Wetland Habitats of North America

ECOLOGY AND CONSERVATION CONCERNS

Edited by

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Cover photograph: Tidal freshwater marsh, Patuxent River, Anne Arundel County, Maryland. Photo by Andrew H. Baldwin.

CHAPTER 9

Northern Peatlands

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Peatlands are best defined by their capacity to accumulate organic matter, thus forming an organic soil named peat. This means that over time, the productivity of the system is greater than its rate of decomposition. Development of peatlands in the landscape is favored in cool, moist climates and in landscapes with poor drainage. Despite their peculiarities, the delineation of peatlands from other wetlands is not always straightforward. For global understanding, we are adopting the following definitions: *peat:* a sedentarily (in situ) accumulated material composed of > 30% (dry mass) of dead and partly decomposed organic matter; and *peatland:* an area with or without vegetation, with a naturally accumulated peat layer of ≥ 30 cm at the surface. Peat accumulation can reach considerable depths, up to 11–15 m, but usually will range between 2–6 m in boreal regions. The minimum depth of 30 cm is often chosen as a somewhat arbitrary threshold for peat formation, but it is useful for classification purposes, such as gathering statistics among different countries or modeling global carbon cycles (IMCG Website, RAMSAR, Wetlands International).

Two main types of northern peatlands are commonly recognized: bogs and fens. Fens are peatland systems influenced by flowthrough drainage, where enriched water coming from the surrounding watershed provides an array of mineral elements for a diverse plant community. This flowing water brings a certain degree of oxygenation to the organic substrate, which accelerates peat decomposition. Hence, fen peat deposits are usually not as thick as bog peat formed in rain-fed-only systems. The different types of vegetation in fens coincide relatively well with the degree of minerotrophy. Fen vegetation is often dominated by sedges (*Carex* and other Cyperaceae) and brown mosses (Amblystegiaceae bryophytes), some shrubs (willows, alders, or dwarf birches), and trees (larches); *Sphagnum* mosses are rare or absent when the pH is high (Amon, Thompson, et al. 2002; Bedford and Godwin 2003).

Bogs are mostly rain-fed systems, and thus poor in mineral nutrients, except when under oceanic influence. They rarely develop directly on mineral substrate (Sundberg, Hansson, et al. 2006), and most often bogs succeed in chronosequence from fen habitats (Kuhry and Turunen 2006). Indeed the accumulation of fen peat with time slowly diminishes plant access to the mineral pool of nutrients. At one point in their development, plant roots can no longer reach the mineral nutrient pool supplied by groundwater, and vegetation better adapted to poor nutrient conditions succeeds. *Sphagnum* mosses are by far the most common and abundant plant component in bogs. Cotton grass *(Eriophorum vaginatum),* ericaceous shrubs, and coniferous trees grow in association with the *Sphagnum* carpet. In North American peatlands, ericaceous shrubs in bogs are composed of a mix of *Kalmia, Ledum, Chamaedaphne, Vaccinium,* and *Gaylussacia* species. Black spruce *(Picea mariana)* is ubiquitous, but tamarack *(Larix laricina)* is also regularly found on wetter, more minerotrophic sites (Montague and Givnish 1996). Simply put, northern peatlands are mossy, spongy habitats. One walks on a soft carpet of vegetation, although it can be through dense black spruce thickets. In a nonpeatland wetland, a person will most likely get muddy feet.

Hydrology

The form and function of fens and bogs are strongly related to hydrological processes, which control the availability of water, dissolved minerals and nutrients, and ultimately the nature of the biotic environment. Fens generally occupy a relatively low position in the landscape, where they receive surface or groundwater from the surrounding mineral sediments. Where suitable climate and landscape exist, peat continues to accumulate, the water table rises, and hydraulic gradients between the fen and the upland decrease and may eventually reverse. The result is a peatland that is entirely ombrogenous (fed only by precipitation, P), and is defined as "bog" (Fig. 9.1).

The regional distribution of bogs and fens is related to landscape factors, but also to latitudinal and zonal gradients. Latitudinal effects control peat accumulation through (1) moisture availability (precipitable moisture), which is a function of atmospheric temperature; (2) the effect of temperature on productivity and decomposition rates; and (3) energy available for evapotranspiration (ET). Zonal (east/west) effects are related to the degree of continentality, i.e., moisture restrictions. Damman (1979) noted that in eastern North America there are northern and southern limits to bog occurrence, since they are reliant on ombrogenous water. Precipitation decreases

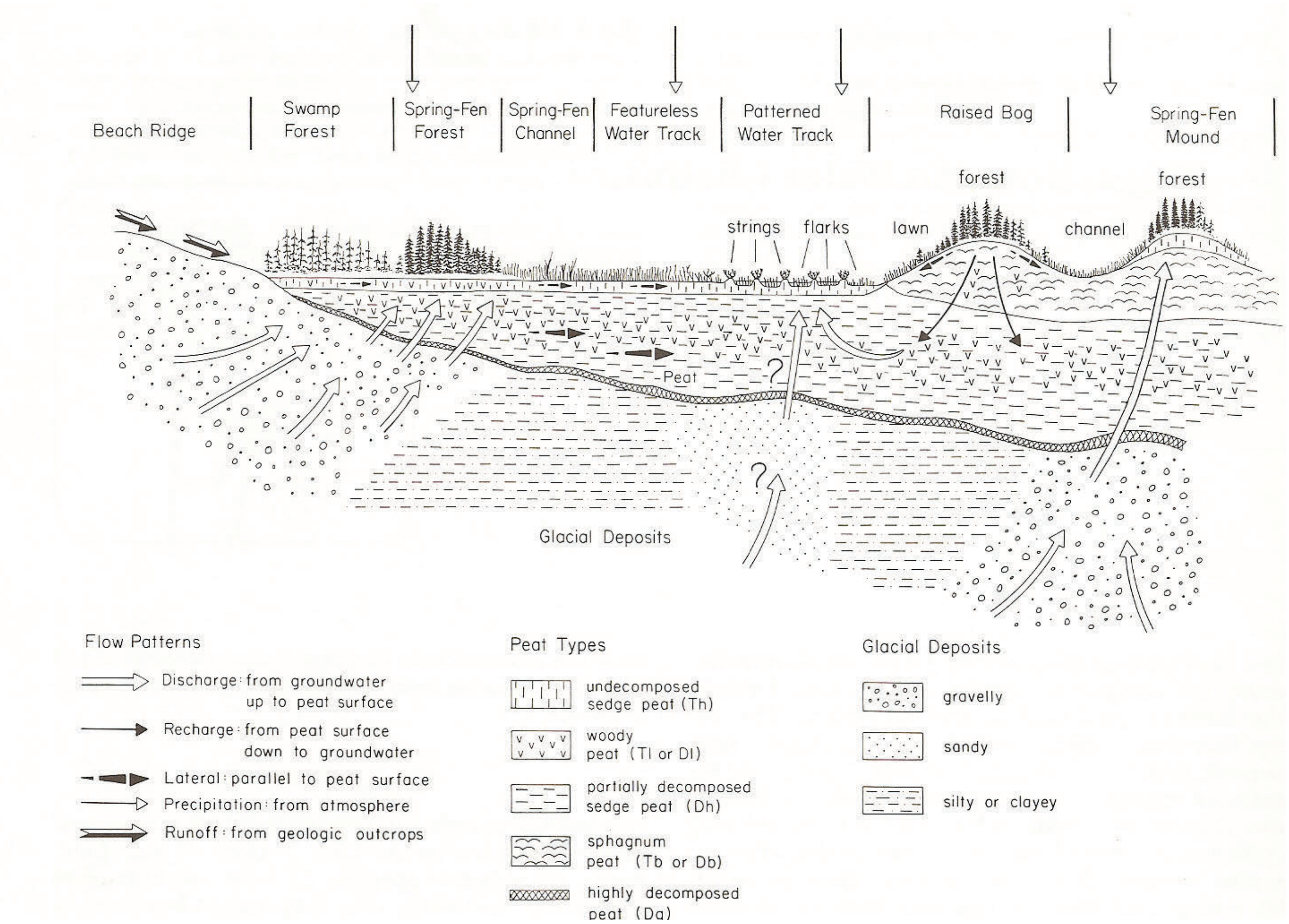

FIG. 9.1. Peatland types according to landform type, water chemistry, and hydrology. The sources of water and mineral ions are indicated by arrows. The alkalinity in the surface water decreases with increasing distance from the source of the groundwater or runoff draining from mineral soils. (Glaser 1992.)

northward and potential evapotranspiration (PET) increases southward; both conditions limit water supply. A similar effect occurs with decreasing precipitation and increasing PET in continental locations. Bogs cannot exist where P < ET, although they occur in the Western Boreal Plain (Vitt, Halsey, et al. 1994), where P < PET and bog ET << PET (Petrone, Silins, et al. 2007). However, since fens have an additional water source through surface and/or groundwater, they become more common than bogs where the atmospheric water deficit is more intense.

Hydrological processes within peatlands and their role in downstream aquatic systems are dominated by the structure and character of the peat soil, which ranges from living and dead but undecomposed plant material near the surface through poorly to well-decomposed materials at depth. Ingram (1978) defines the upper layer (acrotelm) as a variably saturated zone that extends to the depth of the average lowest annual water table and where biological activities are concentrated and nutrient exchange occurs (Fig. 9.2). The lower layer (catotelm) is the permanently saturated layer below which biological activity is considerably reduced, facilitating the accumulation of plant remains. The acrotelm is usually distinct in bogs, typically 35–50 cm in thickness (Belyea and Clymo 2001) and thinner (~10–20 cm) and less distinct in fens (Price and Maloney 1994) because of a higher, less variable water table. The saturated hydraulic conductivity of the acrotelm can decrease from the surface by four or five orders of magnitude in bogs (Hoag and Price 1995; Letts, Roulet, et al. 2000) and three or four orders of magnitude in fens (Price and Maloney 1994; Ferone and Devito 2004).

Peatlands have the ability to self-regulate their hydrology, keeping water levels relatively stable. When water tables are high, such as following snowmelt or during prolonged wet periods, near-surface water flows readily through the permeable acrotelm, facilitating runoff (Quinton, Hayashi, et al. 2008). As the water table declines, the system's transmissivity decreases significantly, and runoff is inhibited. During extended dry periods, runoff from bogs may cease altogether and moderate amounts of rain may not produce any outflow (Bay 1969). Fens, whose water supply is supplemented by groundwater inflow, maintain a higher water table and consequently are less likely to dry (Ingram 1983). Patterned bogs and fens are very effective at retaining water (Price and Maloney 1994). In spring snowmelt, water flows readily around ridges (Quinton and Roulet 1998), but after snowmelt, water must seep through the peat matrix of ridges; thus runoff responses are slow and ET losses dominate (Price and Maloney 1994).

Water flow through the catotelm is minimal (Ingram 1983) because of low hydraulic conductivity; horizontal water flows are also low (Belyea and Clymo 2001). Upward flow from mineral substrates can be important water sources for fens (Devito, Waddington, et al. 1997), while mineral soils underlying bogs typically restrict seepage losses (Ingram 1983). Water content of saturated catotelm peat is frequently at or slightly greater than 0.9 cm^{-3} (Hayward and Clymo 1982), and it is a source of water for evaporation during dry periods as hydraulic gradients reverse from recharge to discharge, even in bogs (Devito, Waddington, et al. 1997; Fraser, Roulet, et al. 2001).

Water-storage changes in peatlands are typically assumed to be manifest entirely by changes in water table as pores drain or refill according to the specific yield of the acrotelm (Ingram 1983). However, dilation and contraction of peat volume (specific storage), causing surface swelling or subsidence, can be more important than pore drainage (specific yield) mechanisms in determining water-storage changes (Price and Schlotzhauer 1999). Seasonal contraction of peat volumes leading to subsidence can also reduce hydraulic conductivity by several orders of magnitude (Price 2003; Hogan, van der Kamp, et al. 2006). The effect is more prominent in fen pool and lawn communities than in more structurally rigid ridges, minimizing water table drop below the (descending) surface (Whittington and Price 2006), having implications for ecological and biogeochemical processes (Strack and Waddington 2007).

Evapotranspiration is the dominant water loss from bogs, ranging up to 4–5 mm d^{-1} (Lafleur, Hember, et al. 2005), but it decreases markedly if *Sphagnum* moss dries (Admiral, Lafleur, et al. 2006); the upward capillary flow that sustains ET (Price, Edwards, et al. 2009) becomes limited by the low hydraulic conductivity of drained moss (Price, Whittington, et al. 2008). In fens, ET can be sustained at or near PET when vascular plants are growing and the water table is within the rooting zone (Kim and Verma 1996). Price and Maloney (1994) noted that evapotranspiration from a fen surface was ~60% greater than from a bog surface. Where surface subsidence keeps the water table near the surface, evapotranspiration rates are higher and more consistent (Lafleur and Roulet 1992).

Hydrological processes in northern peatlands can be strongly affected by freezing and permafrost. Seasonal frost is persistent and permafrost is common in northern peatlands because of the thermally insulative properties of dry moss in the summer and thermally transmissive properties when wet in fall and winter (Brown and Williams 1972). Ice-cored palsas and peat plateaus form up to 2–3 m above the drainage level of some fens (Dever, Hillaire-Marcel, et al. 1984). Their raised profile isolates them from surface water inflows, and hence they are a characteristic bog landform. Water in these features has a relatively short residence time, being quickly translated into runoff (Dever, Laithier, et al. 1982; Quinton and Hayashi 2005). Their elevated position with respect to the regional water table ensures rapid water delivery to adjacent fen peatlands, which are the major regional or watershed conduits for runoff (Price 1987; Quinton and Hayashi 2005). Frost causes a perched water table, which facilitates runoff and keeps the system wetter than it would be otherwise. This can be an important mechanism to explain the occurrence of bogs in the relatively dry Western Boreal Plain (Petrone, Devito, et al. 2008). In winter, differential rates of seasonal frost penetration can alter groundwater flow paths (Price and Woo 1988). Winter drainage produces little flow from bogs, but inflow from mineral uplands can sustain flow into and from fens (Price and FitzGibbon 1987). ET rates in winter are low, but can represent 23–30% of the total annual flux (Lafleur, Hember, et al. 2005).

Biogeochemistry

As with all wetland ecosystems, the oxidation-reduction (or redox) potential is an important control on the availability of chemical elements and cycling of materials in soils. Waterlogged soil conditions limit oxygen availability and result in anaerobic metabolism of organic matter, slowing decomposition and resulting in the substantial accumulation of soil carbon. As a result, northern peatlands are estimated to store between 270 and 455 × 10^{15} g of carbon (Gorham 1991; Turunen, Tomppo, et al. 2002), an amount equivalent to approximately one-third of all soil carbon stocks and 34–57% of the carbon currently held in the atmosphere (IPCC 2007). Northern peatlands are also estimated to contribute 5–10% of global CH_4 emissions (Mikaloff Fletcher, Tans, et al. 2004). Because of this important role in the global carbon cycle, it is not surprising that much peatland biogeochemical research has focused on carbon cycling. Variability in cation concentrations and acidity among northern peatlands has been linked to hydrogeology and availability of elements from atmospheric sources. Lately an increasing interest is being paid to nutrient cycling as atmospheric deposition of nitrogen increases (Limpens, Heijmans, et al. 2006).

Carbon Cycling

Temperate and boreal peatlands have accumulated soil carbon since the last glaciation (~10,000–14,000 years ago), and studies using soil cores give long-term accumulation rates of 19 to 25 g C m^{-2} yr^{-1} (Roulet, Lafleur, et al. 2007). Carbon accumulates in peatlands because uptake of carbon via gross ecosystem photosynthesis (GEP) exceeds losses via decomposition. Changes in stored carbon (ΔC) can be expressed as:

$$\Delta C = -(NEE + F_{CH4} + F_{NMVOC} + F_Q),$$

where NEE is the net flux of carbon as CO_2 from the ecosystem to the atmosphere (i.e., GEP minus autotrophic and heterotrophic respiration), F_{CH4} is the flux of CH_4, F_{NMVOC} is the flux of nonmethane volatile organic compounds, and F_Q is the flux of carbon in particulate and dissolved forms carried by hydrological inputs/outputs to the ecosystem. In all cases fluxes are positive if carbon is lost from the ecosystem.

Contemporary rates of carbon exchange are known to vary widely from year to year, controlled largely by growing season temperature and water table position. Saarnio, Morero, et al. (2007) compiled values for NEE ranging from an uptake of 67 to a release of 80 g C m^{-2} $yr^{-1}$for bogs to an uptake of 98 to release of 101 g C m^{-2} yr^{-1} for fens. These broad ranges likely result from the fact that most studies are conducted for only one or two years and thus poorly represent average conditions at sites. Several peatlands with longer records report similarly large ranges, but average rates of carbon accumulation of ~22–24 g C m^{-2} yr^{-1} (Roulet, Lafleur, et al. 2007; Nilsson, Sagefors, et al. 2008) are similar to long-term accumulation rates determined from cores.

Methane emissions also vary both within and among peatlands. Bogs are reported to emit < 1 to 16 g CH_4–C m^{-2} yr^{-1} and fens < 1 to 42 g CH_4–C m^{-2} yr^{-1} (Saarnio, Morero, et al. 2007). Since CH_4 is produced under highly reduced conditions and may be oxidized to CO_2 above the water table, water table position is an important control on CH_4 emissions, with higher

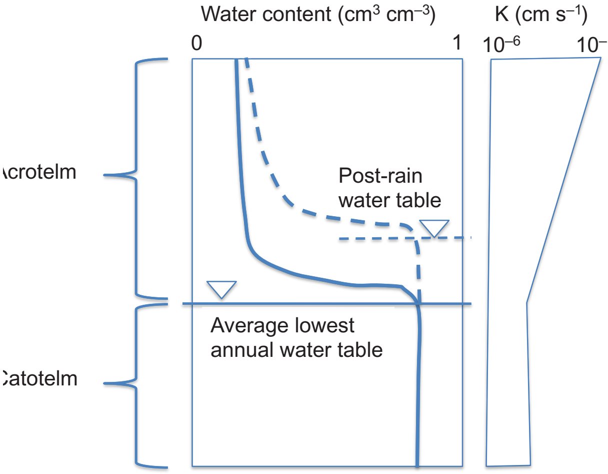

FIG. 9.2. Hydrological processes within peatlands and their role in downstream aquatic systems are dominated by the structure and character of the peat soil.

fluxes from wetter sites. Temperature is positively correlated to CH_4 emissions in many studies (e.g., Dise, Gorham, et al. 1993). Vegetation type (Bubier 1995) and productivity (Waddington, Roulet, et al. 1996; Tuittila, Komulainen, et al. 2000) are also related to CH_4 flux because plants provide labile substrate for CH_4 production and some species can transport CH_4 from the soil to the atmosphere. Once produced in soil, CH_4 can also accumulate as free-phase gas, or bubbles (Strack, Kellner, et al. 2005; Comas, Slater, et al. 2008; Waddington, Harrison, et al. 2009), and recent research suggests that CH_4 release via bubbling (ebullition) may account for a substantial portion of total peatland CH_4 emissions (Glaser, Chanton, et al. 2004; Comas, Slater, et al. 2008).

Carbon is also lost from peatlands via hydrologic output in both particulate and dissolved organic and inorganic forms. These outputs may account for a significant portion of peatland carbon cycles (Billett, Palmer, et al. 2004). Some suggest that hydrologic export of carbon from peatlands is increasing (Freeman, Evans, et al. 2001), leading to concerns over destabilization of these soil carbon stocks. Causes of increasing exports, particularly of dissolved organic carbon (DOC), are still uncertain, but possible mechanisms include warming temperatures (Freeman, Evans, et al. 2001), severe drought (Worrall, Burt, et al. 2004), increasing vegetation productivity (Freeman, Fenner, et al. 2004), and decreasing atmospheric deposition of sulphate (Evans, Chapman, et al. 2006).

Recent research has also shown that release of carbon to the atmosphere as nonmethane volatile organic compounds (NMVOCs) may account for up to 5% of the total carbon balance of northern peatlands (Bäckstrand, Crill, et al. 2008). Efflux of NMVOCs appears correlated to temperature, water table, and vegetation type (Bäckstrand, Crill, et al. 2008), with vascular plants likely responsible for most emissions (Tiiva, Faubert, et al. 2009).

Mineral and Nutrient Availability

Mineral concentrations in peatlands are largely controlled by the source of hydrologic inputs. Because fens receive inputs of surface and groundwater that has interacted with mineral soil, concentrations of cations and alkalinity are higher than bogs receiving only precipitation (Table 9.1). Mineral inputs can also be atmospherically derived. Gorham and Janssens (2005) assessed peat chemistry in five bogs and observed a higher concentration of sea salt–derived minerals (Cl, S, Br) in maritime locations and more wind-blown soil-derived minerals (Al, Ce, Cr) in midcontinental sites.

Several studies have found that the hydrogeologic setting of the peatland can have an important control on mineral and nutrient concentrations and turnovers. For example, Devito and Hill (1997) observed that small headwater peatlands exhibited variable sulphate retention depending on till depth in the catchment. Shallow till depth resulted in elimination of groundwater inputs in dry summers, resulting in water table drawdown and sulphate mobilization. Similarly, Mitchell, Branfireun, et al. (2009) compared porewater chemistry at peatland sites with variable upland slope geometries. They found higher concentrations of methylmercury in porewater adjacent to concave slopes, likely due to larger hydrologic inputs supplying sulphate and DOC, important for mercury methylation.

In general, concentrations of nutrients such as nitrogen and phosphorus are relatively low in peatlands and may vary inconsistently along bog-fen gradients (Table 9.1). However, minerotrophic peatlands are often slightly more nutrient rich than ombrotrophic sites (Laine, Komulainen, et al. 2004; Keller, Bauers, et al. 2006). At many sites, primary productivity is phosphorus limited (Kellogg and Bridgham 2003). Despite low nutrient availability, peat accumulation into thick organic soils represents a long-term accumulation of nutrients (Laine, Komulainen, et al. 2004; Gorham and Janssens 2005).

Because northern peatlands are dominated by vegetation and microbial communities adapted to low nutrient conditions, ecosystem response to fertilization, particularly atmospheric nitrogen deposition, has been the focus of many recent experiments. Fertilization with N has been observed to increase the abundance of vascular vegetation at the expense of bryophytes, particularly *Sphagnum* (Limpens and Berendse 2003; Keller, Bauers, et al. 2006; Bubier, Moore, et al. 2007). This shift in vegetation can increase GEP and ecosystem respiration (Lund, Christensen, et al. 2009); however, in some cases, net uptake of CO_2 is reduced by fertilization because of the loss of mosses (Bubier, Moore, et al. 2007). A meta-analysis of N-fertilization experiments in *Sphagnum*-dominated peatlands (Limpens, Granath, et al. 2011) determined that low levels of N addition enhance *Sphagnum* production, whereas higher levels reduce production. The rate of N application that reduces moss production is lower when background N deposition is high. Higher temperatures and low phosphorus levels exacerbated detrimental effects of N application. Generally fertilization has little effect on CH_4 emissions (Keller, Bridgham, et al. 2005; Lund, Christensen, et al. 2009); however, emissions of the greenhouse gas nitrous oxide (N_2O) are increased when N is added (Lund, Christensen, et al. 2009).

Microtopography and Peatland Biogeochemistry

While it is clear that biogeochemistry varies among peatlands ecosystems, within-site variability is also important. Water tracks within a peatland complex support vegetation communities adapted to more nutrient-rich conditions because the water flow provides a constant supply of nutrients (Malmer 1986). In addition, differences in elevation of the peatland surface create zones with varying water table and vegetation

TABLE 9.1

Summary of chemical data for surface water for four peatlands in western Canada

	Bog	Poor fen	Moderately rich fen	Extremely rich fen
pH	3.96 (0.07)	5.38 (0.13)	6.14 (0.27)	6.88 (0.30)
Conductivity (µS/cm)	39.0 (11.0)	48.0 (14.0)	85.0 (16.3)	187.0 (35.0)
Ca^{2+} (mg/L)	3.00 (0.96)	5.88 (1.88)	11.09 (2.92)	23.28 (6.52)
Mg^{2+} (mg/L)	0.72 (0.35)	3.14 (1.05)	5.07 (1.37)	7.78 (1.76)
Alkalinity (µequiv./L)	< 0 (–)	198.0 (51.0)	694.0 (186.0)	1,716.0 (401.0)
NO_3^--N (µg/L)	5.74 (2.10)	4.90 (1.68)	4.48 (2.55)	3.64 (1.82)
NH_4 (µg/L)	17.6 (8.40)	13.2 (8.82)	12.2 (10.5)	6.44 (5.88)
SRP (µg/L)	8.27 (6.10)	52.7 (27.9)	77.7 (101.0)	7.34 (7.03)

NOTE: Modified from Vitt, Bayley, and Jin 1995. Values are averages of 18 water samples (36 for moderately rich fen) with standard deviation in parenthesis. SRP is soluble reactive phosphorus.

communities. These features, often called microforms, may be one to several meters in extent and centimeters to meters in height. Because water table and vegetation are such important controls on carbon and nutrient cycling, microforms have been observed to have significant differences in carbon accumulation (Belyea and Clymo 2001), CH_4 fluxes (Waddington and Roulet 1996), nutrient (Eppinga, Rietkerk, et al. 2010), and methylmercury concentrations (Branfireun 2004). Microforms also respond differently to disturbances such as drought and warming (Strack and Waddington 2007; Sullivan, Arens, et al. 2008). More than simple differences between microforms, it is clear that the composition and distribution of these features within a peatland can affect whole ecosystem function (Waddington and Roulet 2000; Becker, Kutzbach, et al. 2008; Baird, Belyea, et al. 2009). Thus, in addition to local and regional hydrogeology, microtopography should be considered when studying peatland biogeochemistry.

Vegetation Gradients

Vegetation gradients exist at several spatial scales in northern peatlands. A vegetation gradient is defined as a change in abundance, composition, or growth of plant species or communities in relation to space or another physical, chemical, or biological gradient. One reason why gradients have received so much attention by scientists is their clear expression in peatland landscapes (Sjörs 1948; Bridgham, Pastor, et al. 1996; Økland, Økland, et al. 2001). Bryophytes have a different nutrient acquisition strategy than vascular plants. Given their lack of vascular structure and unistratose cellular leaf composition, bryophytes are more influenced by growing conditions at the soil-atmosphere interface than vascular plants depending more on deeper substrate layers. Consequently, changes of vascular plants and bryophytes along gradients are not always controlled in similar ways (Glaser, Janssens, et al. 1990; Vitt and Chee 1990; Bragazza and Gerdol 2002).

Sjörs (1948) identified three gradients that are important to determining patterns in peatland vegetation: (1) the microtopographical gradient between vegetation and the water table (often referred to as the hummock-hollow gradient); (2) the degree of openness from peatland margin to peatland expanse; and (3) the degree of minerotrophy (as defined by pH and cation base richness, referred to as the pH-alkalinity gradient). When discussing chemical gradients, the term *minerotrophy* strictly refers to base richness (metallic cations and pH), whereas the terms *oligotrophic, mesotrophic,* and *eutrophic* refer only to nutrient richness (mainly N and P) as used in limnology. Lately, a gradient in fertility related to the availability of the limiting nutrient elements N and P has been revealed for vascular plants (Bridgham, Pastor, et al. 1996; Wheeler and Proctor 2000). In terms of predicting the response of plant communities of northern peatlands to climate change and a wide-scale pattern of nitrogen depositions, both pH-alkalinity and nutrient gradients must be addressed and vegetation surveys must include both mosses and vascular plants (Bedford, Walbridge, et al. 1999; Limpens, Granath, et al. 2011) to adequately assess responses of peat moss–dominated peatlands.

Hummock-Hollow Gradient

The hummock-hollow gradient is the linear sequence over a few meters of microstructure. Microtopographical levels along a water table gradient are identified as hummock, lawn, carpet, and hollow/mud-bottom/pool (Fig. 9.3). This gradient is usually described by the distribution of *Sphagnum* mosses or other bryophytes (e.g., Vitt, Crum, et al. 1975; Wagner and Titus 1984; Bubier 1995), but vascular plants can also be useful (Damman and Dowhan 1981). Hummocks are raised 20–80 cm above the water surface and are characterized by dwarf shrubs and *Sphagnum fuscum* (Fig. 9.4a). Lawns are 5–20 cm above the water level and are characterized by graminoids and *Sphagnum* species such as *S. rubellum* and *S. magellanicum.* Floating carpets or hollows are between 5 cm below to 5 cm above the surface and have a sparser cover of graminoids and mosses (e.g., *S. angustifolium*). Mud-bottoms are often flooded and may lack vascular plant cover. They may support mosses or liverworts, but are often simply bare peat with a cover of algae (Karofeld and Toom 1999). Pools are water basins that are permanently filled, often with vegetation such as *Warnstorfia fluitans* (Fig. 9.4a) around the edges. In bogs (sensu lato for *Sphagnum*-dominated peatlands), hummock mosses are dominated by species

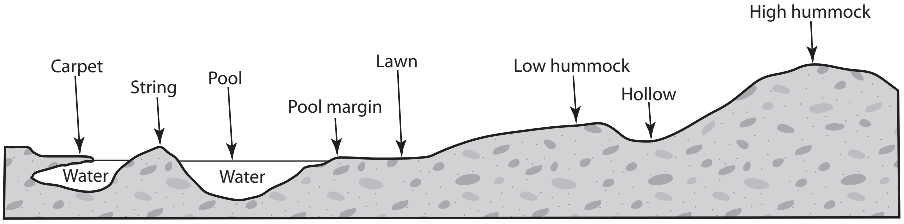

FIG. 9.3. Schematic drawing representing typical microstructures encountered in peatlands. (Drawing by Denis Bastien.)

from the Acutifolia taxonomic section of Sphagna, whereas species from the Cuspidata section frequently grow in wet hollow habitat.

Although less studied, microtopographical gradients also exist in moderate-rich and rich fens (Fig. 9.4b). Vitt (1990) described this gradient as hummock (or string), carpet, lawn, and flark (or marl pool). In fens, the microtopographical gradient is more difficult to study because the topographical height gradient is superposed with a minerotrophic gradient between hummocks and depressions. Hence, in relatively rich fens, *Sphagnum fuscum,* a typical bog species, can be found on high hummocks or well-developed strings. Note that the indicative species enumerated in Fig. 9.4 do not correspond to plant communities, but are just presented as examples of species distributed along the bog or fen microtopographical gradient. The duality of middle-range topographical gradient and minerotrophic gradient is exemplified by *Scirpus cespitosus, S. hudsonianus, Carex exilis,* and *Potentilla palustris* for vascular plants and *Loeskhypnum badium* for bryophytes (Bubier 1995; Campbell and Rochefort 2001).

Swamp Forest–Open Peatland Gradient

The swamp forest–open peatland gradient described by Sjörs (1948) is evident when one walks from upland forests through a forested peatland into a less densely forested peatland, and finally into an open peatland. Vitt and Slack (1984) describe the following moss indicator species for the shade gradient of bogs and forested fens of northern Minnesota: (1) communities within a closed tree canopy, dominated by *Sphagnum teres* and *S. warnstorfii;* (2) those with scattered, individual trees to those with an open tree cover, dominated by *S. fuscum, S. capillifolium, S. magellanicum, S. angustifolium,* and *S. fimbriatum;* and (3) those with no shade, dominated by *S. papillosum, S. rubellum, S. centrale, S. obtusum,* and *S. contortum.* But it is more the tree and shrub spatial pattern that reveals the margin-expanse gradient. When approaching the margin of a peatland, the density and size of trees of species such as *Picea mariana* and *Larix laricina* increase, forming a swampy forested zone (Bubier 1991). Shrubs such as *Viburnum nudum* ssp. *cassinoides, Ilex (Nemopanthus) mucronatus,* and *Alnus incana* ssp. *rugosa* have greater abundance in that zone (Damman and Dowhan 1981). The lagg, an ecotone quite variable in species composition at the transition between peatland and forest ecosystems but usually rich in species, exists at the margin of some peatlands (Conway 1949). Typical lagg species include *Carex riparia, C. rostrata, Osmunda cinnamomea,* and *Calamagrostis canadensis.*

Although this gradient is mostly influenced by shade (Vitt and Slack 1984; Anderson, Davis, et al. 1995), it is conditioned by hydrogeological conditions. The deeper and more variable water table at the margins (Damman and Dowhan 1981) enables trees to grow larger. The gradient also parallels minerotrophy change, as swamp forest margins are close to the mineral soil beneath, which most likely sustains the greater biomass found at peatland-forest margins. Along with the presence of more shrubs and trees, light availability is diminished, causing a change in bryophyte communities, as not all *Sphagnum* species have similar requirements in term of irradiance (Gignac 1992). Some ecologists studying temperate peatlands argue that the swamp forest–open peatland gradient may lack ecological usefulness (Wheeler and Proctor 2000); most admit that the direction of variation in vegetation remains unclear but still argue that this gradient is caused by a specific set of factors (Økland, Økland, et al. 2001). In North American peatlands, scant attention has been given to the study of the swampy forest–open peatland margin ecotone.

Ombrotrophy-Minerotrophy Gradient

A gradient of vegetation going from "poor in indicative species" to "rich in indicative species" exists among bogs, and poor, moderate, and rich fens (Sjörs 1963). This gradient is defined by the presence of indicative species, particularly minerotrophic species. Bogs have very few or no minerotrophic indicative species, whereas fens have few, several, or many indicative species according to the degree of minerotrophy. Some examples of moss species indicative of minerotrophic conditions in boreal North America are *Campylium stellatum, Scorpidium scorpioides, S. cossinii, Sphagnum warnstorfii, S. subsecundum,* and *Warnstorfia exannulata,* and vascular plant species include *Carex aquatilis, C. lasiocarpa, C. exilis, Calamagrostis canadensis,* and *Myrica gale.* Although ombrotrophic peatlands are characterized by a lack of indicative species, an abundance of *Sphagnum fuscum, S. magellanicum, S. angustifolium,* and *S. cuspidatum,* along with the vascular plants *Eriophorum spissum, Kalmia angustifolia, K. polifolia,* and *Rubus chamaemorus,* can indicate a bog environment.

Floristic multivariate analyses of peatland vegetation point to a primary division between *Sphagnum*-dominated and brown moss–dominated (Amblystegiaceae) peatlands. This plant division corresponds well to the bimodal frequency distribution of peatlands related to pH (Gorham and Janssens 1992). Experts believe that grouping peatlands into *Sphagnum*-dominated (bogs and poor fens with pH lower than 5.5–5.7) and brown moss–dominated (moderately rich and rich fens with pH greater than 5.5) habitats makes more ecological sense than using the strict concept of bog (fed only by precipitation) and DuRietz's (1949) notion of indicative species (Vitt 2000; Wheeler and Proctor 2000). With such a system, the categories of bog and poor fen in Table 9.1 would be merged to represent chemistry of *Sphagnum*-dominated peatlands.

The ombrotrophy-minerotrophy gradient is expressed at

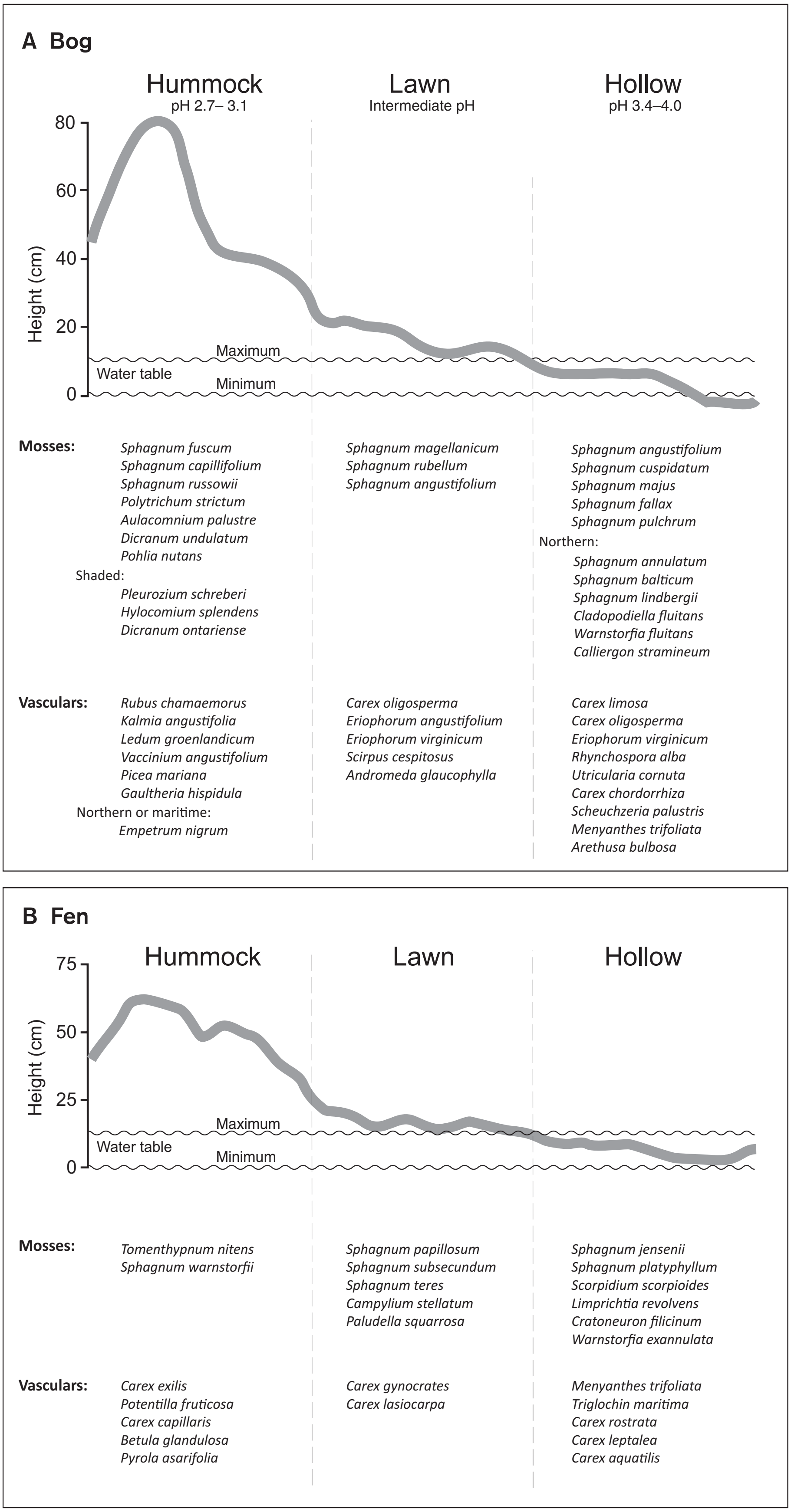

FIG. 9.4. Hummock-hollow gradient showing typical eastern North American species for each microhabitat: A. bog species along with average pH; and B. fen species.

regional scales across different peatlands. But it can also be observed within a peatland complex, such as the extensively studied Red Lake peatlands in Minnesota (Janssens and Glaser 1986) and the Mariana Lakes region in Alberta (Nicholson and Vitt 1990). Changes in species in the ombrotrophy-minerotrophy gradient tend to follow a gradient of pH and conductivity/alkalinity/base cations (Sjörs 1950; Gorham 1953). Factors that explain the distribution of plants along this gradient are not well understood. However, two important factors are the presence of *Sphagnum* mosses (which can lower pH) and the development of the peatland (which, with time, reduces the influence of flow-through runoff). A fertility gradient, or one of nutrient supply during a given time, may also explain the distribution of plants along the ombrotrophic-minetrophic gradient. Difficulties in studying fertility gradients stem from the time and costs associated with complete nutrient budgets involving annual water balance, rate of water flow, and nutrient assimilation and decomposition rates of plants (Bridgham, Pastor, et al. 1996).

Biogeographical Gradient (Distance from the Sea)

To the original work of Sjors (1948), Malmer (1986) adds a fourth gradient: a biogeographical wetness gradient, most evident in raised bogs, that influences vegetation structure of peatlands. Broadly, three types are recognized in North America: (1) continental regions that broadly support forested (often densely) or shrubby peatlands; (2) wetter areas that harbor semiforested peatlands; and (3) the wettest areas, which have open peatlands with pools. Tree and shrub density gradually decreases in peatlands as you move farther east until you reach open peatlands with pools of the maritime region (Glaser and Janssens 1986). In Europe, Malmer (1986) ascertained that climatic conditions were most important in establishing regional differences, whereas in North America, Glaser and Janssens (1986) revealed the importance of autogenic processes and age of the peatlands to the structure of raised bogs.

Plant Adaptations in Peatlands

Sphagnum mosses are often considered eco-engineers in the sense that once established in a peatland, they induce changes in water regimes, acidity of the environment, and the sequestration of nutrients through slowly decomposing peat (van Breemen 1995). Peatland vascular plants grow in wet, partly anoxic, often nutrient-poor and acidic environments. According to Grime's (2001) plant strategies, peatland vascular plants are "stress-tolerators" due to slow growth rate and longevity and because they invest little in the production of seeds. Strategies to deal with environmental stress are more pronounced in bog species and become less pronounced in moderate-rich and rich fens. Ericaceous shrubs in particular have developed adaptations to the wet, acid-poor environment of bogs: persistent resinous leaves and involuted margins of the leaves conserve humidity, and association with ericoid mycorrhizae helps in nutrient sequestration.

Low Nutrient Availability

Several strategies allow peatland plants to live in nutrient-poor environments. Most peatland vascular plants are perennial, an efficient way to ensure large biomass above- and belowground (Rydin and Jeglum 2006). A large underground biomass is essential to procure enough nutrients in a nutrient-poor habitat. Additionally, some ericaceous shrubs *(Rhododendron, Chamaedaphne, Andromeda)* conserve nutrients by retaining their leaves over several growth seasons (Crawford 1993). In deciduous peatland species (e.g., *Rubus chamaemorus* and *Vaccinium* spp. in bogs and many grasses and sedges in fens), nutrients are transferred from leaves to the roots and rhizomes in autumn and then back to new leaves in spring (Grace 1993). Sedges additionally conserve nutrients by reproducing asexually by either aboveground stolons or belowground rhizomes. Nutrients are conserved by translocating them from the old tissue to the new plant.

Some peatland species increase nutrient intake (P, N, and K) through mycorrhizal associations between the plant roots and fungi. The plant has an increased ability to capture water, phosphorus, and other nutrients, and the fungi receive carbohydrate in return. Species that benefit from mycorrhizal associations include various peatland woody species, such as *Larix laricina, Picea mariana, Alnus incana, Betula glandulosa,* and *B. pumila,* as well as ericaceous and orchid species (Cronk and Fennessy 2001). However, sedges and cotton grass, dominant vascular species in many peatlands, generally do not have mycorrhizae (Thormann, Currah, et al. 1999).

The most spectacular example of a plant adaptation to nutrient-poor environments is carnivory in such plants as *Drosera, Utricularia,* and *Sarracenia* species. These plants increase nutrient intake by trapping and digesting invertebrates. The benefits of carnivory must balance the cost of making and maintaining the traps (Cronk and Fennessy 2001). Some carnivorous plants are facultative carnivores, relying on carnivory only in nutritionally hard times, such as a prolonged period without fire (Folkerts 1982).

Waterlogging

Anoxic conditions common in peatlands can hinder root growth and the uptake of minerals and nutrients. Some vascular peatland plants have adapted to these conditions by developing large intercellular spaces, called aerenchyma, that extend from leaves through stems and down into roots or rhizomes. This space transports oxygen to belowground parts (Crawford 1978).

Additional adaptations help peatland vegetation cope with variable water levels, such as after snowmelt or heavy precipitation. The sedge family Cyperacae forms tussocks to elevate leaves above the water. Floating mats, common where fens border lakes, allow vegetation to cope with water fluctuation by moving with the water surface (Rydin and Jeglum 2006). Some peatland plants, especially woody species, adapt their roots to cope with flooded conditions. Two common root adaptations are the development of shallow rooting and adventitious roots (roots made from tissue other than root tissue) (Crawford 1978). Due to a lack of aerenchyma and a reliance on mycorrhizae, many peatland woody species have shallow root systems. These species, such as *Picea mariana, Larix laricina,* and *Thuja occidentalis,* grow in the aerated zone, which is often just tens of centimeters deep (Rydin and Jeglum 2006).

As peatland trees grow, their weight may cause them to sink into the peat, exacerbating anoxic conditions. *Sphagnum* species also grow up around the trees and slowly raise the water level. *Salix* spp., *Alnus glutinosa, Pinus contorta, Larix laricina,* and *Picea mariana* are all peatland species that can form adventitious roots (Cronk and Fennessy 2001; Rydin and Jeglum 2006). Adventitious roots grow either directly on the trunk or can form from low branches. These new branches grow new roots and a new main shoot, leading to clonal reproduction.

Fauna

Peatlands are home to a high diversity of invertebrates; individual peatlands with well over 1,000 arthropod species are not uncommon (Blades and Marshall 1994). Together, vertebrate and invertebrate species assemblages of northern peatlands are unique. In fact, peatlands often contribute significantly to regional wildlife diversity, especially in temperate latitudes bordering the boreal biome (Calmé, Desrochers, et al. 2002; Spitzer and Danks 2006). Although most invertebrates found in peatlands occur in a variety of habitats, several species are found almost exclusively in bogs or fens (Spitzer and Danks 2006). Herbivore insects restricted to peatland plants, such as aphids and moths, dominate this group, but insect predators and parasitoids also occur as peatland specialists (Gotelli and Ellison 2002; Spitzer and Danks 2006). Peatland pools in particular harbor highly specialized invertebrate predators, including dragonflies *(Aeshna)* and water bugs *(Notonecta).*

In contrast to invertebrates, no vertebrate species is thought to occur only in peatlands, even though species of every vertebrate class will use peatlands. Bogs rarely harbor fishes in their pools due to acidic condition and isolation. Occasionally, small fish such as mudminnows *(Umbra limi)* can be found in bogs. Because of the high acidity, bogs have long been presumed hostile to amphibians, as amphibians undergo major exchanges with their environment through their skin (Pough 1976; Leuven, den Hartog, et al. 1986). However, recent investigations indicate that bogs and fens harbor abundant amphibian populations and even offer opportunities for reproduction (Mazerolle and Cormier 2003). One rare amphibian species, the four-toed salamander *(Hemidactylium scutatum),* may occur in peatlands because of its association with *Sphagnum* (Wood 1955), but its occurrence in peatlands remains to be documented (Mazerolle 2003). Few reptiles are reported in peatlands; scarcity may result from northern latitudes or a lack of detailed studies.

By far, birds are the most studied peatland vertebrates, and over 100 bird species are known to breed in North American peatlands (Desrochers and van Duinen 2006). North American peatlands are characterized by a high diversity of lesser-known songbirds. Among the most frequent birds are ubiquitous species such as white-throated sparrow *(Zonotrichia albicollis),* common yellowthroat *(Geothlypis trichas),* and hermit thrush *(Catharus guttatus),* and more specialized species such as palm warbler *(Dencroida palmarum)* and Lincoln's sparrow *(Melospiza lincolnii).* Those birds can reach high population densities on the order of 5 to 10 pairs per ha (A. Desrochers unpublished data). The species listed can be found either in bogs or fens, but fens often harbor additional species such as American bittern *(Botaurus lentiginosus),* swamp sparrow *(Melospiza georgiana),* and the ubiquitous red-winged blackbird *(Agelaius phoeniceus).*

Bogs in particular are attractive to game birds such as spruce grouse *(Falcipennis canadensis)* and sharp-tailed grouse *(Tympanuchus phasianellus).* The impressively large sandhill crane *(Grus canadensis)* is a noteworthy resident in western boreal peatlands, and appears to be expanding in eastern boreal peatlands. Other significant peatland birds are those where recent population declines have raised concerns, including rusty blackbird *(Euphagus carolinus),* a common breeder of boreal muskeg whose numbers have plummeted since the mid-1960s (Sauer, Hines, et al. 2008); upland sandpiper *(Bartramia longicauda);* and most species of shorebirds (Morrison, Aubry, et al. 2001). The role of peatlands as staging areas for migrating shorebirds merits more investigation. Interestingly, migrating shorebirds occur not only in natural peatlands, but migrating flocks also occur regularly in barren expanses of peatlands cut over by the *Sphagnum* peat moss industry (A. Desrochers unpublished data). It is likely that the extinct Eskimo curlew *(Numenius borealis)* used northeastern peatlands regularly in the fall, in search of crowberries *(Empetrum nigrum)* as fuel for their journey south (Bent 1962).

Mammals are rarely abundant in peatlands. Like most terrestrial ecosystems, peatlands support a suite of small rodents, but none are specifically associated to this habitat. Mazerolle, Drolet, et al. (2001) found that only 2 of 15 small-mammal species encountered in eastern Canadian bogs exhibited a preference for bogs: the Arctic shrew *(Sorex arcticus)* and the southern bog lemming *(Synaptomys cooperi).* Moose *(Alces alces)* are often found in peatlands, particularly near edges between adjoining forest patches and open ericaceous habitats that provide food and cover against predators and extreme weather.

Ecological Controls

Peatland Development

Peatlands form by paludification or terrestrialization. These two processes describe the transformation of aquatic or terrestrial habitat into peatlands following changes in hydrological conditions of the substrate or climatic conditions. Specifically, paludification is the swamping of a terrestrial site and terrestrialization is the filling-in of a lake or shallow water body. These two processes do not operate necessarily in an exclusive manner, but it is generally recognized that the inception of peatlands is mostly climatically controlled, whereas their subsequent development is dominated by autogenic processes (Vitt 2006). The interplay between the influence of allogenic factors (external influences to the ecosystem such as climate, fire, large-scale human impact) and autogenic factors (internal influences such as plant succession) is well described by Payette and Rochefort (2001), Charman (2002), and Rydin and Jeglum (2006).

Peatlands are characterized by a striking heterogeneous surface topography that is expressed at several spatial scales: from a few meters (hummock-hollow microstructures) to hundreds of meters (pool macrostructure) to landscape scales (bog islands; Weltzin, Harth, et al. 2001). The main macrostructures in northern peatlands are the alternating pattern of strings and flarks or the presence of pools. Several hypotheses have been formulated about mechanisms of control (an active area of research among peatland ecologists), but none is yet universally recognized.

Macrostructures

Among allogenic processes, the influence of freeze-thaw actions, gravity through solifluxion, and permafrost creation of surface polygons shaped by the presence of ice wedges are considered important to macrostructure (Seppälä and Koutaniemi 1985; Swanson and Grigal 1988). However, in general, minimal quantitative data support allogenic development of macrostructures in boreal peatlands (Payette 2001). On the other hand, autogenic biotic processes are gaining support to explain the formation of strings and pools. From stratigraphic analyses of several peat profiles within a region, Anderson, Foster, et al. (2003) have shown that plant abundance will vary even if plant succession is under the influence of a uniform climate, suggesting that it is mostly autogenic factors controlling peat accumulation and in turn the development of macrostructures. Indeed, pools do not appear synchronously within the same climatic region or even the same site (Foster, Wright, et al. 1988; Tallis and Livett 1994; Karofeld 1998), implying a stronger influence from local variation in vegetation or hydrology (Charman 2002). Glaser and Janssens (1986) maintained that peat accumulation per se can induce changes in the hydraulic properties of peat, leading to a subsequent influence on macrostructure development. Lately, several researchers (reviewed in Kuhry and Turunen 2006) advocated that the interplay of both allogenic and autogenic factors (such as plant productivity, decomposition, peat accumulation, and *Sphagnum* acidification) is basic to the presence of macrostructrure, but that the inception and rate of change are more related to external factors, particularly the influence of climate on hydrological conditions and water table fluctuations. Some simulation models support the interplay of both internal and external factors (Belyea and Baird 2006).

Microstructures

Patterns of hummock-hollow formation and their resilience through time can be explained by various factors, such as intrinsic decomposition rates of *Sphagnum* species (Johnson and Damman 1993; Belyea 1996), water table position and climatic conditions (Rydin 1985; Belyea 1996; Karofeld 1998), interactions among plant species (Vitt, Achuff, et al. 1975; Malmer, Svensson, et al. 1994; Malmer, Albinsson, et al. 2003), nutrient regimes (Damman 1978; Luken 1985), and pH (Clymo 1963). These factors influence the development of the microtopographical gradient and the resulting thickness of the acrotelm.

Water table levels do not follow the relief of the microtopographical gradient; thus a wet-moist to drier gradient from hollows to hummocks is created. Hydrological influences on species distribution along the wetness gradient come from the fact that certain *Sphagnum* mosses have a higher resistance to desiccation conditions that develop on hummocks. This resistance results from their habit of living in tight colonies or communities where fascicle of branches are intermixed together and the structural architecture of the Acutifolia species (the most common peat mosses on hummocks), which has more branches and a denser cover of stem leaves, aiding the transmission of water upward (Hayward and Clymo 1982). This relation does not hold when isolated individual stems of hummock species are submitted to drying conditions (Sagot and Rochefort 1996). In fact, individuals can be less tolerant than hollow species, which survive cycles of drought through rapid physiological recovery in photosynthetic rates (Wagner and Titus 1984). Differences in pH and nutrient elements can also explain hummock-hollow gradients. The lower pH of hummocks, caused by the presence of efficient acid-producing species, such as *S. fuscum,* and the higher relief, impeding dilution of the acids, would exclude species less resistant to low pH (Vitt, Crum, et al. 1975). Concentrations of nutrients can be higher in depressions than on hummocks (Damman 1978). Higher concentrations of nutrients and mineral elements in the upper part of the acrotelm where the depressions are found (hollows, mud-bottoms, pools) would come in part from the buoyancy-driven water flow found in *Sphagnum* bogs (Adema, Baaijens, et al. 2006).

Finally, differences in production and decomposition between hummock and hollow habitats can also maintain microtopographical gradients. *Sphagnum* mosses decompose at a much slower rate on hummocks, even though the microhabitat is more oxygenated than the more anaerobic hollow habitat. Thus intrinsic structural properties of each *Sphagnum* species are more important in defining microtopographical gradients than the wet environment. Once established, hummock species can initiate and maintain differences in microtopography (Pouliot, Rochefort, et al. 2011).

Habitat Size

We have established that peatlands, like most ecosystems, are not homogeneous. They often harbor a high structural diversity, leading to well-defined and often predictable species distribution patterns. Large peatlands, in particular, typically offer many more habitats for wildlife than small ones, for two reasons: (1) large areas provide a greater diversity of microhabitats, and (2) many animal species are partial to large patches of habitat as opposed to small ones. As a result, species found in small peatlands are often simply subsets of species found in larger peatlands, leading to a system of nested species assemblages (Calmé and Desrochers 1999). Species associated to large peatlands include savannah sparrow *(Passerculus sandwichensis),* palm warbler, upland sandpiper *(Bartramia longicauda),* and sandhill crane. All of those species, except the warbler, appear to be attracted to large peatlands because they generally offer expanses of grassy habitats not generally found in small peatlands. The reason why palm warblers occur predominantly in large peatlands is not known, but it may be because of its tendency to congregate in loose "colonies" (Bourque and Desrochers 2006). Perhaps the most conspicuous features of large peatlands are pools. Those small bodies of open water are often the first feature to disappear as a result of land use by humans, leading to significant losses of aquatic insects, amphibians, and migrant birds, particularly ducks *(Anas crecca, A. rubripes)* and shorebirds *(Calidris melanotos, Tringa solitaria).*

For species with large home ranges or territories, peatlands may be important as part of their daily or annual movements. For example, spruce grouse and moose normally require the presence of extensive conifer or mixed forests in their home ranges, but typically venture into open bogs either to feed or, in the case of grouse, nest and raise their broods. Also, owing to their complex life cycles, amphibians may use peatlands only during certain stages, e.g., during dispersal between other types of wetlands, or as wet refuges during periods of the year when other wetlands are dry.

Fire as a Natural and Anthropogenic Disturbance

Fire is one of the few natural disturbances in North American peatlands, being especially common in the western boreal region. During drought, water table levels of bogs may rapidly drop, creating conditions propitious to surface fires, especially where inflammable ericaceous shrubs dominate. About 1,850 ha of bogs and 375 ha of fens burn each year in central Alberta, compared to 5,900 ha of uplands (Turetsky, Amiro, et al. 2004).

In western Canada, mean fire-free intervals (time between two consecutive fires) estimated from analysis of charcoal layers in peat cores are about 600 to 2,900 years (Kuhry 1994; Robinson and Moore 2000; Camill, Barry, et al. 2009). Data from bogs in eastern Québec (Canada) suggest natural fire-free intervals were 2,000 to 2,500 years prior to the 19th century. Fire-free intervals became much shorter (10 times) during the 19th and 20th centuries because until recently, farmers used fire to clear tree stumps before cultivation, and fire can easily spread from clearings to adjacent bogs on dry summer days (Lavoie and Pellerin 2007).

A 100-year postfire chronosequence of vegetation changes has been documented for *Sphagnum*-dominated bogs of central Alberta (Fig. 9.5) (Benscoter 2006; Benscoter and Vitt 2008). Because fire eliminates vascular plants, evapotranspirational water losses are diminished, which contributes to a rise in the water table (Wieder, Scott, et al. 2009). The greatest changes in the vegetation cover occur during the first 10 years, during which bare and burned peat is rapidly colonized by true mosses (mainly *Polytrichum strictum*), *Sphagnum* species, and vascular plants. True mosses are initially abundant because of their ability to colonize bare peat (Groeneveld, Massé, et al. 2007), competition from *Sphagnum* species has been removed, and they benefit from the release of nutrients from the burning of plants. Cover of true mosses rapidly declines after about 10 years, whereas abundance of *Sphagnum* species (mainly *S. fuscum*) and vascular plants continues to increase. Once *S. fuscum* dominates, plant assemblages remain relatively stable. As time progresses, canopy closure and microtopographic elevation facilitate establishment of feathermoss species (e.g., *Pleurozium schreberi*) on hummocks (Benscoter and Vitt 2008).

Fire has an impact on the carbon (C) balance of boreal bogs. Direct combustion of peat releases on average 3.2 ± 0.4 kg m^{-2} yr^{-1} of C (Turetsky and Wieder 2001; Turetsky, Wieder, et al. 2002). Immediately after fire, the bog understory (including the underlying peat) is a net source of C. About 12 to 13 years postfire, bogs switch from a source to a net C sink. This sink increases as bog trees produce roots and aboveground tissues, and reaches a maximum 75 years after fire. Then, as tree growth rates decline, C accumulation decreases (Wieder, Scott, et al. 2009).

Conservation Concerns

Few organizations specifically promote conservation of peatlands in North America. Typically programs for conserving wetlands are based on their capacity to support animal populations, and sites are evaluated and ranked according to productivity. This puts peatlands at a disadvantage since they are relatively poor or unproductive systems, especially bogs. By 2004, the North American Waterfowl Management Plan, signed by Canada and the United States in 1986, had 130,000 ha of wetlands protected, but a small proportion of this area was composed of peatlands. In 1996, less than 6% of sites protected by the international Ramsar wetland convention were peatlands (Lindsay 1996), but recent political pressure has increased this to more than 30%.

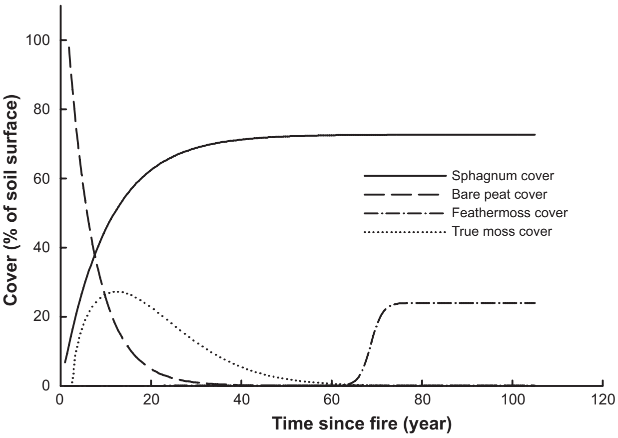

FIG. 9.5. Cover changes of main groups of moss species over time since the last fire (year zero) in bogs of north central Alberta, Canada (modified from Benscoter and Vitt 2008).

Conservation concepts specific to peatlands are emerging (Poulin, Rochefort, et al. 2004; Poulin et al. 2006), beyond only protecting large areas or huge peat volumes. Peatlands are now facing important threats that should be considered when setting conservation priorities. For instance, peatland vegetation structure and species composition are often believed to remain stable in time (centuries). This may be true for peatlands that do not face anthropogenic disturbances, but the combined effect of anthropogenic fire and of a drier-than-average climate may initiate afforestation of peatlands (Pellerin and Lavoie 2003), undermining initial conservation objectives. Anthropogenic drainage can directly affect plant communities, especially in cases where the peat is fibric (with high hydraulic conductivity) (Boelter 1972; Braekke 1983; Rothwell, Silins, et al. 1996). *Carex* species are among the first plants to decline following drainage, and may disappear within 10 years (Vasander and Laiho 1995). Following postdrainage increases in tree cover and associated shade, forest mosses may replace *Sphagnum* (Laine and Vanha-Majamaa 1992). Even natural remnants near mined areas are susceptible to afforestation by peripheral drainage (Poulin, Rochefort, et al. 1999). Afforestation is a major impact on peatland biodiversity, especially in bogs, when vascular plant and bird diversity declines after forest cover increases (Lachance, Lavoie, et al. 2005). Management plans should minimize drainage and tree invasion of peatlands.

Peat extraction for the production of horticultural compost is another threat to North American peatlands. Peat extraction severely damages peatlands, mainly due to intensive drainage, and abandoned sites are poorly recolonized spontaneously by peatland plants (Poulin, Rochefort, et al. 2005; Graf, Rochefort, et al. 2008). *Sphagnum* mosses are completely absent from residual peat surfaces, even decades after peat extraction activities have ceased (Poulin, Rochefort, et al. 2005). Fortunately, the horticultural peat industry affects only a small fraction of peatlands in North America (0.02% of Canadian peatland areas; Rubec 1996) and is limited to specific regions. Bog habitats can now be re-created in the landscape after peat extraction due to efficient restoration techniques, which are also being developed for fens (see chapter 14).

Energy production is a major threat to boreal peatlands in North America. Construction of hydroelectric dams has flooded more than 1,000,000 ha of peatlands in Québec, Manitoba, and Alberta (Rubec 1991). More recently, energy production from oil sands has expanded dramatically, and presents perhaps the greatest source of disturbance to peatlands of boreal Alberta (Forest 2001), where nearly 50% of the landscape is peatland (Vitt, Halsey, et al. 1996). One-third of the 500 km^2 of land impacted by open-pit mining to extract oil from sands were peatlands. If all available resources are mined, new oil extracting techniques such as in situ mining may eventually affect 138,000 km^2 (Schneider and Dyer 2006), an area the size of Florida and 50 times more area than that affected by actual open-pit mining activity.

One of the most influential properties of peatlands for wildlife conservation is their area. Large peatlands are not only more diverse in microhabitats and bird species but, more importantly, they support biotic assemblages rarely found in smaller, less diverse peatlands. Birds such as palm warbler *(Dendroica palmarum)* and upland sandpiper *(Bartramia longicauda)* are found only in large peatlands (Calmé and Haddad 1996; Calmé and Desrochers 2000). Smaller peatlands are often isolated, and this isolation may compound problems of small area. Distributions of palm warblers and upland sandpipers depend both on peatland area and the amount of peatland habitats available in a 10-km radius (Calmé and Desrochers 2000). As palm warbler is strictly associated to peatlands of southern Canada (Calmé and Desrochers 1999), it is a species of special concern when selecting conservation sites. Peatlands should be considered as a network, and protecting very isolated sites, especially if they are small, may be unproductive unless they support rare species.

Mapping peatland habitats using remote sensing tools may facilitate conservation network planning. Peatlands can easily be delineated in the landscape and characterized into habitat types with Landsat imagery (Poulin, Careau, et al. 2002), including habitats of special interest for conservation. For example, herbs-dominated habitats are often highly variable in terms of species composition from site to site (Poulin, Careau, et al. 2002). Although fens are not individually richer in bryophyte species than bogs, their variability from site to site leads to a higher total diversity of species when a group of fens is considered (Vitt, Bayley, et al. 1995). Variation among sites might thus complement species diversity when setting conservation priorities, because these two variables are not necessarily correlated.

Pools are a critical habitat for the conservation of peatland plant diversity. They are particularly distinct habitats in terms of species composition (Poulin, Careau, et al. 2002), and significantly increase species richness within peatlands (Fontaine, Poulin, et al. 2007). In southeastern Canada, natural bogs average 35 plant species. but this figure drops to 24 if surveys around pools are omitted (Fontaine, Poulin, et al. 2007). Thus pools deserve special attention in conservation planning. More globally, information on habitat diversity and distinctiveness is of considerable value when deciding whether all habitats deserve equal levels of protection, and determining amounts of habitat to set aside for conservation. This can be coupled with other criteria (habitat rarity, vulnerability) to set conservation targets (Pressey and Taffs 2001).

Representativeness should also include ecological diversity (Noss 1990), meaning that each type of peatland should have its own representative in a conservation network. This should maximize not only species diversity but also structural diversity, which is related to the physical organization or patterns of habitats, from the communities to the landscape scale. The Canadian wetland classification recognizes 16 forms of bogs (e.g., palsa bogs, blanket bogs, plateau bogs, polygonal peat plateau bogs, and string bogs; National Wetlands Working Group 1997). These bogs represent different shapes and surface patterning as well as different development processes, and should be considered as part of ecological diversity or biodiversity (Noss 1990). Representing each peatland type within a conservation network would favor preservation of different functions such as nutrient cycling and water regulation.

Finally, the distribution of peatlands in regard to hot spots of disturbances should be considered. For example, in North America, peatlands reach very high concentrations in the laregly uninhabited Hudson Bay lowlands, whereas they are much more scattered in more densely populated areas. Conservation efforts should probably focus on populated areas, where peatlands are more susceptible to being disturbed. Remote areas in the boreal zones should not be ignored, however, since hydroelectric projects and oil sand mining now threaten peatlands there. On an international scale, North America encompasses one-third of the world's peatland (Gorham 1990), and thus we have major responsibility in regard to peatland conservation, particularly in regard to processes associated with carbon fluxes (Gorham 1991).

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