems tend to develop within peatlands that cover porous sand and gravel deposits, whereas horizontal flow systems are associated with peatlands underlain by less permeable soils of clayey silt. These coupled models also showed that inorganic solutes could be advected upward from the mineral substratum to the peat surface by transverse dispersion and dispersive mixing along lateral flow paths.

Numerical groundwater models provide valuable insights into the functioning of peatlands because they can be directly tested by explicit hydrological or geophysical measurements. They, therefore, can be used as an initial exploratory tool to guide field investigations and generate hypotheses on peatland formation. The models also serve as heuristic tools to analyze complex and otherwise inexplicable datasets. Among the most perplexing problems in peatland hydrology is the response of peatland ecosystems to transient changes in climate, biota, or geology.

13.4 Transient Hydraulic Conditions

Most peatland groundwater models are designed for steady-state conditions in which hydraulic head varies in space but not time. In the field, however, hydraulic head often varies temporally in response to external (e.g., climatic, geomorphic) or internal (e.g., biotic or diagenetic) drivers. Siegel and Glaser (1987), for example, reported seasonal flow reversals within the deeper peat of a raised bog in northern Minnesota. These flow reversals were associated with a persistent zone of overpressure at 1-m depth (Siegel and Glaser 1987) and topographic oscillations in excess of 10 cm (Almendinger et al. 1986). Subsequent studies showed that both the zone of overpressure and flow reversals were not only characteristic of many raised bogs across northern Minnesota, but were also driven by the regional drought cycle (Romanowicz et al. 1993; 1995; Siegel et al. 1995; Glaser et al. 1997). In this relatively dry region, raised bogs appear to have formed over regional discharge zones for ground water, which upwells into the deeper portion of the peat profile. During wet years, water-table mounds under the bogs drive flow downward into the deeper peat and deflect the upwelling ground water laterally to the bog margins (Fig. 13.1). After several years of drought, however, the water-table mounds dissipate and upwelling ground water can then rise higher in the peat profile (Siegel et al. 1995).

Despite their rapidity, these flow reversals only produce noticeable changes in the pore-water chemistry over decadal timescales (Fig. 13.3). The chemical profiles in bogs and fens hardly change from year to year (Siegel and Glaser 1987; Romanowicz et al. 1993, 1995), but over a decade, a convex chemical profile typical of a discharge system can completely switch to a concave chemical profile typical of a local recharge cell (Siegel et al. 1995; Glaser et al. 1996, 1997). The dynamics of these flow reversals were simulated by a coupled groundwater flow–solute transport model that closely reproduced the actual profiles of pore-water chemistry measured in the Lost River peatland over a 10-year period (Siegel et al. 1995). In addition, plant macrofossils and geochemical evidence indicate that peatland development at this site was driven by at least two major flow reversals at 1,200 and 2,000 BP (uncalibrated radiocarbon years before AD 1950; Glaser et al. 1990, 1996).

Seasonal flow reversals and overpressures were subsequently observed in other peatlands where these phenomena may be related to a slow dissipation of excess pore pressure following a drop in the water table

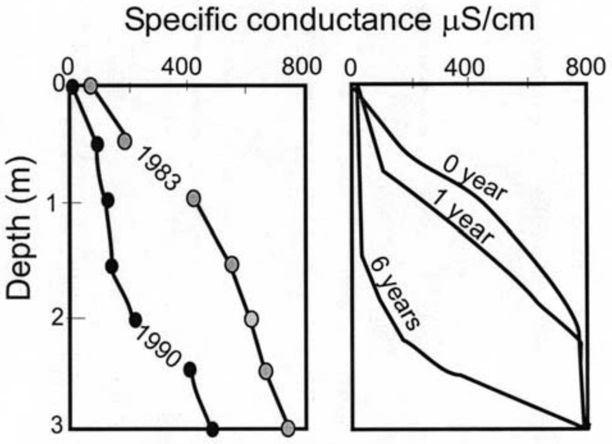

Fig. 13.3. Decadal scale changes in pore water chemistry and simulation results at the Lost River peatland. The *left panel* presents measured temporal field data, whereas the *right panel* presents modeled results. (After Siegel et al. 1995)

(Waddington and Roulet 1997; Devito et al. 1997; Fraser et al. 2001; Van Setens and Price 2001). Alternatively, biogenic gas bubbles may generate overpressure by locally occluding at pores and forming confining layers as originally hypothesized by Romanowicz et al. (1995). The capacity for methane bubbles to occlude peat pores was first suggested by Dinel et al. (1988) and Brown et al. (1989) and was later supported by laboratory and field studies (Reynolds et al. 1992; Beckwith and Baird 2001; Fraser et al. 2001). In the Red Lake peatland, gas bubbles have a greater tendency to become trapped under wood layers in which woody elements confer greater tensile/shear strength to the peat (Glaser et al. 2004a). The accumulation of free-phase gas under these wood layers forms local overpressured compartments that periodically rupture in response to external (e.g., changes in the water table or atmospheric pressure) or internal (e.g., excess gas accumulation) drivers. These ruptures trigger a massive release of methane to the atmosphere that may exceed 35 g CH_4 per event associated with topographic oscillations in excess of 16 cm in a 4-h period (Glaser et al. 2004a). Smaller topographic oscillations were observed by Fechner-Levy and Hemmond (1996) in a small peatland elsewhere that they related to the accumulation and release of trapped gas.

Because pore pressure is almost the same as lithostatic pressure in peatlands, the methane reservoir, when present, causes the land surface to behave as a hydraulic "barometer," contracting and expanding in response to changes in atmospheric pressure or the pressure from the overlying saturated peat (Glaser et al. 2004a;). In addition, these overpressured gas reservoirs will alter the hydrodynamical interactions between local and regional flow systems that are normally controlled in peatlands by the hydrogeologic setting. The superposition of geologically defined flow systems with overpressures generated by microbial metabolism creates an additional level of complexity in considering the hydroecology of large peatlands. Multiple tools and approaches are therefore needed to characterize groundwater flow and solute transport in large peatlands. Some of the more robust of these approaches are geochemical in nature.

13.5 Geochemical Methods to Verify Groundwater Models

13.5.1 Geochemical Tracers

Geochemical methods provide an independent means to trace the geometry and hydrodynamics of groundwater flow systems. Because the deeper pore waters are only flushed slowly over decadal time scales, the solute profiles in a peat deposit will integrate the longer-term hydrodynamic trends. The chemical composition of peat pore waters depends partly on the source of the water and also on biogeochemical reactions within the peat. The surface of a raised bog, for example, only receives water from the atmosphere, which has insufficient alkalinity (in the form of dissolved CO_2 and dustfall base cations) to neutralize the strong organic acids released from decomposing peat. Bog surface waters are therefore acid ($pH<4.2$) with low concentrations of inorganic salts (e.g., Ca less than 2 mg L^{-1}), but much higher concentrations of organic acids, which produce large anion charge imbalances (Hemond 1980; Gorham et al. 1985; Reeve et al. 1996; Glaser et al. 2004b; Siegel et al. 2006). However, both the pH and the calcium concentrations in bog pore waters will rise with increasing depth if precipitation moving downward into the deeper peat mixes with circumneutral ground water upwelling from the mineral substratum below (Siegel et al. 1995; Glaser et al. 1997).

In contrast, the surface waters on fens are mixtures of precipitation and ground water that was transported from mineral sediments, either at the base or at lateral margins of a peat deposit. As a result, fen waters have a much greater range of pH (4.2–8.0) and inorganic base cations (e.g., Ca concentrations 2–60 mg L^{-1}) but apparently weaker organic acids than those found in the bogs (Siegel et al. 2006). With increasing depth the pH and calcium concentrations of the fen pore waters also rise owing to either the upwelling of ground water from the mineral substratum (Siegel and Glaser 1987) or upward transverse dispersion and dispersive mixing of solutes along lateral flow paths (Reeve et al. 2001).

Relatively simple mathematical tools can be used to determine the volume of ground water that discharges into peat profiles from mineral sediment. These methods are most useful at sites where there is a sharp chemical contrast between the surface waters of the peatland and ground water in the underlying mineral sediments. The simplest approach uses a major solute (e.g., Mg or Na) that behaves as a conservative "nonreactive" tracer (Siegel and Glaser 1987). Other major solutes are less effective as tracers because of (1) uptake by organisms (e.g., Ca and K), (2) reduction in anoxic condition (e.g., S or Fe), or (3) insufficient contrast between surface water and ground water (e.g., Cl). Specific conductance (millisiemens per centimeter) can be used as a surrogate for the combined concentration of nonreactive solutes when it is calibrated against total dissolved solids.

The proportions of ground water and surface water in a representative volume of peat pore water can be calculated from the concentrations of relatively nonreactive solutes in a simple bivariate mixing model:

$$n_{gw}=(C_{mix}-C_{p})/(C_{gw}-C_{p}), \tag{13.7}$$

where n_{gw} is the fraction of ground water in pore water at a particular depth in the peat column, C_{mix} is the concentration (or measurement) of the tracer in the mixture, C_p is the concentration (or measurement) of the tracer in precipitation, and C_{gw} is the concentration (or measurement) of the tracer in the ground water.

To optimize this approach, the percentage of ground water in a sample should be calculated from several different tracers for consistency (Siegel and Glaser 1987; Glaser et al. 1990). Once the percentage of ground water has been determined geochemically, it can be checked for reliability against the values calculated by numerical groundwater flow models (Siegel et al. 1995).

The shape of a solute curve in a peat profile sometimes indicates the direction and extent of local flow systems. These shapes are controlled by the prevailing direction of water movements in the peat and the mechanism for solute mixing. There are two kinds of solute mixing: chemical diffusion and hydrodynamic dispersion. A one-dimensional solution to the mathematical equation (called the advective–dispersive equation) defining both processes is

$$C(_{z,t})=1/2C_{o}\mathrm{erfc}\{[(z-vt)/(D_{z}vt)^{0.5}]+\exp(vz/D_{z})\mathrm{erfc}[(z+vt)/(D_{z}vt)^{0.5}\}, \tag{13.8}$$

where $C(_{z,t})$ is the concentration (dimensions of mass per unit volume) of the solute at a given depth (z) at a given time (t) when solute transport began, v is the vertical seepage velocity (dimensions of length per unit time) from Darcy's Law, z is the depth from where solute transport began, t is the time since solute transport began, and erfc is the complementary error function of the argument in the following brackets. The complementary error function takes on the form of a statistical distribution common to diffusive processes. D_z is the coefficient of hydrodynamic dispersion (dimensions of the product of length squared and time), $D_z\alpha v+D^*$, where α is dispersivity (dimensions of length) and D^* is the coefficient of molecular diffusion (dimensions of the product of length squared and time).

When the seepage velocity is zero, the solution to the advective dispersion equation reduces to Fick's Law for chemical diffusion:

$$C_{(z,t)}=1/2C_{o}\mathrm{erfc}[(z)/(D_{z}{}^{*}t)^{0.5}].$$

Molecular diffusion is usually considered from the bottom to the top of a peat profile because (1) inorganic solute concentrations are usually higher in the underlying mineral sediments and (2) molecules diffuse from regions of higher to lower chemical potential. The concentration of solutes in the peat pore waters must fall between those of the two end members, which in this case will be the surface waters and underlying ground water. Assuming that the rate of peat accumulation is greater than the rate of chemical diffusion, we can calculate a theoretical concentration versus depth curve for diffusive transport for any solute of interest. The total time used for transport in the equation is determined from the radiocarbon age of the basal peat.

The theoretical diffusion profile defines an upwardly concave curve. Whether the *net* direction of groundwater flow is upward, downward, or horizontal is determined by comparing the observed solute profile with the one calculated for diffusion alone. If advective transport is downward from the peat surface, the observed concentration profile will plot *below* the diffusive profile because advective transport is opposite to the direction of diffusive transport. If there is substantial groundwater advection upward, the profile will be *convex* upward since advective transport upward will be in the same direction as diffusive transport (Siegel and Glaser 1987; Siegel 1988a, b).

Siegel (1988a,b) used this approach to confirm vertical flow relationships determined from head measurements in sloping Alaskan peatlands underlain by gravel and sand. In a more sophisticated approach, Siegel et al. (1995) solved the advective dispersive equation numerically, incorporating both downward recharge and upward discharge to determine the residence time of water in a bog at the Glacial Lake Agassiz peatlands. There, the modeling effort suggested that active pore water in bogs can be replenished almost completely within a decade (Fig. 13.4).

The simple approach described previously, solving the advective dispersion equation in the vertical dimension, is not suitable for all situations. First, it can only be used where solute concentrations near the peat surface are different from those in the underlying mineral sediments by an order of several factors or more. The best examples are where acidic raised bogs cover calcareous mineral sediments as cited earlier or where peatlands are subject to high loadings of nutrients or acidic anions. Thus, this analysis is not useful for peatlands covering granitic or highly leached mineral deposits or extremely rich fens over calcareous substrates. Also, Reeve et al. (2001) determined from detailed numerical modeling experiments that the deeper pore waters in bogs could have substantial geogenous composition beyond that predicted by diffusion, even where there is no upward vertical flow. Along long horizontal flow paths a statistically small amount of solute movement is transverse to the direction of flow. Over long timescales (10^3 years) and distances (kilometers), dispersive transport can flood the deeper pore waters with geogenous solutes from below.

At scales where dispersion is not a significant transport mechanism, solid-phase geochemical tracers can provide indicators for paleo-flow paths. A period of deep recharge under two peat mounds in northern Minnesota, for example, was inferred by the depletion of acid-soluble

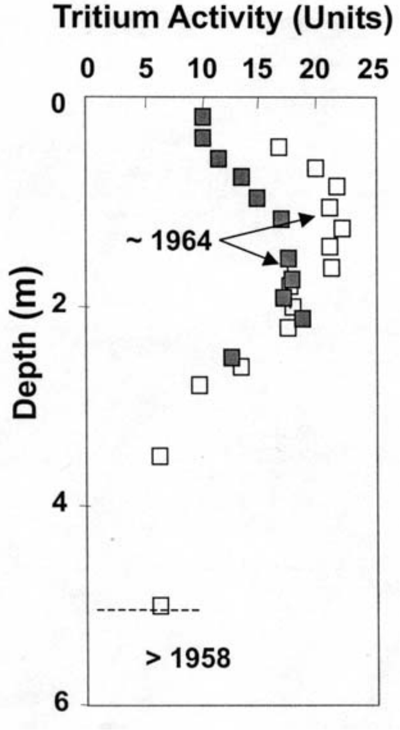

Fig. 13.4. Tritium content in fen water in some Minnesotan fens. The largest values for tritium reflect water that recharged the peat surface ca. 1965. (Siegel, unpublished data)

minerals such as calcite in the mineral sediments under the peat (Bennett et al. 1990; Glaser et al. 1996). In contrast, the sudden discharge of ground water at the surface of one of these mounds is indicated by the weathering pattern of silicate grains embedded in the peat profile and the abrupt switch from bog to fen macrofossil assemblages around 1,200 BP (Glaser et al. 1990, 1996).

These flow reversals were apparently driven by the formation of high water-table mounds within raised bogs during wet periods, followed by the dissipation of these mounds during dry periods, punctuated by extreme droughts that allowed ground water to upwell higher into the peat profile. One way to possibly assess the net steady-state direction of groundwater flow in bogs is to compare the solute concentration in the peat matrix with that in the pore water. The peat matrix should record the long-term history of groundwater flow in the bog because the peat sorbs trace metals as well as some major base cations (Hill and Siegel 1991).

13.5.2 Isotopic Geochemical Methods

Environmental isotopes have broad applications in peatland hydrology such as (1) tracing the geometry of groundwater flow paths, (2) determining the residence times for pore water at any point along a flow path, and (3) determining the sources for any pore-water sample regardless of its complexity. The most commonly used isotopes in peatland studies are those of hydrogen, oxygen, and strontium. The isotopes of any element are distinguished by their number of neutrons and therefore the relationship between atomic number and mass. The most common isotopes of hydrogen, for example, are protium with no neutrons, deuterium with one neutron, and tritium, which has two neutrons and is unstable with a half life of 12.3 years. In contrast, the environmental isotopes of oxygen most commonly used in hydrogeological studies are ^{16}O (the most common form) and ^{18}O (with an atomic mass of 18), whereas those for strontium are ^{86}Sr (the most common) and ^{87}Sr.

13.5.2.1 The Stable Isotopes of Water

The stable isotopes of hydrogen and oxygen can be used to identify the source regions for precipitation that enters a peat profile as well as the seasonality for recharge. Hydrogen and oxygen isotopes are fractionated as air masses move from warmer oceanic source areas to cooler continental regions (Clark and Fritz 1997). Lighter isotopes preferentially evaporate from open water bodies, whereas the heavier isotopes more readily condense from water vapor and are lost in precipitation. Thus, the isotopic compositions of oxygen and hydrogen will evolve along a storm track, while maintaining a nearly linear relationship to each other.

The isotopic ratios for peat pore water should plot on the local linear isotopic curve (called the local meteoric water line, LMWL), which corresponds to that of the precipitation that recharged the bog or fen. If the peatland is recharged by waters that have partly evaporated in the acrotelm, the isotopic values for the peat pore waters will plot at higher values on the LMWL or below it at an acute angle. In contrast, if peat pore waters become enriched in the heavy isotope of hydrogen by the preferential uptake of the lighter isotope during methanogenesis, the isotopic ratio of the pore water will plot along a vertical trend above the LMWL (Siegel et al. 2001; Fig. 13.5).

13.5.2.2 Isotopes Related to Radiogenic Decay

Two radiogenic isotopes are useful for characterizing groundwater flow systems in peatlands: tritium and ^{87}Sr. Tritium is naturally formed by cosmic radiation bombarding helium in the high atmosphere. However, during the 1960s precipitation in the northern hemisphere became enriched in tritium by over 1,000 times because of nuclear weapon testing in the

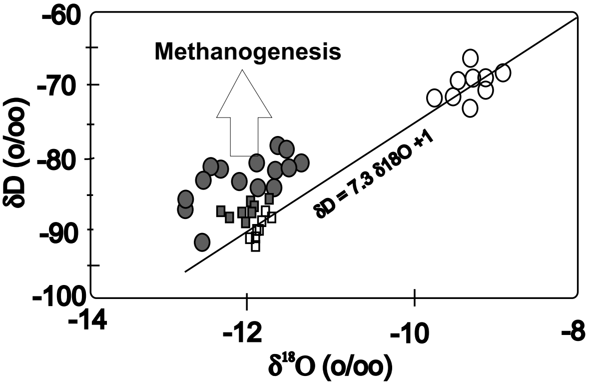

Fig. 13.5. Isotopic composition of peat pore water in two Minnesotan bogs and adjacent fens. One bog–fen complex is shown as *unfilled squares* (fen) and *filled squares* (bog). The other bog–fen complex is shown as *unfilled circles* (fen) and *filled circles* (bog). Note how the isotopic composition of pore water in the bogs plots above the local meteoric water line, consistent with isotopic enrichment associated with methanogenesis. Also, note the remarkable divergence of isotopic values between one bog and its adjacent fen, located only a few kilometers away. This divergence may be caused by the discharge of ground water at the fen from a flow system much farther away than the adjacent bog. In contrast, the isotopic data for the other bog and fen pore waters (*squares*) are near each other, indicating a common source of the waters. (After Siegel et al. 2001; Siegel, unpublished data)

atmosphere. Because of its short half life, the location of this bomb peak can be effectively located in soil profiles to determine groundwater age and flow velocities.

In contrast, ^{87}Sr is produced by the radioactive decay of ^{87}Rb in feldspars and other igneous minerals (Faure 1986); therefore, the ratio of ^{87}Sr to ^{86}Sr of dissolved ground water in mineral soils is inherently different than that found in precipitation, conditioned by oceanic strontium. A plot of the ratio of ^{87}Sr to ^{86}Sr versus the reciprocal of the amount of strontium for peat pore water will produce a linear trend showing mixing of upwelling ground water with acrotelmic pore water originating as precipitation. Figure 13.6 shows such a plot for a bog and fen in the Glacial Lake Agassiz peatlands that defines two linear trends, implying two different groundwater sources for discharge zones less than 2 km apart (Hogan et al. 2000). This study highlights the complexity of local and regional flow systems in large peat basins where the geologic setting imposes important constraints on peatland development.

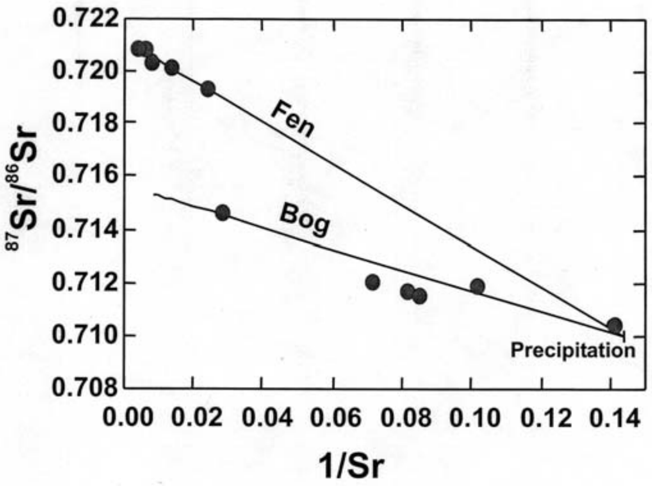

Fig. 13.6. Strontium isotopic composition of peat pore water in a fen and a bog in the Glacial Lake Agassiz peatlands, northern Minnesota. Note the very different mixing lines for proximate bogs and fens, suggesting different groundwater sources. (After Hogan et al. 2000)

13.6 Conclusions

Hydrogeologic investigations over the past 20 years have largely confirmed the concepts developed by peatland ecologists that stress the close linkage between hydrology and peatland ecology. However, these studies have also shown how groundwater flow systems interacting with the climate, geology, and biota of large peat basins largely shape the ecological development of these waterlogged ecosystems. Hydrogeologic methodology therefore provides a rigorous quantitative approach based on first principles of chemistry and physics to constrain the largely empirical statistical methods favored by ecologists.

References

Almendinger JC, Almendinger JE, Glaser PH (1986) Topographic fluctuations across a spring-fen and raised bog in the Lost River peatland, northern Minnesota. J Ecol 74:393–401

Anderson MP, Woessner WW (1992) Applied groundwater modeling. Academic, New York

Armstrong AC (1995) Hydrogeological model of peat-mound form with vertically varying hydraulic conductivity. Earth Surf Processes Landforms 20:473–477

Baden W, Eggelsmann R (1963) Zur Durchlässigkeit der Moorböden. Z Kult Tech 4:226–254

Baird AJ, Gaffney SW (1994) Cylindrical piezometer responses in a humified fen peat. Nord Hydrol 25:167–182

Beard J (1972) Dynamics of fluids in porous media. Elsevier, New York

Beckwith CW, Baird AJ (2001) The effect of biogenic gas bubbles on water flow through poorly decomposed blanket peat. Water Resour Res 37:551–558

Belyea LR, Clymo RS (2001) Feedback control of the rate of peat formation. Proc R Soc Lond Ser B 268:1315–1321

Bennett PC, Siegel DI, Hill B, Glaser PH (1990) The fate of silica in a peat bog. Geology 19:328–331

Boelter DH (1969) Physical properties of peats related to degree of decomposition. Oil Sci Soc Am Proc 33:606–609

Boelter DH, Verry ES (1977) Peatland water in the northern Lake States. U S Dep Agric Tech Rep NC-31:1–22

Boldt DR (1986) Computer simulations of groundwater flow in a raised bog system, Glacial Lake Agassiz peatlands, northern Minnesota. MS thesis, Syracuse University, Syracuse

Brown A, Mathur SP, Kushhner DJ (1989) An ombrotrophic bog as a methane/reservoir. Global Biogeochem Cycles 3:205–213

Chason D, Siegel D (1986) Hydraulic conductivity and related physical properties of peat, Lost River peatland, northern Minnesota. Soil Sci 142:91–99

Childs EC (1969) Introduction to the physical principles of soil water phenomena. Wiley, London, pp 338–340, 406–408

Clark I, Fritz P (1997) Environmental isotopes in hydrogeology. CRC, Lewis

Clymo RS (1984). The limits to peat bog growth. Philos Trans R Soc Lond 303:605–654

Clymo RS (1991) Peat growth. In: Shane LCK, Cushing EJ (eds) Quaternary landscapes. University of Minnesota Press, Minneapolis

Dau JHC (1823) Neues Handbuch über den Torf. JC Hinrichsche Buchhandlung, Leipzig

Devito KJ, Waddington JM, Fowle BA (1997) Flow reversals in peatlands influenced by local groundwater systems. Hydrol Processes 11:103

Dinel H, Mathur SP, Brown A, Levesque M (1988) A field study of the effect of depth on methane production in peatland waters: equipment and preliminary results. J Ecol 76:1083–1091

Faure G (1986) Principles of isotope geochemistry, 2nd edn. Wiley, New York

Fechner-Levy E, Hemond HF (1996) Trapped methane volume and potential effects on methane ebullition in a northern peatland. Limnol Oceanogr 41:1375–1383

Fetter CW (2000) Applied hydrogeology, 4th edn. Prentice-Hall, Englewood Cliffs

Fraser CJD, Roulet NT, Lafleur PM (2001) Groundwater flow patterns in a large peatland. J Hydrol 246:142–154

Freeze RA, Cherry JA (1979) Groundwater. Prentice-Hall, Englewood Cliffs

Freeze RA, Witherspoon PA (1978) Theoretical analysis of regional groundwater flow: 1. Analytical and numerical solutions to the mathematical model. Water Resour Res 2:641–656

Gilman K, Newsome MD (1980) Soil pipes and pipeflow – a hydrological study in upland Wales. British Geomorphological Research Group research monograph series, no 1. Geo Books, Norwich

Glaser PH (1987) The development of streamlined bog islands in the interior of North America. Arct Alp Res 19:402–413

Glaser PH (1992) Raised bogs in eastern North America: regional controls on species richness and floristic assemblages. J Ecol 80:535–554

Glaser PH (2002) CA Weber's benchmark treatise on the Augstumal bog: reflections on its impact and significance to peatland ecology. In: Couwenberg J, Joosten H (eds.) CA Weber and the raised bog of Augstmal. IMCG and Grif & K, Tula, pp 6–21

Glaser PH, Janssens JA (1986) Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. Can J Bot 64:395–415

Glaser PH, Wheeler GA, Gorham E, Wright HE Jr (1981) The patterned peatlands of the Red Lake peatland, northern Minnesota: vegetation, water chemistry, and landforms. J Ecol 69:575–599

Glaser PH, Janssens JA, Siegel DI (1990) The response of vegetation to hydrological and chemical gradients in the Lost River peatland, northern Minnesota. J Ecol 78:1021–1048

Glaser PH, Bennett PC, Siegel DI, Romanowicz EA (1996) Paleo-reversals in groundwater flow and peatland development; in the Lost River peatland, northern Minnesota, USA. Holocene 6:413–421

Glaser PH, Siegel DI, Shen YP, Romanowicz EA (1997) Regional linkages between raised bogs and the climate, groundwater, and landscape features of northwestern Minnesota. J Ecol 85:3–16

Glaser PH, Chanton JP, Morin P, Rosenberry DO, Siegel DI, Ruud O, Chasar LI, Reeve AS (2004a) Surface deformations as indicators of deep ebullition fluxes in a large northern peatland. Global Biogeochem Cycles 18:GB1003. DOI 10.1029/2003 GBO02069

Glaser PH, Siegel DI, Reeve AS, Janssens JA, Janecky DR (2004b). Tectonic drivers for vegetation patterning and landscape evolution in the Albany River region of the Hudson Bay lowlands. J Ecol 92:1054–1070

Glaser PH, Hansen BCS, Siegel DI, Reeve AS, Morin PJ (2004 c) Rates, pathways, and drivers for peatland development in the Hudson Bay lowlands, northern Ontario. J Ecol 92:1036–1052

Gorham E (1953) Some early ideas concerning the nature, origin, and development of peat lands. J Ecol 41:257–274

Gorham E, Eisenreich SJ, Ford J, Sandtelmann MV (1985) The chemistry of bog waters. In: Stumm W (ed) The chemical processes in lakes. Wiley, New York, pp 330–363

Hemond HF (1980) Biogeochemistry of Thoreau's Bog. Concord, Massachusetts. Ecol Monogr 50:507–526

Hill BM, Siegel DI (1991) Groundwater flow and the metal content of peat. J Hydrol 78:1021–1048

Hobbs NB (1986) Mire morphology and the properties and behaviour of some British and foreign peats. Quart J Eng Geol Lond 19:7–80

Hogan JF, Blum JD, Siegel DI, Glaser PH (2000) $^{87}Sr/^{86}Sr$ as a tracer of groundwater discharge and precipitation recharge in the Glacial Lake Agassiz peatlands, northern Minnesota. Water Resour Res 36:3701–3710

Hvorslev JM (1951) Time lag and soil permeability in ground-water observations. Bulletin no 36, US Corps of Engineers, Waterway Experiment Station, Vicksburg

Ingram HAP (1978) Soil layers in mires: function and terminology. J Soil Sci 29:224–227

Ingram HAP (1982) Size and shape in raised mire ecosystems: a geophysical model. Nature 297:300–303

Ingram HAP (1983} Hydrology. In: Gore AJP (ed) Ecosystems of the world 4A. Mires: swamp, bog, fen, and moor. General studies. Elsevier, Amsterdam, pp 67–158

Ivanov KE (1981) Water movement in mirelands. Translated by Thomson A, Ingram HAP (1975) Vodoobmen v bolotnykh landshaftakh. Academic, London

Iverson J (1973) The development of Denmark's nature since the last glacial. Reitzels, Copenhagen

Jones JAA (1981) The nature of soil piping: a review of research. British Geomorphological Research Group research monograph series. Geo Books, Norwich

Kneale P (1987) Sensitivity of the groundwater mound model for predicting mire topography, Nordic Hydrol 18:193–202

Konikow LF, Bredehoeft JD (1992) Ground-water models cannot be validated. Adv Water Resour 15:75–83

Miller P, Shaw GH, Glaser PH, Siegel DI (1992) Bedrock topography beneath the Red Lake peatlands. Geological Society of America, National Meeting, Cincinnati

Nuttle WK, Hemond HF, Stolzenbach KD (1990) Mechanisms of water storage in salt marsh sediments: the importance of dilation. Hydrol Processes 4:1–13

Ours DP, Siegel DI, Glaser PH (1997) Chemical dilation and the dual porosity of humified bog peat. J Hydrol 196:348–360

Price JS, Schlotzhauer SM (1999) Importance of shrinkage and compression in determining water storage changes in peat: the case of a mined peatland. Hydrol Processes 13:2591–2601

Reeve AS (1996). Numerical and multivariate statistical analysis of hydrogeology and geochemistry in large peatlands. PhD dissertation, Syracuse University, Syracuse

Reeve AS, Siegel DI, Glaser PH (2000) Simulating vertical flow in large peatlands. J Hydrol 227:207–217

Reeve AS, Siegel DI, Glaser PH (2001) Simulating dispersive mixing in large peatlands. J Hydrol 242:103–114

Reynolds WD, Brown DA, Mathur SP, Overend RP (1992) Effect of in-situ gas accumulation on the hydraulic conductivity of peat. Soil Sci 153:397–408

Romanowicz EA, Siegel DI, Glaser PH (1993) Hydraulic reversals and episodic methane emissions during drought cycles in mires. Geology 21:231–234

Romanowicz EA, Siegel DI, Chanton JP, Glaser PH (1995) Temporal variations in dissolved methane deep in the Lake Agassiz peatlands, Minnesota (USA). Global Biogeochem Cycles 9:197–212

Rosenberry DO, Glaser PH, Siegel DI, Weeks ED (2003) Use of hydraulic head to estimate volumetric gas content and ebullition flux in northern peatlands. Water Resour Res 39:1066

Roulet NT, McKenzie JW (1998) Role of groundwater in determining the pattern of peatlands in the Hudson Bay lowlands. Geological Society of America annual meeting abstracts with programs 3O(7):A–119

Rycroft DW, Williams DJA, Ingram HAP (1975) The transmission of water through peat. I. Review. J Ecol 63:535–556

Siegel DI (1981) Hydrogeologic setting of the Glacial Lake Agassiz peatlands, northern Minnesota. US Geol Sur Water Resour Invest 81-24a:1–30

Siegel DI (1983) Groundwater and the evolution of patterned mires, Glacial Lake Agassiz peatlands, northern Minnesota. J Ecol 71:913–923

Siegel DI (1988a) The recharge discharge function of wetlands near Juneau, Alaska: part I. Hydrologic investigations. J Ground Water 26:427–434

Siegel DI (1988b) The recharge discharge function of wetlands near Juneau, Alaska: part II. Geochemical investigations. J Ground Water 26:580–586

Siegel DI, Glaser PH (1987) Groundwater flow in a bog-fen complex, Lost River peatland, northern Minnesota. J Ecol 75:743–754

Siegel DI, Reeve AS, Glaser PH, Romanowicz E (1995) Climate-driven flushing of pore water in humified peat. Nature 374:531–533

Siegel DI, Chanton JP, Glaser PH, Chasar LS, Rosenberry DO (2001) Estimating methane production rates in bogs and landfills by deuterium enrichment of pore-water. Global Biogeochem Cycles 15:967–975

Siegel DI, Glaser PH, So J, Janecky DR (2006) The dynamic balance between organic acids and circumneutral groundwater in a large boreal peat basin. J Hydrol (in press)

Sjörs H (1963) Bogs and fens on Attawapiskat River, northern Ontario. Nat Mus Can Bull Contrib Bot 171:1–31

Sjörs H (1983) Mires of Sweden. In: Gore AJP (ed) Ecosystems of the world 4B. Mires: swamp, bog, fen and moor. Regional studies. Elsevier, Amsterdam, pp 69–94

Van Seters T, Price JS (2001) The impact of peat harvesting and natural regeneration on the water balance of an abandoned bog, Quebec. Hydrol Processes 15:233–248

Waddington JM, Roulet NT (1997) Groundwater flow and dissolved carbon movement in a boreal peatland. J Hydrol 191:122–138

Wang H F, Anderson MP (1982) Introduction to groundwater models. Finite difference and finite element methods. Academic, San Diego

Weber CA (1902) Über die Vegetation und Entstehung des Hochmoors von Augstumal im Memeldelta mit vergleichenden Ausblicken auf andere Hochmoore der Erde. Parey, Berlin

Wickman FE (1951) The maximum limiting height of raised bogs and a note on the motion of water in soligenous mires. Geol Foren Stockholm Foerh 73:413–422

Wilcox DA, Shedlock RJ, Henderson WH (1986) Hydrology, water chemistry and ecological relations in the raised mound of Cowles Bog. J Ecol 74:1103–1117

Winston RB (1994) Models of the geomorphology, hydrology, and development of domed peat bodies. Geol Soc Am Bull 106:1594–1604

14 Modeling Ecosystem Processes and Peat Accumulation in Boreal Peatlands

Zicheng Yu

14.1 Introduction

Northern peatlands have accumulated up to about 450 Gt of carbon, mostly during the Holocene (the last 12,000 years) after the last glaciation (Gorham 1991; Clymo et al. 1998). Although northern peatlands have a relatively low average net accumulation rate (e.g., 19.4 g C m^{-2} $year^{-1}$ in western interior Canada; Vitt et al. 2000), their extent, high-latitude location, and the large size of their carbon pool raise concerns that northern peatlands may become significant sources for atmospheric carbon under a changing climate. However, significant uncertainties exist in addressing peatland carbon responses to climate change. The credible assessment of carbon sink–source relationships in peatlands must be based on the understanding of processes responsible for carbon-accumulation patterns over short and long terms.

Peatland dynamics are a function of the balance of photosynthetic production of living plants atop the acrotelm (surface and upper oxic layer) and decomposition of litter and peat in both the acrotelm and the catotelm (underlying anoxic layer) (Ingram 1978; Clymo 1984). Owing to the complex interactions involved in peatland dynamics, a model is often used to facilitate understanding of processes and to make projections. Because peatlands are ecosystems bordering between upland and aquatic ecosystems, they have some unique features that cannot be easily accommodated in standard ways as for other ecosystems. The objective of this chapter is to review some existing models that have been used to simulate peatland carbon dynamics.

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14.2 Model Overview

Yu et al. (2001a) reviewed several models by grouping them into two main categories: conceptual models and simulation models. Conceptual models describe relationships of different processes and can be used to examine the consequences of various assumptions (Clymo 1992). A simulation model is used to mimic and reproduce the behavior of the systems in as much detail as possible. However, this division is not always straightforward. Here we further divide simulation models, based on model complexity, into ecosystem models and hybrid models (Table 14.1). Ecosystem models attempt to consider all the essential parameters that would determine the ecosystem processes concerned, based on a modeler's understanding and preference of important parameters. Hybrid models can be considered as models with complexity intermediate between that of the simplest conceptual models and that of detailed ecosystem models, which are often specifically designed for peatlands.

Table 14.1. Summary of three categories of models for analyzing peatland dynamics

Type	Key feature	Usefulness	Example
Conceptual models	Use the most generalized parameters to capture the first-order patterns and trajectories of peatland dynamics	Understanding long-term fundamental dynamics, and interpreting peat-core data	Clymo (1984); Yu et al. (2003a)
Hybrid/intermediate models	Include the unique features of peatlands by using functional groups as an integration approach	Integration of processes at various time scales, and projections of future changes in peatlands	Hilbert et al. (2000); Frolking et al. (2001); Bauer (2004); Belyea and Malmer (2004)
Ecosystem models	Parameterized for detailed ecosystem processes, through either modifying existing ecosystem models or developing models specifically for peatlands	Understanding the importance and interactions of various parameters and processes responsible for peatland dynamics	Frolking et al. (2002); Zhang et al. (2002); Chimnar et al. (2002)

14.3 Long-Term Trajectory of Peat Accumulation

The simplest model of peatland functions can be used to provide insights into the trajectory or the first-order prediction of the overall long-term dynamics. When we examine a peat-core record, we know that the peat has accumulated a certain amount of mass over the time period determined by basal age. However, the peatland may have reached that mass through very different trajectories (Fig. 14.1). Different trajectories imply different underlying fundamental processes. One such model is the peat growth model proposed by Clymo (1978), which treats the accumulating peat as a two-layer system: the acrotelm (thin, oxic, upper layer) and the catotelm (thick, anoxic, underlying layer) (Ingram 1978; Ivanov 1981). The acrotelm represents the freshly deposited organic materials that are still mostly above the water level, whereas the catotelm is the peat permanently under the water table, representing the long-term, millennial-scale peat deposit. The boundary between these two layers is approximately at the mean depth of the lowest summer water table (maximum water-table depth) for bogs (Clymo 1984), but may be determined by variables other than water-table depth in rich fens, such as redox conditions. The model is originally based on the concept of Ingram's (1982) hydrologically oriented two-dimensional representation of raised bogs in an oceanic climate. The major feature of this model is the use of a proportional decay function (e.g., a single-exponential model; Jenny et al. 1949; Olson 1963; Wieder

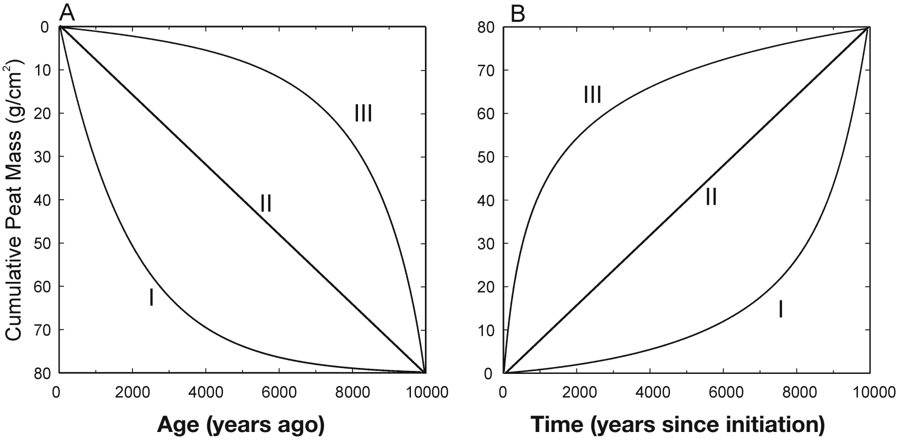

Fig. 14.1. Trajectories of the long-term carbon accumulation in peatlands: **A** derived from peat-core data; **B** simulated over time. There are three first-order scenarios: *I* higher apparent accumulation rates in younger peat and lower rates in older peat (concave pattern); *II* constant apparent accumulation rates; and *III* lower apparent accumulation rates in younger peat and higher rates in older peat (convex pattern)

and Lang 1982) to represent decay processes in both the acrotelm and the catotelm, which assumes that the rate of mass loss is directly proportional to the amount of material remaining.

Carbon accumulation in peatlands is a function of the balance between production of living plants atop the acrotelm and decomposition in both the acrotelm and the catotelm (Clymo 1984). As litter and new peat in the acrotelm are exposed to oxygen and varying water levels, they are subject to a higher decay rate. Once litter and peat are in the catotelm, the decay rate declines sharply and becomes independent of minor climatic fluctuations. The rate of peat transfer from acrotelm to catotelm, or the acrotelm residence time, therefore largely determines net peat accumulation. Water-table depth and the balance of acrotelm production and decay in turn regulate the acrotelm residence time. Clymo (1984) proposed a conceptual model of bog growth, in which constant productivity and exponential decomposition produce a concave cumulative peat mass–age curve, evidenced in most nonboreal oceanic bogs (Fig. 14.2a).

It has been assumed that the processes causing peat to accumulate in continental regions are similar to those in oceanic regions and also that fens are similar to bogs, although with more complicated hydrology (Clymo 1984). There are, however, limited data available to test the valid-

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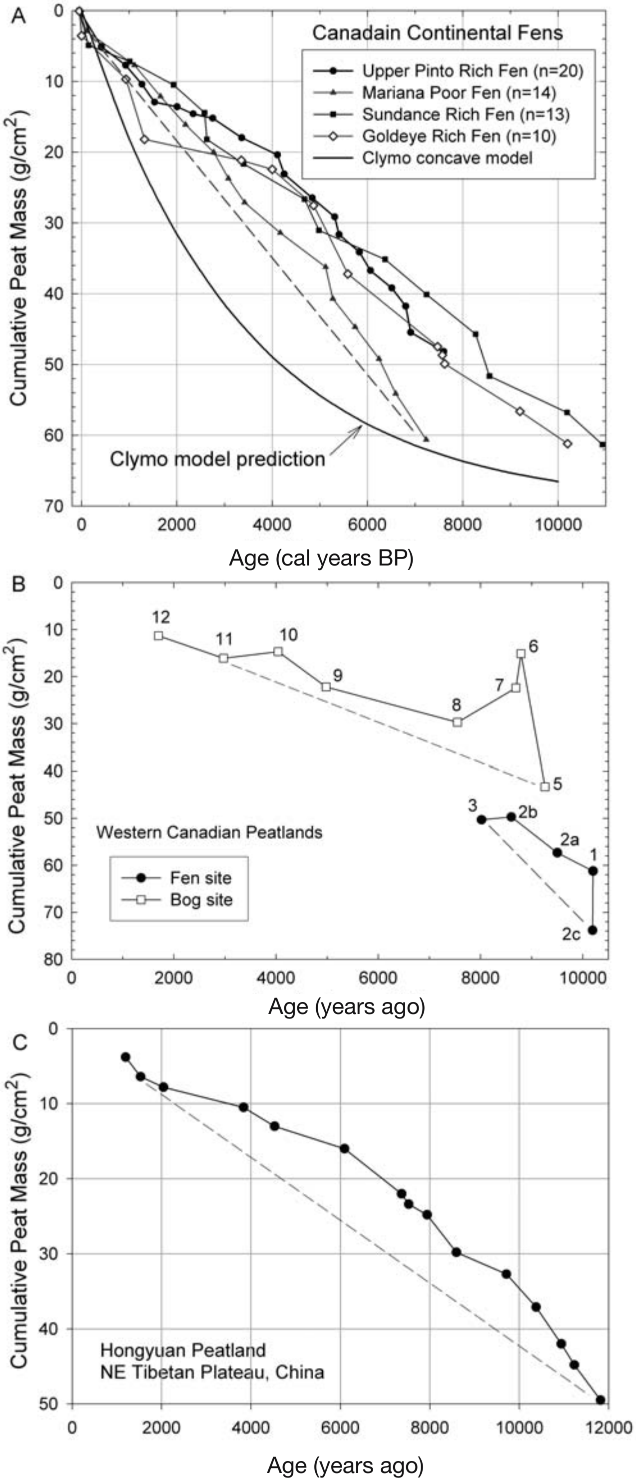
Fig. 14.2. A Peat accumulation pattern from four continental peatlands in western Canada, which have more than ten dating points (*n*; ^{14}C dates and tephra markers with known ages) (Yu et al. 2003a; and unpublished data). Upper Pinto Fen (*UPF*; Yu et al. 2003a), Sundance Fen, and Goldeye Fen (unpublished data) are from the Rocky Mountain Foothills region of Alberta, while Mariana Fen (unpublished data) is in boreal plain of north-central Alberta. The concave pattern ("Clymo model prediction") as often documented in oceanic bogs is also shown schematically for comparison (Clymo 1984). **B** Regional synthesis curves of continental fens and bogs in western Canada, with each point representing the basal date and cumulative peat mass from an individual site. Fens tend to be older and accumulate more peat than bogs do; and both fens and bogs seem to show "convex" accumulation trajectories. For some bogs, if they succeeded from fens, then the age for the bog base rather than basal peatland was used. *1* Goldeye Fen, AB (unpublished data), *2* Muskiki Fen, AB (three cores; Kubiew et al. 1989), *3* UPF, AB (Yu et al. 2003a), *5* Slave Lake Bog, AB (Kuhry and Vitt 1996), *6* Legend Lake Bog, AB (Kuhry 1994), *7* Buffalo Narrows Bog, SK (Kuhry 1994), *8* Mariana Lake site 16 Bog, AB (Nicholson and Vitt 1990), *9* Wathaman Bog, SK (Kuhry 1994), *10* La Ronge Bog, SK (Kuhry et al. 1992), *11* Beauval Bog, SK (Kuhry 1997), *12* Gypsumville Bog, MB (Kuhry 1997). **C** Peat accumulation pattern of Hongyuan sedge-dominated peatland on the northeastern Tibetan Plateau, southwest China, based on 15 ^{14}C accelerator mass spectrometry dates (Hong et al. 2003). Bulk density and organic matter content are not available from the site, so we assumed a constant bulk density of 0.1 g cm^{-3}. The core is dominated mostly by yellowish-brown and brownish-black herbal peat, so likely slight variations in bulk density may not change the general accumulation pattern


A
Canadain Continental Fens
Upper Pinto Rich Fen (n=20)
Mariana Poor Fen (n=14)
Sundance Rich Fen (n=13)
Goldeye Rich Fen (n=10)
Clymo concave model
Clymo model prediction
Cumulative Peat Mass (g/cm^2)
0
10
20
30
40
50
60
70
0
2000
4000
6000
8000
10000
Age (cal years BP)
B
12
11
10
9
8
7
6
5
3
2b
2a
1
2c
Western Canadian Peatlands
Fen site
Bog site
Cumulative Peat Mass (g/cm^2)
0
10
20
30
40
50
60
70
80
0
2000
4000
6000
8000
10000
Age (years ago)
C
Hongyuan Peatland
NE Tibetan Plateau, China
Cumulative Peat Mass (g/cm^2)
0
10
20
30
40
50
0
2000
4000
6000
8000
10000
12000
Age (years ago)

ity of the bog model in continental fens as well as bogs (Kubiw et al. 1989; Charman et al. 1994; Kuhry and Vitt 1996). My focus has been on studies of continental peatlands in western Canada, because there are two main aspects in which the peatlands there differ from the raised bogs that form the basic Clymo model: (1) peatlands are dominantly fens and (2) they are under a continental climate (strong seasonality and lower effective moisture). In continental western Canada (the provinces of Alberta, Saskatchewan, and Manitoba), peatlands cover 365,157 km^2 (approximately 20 % of the land area) and store approximately 50 Gt C (Vitt et al. 2000). However, the majority of these peatlands are fens (64 % of the peatland area, including 35 % treed fens and 29 % open fens), and only 36 % are bogs, with permafrost bogs accounting for 28 % of the total peatland area. About half of the fens are rich fens, which thus comprise the dominant peatland type in continental western Canada. The continental climate has a relatively limited water supply, with strong seasonal and interannual variability. While several western Canadian fens have been moderately well studied (Vitt et al. 1994, 2000), more data will be needed to fully establish the functional differences between continental fens/bogs and the more maritime bogs envisaged by Clymo and others. In the following is a summary of recently published and ongoing work on continental fens and a synthesis of previously published data related to peat accumulation patterns.

Several detailed studies on fens have been published (Kubiw et al. 1989; Yu et al. 2003a) that indicate fens behave differently from bogs in terms of peat accumulation pattern, implying different processes and mechanisms. A detailed record of 20 accelerator mass spectrometry (AMS) dates and centimeter-resolution bulk density and macrofossil analysis from a rich fen (Yu et al. 2003a) and other high-resolution fen records from our ongoing work in Alberta show convex patterns of the age–depth curves (Fig. 14.2a), significantly different from well-documented patterns in oceanic raised bogs (Clymo 1984). From a regional perspective, I have reviewed published sites from western Canada that have multiple radiocarbon dates and bulk density measurements to evaluate the regional patterns of peat accumulation in both bogs and fens. I found that at regional and multiple-site scale these continental peatlands tend to show a convex cumulative mass–age curve (Fig. 14.2b). Similarly other studies on continental bogs also show a convex age–depth pattern (e.g., in Alberta, Kuhry and Vitt 1996; in Siberia, Turunen et al. 2001). A continental peatland dominated by sedges (e.g., *Carex mulieensis*) in southwestern China also showed an unequivocal convex pattern (Hong et al. 2003; Fig. 14.2 c). The peatland is located on the northeastern Tibetan Plateau at an elevation of 3,466 m above sea level, under a continental monsoonal climate with a mean annual precipitation of 700 mm. The 495-cm core of sedge peat was dated by 15 AMS dates, covering the entire Holocene.

Fens tend to be older than bogs, at least in the Rocky Mountain Foothills, and fens of the same ages contain more carbon than bogs. By comparing sites from oceanic regions, Draved Mose accumulated 25 g cm^{-2} dry mass during its 7,000-year history (Aaby and Tauber 1975; Clymo 1984), while a bog at Psaansuo in Finland accumulated 36 g cm^{-2} dry mass over 8,000 years (Ikonen 1993), mostly because of a low bulk density of approximately 0.06 g cm^{-3}. In western Canada, fens accumulated more than 50 g cm^{-2} peat mass over the 8,000-year period.

Greater amounts of peat accumulated at individual sites, together with larger fen areas (Vitt et al. 2000), indicating that fens are much more important in carbon dynamics of northern peatlands, at least in western North America. Also, the fact that fens tend to be more sensitive to climate and hydrological changes (Hilbert et al. 2000; Beilman et al. 2001) implies that fens could play an important role in determining the carbon budget of boreal forests in projected future climate change.

14.4 Causes of Convex Accumulation Patterns

What could have caused the convex age–depth shape of the peat accumulation curves as documented for continental boreal peatlands? Peat addition rates (PARs) and decomposition rates determine long-term peat accumulation in the catotelm. Both variables can change over time, but the PAR is likely to be more sensitive to vegetation type and environmental parameters and thus more variable than the catotelm decomposition rate. The PAR is determined by production and aerobic decomposition above the acrotelm–catotelm interface that usually lies 50 cm or less below the peat surface, where environmental conditions (e.g., temperature, moisture, and chemistry) vary greatly. In contrast, the catotelm decomposition is determined by conditions within the catotelm, and deeper peat is less susceptible to environmental influences acting from the surface.

Here the core data from the Upper Pinto Fen (UPF) core in Alberta are used as an example to explore the underlying processes that might explain the observed pattern (Fig. 14.3a). The peat core was dominated by *Scorpidium scorpioides* between 6,700 and 1,300 calibrated years before the present, and the 15 dating points during that period were analyzed using an extended model with variable PARs (Yu et al. 2003a; Fig. 14.3b). Assuming the catotelm decomposition rate is relatively constant over the 5,400-year period, the extended model suggests that the PAR was initially 191.8 g m^{-2} $year^{-1}$, decreasing exponentially at a rate of 0.00037 $year^{-1}$ to 26.0 g m^{-2} $year^{-1}$ at the end of the period. It is likely that a newly initiated fen on a mineral-rich landscape would have much higher plant production, or lower acrotelm decomposition. A sensitivity analysis reveals the

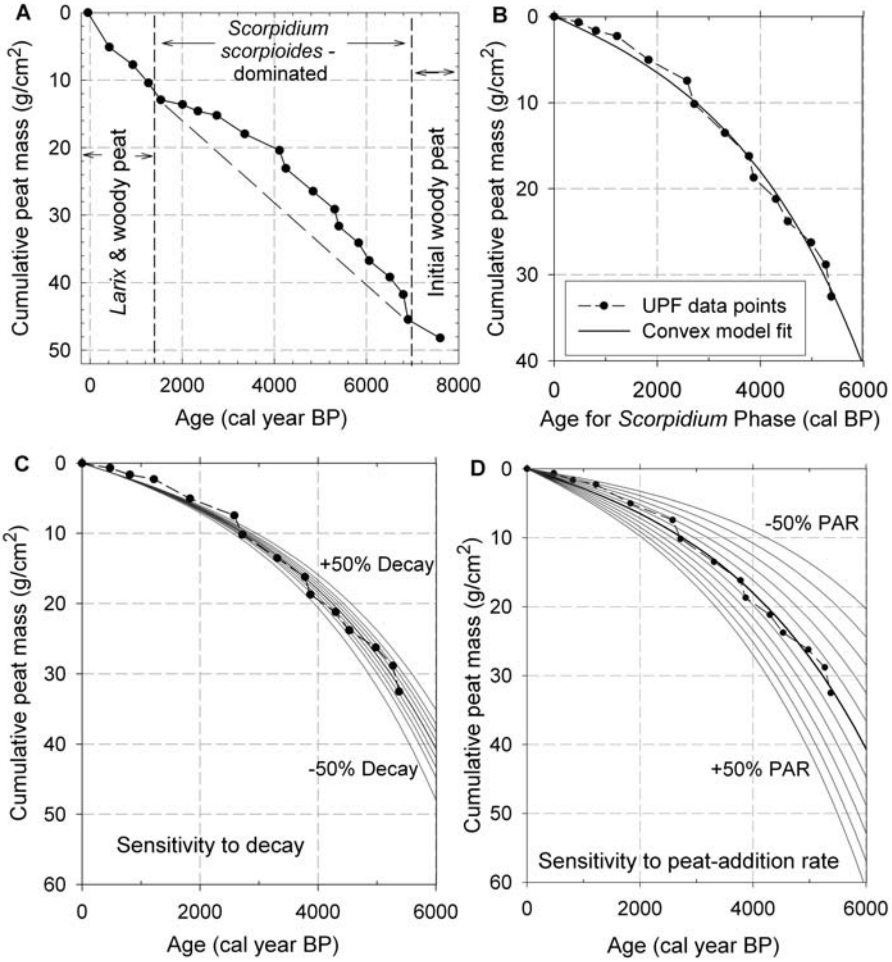


Fig. 14.3. Modeling and sensitivity analysis of the UPF core from Alberta (Yu et al. 2003a). **A** Cumulative peat mass from the UPF core, based on 20 AMS ^{14}C dates and 398 bulk-density measurements. **B** Cumulative peat mass during the period dominated by *Scorpidium* between 6,700 and 1,300 calibrated years before the present for the UPF core (n=15 data points; *dots* and *dashed line*) and modeled fit curve using an extended model with variable peat-addition rates (*PARs*). The model used a fixed decomposition (decay) rate of 0.0002 year^{-1}, which yields an eventual PAR of 26.0 g m^{-2} year^{-1} and an initial PAR value of 191.8 g m^{-2} year^{-1} for that 5,400-year convex period. **C** Sensitivity analyses of changing decomposition rate using the base value of 0.0002 year^{-1} (*thick line*), showing changes from 50 % less (0.0001 year^{-1}) to 50 % more (0.0003 year^{-1}). **D** Sensitivity analysis of changing PAR with an eventual PAR of 26.0 g m^{-2} year^{-1} as the base case (50 % increase to 39.0 g m^{-2} year^{-1}, and 50 % decrease to 13.0 g m^{-2} year^{-1})

effects of changing model parameters on the overall pattern of peat accumulation. As with the case for the concave accumulation pattern (Yu et al. 2001b), changing the decomposition rate has only a relatively limited influence, especially on recently formed peat (Fig. 14.3 c). In contrast, changing the PAR has a noticeable effect on the amount of peat accumulated, including the amount of younger peat as well as older peat in the final profile (Fig. 14.3d).

Why would the rate of peat addition to the catotelm show a unidirectional decrease over time in continental fens? Such a decline may be related to the moisture-limited continental climate and to the particular hydrology of fens and some continental bogs having groundwater (geogeneous water) influences (Glaser et al. 1997). Both autogenic and allogenic processes control the hydrology of peatlands and peatland development (Damman 1986). Local moisture conditions on a peatland surface are determined by a combination of three factors at different temporal and spatial scales: (1) long-term growth of the peatland and associated progressive isolation from the surrounding regional water table (autogenic); (2) regional climatic trends and fluctuations (allogenic; documented in Yu et al. 2003b); and (3) noise from local site disturbances and short-term hydrologic events. The first factor is more important in determining surface moisture conditions in groundwater-dependent continental fens than in the classic raised and blanket bogs of oceanic regions, and a long-term drying trend caused solely by vertical growth of continental rich fens is hypothesized. This reduces the production of moisture-sensitive mosses or increases the acrotelm decomposition, or both, causing a decrease in the PAR. Although this phenomenon might also occur in ombrotrophic bogs because continuous bog growth will accelerate drainage and limit *Sphagnum* production (Damman 1986) or increase acrotelm decomposition (Aaby 1976), it will be more pronounced in continental fens or groundwater-fed bogs owing to greater dependence of these peatlands on local hydrology.

14.5 Modeling Ecosystem Processes in Peatlands

There are several well-established ecosystem models that were originally designed and mostly used to simulate ecological processes in upland ecosystems; for example, TEM (McGuire et al. 2001), CENTURY (Parton et al. 1993), and LINKAGES (Pastor and Post 1986). However, peatland ecosystems have some unique features that need to be considered before any existing upland ecosystem models can be applied to peatlands. These features include waterlogged hydrology, organic soils, a large anaerobic zone, and nonvascular plant dominance. Because of these features, there are strong, coupled interactions and feedbacks among different components of the system, inducing self-regulation to the system dynamics (Beleya and Clymo 2001). Some models for peatlands are based on modification of an existing upland ecosystem model, while others are developed specifically for peatland ecosystems. Some peatland models are generic and can be used for different peatlands, while others are heavily prescribed using site-specific parameters. In any case, peatland ecosystem models consider many more parameters that are responsible for controlling the dynamics than the simple conceptual models do. Many models consider the influence of common environmental conditions (light, temperature, moisture conditions, and chemistry) on net primary production, decomposition, and gas flux rates.

The peatland carbon simulator (PCARS) developed by Frolking et al. (2002) includes components of photosynthesis and respiration of vascular and nonvascular plants, net aboveground and belowground production, and litterfall, aerobic, and anaerobic decomposition of peat. In addition, the model considers production, oxidation, and emission of methane, and dissolved organic carbon loss (Fig. 14.4). The PCARS has been designed in a generalized form that can be applied to all northern peatlands, although it has been more extensively tested against field measurements at one bog in southern Ontario. A unique feature of this model is its ability to link to a model that simulates long-term peat accumulation (Frolking et al. 2001), as a proper peat profile is essential to simulate anaerobic decomposition, a part of the carbon balance term. Also, the model could be coupled to CLASS, the land surface component of the Canadian climate model (Verseghy 2000).

Other attempts have been made to simulate peatland ecosystem processes. Potter et al (2001) applied a NASA-CASA ecosystem model to simulate peatland dynamics over short time scales in western Canada, with major modifications of hydrology (adding run-on) and moss layer for peatlands. Chimnar et al. (2002) modified the CENTURY model, an upland (grassland) soil dynamics model (Parton et al. 1993), in simulating long-term peat accumulation at montane fens in Colorado. In order to mimic conditions in peatlands, they added parameters calculated from effective moisture balance for inducing anaerobic conditions and made adjustments to drainage variables to maintain the water table. Zhang et al. (2002) modified the upland ecosystem model, PnET-N-DNDC, and developed a wetland version of the model, wetland-DNDC. Wildi's (1978) model was designed for testing a specific site, which requires a large number of site-specific parameters, including nutrient information. It simulates a two-dimensional cross section of the peatland and is designed for investigating controls on bog form. Nungesser (2003) designed a model that simulates bog microtopography (hummocks and hollows) in boreal peatlands, which includes submodels of hydrology,

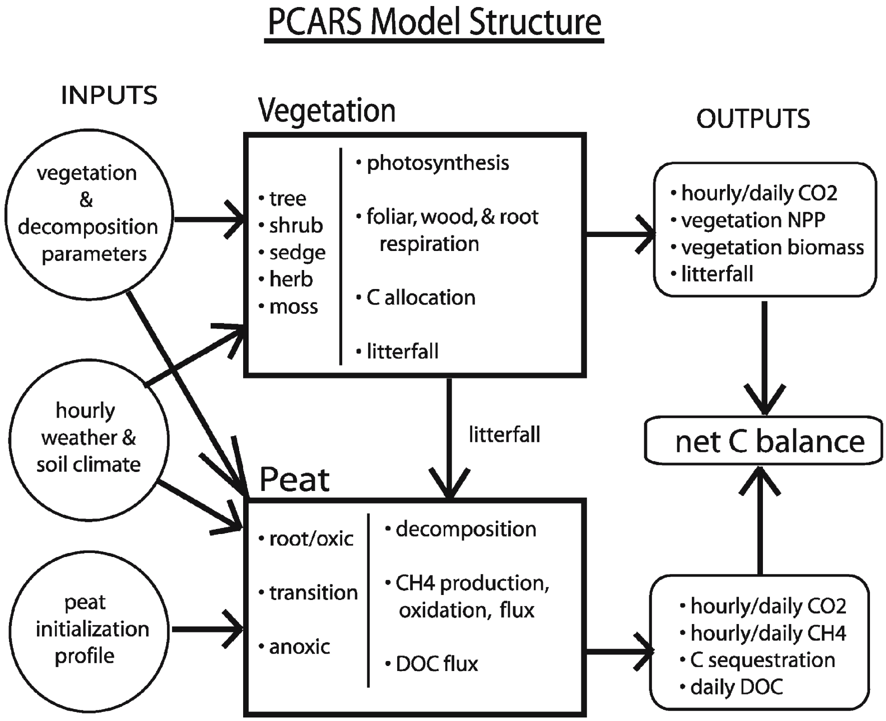


Fig. 14.4. Model structure of peatland carbon simulator (*PCARS*), with an overview of model components (from Frolking et al. 2002)

vegetation, and peat column, and found that microtopography results from the interactions between moss species properties and surrounding physical environment.

14.6 Intermediate Models and Projecting Peatland Dynamics

Some models are specifically designed for studying peatland dynamics, through integrating short-term ecosystem processes with long-term accumulation patterns. A popular approach used for such an integration is cohort treatment of litter inputs and peat column. These models tend to be intermediate in their complexity and details that take into consideration of the unique features of peatlands, especially hydrology and the layered structure, and also use functional types and groups to represent plants and organic fractions. These models have been used to investigate the interactions and feedbacks of biological and physical (hydrological) processes and to provide projections of future changes in carbon sequestration potentials.

Hilbert et al. (2000) modeled the interaction between hydrology (water-table depth) and organic matter (peat production) in peatlands using a system dynamics approach. The model consisting of two coupled nonlinear differential equations shows two possible steady-state configurations for a peatland, depending on water relations, to which the authors ascribe the characters of bogs and fens. There are no interactions between the acrotelm and the catotelm. This model can be seen as an outgrowth of Clymo's conceptual model, but with significant improvement by adding further explicit functional relationships between hydrology and production. Pastor et al. (2002) developed a model of six coupled differential equations that define the interactions between plant species and nutrient

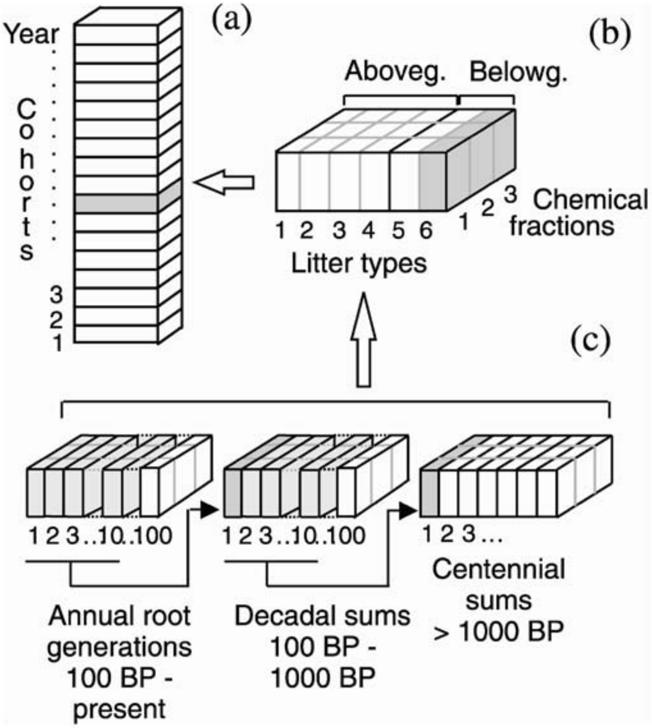


Fig. 14.5. A cohort approach to partitioning organic matter within the peat column as in the model by Bauer (2004). *a* The model follows the fate of a series of annual peat cohorts. *b* Each cohort contains six litter types (aboveground remains from herbaceous, woody, bryophyte and *Sphagnum*, and belowground remains from herbaceous and woody taxa), and mass for each litter type is subdivided into three chemical fractions (soluble, holocellulose, and lignin). *c* Integration of cohorts over time, summarized into 10- or 100-year mass bins

availability, which also result in multiple stable equilibria that represent different types of peatlands.

Frolking et al. (2001) developed a cohort-based peat decomposition model (PDM), in which long-term peat accumulation is directly related to decomposition rates of fresh vegetation litter. The model considers two vegetation types (vascular plant and moss) and root input from vascular plants to deep peat for bogs and fens. The PDM is a static model, assuming constant vegetation production and constant initial litter decomposition. The acrotelm and catotelm are integrated by use of prescribed anoxic factors and bulk density profiles. Bauer (2004) constructed a model to investigate potential effects of environment and vegetation properties on peat accumulation. The model simulates the production and decomposition of annual peat cohorts, which are subsequently integrated over millennial time scales (Fig. 14.5). She found that the factors controlling short-term decomposition are often different from the ones determining long-term decomposition. This highlights the difficulty and challenge of integrating processes over vastly different time scales.

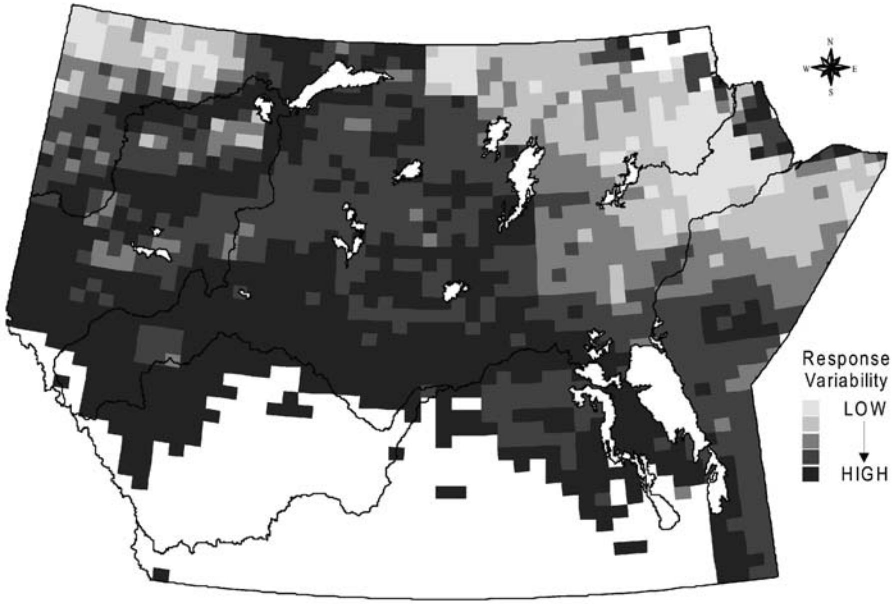


Fig. 14.6. Variability in carbon sequestration between warm/wet and warm/dry climate change scenarios. Calculated as the difference of mean carbon accumulation rate per grid cell between the two scenarios results. Variability in carbon sequestration between warm/wet and warm/dry climate change scenarios calculated as the difference of mean carbon accumulation rate per grid cell. Values range from low (less than 30 g C m^{-2} $year^{-1}$) to high (more than 60 g C m^{-2} $year^{-1}$). (From Beilman et al. 2001)

Belyea and Malmer (2004) linked a model of peat accumulation as described in Yu et al. (2003a) to a model of peatland hydrology and then applied the integrated model to investigate the response of carbon sequestration to climate change in a peatland in Sweden. Some empirical models that are driven by observed data have also been developed and used to make sensitivity analysis and projections. Wieder (2001) presented an empirical model based on ^{210}Pb-dated peat cores, which used depth-dependent decay rates of near-surface (acrotelm) peat to evaluate peatland carbon balance during the last 100–200 years and assessed the sensitivity of peatlands to future climate change. Beilman et al. (2001) took advantage of the extensive peatland survey and database available from western Canada (Zoltai et al. 2000; Vitt et al. 2000) to investigate regional variability and sensitivity of three main types of peatlands (permafrost peatlands, continental bogs, and continental fens). They found that fens located in southern portions of the region appear to show higher variability (Fig. 14.6), implying a large source of uncertainty in response to change in temperature and moisture regimes.

14.7 Conclusions

Various models have been used to investigate processes and dynamics of peatlands. These models range from the simplest conceptual models that intend to understand the first-order trajectory of long-term peat accumulation (carbon sequestration) to the most elaborate ecosystem models that incorporate detailed processes responsible for production, decomposition, and gas fluxes in peatland ecosystems. Some models are modified from existing ecosystem models, while others are deliberately developed to study peatlands by considering their unique characteristics. The peat profiles are an integrated part of peatland ecosystems and make important contributions to heterotrophic respiration of the entire ecosystem, so their inclusion in any model is essential. On the other hand, some key ecosystem parameters, including species composition, production, nutrients, and decomposition, are important for making comparisons with the results from other types of ecosystems. Therefore, it appears that the challenge is to integrate processes that operate over very different time scales, which would be able to offer useful insight to understanding the ecosystem dynamics and to provide robust projections for possible future change.

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References

Aaby B (1976) Cyclic climatic variations in climate over the past 5,500 yr reflected in raised bogs. Nature 263:281–284

Aaby B, Tauber H (1975) Rates of peat formation in relation to humification and local environment, as shown by studies of a raised bog in Denmark. Boreas 4:1–17

Bauer I (2004) Modelling effects of litter quality and environment on peat accumulation over different time-scales. J Ecol 92:661–674

Beilman DW, Yu ZC, Vitt DH (2001) Modelling regional variability in peat accumulation response to climate in continental western Canada. In: Vasiliev SV, Titlyanova AA, Velichko AA (eds) West Siberian peatlands and carbon cycle: past and present. Proceedings of the international field symposium (WSPCC 2001), Noyabrsk, Russia, 18–22 August 2001, pp 15–18

Belyea LR, Clymo RS (2001) Feedback control of the rate of peat formation. Proc R Soc Lond Ser B 268:1315–1321

Belyea LR, Malmer N (2004) Carbon sequestration in peatland: patterns and mechanisms of response to climate change. Global Change Biol 10:1–10

Charman DJ, Aravena R, Warner BG (1994) Carbon dynamics in a forested peatland in north-eastern Ontario, Canada. J Ecol 82:55–62

Chimnar RA, Cooper DJ, Parton WJ (2002) Modelling carbon accumulation in Rocky Mountain fens. Wetlands 22:100–110

Clymo RS (1978) A model of peat bog growth. In: Heal OW, Perkins DF (eds) Production ecology of British moors and montane grasslands. Springer, Berlin Heidelberg New York, pp. 183–223

Clymo RS (1984) The limits to peat bog growth. Philos Trans R Soc Lond Ser B 303:605–654

Clymo RS (1992) Models of peat growth. Suo 43:127–136

Clymo RS, Turunen J, Tolonen K (1998) Carbon accumulation in peatland. Oikos 81:368–388

Damman AWH (1986) Hydrology, development, and biogeochemistry of ombrogenous peat bogs with special reference to nutrient relation in a western Newfoundland bog. Can J Bot 64:384–394

Frolking S, Roulet NT, Moore TR, Richard PJH, Lavoie M, Muller SD (2001) Modeling northern peatland decomposition and peat accumulation. Ecosystems 4:479–498

Frolking S, Roulet NT, Moore TR, Lafleur PM, Bubier JL, Crill PM (2002) Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada. Global Biogeochem Cycles 16. DOI 10.1029/2001GB001457

Gorham E (1991) Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. Ecol Applications 1:182–195

Glaser PH, Siegel DI, Romanowicz EA, Chen YP (1997) Regional linkages between raised bogs and the climate, groundwater, and landscape of north-western Minnesota. J Ecol 85:3–16

Hilbert DW, Roulet N, Moore T (2000) Modelling and analysis of peatlands as dynamical systems. J Ecol 88:230–242

Hong YT, Hong B, Lin QH, Zhu YX, Shibata Y, Hirota M, Uchida M, Leng XT, Jiang HB, Xu H, Wang H, Yi L (2003) Correlation between Indian Ocean summer monsoon and North Atlantic climate during the Holocene. Earth Planet Sci Lett 211:371–380

Ingram HAP (1978) Soil layers in mires: function and terminology. J Soil Sci 29:224–227

Ingram HAP (1982) Size and shape in raised mire ecosystems: a geophysical model. Nature 297:300–303

Ivanov KE (1981) Water movement in mirelands (translated from Russian by Thomson A and Ingram HAP). Academic, Toronto

Ikonen L (1993) Holocene development and peat growth of the raised bog Pesänsuo in southwestern Finland. Geol Surv Finl Bull 370

Jenny H, Gessel S, Bingham FT (1949) Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci 68:419–432

Kubiw H, Hickman M, Vitt DH (1989) The developmental history of peatlands at Muskiki and Marguerite Lakes, Alberta. Can J Bot 67:3534–3544

Kuhry P (1994) The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. J Ecol 82:899–910

Kuhry P (1997) The palaeoecology of a treed bog in western boreal Canada: a study based on microfossils, macrofossils and physico-chemical properties. Rev Palaeobot Palynol 96:183–224

Kuhry P, Vitt DH (1996) Fossils carbon/nitrogen ratios as a measure of peat decomposition. Ecology 77:271–275

Kuhry P, Halsey LA, Bayley SE, Vitt DH (1992) Peatland development in relation to Holocene climatic change in Manitoba and Saskatchewan (Canada). Can J Earth Sci 29:1070–1090

McGuire AD, Sitch S, Clein JS, Dargaville R, Esser G, Foley J, Heimann M, Joos F, Kaplan J, Kicklighter DW, Meier RA, Melillo JM, Moore III B, Prentice IC, Ramankutty N, Reichenau T, Schloss A, Tian H, Williams LJ, Wittenberg U (2001) Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO_2, climate and land-use effects with four process-based models. Global Biogeochem Cycles 15:183–206

Nicholson BJ, Vitt DH (1990) The paleoecology of a peatland complex in continental western Canada. Can J Bot 68:121–138

Nungesser MK (2003) Modelling microtopography in boreal peatlands; hummocks and hollows. Ecol Model 165:175–207

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–331

Parton WJ, Scurlock JMO, Ojima DS, Gilmanov TG, Scholes RJ, Schimel DS, Kirchner T, Menaut J-C, Seastedt T, Garcia Moya E, Apinan Kamnalrut, Kinyamario JI (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochem Cycles 7:785–809

Pastor J, Post WM (1986) Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2:3–27

Pastor J, Peckham B, Bridgham S, Weltzin J, Chen J (2002) Plant community dynamics, nutrient cycling, and alternative stable equilibria in peatlands. Am Nat 160:553–568

Potter CS, Bubier JL, Crill PM, Lafleur P (2001) Ecosystem modeling of methane and carbon dioxide fluxes for boreal forest sites. Can J For Res 31:208–223

Turunen J, Tahvanainen T, Tolonen K (2001) Carbon accumulation in West Siberian mires, Russia. Global Biogeochem Cycles 15:285–296

Verseghy DL (2000) The Canadian land surface scheme (CLASS), its history and future. Atmos Ocean 38:1–13

Vitt DH, Halsey LA, Zoltai SC (1994) Bog landforms of continental western Canada in relation to climate and permafrost patterns. Arct Alp Res 26:1–13

Vitt DH, Halsey LA, Bauer IE, Campbell C (2000) Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. Can J Earth Sci 37:683–693

Wieder RK (2001) Past, present, and future peatland carbon balance – an empirical model based on ^{210}Pb-dated cores. Ecol Appl 7:321–336

Wieder RK, Lang GE (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63:1636–1642

Wildi O (1978) Simulating the development of peat bogs. Vegetatio 37:1–17

Yu ZC, Campbell ID, Vitt DH, Apps MJ (2001a) Modelling long-term peatland dynamics. I. Concepts, review, and proposed design. Ecol Model 145:197–210

Yu ZC, Turetsky MR, Campbell ID, Vitt DH (2001b) Modelling long-term peatland dynamics. II. Processes and rates as inferred from litter and peat-core data. Ecol Model 145:159–173

Yu ZC, Vitt DH, Campbell ID, Apps MJ (2003a) Understanding Holocene peat accumulation pattern of continental fens in western Canada. Can J Bot 81:267–282

Yu ZC, Campbell ID, Campbell C, Vitt DH, Bond GC, Apps MJ (2003b). Carbon sequestration in peat highly sensitive to Holocene wet–dry climate cycles at millennial time scales. Holocene 13:801–808

Zhang Y, Li C, Trettin CT, Li H, Sun G (2002) An integrated model of soil, hydrology, and vegetation for carbon dynamics in wetland ecosystems. Global Biogeochem Cycles 16. DOI 10.1029/2001GB001838

Zoltai SC, Siltanen RM, Johnson JD (2000) A wetland data base for the western boreal, subarctic, and arctic regions of Canada. Canadian Forest Service, Northern Forestry Centre information report NOR-X-368, Edmonton, Alberta, Canada

15 Forestry and Boreal Peatlands

Jukka Laine, Raija Laiho, Kari Minkkinen, and Harri Vasander

15.1 Introduction

Drainage of peatlands to improve forest growth has a long history and was already a well-known practice in the middle of the nineteenth century in Scandinavia (Lundberg 1926) and in Russia, as discussed by Tanttu (1915). In Great Britain the first afforestation attempts on peat had already taken place in the 1730s (Zehetmayr 1954).

During the 1960s and 1970s forest drainage became an important forestry practice in northern and eastern Europe, the British Isles, and some parts of North America. Currently, some 15×10^6 ha of northern peatlands and other wetlands have been drained for forestry. More than 90 % of this area is found in Scandinavia and Russia (Paavilainen and Päivänen 1995). The area drained annually has, however, been declining and, in Finland, for instance, the drainage activity has practically ceased.

In maritime climates such as that of the British Isles, peatlands are treeless, and consequently afforestation, often using exotic tree species followed by fertilization, has been part of the forest drainage process (Zehetmayr 1954). In the more continental climates the predrainage tree stands, even if sparse and stunted, have been utilized as the basis for the production forestry stands after drainage. Afforestation has thus been only of minor importance (Paavilainen and Päivänen 1995).

The aim of drainage has been to adjust the water content of the surface soil to a level that ensures sufficient aeration for tree roots (Päivänen 1973; Boggie 1977). This is achieved by lowering the water table level in the soil by means of drainage ditches. The sufficient minimum drainage depth (the distance between the soil surface and the water table during the growing season) has been given as between 35 and 55 cm, depending on the physical properties of the peat (Heikurainen 1967; Toth and Gillard 1988).

Forestry in peatlands may have national importance in countries like Finland, where the annual growth of tree stands in forested peatlands

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(approximately 20 × 10^6 m^3 $year^{-1}$) is more than 25 % of the total annual growth of Finnish forests (Tomppo 1999).

The environmental impacts of peatland drainage for forestry have been discussed in detail by Laine et al. (1995a), and the present chapter is partially based on that review.

15.2 Effects of Water-Level Drawdown on the Soil Environment

15.2.1 Increase in Aerobic Limit

Lowering the water table level after drainage increases the aeration of the surface peat (Lähde 1969; Lees 1972; Silins and Rothwell 1999). Measurements of the aerobic limit have shown that it closely follows fluctuations in the water table, especially in the falling direction, but remains somewhat above this level (Lähde 1969). Generally, the redox potential decreases towards the water table (Lähde 1969) together with the decreasing proportion of air-filled porosity (Boelter 1964; Päivänen 1973).

15.2.2 Increased Acidity

In addition to increased aeration, other noteworthy physicochemical changes take place in the surface peat. The oxidation of organic and inorganic (e.g., Fe, S, and Al) compounds releases protons in the system and thus increases acidity (De Vries and Breeuwsma 1987). These processes are enhanced after drainage, and lead to increasing acidity in the surface peat (Laiho and Laine 1990; Minkkinen et al. 1999).

In undrained minerotrophic sites, the organic acidity produced by peatland vegetation and decomposition processes is efficiently neutralized by the base cation flow in the inflowing groundwater. After drainage, the groundwater influx is largely cut away by the ditches, decreasing this form of neutralizing process. The uptake of base cations by the increasing tree stand, together with the longer nutrient retention in the biomass, may also be expected to further increase the acidity in the surface soil (Laiho et al. 1999).

Laiho and Laine (1990) found an average decrease in pH (dry peat in $CaCl_2$ suspension) of approximately 0.5 units (from 3.5 to 3.0) for mesotrophic sites and less than 0.2 units (from 3.0 to 2.8) for oligotrophic sites. However, when acidity is measured as an increase of proton concentrations, this means a more or less similar increase in both site types.

15.2.3 Changes in Soil Physical Properties

Drainage initiates subsidence of the peatland surface. At first, the removal of water causes a physical collapse and compression in peat, and later, decomposition of the organic matrix and the increasing mass of the tree stand may further contribute to the subsidence. The amount of subsidence measured in Finnish conditions has varied between 7 and 70 cm, depending on the site type and its wetness, the thickness of the peat layer, and the effectiveness and duration of drainage (Lukkala 1949; Minkkinen and Laine 1998a). Most of the subsidence takes place within the first few years after drainage (Lukkala 1949), which indicates that peat oxidation is of minor importance.

Subsidence and compaction result in increased bulk densities of surface peat (Minkkinen and Laine 1998b; Silins and Rothwell 1998). In data on peats drained approximately 55 years previously in southern Finland, postdrainage increases as high as 20–70 kg m^{-3} were found (undrained peat bulk densities 66–122 kg m^{-3}, drained peat bulk densities 106–160 kg m^{-3}; Minkkinen and Laine 1998b).

Changes in bulk density affect the water retention properties and hydraulic conductivity of peat. Slightly decomposed peats retain a large quantity of water at saturation, whereas peats with higher bulk densities contain less water at this stage but the loss of water with increasing matrix suction is also smaller (Boelter 1964; Päivänen 1973). The hydraulic conductivity of slightly decomposed, undisturbed surface peat may be fairly high (on average 10^{-1}–10^{-3} cm s^{-1}; Päivänen 1973; Rycroft et al. 1975). The increasing degree of decomposition (or increase in compaction and bulk density) decreases conductivity to values as low as 10^{-6}–10^{-8} cm s^{-1} (Päivänen 1973; Rycroft et al. 1975; Belair 1991; Plamondon and Belleau 1991).

The temperature conditions of the dried surface peat are also changed because both thermal conductivity and specific heat decrease as the proportion of air-filled pores increases. Initially, during 1–3 years following water-level drawdown, the growing-season temperatures in surface peat may increase (Lieffers and Rothwell 1987; Lieffers 1988). Generally, however, in drained peatlands with a tree cover, soil temperatures remain colder than in pristine sites (Hökkä et al. 1997; Venäläinen et al. 1999). Minkkinen et al. (1999) observed that this difference may extend at least to a depth of 50 cm. More extreme temperature ranges at surface level have also been reported after drainage (Rothwell 1991).

Results reported on the effects of drainage on the soil frost penetration in peat are fairly ambiguous, as discussed by Laiho and Laine (1992). For instance, Eurola (1968) reported an initial increase in soil frost penetration after drainage, but this trend diminished later as the closing tree stand canopy diminished the longwave radiation flux to the atmosphere. The increase in soil frost depth was more marked in those sites that were originally wetter (Eurola 1975); however, contradictory results on the drainage effects on soil frost penetration have also been reported (Swanson and Rothwell 1989). Even if soil frost penetration in drained peats is shallower than in undisturbed peats, the frost may persist much longer into the summer (Swanson and Rothwell 1989). In the conditions of southern Finland (mean annual temperature approximately 3–4 °C) the reported penetration depths vary between 15 and 40 cm for various study sites and winters, and are clearly lower than in mineral soils (Soveri and Varjo 1977).

15.2.4 Effects on Microbial Environment

The postdrainage improved aeration allows for an increase in the populations and activity of aerobic decomposers (Chmielewski 1991) but the increase may remain rather superficial (Paarlahti and Vartiovaara 1958). The highest activities have been found in the 0–10-cm layer even when water tables stayed below 50 cm during most of the growing season (Paarlahti and Vartiovaara 1958; Karsisto 1979). Results from cellulose decomposition field experiments show, however, a clear correlation between mass loss at greater depths (20–50 cm) and water table level (Karsisto 1979).

As microbial activity is generally pH-dependent, the postdrainage increase in acidity may have a restricting effect, for instance, on decay rates of organic matter. However, Williams and Crawford (1983) found that most bacteria have their optimal mineralization rates around pH 4–5 (soil solution), which suggests that the lowered pH might not seriously affect the decomposition of the surface peat. On the other hand, Ivarson (1977) observed a clear increase in decomposition rates of acid peat samples after liming and a consequent rise in pH from approximately 4 up to 7. The differences in the results may be explained by the great physiological diversity among peatland microbes (Williams and Crawford 1983).

15.2.5 Nutrient Conditions

Drainage initiates many processes that, directly or indirectly, affect the nutrient conditions in the surface soil. Tree stand biomasses increase after drainage relative to other vegetation components and also in absolute terms (Laiho et al. 2003; Sect. 15.3.1). Simultaneously with the change in growth form dominance, the quantity and allocation of total annual nutrient uptake by vegetation changes. While in pristine peatlands organic matter and nutrient fluxes are characterized by annual cycling through graminoids and/or mosses (Verry and Urban 1992; Laiho et al. 2003), following drainage the developing tree stands accumulate large quantities of nutrients to long-term cycle through the cumulatively growing biomass. As an example, on drained meso-oligotrophic sites in Finland, the annual uptake of N was 26-42, that of Ca 12–21, K 4.6–7.2, P 2.5–3.4, Fe 2.0–6.5, and Mg 2–4 kg ha^{-1} in tree stands, with annual net biomass accumulation ranging from 5,800 to 8,400 kg ha^{-1} (Finér 1989).

Along with increased annual runoff (Seuna 1988), drainage usually increases the leaching of nutrients from peatlands (Ahtiainen 1988; Sallantaus 1992). Sallantaus (1992) found a net loss of Ca, Mg, and K with runoff water from drained peatland catchments, whereas on the undrained parts of the same catchments, the inputs and outputs of these elements were more or less balanced. Mg and Ca were leached relatively more easily than K, which is effectively retained by the vegetation (Laiho et al. 1999). However, there is some evidence that the annual runoff approaches the predrainage level and possibly drops below it as the transpiration and interception of the tree stands increase (Seuna 1981), and consequently leaching of nutrients may return to the predrainage level.

The subsidence of the peatland surface initiated by drainage brings some of the nutrient stores immobilized in the deeper layers during peat accumulation back to nutrient cycling in the drained peatland forest ecosystem. Because of subsidence and peat compaction, peat layers of a certain thickness, for instance 30 cm, are not stratigraphically comparable across a postdrainage time gradient. A 30 cm-thick surface layer in a drained peatland includes peat material that was below the 30-cm level at the time of drainage. As the major rooting zone simultaneously becomes slightly thicker, plant roots in a drained site may access nutrient stores that were below their reach before drainage. This phenomenon has been discussed by Laiho et al. (1999) and Westman and Laiho (2003).

In addition to peat subsidence and compaction, another factor compensating for the removal of elements from the surface peat may be the ability of an increased tree stand canopy biomass to capture dry deposition (Schauffler et al. 1996).

The net change in the nutrient pools of surface peat after drainage is determined by the balance between input processes (deposition and addition from deeper peat layers through subsidence), and output processes (leaching and immobilization in the biomass). Inventory data on the changes in the nutrient stores of the surface peat in Finland (Laiho and Laine 1994, 1995; Westman and Laiho 2003) show that the stores of most nutrients remained rather unaltered during the first tree stand rotation after drainage, and were relatively large compared with stores in the biomasses, even in the oldest drainage areas studied. However, the stores of some nutrients, especially those of K, may become critical, because the amounts are generally small, and more than half of the store in the system may be found in the biomass (Kaunisto and Paavilainen 1988; Laiho and Laine 1995; Westman and Laiho 2003). Continued leaching of Ca and Mg (Sallantaus 1992) may lead to decreased stores of these base cations in the long run (Laiho et al. 1999; Westman and Laiho 2003).

Production forestry involves partial removal of tree stand biomass from the site. The major part of the aboveground nutrient stores in the tree stands is in the crowns (Finér 1989). The amounts removed by traditional stemwood harvesting would thus be less than half of the aboveground stores at the end of the first rotation on these site types (Kaunisto and Paavilainen 1988). Whole tree harvesting, however, might have serious implications for the P conditions of the surface peat (Holmen 1964; Finér 1989), and especially K stores might be seriously depleted (Laiho et al. 1999).

15.3 Plant-Mediated Organic Matter Dynamics

15.3.1 Plant Biomass Production

Forest drainage operations have been directed to sites where the high water level and the consequent deficiency of oxygen in the rooting zone are the primary constraints for tree growth. This is commonly the case in peatland sites (Jeglum 1974), even though the soil nutrient regime may also act at least as a secondary constraint (Lähde 1971). After the water level has been lowered by ditching, the soil nutrient regime becomes the primary edaphic constraint for vegetation composition (Laine and Vanha-Majamaa 1992; Laine et al. 1995b) and production, including tree growth (Keltikangas et al. 1986). Temperature is another major control on tree growth in drained peatlands (Heikurainen and Seppälä 1973).

By changing several crucial soil properties, as reviewed in previous sections, drainage induces secondary vegetation succession that continues until the plant community has adjusted to the new growth conditions. A persistent change in the water level induces adaptation first within the existing community as changes in root-to-shoot ratios and species abundances (Weltzin et al. 2000, 2003), followed by slower but more drastic changes in vegetation composition when species better adapted to the new conditions gain dominance (Laine et al. 1995b). The extent and speed of the secondary succession depend on the nutrient status and original wetness of the site (Laine and Vanha-Majamaa 1992; Laine et al. 1995b). The wetter the site was (i.e., the more that genuine peatland species adapted to waterlogged conditions dominated the vegetation) and the more nutrient-rich the site was [i.e., the higher the number of (upland) plant species that are potentially able to grow there], the greater and faster the changes in species composition will be following drainage. Generally, trees and shrubs proliferate, and graminoids decline following drainage (Laine et al. 1995b; Laiho et al. 2003; Fig. 15.1). Mosses may retain their functional importance after adaptation at the community level (Laiho et al. 2003). Peatland species adapted to waterlogged conditions, i.e., those found in hollows and lawns, are replaced by (upland) forest species (Laine et al. 1995b; Vasander et al. 1997). Hummock species, however, may remain in the species assemblage, especially in nutrient-poor sites (Laine et al. 1995b).

The increase in shrub biomass may be very fast and rapid in sites where shrubs occur already before drainage (Laiho et al. 2003). The decline in the coverage and biomass of sedges, such as *Carex rostrata* Stokes and

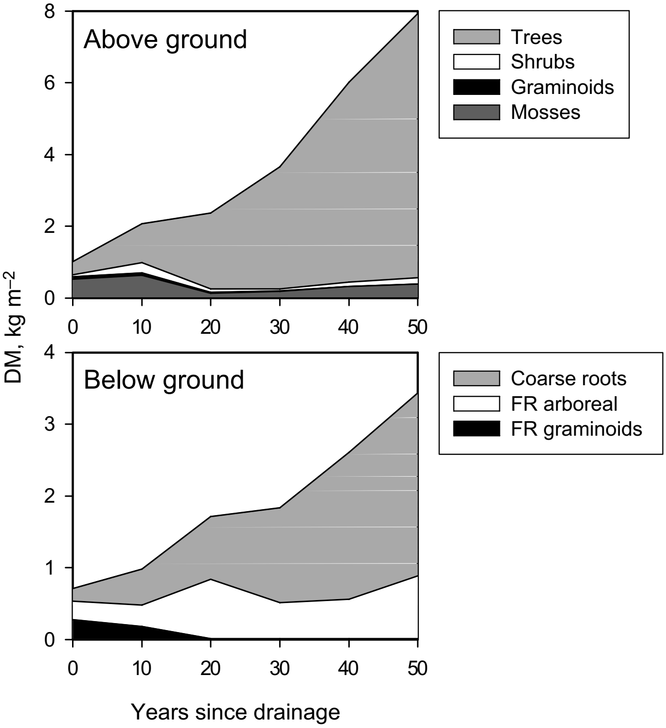

Fig. 15.1. Evolution of aboveground and belowground plant biomass, expressed as dry mass (105 °C), in a drainage succession chronosequence of sedge pine fens. These sites are oligotrophic, or poor fens, in their pristine condition, and are characterized by sedges such as *Carex rostrata* Stokes and/or *C. lasiocarpa* Ehrh. in the field layer, and Scots pine, *Pinus sylvestris* L., in the sparse tree layer occurring on low hummocks. On the *x*-axis, zero denotes the pristine situation. The *y*-axis scales differ for aboveground and belowground situations. *FR* fine roots (diameter 10 mm or less). (Redrawn from Laiho et al. 2003)

C. lasiocarpa Ehrh., also usually commences fast (within a few years) and cottongrass, *Eriophorum vaginatum* L., is one of the few peatland graminoids that has been observed to survive in the drainage succession unless the shading from the tree and shrub layers is heavy (Laine et al. 1995b; Laiho et al. 2003). Shrubs in turn start to decline if and when the growth of the tree layer has revived to the extent of canopy closure, with increased competition for light and nutrients. At that stage, peatland shrubs especially decline dramatically, while forest shrubs still may increase (Laine et al. 1995b; Laiho et al. 2003). Because plants may also plastically react to the changing environment, the changes in biomass may be faster and/or greater than changes in coverage (Laiho 1996). In general, the aboveground biomass of ground vegetation correlates negatively with the biomass or stem volume of the tree stand. The more tree biomass, the less ground vegetation biomass there is, and this decrease is exponential (Reinikainen et al. 1984). Below ground, the situation is not quite as simple because shrubs have relatively more fine roots than trees (Paavilainen 1980). However, the coarse root systems of trees add a new significant biomass component below ground (Fig. 15.1).

The increase in tree stand stem volume and biomass is at first caused by drainage-induced release growth of existing trees (Seppälä 1969; Macdonald and Yin 1999), as well as regeneration and ingrowth of new trees (Sarkkola et al. 2003). The increase in stem number caused by regeneration and ingrowth is most pronounced where the predrainage tree stand was sparse, i.e., in initially wetter sites (Sarkkola et al. 2005). How fast existing trees respond to the lowered water level depends on tree species, size, and age (Seppälä 1969; Macdonald and Yin 1999). A response may usually be seen within 5 years; first in fine roots and needles, then in radial growth (Seppälä 1969; Macdonald and Yin 1999; Mugasha et al. 1993). It may take 5–30 years for the release growth to reach its maximum, depending on tree species, size, and age, as well as site nutrient regime (Seppälä 1969). Thereafter, the growth rate largely depends on the available resources. The increase in tree stand stem volume and biomass may continue for decades, even centuries (Minkkinen et al. 2001; Sarkkola et al. 2003; Fig. 15.1). This depends on how much "growth potential" was released by drainage, which is determined by the nutrient regime of the site as well as the initial size of the tree stand.

For peatland sites where the nutrient regime is too poor for tree growth, however, the patterns of vegetation change following water-level drawdown will be different. In naturally dry, nutrient-poor ombrotrophic peatlands the species composition, biomass, and production are not affected by drainage to any great extent (Vasander 1982). Wet, nutrient-poor ombrotrophic sites lose the plant species adapted to wetness, and develop a lichen cover with some shrubs, mostly clonally spreading, ombrotrophic hummock species (Jauhiainen et al. 2002).

15.3.2 Litter Inputs

Along with the changes in vegetation composition and total biomass, the amount and tissue type composition of litterfall change. In pristine peatlands, *Sphagnum* mosses, sedges, and shrubs are the major litter sources. After drainage, the tree stand, especially its foliage and fine roots, becomes the major litter source (Laiho et al. 2003).

The effects of long-term vegetation succession on litter inputs has so far been investigated only for one peatland site type, an oligotrophic sedge fen with a sparse predrainage Scots pine stand, a site type commonly found in boreal Eurasia (Laiho et al. 2003). The clearest changes were the dramatic decline in sedge root litter, the fluctuations in the amount of moss litter, and the increase in tree litter (Fig. 15.2). Also, the composition of litterfall from trees changed gradually over time as the proportion of woody debris increased.

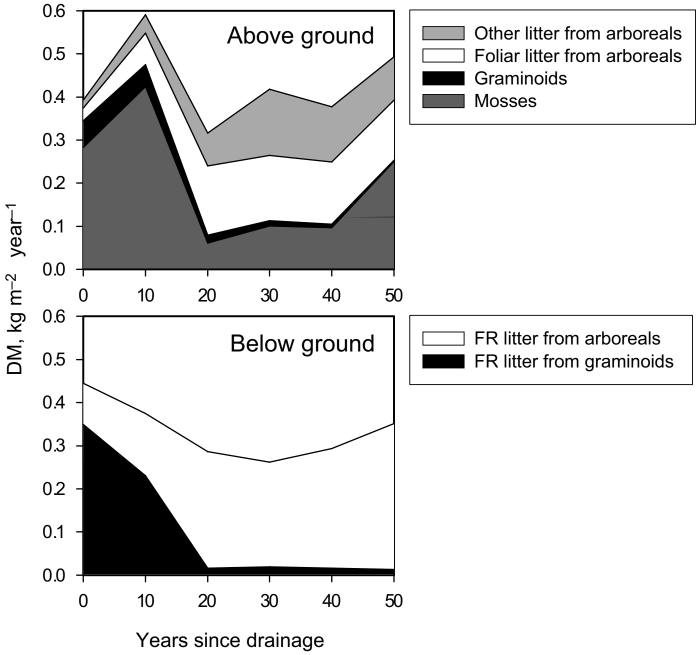

Fig. 15.2. Evolution of annual litterfall from different vegetation components, expressed as dry mass (105 °C), in a drainage succession chronosequence of sedge pine fens. *Foliar litter* includes needles and leaves, while all other arboreal litter, e.g., branches, twigs, and cones, is summed under *other litter*. *FR* fine roots (diameter 10 mm or less). (Redrawn from Laiho et al. 2003)

15.3.3 Decomposition

Considering all the changes in the tissue type composition of litterfall and in the physical environment for decomposition, reviewed in previous sections, it is evident that the effect of drainage on decomposition rates of organic matter may not be unambiguous. Increased aeration is the only factor affecting decomposition positively, while lowered soil temperatures and increased acidity may have negative effects. In a thin surface layer, drought may constrain decomposition in drained sites (Lieffers 1988; Laiho et al. 2004). Correspondingly, in decomposition experiments using standard litter materials, increased, decreased, and unaltered rates of decomposition have all been observed for drained sites, varying with sites and measurement depths (Lieffers 1988; Minkkinen et al. 1999; Domisch et al. 2000; Laiho et al. 2004).

Technically, the carbon fluxes following drainage may be divided into two compartments: those pertaining to the "old" peat soil brought under aerobic conditions by the water-level drawdown (decomposition only) and those pertaining to the "fresh" organic matter that enters the soil matrix under the changed conditions (both input and decomposition). Potential changes in the decomposition rate of the old peat following water-level drawdown largely depend on the conditions under which the peat was deposited. Peats that have already been exposed to long periods of aerobic decay may be highly resistant to further decay (Hogg et al. 1992). The carbon fluxes of the fresh organic matter in part depend on the vegetation succession, through the quantity and tissue type composition of litterfall, both of which may undergo significant changes as pointed out in the previous section.

Changes in litter quality following drainage may be of even greater significance for organic matter balance following drainage than the changes occurring in the physical environment for decomposition. Graminoid and herbaceous litters, which are the major vascular plant litter types in undrained peatlands, generally decompose faster than foliage and root litter from shrubs and trees, which are the major litter types in forested sites (Taylor et al. 1991; Hobbie 1996; Szumigalski and Bayley 1996; Thormann et al. 2001). Woody materials, twigs, branches, cones, and tree trunks decompose especially slowly (Taylor et al. 1991; Hobbie 1996; Laiho and Prescott 1999). Also the tree species gaining dominance may have an effect on the organic matter fluxes. It has been observed that rates of decomposition may be higher under deciduous stands than under coniferous stands (Priha and Smolander 1997; Prescott et al. 2000; Priha et al. 2001), and that this may not be due to litter quality only (Prescott et al. 2000). Decomposition rates of mosses vary with species, but may generally be considered low (Hobbie 1996; Karsisto et al. 1996; Szumigalski and Bayley 1996).

In plant-mediated organic matter fluxes, complex changes in both "input" (production, biomass duration) and "output" (decomposition of the litter produced) processes follow drainage. Thus, it may not be surprising that in single studies dealing with ecosystem or soil carbon balance, it has been suggested that a peatland site may become a source of carbon release into the atmosphere, remain a sink, or become a stronger sink (Sakovets and Germanova 1992; Vompersky et al. 1992; Minkkinen and Laine 1998b; Minkkinen et al. 1999; Hargreaves et al. 2003).

15.4 Effect on Carbon Balance and Greenhouse Gas Fluxes

15.4.1 Carbon and Nitrogen Cycle in Peatlands

Natural peatlands accumulate atmospheric carbon (CO_2) and nitrogen (N_2) in peat (Chap. 7). In turn, they emit some of the fixed carbon back into the atmosphere as methane (CH_4), which is formed in the anaerobic decomposition processes in peat and transported to the atmosphere by diffusion through the peat matrix or plant aerenchymes, or by ebullition. Carbon also flows in and out of peatlands dissolved (i.e., dissolved organic carbon) in the groundwater. As peatlands have very high carbon densities, the carbon outflow is usually higher than the inflow, i.e., there is a net loss of carbon from the peat by the throughflow of water. Nitrous oxide (N_2O) is formed as a byproduct of organic N decomposition in nitrification and denitrification processes. As nitrification demands aerobic conditions, N_2O emissions from natural peatlands are insignificant (Martikainen et al. 1993; Regina et al. 1996, 1998). Following drainage, the numerous physical and chemical changes in the peat soil and in the plant communities alter the fluxes of these greenhouse gases markedly. These changes are described in the following sections.

15.4.2 Changes in Carbon Dioxide Fluxes

Because of the increased aeration the CO_2 emissions (soil respiration) usually clearly increase following drainage (Silvola 1986; Moore and Dalva 1993; Silvola et al. 1996). In Finnish peatlands, annual CO_2 emissions from peat have been reported to increase by 6–190 % (mean 50 %; increase from 135–340 g C m^{-2} $year^{-1}$ on undrained sites to approximately 160–460 g C m^{-2} $year^{-1}$ on those drained; Silvola et al. 1996) depending on the drainage intensity (water-level drawdown) and peatland site type (Chap. 9).

The increase in soil respiration has often been regarded as an indicator of carbon loss from peat deposits (Silvola 1986; Gorham 1991). Soil respiration is, however, not derived only from the heterotrophic decomposition of old peat, but also from the decay of new litter and from autotrophic respiration of living roots. Following drainage, the net primary production and biomass of the vegetation increase overall, the greatest increase occurring in the tree stand with some decrease in the moss layer (Reinikainen 1981; Reinikainen et al. 1984; Laiho 1996; Laiho and Laine 1997; Laiho et al. 2003). Understandably, also litterfall and autotrophic respiration increase. Thus, roots (Silvola et al. 1992) and new decomposing litter may together comprise even two thirds of the measured carbon efflux (i.e., soil respiration) from old forestry drainage areas (Minkkinen et al., unpublished data).

Direct measurements of peat carbon balances are rare, probably because of methodological difficulties, but both decreases (Sakovets and Germanova 1992; Braekke and Finer 1991; Gustafsson 2001) and increases (Minkkinen and Laine 1998a; Minkkinen et al. 1999) in peat carbon stores following drainage have been reported.

Not only do peat carbon changes determine the carbon balance of peatland ecosystems but changes in primary productivity and carbon storage of the peat-forming vegetation, including trees, are equally important in understanding the effects of water-level drawdown, as discussed by Gorham (1991) and Hogg et al. (1992). As carbon stores in vegetation nearly always increase following forestry drainage, peatlands may remain carbon sinks despite possible carbon losses from the peat (Minkkinen et al. 2002; Hargreaves et al. 2003).

15.4.3 Leaching of Carbon

The leaching of dissolved organic carbon increases during and immediately after digging the drainage network (Bergquist et al. 1984; Ahtiainen 1988), but because the groundwater flow through the peatland is decreased by ditches trapping the inflowing water, the long-term increase in organic carbon leaching is small (approximately 10 %; Ahtiainen 1988; Sallantaus 1994) or may even decrease (Heikurainen et al. 1978; Lundin and Bergquist 1990). Leaching of carbon downwards in the peat profile may be expected to increase because of the increased fluctuation in the water table after rainfall events. This would form a further outflow of carbon from the peatland as well as rapider relocation of carbon downwards in the peat deposit (Domisch et al. 2000).

15.4.4 Decrease in Methane Emissions

Drainage lowers the water table level, thus decreasing the anaerobic peat volume, in which CH_4 is formed. The aerobic peat volume is occupied by methanotrophic microbes which oxidise upwards-moving CH_4 into CO_2, thus decreasing emissions of CH_4. However, most of CH_4 emitted from undrained peatlands originates from new carbon, photosynthates, deposited directly into anoxic conditions by deep-rooted sedges (Whiting and Chanton 1993; Mikkelä et al. 1995; Bubier 1995; Ström et al. 2003). Thus, a more distinctive change in CH_4 dynamics takes place, when sedges are replaced by vegetation adapted to drier conditions, and direct carbon deposition into anaerobic layers is diminished.

In Finnish peatlands CH_4 emissions have decreased by 30 to over 100 % (from 3 to 30 g C m^{-2} $year^{-1}$ on the undrained sites to 5–6 g C m^{-2} $year^{-1}$ on the drained sites; Nykänen et al. 1998) following drainage. The decrease is smallest in ombrotrophic pine bogs and greatest in meso-oligotrophic sedge fens, which also undergo the greatest change in vegetation and physicochemical environment (Minkkinen et al. 1999) and often act as net sinks for atmospheric CH_4 after drainage (Lien et al. 1992; Glenn et al. 1993; Martikainen et al. 1995; Nykänen et al. 1998).

Ebullition of CH_4 is diminished because of the disappearance of wet surfaces (flarks) following drainage; however, ebullition (and diffusion) of CH_4 may continue in drainage ditches if they become dammed by vegetation or by beavers, thus forming new stagnant-water pools on the peatland. The impact of ditch emissions may be significant, if ditch emissions are high and the predrainage emissions have been fairly small as observed, for instance, in northern Ontario (Roulet et al. 1993; Roulet and Moore 1995). In Finnish conditions the ditch emissions are usually at the same level with natural peatlands and contribute to the postdrainage emissions only a little (Minkkinen et al. 1997).

15.4.5 Increase in Nitrous Oxide Emissions in Nutrient-Rich Peatlands

Drainage for forestry has been shown to increase N_2O emissions only at nutrient-rich peatland sites (Martikainen et al. 1993; Regina et al. 1996, 1998), where pH is high enough for nitrate formation through nitrification. Tree stand fellings and consequent N input from slash may, however, create environmental conditions favorable for N_2O formation, and some high emissions have been observed in felling experiments (Minkkinen et al., unpublished data; Chap. 10).

15.4.6 Greenhouse Impact of Drainage

The greenhouse impact of any land use or land use change can be expressed as the change in radiative forcing (RF, i.e., perturbation in the earth's energy balance, units of watts per square meter), positive values indicating a warming effect and negative ones a cooling effect. That is, emissions of different greenhouse gases can be made commensurable by calculating their RF. Not only do the emitted amounts of a certain gas affect the RF but also the ability of the gas to absorb longwave radiation and its lifetime in the atmosphere. Comparisons between gas emissions can be simplified by calculating their RF relative to that of CO_2 for a selected time period. Thus, for example, CH_4 is 23 times and N_2O 296 times more effective as a greenhouse gas than CO_2, in a 100-year time horizon (Intergovernmental Panel on Climate Change 2001). These kinds of RF averages over certain time periods are called global warming potentials (GWP), and greenhouse impacts of, for example, forestry operations can be illustrated using them; however, for studies of dynamical phenomena, like the development of peatlands and their greenhouse-gas fluxes in the course of time, RF simulation models (e.g., REFUGE; Sinisalo 1998) provide a better and a more accurate tool.

In the natural state most peatlands (bogs, swamps) usually have a negative RF ("cooling impact") on climate, since the impact of carbon sequestration into peat from atmosphere exceeds that of CH_4 emissions (Laine et al. 1996; Fig. 15.3). However, in mire site types that have high CH_4 emissions and relatively small carbon sequestration rates (sedge fens), the RF may be positive ("warming"; Fig. 15.3). Drainage of mires for forestry decreases CH_4 emissions, increases N_2O and CO_2 emissions, and increases carbon sequestration from peat, but increases carbon sequestration to the ecosystem during the first tree stand rotation. In sedge fens, a big decrease in RF takes place after drainage, when high CH_4 emissions virtually cease, while a smaller decrease in RF is predicted for bogs (Fig. 15.3). On the whole the RF impact of forest drainage is estimated to be negative, i.e., drainage has a "cooling" effect on the global climate during the first 50–500 years (Laine et al. 1996; Minkkinen et al. 2002), depending on the site type. This shift is mainly caused by the decrease in CH_4 emissions, which is well documented and a widely agreed phenomenon. Estimates of changes in N_2O emissions and ecosystem carbon sequestration rates include much higher uncertainty, which is also reflected in future predictions (Minkkinen et al. 2002).

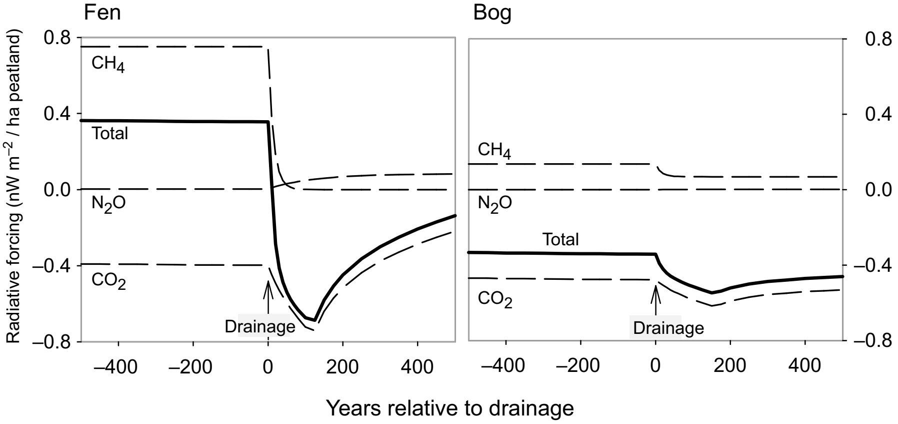

Fig. 15.3. The effect of drainage on the radiative forcing of a mire ecosystem in the minerotrophic fen and ombrotrophic bog sites in Lakkasuo mire, central Finland. Notice the unit of radiative forcing of nanowatts per square meter per drained hectare of peatland. The emission estimates behind this figure are from Laine et al. 1996. *CO_2* includes the effect of increasing tree stand biomass

15.5 Restoration of Peatlands Drained for Forestry

15.5.1 Needs and Aims of Restoration

Environmental management of peatlands and protection of key biotopes have created needs and pressures to restore peatlands drained for forestry back to peatland ecosystems. Peatland restoration aims at revitalizing a self-sustaining naturally functioning peatland ecosystem which accumulates carbon and retains nutrients from through-flowing waters (Wheeler and Shaw 1995). The first step is to raise the water table and ideally stabilize the water table level close to the peat surface. In successful restoration, the recolonization of peatland plant species follows rewetting, and finally, the carbon cycle typical of the peatland ecosystem, including anoxic decomposition, begins once again (Pfadenhauer and Klötzli 1996; Chap. 17).

The aims of restoration of peatlands drained for forestry are diverse. As forestry is most profitable on nutrient-rich peatland sites (Paavilainen and Päivänen 1995), those sites have been selected for drainage first, and thus are now the rarest in pristine condition. Nutrient-rich peatlands have threatened species requiring habitats with flowing water, and often also have a special landscape value (Aapala et al. 1996; Finnish Forest and Park Service 1999; Virkkala et al. 2000). One type of peatland that has been used intensively for forestry is the spruce swamp that can be found as narrow strips in the ecotone between forest and peatland ecosystems. These ecotones are ecological hot spots for biodiversity (Aapala et al. 1996) but may be easily destroyed by a single ditch.

Other priority sites to be restored include areas with special landscape value where the natural mosaic of forests and open or sparsely treed peatlands should be returned. Also, the need to create buffer zones between terrestrial and water ecosystems to capture liberated nutrients from the forestry operation areas can be achieved by restoring small areas of peatlands drained for forestry (Sallantaus et al. 1998).

15.5.2 Restoring Drained Peatlands to Promote Landscape and Species Diversity

Residual parts of pristine peatlands are often too small and fragmented to allow natural processes of spontaneous regeneration to take place. In such cases restoration management can be used to combine and enlarge smaller areas to form a larger landscape unit together with integrated functions of subunits (Virkkala et al. 2000).

The planning for peatland restoration should be done on a peatland ecosystem level. Attempts should be made to restore the hydrological aspects of the whole watershed, including mineral soil and peat covered areas, although this is often difficult owing to the local land ownership conditions (Aapala and Lindholm 1999).

In recently drained areas, it is likely that through restoration the area reverts almost to its original habitat type. The longer the area has been drained, the more difficult it is to fully recreate the original state. In such cases, successful restoration leads to a "new natural state," different from the original, but nevertheless recognizable as some other peatland habitat type (Heikkilä and Lindholm 1996; Finnish Forest and Park Service 1999).

The restoration of hydrology is achieved by damming or filling in the ditches (Vasander et al. 1992; Heikkilä and Lindholm 1995). Drainage has caused peat subsidence to be most pronounced near the ditches (Lukkala 1949; Minkkinen and Laine 1998a); thus, water may continue to flow along or stay in the dammed or filled-in ditches, instead of spreading across the peatland. Therefore, appropriate water conditions for the initiation of restoration processes are difficult to achieve, and the result is usually a mosaic of drier and wetter areas much unlike the moisture conditions in pristine peatlands. Also the fluctuations of the water table are expected to increase owing to the increased bulk density of the surface peat after drainage (Minkkinen and Laine 1998b). Extending dams several meters to the sides of the ditches will spread the water flow more evenly across the peatland (Seppä et al. 1993). Handmade dams are expensive and very often do not hold water in peatland. That is why excavators are usually used in damming or filling in the ditches (Sallantaus et al. 2003).

Tree stands which have developed since drainage can be removed partially or totally. In peatlands which originally had a dense tree cover, particularly spruce peatlands, the whole tree cover is usually left intact during restoration (Finnish Forest and Park Service 1999). This will increase the amount of windfall and decaying wood on the site, increasing the future fungi and insect biodiversity. On topographically flat areas, large stands of dead trees may be formed. If the tree stand is manipulated, typical characteristics of pristine spruce peatlands, such as long continuity, trees of all sizes and ages, large amounts of dead wood, and gap-phase dynamics (Kuuluvainen 1994; Hörnberg et al. 1997), should be taken into account. Restoring the hardwood component of the natural tree stand structure is usually not a problem since birches as pioneer tree species readily recolonize restored habitats. The structure of predrainage tree stands may be clarified with the aid of old aerial photographs. On peatlands which were treeless before drainage, the whole tree layer is usually cut and taken away. On ombrotrophic peatlands, the slash might also be taken away to diminish the amount of nutrients left on the site. Vegetation recovery after restoration in peatlands drained for forestry is usually fast after rewetting as diaspores of peatland plants are nearby (Jauhiainen et al. 2002). No seeding or planting is needed in contrast to the situation on large cut-away peatlands (Sliva and Pfadenhauer 1999, Rochefort 2001). However, species compositions in restored sites may remain different from pristine for a long time (Soro et al. 1999).

15.5.3 Changes in Water Quality After Restoration

Before large-scale forestry drainage, the water discharged from forested peatlands was naturally filtered through the existing peat deposit. The even topography, dense moss cover, and the favorable physical, chemical, and biological properties of surface peat (e.g., anoxia, porosity, cation-exchange capacity, and microbial retention) facilitate versatile buffering functions in these systems. As a result of forest drainage, the major part of these buffering systems are lost. Restoring drained peatlands, being potentially well suited to act as buffer zones between forestry land and a watercourse, is an important reason for rewetting outside nature reserves (Sallantaus et al. 1998). These restored buffer zones are important in reducing the nutrient loading (especially N and P) imposed on watercourses from the forestry operation areas (Hyvönen et al. 2000; Silvan et al. 2002, 2003, 2004).

Restoration has also been noted to cause an immediate increase in phosphorus concentration in the outflow (Sallantaus 1999; Vasander et al.

1988, 2003). Drained peatland forests have often been fertilized with phosphorus, and in the restoration site felling slash has been left on the site. Although peatlands were restored in late fall or early winter, the increase in phosphorus concentration may take place late in the summer and in early fall, showing that biological processes are involved, directly or indirectly, in the phosphorus release. As the water level is raised abruptly, phosphorus bound in roots and mycorrhizae may be released owing to anoxic conditions (Sallantaus et al. 2003).

Also other changes in water quality take place after restoration. Leaching of dissolved organic carbon increases for some time after restoration, when increased amounts of water reach the decomposed surface peat of the drained area. The higher concentrations of organic acids increase the acidity of runoff waters as well, and the increased acidity may be the reason why the establishment of so-called brown mosses (Amblystegiaceae) is very poor after restoration of sites where they used to thrive in the natural state (Sallantaus 1999).

Silvan et al. (2002, 2003, 2004) noticed that a restored peatland was very effective in retaining N and P. Approximately 15 and 25 % of experimentally added high loads of N and P, respectively, were retained by microbes during the first 2 years, while the retention by vegetation was 70 % for N and 25 % for P. Karsisto et al. (2003) noted that also the concentrations of dissolved carbon and iron in the smallest molecular size fraction and iron also from high molecular compounds were lower after the water had passed this restored area. These promising results show that whenever possible each drainage area should include a restored buffer zone through which the outgoing waters from the drainage area and the surrounding upland forest catchment would be filtered.

15.5.4 Conclusions

The first experiences of restoration are quite promising. Peatlands restored after drainage for forestry are, however, in the very early stages of postrestoration succession and many questions remain. Practical restoration projects should be closely linked with monitoring and research whenever possible (Heikkilä and Lindholm 1997; Finnish Forest Park Service 1999). Restoration of nutrient-rich peatlands might not be easy since changes in peatland vegetation and peat properties are most pronounced after disturbance in these sites. Restored habitats will be colonized by their typical species most likely if restored fragments are close to existing sources of potential colonists (Campbell and Rochefort 2003). So sites where targeted plant and animal species still exist in the surrounding areas should be prioritized for restoration. Monitoring enables corrective future actions in order to better achieve the restoration goals (adaptive management; Walters and Holling 1990). Incorporation of research into management generates synergy benefits, for example, by enabling experiments to be set up at scales that are relevant both ecologically and for management. This also helps to ensure the formation of a knowledge base about the long-term effects of restoration, which in turn can be used in planning future restoration efforts (Kuuluvainen et al. 2002). Other questions concerning the restoration of peatlands drained for forestry are linked with physicochemical changes in the surface peat and changed hydrology after restoration. It is still unclear how common the increased leaching of P is and how it could be reduced or avoided. Also the metapopulation dynamics of specialized peatland animals (e.g., butterflies) and rich-fen vascular plants should be better known to ensure that restoration activities lead to successful results (Rassi et al. 2003).

References

Aapala K, Lindholm T (1999) Suojelusoiden ekologinen rajaaminen (Abstract: Ecological evaluation of the boundaries of protected peatlands). Metsähallituksen luonnonsuojelujulkaisuja. Series A 95. Metsähallitus, Vantaa

Aapala K, Heikkilä R, Lindholm T (1996) Protecting the diversity of Finnish peatlands. In: Vasander H (ed) Peatlands in Finland. Finnish Peatland Society, Jyväskylä, pp 45–57

Ahtiainen M (1988) Effects of clear-cutting and forestry drainage on water quality in the Nurmes-study. Proceedings of the international symposium on the hydrology of wetlands in temperate and cold regions, Joensuu, Finland, pp 206–219

Belair JL (1991) Low hydraulic conductivity in catotelm limits effectiveness of drainage. In: Jeglum J K, Overend R P (eds) Proceedings of the symposium '89 – peat and peatlands diversification and innovation, vol 1. Peatland forestry. The Canadian Society for Peat and Peatlands, pp 141–145

Bergquist B, Lundin L, Andersson A (1984) Hydrologiska och limnologiska konsekvenser av skogs- och myrdikning. Sicksjöbäckområdet. Uppsala universitet limnologiska institutionen forskningsrapport 8:1–140

Boelter DH (1964) Water storage characteristics of several peats in situ. Soil Sci Soc Am Proc 28:433–435

Boggie R (1977) Water-table depth and oxygen content of deep peat in relation to root growth of Pinus contorta. Plant Soil 48:447–454.

Braekke FH, Finer L (1991) Fertilization effects on surface peat of pine bogs. Scand J For Res 6:433–449

Bubier J (1995) The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. J Ecol 83:403–420

Campbell D, Rochefort L (2003) Germination and seedling growth of bog plants in relation to the recolonization of milled peatlands. Plant Ecol 169:71–84

Chmielewski K (1991) The effect of habitat conditions on microbiological activity of peat soils. Pol Ecol Stud 17:143–153

De Vries W, Breeuwsma A (1987) The relation between soil acidification and element cycling. Water Air Soil Pollut 35:293–310

Domisch T, Finér L, Laiho R, Karsisto M, Laine J (2000) Decomposition of Scots pine litter and the fate of released carbon in pristine and drained pine peatlands. Soil Biol Biochem 32:1571–1580

Eurola S (1968) Über die ökologie der nordfinnischen Moorvegetation im Herbst Winter und Frühling. Ann Bot Fenn 5:83–97

Eurola S (1975) Snow and ground frost conditions of some Finnish peatland types. Ann Bot Fenn 12:1–16

Finér L (1989) Biomass and nutrient cycle in fertilized and unfertilized pine mixed birch and spruce stands on a drained peatland. Acta For Fenn 208:1–63

Finnish Forest and Park Service (1999) The principles of protected area management in Finland, guidelines on the aims, function and management of state-owned protected areas. Nat Prot Publ Ser B 54

Glenn S, Heyes A, Moore T (1993) Carbon dioxide and methane emissions from drained peatland soils, southern Quebec. Global Biogeochem Cycles 7:247–258

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195

Gustafsson M (2001) Carbon loss after forest drainage of three peatlands in southern Sweden. Masters thesis, Department of Forest Soils, SLU, Uppsala

Hargreaves KJ, Milne R, Cannell MGR (2003) Carbon balance of afforested peatland in Scotland. Forestry 76:299–317

Heikkilä H, Lindholm T (1995) The basis of peatland restoration in Finland. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) Restoration of temperate wetlands. Wiley, Chichester, pp 548–556

Heikkilä H, Lindholm T (1996) Metsäojitettujen soiden ennallistamisopas, 2nd edn. Metsähallituksen luonnonsuojelujulkaisuja. Series B 25. Metsähallitus, Vantaa

Heikkilä H, Lindholm T (1997) Soiden ennallistamistutkimus vuosina 1987–1996 (Abstract: The peatland restoration study from 1987 to 1996). Metsähallituksen luonnonsuojelujulkaisuja. Series A 81. Metsähallitus, Vantaa

Heikurainen L (1967) On the possibilities of optimum drainage in peat lands. 14th IUFRO Congr Pap 4:264–277

Heikurainen L, Seppälä K (1973) Ojitusalueiden puuston kasvun jatkumisesta ja alueellisuudesta (Summary: Regionality and continuity of stand growth in old forest drainage areas). Acta For Fenn 132:1–36

Heikurainen L, Kenttämies K, Laine J (1978) The environmental effects of forest drainage. Suo 29:49–58

Hobbie SE (1996). Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol Monogr 66:503–522

Hogg EH, Lieffers VJ, Wein RW (1992). Potential carbon losses from peat profiles: effects of temperature, drought cycles, and fire. Ecol Appl 2:298–306

Hökkä H, Penttilä T, Siipola M (1997). Relationships between groundwater level and temperature in peat. In: Trettin CC, Jurgensen MF, Gale MR, Jeglum JK (eds) Northern forested wetlands: ecology and management. CRC, Boca Raton, pp 287–296

Holmen H (1964) Forest ecological studies on drained peatland in the province of Uppland, Sweden. Stud For Suec 16:1–236

Hörnberg G, Ohlson M, Zackrisson O (1997) Influence of bryophytes and microrelief conditions on Picea abies seed regeneration patterns in boreal old-growth swamp forests. Can J For Res 27:1015–1023

Hyvönen R, Olsson BA, Lundkvist H, Staaf H (2000) Decomposition and nutrient release from Picea abies (L.) Karst. and Pinus sylvestris (L.) logging residues. For Ecol Manage 126: 97–112

Intergovernmental Panel on Climate Change (2001) Climate change 2001: the scientific basis. Cambridge University Press, Cambridge

Ivarson KC (1977) Changes in decomposition rate, microbial population and carbohydrate content of an acid peat bog after liming and reclamation. Can J Soil Sci 57:129–137

Jauhiainen S, Laiho R, Vasander H (2002) Ecohydrological and vegetational changes in a restored bog and fen. Ann Bot Fenn 39:185–199

Jeglum JK (1974) Relative influence of moisture-aeration and nutrients on vegetation and black spruce growth in northern Ontario. Can J For Res 4:114–126

Karsisto M (1979) Maanparannustoimenpiteiden vaikutuksista orgaanista ainetta hajottavien mikrobien aktiivisuuteen suometsissä. Osa I Pohjaveden etäisyyden ja NPK-lannoituksen vaikutus Vilppulan ja Kivalon rämeellä ja korvessa (Summary: Effect of forest improvement measures on activity of organic matter decomposing micro-organisms in forested peatlands. Part I. Effect of drainage and NPK fertilization in the spruce and pine swamps at Kivalo and Vilppula). Suo 30:49–58

Karsisto M, Varjola I, Kitunen V, Domisch T (1996) Decomposition of mosses in different peats. In: Laiho R, Laine J, Vasander H (eds) Northern peatlands in global climatic change. Edita, Helsinki, pp 47–53

Karsisto M, Kitunen V, Laine J (2003) Peatland as buffer zone in a constructed overland flow area. In: Järvet A, Lode E (eds) Ecohydrological processes in northern wetland, Tartu University Press, Tartu, pp 290–293

Kaunisto S, Paavilainen E (1988) Nutrient stores in old drainage areas and growth of stands. Commun Inst For Fenn 145:1–39

Keltikangas M, Laine J, Puttonen P, Seppälä K (1986) Vuosina 1930–1978 metsäojitetut suot: ojitusalueiden inventoinnin tuloksia. (Summary: Peatlands drained for forestry during 1930–1978: results from field surveys of drained areas). Acta For Fenn 193:1–94

Kuuluvainen T (1994) Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland, a review. Ann Zool Fenn 31:35–51

Kuuluvainen T, Aapala K, Ahlroth P, Kuusinen M, Lindholm T, Sallantaus T, Siitonen J, Tukia H (2002) Principles of ecological restoration of boreal forested ecosystems: Finland as an example. Silva Fenn 36: 409–422

Lähde E (1969) Biological activity in some natural and drained peat soils with special reference to oxidation-reduction conditions. Acta For Fenn 94:1–69

Lähde E (1971) Anaerobisten olosuhteiden ja aerobisuusrajan esiintymisestä erilaisilla luonnontilaisilla turvemailla ja merkityksestä suotyypin kuvaajana (Summary: On anaerobic conditions in various virgin peat soils and the significance of the aerobic limit as an indicator of site quality). Silva Fenn 5:36–48.

Laiho R (1996) Changes in understorey biomass and species composition after water-level drawdown on pine peatlands in southern Finland. Suo 47:59–69

Laiho R, Laine J (1990) Post-drainage nutrient stores in peat. In: Hånell B (ed) Biomass production and element fluxes in forested peatland ecosystems. Swedish University of Agricultural Sciences, Umeå, pp 81–91

Laiho R, Laine J (1992) Effect of forest drainage on soil frost conditions. In: Bragg OM, Hulme PD, Ingram HAP, Robertson RA (eds) Peatland ecosystems and man: an impact assessment. Department of Biological Sciences, University of Dundee, Dundee, pp 149–152

Laiho R, Laine J (1994) Nitrogen and phosphorus stores in peatlands drained for forestry in Finland. Scand J For Res 9:251–260

Laiho R, Laine J (1995) Changes in mineral element concentrations in peat soils drained for forestry in Finland. Scand J For Res 10:218–224

Laiho R, Laine J (1997) Tree stand biomass and carbon content in an age sequence of drained pine peatlands in southern Finland. For Ecol Manage 93:161–169

Laiho R, Prescott CE (1999) The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. Can J For Res 29:1592–1603.

Laiho R, Sallantaus T, Laine J (1999) The effect of forestry drainage on vertical distributions of major plant nutrients in peat soils. Plant Soil 207:169–181

Laiho R, Vasander H, Penttilä T, Laine J (2003) Dynamics of plant-mediated organic matter and nutrient cycling following long-term water-level drawdown in boreal peatlands. Global Biogeochem Cycles 17:1053. DOI 10 1029/2002GB002015

Laiho R, Laine J, Trettin CC, Finér L (2004) Scots pine litter decomposition along soil moisture and nutrient gradients in peatland forests, and the effects of interannual weather variation. Soil Biol Biochem 36:1095–1109

Laine J, Vanha-Majamaa I (1992) Vegetation ecology along a trophic gradient on drained pine peatlands in southern Finland. Ann Bot Fenn 29:213–233

Laine J, Vasander H, Sallantaus T (1995a) Ecological effects of peatland drainage for forestry. Environ Rev 3:286–303

Laine J, Vasander H, Laiho R (1995b) Long-term effects of water level drawdown on the vegetation of drained pine peatlands in southern Finland. J Appl Ecol 32:785–802

Laine J, Silvola J, Tolonen K, Alm J, Nykänen H, Vasander H, Sallantaus T, Savolainen I, Sinisalo J, Martikainen PJ (1996) Effect of water level drawdown in northern peatlands on the global climatic warming. Ambio 25:179–184

Lees JC (1972) Soil aeration response to draining intensity in basin peat. J Soc For 45:135–143

Lieffers VJ (1988) *Sphagnum* and cellulose decomposition in drained and natural areas of an Alberta peatland. Can J Soil Sci 68:755–761

Lieffers VJ, Rothwell RL (1987) Effects of drainage on substrate temperature and phenology of some trees and shrubs in an Alberta peatland. Can J For Res 17:97–104.

Lien T, Martikainen PJ, Nykänen H, Bakken L (1992) Methane oxidation and methane fluxes in two drained peat soils. Suo 43:231–236

Lukkala OJ (1949) Soiden turvekerroksen painuminen ojituksen vaikutuksesta (Referat: Über die Setzung des Moortorfes als Folge der Entwässerung). Commun Inst For Fenn 37:1–67

Lundberg G (1926) Drainage of swamp lands for forestry purposes. J For 24:19–37

Lundin L, Bergquist B (1990) Effects on water chemistry after drainage of a bog for forestry. Hydrobiologia 196:167–181

MacDonald SE, Yin F (1999) Factors influencing size inequality in peatland black spruce and tamarack: evidence from post-drainage release growth. J Ecol 87:404–412.

Martikainen PJ, Nykänen H, Crill P, Silvola J (1993) Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. Nature 366:51–53

Martikainen PJ, Nykänen H, Alm J, Silvola J (1995) Change in fluxes of carbon dioxide methane and nitrous oxide due to forest drainage of peatland sires of different trophy. Plant Soil 168-169:571–577

Mikkelä C, Sundh I, Svensson BH, Nilsson M (1995) Diurnal variation in methane emission in relation to the water table soil temperature climate and vegetation cover in a Swedish acid peatland. Biogeochemistry 28:93–114

Minkkinen K, Laine J (1998a) Long-term effect of forest drainage on the peat carbon stores of pine peatlands in Finland. Can J For Res 28:1267–1275

Minkkinen K, Laine J (1998b) Effect of forest drainage on the peat bulk density of pine peatlands in Finland. Can J For Res 28:178–186

Minkkinen K, Laine J, Nykänen H, Martikainen PJ (1997) Importance of drainage ditches in emissions of methane from peatlands drained for forestry. Can J For Res 27:949–952

Minkkinen K, Vasander H, Jauhiainen S, Karsisto M, Laine J (1999) Post-drainage changes in vegetation composition and carbon balance in Lakkasuo peatland, central Finland. Plant Soil 207:107–120

Minkkinen K, Laine J, Hökkä H (2001) Tree stand development and carbon sequestration in drained peatland stands in Finland – a simulation study. Silva Fenn 35:55–69

Minkkinen K, Korhonen R, Savolainen I, Laine J (2002) Carbon balance and radiative forcing of Finnish peatlands 1900–2100 – the impact of forestry drainage. Global Change Biol 8:785–799

Moore TR, Dalva M (1993) The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. J Soil Sci 44:651–664

Mugasha AG, Pluth DJ, Hillman GR (1993) Foliar responses of tamarack and black spruce to drainage and fertilization of a minerotrophic peatland. Can J For Res 23:166–180

Nykänen H, Alm J, Silvola J, Tolonen K, Martikainen PJ (1998) Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. Global Biogeochem Cycles 12:53–69

Paarlahti K, Vartiovaara U (1958) Havaintoja luonnontilaisten ja metsäojitettujen soiden pieneliöstöistä (Summary: Observations concerning the microbial populations in virgin and drained bogs). Commun Inst For Fenn 50: 1–38

Paavilainen E (1980). Effect of fertilization on plant biomass and nutrient cycle on a drained dwarf shrub pine swamp. Commun Inst For Fenn 98:1–71

Paavilainen E, Päivänen J (1995) Peatland forestry – ecology and principles. Springer, Berlin Heidelberg New York

Päivänen J (1973) Hydraulic conductivity and water retention in peat soils. Acta For Fenn 129:1–70

Pfadenhauer J, Klötzli F (1996) Restoration experiments in middle European wet terrestrial ecosystems: an overview. Vegetatio 126:101–115

Plamondon AP, Belleau P (1991) Estimation of the hydraulic conductivity of peat from bulk density and von Post decomposition. In: Jeglum JK, Overend RP (eds) Proceedings of the symposium '89 – peat and peatlands diversification and innovation, vol 1. Peatland forestry. The Canadian Society for Peat and Peatlands, Quebec City, pp 146–152

Prescott CE, Zabek LM, Staley CL, Kabzems R (2000) Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Can J For Res 30:1742–1750

Priha O, Smolander A (1997) Microbial biomass and activity in soil and litter under Pinus sylvestris, Picea abies and Betula pendula at originally similar field afforestation sites. Biol Fertil Soils 24:45–51

Priha O, Grayston SJ, Hiukka R, Pennanen T, Smolander A (2001) Microbial community structure and characteristics of the organic matter in soils under Pinus sylvestris, Picea abies and Betula pendula at two forest sites. Biol Fertil Soils 33:17–24

Rassi P, Aapala K, Suikki A, Ahti E, Eerola L, Kouki j, Kurikka T, Kuuluvainen T, Kuusinen M, Lindholm T, Merisaari H, Virolainen E (2003) Restoration in protected areas: report by the working group on restoration (in Finnish). Finn Environ 618:1–220

Regina K, Nykänen H, Silvola J, Martikainen PJ (1996) Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity. Biogeochemistry 35 401–418

Regina K, Nykänen H, Maljanen M, Silvola J, Martikainen PJ (1998) Emissions of N_2O and NO and net nitrogen mineralization in a boreal forested peatland treated with different nitrogen compounds. Can J For Res 28:132–140

Reinikainen A (1981) Metsänparannustoimenpiteiden vaikutuksesta suoekosysteemien kasvibiomassaan ja perustuotantoon (Summary: Effect of drainage and fertilization on plant biomass and primary production). Suo 32:110–113

Reinikainen A, Vasander H, Lindholm T (1984) Plant biomass and primary production of southern boreal peatland-ecosystems in Finland. In: Proceedings of the 7th international peat congress, Dublin, Ireland IV. The Irish National Peat Committee/International Peat Society, Dublin, pp. 1–20

Rochefort L (2001) Restauration écologique. In: Payette S, Rochefort L (eds), Écologie des tourbières du Québec-Labrador, Les Presses de l'Université Laval, Sainte-Foy, pp 449–504

Rothwell RL (1991) Substrate environments on drained and undrained peatlands Wally Creek experimental drainage area Cochrane Ontario. In: Jeglum JK, Overend RP (eds) Proceedings of the symposium '89 – peat and peatlands diversification and innovation, vol 1. Peatland forestry. The Canadian Society for Peat and Peatlands, pp 103–108

Roulet NT, Moore TR (1995) The effect of forestry drainage practices on the emission of methane from northern peatlands. Can J For Res 25:491–499

Roulet NT, Ash R, Quinton W, Moore T (1993) Methane flux from drained northern peatlands: Effect of a persistent water table lowering on flux. Global Biogeochem Cycles 7:749–769

Rycroft DW, Williams DJA, Ingram HAP (1975) The transmission of water through peat II: field experiments. J Ecol 63:557–568

Sakovets VV, Germanova NI (1992) Changes in the carbon balance of forested peatlands in Karelia due to drainage. Suo 43:249-252

Sallantaus T (1992) Leaching in the material balance of peatlands – preliminary results. Suo 43: 253–358

Sallantaus T (1994) Response of leaching from mire ecosystems to changing climate. In: Kanninen M (ed) The Finnish Research Programme on Climate Change. Second progress report. The Academy of Finland, Helsinki, pp 291–296

Sallantaus T (1999) Seitsemisen soiden hydrologinen seuranta (Hydrological monitoring in the peatlands of Seitseminen National Park). Subreport of the project: restoration of active raised bogs, aapapeatlands and bog woodland in Natura 2000 sites. Life project B4-3200/96/542

Sallantaus T, Vasander H, Laine J (1998) Metsätalouden vesistöhaittojen torjuminen ojitetuista soista muodostettujen puskurivyöhykkeiden avulla. (Summary: Prevention of detrimental impacts of forestry operations on water bodies using buffer zones created from drained peatlands). Suo 49:125–133

Sallantaus T, Kondelin H, Heikkilä R (2003) Hydrological problems associated with peatland restoration. In: Heikkilä R, Lindholm T (eds) Biodiversity and conservation of boreal nature. Finn Environ 485:256–261

Sarkkola S, Alenius V, Hökkä H, Laiho R, Päivänen J, Penttilä T (2003) Changes in structural inequality in Norway spruce stands on peatland sites after water-level drawdown. Can J For Res 33:222–231

Sarkkola S, Hökkä H, Laiho R, Päivänen J, Penttilä T (2005) Stand structural dynamics on drained peatlands dominated by Scots pine. For Ecol Manage 206:135–152

Schauffler M, Jacobson GL, Pugh AL, Norton SA (1996) Influence of vegetational structure on capture of salt and nutrient aerosols in a Maine peatland. Ecol Appl 6:263–268

Seppä H, Lindholm T, Vasander H (1993) Rehabilitation of peatlands drained for forestry. Metsähallituksen luonnonsuojelujulkaisuja. Series A 7. Metsähallitus, Vantaa (in Finnish)

Seppälä K (1969) Kuusen ja männyn kasvun kehitys ojitetuilla turvemailla (Post-drainage growth rate of Norway spruce and Scots pine on peat). Acta For Fenn 93:1–89

Seuna P (1981) Long-term influence of forestry drainage on the hydrology of an open bog in Finland. Publ Water Res Inst 43:3–14

Seuna P (1988) Effects of clear-cutting and forestry drainage on runoff in the Nurmes-study. Proceedings of the international symposium on the hydrology of wetlands in temperate and cold regions, Joensuu, Finland. pp 122–134

Silins U, Rothwell RL (1998) Forest peatland drainage and subsidence affect soil water retention and transport properties in an Alberta peatland. Soil Sci Soc Am J 62:1048–1056

Silins U, Rothwell RL (1999) Spatial patterns of aerobic limit depth and oxygen diffusion rate at two peatlands drained for forestry in Alberta. Can J For Res 29:53–61

Silvan N, Regina K, Kitunen V, Vasander H, Laine J (2002) Gaseous nitrogen loss from a restored peatland buffer zone. Soil Biol Biochem 34:721–728

Silvan N, Vasander H, Karsisto M, Laine J (2003) Microbial immobilisation of added nitrogen and phosphorus in constructed wetland buffer. Appl Soil Ecol 24:143–149

Silvan N, Vasander H, Laine J (2004) Vegetation is the main factor in nutrient retention in a constructed wetland buffer. Plant Soil 258:179–187

Silvola J (1986) Carbon dioxide dynamics in peatlands reclaimed for forestry in eastern Finland. Ann Bot Fenn 23:59–67

Silvola J, Alm J, Ahlholm U (1992) The effect of plant roots on CO_2 release from peat soil. Suo 43:259–262

Silvola J, Alm J, Ahlholm U, Nykänen H, Martikainen PJ (1996) CO_2 fluxes from peat in boreal peatlands under varying temperature and moisture conditions. J Ecol 84:219–228

Sinisalo J (1998) Estimation of greenhouse impacts of continuous regional emissions. VTT publication 338. Technical Research Centre of Finland, Espoo

Sliva J, Pfadenhauer J (1999) Restoration of cut-over raised bogs in southern Germany – a comparison of methods. Appl Veg Sci 2: 37–148

Soro A, Sundberg S, Rydin H (1999) Species diversity, niche metrics and species associations in harvested and undisturbed bogs. J Veg Sci 10:549–560

Soveri J, Varjo M (1977) Roudan muodostumisesta ja esiintymisestä Suomessa vuosina 1955–1975 (Summary: On the formation and occurrence of soil frost in Finland 1955 to 1975). Publ Water Res Inst 20:1–66

Ström L, Ekberg A, Mastepanov M, Christensen TR (2003) The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Global Change Biol 9:1185–1192

Swanson LE, Rothwell RL (1989) Substrate freeze–thaw in a drained Alberta fen. Can J For Res 19:1024–1029

Szumigalski AR, Bayley SE (1996) Decomposition along a bog to rich fen gradient in central Alberta, Canada. Can J Bot 74:573–581

Tanttu A (1915) Tutkimuksia ojitettujen soiden metsittymisestä (Referat: Studien über Aufforstungsfähigkeit der entwässerten Moore). Acta For Fenn 5:1–211

Taylor BR, Prescott CE, Parsons WJF, Parkinson D (1991) Substrate control of litter decomposition in four Rocky Mountain coniferous forests. Can J Bot 69:2242–2250

Thormann MN, Bayley SE, Currah RS (2001) Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. Can J Bot 79:9–22

Tomppo E (1999) Forest resources of Finnish peatlands in 1951–1994. Int Peat J 9:38–44

Toth J, Gillard D (1988) Experimental design and evaluation of a peatland drainage system for forestry by optimization of synthetic hydrographs. Can J For Res 18:353–373

Vasander H (1982). Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Ann Bot Fenn 19:103–125

Vasander H, Leivo A, Tanninen T (1992) Rehabilitation of a drained peatland area in the Seitseminen national park in southern Finland. In: Bragg OM, Hulme PD, Ingram HAP, Robertson RA (eds) Peatland ecosystems and man: an impact assessment. International Peat Society, University of Dundee, Dundee, pp 381–387

Vasander H, Laiho R, Laine J (1997) Changes in species diversity in peatlands drained for forestry. In: Trettin CC, Jurgensen MF, Grigal DF, Gale MR, Jeglum JK (eds) Northern forested wetlands, ecology and management. CRC, Boca Raton, pp 109–119

Vasander H, Tuittila E-S, Komulainen V-M, Laine J, Sallantaus T (1998) Restoration of peatlands drained for forestry in Finland. In: Malterer T, Johnson K, Stewart J (eds) Peatland restoration and reclamation – techniques and regulatory considerations. International Peat Society, Jyväskylä, Finland, pp 88–93

Vasander H, Tuittila E-S, Lode E, Lundin L, Ilomets M, Sallantaus T, Heikkilä R, Pitkänen M-L, Laine J (2003) Status and restoration of peatlands in northern Europe. Wetland Ecol Manage 11:51–53

Venäläinen A, Rontu L, Solantie R (1999) On the influence of peatland draining on local climate. Boreal Environ Res 4:89–100

Verry ES, Urban NR (1992). Nutrient cycling at Marcell bog, Minnesota. Suo 43:147–153

Virkkala R, Korhonen KT, Haapanen R, Aapala K (2000) Protected forests and peatlands in forest and peatland vegetation zones in Finland based on the 8th National Forest Inventory. (In Finnish) Suomen ympäristö 395:1–49

Vompersky SE, Smagina MV, Ivanov AI, Glukhova TV (1992) The effect of forest drainage on the balance of organic matter in forest mires. In: Bragg OM, Hulme PD, Ingram HAP, Robertson RA (eds) Peatland ecosystems and man: an impact assessment. International Peat Society, University of Dundee, Dundee, pp 17–22

Walters CJ, Holling CS (1990) Large-scale management experiments and learning by doing. Ecology 71:2060–2068

Weltzin JF, Pastor J, Harth C, Bridgham SD, Updegraff K, Chapin CT (2000) Response of bog and fen plant communities to warming and water-table manipulations. Ecology 81:3464–3478

Weltzin JF, Bridgham SD, Pastor, J, Chen JQ, Harth C (2003) Potential effects of warming and drying on peatland plant community composition. Global Change Biol 9:141–151

Westman CJ, Laiho R (2003) Nutrient dynamics of peatland forests after water-level drawdown. Biogeochemistry 63:269–298

Wheeler BD, Shaw SC (1995) Restoration of damaged peatlands with particular reference to lowland raised bogs affected by peat extraction. HMSO, London

Whiting GJ, Chanton JP (1993) Primary production control of methane emission from wetlands. Nature 364:794–795

Williams RT, Crawford R (1983) Effects of various physiochemical factors on microbial activity in peatlands: aerobic biodegradation processes. Can J Microbiol 61:1430–1437

Zehetmayr JWL (1954) Experiments in tree planting on peat. For Comm Bull 22:1–110

16 Disturbance in Boreal Peatlands

Merritt R. Turetsky and Vincent L. St. Louis

16.1 Introduction

Over the past several hundred years, approximately 50 % of wetlands globally have been degraded (IUCN 2000), largely owing to agricultural intensification, pollution, energy and forestry practices, and urban development. Wetland loss has occurred over the past several centuries in Europe (Immirzi et al. 1992; Jones et al. 1993), more recently since settlement in North America (Tiner 1984; National Wetlands Working Group 1988; Dahl 1990), and may be intensifying today in many less industrialized nations (Brinson et al. 2002).

Disturbances are particularly important to the boreal forest biome, where the structure and function of the boreal forest both determines and is influenced by its disturbance regime. In pristine boreal forest, disturbances such as fire and insect outbreaks are common and alter landscape structure and species composition. In many boreal regions, however, human activities also influence ecosystem structure and function, and can alter natural disturbance regimes. Fires, for example, are a function of both natural conditions and human activities. The increasing area burned in Canada is most likely due to a combination of changing climate and increased human activities in formerly remote areas (Podur et al. 2002; Stocks et al. 2003). Most of our knowledge on disturbances in boreal regions is based on upland ecosystems, while less attention has been devoted to the role of disturbance in poorly drained landscapes, especially peatlands that cover significant areas of the boreal forest region.

As noted in other chapters in this volume, peatlands play a significant role in many ecosystem services, including C sequestration, water storage and supply, and species and landscape diversity. Changes in disturbance regimes could compromise these ecosystem functions. Here, we briefly review the most common disturbances that influence boreal peatlands, focusing on disturbance impacts on plant structure, hydrology, and bio-

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geochemical cycling in peatlands. Similar to well-drained ecosystems, disturbances in peatlands are a function of both natural conditions and human activities. We classify disturbances into perturbations that involve (1) herbivory and grazing, (2) biomass burning, (3) flooding or inundation, (4) water table drawdown, and (5) pollution.

Disturbance can be defined as discrete events in space and time that disrupt ecosystem structure (Pickett and White 1985) or induce widespread mortality of dominant species in an ecosystem (Aber and Melillo 1991). These definitions distinguish disturbances from more chronic stresses or variability present in many ecosystems. However, as noted throughout this chapter, determining whether a perturbation is discrete or is caused by an external versus an internal agent (Pickett et al. 1989) can be difficult and is often influenced by the temporal or spatial scale being considered.

16.2 Herbivory/Grazing

16.2.1 Herbivory

The high phytomass production ratios of bryophytes and lichens are consistent with low levels of herbivory (Longton 1992). Low herbivory of peatland vegetation such as lichen and *Sphagnum* spp. likely is due to a combination of low nutrient content and the production of defensive chemicals (Clymo and Hayward 1982; Lawrey 1986; Davidson et al. 1990). However, certain species of bryophytes and lichens do serve as food sources for animals and insects (Lawrey 1986). Depending upon its history and severity, herbivory may represent an intrinsic perturbation rather than a disturbance (see definition earlier). For example, caribou (*Rangifer tarandus*) periodically use treed peatlands throughout the year (Bradshaw et al. 1995; Rettie and Messier 2000) for protection against wolf predation and food availability. Individual caribou can graze over 2,000 m^2 during winter months, consuming up to 2 kg dry weight of lichen daily (Slack 1988). Because lichens are generally slow-growing, caribou consumption will influence plant structure and inputs to soil organic matter in treed peatlands. However, because lichens often preferentially decompose in peat profiles, lichen consumption by caribou is not likely to influence long-term trends in peat accumulation.

16.2.2 Animal Husbandry

Peatlands, particularly in Europe, have served as important grazing sites for sheep and other ungulates/animals. Overgrazing is caused by animal overstocking and has been identified as a problem for habitat integrity and biodiversity in peatlands (Mackay and Tallis 1996). Grazing influences plant community composition (Cooper et al. 1997, 2001; Segerstrom 1997; Segerstrom and Emanuelsson 2002), though light grazing and haymaking practices may actually increase species diversity in some peatlands. On decadal to century time scales, grazing in preindustrial Sweden may have favored the stability of pine forests over mixed deciduous–conifer forests (Segerstrom and Emanuelsson 2002).

Generally, animal husbandry in peatlands removes aboveground biomass, alters microtopography and soil structure, and increases soil erosion in peatlands (Evans 1997; Garnett et al. 2000). Changes in soil structure and nutrient inputs with grazing activities can influence microbial activity. For example, grazing stimulated nitrous oxide (N_2O) fluxes from peat soils (Koops et al. 1997). However, light sheep grazing did not alter decadal rates of peat accumulation in the UK (Garnett et al. 2000).

16.3 Biomass Burning

Fire is a common disturbance in many parts of the boreal forest. Between 5×10^6 and 12×10^6 ha of boreal forest burn every year, directly releasing an estimated approximately 10–40 t C ha^{-1} to the atmosphere (Stocks and Kaufman 1997; Kasischke et al. 2000; Levine and Cofer 2000). Fires generally release C, N, and Hg to the atmosphere immediately through organic matter combustion, and influence longer-term ecosystem processes by redistributing elements on the forest floor (Harden et al. 2004), reducing autotrophic respiration, and altering heterotrophic respiration (Van Cleve et al. 1996; Amiro et al. 2003). Fire has been invoked as a mechanism contributing to peat initiation and paludification in boreal regions, as conditions after fire can be more saturated and oligotrophic than prior to burning (Tolonen 1985); however, Efremova and Efremov (1994) concluded that fires mobilize nutrients and thus can stimulate stand productivity in forested bogs.

Several landscape factors contribute to the risk of burning, including the rate of fuel accumulation, the distribution of fuels, fuel flammability, and landscape connectivity. Flinn and Wein (1977) concluded that northern peatlands are too wet to burn during years of average precipitation. In western Canada, the area of large fires was positively correlated to the abundance of peatlands on the landscape, suggesting that peatland fuels might promote fire activity during extreme fire conditions (Turetsky 2004). While fire return intervals range from 50 to 500 years in boreal upland systems (Zackrisson 1977; Ritchie 1987; Laberge and Payette 1995; Stocks and Kaufman 1997), fire return intervals ranged from 80 to 200 years in treed peatlands in Minnesota, Quebec, and southwestern Finland (Heinselman 1973; Cogbill 1985; Tolonen 1985). Kuhry (1994) estimated longer fire return intervals (450–1,700 years) for several treed peatlands in western Canada.

Grass and sedge biomass in open fens burns readily in the spring, while treed peatlands typically burn later in the fire season with the drying of moss layers (Heinselman 1973). Generally, fire severity in peatlands depends on fuel loads, oxygen availability, and the moisture content of peat (Maltby et al. 1990; Morrissey et al. 2000). Severe fire activity in peatlands results in the combustion of peat layers and can last for several months. Zoltai et al. (1998) estimated that 15 % of all fires affecting peatlands in Canada burn deeply into peat layers; however, these severe burning events account for the majority of regional C emissions from peatland fires. Lower combustion efficiencies during the smoldering of peat likely increase CH_3Br and CH_3Cl emissions during burning (Manö and Andreae 1994). Fires generally reduce soil C sequestration in Canadian peatlands (Kuhry 1994; Zoltai et al. 1998; Turetsky et al. 2002a). For example, peat plateaus have low rates of C storage likely owing, at least in part, to high fire frequencies (Robinson and Moore 2000). Regional C budgets in western Canada suggest that small increases in fire frequency or severity would cause peatlands to switch from net C sinks to sources (Turetsky et al. 2002a). However, western Siberian peatlands burned only 2–3 times over the past 8,000 years, with no evidence of decreasing soil C accumulation with fire activity (Turunen et al. 2001).

Humans have used rotational burning in peatlands to increase plant diversity and improve grazing value (Hobbs and Gimingham 1980). Plant composition and soil C storage was affected more by rotational burning than by light grazing in a UK peatland (Hobbs 1984; Garnett et al. 2000). Combustion of drained peat can be severe if managed peatlands burn (Maltby and Immirzi 1993; Sect. 16.5).

16.4 Flooding/Inundation

16.4.1 Beaver Damming

Beaver (*Castor fiber* and *C. canadensis*) populations have declined dramatically owing to trapping for their fur. Though populations are not near their historical densities, beaver today serve as important ecosystem engineers in the northern hemisphere, creating open-water wetland habitats and increasing the diversity of boreal and temperate landscapes (Wright et al. 2002). Beavers create shallow open-water bodies in peatlands that are colonized by emergent and floating macrophytes. Beaver activity along with increased sedimentation and erosion in beaver ponds lead to greater organic matter inputs (Naiman et al. 1986). Beaver ponds in Ontario, Canada, did not differ from poor fens in surface water chemistry (cations, pH, etc.) but had greater sediment heat flux (Roulet et al. 1992), which is likely to influence microbial activity. Methane fluxes from beaver ponds are generally high (Roulet et al. 1997), largely owing to transport through ebullition (Dove et al. 1999). Roulet et al. (1992) estimated that beaver ponds could be responsible for up to 32 % of total methane emissions from boreal wetlands. Ponds created by beaver activity also serve as important habitats for a number of species such as the green-winged teal (Nummi and Poysa 1997). Eventually, beaver dams are abandoned, ponds drain or dry out, and grasses and other herbaceous species colonize to form rich meadow communities.

16.4.2 Reservoir Creation

Reservoir creation is common in association with hydroelectric power generation, but reservoirs are also used for water supply, recreation, and aquaculture. Reservoirs that flood peatlands represent a “worst-case scenario” for greenhouse gas emissions because of the large stores of organic C in peat available for decomposition (St. Louis et al. 2000). Flooding kills terrestrial plants, thus removing the C sink potential of peatlands, and increases the emissions of CH_4 and other C greenhouse gases (Kelly et al. 1997; St. Louis et al. 2000). Experimental flooding of a peatland in Ontario led to a 40-fold net yield of methylmercury, which was available to bioaccumulate through the food web to concentrations in fish that are known to be toxic to consumers. More generally, reservoir creation can also result in a loss in biodiversity, but it may increase the stability of local water and energy supplies (Watson et al. 2000). In Canada, reservoirs occupy more than 70,000 km^2 across Ontario, Quebec, Manitoba, and Labrador, and much of this flooding likely occurred in landscapes dominated by peatlands. At least 800 km^2 of peatlands have been flooded in Manitoba alone (Turetsky et al. 2002a).

16.4.3 Thermokarst

Across much of the boreal forest, distributions of permafrost are discontinuous, and permafrost is found primarily in peatlands owing to their thick layers of insulating soil organic matter and relatively dense canopies of black spruce. Over the past approximately 100 years, permafrost in peatlands has been degrading across the southern limit of permafrost in North America (Vitt et al. 1994, 2000), creating saturated fens called internal lawns. Distributions of internal lawns in North America are generally well correlated to mean annual temperatures, suggesting that permafrost collapse in boreal peatlands is related to regional climate warming since the Little Ice Age (Vitt et al. 1994; Halsey et al. 1997). Further north in high boreal and subarctic regions, permafrost collapse in peat plateaus (creating thaw features called collapse scars) can be triggered by autogenic processes, local disturbance, or fire activity (Robinson, personal communication).

Internal lawns and collapse scars are initially colonized by semiaquatic sedge and moss species (Camill 1999; Beilman 2001). These thaw features often have faster rates of peat accumulation than adjacent frozen peatlands (Robinson and Moore 2000; Turetsky et al. 2000; Camill et al. 2001); however, decomposition is also stimulated by permafrost thaw (Liblik et al. 1997; Turetsky et al. 2002b; 2004), suggesting that increases in soil organic matter formation after thawing are driven by high rates of plant productivity. Permafrost degradation has occurred over more than 2,500 km^2 of peatland across western Canada (Vitt et al. 2000; Beilman et al. 2001) and may have increased regional peatland C stocks by an estimated 100±12 Gg C (Turetsky et al. 2002a). These enhanced C stocks likely are protected from fire activity owing to a saturated condition, until peat accumulates well above the water table and more mesic plant species colonize.

16.5 Water Table Drawdown

Multiple human activities in peatlands (forestry, agriculture, and peat extraction for horticulture or fuels) manipulate water tables through open ditches, subsurface drains, and/or pumps. Generally, drainage affects many ecosystem processes in peatlands (Chap. 13). Drained peatlands often release more CO_2 and N_2O owing to accelerated rates of aerobic decomposition (Martikainen et al. 1995; Augustin et al. 1996; Regina et al.

1998; Waddington et al. 2000) and consume more CH_4 (Willison et al. 1998) than pristine sites (Chap. 9). However, CO_2 uptake in peatlands with open-water sites can be enhanced under the drier (drained) conditions (Strack et al. 2003). While the production of CH_4 generally also declines with peat drainage (Cannell et al. 1993), Strack et al. (2004) noted that "wet" areas of a managed peatland showed no significant change in CH_4 emissions.

CO_2 and other greenhouse gas emissions from peatlands drained for agriculture or other land uses likely decrease over time as peat is oxidized. However, rewetting of drained peatland soils can lead to large losses of N_2O (Ruckauf et al. 2004). Under certain climatic conditions, drained peatlands can serve as a net C sink owing to increased tree growth (Minkkinen and Laine 1998). Increased aerobic decomposition may stimulate dissolved organic C production, though dissolved organic export may decrease with diminished water flow (Moore et al. 1998).

Peatland drainage can adversely affect water quality, which has implications for aquatic communities. Drainage waters tend to have high nutrient concentrations, and excess nutrients can lead to eutrophication and oxygen depletion. Nitrogen and some pesticides leached from organic soils may be harmful or lethal to aquatic organisms (Coote and Gregorich 2000). Peatland drainage also can increase exports of particulate matter, high molecular weight dissolved organic matter, and heavy metals to aquatic systems, which can cause impairment of reproductive success of riverine brown trout and salmon in Finland (Laine 2001) and the impoverishment of benthic communities (Vuori et al. 1998).

16.5.1 Peat Extraction

Peat is widely used for energy, as a fertilizer, and as raw material for chemical products. The use of peat for fuel in recent decades accounts for about 50 % of peat extracted globally, and can provide an important source of local heat and power. The International Peat Society (2002) estimates that 21×10^6 t of peat generates about $5–6 \times 10^6$ t of oil equivalent annually. Extraction rates likely will decline with the development of new electricity markets around the world, increased awareness of greenhouse gas emissions from land use and biomass burning, and declining peat supplies. Peat also has been used for organic fertilizers and a soil amendment in agricultural settings, though this use may be declining globally with the development of cheaper fertilizers and management alternatives.

Utilization of peat in horticulture is increasing globally, particularly in the Baltic States and Canada. The use of peat in fiberboards and peat bricks also is expanding commercially in China (Zhao and Päivänen 1986). In 1999, nearly 40×10^6 m^3 of peat was used globally in horticulture.

The International Peat Society (2002) estimates that peat extraction worldwide affects around 2,000 km^2 of peatland.

Today, peat extraction commonly involves the drainage of large *Sphagnum*-dominated peatlands. During this process, the vegetation layer is removed and peat is milled before organic matter is harvested with large vacuums or tractors (Rochefort 2000; Strack et al. 2003). Drainage and removal of surface vegetation and soil layers in peatlands alters soil structure, water balance, and microbial activity (Strack et al. 2003). Emissions of CO_2 can increase up to 400 % with drainage (Silvola 1986; Waddington et al. 2002); however, as noted earlier, CH_4 fluxes also will decline (Laine et al. 1996). Removing the vegetated layer and lowering the water table of a peatland disrupts the feedback between peatland development and hydrology. Increased peat subsidence (with shrinkage, compression, and oxidation) decreases peat pore size and specific yield, and reduces water storage capacity and saturated hydraulic conductivity (Price and Whitehead 2001; Price et al. 2003).

Restoration efforts in Canada have led to the large-scale reestablishment of *Sphagnum* cover in vacuum-harvested bogs. One goal of this peatland restoration is to restore harvested sites to peat-accumulating systems (Chap. 17). The reintroduction of *Sphagnum* during restoration activities involves rewetting soil layers, spreading plant diaspores to the harvested fields, and covering the surface with mulch or straw (LaRose et al. 1997; Rochefort 2000; Waddington and Price 2000). Waddington et al. (2003) found that plant production rates in recently restored peatlands were similar to those in adjacent natural sites. Restoration enhances CO_2 uptake, though it is not clear whether C sequestration in harvested peatlands is restored at rates comparable to those in natural sites (Waddington and Price 2000).

16.5.2 Forestry

Saturated conditions inhibit tree production in peatlands (Chap. 15). Globally, large areas of peatlands (estimated by the International Peat Society to represent approximately 150,000 km^2) have been drained to support commercial forestry operations. Proe et al. (1996) suggest that peatlands will face increasing pressures from afforestation operations as land capability classifications change. As mentioned before, drainage generally increases CO_2 emissions from peatlands owing to increased heterotrophic respiration and reduces CH_4 emissions; however, increased tree establishment and production can offset these C releases (Minkkinen and Laine 1998; Sarkkola et al. 2003). Conversion of peatlands for forestry activities may generally lead to decreased water availability and a loss in biodiversity.

16.5.3 Agriculture

Agriculture has been a common land use in peatlands for several centuries, impacting about 125,000 km^2 of peatland globally (International Peat Society). Organic soils can be extremely productive, particularly fen peats that are rich in nutrients and are less acidic than bog peats. However, peat in agricultural sites can degrade rapidly, potentially leading to rapid declines in productivity. Before use in agricultural activities, peatlands are generally drained and tilled, and organic soils are often amended with mineral soils or fertilizers (Zhao and Päivänen 1986).

Organic soil drainage for agriculture usually triggers land subsidence, owing to a combination of compaction, desiccation, wind/water erosion, and/or burning (Schothorst 1977; Nieuwenhuis and Schokking 1997). Drained organic soils in many ecosystems contribute substantial amounts of CO_2 and N_2O to the atmosphere (Kasimir-Klemedtsson et al. 1997; Maljanen et al. 2003; Smith et al. 2003), particularly sites that have been fertilized (Augustin et al. 1998). A drained fen in Finland used for pasturing and fodder production was a large source of greenhouse gases, equivalent to about 2.6×10^4 kg CO_2 ha^{-1} year^{-1}, and may have accumulated up to 600 kg CO_2 ha^{-1} year^{-1} prior to management. Maljanen et al. 2001 found that organic soils planted as grasslands served as a net C source during the growing season, while a barley field served as a net sink for CO_2, and they concluded that C balance is influenced by the prevailing plant cover. Additionally, the intensity of soil disturbance during land use is likely to influence N_2O emissions.

Minerotrophic peatlands are not isolated from the surrounding watershed; thus, agricultural practices in watersheds can have indirect influences on peatlands. Eutrophication from neighboring fields can reduce biodiversity and influence the nutrient status of peatlands (Coote and Gregorich 2000; Bedford and Godwin 2003). While agricultural development increases food availability, such developments on or near peatlands decrease water quality, alter pathways of C and N cycling, and reduce biodiversity (Watson et al. 2000).

16.6 Acid Rain

Air pollution represents a major threat to European peatlands, and will become more important to boreal peatlands under increasing land use and development at high latitudes. Acid deposition may not be considered a discrete perturbation over short time scales; however, peatlands are generally considered to be sensitive to acid rain, which has been associated with *Sphagnum* declines in peatlands across the UK (Press et al. 1986).

Nitrogen is a limiting nutrient to most terrestrial vegetation, and N fertilization has stimulated net primary productivity in peatlands (Aerts et al. 1992; Vitt et al. 2003; Chap. 10). Other studies, however, have not observed increases in productivity with N additions (Walker et al. 1996; Thormann and Bayley 1997; Press et al. 1998; Davey 1999). At critical N loads between 14.8 and 15.7 kg N ha^{-1} $year^{-1}$, N becomes toxic to *Sphagnum fuscum* and inhibits net primary production in peatlands (Gunnarsson and Rydin 2000; Vitt et al. 2003).

Increased N loading can generally stimulate decomposition by decreasing C/N ratios of organic matter, though this may not occur if net primary production also increases in response to greater N concentrations (Vitt et al. 2003). Additions of NH_4^+–N may inhibit methanotrophy in aerobic peat layers (Crill et al. 1994). Alternatively, enhanced NO_3^-–N loading in peatlands can directly inhibit methanogenesis (Wang et al. 1992). Combined additions of NO_3^-–N and NH_4^+–N to peatlands result in a small increase in CH_4 emissions (Saarnio et al. 2000), though this effect may be moderated by increasing levels of atmosphere CO_2 (Saarnio and Silvola 1999).

Sulfate derived from fossil fuel combustion can be a dominant component of acid rain. Anaerobic peatland soils can serve as a net sink for atmospheric SO_4^{2-} through sulfate reduction, though increased oxidation of peat layers can stimulate SO_4^{2-} release (Brown 1985; Chap. 12). The fate of peatland sulfur stocks under changing disturbance or climatic regimes is not clear, and is of particular concern in peatlands that have been exposed to high atmospheric sulfur loads (Vile et al. 2003). Sulfur inhibition of methanogenesis also could have important implications for greenhouse gas emissions from peatlands (Winfrey and Zeikus 1977; Vile et al. 2003).

16.7 Other Disturbances

Several disturbances, including ice storms and insect outbreaks, have been identified as important in boreal and temperate forest ecosystems (Dale et al. 2001); however, to our knowledge, these disturbances have not been investigated specifically in boreal peatlands. Future work should determine how these perturbations influence vegetation/soil structure and hydrological and/or biogeochemical function in peatland ecosystems.

16.7.1 Ice Storms

Wind throw and ice damage following winter storms may alter canopy structure and the distribution of aboveground biomass and fuels in treed peatlands. Downed woody debris could increase the vulnerability of peatlands to burning, particularly in drought years. However, because vegetation in peatlands can be dominated by bryophyte and herbaceous biomass, the influence of ice storms on ecosystem function likely is more important in upland settings.

16.7.2 Insect Outbreaks

Insect outbreaks are important to the ecology and management of temperate and boreal forests. For example, in North America, populations of the spruce budworm (*Choristoneura fumiferana*) oscillate on cycles of 30–35 years and are synchronous across large regions of the boreal forest. Spruce budworms are strong defoliators, resulting in the reduced growth and increased mortality of spruce and fir (Ostaff and MacLean 1989). Black spruce is a suitable host for spruce budworm, though the insect is considered more of a pest for fir and white spruce. However, spruce budworm outbreaks have been correlated to reduced growth and increased mortality of black spruce in Canada (Lussier et al. 2002). Spruce budworm could decrease tree productivity and mortality in treed peatlands, particularly during severe outbreaks or in peatlands adjacent to white spruce or fir stands. Permafrost peatlands, with dense canopies of black spruce, likely are at the highest risk during outbreaks. Insect-caused mortality of trees can generally increase vulnerability of secondary infections, including the spruce beetle (*Dendroctonus rufipennis*) (McCullough et al. 1998).

16.7.3 Linear Disturbances

Globally, the loss of peatlands owing to road construction is estimated to be less than 5 % (Joosten and Clarke 2002), but linear disturbances will increase in northern regions with ongoing development and land-use changes. Roads can have severe local impacts on hydrologic flow and nutrient retention. Both the forestry and the oil and gas industries create linear corridors in boreal regions. For example, a 6,000 km^2 study area in northern Alberta, Canada, was crossed by 236 gravel roads, 7,111 km of seismic lines and 1,600 well sites (Alberta's Boreal Caribou Research Program 1999). Across the entire province of Alberta, more than 1×10^6 km of seismic lines have been created to support industrial activities (Alberta's Boreal Caribou Research Program 1999).

The influence of linear disturbances on plant soil processes in peatlands is not well understood; however, linear disturbances likely contribute to peatland fragmentation and alter peatland hydrology at large scales. In western Canada, linear disturbances in peatlands have negatively influenced populations of the endangered woodland caribou. As noted before, caribou preferentially use treed peatlands but tend to avoid roads, wells, and seismic lines throughout their ranges. Caribou near seismic lines and roads were at higher risk of being killed by wolves (James and Stuart-Smith 2000; McLoughlin et al. 2002).

16.8 Feedbacks

16.8.1 Cumulative Impacts

Cumulative impacts are environmental changes caused by an activity in combination with other past or present human activities. Thus, cumulative impacts can increase the severity of effects on a particular peatland function above the sum of individual disturbances alone. For example, many boreal peatlands have the capacity to store large amounts of SO_4^{2-}, but oxidation and release of reduced sulfate could occur with drainage of peat layers (Wieder and Lang 1986; Bayley et al. 1986; Chap. 12). Human activities in peatlands that involve drainage, such as forestry and agriculture, also increase the susceptibility of peatlands to fire. Fire severity under these conditions also may be exacerbated (Maltby and Immirzi 1993). Insect-caused mortality of trees could increase the risk of burning in boreal ecosystems (McCullough et al. 1998). Conversely, Cappuccino et al. (1998) concluded that lower rates of budworm-induced mortality occurred in boreal regions that experience more frequent fire activity. Outbreaks of *Choristoneura* spp. may be increasing in severity owing to the influence of land uses (grazing, forestry) on forest structure (Weber and Schweingruber 1995).

Fire events can trigger thermokarst in permafrost peatlands, which has implications for surface topography, water availability, and plant structure. Conversely, permafrost thaw creates saturated peatland features called internal lawns or collapse scars. Vegetation and soil layers in these thaw features likely are protected from burning owing to saturated conditions, at least until peat accumulates well above the water table and allows the colonization of more xeric peatland species.

16.8.2 Climate–Disturbance Interactions

Climate can serve as a strong control on the frequency or severity of disturbances in terrestrial ecosystems (Dale et al. 2001). For example, cold climatic conditions, including spring frost events, may limit the magnitude of insect outbreaks and the survival and/or growth rates of individual pests (Volney and Fleming 2000). Many boreal regions are expected to receive less precipitation under climate warming. The response of insect outbreaks to changing precipitation is not clear, as drought conditions might have positive or negative influences on insects such as the spruce budworm (Hogg and Schwarz 1999; (Volney and Fleming 2000).

Fire frequencies appear to be increasing in many boreal regions (Kasischke and Stocks 2000; Podur et al. 2002). Positive relationships between burn area in western Canadian peatlands and weather variables suggest that warmer and drier climates will lead to increased burning in boreal and subarctic peatlands (Turetsky 2004). Given that peatlands store significant amounts of soil C and that biomass burning represents a direct release of C to the atmosphere, more frequent and/or severe burning of peat layers could represent a positive feedback to ongoing climate change.

Like fire, land uses in peatlands have the potential to serve as either positive or negative feedbacks to climate. Human activities in peatlands that involve drainage lead to increased emissions of CO_2 and N_2O to the atmosphere, but will decrease CH_4 emissions. Flooding for hydroelectric power generation likely leads to increases in emissions of both CO_2 and CH_4 to the atmosphere owing to increased decomposition. Both CH_4 and N_2O are more effective greenhouse gases than CO_2. Thus, the balance between net CH_4, N_2O, and CO_2 emissions will be important in determining whether management in peatlands increases greenhouse gas emissions (Maltby and Proctor 1996).

16.9 Conclusions

A variety of disturbances influence boreal peatlands. Disturbances that influence pristine peatlands include herbivory, fire, beaver flooding, and permafrost thaw. Climate change leading to warmer and/or drier conditions in some boreal regions may increase peatland burning and trigger more widespread collapse of permafrost. A variety of land uses also commonly influence peatland ecosystems, including flooding for reservoir creation and drainage for forestry, peat extraction, and agricultural activities. Many disturbances reviewed here result in similar effects on peatland communities, hydrology, and greenhouse gas emissions. For example, higher water tables caused by beaver damming, permafrost thaw, and reservoir creation will favor aquatic or semiaquatic plant communities, and likely will increase the emissions of anaerobic greenhouse gases such as CH_4. Alternatively, peatland drainage leads to colonization of woody vegetation, and increased emissions of CO_2 and N_2O owing to greater oxidation and mineralization of soil organic matter.

Northern peatlands may be vulnerable to cumulative impacts, such as increased threats of fire severity following peatland drainage for forestry. The cumulative effects of disturbances on peatland structure and function are far from understood as a whole, and may be accentuated further by climate change. We recommend that future research focus on the potential interactions between land use (reservoirs, drainage) and natural disturbances (insect outbreaks, fire). Additionally, while much research has focused on forestry and peat extraction activities in peatlands, less is known about linear disturbances in boreal peatlands. Roads, pipelines, and other linear corridors are increasingly fragmenting boreal landscapes, and more information on how they influence peatland hydrology and biogeochemical function is needed.

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References

Aber JD, Melillo JM (1991) Terrestrial ecosystems. Saunders College Publishing, Philadelphia

Aerts R, Wallen B, Malmer N (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. J Ecol 80:131–140

Alberta's Boreal Caribou Research Program (1999) http://www.deer.rr.ualberta.ca/caribou/BCRP.htm

Amiro BD, MacPherson JI, Desjardins RL, Chen JM, Liu J (2003) Post-fire carbon dioxide fluxes in the western Canadian boreal forest: evidence from towers, aircraft and remote sensing. Agric For Meteorol 115: 91–107

Augustin J, Merbach W, Schmidt W, Reining E (1996) Effect of changing temperature and water table on trace gas emission from minerotrophic mires. Angew Bot 70:45–51

Augustin J, Merbach W, Rogasik J (1998) Factors influencing nitrous oxide and methane emissions from minerotrophic fens in northeast Germany. Biol Fertil Soils 28:1–4

Bayley SE, Behr RS, Kelly CA (1986) Retention and release of S from a freshwater wetland. Water Air Soil Pollut 31:101–114

Bedford BL, Godwin KS (2003) Fens of the United States: distribution, characteristics, and scientific connection versus legal isolation. Wetlands 23:608–629

Beilman DW (2001) Plant community and diversity change due to localized permafrost dynamics in bogs of western Canada. Can J Bot 79:983–993

Beilman DW, Vitt DH, Halsey LA (2001) Localized permafrost peatlands in western Canada: definitions, distributions and degradation. Arct Antarct Alp Res 33:70–77

Bradshaw CJA, Hebert DM, Rippin AB, Boutin S (1995) Winter peatland habitat selection by woodland caribou in northeastern Alberta. Can J Zool 73:1567–1574

Brinson MM, Malvarez AI (2002) Temperate freshwater wetlands: types, status, and threats. Environ Conserv 29:115–133

Brown K (1985) Sulphur distribution and metabolism in waterlogged peat. Soil Biol Biochem 17:39–45

Camill P (1999) Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. Can J Bot 77:721–733

Camill P, Lynch JA, Clark JS, Adam JB, Jordan B (2001) Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. Ecosystems 4:461–478

Cannell MGR, Dewar RC, Pyatt DG (1993) Conifer plantations on drained peat in Britain: a net gain or loss of carbon? Forestry 66:356–369

Cappuccino N, Lavertu D, Bergeron Y, Régnicre J (1998) Spruce budworm impact, abundance and parasitism rate in a patchy landscape. Oecologia 114:236–242

Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. Chapman and Hall, London, pp 229–289

Cogbill CV (1985) Dynamics of the boreal forests of the Laurentian Highlands, Canada. Can J For Res 15:252–261

Cooper A, McCann T, Power J (1997) Regional variation in the cover, species composition and management of blanket bog. Landscape Urban Plan 37:19–28

Cooper A, McCann TP, Hamill B (2001) Vegetation regeneration on blanket mire after mechanized peat-cutting. Global Ecol Biogeogr 10:275–289

Coote DR, Gregorich LJ (eds) (2000) The health of our water – toward sustainable agriculture in Canada. Research Planning and Coordination Directorate, Research Branch, Agriculture and AgriFood Canada, Ottawa

Crill PM, Martikainen PJ, Nykänen H, Silvola J (1994) Temperature and N fertilization effects on methane oxidation in a drained peatland soil. Soil Biol Biochem 26:1331–1339

Dahl TE (1990) Wetlands losses in the United States 1780's to 1980's. US Department of the Interior, Fish and Wildlife Service, Washington, DC, Jamestown: Northern Prairie Wildlife Research Center. http://www.npwrc.usgs.gov/resource/othrdata/wetloss/wetloss.htm. Version 16 July 1997

Dale VH, Joyce LA, McNaulty S, Neilson RP, Ayres MR, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BM (2001) Climate change and forest disturbances. BioScience 51:723–734

Davey MC (1999) The elemental and biochemical composition of bryophytes from the maritime Antarctic. Antarct Sci 11:157–159

Davidson AJ, Harborne JB, Longton RE (1990) The acceptability of mosses as food for generalist herbivores, slugs in the Arionidea. Bot J Linn Soc 104:99–113

Dove A, Roulet NT, Crill P, Chanton J, Bourbornierre R (1999) Methane dynamics of a northern boreal beaver pond. Écoscience 6:577–586

Efremova TT, Efremov SP (1994) Peat fires as an ecological factor in the development of forest-bog ecosystems. Russ J Ecol 25:330–335

Evans R (1997) Soil erosion in the UK initiated by grazing animals: a need for a national survey. Appl Geogr 17:127–141

Flinn MA, Wein RW (1977) Depth of underground plant organs and theoretical survival during fire. Can J Bot 55:2550–2554

Garnett MH, Ineson P, Stevenson AC (2000) Effects of burning and grazing on carbon sequestration in a Pennine blanket bog, UK. Holocene 10:729–736

Gunnarsson U, Rydin H (2000) Nitrogen fertilization reduces *Sphagnum* production in bog communities. New Phytol 147:527–537

Halsey L, Vitt D, Zoltai S (1997) Climatic and physiographic controls on wetland type and distribution in Manitoba, Canada. Wetlands 17:243–262

Harden JH, Neff JC, Sandberg DV, Turetsky MR, Ottmar R, Gleixner G, Fries TL, Manies KL (2004) The chemistry of burning the forest floor during the FROSTFIRE experimental burn, interior Alaska. Global Biogeochem Cycles 18:GB3014. DOI 10.1029/2003GB002194

Heinselman ML (1973) Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat Res 3:329–382

Hobbs RJ (1984) Length of burning rotation and community composition in high-level *Calluna-Eriophorum* bog in northern England. Vegetatio 57:129–136

Hobbs RJ, Gimingham CH (1980) Some effects of fire and grazing on heath vegetation. Bull Ecol 11:709–715

Hogg EH, Schwarz AG (1999) Tree-ring analysis of declining aspen stands in west-central Saskatchewan. Canadian Forest Service, Northern Forestry Centre, information report NOR-X-359, Edmonton

Immirzi CP, Maltby E, Clymo, RS (1992) The global status of peatlands and their role in carbon cycling. A report for Friends of the Earth by the Wetland Ecosystems Research Group, Department of Geography, University of Exeter. Friends of the Earth, London

International Peat Society (2002) Statement on the wise use of peatlands. http://www.imcg.net/docum/wise0204.pdf

IUCN (2000) Executive Summary of the WWDR (2000) vision for water and nature. a world strategy for conservation and sustainable management of water resources in the 21st century – compilation of all project Documents. Cambridge

James ARC, Stuart-Smith AK (2000) Distribution of caribou and wolves in relation to linear corridors. J Wild Manage 64:154–159

Jones TA, Hughes JMR (1993) Waterfowl and wetland conservation in the 1990s – a global perspective. Wetland inventories and wetland loss studies – a European perspective. Proceedings of the IWRB symposium, St Petersburg Beach, Florida, USA. IWRB special publication no 26. IWRB, Slimbridge, pp 164–169

Joosten H, Clarke D (2002) Wise use of mires and peatlands. Background and principles including a framework for decision making. International Mire Society and the International Peat Conservation Group. http://www.mirewiseuse.com

Kasimir-Klemedtsson A, Klemdtsson L, Berglund K, Marikainen PJ, Silvola J, Oenema O (1997) Greenhouse gas emissions from farmed organic soils: a review. Soil Use Manage 13:245–250

Kasischke E, Stocks BJ (2000) Introduction. In: Kasischke E, Stocks BJ (eds) Fire, climate change, and carbon cycling in the boreal forest. Ecological studies 138. Springer, Berlin Heidelberg New York, pp 1–6

Kasischke ES, O'Neill KP, French NHF, Bourgeau-Chavez LL (2000) Patterns of biomass burning in Alaskan boreal forests. In: Kasischke E, Stocks BJ (eds) Fire, climate change, and carbon cycling in the boreal forest. Ecological studies 138. Springer, Berlin Heidelberg New York, pp 173–196

Kelly CA, Rudd JWM, Bodaly RA, Roulet NT, St. Louis VL, Heyes A, Moore TR, Schiff S, Aravena R, Scott KJ, Dyck B, Harris R, Warner B, Edwards G (1997) Increases in fluxes of greenhouse gases and methyl mercury following flooding of an experimental reservoir. Environ Sci Technol 31:1334–1344

Koops JG, van Beusichem ML, Oenema O (1997) Nitrogen loss from grassland on peat soils through nitrous oxide production. Plant Soil 188:119–130

Kuhry P (1994) The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. J Ecol 82:899–910

Laberge M, Payette S (1995) Long-term monitoring of permafrost change in a palsa peatland in northern Quebec, Canada: 1983–1993. Arct Alp Res 27:157–171

Laine A (2001) Effects of peatland drainage on the size and diet of yearling salmon in a humic northern river. Arch Hydrobiol 151:83–89

Laine J, Silvola J, Tolonen K, Alm J, Nykänen H, Vasander H, Sallantaus T, Savolainen I, Sinisalo J, Martikainen PJ (1996) Effect of water-level drawdown in northern peatlands on the global climatic warming. Ambio 25:179–184

LaRose S, Price J, Rochefort L (1997) Rewetting of a cutover peatland: hydrologic assessment. Wetlands 17:416–423

Lawrey JD (1986) Biological role of lichen substances. Bryologist 89:111–122

Levine JS, Cofer WRI (2000) Boreal forest fire emisions and the chemistry of the atmosphere. In: Kasischke E, Stocks BJ (eds) Fire, climate change, and carbon cycling in the boreal forest. Ecological studies 138. Springer, Berlin Heidelberg New York, pp 31–48

Liblik LK, Moore TR, Bubier JL, Robinson SD (1997) Methane emissions from wetlands in the zone of discontinuous permafrost: Fort Simpson, Northwest Territories, Canada. Global Biogeochem Cycles 11:484–494

Longton RE (1992) The role of bryophytes and lichens in terrestrial ecosystems. In: Bates JW, Farmer AM (eds) Bryophytes and lichens in a changing environment. Oxford University Press, Oxford, pp 32–76

Lussier JM, Morin H, Gagnon R (2002) Mortality in black spruce stands of fire or clear-cut origin. Can J For Res 32:539–547

Mackay AW, Tallis JH (1996) Summit-type blanket mire erosion in the Forest of Bowland, Lancashire, UK: predisposing factors and implications for conservation. Biol Conserv 76:31–44

Maljanen M, Martikainen PJ, Walden J, Silvola J (2001) CO_2 exchange in an organic field growing barley or grass in eastern Finland. Global Change Biol 7:679–692

Maljanen M, Liikanen A, Silvola J, Martikainen PJ (2003) Measuring N_2O emissions from organic soils by closed chamber or soil/snow N_2O gradient methods. Eur J Soil Sci 54:625–631

Maltby E, Immirzi CP (1993) Carbon dynamics in peatlands and other wetland soils – regional and global perspectives. Chemosphere 27:999–1023

Maltby E, Proctor MCF (1996) Peatlands: their nature and role in the biosphere. International Peat Society and Geological Survey of Finland, Jyska, pp 11–19

Maltby E, Legg CJ, Proctor MCF (1990) The ecology of severe moorland fire on the North York Moors – effects of the 1976 fires, and subsequent surface and vegetation development. J Ecol 78:490–518

Manö S, Andreae MO (1994) Emission of methyl bromide from biomass burning. Science 263:1255–1257

Martikainen PJ, Nykanen H, Alm J, Silvola J (1995) Change in fluxes of carbon dioxide, methane and nitrous oxide due to forest drainage of mire sites of different trophy. Plant Soil 169:571–577

McCullough DG, Werner RA, Neumann D (1998) Fire and insects in northern and boreal forest ecosystems of North America. Ann Rev Entomol 43:107–127

McLoughlin PD, Dzus E, Wynes B, Boutin S (2002) Declines in populations of woodland caribou. J Wild Manage 67:755–761

Minkkinen K, Laine J (1998) Long-term effect of forest drainage on the peat carbon stores of pine mires in Finland. Can J For Res 28:1267–1275

Moore TR, Roulet NT, Waddington JM (1998) Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. Clim Change 40:229–245

Morrissey LA, Livingston GP, Zoltai SC (2000) Influence of fire and climate change on patterns of carbon emissions in boreal peatlands. In: Kasischke E, Stocks BJ (eds) Fire, climate change, and carbon cycling in the boreal forest. Ecological studies 138. Springer, Berlin Heidelberg New York, pp 423–439

Naiman RJ, Melillo JM, Hobbie JE (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67:1254–1269

National Wetlands Working Group (1988) Wetlands of Canada. Ecological land classification series, no 24. Sustainable Development Branch, Environment Canada, Ottawa, and Polyscience, Montreal

Nieuwenhuis HS, Schokking F (1997) Land subsidence in drained peat areas of the Province of Friesland, The Netherlands. Q J Eng Geol 30:37–48

Nummi P, Poysa H (1997) Population and community level responses in *Anas*-species to patch disturbance caused by an ecosystem engineer, the beaver. Ecography 20:580–584

Ostaff DP, MacLean DA (1989) Spruce budworm populations, defoliation, and changes in stand condition during an uncontrolled spruce budworm outbreak on Cape Breton Island, Nova Scotia. Can J For Res 19:1077–1086

Pickett STA, White PS (eds) (1985) The ecology of natural disturbance and patch dynamics. Academic, New York

Pickett STA, Amesto JJ, Collins SL (1989) The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129–136

Podur J, Martell DL, Knight K (2002) Statistical quality control analysis of forest fire activity in Canada. Can J For Res 32:195–205

Press MC, Woodin SJ, Lee JA (1986) The potential importance of an increased atmospheric nitrogen supply to the growth of ombrotrophic *Sphagnum* species. New Phytol 103:45–55

Press MC, Potter JA, Burke MJW, Callaghan TV, Lee JA (1998) Responses of a subarctic dwarf shrub heath community to simulated environmental change. J Ecol 86:315–327

Price JS, Whitehead GS (2001) Developing hydrologic thresholds for *Sphagnum* recolonization on an abandoned cutover bog. Wetlands 21:32–40

Price JS, Heathwaite AL, Baird AJ (2003) Hydrological processes in abandoned and restored peatlands: an overview of management approaches. Wetlands Ecol Manage 11:65–83

Proe MF, Allison SM, Matthews KB (1996) Assessment of the impact of climate change on the growth of Sitka spruce in Scotland. Can J For Res 26:1914–1921

Regina K, Nykanen H, Maljanen M, Silvola J, Martikainen PJ (1998) Emissions of N_2O and NO and net nitrogen mineralization in a boreal forested peatland treated with different nitrogen compounds. Can J For Res 28:132–140

Rettie WJ, Messier F (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466–478

Ritchie JC (1987) Postglacial vegetation of Canada. Cambridge University Press, New York

Robinson SD, Moore TR (2000) The influence of permafrost and fire upon carbon accumulation in high boreal peatlands, Northwest Territories, Canada. Arct Antarct Alp Res 32:155–166

Rochefort L (2000) *Sphagnum* – a keystone genus in habitat restoration. Bryologist 103:503–508

Roulet NT, Ash R, Moore TR (1992) Low boreal wetlands as a source of atmospheric methane. J Geophys Res 97:3739–3749

Roulet NT, Crill PM, Comer NT, Dove AE, Bourbonniere RA (1997) CO_2 and CH_4 flux between a boreal beaver pond and the atmosphere. J Geophys Res 102:29313–29319

Ruckauf U, Augustin J, Russow R, Merbach W (2004) Nitrate removal from drained and reflooded fen soils affected by soil N transformation processes and plant uptake. Soil Biol Biochem 36:77–90

Saarnio S, Silvola J (1999) The effects of raised CO_2 and N supply on CH_4 efflux from a boreal peat: a growth cabin experiment. Oecologia 119:349–356

Saarnio S, Saarinen T, Vasander H, Silvola J (2000) A moderate increase in the annual CH_4 efflux by raised CO_2 or NH_4NO_3 supply in a boreal oligotrophic mire. Global Change Biol 6:137–144

Sarkkola S, Alenius V, Hökkä H, Laiho R, Päivänen J, Penttilä T (2003) Changes in structural inequality in Norway spruce stands on peatland sites after water-level drawdown. Can J For Res 33:222–231

Schothorst CJ (1977) Subsidence of low moor peat soils in the western Netherlands. Geoderma 17:265–291

Segerstrom U (1997) Long-term dynamics of vegetation and disturbance of a southern boreal spruce forest. J Veg Sci 8:295–306

Segerstrom U, Emanuelsson M (2002) Extensive forest grazing and hay-making on mires – vegetation changes in south-central Sweden due to land use since Medieval times. Veg Hist Archaeobot 11:181–190

Silvola J (1986) Carbon dioxide dynamics in mires reclaimed for forestry in eastern Finland. Ann Bot Fenn 23:59–67

Slack NG (1988) The ecological importance of lichens and bryophytes. In: Nash TH III (ed) Lichens, bryophytes and air quality. Bibliotheca Lichenologica 30. Cramer, Berlin, pp 1–53

Smith KA, Ball T, Conen F, Dobbie KE, Massheder J, Rey A (2003) Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. Eur J Soil Sci 54:779–791

St Louis V, Kelly CA, Duchemin E, Rudd JWM, Rosenberg DM (2000) Reservoir surfaces as sources of greenhouse gases to the atmosphere: a global estimate. BioScience 50:766–775

Stocks BJ, Kaufman JB (1997) Biomass consumption and behavior of wildland fires in boreal, temperate, and tropical ecosystems: parameters necessary to interpret historic fire regimes and future fire scenarios. In: Clark JS, Cachier H, Gold ammer JG, Stocks BJ (eds) Sediment records of biomass burning and global change. NATO ASI series 151, Springer, Berlin Heidelberg New York, pp 169–188

Stocks BJ, Mason JA, Todd JB, Bosch EM, Wotton BM, Amiro BD, Flannigan MD, Hirsch KG, Logan KA, Martell DL, Skinner WR (2003) Large forest fires in Canada, 1959-1997. J Geophys Res. DOI 10.1029/2001JD000484

Strack M, Waddington JM, Tuittila E-S, Kellner E, Price JS, Rochefort L (2003) Methane emissions and storage at a natural and drained peatland fen in central Québec. Järvet E, Lode E. (eds) Proceedings of the international conference on ecohydrological processes in northern wetlands. Tartu University Press, Tallinn, pp 227–232

Strack M, Waddington JM, Tuittila E-S (2004) The effect of water table drawdown on northern peatland methane dynamics: Implications for climate change. Global Biogeochem Cycles 18. DOI 10.1029/2003GB002209

Thormann MN, Bayley SE (1997) Response of aboveground net primary plant production to nitrogen and phosphorus fertilization in peatlands in southern boreal Alberta, Canada. Wetlands 17:502–512

Tiner RW (1984) Wetlands of the United States: current status and recent trends. US Fish and Wildlife Service, US Government Printing Office, Washington, DC

Tolonen M (1985) Paleoecological record of local fire history from a peat deposit in SW Finland. Ann Bot Fenn 22:15–29

Turetsky MR (2004) Decomposition and organic matter quality in peatlands. Ecosystems 7:740–750

Turetsky MR, Wieder RK, Williams CJ, Vitt DH (2000) Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta. Écoscience 7:379–392

Turetsky MR, Wieder RK, Halsey LA, Vitt. DH (2002a) Current disturbance and the diminishing peatland carbon sink. Geophys Res Lett 29. DOI 10.1029/2001 GL014000

Turetsky MR, Wieder RK, Vitt DH (2002b) Boreal peatland C fluxes under varying permafrost regimes. Soil Biol Biochem 34:907–912

Turetsky MR, Amiro BD, Bosch E, Bhatti, JS (2004) Historical burn area in western Canadian peatlands and its relationship to fire weather indices. Global Biogeochem Cycles 18:GB4014. DOI 10.1029/2004GB002222

Turunen J, Tahvanainen T, Tolonen K, Pitkanen A (2001) Carbon accumulation in west Siberian mires, Russia. Global Biogeochem Cycles 15:285–296

Van Cleve K, Viereck LA, Dryness CT (1996) State factor control of soils and forest succession along the Tanana River in interior Alaska, USA. Arct Alp Res 28:388–400

Vile MA, Bridgham SD, Wieder RK, Novák M (2003) Atmospheric sulfur deposition alters gaseous carbon production from peatlands. Global Biogeochem Cycles 17:1058

Vitt D, Halsey L, Zoltai S (1994) The bog landforms of continental western Canada in relation to climate and permafrost patterns. Arct Alp Res 26:1–13

Vitt DH, Halsey LA, Zoltai SC (2000) The changing landscape of Canada's western boreal forest: the current dynamics of permafrost. Can J For Res 30:283–287

Vitt DH, Wieder RK, Halsey LA, Turetsky MR (2003) Response of *Sphagnum fuscum* to nitrogen deposition: a case study of ombrogenous peatlands in Alberta, Canada. Bryologist 106:235–245

Volney WJA, Fleming RA (2002) Climate change and impacts of boreal forest insects. Agric Ecosyst Environ 82:283–294

Vuori K-M, Joensuu I, Latvala J, Jutila E, Ahvonen A (1998) Forest drainage: a threat to benthic biodiversity of boreal headwater streams? Aquat Conserv Mar Freshwater Ecosyst 8:745–759

Waddington JM, Price JS (2000) Effect of peatland drainage, harvesting, and restoration on atmospheric water and carbon exchange. Phys Geogr 21:433–451

Waddington JM, Warner KD, Kennedy G (2002) Cutover peatlands: a persistent source of atmospheric CO_2. Global Biogeochem Cycles. DOI 10.1029/2001 GB001398

Waddington JM, Campeau S, Rochefort L (2003) *Sphagnum* production and decomposition in a restored peatland. Wetland Ecol Manage 11:85–95

Walker LR, Zimmerman JK, Lodge DJ, Guzman-Grajales S (1996) An altitudinal comparison of growth and species composition in hurricane damaged forests in Puerto Rico. J Ecol 84:877–889

Wang Z, Delaune RD, Lindau CW, Patrick WH (1992) Methane production from anaerobic soil amended with rice straw and nitrogen fertilizers. Fert Res 33:115–121

Watson RT, Noble IR, Bolin B, Ravindranath NH, Verardo DJ, Dokken DJ (eds) (2000) Land use, land-use change, and forestry 2000. Special report of the intergovernmental panel on climate change, Cambridge University Press, Cambridge

Weber UM, Schweingruber FH (1995) A dendroecological reconstruction of western budworm outbreaks (Choristoneura occidentalis) in the Front Range, Colorado, from 1720 to 1986. Trees 9:204–213

Wieder RK, Lang GE (1986) Fe, Al, Mn, and S chemistry of *Sphagnum* peat in four peatlands with different metal and sulfur input. Water Air Soil Pollut 29:309–320

Willison TW, Baker JC, Murphy DV (1998) Methane fluxes and nitrogen dynamics from a drained fenland peat. Biol Fertil Soil 27:279–283

Winfrey MR, Zeikus JG (1977) Effect of sulfate on carbon and electron flow during microbial methanogenesis in freshwater sediments. Appl Environ Microbiol 275–281

Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96–101

Zackrisson O (1977) Influence of forest fires on the north Swedish boreal forest. Oikos 29:22–32

Zhao K, Päivänen J (1986) Peatlands and their utilization in northeast China. Suo 37:57–65

Zoltai SC, Morrissey LA, Livingston GP, de Groot WJ (1998) Effects of fire on carbon cycling in North American boreal peatlands. Environ Rev 6:13–24

17 Restoration of Degraded Boreal Peatlands

LINE ROCHEFORT and ELVE LODE

17.1 Introduction

The ecological restoration of a habitat is the process of assisting the recovery of an ecosystem that has been damaged, degraded, or destroyed (Society for Ecological Restoration Science, Policy Working Group 2004; Chap. 16). Owing to the fact that the restoration of complex wetland ecosystems to their former patterns is almost impossible, the existing wetlands or peatlands should be improved and restored as far as is possible to former wetlands within socioeconomic and environmental limiting conditions (Anonymous 1995; Wheeler 1995; Charman 2002). Environmental limitations can refer to controllable conditions, e.g., hydrological or biological management, or to uncontrollable conditions, e.g., climate (Streefkerk and Casparie 1989). Socioeconomic conditions can limit the restoration approach owing to poor economy or lack of environmental knowledge of a society. The historical conditions established by different peatland utilization systems also influence future possibilities for restoration (Girard et al. 2002). There is considerable variation in restoration costs and in the duration of the recovery process, variation that is strongly related to the scale and length of time of the changes made in the peat landscapes.

In view of these constraints, we define the general goal of peatland restoration as the return of degraded or destroyed peatland sites to wetland ecosystems. Over time and through plant succession, these wetlands should lead back to peat-accumulating ecosystems. The notions discussed in this chapter apply mostly to the boreal biome of the northern hemisphere.

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17.1.1 Goals of Peatland Restoration

The restoration of peatlands will seek to reestablish a plant cover dominated by *Sphagnum* or brown mosses depending on the substrate minerotrophy, as well as a hydrological regime typical of peatlands (Rochefort 2000). Nonetheless, the restoration process should ensure the return of functions of the ecosystem necessary to its self-perpetuity (Lode 2001). Among these functions are adequate productivity permitting the accumulation of carbon, cycling of nutrients, recovery of the vegetation structure that will favor animal and plant biodiversity, and characteristics that permit the ecosystem to resist biological invasions.

Peatland restoration is one way of reaching the objective of "no net loss" promoted by the North American council for the conservation of wetlands (Lynch-Stewart 1992) and the European community (Anonymous 1995). The no net loss objective is based on the principle that the obligatory loss of wetlands should be compensated. Compensation can be achieved by the restoration of former wetlands or the creation of new wetlands of at least the same area that perform the same functions and provide similar ecological values. Improvement and restoration should have priority over the creation of new wetlands. It is not possible to completely end disturbance of wetlands. Some disturbances occur naturally, some are from past activities, while others are unavoidable and result from human activities that are beneficial. However, attempts toward "wise use" of peatlands (Joosten and Clark 2002) via "reasonable" manmade management including conservation and nondestructive uses will hopefully increase in the near future.

The concept of peatland restoration retained in this chapter subscribes to the notion of "sustainable use" of peatlands. This means that after any type of disturbance, the peatland ecosystem and its main functions are restored back within a human lifetime, so that future generations can appreciate the presence of this special habitat, often little known by the general public. Thus, the general goal of restoration is not to renew peat as a natural resource, but rather to manage the ecosystem so as to impede its loss in certain regions or localities and maintain the biodiversity of habitats.

Mire restoration has become a central practice of nature conservation in European countries where mires have become rare (Wheeler and Shaw 1995; Wheeler et al. 1995; Lamers et al. 2002; Blankenburg and Tonnis 2004). In North America and in Europe, commitments toward peatland restoration have been adopted as a common practice among the peat industries (Rochefort and Price 2003; Vasander et al. 2003). In European countries where there is still a considerable amount of both peat resources and mires in a natural state (Estonia, Finland, Sweden, Russia), bog restoration is not the prevailing aim of peatland management. Management options are often the creation of shallow wetlands to favor bird habitats, the creation of fen-type landscapes, or the establishment of agricultural or forestry practices. But if in a particular landscape setting bogs are recognized to be important in maintaining the groundwater table, then a restoration approach is favored (Schouten et al. 2002).

17.1.2 Conservation

It would be unwise to only rely on restored peatlands as a conservation strategy for a given geographical region. Indeed we know little about how new restoration sites are recolonized by animal peatland species. To ensure the maintenance of regional biodiversity, it appears important to maintain pristine peatlands on the landscape, or at the scale of a peatland complex to preserve undisturbed fragments adjacent to extracted areas (Poulin et al. 1999; Pellerin and Lavoie 2000). The undisturbed peat deposits of mires are like a book, and through palaeoecological analyses, the history of past climate, landscape development since the last glaciation, and environmental changes can be decoded. Any peat utilization destroys these archives forever, and this is part of the reason why the spatial distribution of peatlands for conservation should be chosen with care. The preservation of natural remnants within a peatland site or complex is also recommended as it can ensure the supply of plant material for future restoration plans or as a refuge for an array of animal species while waiting for the restoration of the entire ecosystem.

17.1.3 Topics of This Chapter

Peatland restoration is a relatively new field of investigation that was the object of significant advances in the 1990s (Lode 2001; Price et al. 2003; Rochefort et al. 2003). Currently the conservation and restoration of peatlands in Europe stem from the fact that Europe has lost or degraded the major part of its peatlands. This chapter will mostly discuss the restoration of *Sphagnum*-dominated peatlands (bogs) that have been affected by peat mining (Chap. 16), but the overall approach can easily be adapted to the restoration of ombrotrophic peatlands that have been damaged by agriculture, fires, or certain types of erosion. The restoration of peatlands after forestry practices and drainage is discussed in depth by Laine et al. (Chap. 15). For the particular case of peatlands with serious erosion problems, the report on blanket mire degradation (Tallis et al. 1997) should be consulted.

The first section of this chapter overviews the extent of habitat loss in the boreal biome. The next section describes the factors influencing plant establishment on degraded peatlands, and the subsequent section gives an overview of restoration practices. Concluding sections discuss the success of recovery and end with the needs of research in peatland restoration.

17.2 Background on Habitat Loss

During the last decade, intensive work has been done in the field of peatland inventories (Pfadenhauer et al. 1993; Lappalainen 1996; Mitsch and Gosselink 2000). In spite of greatly improved overviews concerning the location of peatlands and extension, there is still lack of comprehensive and comparable data in reports at the national level (compare for instance Joosten and Clarke 2002 with Vasander et al. 2003). In spite of uncertainties in data or different definitions used, one trend is clearly observed – a trend of decreasing the area of peatlands in the world, especially in Europe (Fig. 17.1).

Owing to a long history of high population and climatic suitability for agriculture, Europe has experienced one of the largest mire losses in the world. Currently over 50 % of European peatlands have ceased to accumulate peat and almost 20 % of the original mire area no longer exists as peatland. In many countries only 1 %, or less than 1 %, of the original resources remains (Joosten and Clarke 2002).

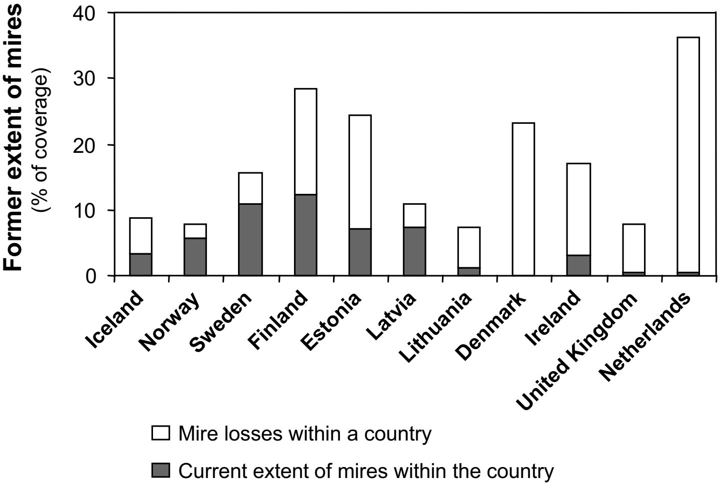

Fig. 17.1. Former extent of mires expressed as a percentage over the total area of a country (*total bars*), mire losses within a country (*white part of the bar*), and current extent of mires within a country (*shaded part of the bar*) in northern Europe, estimated after Joosten and Clarke (2002)

In Canada, it is estimated that since European colonization, close to 20×10^6 ha of wetlands have been affected by human activities (Rubec 1996). Out of that 20×10^6 ha of wetland lost, it is estimated that 1×10^6 ha are ombrotrophic peatlands (bogs). So far, the peat industry has been working on a total area of 17,000 ha of bogs over the country (Daigle and Gautreau-Daigle 2001). The main loss of bog habitats in North America is mostly caused by flooding from the building of dams for hydroelectricity or from agriculture, which has impacted mostly fens and wetlands. In the USA, there are 21.4×10^6 ha of peatlands, of which 50 % occur in Alaska in their natural state. Only about 2 % of the contiguous USA is ombrotrophic peatlands (high fiber, low-decomposition fibrists peat type; Malterer 1996), and nearly all are in their natural state.

17.3 Factors Influencing Plant Establishment on Degraded Peatlands

Sphagnum-dominated peatlands (bogs and poor fens) are characterized by a strong relationship between vegetation and hydrology (Ingram 1983; Chap. 4). *Sphagnum* mosses are abundant and dominant in these ecosystems and they are able to modify their physicochemical environment to the point of impeding the processes of decomposition (Clymo 1987). With time, peat accumulates, which slowly raises the peat layers above surface runoff, causing an impoverishment in mineral input as the peatlands become fed only by atmospheric precipitation (Glaser and Janssens 1986). The highly fibric and porous structure of the Sphagnum carpet can store atmospheric water and limits considerably water table fluctuations (Ingram 1983; Wheeler 1999). In natural bogs, the *Sphagnum* mosses keep the eco-hydrologic self-regulating systems favorable to their own growth (van Breemen 1995). This is the reason why so much attention has been given to the long-term reestablishment success of *Sphagnum* mosses during the development of restoration techniques (Money 1995; Rochefort 2000; Tuittila et al. 2003).

17.3.1 General Approach

Sphagnum mosses possess a high potential for regeneration from vegetative fragments (Table 17.1), but factors allowing this expression under field conditions have only begun to be understood. Numerous field observations show that spontaneous recolonization of peatland ecosystems by *Sphagnum* mosses is not a common phenomenon on milled peatlands (presently the most common type of abandoned peat fields). Indeed, very

Table 17.1. Regeneration potential of different *Sphagnum* organs removed from the gametophyte in experimental conditions (adapted from Gauthier 2001)

Bibliographical source	Oehlmann (1898)			Woesler (1934)	Noguchi and Muraoka (1959)
Species	6	7	8	2	10
Green part					
Apical bud					
• With leaf and branch primordia					
• Without leaf and branch primordia	+	+	+		
Whole capitulum					
Branch of the capitulum					
• Length not specified					
• Long	+	+	+		
• Medium	+	+	+		
• Short	+	+	+	+	
Thin section of the stem between the capitulum and the first fascicle					
Stem portion					
• Not specified	–	–	–		
• Between the capitulum and the first fascicle					
• With at least 1 branch fascicle					
• Between 2 branch fascicles					
• Without leaves and branches					
Whole branch fascicle					
Branch (type not specified)	+	+	+	+	
Divergent branch					
• With leaves					
• Without leaves					
Pendent branch					
• With leaves					
• Without leaves					
Branch leaf					
• Origin not specified	+	+	+		+
• From branches of the capitulum				+	
• From divergent branches of the stem					
Brown part – stem portion					
• With at least 1 branch fascicle					
• Between 2 branch fascicles					
• Without leaves and branches					

+ expresses a positive result and – a negative result.
1 S. magellanicum, 2 S. palustre, 3 S. papillosum, 4 S. squarrosum, 5 S. angustifolium, 6 S. cuspidatum, 7 S. fallax, 8 S. rufescens (= *S. denticulatum*), *9 S. subsecundum, 10 S. capillifolium, 11 S. rubellum, 12 S. subnitens*

Sobotka (1976)	Poschlod and Pfadenhauer (1989)								Rochefort et al. (1995)			
2	1	2	3	4	6	9	11	12	1	3	5	11
									+			+
										−		
+	+	+	+	−	+	+	+	+				
	+	+	+	+	+	+	+	+				
										+		
										+		
										+		
									+			
									+	−		
	+	+	+	+	+	+	+	+		+		
	+	+	+	+	+	+	+	+	−	+		
+												
	+	+	+	+	+	+	+	+				
+	+	+	+	+	+	+	+	+	−		+	+
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									−			
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−	−	−	−	−	−	−	−	−				
									+		−	+
	+	+	+	+	+	−	+	+				
	+	+	+	+	+	−	+	−				
+												

few postmilled peatlands that have been abandoned for the last 15–25 years have readily been recolonized by *Sphagnum* plants over extensive bare peat areas (e.g., less than 1 % in Canada; Rochefort 2001; Poulin et al. 2005).

The first years of trials to reintroduce Sphagna on bare peat were unsuccessful (at the end of the 1980s and the beginning of the 1990s). All moss reintroductions were done by spreading fragments on bare peat, by either reintroducing whole *Sphagnum* individuals in wet hollows and water-filled ditches or by the transplantation of entire *Sphagnum* cores ("plugs") of different size (small cores of 10 cm × 10 cm × 10 cm or blocks of 1 m × 1 m × 50-cm depth), and resulted in dead plant material after one or two field seasons or at most they just barely survived (the large "plugs") without any spatial extension after 10 years of monitoring. *Sphagnum* moss establishment became successful only once the importance of providing a favorable humid microclimate at the interface of the air–peat surface and of protecting the vegetative moss fragments against desiccation was realized. Then it became possible to develop efficient restoration techniques.

In the first peatland restoration projects, careful attention was given to match the *Sphagnum* species and the residual substrate in terms of physicochemical conditions. Those detailed substrate characterizations were costly and now several field observations indicate that there is little relation between the specific *Sphagnum* habitat niche and its ability to colonize bare peat when working on *Sphagnum* residual peat (fibric material of von Post 4–5 or less). Usually though, *Sphagnum* material should not be reintroduced on residual sedge peat.

Ten years of restoration practices in North America have shown that there are three management interventions that are paramount to the success of *Sphagnum* establishment on bare peat surfaces: (1) the active reintroduction of plant diaspores[3]; (2) the application of a protective mulch cover; and (3) the rewetting of the site by a combination of blocking drainage and field surface preparation (ellipses in Fig. 17.2). For the sites prone to frost heaving (Groeneveld and Rochefort 2002), phosphorus fertilization is also compulsory. It is currently questioned if fertilization is needed for all restoration conditions and only long-term monitoring of projects will determine its necessity.

The following sections describe how the different factors represented in rectangles in Fig. 17.2 affect the establishment of *Sphagnum*.

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[3] Any part of a plant capable of growing as a new plant. This includes seeds and spores, but also rhizomes, stems, leaves, and branches.

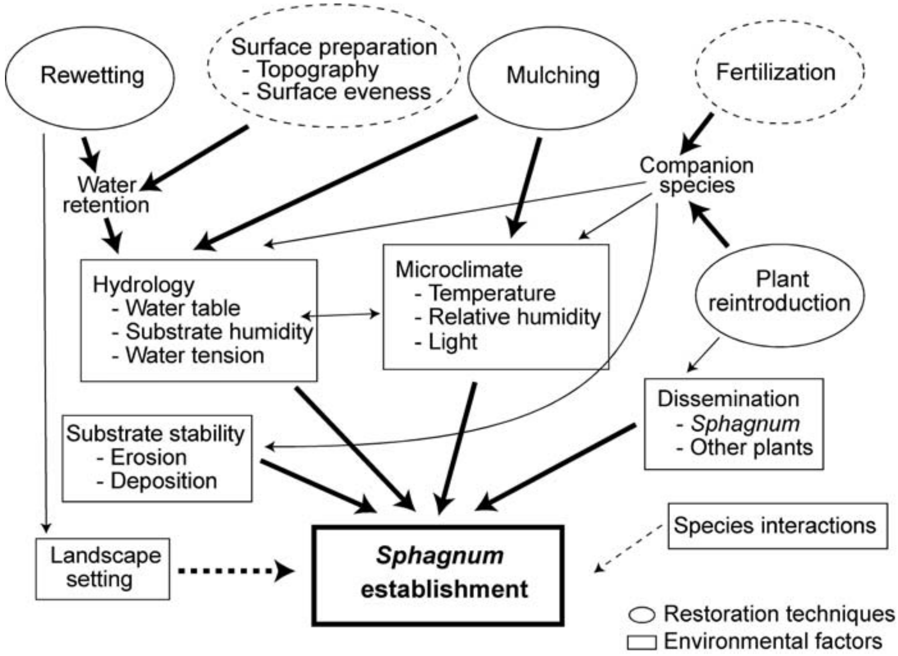


Fig. 17.2. Factors affecting the success of *Sphagnum* establishment on bare peat substrates. *Rectangles* represent the factors directly responsible for the success of moss establishment. Management practices (actions) – absolutely necessary to reestablish a moss cover when degradation is extreme such as in a cutover peatland – are represented in *ellipses*. The *dashed-line ellipse* represent optional management practices, specific of each case study, or factors suspected to be compulsory (fertilization) but still under study. The *full-line arrows* point to relationships that have often been demonstrated through several field trials; *the dashed-line arrows* are relationship still under study. (Adapted from Rochefort 2000)

17.3.2 Dissemination

It was obvious from the start that natural recolonization of milled peatlands is far from sufficient to restore a functional peatland (Salonen 1987; Desrochers et al. 1998; Bérubé and Lavoie 2000; Campbell et al. 2003; Lavoie et al. 2003; Fig. 17.3). Plant dispersal by wind to bare peat sites does not appear to be a problem. Indeed, spores of mosses, particularly *Polytrichum strictum*, seeds of several ericaceous species, notably *Kalmia angustifolia* and *Rhododendron groenlandicum*, and seeds from trees, mostly *Betula* spp. and *Picea mariana*, are easily and abundantly dispersed by wind (Soro et al. 1999; Campbell et al. 2000). That is true if the surrounding edges of the site to be rehabilitated are in a relatively natural

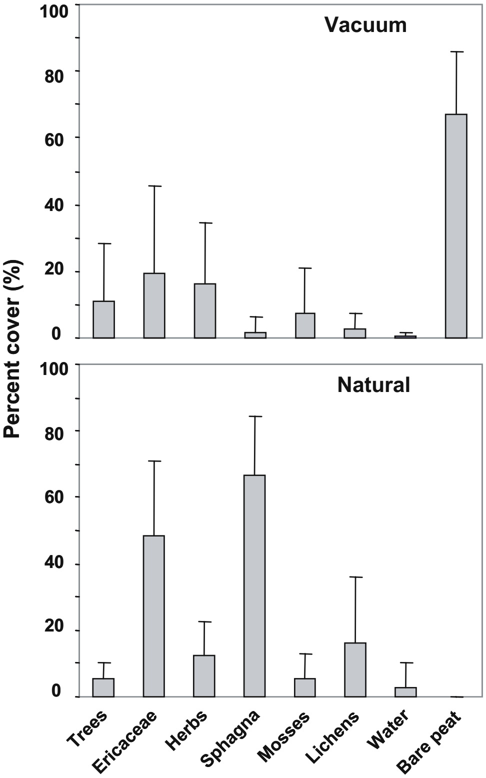


Fig. 17.3. Mean vegetation cover in 18 abandoned milled peatlands and 24 nearby natural peatlands in eastern Canada. The average age of abandonment was 11±7 years (mean ± standard deviation). Details on the methodological surveys are available from Poulin et al. (2005). Surveys in milled peatlands were conducted in 1994–1995 and those in natural peatlands were conducted in 1997 (see Poulin et al. 1999 for more details). (Adapted from Poulin et al. 2005)

state and are not dominated by invasive species such as *Betula* spp. which then can create a serious barrier to peatland plant dispersal. But usually, the discrepancies between immigration potential and the actual recolonization for several species suggest that other factors after immigration control their colonization success. In fact, it resides mostly in their inability to germinate, to establish, or to grow to maturity.

But why *Sphagnum* species are not found at all recolonizing milled peat surfaces is a key question on the road to successful restoration. A great part of the solution resides in the fact that *Sphagnum* spores seem to require very specific and stable conditions to germinate (Clymo and Duckett 1986). It is quite easy to get *Sphagnum* spores to germinate on bare peat when the peat is at a constant humidity and at 22 °C in a sealed Petri dish. But to our knowledge, no one has succeeded in germinating *Sphagnum* spores in the field. Recolonization is relatively easy with vegetative *Sphagnum* fragments when conditions are created to provide a favorable growing substrate (Poschlod and Pfadenhauer 1989; Rochefort et al. 1995). Thus, it was concluded early in the development of a restoration approach for *Sphagnum*-dominated peatlands that vegetative *Sphagnum* moss material had to be reintroduced to initiate the restoration process of abandoned milled peatlands. Once a *Sphagnum* carpet is established, it does not appear necessary to introduce other peatland plants as several will establish themselves from the diaspore bank brought in by the reintroduced *Sphagnum* plant material or they will simply immigrate from the residual fragments surrounding the restoration site and germinate. The usual biodiversity of the peatland might not be completely restored by this restoration approach, but only the long-term monitoring of restored sites will reveal if further actions are necessary.

17.3.3 Microclimate

The extreme microclimate of the bare peat surface is one of the main factors prohibiting the successful restoration of postharvested bogs. Owing to low conductivity, absence of shade, and temporary aridity, surface temperature can reach over 70 °C on bare peat surfaces, effectively disabling the establishment and recolonization of bog species (Sliva 1998). The microclimate conditions at the air–peat interface seem to be more important when the mosses are growing as isolated plants spread over the field than when growing as a uniform cover of *Sphagnum* carpets in undamaged bogs (Grosvernier et al. 1995) or in well self-recovered peat block-cutting pits (Lode 2001).

Laboratory trials have established that regenerating *Sphagnum* fragments can survive lengthy periods without a supply of water, despite the fact that they are wetland plants with little mechanism of water retention or water transport. In a study on desiccation tolerance, Sagot and Rochefort (1996) isolated *Sphagnum* fragments and left them to air dry (average temperature of 21 °C, average relative humidity, RH, of 60 %) for periods up to 61 days and then placed them in culture (for 8 weeks) in Petri dishes with nutrient solutions to determine their survival rate. The three species tested (*Sphagnum fuscum*, *S. fallax*, and *S. magellanicum*) survived quite well for periods of desiccation lasting up to 14 days, after which a sharp decline in survival was evident. But if the temperature was increased to a constant 30 or 40 °C, it appeared that most species could not survive 2 days of desiccation (six species tested; Sagot and Rochefort 1996). In fact, the ability of *Sphagnum* fragments to tolerate desiccation is directly dependent on the RH of the air to which they are exposed (Rochefort, unpublished data). At 14 % RH with an air temperature of 21 °C, survival of *Sphagnum* fragments without capitula was zero after 12 h. When the air RH was maintained at 76 %, the *Sphagnum* fragments could tolerate 3 days without a supply of water. At 94 % RH, two of the species tested could survive 28 days of no watering. In conclusion, *Sphag-*

num fragments can survive and regenerate despite periods of several days without rain in conditions of temperature and RH averaging 21 °C and 60 %. Consequently, if a higher temperature of the residual peat surface is experienced, fragments will need to have an environment of greater RH. Abandoned peat surface conditions (in terms of temperature and RH) are known to exceed the conditions needed for the survival of *Sphagnum* fragments for a long period without rain (Price et al. 1998). It is thus imperative to use a protective device that gives preference to the survival and establishment of *Sphagnum* mosses.

The use of natural or artificial mulch is a management practice largely in use in agriculture to decrease the thermal variation of soil and to reduce evaporation (Rosenberg et al. 1983; Enz et al. 1988). A wide array of "mulching" material has been tested in peatland restoration (Rochefort 2001): polyethylene plastic cover, plastic material usually used for making snow fences, greenhouse shading screen, straw mulch, and root residues rejected by the peat screening process when baling peat. Even if in most cases moss fragments did establish themselves better under a cover rather than under no cover, the results varied greatly in efficiency between the material types used for protection. After several trials and a few years of monitoring the recovery success of different protecting materials, straw mulch proved to be the most effective protection through reducing day temperature, reducing evaporation losses, and improving soil moisture and pore water pressure (Price et al. 1998, 2003; Fig. 17.4, Table 17.2). Not only did it improve the regenerating conditions for the mosses, but it also proved to be the most economical solution.

The use of mulch might well provide a favorable humid microclimate for the mosses but it also reduces the quantity of incident light that is needed for photosynthesis and growth. Again, the requirement for light in the habitat niche might be quite different from that in the regeneration niche, especially when the moss is reintroduced as fragments. Experiments conducted in growth chambers and greenhouses (Rochefort 2001) showed that there is a decrease in *Sphagnum* regeneration from fragments only when light is cut by 80 % or more. Thus, it is possible that the potential negative effect of reducing incident light is more than counterbalanced by the amelioration of RH for the regeneration of the *Sphagnum* mosses. In fact, the photosynthetic capacity of *Sphagnum* mosses is reduced when incident light was found to be greater than 175 W m^{-2} (photoinhibition; Murray et al. 1993). Thus, the reduction of light by the straw mulch could also be beneficial, but this hypothesis remains to be tested.

Microclimate conditions for *Sphagnum* recolonization of bare peat surfaces can also be improved by the use of companion species (Grosvernier et al. 1995; Boudreau and Rochefort 1999; Tuittila et al. 2000). Vascular plants, such as the ericaceous shrubs or *Eriophorum* species, used to promote moss establishment could be interesting. One must keep in mind

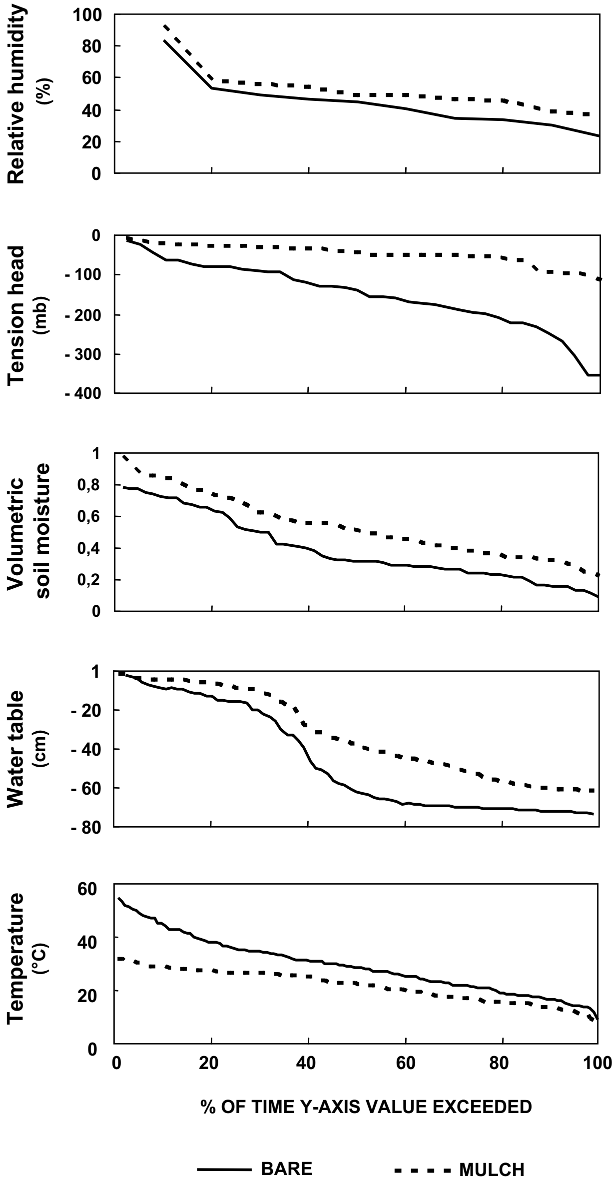


Fig. 17.4. Hydrological and microclimatic variables duration curves for bare and mulched peat substrate showing the percentage of the time the variable was greater than the level shown

that ericaceous shrubs are slow to propagate and to grow and *Eriophorum* species can be invasive and totally cover the ground. A better knowledge of their propagation and population development will be needed before they can be used effectively, although some light is now being shed in the population dynamics of *Eriophorum spissum* on abandoned peatlands (Lavoie et al. 2005a, b). Furthermore, vascular plants can enhance evapo-

Table 17.2. Average daily net radiation (Q^*), ground (Q_g) and latent heat (Q_e) flux (W m^{-2}), and evaporation (E, mm) from a bare peat surface, and a similar surface covered with straw mulch (2,250 kg ha^{-1}). Measurements are from Lac St. Jean peatland, Quebec, Canada, between June and October 1995. (Adapted from Price et al. 2003)

	Q^*	Q_g	Q_e	E
Bare peat	128.2	16.4	88.3	3.1
Mulch covered	112.0	2.2	74.2	2.6

rative losses from a site (Lafleur 1990; Spieksma et al. 1997) but water losses are from deeper in the peat profile; thus, *Sphagnum* mosses might access water directly from the surface of the bare peat in addition to direct precipitation (Price et al. 2003). In counterpart, mosses such as *Polytrichum strictum* or *Campylopus introflexus* (introduced in Ireland) are promising nursing plants (Groeneveld and Rochefort 2002). *Polytrichum* fragments or *Polytrichum* carpets can improve the microclimate over a cutover peat surface (Groeneveld and Rochefort 2005) and the survival of surrogate seedlings but the direct nursing effect to directly help *Sphagnum* establishment remains to be tested.

Similar to the restoration of *Sphagnum*-dominated peatlands, amelioration of microclimatic conditions at the air–peat interface also seems to be important for restoration of fens when plant reintroduction approach is used. A first attempt to fen restoration with Sphagna and brown mosses was done by reintroducing two different types of fen vegetation in combination with straw mulch on sedge peat (Cobbaert et al. 2004). Vegetation from natural fens was introduced as a donor diaspore bank, containing seeds, rhizomes, moss fragments, and other plant propagules. Two natural fens were chosen with contrasting vegetation types: one was dominated by mosses (*S. centrale* and *S. flexuosum* species), the other was dominated by vascular plants (*Calamagrostis canadensis)*. Even though there were problems to fully rewet the experimental site, the application of straw mulch improved the establishment success of the fen vegetation. It can be suspected that this was through the amelioration of growing conditions at the air–peat interface as for *Sphagnum* cutover peatlands.

17.3.4 Hydrology

In peatland management, it might appear easy to reverse the effects of drainage by simply rewetting. In reality, new soil profile conditions have developed after peat utilization, and these differ significantly from the natural mire soil profile of any former developmental stage (Price et al. 2003). Therefore, restoration actions, especially after peat cutting or agricultural management, should consider the restoration site as a new environment with new physical properties, especially on the upper layer of the soil column.

Starting conditions for peatland restoration are influenced by the historical management of the site and by the stratigraphy of the mire massif before human activities started. Since water is one of the main prerequisites for the development of peatlands (Chap. 13), further development of the ecosystem after restoration will be greatly influenced by two of the fundamental physical properties of the peat – porosity and hydraulic conductivity. Values of both porosity and hydraulic conductivity usually have a decreasing trend from the upper peat massif layers toward the bottom layers. This is correlated with the higher decomposition state of the vegetation debris. In most peatland areas, the bottom peat or gyttja layers act as a water seal against the underlying mineral deposits. Thus, two different aquifers are created – an upper one with free water influenced by atmospheric pressure and a lower one with water at a pressure greater than atmospheric pressure (Franzen 1985). The distribution of different porosity and hydraulic conductivity within the peat determines the water movement through the peat layer. The drained and cutaway peat massif surface therefore reflects the earlier peat hydrophysical conditions and the later degraded (by shrinkage, compaction, and oxidation) peat at the upper part of the remnant surface layer. Owing to increased mineralization, the decomposition of the peat is higher and water permeability properties lower; therefore the water table sinks far below the peat surface, especially in dry periods of the year. The supply of moisture for peat-moss growth is insufficient, which makes the substrate often unsuitable for the growth of raised bog plants (Streefkerk and Casparie 1989; Eggelsmann et al. 1993; van Seters and Price 2002; Kennedy and Price 2004). Finally, in cutover mires some of the hydrophysical attributes of the original mire are irreversibly altered (Eggelsmann et al. 1993; Schlotzhauer and Price 1999).

Here it is important to keep in mind that in natural peatlands, *Sphagnum* mosses are adapted to grow on dead, but essentially undecomposed versions of themselves. The high water storage imparted by these loosely packed, and poorly or undecomposed mosses, maintains a high and stable water table, so only a relatively small capillary rise is necessary to ensure an adequate moisture supply to the growing part of the plant. The *Sphagnum* carpet can only generate relatively weak capillary pressures within the intracellular spaces (hyaline cells) and intercellular pores (between branches and leaves of adjacent plants). Hayward and Clymo (1982) found that drainage of hyaline cells in *Sphagnum* occurred when the pore-water pressure is below about –100 mbar. The corollary of this is that *Sphagnum* plants are unable to withdraw moisture from a substrate where the pore-water pressure is lower than –100 mb. Several measurements done on terminated peat cuttings at different sites in different years reveal conditions of pore-water pressure of less than –100 mbar (–355 mbar in Price 1997; –170 mbar in Price and Whitehead 2001) to the extent that water management measures are as necessary as plant reintroduction to alleviate the problem of poor regeneration or germination and mulching to improve microclimate growing conditions (Price et al. 2003).

Hydrological conditions for restoration can be approximated from the study of old block peat cutting sites. A study of the vegetation–water–soil relationships in block peat cuttings in Sweden that were left to spontaneous recolonization in the last 30–50 years revealed the primary importance of water inundation depths and water regulation intensities in the development of different plant communities (Lode 2001). It was found that sites with reestablished (1) *Sphagnum* species (*Sphagnum* carpet) had a large range of average inundation water depths (from 0.2 to 1.0 m above the soil surface), along with small annual water level fluctuations around the year, standard deviation, SD, 1.2–2.6, (2) *E. vaginatum* had on average lower inundation levels (up to 25 cm), but more fluctuating water levels (SD 3.7–4.8), and (3) dwarf shrubs, *Pinus sylvestris*, and *Betula pubescens* accompanied by *E. vaginatum* had as a rule average groundwater level around 4–20 cm below the peat soil surface, with a relatively larger fluctuation of the water table (SD 2.3–6.9). The poorly revegetated sites had a deeper water table of 50–60 cm and a strongly fluctuating water level (SD 12–19), as a result of the functioning drainage. When the average groundwater depth was 6 cm below the surface with corresponding SDs of 4.5 the surface remained "muddy" owing to soil surface freezing and swelling events in autumn and spring, impeding young plant establishment.

The work of McNeil and Waddington (2003) in block peat cuttings in Canada also emphasizes the importance of limiting water fluctuations in restoration sites. Indeed, they found that drying and wetting cycles negatively affect *Sphagnum* net primary production and net ecosystem CO_2 exchange. *Sphagnum* and peat respiration increased 4–14-fold upon rewetting, whereas *Sphagnum* photosynthesis did not recover until 20 days of saturation. In conclusion, they suggest that restoration techniques should include the establishment of companion species to help the newly *Sphagnum* cushions to survive while a proper acrotelm, which will in turn regulate water fluctuations, is being formed.

Site preparation for restoration of milled peatlands frequently involves the construction of berms or shallow basins to enhance peat moisture content (Wheeler and Shaw 1995; Farrell and Doyle 2003; Price et al. 2003; Table 17.3). As a consequence, *Sphagnum* reintroduced within restored areas may be subject to extended periods of flooding, particularly following snowmelt or heavy rainfall. Different *Sphagnum* species were tested to

Table 17.3. Changes to water table, soil moisture at –2 cm, and water tension at –1 cm in basins vs. flat restored surfaces. Measurements are from Lac St. Jean peatland, Quebec, Canada. (Adapted from Price et al. 2002)

	Water table (cm)	Soil moisture (cm^3 cm^{-3})	Tension (cm)
Control (flat surface)	–27.5±13.2 (–30.2)	0.67±0.07 (0.65)	–26.4±19.3 (–25.7)
20-m basin	–0.3±10.3 (1.2)	ND	ND
10-m basin	–19.2±11.4 (–19.2)	0.80±0.05 (0.72)	–15.4±9.3 (–15.5)[a]
4-m basin	–16.1±12.1 (–16.5)	0.78±0.06 (0.71)	–8.2±11.7 (–7.4)
Mulch covered	–17.8±10.5 (–18.6)	ND	–13.5±11.0 (–13.5)

Values are means ± standard deviation, with medians in *parentheses*, collected daily between May and August 1996

ND data for this variable were not collected at this location.

[a] Data missing but generated by regression (r^2=0.92)

evaluate the effect of flooding on their growth and development (Rochefort et al. 2002). It was found that *Sphagnum* can physiologically tolerate and even benefit from shallow temporary flooding. Areas that tend to be temporarily flooded (lower depressions, downslope ends of sites) are also often the same areas that tend to stay wetter throughout the growing season. In such areas, establishment of reintroduced *Sphagnum* will be enhanced, as establishment success is strongly linked to the level of humidity at the peat surface during summer (Price and Whitehead 2001; Girard et al. 2002). However, it must be underlined that flooding is by no means an absolute necessity for *Sphagnum* establishment. On the contrary, severe or lengthy flooding in the field, and even limited flooding of unstabilized fine peat, can lead to erosion and peat deposition, that in turn retard or impede vegetation establishment (Quinty and Rochefort 2000; Faubert and Rochefort 2002). Thus, for successful *Sphagnum* establishment, a fine balance between rewetting and substrate stability must be found.

In conclusion, milled landscapes were designed (cambered surfaces) to efficiently shed surface water quickly with usually little variation in topography over extensive areas. Furthermore, with the repeated passages of heavy machinery to extract peat, the residual peat profile is strongly compressed, and dries quickly, which then impedes the capillary water flow to the surface and to any establishing *Sphagnum* propagules. In short, the residual peat profile of milled extracted area is a harsher environment for spontaneous recolonization than the former block cutting method.

17.3.5 Peat Stability and Quality

17.3.5.1 Erosion

In addition to microclimate, substrate instability has been suggested as one of the potential barriers to natural recolonization of bare milled peat surfaces (Rochefort 2000). But compared with hydrology and microclimate, the role of peat surface stability in *Sphagnum* establishment has received scant attention. Peatlands for commercial uses need to be drained to allow the extraction of peat. After drainage has ceased, subsidence of these peatlands continues (Price and Schlotzhauer 1999). This subsidence is usually attributed to shrinkage, compression, and biochemical oxidation of the peat (Schothorst 1997) but wind erosion has been suspected to play a role as well (McNeil et al. 2000; Campbell 2002).

According to Eggelsmann et al. (1993), drainage and the resulting drying of the peat causes the coherent peat matrix to break down into structural units of aggregates. Although peat fibers or peat-derived aggregates are very stable and resist physically disruptive process such as ploughing, they are light in weight and therefore up to diameters of 0.5–2 mm they could be very susceptible to wind erosion. Campbell et al. (2002) have found that wind erosion during summers is not an important cause of subsidence in milled peatlands as was previously suspected. This is attributed to the crusting of the surface that makes the bare peat surfaces very resistant to wind erosion and may impede diaspore germination. This is the reason why if an extensive peat surface has been abandoned for a long time before a restorative intervention, it is recommended to refresh the surface by breaking up the crust. The scraping of the peat surface facilitates the contact between diaspores and the substrate.

Shrinkage is another component of drained peat erosion and takes place in peat surfaces as a result of high rates of evaporation (Heathwaite et al. 1993). In warm and dry periods, cracks or fissures may appear in the peat surface. These may be up to 15-cm wide and over 0.5-m deep and have height losses of 10–30 cm (Eggelsmann et al. 1993). From the experience of agricultural use of peatlands, lost of peat due to mineralization can reach up to 30 mm year^{-1} in humid regions, and in fen types mineralization can be much greater than in raised bogs (Heathwaite et al. 1993). In a cutover peatland in eastern Canada, the loss was estimated to be 6 mm year^{-1} (Waddington and McNeil 2002). In agriculture, the groundwater levels are perched to minimize the losses caused by mineralization; likewise high water levels should be maintained in cutover peatlands to impede oxidation.

Shrinkage, mineralization, wind erosion, and peat surface fires typically occur in the dry seasons of the year, whereas water-derived erosion

Fig. 17.5. Example of a large-scale restored surface prepared with small basins. (Photograph taken by Jacques Gagnon)

occurs during intensive rain periods or flooding seasons after the winter snowmelt. Water erosion can be quite disruptive on recently restored sites (Quinty and Rochefort 2000). Compartmentalization of extensive bare peat areas or the creation of shallow basins can be effective in controlling sites prone to water erosion (Fig. 17.5).

17.3.5.2 Frost Heaving

Surfaces of milled peatlands often show an initial bumpy appearance in the spring that gets smoother with time as the summer season advances (Campbell et al. 2002). These surface irregularities appear largely connected to frost heaving (Quinty and Rochefort 2000; Fig. 17.6a). Groeneveld and Rochefort (2002) gave a description of the problem of frost heaving in cutover peatlands (Fig. 17.6b) and an array of means by which it can be diminished. Unforeseen in earlier work on peatland restoration, frost-heaving problems were exacerbated by the rewetting of former drained peatlands. As most peatlands are located in the boreal and tem-

Fig. 17.6. **A** Extensive effect of frost heaving in an Estonian peatland (Viiru bog) after several years of no harvesting activities. **B** Ice-needle formation within peat. (**A** Photograph taken by Edgard Karofeld; **B** photograph taken by Ian Roul)

perate zone (Lappalainen 1996) that experiences freezing weather, peat substrate instability caused by frost heaving might be among the main factors impeding total success of restoration projects. Field experiments were used to determine the effectiveness of straw mulch or the use of the moss *Polytrichum strictum* against frost heaving (Groeneveld and Rochefort 2005). Wooden dowels and seedlings of fir trees placed in a *Polytrichum strictum* carpet experienced almost no frost heaving, whereas heaving was severe on bare peat (up to 6 cm; Fig. 17.7). Straw mulch, a protective cover recommended in peatland restoration to protect *Sphagnum* diaspores against desiccation, effectively reduced heaving in the fall, but was less effective in the spring because it had partially decomposed. The *Polytrichum* carpet and the straw mulch reduced frost heaving by reducing the number of freeze–thaw cycles, by slowing the rate of ground thaw in the spring, and by reducing the unfrozen water content of the peat during the spring thaw. From these experiments, we suspect that *Polytrichum*

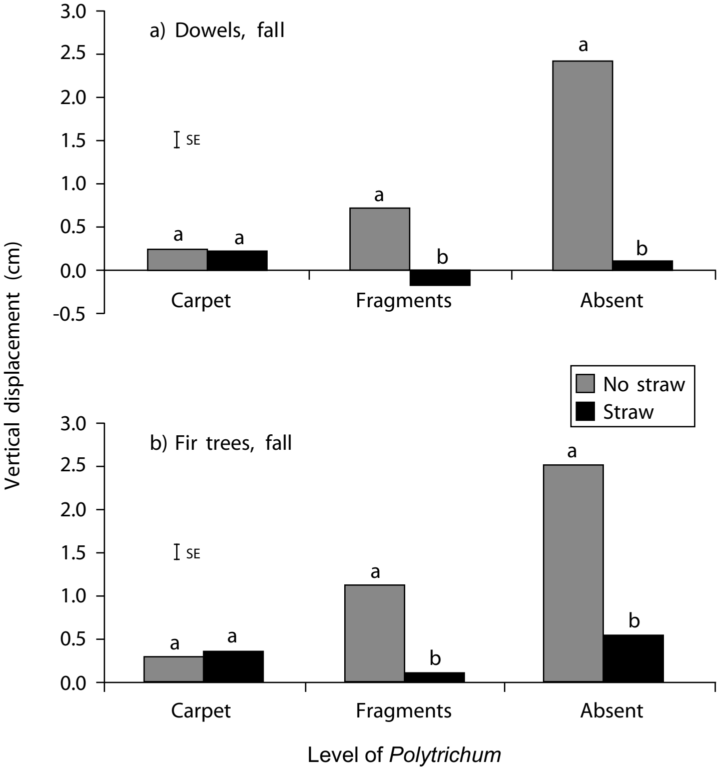


Fig. 17.7. Vertical displacement of dowels and fir trees in spring 2001 (10 months of cumulative frost heave from 24 August 2000 to 29 May 2001) due to frost heaving on an abandoned vacuum-harvested bog, Premier St-Laurent, Rivière-du-Loup, Quebec. (Adapted from Groeneveld and Rochefort 2005)

strictum could potentially be a good nursing plant for the *Sphagnum* fragments, not only in terms of stabilizing the peat surface, but also in helping to ameliorate the microclimate at the peat surface. The extent of competition between *Polytrichum strictum* and its benefactor plant, *Sphagnum*, remains unclear at this time. An interesting question is: Under what conditions does *Polytrichum strictum* enhance the establishment of *Sphagnum*, and under what conditions does competition negate the positive facilitation? Further research is needed.

17.3.6 Species Interactions

Much of the effort done in peatland restoration has been to evaluate *Sphagnum* establishment success in relation to abiotic factors (Chap. 4). Biotic interaction studies are just beginning as the implementation of large-scale restoration projects was needed to assess plant species interactions on vegetation establishment success and biodiversity.

In Europe, cotton grass (*Eriophorum vaginatum*) has been found to facilitate the establishment of other bog plant species in mined bogs (Matthey 1996; Tuitilla et al. 2000), but detailed studies conducted in North America by Lavoie et al. (2005a, b) did not provide evidence for the facilitation hypothesis. The presence of mosses or liverworts was more associated with favorable hydrological conditions than with the presence of cotton-grass cover (Fig. 17.8). Also to be noted from Fig. 17.8 is the decline in the number of cotton-grass tussocks, which is surprising given their potential long-lived tussocks and their many characteristics facilitating their invasion on bare peat (Lavoie et al. 2005a). We now know that with only minimal water management, it is possible to induce a rapid cotton-grass invasion on an abandoned milled peatland (Lavoie et al. 2005b); but once a cotton-grass cover is established it can take 60–600 years before it is succeeded by a *Sphagnum*-dominated community or other wetland vegetation types (Buttler et al. 1996; Hughes and Cymayne-Peaty 2002). Thus, if one has in mind a restoration goal of reestablishing a *Sphagum* plant cover within5 years, use of cotton grass is not a suitable restoration option as the minimal water management option using cotton-grass invasion is not suitable for a short to midterm basis (less than 100 years). But in countries where a natural source of *Sphagnum* diaspores is not readily available, cotton-grass invasions might represent a suitable restoration option.

Little is known about moss interactions. During the establishment phase, does the reintroduction of several *Sphagnum* species together benefit the biodiversity of the carpet or does it help the establishment of recalcitrant *Sphagnum* species (as noted for *S. magellanicum*; L. Rochefort, personal observation)? Or does it negatively impact the establishment success rate because of competition for resources? For answers, a long-

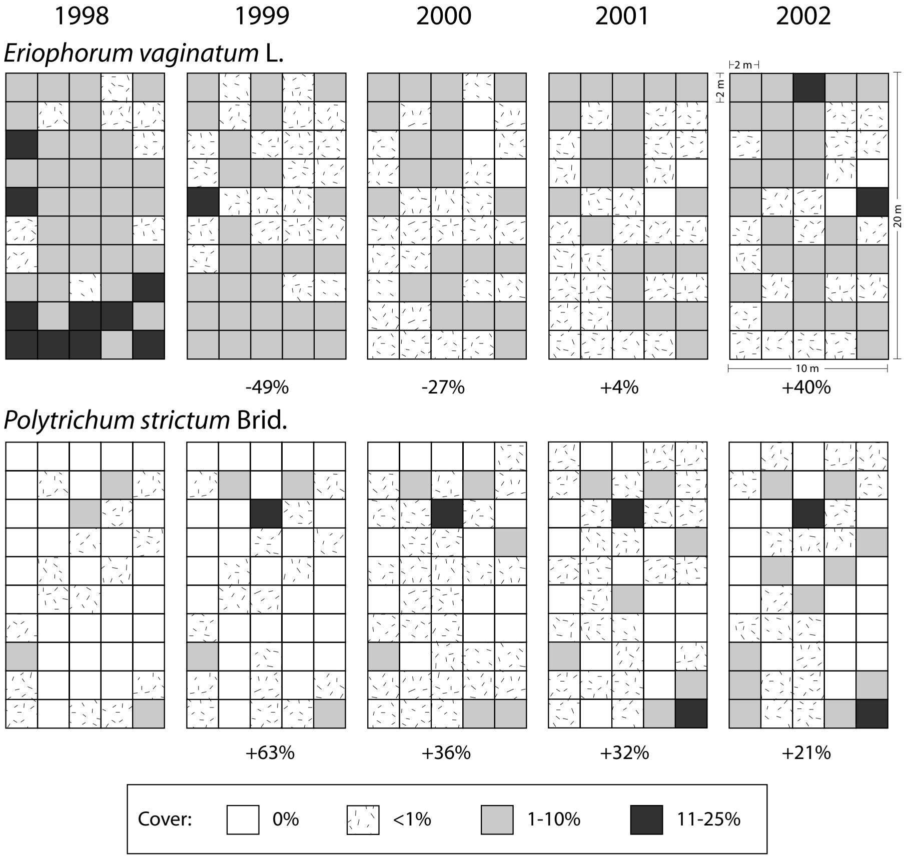


Fig. 17.8. Monitoring of the cover of *Eriophorum vaginatum* L. and *Polytrichum strictum* Brid. in a 10 m × 20 m quadrat installed in a 14-year-old abandoned vacuum-milled site over a 5-year period. See Lavoie et al. (2005a) for more details

term experiment was established in an abandoned milled peat field by Chirino and Rochefort (2000) in 1998 to assess the establishment capabilities of four species of *Sphagnum*: *S. fuscum*, *S. rubellum*, *S. magellanicum*, and *S. angustifolium*. The reintroductions were done on single species or multiple-species combinations in nine treatments. Most percentage combinations with ratios of 100, 50:50, 50:25:25, or 25:25:25:25 were applied in experimental plots of 30 m^2 in area. This was repeated six times and the development of the carpet was monitored for 4 years. It was found that *S. fuscum* and *S. rubellum* are two widespread species that easily recolonize bare peat substrates and show good success of establishment, be it in monospecific or plurispecific reintroductions. It was also found that a species like *S. magellanicum* had a greater establishment rate in the presence of *S. fuscum* or *S. rubellum* than when reintroduced in a monospecific carpet. This result is interesting because if one aims to favor the establishment of a species from the section *Sphagnum* then plurispecific reintroductions including species from the section Acutifolia should be considered. These conclusions were reached during the early development of the moss carpet. Continued monitoring is necessary to follow the evolution and specific interactions of completely closed carpets to determine the long-term establishment success.

17.3.7 Climatic Conditions

A similar long-term experiment was done to study the responses of specific *Sphagnum* species and their morphological structure in relation to interannual variations in climate (Chirino et al. 2006). In order to compare results under a variety of climatic conditions, the whole experimental setting as described earlier was repeated four times (trials), i.e., repeated in the springs of 1995, 1996, 1997, and 1998 with a 4-year follow-up for each trial. The establishment rate of the moss carpet varied according to the year, in response to climatic variations between growing seasons. Climate in the reintroduction year was particularly important in determining the long-term establishment success, mostly in terms of rainfall distribution over the growing season. The relative success of different moss species and combination of species, however, did not vary within or between trials. Thus, the species and combinations of species resulting in the highest short-term or long-term establishment rates remained the same for all trials, independent of the climatic conditions at the time of reintroduction and the season of growth. Our results showed no link between the number of species in the *Sphagnum* reintroduction mixture and successful establishment of the moss carpet. Yet successful regeneration was clearly influenced by the identity of the species chosen for reintroduction. *S. fuscum*, alone or in combination, was the species found to lead to the most extensive development of the moss carpet under the conditions tested.

17.4 Overview of Restoration Practices

Practical considerations for implementing restoration projects on a large scale have been well described by several reviews: Wheeler and Shaw (1995); Brooks and Stoneman (1997); Dupieux (1998); Blankenburg and Tonnis (2004); Schouten (2002); and Quinty and Rochefort (2003).

Thus, for this section, only general guidelines that can be applied to any peatland restoration project will be discussed.

17.4.1 Planning

Any restoration project should begin with the preparation of a restoration plan to make sure that the right options and timeframe are set up. Planning and design considerations are key elements in the success of restoration as it is essential to set the appropriate goal and objectives; it allows greater efficiency in conducting the operations and it contributes largely to the cost reduction of restoration. A good restoration plan should have two different components: site conditions, goals, and objectives and planning restoration operations.

Identification of the conditions of the site is a necessary step because site characteristics dictate the correct goal to be achieved: restoration or reclamation. The second step consists of defining the operations that need to be done, planning resources and time required, setting up a schedule, and evaluating costs. This information should include the following elements: site characteristics prior to peat extraction; hydrologic environment; topography; peat characteristics; chemical aspects; existing vegetation of the restoration site; surrounding landscape; setting the right goal; setting the right objectives; identification of a donor site (source of plant material to be reintroduced); identification of a reference site; identification of a nonrestored section (optional); and monitoring protocol.

The overall water budget should be evaluated to see if primary positive moisture conditions still exist, mostly for the case of *Sphagnum* peatland development. A hydrological approach as used by van Seters and Price (2001, 2002) should provide useful clues on restoration potential, mostly when peatlands are at the limits of their normal climatic distribution. For example, it might prove quite difficult to restore a *Sphagnum*-dominated peatland located at the edge between the prairies and the boreal forest in North America in the context of global warming. In such a case, reclamation may be a more appropriate goal, and this should be known from the beginning.

To prepare functional restoration goals, a reference ecosystem should be described as the model for planning the project, and should later serve in the evaluation of the project. Typically, the reference represents a point of advanced development that lies somewhere along the intended trajectory of the restoration (Society for Ecological Restoration Science, Policy Working Group 2004). In other words, the restored ecosystem is eventually expected to emulate the attributes of the reference, and project goals and strategies are developed in light of that expectation. The reference can consist of one or several specified locations that contain model ecosystems, written descriptions, or a combination of both. The value of the reference increases with the amount of information it contains, but every inventory is compromised by limitations of time and funding. Minimally, a baseline ecological inventory describes the salient attributes of the abiotic environment and important aspects of biodiversity such as species composition and community structure. In addition, it identifies the normal periodic stress events that maintain ecosystem integrity (Society for Ecological Restoration Science, Policy Working Group 2004). With peatland ecosystems, paleoecology can also be a useful tool to define the reference ecosystem (Lavoie et al 2001; Gorham and Rochefort 2003).

The amount of work for this planning stage depends on the restoration starting conditions, and the agreed restoration end option. In many cases, financial limitations are the main factor influencing the measures planned and consequently the intensity of preparatory work. A good-quality preparatory plan should include both desk and laboratory work (literature search, climatic and hydrological data compilations, chemical analyses, computer mapping) and field work.

17.4.2 Surface Preparation

The preparation of an abandoned bare peat surface for restoration has two main purposes. One is to remove the surface crust that might have formed between the time that the extracting activities ceased and the start of the restoration project (Fig. 17.9a). A fresh peat surface will allow better contact between the newly reintroduced plant diaspores and the peat substrate as well as greater access to the soil moisture, particularly for mosses that can gain their moisture from the soil only by capillarity, because they have no roots. The second one is to prepare the surface to increase water availability and its distribution over the site to favor the establishment of the *Sphagnum* fragments.

As discussed in Sects. 17.3.3 and 17.3.4, water availability is preponderant in peatland restoration. As peat-extracted peatlands have lost their natural ability to store water and regulate water table fluctuation, management procedures must be undertaken to reduce water losses and to provide a water supply to *Sphagnum* and other introduced plants. To achieve these goals, two types of action can be undertaken: (1) redesign the surface topography and (2) blockage of the former drainage system (Fig. 17.2). Blocking the former drainage system is a necessary action (Money 1995; Rochefort 2001) as illustrated in Fig. 17.2 by the ellipse. Blocking drainage should be done only at the end of all the restoration actions to make sure that the site can support the repeated passage of machinery to the end of the restoration project. The step of blocking drainage will be discussed later.

Surface preparation includes an array of actions that can help to improve site conditions, but the implementation of any surface management needs to be decided on a case-by-case basis. If a site is naturally well supplied with water, either by an artesian aquifer or by an oceanic climate, surface preparation might not be needed much as illustrated by the discontinuous ellipse in Fig. 17.2, but this remains to be better substantiated. Among the options for surface preparation, there are (1) the reprofiling of peat fields to favor a better distribution of water (Bugnon et al. 1997); (2) the filling of ditches where convenient to facilitate the work of the machinery; (3) the building of peripheral berms to retain water in situ or act as a windbreak; (4) the building of berms across the slope or chessboard-like berms and the creation of shallow basins (Price et al. 2002, 2003; Campeau et al. 2004) that on top of acting as options 1 and 3 will prevent flooding over large areas and remove loose peat surface and crust; and (5) the removal of existing vegetation to reduce evapotranspiration and plant competition and to facilitate the work with machinery.

Further rationales for surface preparation options can be found in Wheeler and Shaw (1995), Quinty and Rochefort (2003), and Price et al. (2003).

17.4.3 Plant Material Choice and Spreading

Active introduction of plants is done when one wants to accelerate the formation of a new plant carpet. The most important feature of this plant carpet is the presence of *Sphagnum* mosses, which are largely responsible for the unique characteristics of peat bogs and for the accumulation of peat. Thus, the plant material that is introduced must contain an important fraction of *Sphagnum*. Species from the Acutifolia group such as *S. fuscum* or *S. rubellum* are among the best species tested so far (Rochefort et al. 2002) along with other mosses like *Polytrichum* that can contribute substantially to the success of restoration because *Sphagnum* mosses are poor primary colonizers. The quality of plant material in terms of plant species is a major factor responsible for the success of restoration. A site dominated by these plants is the best source for acquiring replacement material, while a site lacking *Sphagnum* should be discarded. The most practical and abundant source of peat bog plant diaspores is a bog itself, but there is ongoing research to develop *Sphagnum* “farms” to produce *Sphagnum* diaspores for restoration that would be very useful for countries where mires are not abundant (Joosten 1998; Campeau and Rochefort 2002; Gaudig and Joosten 2002). Ideally, plant material is collected near the site to be restored in order to minimize transportation and differences in population genetics from out-of-region donor sites.

In North America, natural remnants of harvested peatlands or small peat bogs are commonly available and accessible at short distances from restoration sites. Collection of plants consists essentially in shredding the surface vegetation and in picking it up (Fig. 17.9b). This plant material will be spread over the restoration site to form a new plant carpet. Collection

Fig. 17.9. The six main mechanical steps proposed for successful restoration of milled harvested peatlands. (Photographs taken by Peatland Ecology Research Group, *PERG*)

of plants, when done properly, allows rapid recovery of donor sites and does not result in permanent damage (Rochefort and Campeau 2002).

The quantity of plant material to be used for restoration was determined experimentally in order to ensure rapid establishment of new plant carpets on the restored site, minimize the amount of work required for plant collection and transportation, and minimize impacts to natural sites.

The quantity of plant material for reintroduction is generally reported as a ratio of the area of the collection site to the area of the site to be

C. Diaspore spreading

D. Sraw mulch appllcation

E. Fertilization

F. Ditch blocking

restored. A ratio of 1:10–1:15 is suggested, i.e., the donor site is 10 or 15 times smaller than the area to be restored when harvested on a 6–10-cm-thick surface layer (Campeau and Rochefort 1996). Collecting only the top 5–10 cm of the surface vegetation has the advantage of favoring a rapid recovery of donor sites (Rochefort 2002). During the collection process, the plant material must be shredded to an ideal fragment size between 1 and 3 cm. If worked properly, a donor site could be used more than once on a sustainable basis.

Well-loosened fragments spread better and regenerate more successfully as they make better contact with the substrate. The root system of shrubs and sedges stays in place and moss fragments that are left behind can regenerate easily. Theoretically when spreading in the field, plant diaspores should cover the ground but not overlap. Some sedge and shrub diaspores will occur in the collected material along with the moss species and help to more quickly rehabilitate the biodiversity typical of peatlands.

The choice of donor sites should always minimize impacts to pristine sites. Whenever possible, plants should be collected on fields that are being opened for future extraction activities. Plant material of peatlands that are condemned for industrial or agricultural development should be saved for restoration projects.

Once the plants have been shredded with the help of a rotovator (Fig. 17.9b), picked up (Fig. 17.9b), and transported to the restoration site, moss fragments are spread using a standard box manure spreader (Fig. 17.9 c). Biologically, *Sphagnum* moss appears to have a lower potential of regeneration in midsummer than in spring or fall (Rochefort 2001); however this is unlikely to affect the restoration success of very wet sites as a moist substrate and a microclimate appear to be much more prevalent influencing factors. The use of heavy manure spreaders should be avoided when the ground is too soft because the machines leave deep tracks. The creation of this type of surface microtopography has proven to be detrimental to *Sphagnum* establishment (Price et al. 1998).

17.4.4 Diaspore Protection

Once spread on the bare peat surface, plant fragments are exposed to the sun and wind and they dry rapidly (Sagot and Rochefort 1996); hence, it is imperative to protect the newly reintroduced diaspores as soon as possible.

For peatland restoration on sites where peat instability does not appear to be a problem, the use of straw mulch alone should be sufficient (Fig. 17.9d). However, on those sites where instability is a severe problem, straw alone is not the best option. Its effect is short term, as it decomposes rapidly, seriously decreasing in efficiency after 1 year of application and being close to nil after 2 years. In these cases, the uses of a pioneer plants such as *Polytrichum strictum*, with better stabilizing capacities, become an interesting addition to restoration techniques (Groeneveld and Rochefort 2005). Straw mulch is still considered necessary, as it takes at least two growing seasons for *Polytrichum strictum* carpets to reach an appreciable size, and it also enhances the *Polytrichum* establishment.

Many other covers aimed at protecting the reintroduced *Sphagnum* fragments have been considered and tested experimentally (Rochefort 2001): clear plastic cover as used in agriculture, shading screens (Bastien 1996), plastic nets used as snow fences or construction fences of different porosity (Quinty and Rochefort 1997), root "mulch" supplied by the screening process when baling peat, ericaceous or *Eriophorum* companion species (Boudreau and Rochefort 1999), and commercial mulch such as *Curlex* and *Eromat*. Among them, the use of straw mulch was always more efficient in *Sphagnum* establishment success and proved to be the most economical option. Visually, an efficient spreading of straw mulch is when it is thick enough to create an air layer, but allows light to pass through and reach plant fragments.

17.4.5 Fertilization

Fertilization aims at facilitating plant establishment (Fig. 17.9e). In restoration experiments, it was shown that phosphorus fertilization increases the development and spreading of mosses like *Polytrichum strictum* (Sottocornola et al. 2002). This moss in turn is suspected to provide suitable conditions for the establishment and growth of *Sphagnum* fragments. Rapid colonization of bare peat substrate by *Polytrichum strictum* also helps to decrease or prevent damage caused by erosion and frost heaving phenomena. In addition to favoring mosses such as *Polytrichum strictum*, phosphorus application may help the germination and establishment of several vascular plant species typical of peatlands (Sottocornola et al. 2002). Phosphorus fertilization is a factor that plays a role in the success of plant establishment, but its usefulness still remains to be properly assessed against the drawback of favoring the growth of nonpeatland plant species. So far, the benefits appear to exceed the drawbacks.

17.4.6 Blocking Drainage and Rewetting

The objective of blocking drainage is to essentially keep water within the restoration site and also to improve the distribution of water. This action is done last, once all other restoration steps have been completed, in order to facilitate the circulation of machinery over the site (Fig. 17.9f). Still it is one of the essential actions (Fig. 17.2) without which *Sphagnum* will not be established. Wet humified peat can be used to make the most efficient and impervious dams. Different experiments done within the Peatland Ecology Research Group (http://www.gret-perg.ulaval.ca) have shown repetitively the synergic effect of mulching and blocking drainage and now no further trials are done without applying these two restoration practices.

Besides blocking the drainage, many other treatments aiming at supplying water to the *Sphagnum* fragments and impeding desiccation have been tested: sprinkler irrigation, pumping water into irrigation ditches, windbreaks to retain snow on the restoration site, and surface inundation distributed by a perforated PVC pipes. All these management practices proved to be equal to mulching or did not significantly improve the *Sphagnum* establishment rate if applied in combination with mulching (Rochefort 2001). As they were costly to implement, mulching and blocking drainage remain the best options.

17.4.7 Pool Creation

Bog pools represent a characteristic feature of peat bogs in oceanic regions. Not all sites have pools, but some peatlands have hundreds of them. Pools are important because they support a wide variety of organisms that contribute to the biological richness of peatlands. Many plant and insect species are found only in or around bog pools and nowhere else in peatlands. In fact, peatlands with pools have a much greater biodiversity than peatlands without pools. Thus, the creation of pools is strongly encouraged because it increases the value of a restored peat bog, especially if the presence of pools has been seriously reduced regionally (Standen et al. 1998; Mazerolle 2001, 2003; Mazerolle and Cormier 2003).

17.4.8 Time to "Recovery"

An example of a simple monitoring program that is suggested to peatland managers after restoring a peatland is given in Quinty and Rochefort (2003) with examples of monitoring forms. We now know that it is possible to revegetate a cutover peatland with peatland plants and stabilize the surface peat substrate within 3–5 years. An example is a restoration project done in eastern Canada (Bois-des-Bel), where it was found that after 5 years of restoration, total plant cover by peatland plants was already 90 % and a moss carpet composed of *Polytrichum* and *Sphagnum* species covered 70 % of the ground. Figure 17.10 illustrates the changes observed through the years.

Here the success is only evaluated in terms of vegetation cover excluding nonpeatland or wetland species. It is only with a long-term monitoring program that we will be able to assess if full biodiversity is restored and if the different ecological functions have been restored in the peatland (Waddington et al. 2003; Tuittila et al. 2004).

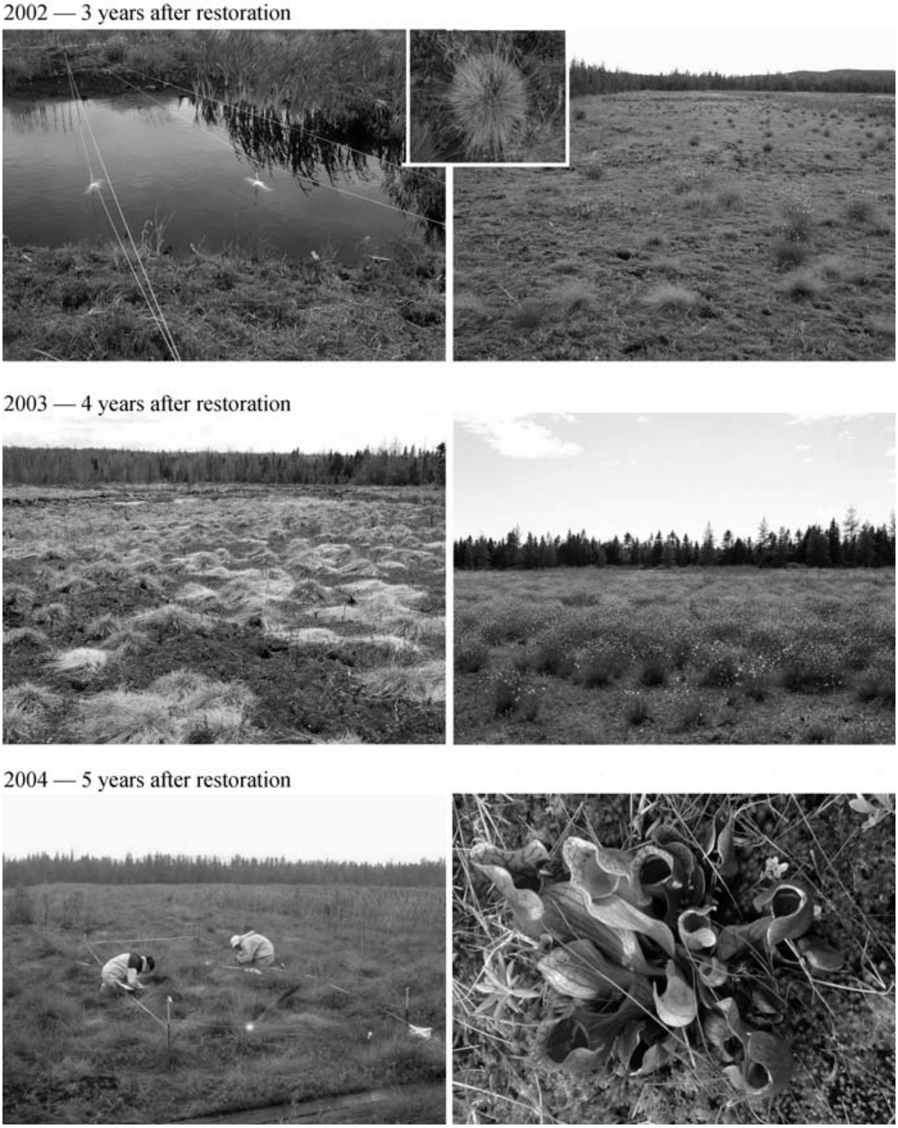
1999 — Before restoration

2002 — Control unrestored zone

2000 — After restoration

2001 — 2 years after restoration

Fig. 17.10. Plant revegetation sequence of the whole ecosystem experiment at Bois-des-Bel peatland showing relatively bare peat substrate prior to restoration in 1999, the year of restoration in 2000 and four years of recovery. In 1999, prior to restoration, bare peat still covered 71 % of the ground after 20 years of abandonment. In the picture from 2002 of the control nonrestored zone, one can see much dead wood that frost-heaved to the surface with time. The picture from 2000 is a general view of the restored site covered with straw mulch atop the spread *Sphagnum* diaspores and the first pair of created pools can be seen in the foreground. In 2001, already 2 years after



2002 — 3 years after restoration

2003 — 4 years after restoration

2004 — 5 years after restoration

Fig. 17.10. (*Continued*)

restoration, the moss carpet covered 62 %, of which 22 % was composed of *Sphagnum* species; part of it is seen atop the straw mulch. In 2002, most of the ground vegetation is dominated by cotton grass (*E. spissum*) and *P. strictum*. Four years after restoration, a moss carpet dominated more and more by sphagna has developed (35 %). The survey of 2005 points to an estimate of 65 % *Sphagnum* cover and 80 % total moss cover, while *Sphagnum* cover is still below 0.2 % in the nonrestored site. (Photographs taken by Peatland Ecology Research Group)

17.5 The Future of Peatland Restoration Research

17.5.1 Climate Influence

A good restoration project will define specific goals in regard to the localization of the decommissioned site in the landscape. The effect of different climates on the success of *Sphagnum* establishment has received little attention as the climate within the current distribution of peatlands has been assumed to be suitable for *Sphagnum* regeneration. Now that several large-scale restoration projects have been undertaken since the beginning of the 1990s, it would be interesting to see if climate can be isolated as a factor that influences the success of peatland restoration.

17.5.2 Management Approach

There is a diversity of approaches and machinery that can be used to implement a restoration project. Different machinery, or timing of work in a season, can have an effect on the restoration success. As we begin to have more large-scale restoration projects, analyses of the management factors should be carried out to pinpoint less efficient practices (e.g., a machine that would mechanically shred too much of the moss material and decrease its regeneration potential during the collection or the spreading steps) and ameliorate overall restoration success.

17.5.3 Restoration of Fens

There is much experience in the restoration of fens after agricultural use in Germany and the Netherlands (Lamers et al. 2002; Blankenburg and Tonnis 2004), but little has been done so far to restore fens in milled peatlands and to reestablish brown mosses. Applying donor diaspores and straw mulch effectively increases fen plant cover and richness (Cobbaert et al. 2004) as shown in a study done on small plots (5 m × 5 m) and evaluated after a short-term recovery (2 years). Another study done in the mountains of Colorado was successful at reimplanting fen vegetation after peat mining, but the cost of the manual plantations was prohibitive (Cooper et al. 1998). So, much remains to be done in improving our abilities to understand the processes that can lead to successful fen restoration. The expertise in fen restoration needs to be improved knowing that as the peat industry ages, more and more fen type residual peat substrates will be decommissioned.

17.5.4 *Sphagnum* Farming and Nursery

Positive results in the area of *Sphagnum* cultivation in North America (Campeau and Rochefort 2002; Rochefort et al. 2003; Campeau et al. 2004) have been facilitated with comparably large interest in European peatland studies and restorations (Money 1995; Sundberg 2000), and might be a key for a new type of professional horticulture that will diminish the management pressure on natural bog landscapes (Gaudig and Joosten 2002). To create outdoor *Sphagnum* nurseries, such as in the trenches of old block peat cuttings, is an interesting option for supplying *Sphagnum* moss vegetative fragments in countries with little natural mire left and is definitely an avenue that deserves more research.

17.5.5 Creation of *Sphagnum*-Dominated Peatlands

In this era of greater environmental awareness, several stakeholders are trying to find solutions to mitigate the pollution created by industrial activities. For example, one of them is to decontaminate the polluted water caused by the piling of mine tailings such as for copper or gold extraction or to ameliorate the quality of the quality exuding from bark piles from sawmills. These tailings can be quite acidic, so it could be interesting to see if creating *Sphagnum*-dominated wetlands will be one of the processes to mitigate the polluting effect via their known ability to filter water.

The development of expertise in peatland reclamation could be useful in regions of high oil sands extraction activities. For example, in northern Alberta, Canada, the oil sands extraction activities take place in a region of abundant natural peatlands. It could be important at a regional biodiversity level to be able to recreate functional peatlands on the soils disturbed by the oil sands industry.

17.6 Conclusions

Even though *Sphagnum* mosses are not easy plants to manipulate on artificial substrates or in nonnatural environments, it is possible to revegetate large expanses of cutover peatland at a relatively low cost (in the range of US $900–1400 per hectare). Only long term monitoring of the current restoration projects will confirm if it is possible to restore the ecological functions of the cutover peatland to bring it back to a peat-accumulating ecosystem. Fen restoration of peat fields used for agriculture has been mostly studied in central Europe but much research is needed to develop sound restoration procedures for cutover peatlands and learn how to grow true mosses. *Sphagnum* farming (cultivation in nurseries) is promising and research in that area should be promoted. Not only would it be useful for supplying plant material for reintroduction in countries with low supply, but it could prove a useful source of biomass to ameliorate growing substrates.

References

Anonymous (1995) EC Wetlands Communication. http://europa.eu.int/comm/environment/nature/docum.htm

Bastien DF (1996) Établissement et croissance des sphaignes dans une tourbière exploitée et abandonnée. MSc thesis, Université Laval, Sainte-Foy

Bérubé MÈ, Lavoie C (2000) The natural revegetation of a vacuum-mined peatland: Eight years of monitoring. Can Field Nat 114:279–286

Blankenburg J, Tonnis W (eds) (2004) Guidelines for wetland restoration of peat cutting areas – results of the BRIDGE-PROJECT. Geological Survey of Lower Saxony, Bremen, Germany

Boudreau S, Rochefort L (1999) Établissement des sphaignes réintroduites sous diverses communautés végétales recolonisant les tourbières après exploitation. Ecologie 30:53–62

Brooks S, Stoneman R (eds)(1997) Conserving bogs. The management handbook. The Stationary Office, Edinburgh

Bugnon JL, Rochefort L, Price JS (1997) Field experiments of *Sphagnum* reintroduction on a dry abandoned peatland in eastern Canada. Wetlands 17:513–517

Buttler A, Warner BG, Grosvernier P, Matthey Y (1996) Vertical patterns of testate amoebae (Protozoa: Rhizopoda) and peat-forming vegetation on cutover bogs in the Jura, Switzerland. New Phytol 134:371–382

Campbell D (2002) Comprendre la mécanique du processus de recolonisation végétale des tourbières exploitées. PhD thesis, Département de phytologie, FSAA. Université Laval, Sainte-Foy

Campbell DR, Rochefort L, Lavoie C (2000) The colonisation potential of peatland plants recolonising post-vacuum-extracted bogs. In: Rochefort L, Daigle JY (eds) Sustaining our peatlands. Proceedings of the 11th international peat congress, vol II. Canadian Society of Peat and Peatlands, International Peat Society, Quebec City, pp 670–674

Campbell DR, Lavoie C, Rochefort L (2002) Wind erosion and surface stability in abandoned milled peatlands. Can J Soil Sci 82:85–95

Campbell DR, Rochefort L, Lavoie C (2003) Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands in Québec. J Appl Ecol 40:78–91

Campeau S, Rochefort L (1996) *Sphagnum* regeneration on bare peat surfaces: field and greenhouse experiments. J Appl Ecol 33:599–608

Campeau S, Rochefort L (2002) Possibilities and limits to *Sphagnum* farming. In: Schmilewski G, Rocheford L (eds) Proceedings of the international peat symposium: peat in horticulture – quality and environmental challenges. A joint symposium of Commission II (industrial utilization of peat and peatlands) and

Commission V (after-use of cut-over peatlands) of the International Peat Society, Pärnu, Estonia, 3–6 September 2002. International Peat Society, Jyväskylä, pp 264–269

Campeau S, Rochefort L, Price JS (2004) On the use of shallow basins to restore cutover peatlands: plant establishment. Restor Ecol 12:471–482

Charman D (2002) Peatlands and environmental change. Wiley., Chicester

Chirino C, Rochefort L (2000) Establishment response of four *Sphagnum* species on cutover peatland. In: Rochefort L, Daigle JY (eds) Sustaining our peatlands. Proceedings of the 11th international peat congress, Quebec City, Canada, 6–12 August 2000, vol II. Canadian Society of Peat and Peatlands and the International Peat Society. Edmonton, pp 694–698

Chirino C, Campeau S, Rochefort L (2006) Peatland restoration: are climatic variability and *Sphagnum* richness important? Appl Veget Sci (in press)

Clymo RS (1983) Peat. In: Gore AJP (ed) Ecosystems of the world 4A. Mires: swamp, bog, fen and moor. General studies. Elsevier, Amsterdam, pp 159–224

Clymo RS (1987) The ecology of peatlands. Sci Prog Oxford 71:593–614

Clymo RS, Duckett JG (1986) Regeneration of *Sphagnum*. New Phytol 102:589–614

Cobbaert D, Rochefort L, Price JS (2004) Experimental restoration of a fen plant community after peat mining. Appl Veg Sci 7:209–220

Cooper DJ, Macdonald LH, Wenger SK, Woods SW (1998) Hydrologic restoration of a fen in Rocky Mountain National Park, Colorado, USA. Wetlands 18:335–345

Daigle JY, Gautreau-Daigle H (2001) Canadian peat harvesting and the environment, 2nd edn. Sustaining wetlands issues paper no 2001-1. North American Wetlands Conservation Council Committee, Ottawa

Desrochers A, Rochefort L, Savard JP (1998) Avian recolonization of eastern Canadian bogs after peat mining. Can J Zool 76:989–997

Dupieux N (1998) La gestion conservatoire des tourbières de France: premiers éléments scientifiques et techniques. Espaces Naturels de France, Orleans

Eggelsmann R, Heathwaite AL, Grosse-Baukmann G, Küster E, Naucke W, Schuch M, Schweickle V (1993) Physical processes and properties of mires. In: Heathwaite AL, Göttlich K (eds) Mires. Process, exploitation and conservation. Wiley, Chichester, pp 171–262

Enz JW, Brun LJ, Larsen JK (1988) Evaporation and energy balance for bare and stubble covered soil. Agric For Meteorol 43:59–70

Farrell CA, Doyle GJ (2003) Rehabilitation of industrial cutaway Atlantic blanket bog in County Mayo, north-eest Ireland. Wetlands Ecol Manage 11:21–35

Franzen L (1985) Peat in Sweden: a method to calculate the resources. GUNI report 21, Göteborg University, Göteborg

Faubert P, Rochefort L (2002) Response of peatland mosses to burial by wind-dispersed peat. Bryologist 105:96–103

Gaudig G, Joosten H (2002) Peat loss (*Sphagnum*) as a renewable resource – an alternative to *Sphagnum* peat in horticulture? In: Schmilewsky G, Rochefort L (eds) Peat in horticulture. Quality and environmental challenges. International Peat Society, Pärnu, pp 117–126

Gauthier R (2001) Les sphaignes. In: Payette S, Rochefort L (eds) Écologie des tourbières du Québec-Labrador. Les Presses de l'Université Laval, Sainte-Foy, Canada, pp 91–127

Girard M, Lavoie C, Thériault M (2002) The regeneration of a highly disturbed ecosystem: a mined peatland in southern Québec. Ecosystems 5:274–288

Glaser PH, Janssens JA (1986) Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. Can J Bot 64:395–415

Gorham E, Rochefort L (2003) Peatland restoration: a brief assessment with special reference to *Sphagnum* bogs. Wetlands Ecol Manage 11:109–119

Groeneveld EVG, Rochefort L (2002) Nursing plants in peatland restoration: on their potential use to alleviate frost heaving problems. Suo 53:73–85

Groeneveld EVG, Rochefort L (2005) *Polytrichum strictum* as a solution to frost heaving in disturbed ecosystems: a case study with milled peatlands. Restor Ecol 13:1–9

Grosvernier P, Matthey Y, Buttler A (1995) Microclimate and physical properties of peat: new clues to the understanding of bog restoration processes. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) Restoration of temperate wetlands. Wiley, Chichester, pp 434–450

Hayward PM, Clymo RS (1982) Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. Proc R Soc Lond Ser B 215:299–-325

Heathwaite AI, Eggelsmann R, Göttlich KH, Kaule G (1993) Ecohydrology, mire drainage and mire conservation. In: Heathwaite AL, Göttlich KH (eds) Mires: process, exploitation and conservation. Wiley, Chichester, pp 418–484

Hughes PDM, Cymayne-Peaty L (2002) Testing theories of mire development for nutrient balance of the cotton sedge, *Eriophorum vaginatum* L. Oecologia 67:511–518

Ingram HAP (1983) Hydrology. In: Gore AJP (ed) Mires: swamp, bog, fen and moor. Elsevier, New-York, pp 67–158

Joosten H (1998) Peat as a renewable resource: the road to paludiculture. In: Maltere T, Johnson K, Stewart J (eds) Peatland restoration and reclamation, Proccedings of the 1998 international peat symposium, Duluth, Minnesota, 14–18 July 1998. International Peat Society, Jyväskylä

Joosten H, Clarke D (2002) Wise use of mires and peatlands – background and principles including a framework for decision-making. International Mire Conservation Group and International Peat Society, Finland. http://www.mirewiseuse.com

Kennedy GW, Price JS (2004) Simulating soil water dynamics in a cutover bog. Water Resour Res 40:W12410. DOI 10.1029/2004WR003099

Lafleur PM (1990) Evapotranspiration from sedge-dominated wetland surfaces. Aquat Bot 37:341–353

Lamers LPM, Smolders AJP, Roelofs JGM (2002). The restoration of fens in the Netherlands. Hydrobiologia 478:107–130

Lappalainen E (1996) General review on world peatland and peat resources. In: Lappalainen E (ed) Global peat resources. International Peat Society, Jyväskylä, pp 53–56

Lavoie C, Zimmermann C, Pellerin S (2001) Peatland restoration in southern Québec (Canada): a paleoecological perspective. Écoscience 8:247–258

Lavoie C, Grosvernier P, Girard M, Marcoux K (2003) Spontaneous revegetation of mined peatlands: an useful restoration tool? Wetlands Ecol Manage 11:97–197

Lavoie C, Saint-Louis A, Lachance D (2005a) The vegetation dynamics of a poorly regenerated mined peatland: five years of monitoring. Wetlands Ecol Manage 13:621–633

Lavoie C, Marcoux K, Saint-Louis A, Price JS (2005b) The dynamics of a cotton-grass (*Eriophorum vaginatum* L.) cover expansion in a vacuum-mined peatland, southern Québec, Canada. Wetlands 25:64–75

Lode E (2001) Natural mire hydrology in restoration of peatland functions. Doctoral thesis, Acta Universitatis Agrivuturae Sueciae, Silvestria 234, Uppsala

Lynch-Stewart P (1992) No net loss – implementing "no net loss" goals to conserve wetlands in Canada. Sustaining wetlands issues paper 1992-2. North American Wetlands Conservation Council, Ottawa

Malterer TJ (1996) Peat resources of the United States. In: Lappalainen E (ed) Global peat resources. International Peat Society, Jyskä, pp 253–266

Matthey Y (1996) Conditions écologiques de la régénération spontanée du *Sphagnion magellanici* dans le Jura suisse. Typologie, pédologie, hydronamique et micrométéorologie. PhD dissertation, Université de Neuchâtel, Neuchâtel, Switzerland

Mazerolle MJ (2001) Amphibian activity, movement patterns, and body size in fragmented peat bogs. J Herpetol 35:13–20

Mazerolle MJ (2003) Detrimental effects of peat mining on amphibian abundance and species richness in bogs. Biol Conserv 113:215–223

Mazerolle M, Cormier M (2003) Effects of peat mining intensity on green frog (*Rana clamitans*) occurrence in bog ponds. Wetlands 23:709–716

McNeil P, Waddington JM (2003) Moisture controls on *Sphagnum* growth and CO_2 exchange on a cutover bog. J Appl Ecol 40:354–367

McNeil P, Waddington JM, Lavoie C, Price JS, Rochefort L (2000) Contemporary and long-term peat oxidation rates in a post-vacuum harvested peatlands. In: Rochefort L, Daigle JY (eds) Sustaining our peatlands. Proceedings of the 11th international peat congress, vol II. Canadian Society of Peat and Peatlands and the International Peat Society, Quebec City, pp 732–741

Mitsch WJ, Gosselink JG (2000) Wetlands, 3rd edn. Wiley, New York

Money R (1995) Restoration of cut-over peatlands: the role of hydrology in determining vegetation quality. In: Hughes J, Heathwaite L (eds) Hydrology and hydrochemistry of British wetlands. Wiley, Chichester, pp 383–400

Murray KJ, Tenhunen JD, Nowak RS (1993). Photoinhibition as a control on photosynthesis and production of *Sphagnum* mosses. Oecologia 96:200–207

Noguchi A, Muraoka S (1959) Sporelings and regenerants in some mosses, 4. Kumamoto J Sci Ser B Sect 2 4:118–149

Oehlmann V (1898) Vegetative Fortpflanzung der Sphagnaceen nebst ihrem Verhalten gegen Kalk. Inaugural-Dissertation. Der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Freiburg in der Schweiz

Pellerin S, Lavoie C (2000) Peatland fragments of southern Quebec: recent evolution of their vegetation structure. Can J Bot 78:255–265

Pfadenhauer J, Schneekloth H, Schneider R, Schneider S (1993) Mire distribution. In: Heathwaite AL, Göttlich K (eds) Mires. Process, exploitation and conservation. Wiley, Chichester, pp 77–121

Poschlod P, Pfadenhauer J (1989) Regeneration of vegetative parts of peat mosses – a comparative study of nine *Sphagnum* species. Telma 19:77–88

Poulin M, Rochefort L, Desrochers A (1999) Conservation of bog plant species assemblages: assessing the role of natural remnants in mined sites. Appl Veg Sci 2:169–180

Poulin M, Rochefort L, Quinty F, Lavoie C (2005) Spontaneous revegetation of mined peatlands in eastern Canada. Can J Bot 83:539–557

Price J (1997) Soil moisture, water tension, and water table relationships in a managed cutover bog. J Hydrol 202:21–32

Price JS, Schlotzhauer SM (1999) Importance of shrinkage and compression in determining water storage changes in peat: the case of a mined peatland. Hydrol Process 13:2591–2601

Price JS, Whitehead GS (2001) Developing hydrologic thresholds for *Sphagnum* recolonization on an abandoned cutover bog. Wetlands 21:32–40

Price JS, Rochefort L, Quinty F (1998) Energy and moisture considerations on cutover peatlands: surface microtopography, mulch cover and *Sphagnum* regeneration. Ecol Eng 10:293–312

Price JS, Rochefort L, Campeau S (2002) Use of shallow basins to restore cutover peatlands: hydrology. Restor Ecol 10:259–266

Price JS, Heathwaite AL, Baird AJ (2003) Hydrological processes in abandoned and restored peatlands: an overview of management approaches. Wetlands Ecol Manage 11:65–83

Quinty F, Rochefort L (1997) Plant reintroduction on a harvested peat bog. In: Trettin CC, Jurgenses MF, Griga DF, Gale MR, Jeglum JK (eds) Northern forested wetlands: ecology and management. CRC, Boca Raton, pp 133–145

Quinty F, Rochefort L (2000) Bare peat substrate instability in peat land restoration: problems and solutions. In: Rochefort L, Daigle JY (eds) Sustaining our peatlands. Proceedings of the 11th international peat congress, vol II. Canadian Society of Peat and Peatlands and International Peat Society, Quebec City, pp 751–756

Quinty F, Rochefort L (2003) Peatland restoration guide, 2nd edn. Canadian Sphagnum Peat Moss Association, New Brunswick Department of Natural Resources and Energy, Quebec, Canada. http://www.peatmoss.com/pm-resre.html

Rochefort L (2000) *Sphagnum* – a keystone genus in habitat restoration. Bryologist 103:503–508

Rochefort L (2001) Restauration écologique. In: Payette S, Rochefort L (eds) Écologie des tourbières du Québec-Labrador. Presses de l'Université Laval, Sainte-Foy, pp 449–504

Rochefort L, Campeau S (2002) Recovery of donor sites used for peatland restoration. In: Schmilewski G, Rochefort L (eds) Proceedings of the international peat symposium: peat in horticulture – quality and environmental challenges. A joint symposium of Commission II (industrial utilization of peat and peatlands) and Commission V (after-use of cut-over peatlands) of the International Peat Society, Pärnu, Estonia, 3–6 September 2002. International Peat Society, Jyväskylä, pp 244–250

Rochefort L, Price J (2003) Restoration of *Sphagnum* dominated peatlands. Wetlands Ecol Manage 11:1–2

Rochefort L, Gauthier R, LeQuéré D (1995) *Sphagnum* regeneration – toward an optimisation of bog restoration. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) Restoration of temperate wetlands. Wiley, Chichester, pp 423–434

Rochefort L, Campeau S, Bugnon JL (2002) Does prolonged flooding prevent or enhance regeneration and growth of *Sphagnum*? Aquat Bot 74:327–341

Rochefort L, Quinty F, Campeau S, Johnson K, Malterer T (2003) North American approach to the restoration of *Sphagnum* dominated peatlands. Wetlands Ecol Manage 11:3–20

Rosenberg NJ, Blad BL, Verma SB (1983) Microclimate: the biological environment, 2nd edn. Wiley, New York

Rubec C (1996) The status of peatland resources in Canada. In: Lappalainen E (ed) Global peat resources. International Peat Society, Jyväskylä, pp 243–252

Sagot C, Rochefort L (1996) Tolérance des sphaignes à la dessication. Cryptogamie Bryol Lichénol 17:171–183

Salonen V (1987) Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. Holarct Ecol 10:171–174

Schlotzhauer SM, Price JS (1999) Soil water flow dynamics in a managed cutover peat field, Quebec: field and laboratory investigations. Water Resour Res 35:3675–3683

Schothorst CJ (1997) Subsidence of low moor peat soil in the western Netherlands. Geoderma 17:265–291

Schouten MGC (ed) (2002) Conservation and restoration of raised bogs; geological, hydrological and ecological studies. Geological, hydrological and ecological studies. Department of the Environment and Local Government Ireland, Geological Survey of Ireland, Staatsbosbeheer, The Netherlands

Schouten MGC, Streefkerk JG, van der Schaaf S, Ryan JB (2002) General conclusions: implications for management and restoration. In: Schouten MGC (ed) Conservation and restoration of raised bogs; geological, hydrological and ecological studies. Geological, hydrological and ecological studies. Department of the Environment and Local Government Ireland, Geological Survey of Ireland, Staatsbosbeheer, The Netherlands, pp 210–217

Sliva J (1998) Regeneration of milled peat bog: a large scale approach in Kollerfilze (Bavaria, southern Germany). In: Malterer T, Johnson K, Stewart J (eds) Peatland restoration and reclamation: proceedings of the 1998 international peat symposium, Duluth, 14–18 July. International Peat Society, Duluth, pp 82–87

Sobotka D (1976) Regeneration and vegetative propagation of Sphagnum palustre as factor of population stability. Acta Soc Bot Pol 45:357–368

Society for Ecological Restoration Science, Policy Working Group (2004) The SER international primer on ecological restoration. Society for Ecological Restoration International, Tucson. http://www.ser.org/

Soro A, Sundberg S, Hakan R (1999) Species diversity, niche metrics and species associations in harvested and undisturbed bogs. J Veg Sci 10:549–560

Sottocornola M, Boudreau S, Rochefort L (2002) Fertilisation aspects in peatland restoration. In: Schmilewski G, Rocheford L (eds) Proceedings of the international peat symposium: peat in horticulture – quality and environmental challenges. A joint symposium of Commission II (industrial utilization of peat and peatlands) and Commission V (after-use of cut-over peatlands) of the International Peat Society, Pärnu, pp 256–261

Spieksma JFM, Moors EJ, Dolman AJ, Schouwenaars JM (1997) Modelling evaporation demand from a drained and rewetted peatland. J. Hydrol. 199:252–271

Standen V, Tallis JH, Meade R (eds)(1998) Patterned mires and mire pools. Origin and development; flora and fauna. British Ecological Society, London

Streefkerk JG, Casparie WA (1989) The hydrology of bog ecosystems. Guidelines for management. Staatsbosbeheer, The Netherlands

Sundberg S (2000) The ecological significance of sexual reproduction in peat mosses (*Sphagnum*). PhD thesis, Acta Universitatis Upsaliensis, Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology 581, Uppsala

Tallis JH, Meade R, Hulme PD (eds) (1997) Blanket mire degradation – causes, consequences and challenges. Proceedings of the Mires Research Group meeting, Manchester, 9–11 April 1997. Macaulay Land Use Research Institute, Aberdeen

Tuittila ES, Rita H, Vasander H, Laine J (2000) Vegetation patterns around *Eriophorum vaginatum* L. tussocks in a cut-away peatland in southern Finland. Can J Bot 78:47–58

Tuittila ES, Vasander H, Laine L (2003) Success of re-introduced *Sphagnum* in a cutaway peatland. Boreal Envir Res 8:245–250

Tuittila ES, Vasander H, Laine J (2004) Sensitivity of C sequestration in reintroduced *Sphagnum* to water-level variation in a cutaway peatland. Restor Ecol 12:483–493

van Breemen N (1995) How *Sphagnum* bogs down other plants. Tree 10:270–275

van Seters TE, Price JS (2001) The impact of peat harvesting and natural regenaration on the water balance of an abandoned cutover bog, Quebec. Hydrol Process 15:233–248

van Seters TE, Price J (2002) Towards a conceptual model of hydrological change on an abandoned cutover bog, Quebec. Hydrol Process 16:1965–1981

Vasander H, Tuittila ES, Lode E, Lundin L, Ilomets M, Sallantaus T, Heikkilä R, Pitkänen ML, Laine J (2003) Status and restoration of peatlands in northern Europe. Wetlands Ecol Manage 11:51–63

Waddington JM, McNeil P (2002) Peat oxidation in an abandoned cutover peatland. Can J Soil Sci 82:279–286

Waddington JM, Greenwood MJ, Petrone RM, Price JS (2003) Mulch decomposition impedes recovery of net carbon sink function in a restored peatlands. Ecol Eng 20:199–210

Wheeler BD (1995) Introduction: Restoration and wetlands. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) Restoration of temperate wetlands. Wiley, Chichester, pp 1–18

Wheeler BD (1999) Water and plants in freshwater wetlands. In: Baird AJ, Wiby RL (eds) Eco-hydrology. Plants and water in terrestrial and aquatic environments. Routledge, London, pp 127–180

Wheeler BD, Shaw SC (1995) Restoration of damaged peatlands. HMSO, London

Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) (1995) Restoration of temperate wetlands. Wiley, Chichester

Woesler A (1934) Beitrag zur Kenntnis der vegetativen Vermehrung von Sphagnum cymbifolium Ehrh. Beitr Biol Pflanzen 22:13-24

18 Boreal Peatland Ecosystems: Our Carbon Heritage

Dale H. Vitt and R. Kelman Wieder

The boreal forest, or taiga, perhaps the last remaining undisturbed forest region in the world, is in reality a mosaic of uplands, peatlands, and lakes. Peatlands currently represent a substantial part of this forest region, and in many cases these carbon-rich ecosystems may dominate the regional landscape, forming complex peatlands of fens and bogs. Much of today's boreal forest lies in glaciated terrain and has developed its current vegetation cover only within the last 10,000–12,000 years. During this time period, the Holocene, the boreal landscape has undergone dramatic change, with peatlands paludifying many boreal landscapes and sequestering a large store of carbon. At present this is estimated to be about 455 Pg or one third of the world's soil carbon. Thus, through their presence, peatlands have substantially changed the boreal landscape (Chap. 3) and sequestered a large amount of atmospheric carbon (Chap. 9).

Throughout the boreal region, peatlands remove carbon from the atmosphere via photosynthesis, depositing the carbon-rich organic matter in dead and decaying plant mass as peat. Carbon storage as peat in the boreal region occurs under extremely variable conditions, for example the pH may vary from 3.5 to 8.5, and deep peat deposits form under both acidic and basic conditions. Peat may form in relatively dry acrotelmic bogs or in fens having water levels at the ground-layer surface. Surface soil temperatures, vegetation, flora, hydrology, and pore water chemistry are all factors that are critical to peat formation and all are highly variable in boreal peatlands. Appreciation of how these ecosystem components vary and how they interact is fundamental to our understanding of peat accumulation (Chap. 14).

Bryophytes play critical roles in boreal peatlands and carbon is sequestered in both undecomposed parts of *Sphagnum* and true mosses. Thus, even though *Sphagnum* mosses may play a pivotal role in the development of bogs and poor fens, true mosses play an equivalent role in rich

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fens (Chap. 2). Unlike cool-temperate, oceanic peatlands that have a predominance of bogs, boreal landscapes are often dominated by fens that are an integral part of boreal watersheds (Chap. 13). Whereas oceanic bogs began development very soon after glacial retreat in the early Holocene, many boreal peatlands were delayed in development, often until as late as 6,000–7,000 years ago in the mid-Holocene (Chap. 3).

Historically, peatlands hold an in situ, continuous record of their initiation and subsequent development, and have been studied in some detail through analyses of macrofossils and physical characteristics (Chap. 3). Perhaps owing to their relatively simple vegetative structure and relatively small number of plant species, plant community ecologists have developed a rich literature describing and classifying northern peatlands (Chap. 2). Likewise, much is known about the habitats and roles of species in the keystone genus, *Sphagnum* (Chap. 4). However, in contrast, few studies have been carried out that describe the fauna, including both invertebrates and vertebrates (Chap. 5). Also, little is known about the diversity of fungi in peatland ecosystems, probably because of the notion that fungi have little importance and do not contribute to the functioning of carbon-based ecosystems. This notion is being shown as incorrect and there appears to be a rich diversity of fungi, including abundant mycorrhizae in peatlands (Chap. 6). These fungi may play important roles in peat accumulation and decomposition about which we know very little.

One of the hallmarks of peatland development is the isolation of the vegetation growing on (nonvascular plants) or near (vascular plants) the peat surface from the underlying mineral geologic substrate (Chap. 3). Lacustrine clays may contribute to the initial isolation, but the horizontal and vertical expansion of the peat deposit perpetuates this separation, with major consequences for peatland biogeochemistry. While fens can deliver supplies of inorganic nutrients to growing vegetation by the movement of water that has interacted with mineral substrates (geogenous waters), peatlands receiving these waters are not in contact with the mineral soil/rock substrates that contribute soluble inorganic nutrient ions to fen waters. The more extreme cases, of course, are ombrotrophic bogs, in which both water and nutrients are supplied exclusively from atmospheric deposition (Chap. 2). An important consequence of geochemical isolation is that the inorganic fraction of soil of peatland ecosystems is contributed by elements in organic forms, not by contamination or admixture of peat with inorganic mineral soil particles. Therefore, with respect to the cycling of elements in both bogs and fens, the "geo" component of biogeochemistry is either missing or of minor importance.

Boreal peatlands, whether bogs or fens, are located in moist to wet environments (Chap. 1). Annual precipitation exceeding annual actual evapotranspiration, geomorphologic setting, and the hydraulic properties of peat combine to produce situations where water tables in boreal peatlands are close to the peat surface, leading to an aerobic acrotelm overlying an anaerobic catotelm (Chap. 13), creating opportunities for oxidation and reduction reactions to occur within close physical proximity, especially as water tables rise and fall.

Because of the absence of N in primary minerals, N cycling in general is dominated by atmosphere–biosphere and within-ecosystem fluxes. Atmospheric deposition of inorganic N and its effects on peatlands has been widely examined (Chap. 10), although much of this research has focused on peatlands that already receive elevated N deposition because of anthropogenic activities. Relatively little attention has been paid to either N inputs by biological N fixation or N losses by denitrification, in part because the few reported rates are quite low compared with rates for other terrestrial ecosystems. However, the low rates of N fixation in peatlands may be comparable to inorganic N deposition in pristine areas of the world. N fixation in boreal bogs and fens may be worthy of further study. Reported denitrification rates in peatlands are also low, in part because of low nitrate concentrations in peatland waters. Low nitrate concentrations are attributable to inhibition of nitrification (in acidic bogs) and/or efficient retranslocation of N in senescing plant tissues along with efficient uptake of ammonia by plants and microbes (bogs and fens). Regardless of the mechanism, N cycling in boreal peatlands can be viewed as incomplete in comparison with that in other terrestrial ecosystems because of the minimal importance of nitrification and denitrification.

In nonpeatland terrestrial ecosystems, P cycling is dominated by mineralization of P from primary and/or secondary minerals, which represent the source of "new P" inputs (in the absence of fertilization and pollution). Some of this P mineralization may be facilitated by soil microbes that are active within the rooting zone of a mineral soil. Once P is released from these minerals, its availability for plant/microbial uptake can be influenced by sorption/desorption from Fe and Al sesquioxides. Neither of these processes occurs in peatlands, because of the geological isolation from P-containing minerals, as well as from Fe- and Al-bearing minerals. As such, the cycling of P in peatlands (both bogs and fens) is dominated by biologically mediated transformations between organic P forms, i.e., mineralization of organic P and uptake of soluble inorganic P by plants and microbes (Chap. 11). Thus, the peatland P cycle is rather unique among terrestrial ecosystems in that it is both incomplete (lacking geochemical pools and pathways) and biologically controlled.

Most of the research on peatland S cycling has focused on bogs or acidic poor fens (Chap. 12). As with P, S cycling is dominated by transformations between organic S forms, without geochemical sorption/desorption reactions involving Fe and Al sesquioxides. A more striking aspect of S cycling in peatlands, however, is the alternating reduction (via dissimilatory sulfate reduction) and oxidation (with uncertainty regarding the electron donor molecules) of S, to an extent not seen in other terrestrial ecosystems. The physically close proximity of aerobic and anaerobic zones (acrotelm and catotelm) in peatlands, along with the likelihood of anaerobic microsites in the zone of water table fluctuation in peatlands, creates unique physicochemical conditions that promote this internal S cycling, with ramifications for C cycling, as well. With increasing atmospheric S deposition, this alternating reduction and oxidation of S within peatlands is stimulated. Therefore, S cycling in peatlands is unusual compared with that in other terrestrial ecosystems in that it is incomplete (lacking geochemical transformations) with strikingly augmented alternating reduction/oxidation pathways.

Ongoing climate change, coupled with the tremendous quantity of C stored in the world's boreal peatlands, has stimulated considerable research over the past decade that has focused on understanding the C cycle on peatlands and its biotic and abiotic controls. Of course, the large global C store in peatlands has resulted from an excess of net primary production over decomposition (Chaps. 7, 8, 14). Carbon cycling in peat is unusual because of the importance of methane production and oxidation pathways (Chap. 9), made possible by the physically close proximity of aerobic and anaerobic zones within the organic peat deposit. Also, as with S, most of the research on C cycling in peatlands has focused on bogs, with comparatively less effort on fens.

From a biogeochemical perspective, the cycling of each of the major elements (C, N, S, and P) in peatlands is unique in comparison with other terrestrial ecosystems. The isolation of the peat surface, where the net primary production and most of the decomposition occurs, from geologic mineral substrates, the absence of primary and secondary mineral particles within peat matrix, and the physicochemical ramifications of water table position with the close physical proximity of aerobic and anaerobic zones within the peat deposit collectively create a unique physicochemical environment. As a result, the cycling of C, N, S, and P in the highly organic soils that characterize boreal peatlands is perhaps better described as biohydrochemical than biogeochemical.

Compared with relatively wet oceanic peatlands, dry boreal peatlands (especially bogs) have been subjected to natural disturbances that alter the succession of individual peatlands and influence the process of peat accumulation. Especially important disturbances in the boreal region are wildfire and permafrost aggradation and degradation (Chap. 16). In the past century, anthropogenic disturbances directed at boreal peatlands, particularly activities (e.g., drainage) related to forestry (Chapt. 15), agriculture, and peat harvesting (Chap. 16) have led to additional disturbance. Atmospheric deposition, oil and gas extraction, and mining activities will add important disturbance components over the next decade that have the potential to alter ecosystem functions on a regional level.

As with all terrestrial ecosystems, boreal peatlands are ephemeral on a millennial scale. Nonetheless, peatlands stand out among extant terrestrial ecosystems because of their truly impressive sequestration of atmospheric carbon as peat over a time period of a few thousand years. Unfortunately this large carbon pool is vulnerable to climatic changes and other natural and anthropogenic disturbances. What remains uncertain is how future boreal peatland functions may be altered by anthropogenic influences that will be manifested at local, regional, and global scales. Of particular concern are predictions that global warming may be most pronounced in the boreal and arctic regions of the northern hemisphere, with as yet uncertain consequences for peatland function.

This volume contains a collection of papers that review what we know about an ecologically important, yet understudied ecosystem – boreal peatlands. Indeed, these papers individually and collectively indicate that we have gained considerable knowledge about boreal peatland structure and function (including carbon sequestration), but also have implicitly and explicitly revealed that much is left to do. The prospects for peatland research in the next decade are especially exciting given the new and existing tools that have become available to ecosystem scientists. These include remote sensing from satellites to ground-based systems, an increasing array of molecular tools to assess microbial community structure and function, minirhizotrons to examine root production and turnover, stable and radioactive isotopes to gain insight into element cycles, statistical approaches to evaluate plant community structure, a modern phylogenetically based classification of keystone bryophyte species, instrumentation to obtain continuous measurements of peatland carbon, water, and energy balances, and increasing sophistication of empirical and predictive models that will be applied to past, present, and future peatland development across a spectrum of spatial scales. We look forward to the next decade as new generations of peatland researchers build upon our current knowledge to reveal new insights into the structure and function of the world's boreal peatland ecosystems.

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