

MULTIPLE LIMITING GRADIENTS IN PEATLANDS: A CALL FOR A NEW PARADIGM

Scott D. Bridgham,¹ John Pastor,² Jan A. Janssens,³ Carmen Chapin,¹
and Thomas J. Malterer²

¹ *Department of Biological Sciences
University of Notre Dame
Notre Dame, IN 46556*

² *Natural Resources Research Institute
University of Minnesota
Duluth, MN 55811*

³ *Department of Ecology, Evolution, and Behavior
University of Minnesota
St. Paul, MN 55108*

*All correspondence concerning this manuscript should be addressed to Scott Bridgham (219) 631–4921,
fax: (219) 631–7413, email: scott.d.bridgham.1@nd.edu*

Abstract: Peatlands often have readily apparent gradients of plant species distributions, biogeochemistry, and hydrology across several spatial scales. Many inferences have been drawn about the colinearity of these gradients, and these assumptions have become ingrained in the terminology that describes and classifies peatlands. We review the literature and present some of our own data that show that many of these inferences are either wrong or correct only under a limited set of ecological conditions. We examine historical classification schemes of peatlands and, in this context, gradients of alkalinity, pH, nutrient availability for plant growth, nutrient mineralization, hydrology, and decomposition. We further suggest a strictly defined set of terms to describe separate gradients of hydrology, alkalinity, and nutrients that limit plant growth in peatlands. Specifically, we make the following suggestions concerning terminology. (1) The suffix “-trophic” should only be used when referring to nutrients that directly limit plant growth at natural availabilities (e.g., eutrophic and oligotrophic). (2) Terms such as circumneutral, moderately acid, and very acidic (or alternatively strong, intermediate, and weak) should be used to describe the pH of peatlands. (3) Ombrogenous and geogenous (or limnogenous, topogenous, and soligenous) should be used to describe the hydrology of peatlands. (4) The terms bog and fen should be defined broadly based on water/soil chemistry and dominant plant species without accompanying assumptions regarding hydrology, topography, ontogeny, nutrient availability, or the presence or absence of nondominant indicator plant species. Better yet, the generic term peatland be used when possible to avoid confusion about conditions that may or may not be present at a particular site.

Key Words: peatlands, multiple limiting gradients, pH, alkalinity, nutrients, hydrology, plant species distributions, decomposition

INTRODUCTION

Peatlands, and wetlands in general, often have readily apparent plant community gradients, sometimes with very abrupt boundaries over distances of only meters. Many northern peatland communities have similar analogs across the circumboreal zone (Moore and Bellamy 1974, Wheeler et al. 1983, National Wetlands Working Group 1988), suggesting a similar, limited set of controlling factors over peatland initiation

and development. This had led to a long history of attempts both to classify individual communities along these gradients and to explain the underlying mechanisms for the existence of such gradients.

Peatland ecology has always had a strong natural history orientation, and while not necessarily negative, it has often led to inferences between biogeochemistry, hydrology, and plant communities when data are limited. Most of the data that do exist are correlational in

nature. In many ways, the understanding of the initiation, development, and succession of peatland communities laid out by Moore and Bellamy (1974) in their classic book has not progressed substantially (cf. Mitsch and Gosselink 1993).

Probably not surprisingly, these same inferences have become ingrained in the terminology of peatlands. For example, once a peatland has been classified as minerotrophic or ombrotrophic, one often assumes its pH, alkalinity, nutrient availability, hydrology, and dominant plant community fall into a neat theoretical framework. Rarely have all of these factors been measured simultaneously to put this theoretical framework to test (cf. Malmer 1986, Vitt and Kuhry 1992, Bridgham and Richardson 1993).

We review the literature and present some of our own data that show that many of these inferences are either wrong or correct only under a limited set of ecological conditions. We further suggest a strictly defined set of terms to describe separate gradients of hydrology, alkalinity, and nutrients that limit plant growth in peatlands.

CLASSIFICATION SCHEMES OF PEATLANDS

The concept of a gradient of peatland types resulting from different relative influences of ground water, surface water, and precipitation dates back to at least the early nineteenth century (Naismith 1807, Aiton 1811, Dau 1823 [as reviewed by Gorham and Janssens 1992], Gorham 1953). In the ensuing centuries, numerous terminologies have been suggested for different kinds of peatlands, resulting in confusion and poorly defined descriptors of peatland type. Most often, peatlands have been classified according to topography, ontogeny, hydrology, water chemistry, and/or plant-community composition (Table 1). Most of these terms are still in common usage today, and many are used interchangeably despite their original definitions being more narrowly defined (Gore 1983). The implicit assumption behind the widening definitions of these terms is that the factors controlling the successional development and present landscape distribution of peatland types act in concert across spatial and temporal scales.

Probably the first widely accepted terms discriminating types of peatland were the hochmoore (= highmoor or raised bog) and niedermoore (= lowmoor or fen) of the German and Fennoscandian schools (Weber 1908, Gore 1983). These terms are largely based on shape or topography, although ontogeny (genesis and successional development) is of great importance in determining peatland topography. Subsequently, Osvald (1925) further differentiated several European raised-bog types based on topography. Moore and Bel-

Table 1. Historical classification schemes for peatlands.

Mineral-Influenced Peatlands	Transition Peatlands	Precipitation-Dominated Peatlands	Basis for Classification	Reference
Niedermoore	Ubergangsmoore	Hochmoore	Topography	Weber 1908, Osvald 1925
Fen		Raised Bog	Topography	General Usage
Fen—various types		Bog—various types	Topography	Moore and Bellamy 1974, Glaser and Janssens 1986
Primary	Secondary	Tertiary	Ontogeny, Hydrology	Moore and Bellamy 1974
Geogenous:		Ombrogenous	Hydrology,	von Post and Granlund 1926,
Soligenous,			Topography	Sjörs 1948, Du Rietz 1949,
Topogenous				Damman 1986
Limnogenous				
Rheophilous	Transition	Ombrophilous	Hydrology	Kulczynski 1949
Rich Fen	Poor Fen	Bog	Hydrology	General Usage
Rich Fen	Poor Fen	Moss (Bog)	Water Chemistry	Sjörs 1948
Minerotrophic	Mesotrophic	Ombrotrophic	Water Chemistry, Hydrology	Du Rietz 1954, Sjörs 1961
Rheotrophic	Mesotrophic	Ombrotrophic	Water Chemistry, Hydrology	Moore and Bellamy 1974
Fen	Transitional	Bog	pH, Bryophytes	Gorham and Janssens 1992
Riekarr	Karr	Moss	Vegetation	Melin 1917
Rich Fen	Poor Fen	Bog	Vegetation	General Usage
Emergent		Moss-Lichen	Vegetation	Cowardin et al. 1979
Fen, Swamp, Marsh	Fen, Swamp	Bog	Ontogeny, Topography, Water Chemistry, Vegetation	National Wetlands Working Group 1988

lamy (1974) recognized a more elaborate geographic zonation of 11 types of European peatlands that were classified according to cross-sectional profile and surface patterning. Using similar classification criteria, Glaser and Janssens (1986) divided the boreal raised bogs of the eastern half of North America into four geographic zones. They hypothesized that the distribution of these landforms was the result of the differing age and ontogeny of the peatlands. The second of the three tiers of the hierarchical Canadian national classification system for wetlands is also largely based on topography (National Wetlands Working Group 1988).

Realizing the importance of hydrology as a master controlling variable for the diversity of peatlands, Kulczynski (1949) introduced the terms rheophilous ("loving of flow") to refer to peatlands influenced by ground water and overland flow and ombrophilous ("loving of rain") to refer to peatlands with only atmospheric inputs. Variants on this, and probably the most commonly used terms today, are minerotrophic and ombrotrophic (Du Rietz 1954, Sjörs 1961), with the suffix "-trophic" implying nourishment of "minerals" by ground water or precipitation. Although with a strong root in hydrology, the minerotrophic—mesotrophic—ombrotrophic gradient is usually operationally defined by the water chemistry of surface waters, with alkalinity-associated variables of predominant importance. Moore and Bellamy (1974) examined previous peatland classification schemes and suggested the use of the term rheotrophic instead of minerotrophic to acknowledge the role of flowing water in the development of fens, while still maintaining the emphasis on mineral nourishment from hydrologic sources. As discussed below, the nutrients that actually limit plant growth and the role of hydrology in supplying those nutrients remain open to question today. The terms bog and fen are also often defined based on water chemistry and/or hydrology (Sjörs 1948, Boelter and Verry 1977, Gore 1983).

A somewhat different conceptual approach emphasizes the ontogeny or autogenic (internally biotic driven) successional development of peatlands. As peatlands accumulate soil organic matter, they gain increasing control over their own hydrology (this is probably the most unique aspect of peatlands). Moore and Bellamy (1974) described such a developmental sequence of peatlands through progressive deposition of primary, secondary, and tertiary peat, resulting in increasing water retention in the basin and culminating in a tertiary peatland with a water table "perched" above the regional ground-water table.

A related concept defines peatlands based on their hydrology, which is a consequence of the topography of the peatland and its surrounding basin (von Post and Granlund 1926, Sjörs 1948, Du Rietz 1949, Dam-

man 1986). This concept explicitly realizes the role of autogenic peatland development as a control over hydrology. Thus, peatlands are divided into four categories (Figure 1): (1) limnogenous peatlands developing along lakes and slow-flowing streams; (2) topogenous peatlands developing in topographic depressions, with a portion of their water derived from the regional ground-water table; (3) soligenous peatlands that are affected by water from outside sources percolating through or over the surface peat; and (4) ombrogenous peatlands with water and nutrient input solely from precipitation. The first three terms can be combined under the heading geogenous.

Geogenous peatlands vegetated mostly with graminoids and ombrogenous peatlands vegetated largely with *Sphagnum* mosses have long been colloquially known as fens and bogs, respectively. Geogenous peatlands vegetated with trees such as northern white-cedar (*Thuja occidentalis* L.) or tamarack (*Larix laricina*) are often termed treed fens (Zoltai 1988). Classification schemes that have tried to formalize this terminology are usually based on plant-community composition (Melin 1917, Malmer 1986) or water chemistry (Sjörs 1950), or a combination of both (Gorham and Janssens 1992). Fens are often further subdivided into poor fens and rich fens, with sometimes several additional divisions such as very poor fens and extremely rich fens (e.g., Du Rietz 1949, Sjörs 1950).

When numerous peatland categories are recognized, there is often overlap among them in environmental conditions, such as soil or water pH, and indicator species are typically the distinguishing factor for classification (Gorham 1950, Sjörs 1950, Glaser *et al.* 1981). Generally, these indicator species are not the dominants in the plant community, and they may represent the persistence of a few individuals from previous conditions (Gorham and Janssens 1992). Floristically, bogs are often defined by a lack "of exclusive fen plants" and "are without characteristic species of their own" (Malmer 1986). Nevertheless, it is the dominant plant species, which often occur across rather broad environmental gradients, that are responsible for the significant autogenic control that peatlands often demonstrate over their biogeochemistry, successional trajectory, and ontogeny.

Gorham and Janssens (1992) examined bryophyte assemblages and surface-water pH in 440 plots across North America (Figure 2). Based on a distinct bimodal distribution of pH that was coincident with Sphagnaceae at low pH and Amblystegiaceae at higher pH, they suggested a bipartite separation into fen and bog. An intermediate transitional community distinction seemed possible, but its boundaries may be only regionally applicable. Despite this bimodal distribution

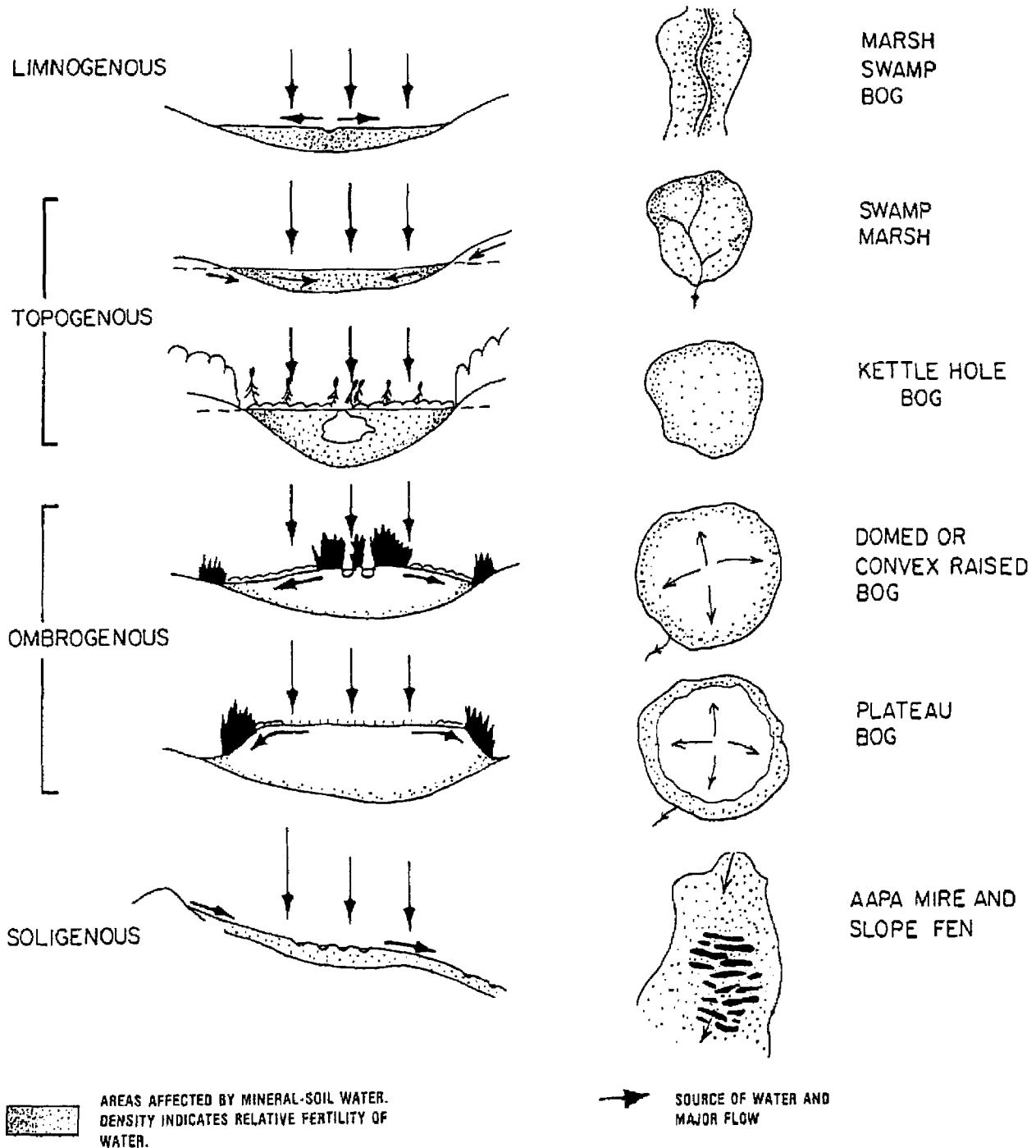


Figure 1. A classification scheme of peatlands based on their hydrology and topography (from Damman 1986, with permission). Note that the degree of contact of peat with geogenous waters is considered the same as, or at least coincident with, site fertility.

at the family level for mosses, individual species within each family had a wide range of optimum pH.

Several more formal classification schemes have been proposed based on phytosociological associations (Tansley 1939, McVean and Ratcliffe 1962, Gauthier and Grandtner 1975, Daniels 1978) or vegetation

structure (Radforth 1969, Botch and Masing 1983). The usefulness of elaborate phytosociological associations is usually limited to the region for which they were originally developed (Gore 1983). Additionally, gradient analyses in both upland (Whittaker 1967) and wetland communities (van der Valk 1981, Glaser

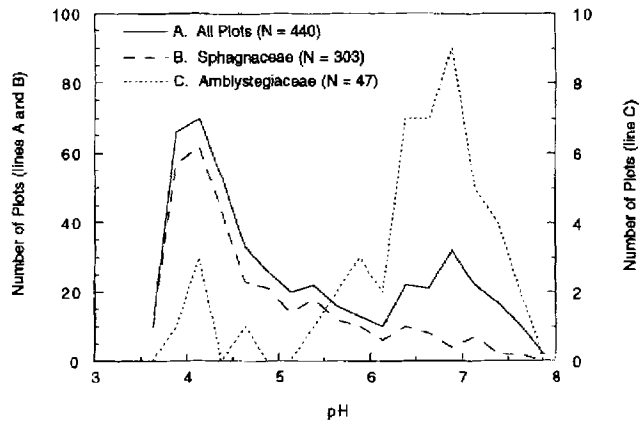


Figure 2. Bryophyte assemblages and surface-water pH in 440 plots across North America. Based on a distinct bimodal distribution of pH and moss communities (Sphagnaceae at low pH and Amblystegiaceae at higher pH) a bipartite separation into fen and bog is suggested (adapted from Gorham and Janssens 1992).

1987) have consistently shown that species assemblages have broadly overlapping population distributions along environmental gradients. Plant-community designations are to some degree a matter of human convenience, and fine distinctions and rigid boundaries among plant communities should be avoided.

Both Canada and the U.S.A. have developed national classification systems for wetlands. In the hierarchical classification scheme of the U.S.A., all peatlands fall into the Palustrine system, so the first useful designation is based on vegetation composition (Cowardin *et al.* 1979). Modifiers indicate hydroperiod and surface-water pH. This classification system is of marginal usefulness for peatlands. The hierarchical classification system of Canada is more explicitly designed for peatlands and defines wetlands based on overall genetic origin, morphology, and vegetation physiology (National Wetlands Working Group 1988).

Although classification schemes for peatlands have been previously reviewed and vigorously debated by other authors (e.g., Moore and Bellamy 1974, Gore 1983, Zoltai 1988), the result has not been narrowly defined terms and consensus among peatland ecologists. Through the remainder of this article, we review individual gradients thought to structure peatland ecosystems, and we suggest appropriate terminology for each.

The various ecological criteria, or lack of any formal criteria, for the usage of the terms bog and fen are especially problematic in the current literature. Note that bogs and fens have been defined with reference to hydrology, topography, water chemistry, and/or plant-community composition (Table 1). Furthermore, bog is also often used by the layman to describe any

wetland. Exactly how to define bog and fen can cause heated debate among otherwise mild-mannered wetland scientists. Given the current lack of definition for these terms, we recommend that they be considered of colloquial usage and inadequate for formal peatland classification or description. When this bipolar distinction between bog and fen is unnecessary, generic use of the terms peatlands or mires is recommended. If the terms bog and fen are used, we suggest it should be in the broadest sense with bogs referring to acidic, low alkalinity peatlands, typically dominated by *Sphagna*, conifers (particularly spruces and pines), and/or various ericaceous shrubs. Similarly, fens should broadly refer to somewhat less acidic, more alkaline peatlands dominated by graminoids, brown mosses, taller shrubs, and coniferous and/or deciduous trees. The particular species assemblage characteristic of bogs and fens is regionally determined, although there is a remarkable degree of convergence of species and genera in the two habitats across the circumboreal region of the globe. No assumptions concerning hydrology, topography, nutrient availability, or ontogeny are inherent in this definition. Additionally, presence or absence of nondominant indicator plant species are not a component of this definition. This definition, based loosely (i.e., with no exact limits) on water chemistry and plant-community composition, predominates in the peatland literature. In this review paper, we have used the terms bog and fen as done by the original authors, which, of necessity, requires use of the broad definition discussed above.

ALKALINITY, pH, AND NUTRIENTS AS CONTROLLING GRADIENTS

Terms such as rich and poor have often been used to differentiate fens, but they refer to pH, cation concentrations (especially Ca^{2+}), and alkalinity levels (e.g., Sjörs 1950). These parameters have been typically measured in surface or pore water, although soil data often give similar relative comparisons. In other ecosystems, rich and poor are commonly used as synonyms for fertile and infertile. In the peatland literature, this ill-chosen use of terms has caused great confusion, and alkalinity gradients (and correlated factors such as pH and Ca^{2+} concentrations) are often implicitly considered to be coincident with nutrient-availability gradients.

A close fidelity between pH/alkalinity/mineral cation concentrations and plant communities has been consistently demonstrated in northern peatlands (Sjörs 1950, Glaser 1987, Grootjans *et al.* 1988, Wassen *et al.* 1989, Vitt and Chee 1990, Gorham and Janssens 1992). An example from Swedish peatlands is shown in Figure 3. Nevertheless, significant variation in these

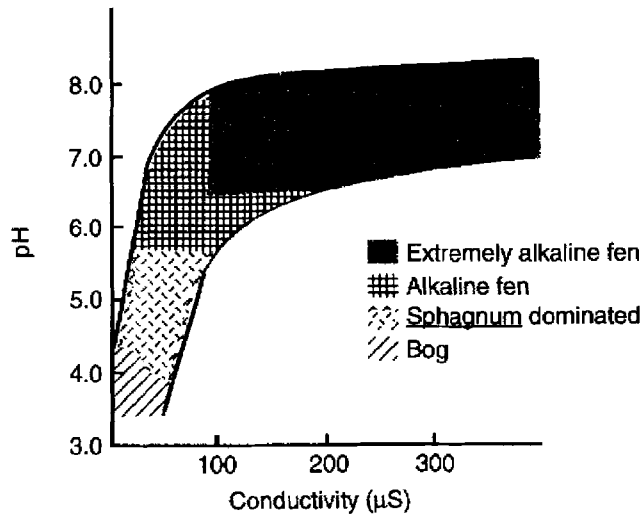


Figure 3. Relationship between pH and conductivity (at 20°C, adjusted for H⁻ ion activity) and peatland vegetation in Sweden (adapted from Malmer 1986, with permission).

relationships has been shown within the microtopography of a particular site, between the center and fringe areas of a peatland, and regionally within a particular peatland category (Gorham 1950, Gorham et al. 1985, Malmer 1986, 1988).

Correlational evidence such as shown in Figure 3 has been used to infer that basic cations, and in particular Ca²⁺, are limiting nutrients for peatland plants. Often, Ca²⁺ concentrations and pH in surface water are used to define the boundaries of different peatland types. Nevertheless, even in ombrotrophic bogs, Ca²⁺ and Mg²⁺ concentrations are high enough to satisfy the nutritional demands of plants (Malmer 1986). Concentrations of Ca²⁺, Mg²⁺, and various micronutrients in *Sphagna* are determined by passive ion-exchange phenomena; this is contrasted with N, P, and K, which are preferentially enriched in *Sphagna* and relocated during growth to the apical parts of the plant (Pakarinen and Tolonen 1977, Malmer 1986, 1988, 1993).

Moreover, Clymo and Hayward (1982, Figure 4) clearly demonstrated that Ca²⁺ is not a limiting nutrient for *Sphagna*. They examined the growth of eight *Sphagnum* species relative to Ca²⁺ concentrations and pH. Seven of the eight species showed a growth decline at high Ca²⁺ concentrations and high pH, with a particularly pronounced decline in hummock-forming ombrogenous species such as *S. capillifolium*. Thus, it seems that high Ca²⁺ concentrations at low pH are actually toxic to most species of *Sphagna*.

Few studies have examined the distinction between pH/alkalinity and nutrient availability in controlling growth of peatland plants. Kooijman and Bakker (1995) examined the successional relationships among four peatland mosses that varied in terms of pH/alka-

linity and nutrient availability in their natural habitats (Table 2). Species-specific responses occurred to manipulations of alkalinity, nutrient availability, and interspecific competition, and the results only could be partially explained by the chemistry of the natural habitats of the species. Although increasing alkalinity did affect growth of three of the four species (two positively, one negatively), the responses likely were due to the physiological tolerances of the species to alkalinity (and pH) gradients rather than basic cations being at a concentration that limited uptake for growth.

Boatman and Lark (1971) demonstrated that for *S. papillosum* protonema, PO₄³⁻ is a limiting nutrient, Ca²⁺ is a toxicant, and NO₃⁻, K⁺, and Mg²⁺ are neutral (Table 2). In North Carolina peatlands, plant community composition, biomass, vegetation stature, and nutrient-cycling efficiency reflect a P-availability gradient on acid peat soils, culminating in a nutrient-rich hardwood swamp-forest community on peat with a pH of about 4.0 (Walbridge 1991, Bridgham and Richardson 1993, Bridgham et al. 1995b).

Calcium may also be important in controlling P availability. Under alkaline conditions, Ca²⁺ will bind with P to form Ca-phosphates, lowering plant-available P. Very alkaline (or "rich") European peatlands have been found to be P-deficient, resulting in low productivity and high species diversity (Wheeler 1980, Wilson and Fitter 1984, Verhoeven and Arts 1987, Boyer and Wheeler 1989, Wassen et al. 1990a, b). High Fe concentrations may also be important in binding P and thus causing P-deficiency in alkaline peatlands (Wassen and Barendregt 1992).

Our discussion above illustrates that Ca²⁺ is important in various ways in determining the species distributions in peatlands, but it is likely not a limiting nutrient. Ca²⁺ is typically associated with the bicarbonate ion that in turn determines the pH of a peatland through its buffering capacity (Kemmers 1986). pH also has a dramatic effect on the availability of many nutrients, with circumneutral to alkaline conditions decreasing the availability of certain nutrients, such as P, K, Mg, Fe, Mn, B, Cu, and Zn (Lucas and Davis 1961). At circumneutral or higher pH, high Ca²⁺ concentrations may also cause P deficiency through formation of Ca-P complexes. High Ca²⁺ concentrations may also cause ion imbalances in plants adapted to low alkaline environments (Kinzel 1983).

In an extensive review of fertilization studies in peatlands, including studies of mosses, graminoids, shrubs, and trees, we generally found N, P, both N and P, or occasionally K to be the limiting nutrient (Table 2). In a few cases, no significant response was found to any nutrient addition (or inhibition for mosses, see below), indicating either that the appropriate nutrient or nutrient concentrations were not added, the plant

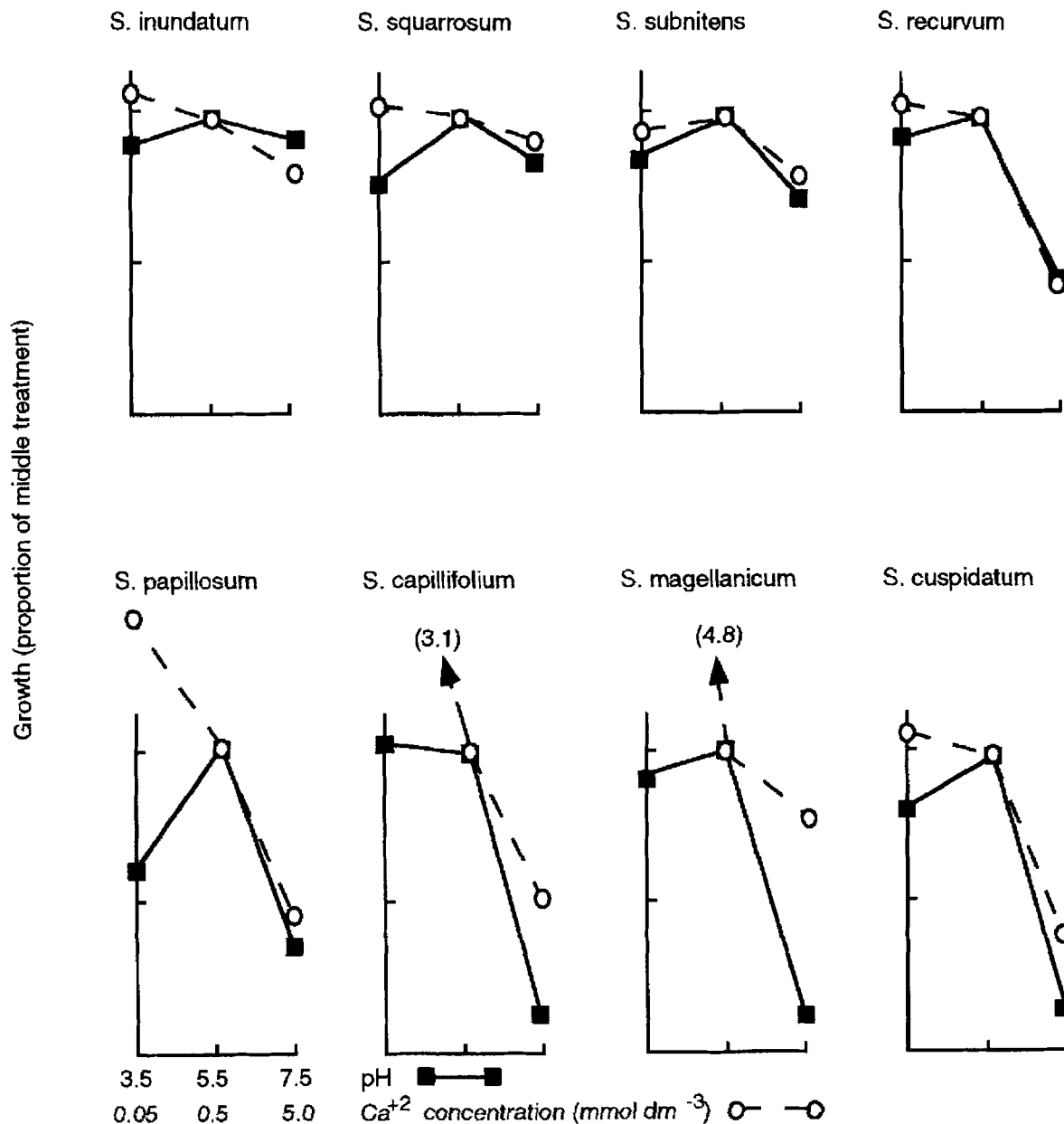


Figure 4. Relative growth rate of eight *Sphagnum* spp. in relation to pH (closed squares) and Ca^{2+} concentration (open circles) in water. Results are scaled to the middle treatment (i.e., pH 5.5 and $0.5\ mmol\ Ca^{2+}\ dm^{-3} = 1.0$). From Clymo and Hayward 1982, with permission. Species authorities not given in Table 2 are *S. inundatum* (= *S. subsecundum* var. *inundatum* (Russ.) C. Jens.), *S. squarrosum* Crome, *S. subnitens* Russ. and Warnst. ex Warnst., and *S. capillifolium* (Ehrhart) Hedwig.

was preadapted to low-nutrient conditions and was physiologically incapable of responding (Chapin 1980), or some other factor was limiting. Interestingly, some species showed varying response to nutrient additions across studies (e.g., *Eriophorum vaginatum*), or in different sites within the same study (e.g. Aerts *et al.* 1992).

Calcium additions were found to stimulate growth in only two studies. In the study by Kooijman and Bakker (1995), the growth of two moss species, *Scor-*

pidium scorpioides and *Calliergonella cuspidata*, were stimulated by increased alkalinity and pH, whereas *Sphagnum squarrosum* had no significant response and *Sphagnum subnitens* was strongly inhibited. As discussed above, we interpret these responses to reflect the physiological tolerances of the species to alkalinity and pH. In a study by MacCarthy and Davey (1976), *Pinus taeda* was planted in pine plantations on converted pocosin soils, although this species is not naturally dominant in pocosins. Despite the positive lime

Table 2. Nutrients limiting plant growth in studies from northern wetlands in which fertilization experiments have been undertaken. Nomenclature for plant species from Radford et al. 1968 and Halliday and Beadle 1983, except mosses which are from Crum et al. 1973.

Species or Plant Community	Limiting Nutrient	Comments ^a	Reference
Bog	P	Field. Raised bog in Sweden. Combinations of N, P, K, Ca, Mg, S, Fe, Mn, Cu, B, Zn, Mo. Growth increase, increased dominance of <i>Eriophorum vaginatum</i> L.	Tamm 1954
Bog	P	Field. Blanket bog in Great Britain. P.	McVean 1959
Bogs	N in low-N site, P in high-N site.	Field. Sites in Sweden with high and low atmospheric N deposition. N, P.	Aerts et al. 1992
Fens with "short" and "tall" vegetation	P	Field. Calcareous fens in Great Britain. Comparisons of growth and biomass of plants with soil and water chemistry, and laboratory experiments, including P additions. More calcareous sites showed greater P limitation.	Boyer and Wheeler 1989
"Mesotrophic" fens	N or P	Field. Netherlands. N, P, K, N or P limitation depended on successional status and mowing. Suggest long-term shift over succession from N to P limitation.	Verhoeven and Schmitz 1991
Floating fen	N	Field. Netherlands. N, P, K. Increased importance of grasses with fertilization in fen and wet grassland.	Vermeer 1986
Wet grassland	N		
Hayfields on peat with low water table	K		
<i>Sphagnum peylosum</i> Lindb.	P	Protonema in lab. N, P, K, Mg, Ca.	Boatman and Lark 1971
<i>Sphagnum cuspidatum</i> Ehrh. ex Hoffm.	P	≈1.0 mM PO ₄ ³⁻ optimum, >0.1 mM Ca ²⁺ inhibitory.	
<i>Sphagnum mugellanicum</i> Brid.	P		
<i>Sphagnum nemoreum</i> (= <i>S. capillaceum</i> (Weiss) Schrank)	N, P	Field. Alaskan <i>Picea mariana</i> (Miller) BSP forest. N, P, K, Mg, Ca. 1.0 mM PO ₄ ³⁻ , 15.75 mM NO ₃ ⁻ , 1.5 mM NH ₄ ⁺ optimum.	Skre and Oechel 1979
<i>Sphagnum magellanicum</i>	NO ₃ ⁻ limited; inhibited by NH ₄ ⁺ .	Lab. Samples from Germany. N. NO ₃ ⁻ favorable to 0.322 mM (highest conc. tested), >0.225 mM NH ₄ ⁺ inhibitory.	Rudolph and Voigt 1986
<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	N, P	Northern Minnesota.	Gardetto 1987
<i>Sphagnum cuspidatum</i>	P	Lab. Plants from peatland in Great Britain. N, P, K, CO ₂ . 0.13 mM PO ₄ ³⁻ , 0.4 mM N, 0.2 K ⁺ optimum.	Baker and Boatman 1990

Table 2. Continued.

Species or Plant Community	Limiting Nutrient	Comments ^a	Reference
<i>Sphagnum papillosum</i>	N and P inhibitory, greatest growth in distilled water.	Lab. Plants from peatland in Great Britain. N, P: 0.006 mM PO ₄ ³⁻ , 0.030 mM NO ₃ ⁻ , 0.030 mM NH ₄ ⁺ inhibitory relative to distilled water (lowest conc. tested, similar to rainfall. High mortality in all treatments).	Clymo 1987
<i>Sphagnum cuspidatum</i>	N inhibitory in areas with high atmospheric N deposition.	Field and lab. Plants from areas in Great Britain with relatively high and low atmospheric N deposition. High N deposition caused accumulation of tissue N conc. and apparent growth reduction. 0.01 mM NO ₃ ⁻ , 0.01 mM NH ₄ ⁺ caused growth inhibition in lab.	Press et al. 1986
<i>Sphagnum fuscum</i>	N and/or S in oligotrophic zone but no response in minerotrophic zone.	Field. "Oligotrophic" middle zone and "minerotrophic" edge zone of a "poor" fen in Ontario. Acidification with SO ₄ ²⁻ and NO ₃ ⁻ . Response diminished over 4 yr in all spp.	Rochefort et al. 1990
<i>Sphagnum magellanicum</i> <i>Sphagnum angustifolium</i> (= <i>S. recurvum</i> var. <i>tenue</i> Klinggr.)	N and/or S in both zones.		
<i>Sphagnum subnitens</i>	Negative growth response to increased alkalinity. No nutrient effect.	Lab. <i>S. subnitens</i> from mineral-poor, nutrient-poor peatland, <i>S. squarrosum</i> from mineral-poor, nutrient-rich peatland, <i>S. scorpioides</i> from mineral-rich, nutrient-poor peatland, and <i>C. cuspidata</i> from mineral-rich, nutrient-rich peatland. N × P; artificial rainwater, artificial groundwater.	Kooijman and Bakker 1995
<i>Sphagnum squarrosum</i>	No alkalinity effect. Positive N × P effect.		
<i>Scorpidium scorpioides</i> (Hedw.) Limpr.	Positive alkalinity effect, positive N × P effect in groundwater.		
<i>Calliergonella cuspidata</i> (Hedw.) Loeske	Positive alkalinity effect, no nutrient effect.		
<i>Scorpidium scorpioides</i> <i>Calliergonella cuspidata</i>	P No nutrient effect.	Lab. Samples from alkaline fens in the Netherlands. N, P, N × P; light, litter.	Kooijman and Bakker 1993
<i>Hylocomium splendens</i> (Hedw. B.S.G.)	Negative growth response, positive photosynthesis response in young tissue.	Field. Alaskan <i>Picea mariana</i> forest. N, P, K, Mg, Ca. For growth, 0.5 mM PO ₄ ³⁻ , 5.25 mM NO ₃ ⁻ , 0.5 mM NH ₄ ⁺ inhibitory relative to distilled water (lowest conc. tested).	Skre and Oechel 1979
<i>Pleurozium schreberi</i> (Brid.) Mitt.	Negative growth response.		
<i>Scorpidium scorpioides</i> (Hedw.) Limpr.	P	Lab. Samples from alkaline fens in the Netherlands. N, P, N × P; light, litter.	Kooijman and Bakker 1993

Table 2. Continued.

Species or Plant Community	Limiting Nutrient	Comments ^a	Reference
<i>Molinia caerulea</i> (L.) Moench.	No effect.	Planted in field plots. Blanket bog in Great Britain. P, Ca, P × Ca.	Gore 1961a
<i>Eriophorum vaginatum</i>	No effect.	Planted in field plots. Blanket and raised bogs in Great Britain. N, P, N × P.	Gore 1961b
<i>Molinia caerulea</i>	N in blanket bog, P and N × P in raised bog	Field. Upland and bog sites in Great Britain. N, P, K, Mg, Ca.	Goodman and Perkins 1968
<i>Dactylis glomerata</i> L.	K > P > N	Field. Alaskan tundra. Various combinations of N, P, K, lime, sugar.	Shaver and Chapin 1980
<i>Eriophorum vaginatum</i>	N, N × P	Lab. P. Spp. showed numerous adaptations for efficient use of P.	Veerkamp et al. 1980
<i>Eriophorum vaginatum</i>	no effect	Field. Beaver meadows on mineral soils in northern Minnesota. Various combinations of N × P.	Erickson 1994
<i>Carex bigelowii</i> Torrey ex Schweinitz	P	Field. Minnesota poor fen. Various combinations of N, P, micronutrients, insects.	Chapin and Pastor 1995
<i>Carex rostrata</i> (Stokes)	P	Field. Alaskan tundra. Various combinations of N, P, K, lime, sugar.	Shaver and Chapin 1980
<i>Carex limosa</i> L.	P		
<i>Carex lasiocarpa</i> Ehrh.	P		
<i>Carex diandra</i> Schrank	P		
<i>Carex acutiformis</i> Ehrh.	P		
<i>Carex</i> spp.	N > P		
<i>Calamagrostis canadensis</i> (Michaux.) Beauv.	N > P		
<i>Scirpus cyperinus</i> (L.) Kunth	N > P		
<i>Sarracenia purpurea</i> L.	No effect on growth, N and P limitation suggested by Timmer and Stone (1978) plots.		
<i>Ledum palustre</i> L.	N, N × P		
<i>Vaccinium vitis-idaea</i> L.	N, N × P		
<i>Vaccinium uliginosum</i> L.	N, P, N × P		
<i>Betula nana</i> L.	N		
<i>Zenobia puberulenta</i> (Bartram) Pollard	N, P, N × P		
<i>Lyonia lucida</i> (Lam.) K. Koch	N, P (weaker response)		
<i>Chamaedaphne calyculata</i> (L.) Moench.	Bog N, P, or K limited; "poor" fen not limited by N × P × K.	Field. Bog and "poor" fen in Maine. N × P × K.	Bartsch and Schwintzer 1994
<i>Pinus serotina</i> Michaux	P, N	Lab. North Carolina pocosins. N, P, K, S, Ca, Mg.	Woodwell 1958
<i>Pinus serotina</i>	P in unburned peat; P, N, N × P in burned peat.	Lab. Samples from North Carolina pocosins. N, P, S, K, Mg, Ca, Fe, micronutrients.	Wilbur and Christensen 1983
<i>Picea mariana</i>	N, P, N × P	Field. Treed bog in Minnesota patented peatland. N, P, N × P.	Watt 1966

Table 2. Continued.

Species or Plant Community	Limiting Nutrient	Comments ^a	Reference
<i>Pinus taeda</i> L.	P, Ca, P × Ca	Field. Pine plantation plots previously burned and disked in North Carolina pocosins. Lime, lime-P mixture.	MacCarthy and Davey 1976
<i>Picea mariana</i>	N	Field. "Minerotrophic" peatland in Alberta. P × K and N × P × K in drained and undrained sites.	Mugasha <i>et al.</i> 1993
<i>Larix laricina</i> (Duroi) C. Koch	N, P		

^a Field or laboratory study, location and wetland type, fertilization treatments, other comments. For mosses, optimum or inhibitory concentrations of nutrients are given when available.

effect on growth, high yields occurred at low soil pH, with the highest yield occurring at pH 4.1.

In several European countries, eutrophication of peatlands, and the consequent loss of species diversity and habitat for rare plants, has become an important problem. Control of the water source, giving high alkalinity and low nutrient availability, has become an important component of the management regime for maintaining species-rich, mesotrophic fens in the Netherlands (Grootjans *et al.* 1988, Wassen *et al.* 1989, 1990a). Mowing is also used to combat eutrophication and lower nutrient availability in these highly disturbed fens (Verhoeven and Schmitz 1991). Thus, this regional example shows the importance of N and P availability in controlling plant-community structure and diversity. It also shows that nutrient-availability and alkalinity gradients are not necessarily coincident and that there are complicated interactions with regional and local hydrology.

Additionally, the importance of nutrients for peatland plants is attested to by their many adaptations to maximize the efficiency of N and P for production by such mechanisms as evergreenness, sclerophylly and defensive compounds to reduce grazing losses, nutrient translocation before leaf abscission, high nutrient-use efficiency, and high root:shoot ratios (Veerkamp *et al.* 1980, Christensen *et al.* 1981, Shaver and Melillo 1984, Walbridge 1991, Bridgham *et al.* 1995b). For example, the peculiarities of N nutrition in the Ericaceae may be responsible for them being the dominant shrubs in many ombrogenous peatlands. NO_3^- concentrations are very low in most acidic peatlands because nitrifying bacteria require a relatively high pH and waterlogged conditions inhibit nitrification and promote denitrification (Waughman 1980, Runge 1983, Gorham *et al.* 1985, Bridgham and Richardson 1993). NO_3^- from precipitation is also very rapidly taken up in surface peat (Urban *et al.* 1988), except under N saturating conditions of high atmospheric N deposition (Press *et al.* 1986, Lee *et al.* 1987). Many ericaceous species are adapted to low NO_3^- conditions, as they have minimal capacity for NO_3^- reduction but can effectively utilize NH_4^+ in a low pH environment because their roots are resistant to acidity (Kinzel 1983, Runge 1983). NH_4^+ utilization by other plants is typically strongly inhibited by decreasing pH due to the excretion of H^+ (to maintain an internal charge balance), which results in a highly acidic rhizosphere and root damage.

Ericaceous shrubs also have relatively low optimal N concentrations, and inhibition can occur at just slightly higher levels (Ingestad 1973). These same experiments found a large luxury consumption (i.e., uptake under nonlimiting conditions) of Ca^{2+} , and high concentrations of K^+ and Ca^{2+} caused growth inhibi-

tion. Thus, ericaceous shrubs typical of ombrogenous peatlands are adapted for NH_4^+ uptake in an acidic environment with low NO_3^- availability, have low N growth requirements, and efficiently scavenge basic cations but are inhibited by high soil cation concentrations.

Concentrations of dissolved organic compounds (DOC) can be very high in peatland waters, and nutrients associated with this DOC have traditionally been thought to be unavailable for plant uptake until microbial mineralization to inorganic forms. Nevertheless, the sedge *Eriophorum vaginatum* was recently found to preferentially take up amino acids over inorganic N (Chapin et al. 1993). Ericaceous peatland shrubs have also recently been found to take up organic N (L. Johnson, Kansas State University, Manhattan, KS, personal communication). Thus, peatland plants may have a much tighter N cycle than previously thought, at least partially bypassing the microbial mineralization loop.

The *Sphagnum* results in Table 2 deserve special mention because of the highly variable results and the importance of *Sphagna* in peatland biogeochemistry and succession. Several laboratory studies have found that N and/or P concentrations in peatlands are limiting for *Sphagnum* protonema development, number of innovations (branches that eventually form new plants in vegetative production), interfascicle length, photosynthesis rate, and dry mass production (Boatman and Lark 1971, Skre and Oechel 1979, Baker and Boatman 1990, Kooijman and Bakker 1995). In fact, Boatman and Lark (1971) concluded that because of low available-P levels in peatlands, *Sphagnum* protonema are unlikely to develop, leaving population expansion largely to vegetative production. Additionally, many *Sphagnum* species form spores only rarely in the natural environment.

Conversely, several other laboratory studies have found very low optimal N and P levels for growth of *Sphagna*, with inhibition at higher concentrations (Press et al. 1986, Rudolph and Voigt 1986, Clymo 1987, Lee et al. 1987). These authors concluded that *Sphagna* are adapted to the low nutrient conditions that are presumed to occur in ombrogenous peatlands (see Nutrient Mineralization below). Interestingly, the various studies cited in Table 2 have found either nutrient deficiency or inhibition by nutrient excess at similar aqueous concentrations for the same *Sphagnum* species. Optimum aqueous nutrient concentrations across studies ranged from <0.006 to 1 mM for PO_4^{3-} , <0.01 to 15.75 mM for NO_3^- , and <0.01 to 1.5 mM for NH_4^+ . In several cases, greatest growth occurred in distilled water, and some of the inhibitory concentrations of nutrients that have been reported are similar to those found in rainfall. However, the higher opti-

mum N concentrations are not dissimilar to those found for two *Vaccinium* species (4–5 mM, Ingestad 1973), which are important ericaceous shrub species in many peatlands.

Rarely have these studies had a salt control (most commercial nutrient solutions come as salts), which may help explain some of the discrepancy in results between studies given the inhibitory effect of low cation concentrations on *Sphagna* (cf. Skre and Oechel 1979). Additionally, the previous nutrient history of the *Sphagnum* specimens may be important. For example, the response of *S. cuspidatum* to N additions was tested from two sites in Great Britain that received relatively high or low atmospheric N deposition (Press et al. 1986). Enhanced N deposition caused accumulation of tissue N to supraoptimal concentrations and apparent growth reduction, and very low additional supplements of NO_3^- and NH_4^+ in the laboratory caused growth inhibition.

As with laboratory studies, field studies give contradictory results concerning the role of N and P as limiting nutrients for *Sphagna*. In Sweden, *Sphagnum*-dominated sites receiving low atmospheric N deposition are N-limited, while those receiving high N deposition are P-limited (Aerts et al. 1992). Other *Sphagnum*-dominated peatlands in Sweden (Tamm 1954) and in Great Britain (McVean 1959) have been found to be P-limited. Several *Sphagnum* species were originally found to be N- and/or S-limited in the oligotrophic zone of a "poor fen" in Canada, but the response diminished over 4 years (Rochefort et al. 1990).

Other field studies have found severe inhibition of *Sphagna* by nutrient additions. The loss of most *Sphagnum* spp. from the peatlands of the Pennine range in Great Britain has been attributed to high N deposition (Lee et al. 1987). We are examining the interactive effects of fertilization (2 and 6 g N m^{-2} , 0.67 and 2 g P m^{-2}) and alkalinity in a bog in northern Minnesota (unpublished data, C. Chapin, S. Bridgman, J. Pastor). After one growing season, the high-N, high-P treatment caused severe inhibition of *Sphagna* growth, whereas the low-N, high-P treatment stimulated growth relative to the control. Liming caused a small, but statistically significant increase in growth. A multi-year fertilization with N and P of an ombrogenous peatland in Maine has caused death and replacement of *Sphagna* by other species (L. Johnson, Kansas State University, Manhattan, KS, personal communication).

The response of any plant to a nutrient-availability gradient ranges from nutrient deficiency at suboptimal concentrations, to an optimal concentration, to a supraoptimal concentration that eventually becomes inhibitory (Ingestad 1973, 1987). Among other factors, this response curve will vary by the previous nutri-

tional history of the plant, the concentrations of other nutrients, pH, and the physiological ability of the plant to respond (Chapin 1980, Runge 1983, Tilman 1988). It is evident from our discussion that much research remains to be done in comparison of intra- and inter-species responses of plants to multiple limiting gradients in peatlands. It is our belief that a manipulative experimental approach is most appropriate to determine the theoretical foundations for the observed distributions of species in peatland plant communities.

Numerous fertilization experiments (Table 2) suggest that N, P, and K are the only nutrients that directly limit plant growth in peatlands, although the relative level of nutrient deficiency of various peatland plant species remains controversial. Given these findings, we suggest that the suffix “-trophic” in peatland terminology should be used only when referring to nutrients that limit plant growth directly at natural availabilities. We suggest oligotrophic for nutrient-poor conditions and eutrophic for nutrient-rich conditions, given the clear understanding of their meaning in other branches of ecology. Additionally, given the inexactness of terms such as rich and poor, we suggest terms such as alkaline, circumneutral, moderately acidic, and very acidic (or alternatively strong, intermediate, and weak) be used to describe ranges of pH. Whichever set of terms is used, they should be quantitatively defined in each study. H^+ ion activity, alkalinity, cation concentrations, and base saturation are important factors determining the physiological tolerance of peatland plant species, and thus in determining plant-community composition and productivity, but they do not determine the trophic status of a peatland except to the extent that they control nutrient mineralization rates and availability.

Nutrient Mineralization

The distinction between pH/alkalinity and nutrient availability becomes somewhat academic if these two environmental gradients are coincident across plant-community gradients. To address this question, we have examined correlations between environmental variables, plant-community type, and nutrient mineralization among a diverse assemblage of northern Minnesota wetlands (Figure 5). Sites were grouped into bogs (soil pH < 4, *Sphagnum*-dominated peatlands, N = 5), acidic fens (soil pH 4.0–4.1, *Sphagnum*-sedge-dominated peatlands, N = 2), intermediate fens (soil pH 4.9–5.6, sedge-dominated peatlands, N = 2), beaver meadows (soil pH 5.8–6.2, grass and sedge-dominated, histic epipedon, N = 2), and swamp forests (soil pH 4.3–6.6, tree-dominated peatlands, N = 6). In this study, we took five 0- to 25-cm depth cores from each site (except for the surface organic layer of vari-

able depth in the beaver meadow). We incubated subsamples from each core at 30°C (an optimal temperature for microbial activity) in the laboratory, leached the samples with 0.01 M $CaCl_2$ at regular intervals, and subsequently determined nutrient concentrations in the leachate. In this manner, nutrient mineralization rates were determined over 59 weeks, and cumulative mineralization during this period is presented in Figure 5. Methods are described in detail in Updegraff *et al.* (1994, 1995).

When N mineralization was expressed as a turnover rate (mg N mineralized /g total soil N, Figure 5A), the bogs and acidic fens had the highest mineralization rates under aerobic conditions. The beaver meadow had the highest anaerobic N turnover rates, with the bogs, acidic fens, and swamp forests relatively similar. The lowest anaerobic N turnover rates were in the intermediate fens. Nutrient mineralization per unit soil volume is a more appropriate measure of nutrient availability for plants. There were large differences in bulk density among wetland types, resulting in dramatically different relative N mineralization rates (Figure 5B). Nitrogen mineralization per unit soil volume, under both aerobic and anaerobic conditions, was highest in the beaver meadows, followed by swamp forest, intermediate fens, and acidic fens and bogs. Thus, N mineralization per unit soil volume supports coincident nutrient-availability and pH/alkalinity gradients, although the small amount of N in the peats of bogs and acidic fens turns over relatively rapidly.

Phosphorus turnover rates were highest in the bog and acidic fen under both aerobic and anaerobic conditions (Figure 5C). Under aerobic conditions, P mineralization per unit soil volume remained highest in the bog sites, although the acidic fen sites had intermediate values (Figure 5D). Under anaerobic conditions, P mineralization per unit soil volume was greatest in bogs, swamp forests, and beaver meadows, with significantly lower rates in the acidic and intermediate fens. Thus, P mineralization, whether expressed as a turnover rate or per unit soil volume, does not appear to be coincident with pH/alkalinity gradients. Furthermore, our results indicate that N and P availability may act in very different ways across pH/alkalinity and community gradients in peatlands.

The relatively high N and P turnover rates in surface bog peat are in direct opposition in many ways to the long held paradigm that bogs are highly oligotrophic and that *Sphagnum*-derived peat is highly recalcitrant (Moore and Bellamy 1974, Malmer 1993). Nutrient mineralization and availability have also been found to be higher in bogs than in fens in European peatlands, although total nutrient concentrations in plants and peat are lower in bogs (Waughman 1980, Verhoeven *et al.* 1990). Nutrient outflow was greater from

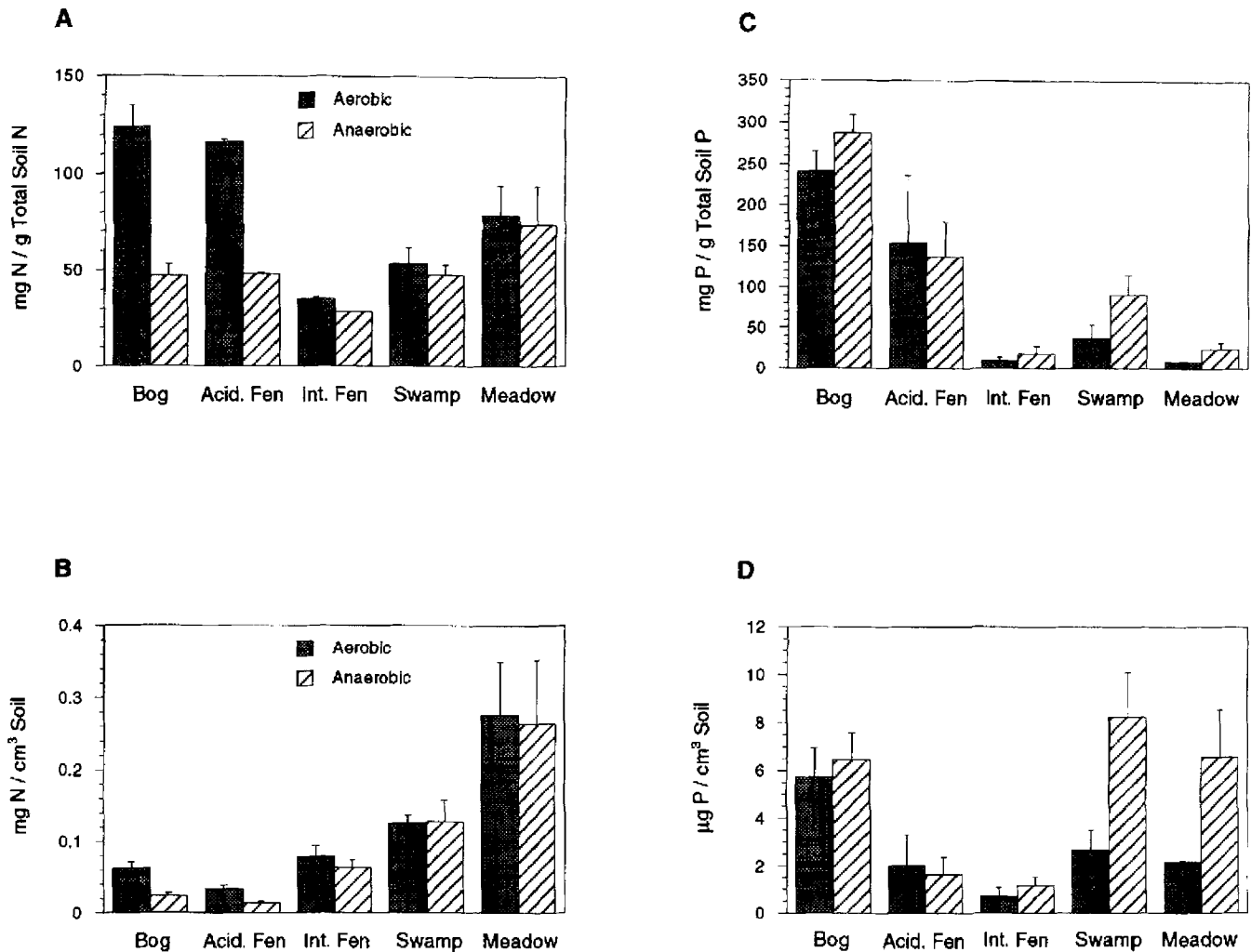


Figure 5. Cumulative mineralization over 59 week incubations in the laboratory at 30°C for (A) mg N mineralized/g total soil N, (B) mg N mineralized/cm³ soil, (C) mg P mineralized/g total soil P, and (D) µg P mineralized/cm³ soil. Organic soils were collected from 5 bogs, 2 acidic fens (Acid. Fen), 2 "intermediate" fens (Int. Fen), 6 minerogenous swamp forests (Swamp), and 2 beaver meadows (Meadow). Bars are 1 standard error.

a northern Minnesota bog with a perched water table than from a nearby, similarly sized ground-water fen, whether expressed on a simple concentration basis or as a flow-weighted concentration (Boelter and Verry 1977). Given the above evidence, we suggest that although bogs have low total nutrient concentrations in soil organic matter, the soil nutrients that are there are mineralized quickly, especially under aerobic conditions.

Litter bag studies show very low decay rates for *Sphagnum* (Clymo and Hayward 1982), and cellulose decay rates have been found to be lower in bogs than in fens (Verhoeven et al. 1990, cf. Bridgham et al. 1991). These results are in contrast to the relatively high nutrient turnover rates (Figure 5, Verhoeven et al. 1990) and high C turnover as CO₂ (Bridgham et al. 1995a) of surface bog peat. Verhoeven et al. (1990)

suggested that these discrepancies can be explained by the unique chemical properties of *Sphagnum* litter. They suggested that *Sphagnum* have a nutrient-rich protoplasm that breaks down rapidly, yielding high nutrient mineralization and C-respiration rates, whereas the majority of the plant is composed of recalcitrant cell wall material such as hyaline cells (cf. Clymo and Hayward 1982).

An alternative explanation is that litter bag studies typically have been done with freshly abscised litter, whereas the mineralization studies of Figure 5, Verhoeven et al. (1990), and Bridgham et al. (1995a) were done with surface peat. As the litter of fen vegetation decays more quickly than *Sphagnum* litter, the surface fen peat is more decomposed and humified. The peat of minerogenous swamp forests is particularly highly decomposed. In contrast, surface bog peat is usually

only slightly decayed and humified, and in even deep peat *Sphagna* remains can often be identified to species. Thus, because of the recalcitrance of *Sphagnum* litter, surface bog peat is relatively undecomposed and may give higher C and nutrient mineralization rates than the highly decomposed surface peats of fens and minerotrophic swamp forests.

Nutrient cycling in *Sphagnum*-dominated peatlands may be unique in another aspect if, as Malmer (1993) suggested, *Sphagnum* rely mainly on atmospheric deposition for their supply of nutrients and, lacking vascular tissue, are relatively divorced from mineralization of the organic matter under the active surface moss layer. Vascular plants would continue to be dependent primarily on nutrient mineralization in the underlying peat for their nutrient-uptake requirements. This may explain the observation of Vitt and Chee (1990) that, in Alberta fens, variation in vascular plant occurrence was associated with nutrient levels, whereas variation in bryophyte occurrence was better correlated with acidity and alkalinity measures.

To our knowledge, this important hypothesized dichotomy between bryophyte and vascular plant nutrient uptake mechanisms remains to be rigorously tested. However, a rapid and quantitatively important transfer of C and P compounds has been demonstrated in *Sphagna* stems over at least 6 to 7 cm (Rydin and Clymo 1989). Thus, *Sphagna* may not be as divorced from mineralizable nutrients in the organic matter below the active moss layer as previously thought.

Microbes and plants directly compete for nutrients, with microbial uptake of P (Richardson and Marshall 1986, Walbridge 1991) much more rapid than plant uptake in low-nutrient peatlands. Thus, rapid nutrient turnover may not result in greater availability of nutrients for plants. However, *Sphagna* rapidly take up NO_3^- from precipitation in the surface peat layers, out-competing denitrifying bacteria in the underlying anaerobic peat (Urban *et al.* 1988). Other soil conditions, such as low pH, may also limit microbial mineralization and immobilization of nutrients (Wilson and Fitter 1984).

We find it perplexing that given the central role nutrients (especially N and P) have been found to play in ecosystem structure and function in both terrestrial and aquatic ecosystems, including plant-community composition and succession, so little research effort has been expended on nutrient relationships in peatlands. The historical biogeochemical peatland literature is focused on cation/anion budgets, and despite its importance as a limiting nutrient, PO_4^{3-} was rarely measured because of its minor importance in anion budgets. The more recent literature has shown modest improvement in our understanding of nutrient cycling in peatlands (e.g., Richardson and Marshall 1986, Ur-

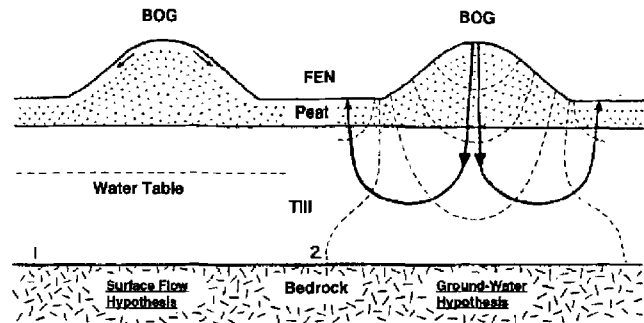


Figure 6. Two opposing hypotheses of peatland hydrology. The traditional surface-flow hypothesis (left) assumes that an ombrogenous bog has a perched water table, isolating it from groundwater influences, and that its outward growth is blocked by alkaline water draining from adjacent uplands (Ingram 1982). The ground-water hypothesis (right) assumes that a bog mound creates a sufficient hydraulic head to drive vertical flow cells, with water flowing from the bog crest down into mineral soil, accumulating cations and alkalinity, and surfacing in adjacent fens (from Glaser 1987).

ban *et al.* 1988, Verhoeven *et al.* 1990, Walbridge 1991, Koch and Reddy 1992, Bridgman and Richardson 1993, Updegraff *et al.* 1995).

HYDROLOGY AS A CONTROLLING GRADIENT

The central role of hydrology in controlling the structure and function of wetland ecosystems is widely accepted (e.g., Mitsch and Gosselink 1993). Additionally, through the build-up of soil organic matter, peatlands have significant autogenic control over their ontogeny and hydrology (Figure 1). Furthermore, it is deductively obvious, and there are ample field data to demonstrate (e.g., Kemmers 1986, Wilcox *et al.* 1986, Siegel and Glaser 1987, Siegel 1988a and b, Verry, *in press*), that the source of water for a peatland will have a significant control over its soil and water chemistry. The generally accepted paradigm is that with increasing input of minerogenous waters, a peatland will have higher pH, cation concentrations, nutrient availability, and hence, productivity (Moore and Bellamy 1974). We have discussed above the limitations of considering cation/alkalinity and nutrient gradients to be coincident. Here, we examine other aspects of the traditional hydrologic paradigm in peatlands.

The traditional surface-flow hypothesis assumes that an ombrogenous bog has a perched water table, isolating it from ground-water influences, and that its outward growth is blocked by alkaline water draining from adjacent uplands (Figure 6, Ingram 1982). This traditional view has been recently challenged (Siegel 1983, Siegel and Glaser 1987). Siegel and his colleagues assume that a bog mound creates a sufficient hydraulic head to drive flow cells, with water flowing

from the bog crest down into mineral soil, accumulating cations and alkalinity, and surfacing in adjacent fens (Figure 6). Thus, their work suggests that "ombrogenous" bogs are intimately linked to regional ground-water flow, at least as recharge zones. Their field data also demonstrate a much more dynamic, complicated picture of the hydrology of bogs and fens, with each capable of switching from being discharge to recharge zones depending on changes in intermediate and regional ground-water systems (Siegel and Glaser 1987). Although presented here as a dichotomy, both of these hydrologic models are probably correct under appropriate circumstances (that are yet to be defined).

While it is certainly true that the degree of water contact with mineral soil will have a major influence on its chemistry, simple inferences drawn from water chemistry (e.g., pH, alkalinity, Ca^{2+} concentrations, base saturation) about the degree of mineral soil influence in a peatland may be incorrect. For example, there are large regional differences in the surface water chemistry of peatlands in North America (Gorham et al. 1985) and the British Isles (Proctor 1992) due to differences in precipitation chemistry. Additionally, internal biotic and abiotic processes can have great effects on the water chemistry of peatlands, including its acidity (Urban et al. 1987, Damman 1990). The effect on water chemistry in minerogenous peatlands of a given amount of ground water will also vary according to the soil chemistry of the underlying mineral-soil strata (Kemmers 1986, Bridgham and Richardson 1993, Verry, in press). We give several examples below of how these effects can cause unexpected water chemistry of peatlands, irrespective of their hydrology.

Damman (1988) examined raised bogs in Japan that had significant atmospheric inputs from frequent volcanic activity. Although topographically and hydrologically these Japanese raised bogs are ombrogenous, the vegetation and water chemistry are representative of other northern peatlands with significant ground-water inputs. Damman (1988) ascribed the fen-like characteristics of these Japanese ombrogenous peatlands to "fertilization" of basic cations from atmospheric inputs of volcanic tephra. The limitations of the current terminology are underscored by the fact that Damman felt forced to use the term, "tephratrophic," to describe these Japanese bogs.

Peatlands growing on naturally acid seeps in the Black Hills, South Dakota have very low pH and plants characteristic of ombrogenous bogs (Chapel and Janssens, unpublished data). Despite their water chemistry and vegetation, these peatlands are clearly minerogenous. Similarly, if the underlying mineral substratum is well-leached sand or low Ca^{2+} bedrock, such as occur in areas of Wisconsin and Michigan (Verry,

in press) and on the Coastal Plain of North Carolina (Bridgham and Richardson 1993), the soil water chemistry of minerogenous peatlands can be quite acid, have low extractable basic cations, and low base saturation.

Therefore, hydrology and pH/alkalinity gradients may not necessarily be coincident. Rarely are intensive hydrologic measurements made in ecological peatland studies, and the degree of ground-water influence is typically deduced from the vegetation cover and soil water chemistry. To the extent that the dynamic hydrology found by Siegel and his colleagues in their study sites can be extrapolated to other peatlands, such simple correlations may prove to be inadequate. Also, regional differences in precipitation chemistry and the differences in the underlying mineral substrata may have profound effects on the water chemistry and vegetation composition of peatlands.

Thus, we caution against inferring hydrology of peatlands from plant-community composition, alkalinity, pH, or Ca^{2+} concentrations alone. We suggest either to measure the hydrology of a site directly or to compare the concentrations of multiple elements (including conservative tracers such as Na^+ and Cl^-) with source strengths in oceanic, atmospheric, and ground-water inputs (e.g., Gorham et al. 1985, Damman 1988). Siegel (1987) further suggested a hydrogeologic systems approach to wetland hydrology, where the recharge-discharge function of a wetland is placed in the larger context of the regional geology and hydrology.

Besides being a conveyor of nutrients and cations to a peatland, hydrology is important in terms of the moisture content and the degree and duration of waterlogging of the soil. Anaerobic soil conditions resulting from prolonged waterlogging can lead to severe physiological stress to many plants; therefore, wetland plants have various physiological and structural adaptations to waterlogging that allow for varying degrees of flood tolerance (Mitsch and Gosselink 1993). On the opposite extreme, ombrogenous peatlands can experience water tables far below the surface during dry years, causing drought stress for plants. Even during normal years, the pronounced microtopography of peatlands leads to extreme variation in soil moisture for *Sphagna*, ranging from waterlogging in hollows to desiccation in hummocks. *Sphagnum* species that normally grow on hummocks are better able to prevent desiccation from occurring than hollow species, although both have similar tolerance to desiccation once it occurs (Rydin 1985).

An extensive survey of northern Minnesota peatlands found that biomass and physiognomy (i.e., vertical stature) were controlled by degree of water logging and disturbance (Swanson and Grigal 1991).

Low-statured, low-biomass communities occurred in both acidic and alkaline peatlands under wet soil conditions, whereas high-biomass communities with an overstory of shrubs and trees occurred in drier peatlands. The gradient between shrubs and trees was ascribed to previous levels of disturbance. A "trophic" gradient (as defined by pH and electrical conductivity of surface water) affected plant-community composition, but was not primarily responsible for standing biomass or physiognomy of the sites. Thus, the species distribution, productivity, and live biomass of peatlands is controlled by the physiological tolerance of the plants to the range of soil moisture conditions in different habitats.

DECOMPOSITION

Our discussion to this point has focused on correlations among environmental gradients (nutrients, pH/alkalinity, hydrology) and their effects on plant-community composition. Previous peatland classification schemes have been built largely upon these variables (Table 1). The defining characteristic of a peatland, though, is its accumulation of soil organic matter, and this accumulation of peat subsequently exerts an important control over the hydrology, biogeochemistry, and plant community composition of a peatland. The degree of peat accumulation among wetlands is controlled by differences in decay, not production (Clymo 1984). Therefore, a conceptual understanding of peatlands, with its attendant terminology, should also incorporate environmental controls over decomposition.

Decomposition in peatlands is controlled by the carbon quality of the organic substrates, pH, temperature, nutrient availability, and hydrology (Clymo 1983, Bridgham *et al.* 1995a). The hydrologic control over the depth of the acrotelm is probably more important than its control over soil and water chemistry. Current theory suggests that peat accumulation only occurs under the continuous anaerobic conditions of the catotelm (Clymo 1992). Nevertheless, the existence of southern peatlands (Bridgham and Richardson 1992, 1993) and midcontinental northern peatlands (Glaser and Janssens 1986) that experience long periods with reduced water-table levels during the growing season suggests that other factors also limit decomposition in peatlands.

The carbon quality of leaf litter (Johnson and Damman 1991) and peat (Valentine *et al.* 1994, Bridgham *et al.* 1995a, Updegraff *et al.* 1995) are additional important constraints on decomposition rates. Nutrient availability and pH seem to be of secondary importance as direct controls over decomposition (Bridgham 1991, Bridgham and Richardson 1992, Valentine *et al.* 1994), although nutrient availability may have an im-

portant indirect control over decomposition through its effect on the quality and quantity of plant litter produced (Bridgham *et al.* 1995a).

The effect of temperature on peat accumulation is perhaps most elegantly illustrated by the distinct peak in peatland occurrence at high latitudes (Matthews and Fung 1987), although large areas of peatlands do occur under warmer climates. We have suggested that southern peatlands can continue to exist due to the highly decomposed, recalcitrant nature of their peats (Bridgham and Richardson 1992, 1993).

In controlled laboratory experiments, we have found significant interactions between carbon and nutrient mineralization rates, temperature, aeration status, and carbon quality in a range of peatland soils (Bridgham *et al.* 1995a, Updegraff *et al.* 1995). Such results suggest the limitations of the accepted paradigm that decomposition rates are low in ombrogenous bogs (as opposed to fens) because of the recalcitrant nature of *Sphagnum*-derived peat, low pH, low nutrient and cation availability, and a limited acrotelm (Moore and Bellamy 1974, Malmer 1986, Moore 1989, Mitsch and Gosselink 1993).

CONCLUSIONS

We suggest that the role of multiple controlling axes be recognized and studied in peatlands (*cf.* Janssens 1992, Vitt and Kuhry 1992, Bridgham *et al.* 1995a). We examined three of the most important axes (pH/alkalinity, nutrient availability, and hydrology) and found that they were not necessarily coincident across community gradients in peatlands. Additionally, other factors such as temperature, presence or absence of permafrost, and shading will be of importance. We further suggest a new terminology for peatlands that allows consideration of each of these variables as independent factors without *a priori* assumptions of collinearity.

Specially, we make the following suggestions concerning terminology:

- (1) The suffix "-trophic" should only be used when referring to nutrients that directly limit plant growth at natural availabilities. We suggest oligotrophic for nutrient-poor conditions and eutrophic for nutrient-rich conditions.
- (2) Given the inexactness of terms such as rich and poor, we suggest that terms such as circumneutral, moderately acid, and very acidic (or alternatively strong, intermediate, and weak) be used to describe the pH of peatlands.
- (3) Because of the multiple, often invalid, assumptions in the use of the suffix "-trophic", we suggest that ombrogenous and geogenous (or limnogenous, topo-

genous, and soligenous) be used to describe the hydrology of peatlands.

(4) We suggest that bog be used colloquially to refer to acidic, low alkalinity peatlands dominated by *Sphagna*, conifers (particularly spruces and pines), and/or various ericaceous shrubs. Similarly, fens should broadly refer to somewhat less acidic, more alkaline peatlands dominated by graminoids, brown mosses, taller shrubs, and coniferous and/or deciduous trees. The typical species assemblage of bogs and fens will be regionally determined. This approximates their predominant usage in the current literature, but our definition carries no assumptions regarding hydrology, topography, ontogeny, nutrient availability, or the presence or absence of nondominant indicator plant species.

(5) Use of the general term peatland, especially when specific hydrologic data are lacking, would reduce confusion and avoid false expectations regarding conditions that may or may not be present at a particular site.

ACKNOWLEDGMENTS

This work was funded by the National Aeronautics and Space Administration (NASA/NAGW-1828), the National Science Foundation (DEB-9306854, DEB 9496305), and a Department of Energy Global Change Distinguished Postdoctoral Fellowship to Scott Bridgman. While we take full responsibility for this paper, we would like to acknowledge others who, some long ago, foreshadowed the ideas developed here (Gorham 1950, Malmer and Sjörs 1955, Gorham 1957, Vitt and Kuhry 1992). Additionally, Drs. Eville Gorham, Antoni Damman, Stephen Zoltai, and Douglas Wilcox provided helpful reviews of this manuscript.

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Manuscript received 21 July 1995; revision received 9 October 1995; accepted 20 November 1995.