DIVISION S-10—WETLAND SOILS

A Comparison of Nutrient Availability Indices Along an Ombrotrophic–Minerotrophic Gradient in Minnesota Wetlands

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ABSTRACT

Despite the importance of nutrient availability in determining ecosystem structure and function, it is difficult to quantify in an absolute sense because of the complexity of nutrient cycles and methodological limitations. Others have compared nutrient availability indices for upland soils, but few comparative studies have been done in organic soils. Objectives of this study were, (i) to determine if N and P availability change in a predictable manner across an ombrotrophic–minerotrophic gradient in 16 wetlands in northern Minnesota, and (ii) to compare various laboratory and field indices of soil nutrient availability in a diverse group of organic soils. Ombrotrophic wetlands receive only atmospheric inputs of ions, while minerotrophic wetlands also receive groundwater or overland water inputs. We compared the following nutrient availability indices: 2- and 59-wk laboratory mineralization potentials, labile P and N pools determined from a kinetic mineralization model, total and extractable soil N and P pools, plant N and P concentrations, and H–OH and HCO_3^- charged resins. Most indices indicated that N availability increases along the ombrotrophic–minerotrophic gradient, and correlations among indices were generally good, suggesting that they can be used somewhat interchangeably. Resins indicated a predominance of NO_3–N availability during the growing season and NH_4–N availability during the winter, and most indices indicated an increasing importance of nitrification in more minerotrophic wetlands. In contrast, P indices gave contrasting results across the gradient and were generally poorly correlated; however, the majority of the methods suggested that P availability is higher in minerotrophic swamp forests or beaver meadows, and that P availability is low in bogs and fens. We suggest that current methods of determining P availability may be inadequate in highly diverse organic soils. Plant nutrient concentrations did not show clear relationships with soil nutrient indices, particularly for N, which probably reflects the complicated relationship between soil nutrient availability and plant response in natural wetlands.

DESPITE THE IMPORTANCE of nutrient availability in determining ecosystem structure and function, it is difficult to quantify in an absolute sense because of the complexity of nutrient cycles and methodological limitations. Dissolved inorganic nutrient pool sizes in soil are typically orders of magnitude less than annual plant uptake and must be continually replenished from other labile pools to maintain soil fertility (Binkley and Hart, 1989). Thus, nutrient availability is most profitably thought of as the rate of replenishment or the buffer capacity of the dissolved inorganic nutrient pool. However, measurement of nutrient supply rates is a difficult endeavor, as they are determined by the relative sizes of the labile, organic, and recalcitrant inorganic pools in the soil, and rates of transformation and transfer among the pools (Stevenson, 1986; Binkley and Hart, 1989). Furthermore, the importance of particular pools and transformations varies among nutrients. Environmental controls over all of these factors must also be considered. Any particular method of determining nutrient availability only measures one to several of these pools and fluxes and the pools are often operationally defined, so any measure of nutrient availability must be considered an index (Binkley and Hart, 1989; Binkley and Vitousek, 1989). In addition, field studies have large amounts of temporal and spatial variability, which is usually poorly quantified.

Researchers are typically interested in (and often define) nutrient availability in terms of plant growth; however, plant growth is a response to soil nutrient availability and is, at best, an indirect measure of it. Nutrient supply rates and nutrient limitation of plants may vary in complex ways in natural communities because of inherent physiological limitations in the capacity of plants adapted to low nutrient environments to respond to increases in nutrient supply (Chapin et al., 1986; Pastor and Bridgham, 1999; Aerts and Chapin, 2000). Thus, nutrient supply rates and nutrient limitation of plant growth may give contradictory results.

Despite our inability to definitively quantify nutrient availability, several studies have measured nutrient gradients across natural community assemblages (e.g., Pastor et al., 1984; Hart and Firestone, 1989; Giblin et al., 1991; Bridgham and Richardson, 1993). These studies have often improved our understanding of the spatial controls over plant community structure and productivity. However, the methods employed by these studies may be limited in their ability to characterize changes in nutrient dynamics across sites with widely varying soil characteristics.

In this study, we focused on how nutrient availability varies among wetlands that occur along an ombrotrophic–minerotrophic gradient. This gradient is a basic structuring paradigm in wetlands with organic soils (Bridgham et al., 1996). Ombrotrophic wetlands are those that receive all their water and associated ions via the atmosphere, usually because of a deep accumulation of soil organic matter causing hydrologic isolation from groundwater inputs. This results in low soil pH and very

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Table 1. Total soil N content, initial 0.01 *M* $CaCl_2$-extractable N, potential N mineralization at 2 and 59 wk, and labile N (N_o) pool from 16 Minnesota wetlands across an ombrotrophic-minerotrophic gradient. Mean ± (SE). Numbers with different letters within a column show significant differences among sites ($P < 0.05$). Data were previously published in Bridgham et al. (1998) and are included here for comparison to other nutrient availability indices.

			Initial $CaCl_2$-extractable N		2 wk mineralization		59 wk mineralization			Labile N Pool (N_o)	
Site	n†	Total soil N	NH_4-N	NO_3-N	Aerobic	Anaerobic	Aerobic	Anaerobic	Nitrification‡	Aerobic	Anaerobic
		mg N cm^{-3}	ug N cm^{-3}						%	mg N g^{-1} total N	
Bog	5	0.51 (0.05)c	0.50 (0.14)d	0.03 (0.03)b	8.0 (2.5)b	11.8 (3.7)c	62.8 (8.2)de	23.8 (3.8)d	1.9 (1.4)d	79 (18)a	35 (5)a
Acidic fen	2	0.29 (0.04)d	0.96 (0.43)cd	0.04 (0.01)b	6.6 (1.0)b	5.5 (0.4)d	33.9 (4.9)e	13.9 (2.2)d	17.4 (13.5)c	79 (22)a	31 (1)a
Intermediate fen	2	2.17 (0.32)b	2.11 (0.08)bc	0.07 (0.07)b	6.4 (0.5)b	10.5 (2.4)c	78.9 (15.0)cd	63.4 (11.0)c	30.3 (17.9)c	14§a	7 (0)a
Cedar swamp	3	2.25 (0.27)b	5.64 (0.96)a	0.06 (0.01)b	6.9 (2.8)b	24.8 (0.5)b	107.0 (12.7)c	86.8 (12.5)c	64.9 (25.9)b	42§a	23 (2)a
Tamarack swamp	2	2.34 (0.32)b	6.31 (2.33)a	0.04 (0.02)b	9.8 (3.6)b	27.0 (3.8)b	155.5 (5.4)b	118.0 (18.3)b	76.0 (18.2)ab	6§a	23 (0)a
Meadow	2	3.50 (0.24)a	3.19 (1.27)b	3.50 (1.20)a	18.4 (5.3)a	45.1 (16.3)a	276.2 (73.3)a	263.6 (89.3)a	98.3 (28.3)a	21 (13)a	46 (20)a

† Number of replicate sites within a community type, with 5 cores taken per site.
‡ Percentage nitrification in aerobic 59-wk mineralization experiment.
§ Kinetic model did not converge for all sites, $n = 1$. Standard error could not be calculated.

high organic matter content, along with other associated chemical and physical soil properties (Bridgham et al., 2000). In contrast, minerotrophic wetlands also have inputs of surface or groundwater that usually impart a higher soil pH and ash content. There are also distinct changes in plant community structure along this gradient (Glaser, 1987; Vitt and Chee, 1990; Gorham and Janssens, 1992). Although fundamentally a hydrology gradient, it has generally been assumed that the ombrotrophic–minerotrophic gradient is coincident with a nutrient availability gradient, with ombrotrophic wetlands being nutrient deficient and minerotrophic sites being relatively nutrient rich (Bridgham et al., 1996). However, the few studies that have examined this assumption have generally found that nutrient availability does not vary in a simple way along this gradient (Waughman, 1980; Verhoeven et al., 1990; Vitt and Chee, 1990; Bridgham et al., 1998; Aerts et al., 1999; Bedford et al., 1999). Furthermore, results have varied among these studies, and it is unclear to what extent this has been because of the different methods employed.

The objectives of this study are twofold. First, we examine how in situ N and P soil availability and nutrient concentrations in foliage change in 16 wetlands that occur across an ombrotrophic–minerotrophic gradient in northern Minnesota. We previously compared long–term laboratory nutrient and C mineralization potentials for these wetlands and found that N mineralization rates were greater in more minerotrophic wetlands, but that P mineralization changed in complex ways across the gradient (Bridgham et al., 1998). However, environmental conditions vary widely among the wetlands, and long incubations probably cause artifacts such as changes in microbial community structure. Thus, we will determine if in situ measurements of nutrient availability show similar changes along the ombrotrophic–minerotrophic gradient. Second, we ask the more methodological question of whether a large variety of commonly used indices of soil nutrient availability give comparable results in a diverse set of organic soils, despite the fact that each index measures a somewhat different pool or rate (Binkley and Hart, 1989; Binkley and Vitousek, 1989). We compared in situ soil nutrient availability as measured by anion–cation exchange resins and nutrient concentrations in foliage reported in this paper with extractable and total soil nutrient pools, cumulative nutrients mineralized over 2 and 59 wk, and the labile N and P pools (N_o and P_o, respectively) from previously published data taken from the same sites (Bridgham et al., 1998). This previously published data are presented in Tables 1 and 2 to allow for a direct comparison between methods.

Table 2. Total soil P content, initial acid-fluoride extractable P, initial 0.01 *M* $CaCl_2$-extractable P, potential P mineralization at 2 and 59 wk, and labile P (P_o) pool from 16 Minnesota wetlands across an ombrotrophic-minerotrophic gradient. Mean ± (SE). Numbers with different letters within a column show significant differences among sites ($P < 0.05$). Data were previously published in Bridgham et al. (1998) and are included here for comparison to other nutrient availability indices.

					2-wk mineralization		59-wk mineralization		Labile P Pool (P_o)	
Site	n†	Total soil P	Initial acid-fluoride extractable P	Initial $CaCl_2$-extractable P	Aerobic	Anaerobic	Aerobic	Anaerobic	Aerobic	Anaerobic
		mg P cm^{-3}	ug P cm^{-3}						mg P g^{-1} total P	
Bog	5	0.024 (0.004)d	0.122 (0.023)d	0.245 (0.111)ab	0.34 (0.17)ab	4.14 (0.97)a	5.72 (1.23)a	6.44 (1.14)b	150 (50)‡a	247 (20)a
Acidic fen	2	0.012 (0.002)e	0.347 (0.308)cd	0.400 (0.242)a	0.45 (0.24)a	0.87 (0.61)c	2.00 (1.31)b	1.63 (0.73)c	98 (62)a	110 (34)b
Intermediate fen	2	0.067 (0.009)c	0.157 (0.047)d	0.071 (0.002)b	0.04 (0.01)c	0.10 (0.02)d	0.70 (0.36)c	1.15 (0.38)c	8 (4)a	11 (8)b
Cedar swamp	3	0.091 (0.011)bc	0.338 (0.123)bc	0.315 (0.143)a	0.31 (0.21)ab	2.81 (0.77)b	3.22 (1.36)b	7.88 (3.25)b	9 (3)§a	80 (23)b
Tamarack swamp	2	0.098 (0.019)b	0.788 (0.563)b	0.213 (0.028)ab	0.10 (0.01)bc	4.99 (0.45)a	2.80 (1.66)b	10.76 (2.43)a	6¶a	95 (35)b
Meadow	2	0.272 (0.000)a	1.224 (0.318)a	0.425 (0.236)a	0.95 (0.12)a	0.49 (0.04)cd	2.15 (0.05)b	6.55 (1.98)b	6 (0)a	23 (15)b

† Number of replicate sites within a community type, with 5 cores taken per site.
‡ Kinetic model did not converge for all sites, $n = 4$.
§ Kinetic model did not converge for all sites, $n = 2$.
¶ Kinetic model did not converge for all sites, $n = 1$. Standard error could not be calculated.

MATERIALS AND METHODS

Study Sites

We sampled 16 different wetland sites in northern Minnesota located between 46° and 49° N that are representative of the ombrotrophic–minerotrophic gradient in this region. The bog sites ($n = 5$) had a mean soil pH of 3.8 and were vegetated with black spruce [*Picea mariana* (P. Mill.) B.S.P.], *Sphagnum* L., and stunted ericaceous shrubs. They were located at Pine Island, Red Lake, Toivola, Arlberg, and Ash River near Voyageurs National Park. Fen sites were dominated by sedges (*Carex* L) and were located at Red Lake, McGregor, Alborn, and Marcel. The fens were separated into acidic fens (= poor fens, $n = 2$) with a mean soil pH of 4.1, and intermediate fens with a mean soil pH of 5.2 ($n = 2$). Plant community composition supported this distinction, with cover of *Sphagnum* and ericaceous shrubs in the acidic fens more similar to bog sites then to intermediate fen sites. Forested swamp sites included cedar swamps (*Thuja occidentalis* L.) near Meadowlands, Isabella and Ash River ($n = 3$), and tamarack swamps [*Larix laricina* (Du Roi) K. Koch] near Meadowlands and Ash River ($n = 2$). They had mean soil pHs of 5.5 and 5.8, respectively. We also sampled two beaver meadows in Voyageurs National Park. They had a mean soil pH of 6.0 and were dominated by Canada blue joint [*Calamagrostis canadensis* (Michx.) Beauv.], wool grass [*Scirpus cyperinus* (L.) Kunth], and sedges (Erickson, 1994).

These sites are described in greater detail in Bridgham et al. (1998), including a site map and an extensive table with their physical and chemical soil characteristics. The bogs are Sphagnic Cryofibrists, the acidic fens are Typic Cryofibrists, the intermediate fens are Typic Cryohemists or Typic Cryosaprists, and the tamarack and cedar swamps are Typic Cryohemists (Soil Survey Staff, 1998). The soils in the beaver meadows had an O horizon of 8- to 21-cm depth over the mineral substratum and are Typic Argiaquolls or Typic Epiaqualfs (Johnston et al., 1995; C. Johnston, personal communication, 1999). Soil bulk density varied dramatically among sites, varying from 0.045 g cm^{-3} in the bogs to 0.224 g cm^{-3} in the beaver meadows (all 0- to 25-cm depth, except O horizon in beaver meadows, Bridgham et al., 1998).

Resins

We put in five H–OH or HCO_3^- charged exchange resins at 10-cm depth in approximately the same locations in the 16 wetlands as the cores were taken for the mineralization experiment reported in Bridgham et al. (1998). Resins were placed in hollows when significant microtopography was present. Resins were placed in the field in mid-May 1993 and removed in the beginning of October, replaced with a fresh set of resins, which were then removed in mid-May 1994. The May 1993 through October 1993 period represents growing season nutrient availability, while the October 1993 through May 1994 period represents winter nutrient availability. Only a small percentage of the exchange capacity of the resins (3.2 meq/g dry resin for HCO_3^-, 3.87 meq/g dry resin for H–OH) was used over these periods.

Bicarbonate-charged resins were used to assess P availability, and H–OH mixed-charge resins were used to assess both N and P availability. Approximately 10-g wet mass of each resin type was placed separately in nylon bags. For HCO_3^- resins, the 20-50 mesh AG 1-X8 anion-exchange resin (Bio-Rad Laboratories, Hercules, CA) was originally in the Cl^- form. It was acid-rinsed in 0.5 M HCl, rinsed with deionized water, and charged with HCO_3^- by several successive soakings in 0.5 M HCO_3^-. Upon retrieval from the field, ≈3 g dry mass of resin was extracted twice in 0.5 M HCl and passed through a Whatman #1 filter (Whatman Chemical Separation, Inc., Clifton, NJ).

The H–OH resins (Rexyn I-300, Fisher Scientific, Pittsburgh, PA) came appropriately charged. Upon retrieval from the field, ≈3-g dry mass resin was extracted twice in 1 M KCl and passed through a Whatman #1 filter (Clifton, NJ). Nitrogen in the extracts was determined on a Lachat autoanalyzer, while P was determined either on the Lachat autoanalyzer or manually with the absorbic acid method (Olsen and Sommers, 1982), depending on concentration.

Plant Nutrient Concentrations

Vegetation samples were taken to determine total N and P concentrations from five 10- by 10-cm quadrats in each wetland in October 1993, immediately adjacent to the resin locations. Since there were no species common to all wetlands, we took all graminoids and mosses from each quadrant and mixed them to give an average ground layer nutrient content for each site. Total P concentrations were determined in dried (70°C) subsamples with a H_2SO_4–H_2O_2 digestion (Lowther, 1980). Total N concentrations were determined on dried subsamples by combustion on a CHN analyzer (Leco Corp., St. Joseph, MI).

Statistics

Data for all variables were log transformed to fit normal distributions. Wetland sites were considered the replicate units ($n = 2$–5). Differences among community types were determined with one-way ANOVAs with the five subreplicates per wetland nested to account for intrasite variation. Pairwise means comparisons were done with Tukey's test using the ANOVA model mean square error term. Spearman rank-order correlation coefficients were performed on all variables using the means for each site. Systat 7.0 was used for all analyses (SPSS Inc., Chicago, IL).

RESULTS AND DISCUSSION

The Ombrotrophic–Minerotrophic Gradient: Nitrogen

Nitrogen recovered from in situ resins was greatest annually in the minerotrophic cedar and tamarack swamp forests, was intermediate in the beaver meadows and fens, and was lowest in the bog sites (Fig. 1A, $P < 0.001$ for community effect). However, there were large seasonal differences in the accumulation of NO_3–N and NH_4–N on the resins. During the growing season, NO_3–N dominated resin N, but during the winter NH_4–N dominated resin N (Fig. 1A). Cumulative over the entire year, about twice as much NO_3–N as NH_4–N was captured on the resins in most sites, with the exception that NO_3–N was 4- and 10-fold higher than NH_4–N in the beaver meadows and tamarack swamps, respectively (Fig. 1B).

Nitrogen concentration in vegetation was highest in the herbaceous vegetation of the cedar and tamarack swamp forests and similar in the rest of the wetland communities (Fig. 2, $P < 0.001$ for community effect).

The greater resin N and plant N concentration in the minerotrophic swamp forests suggests that in situ soil

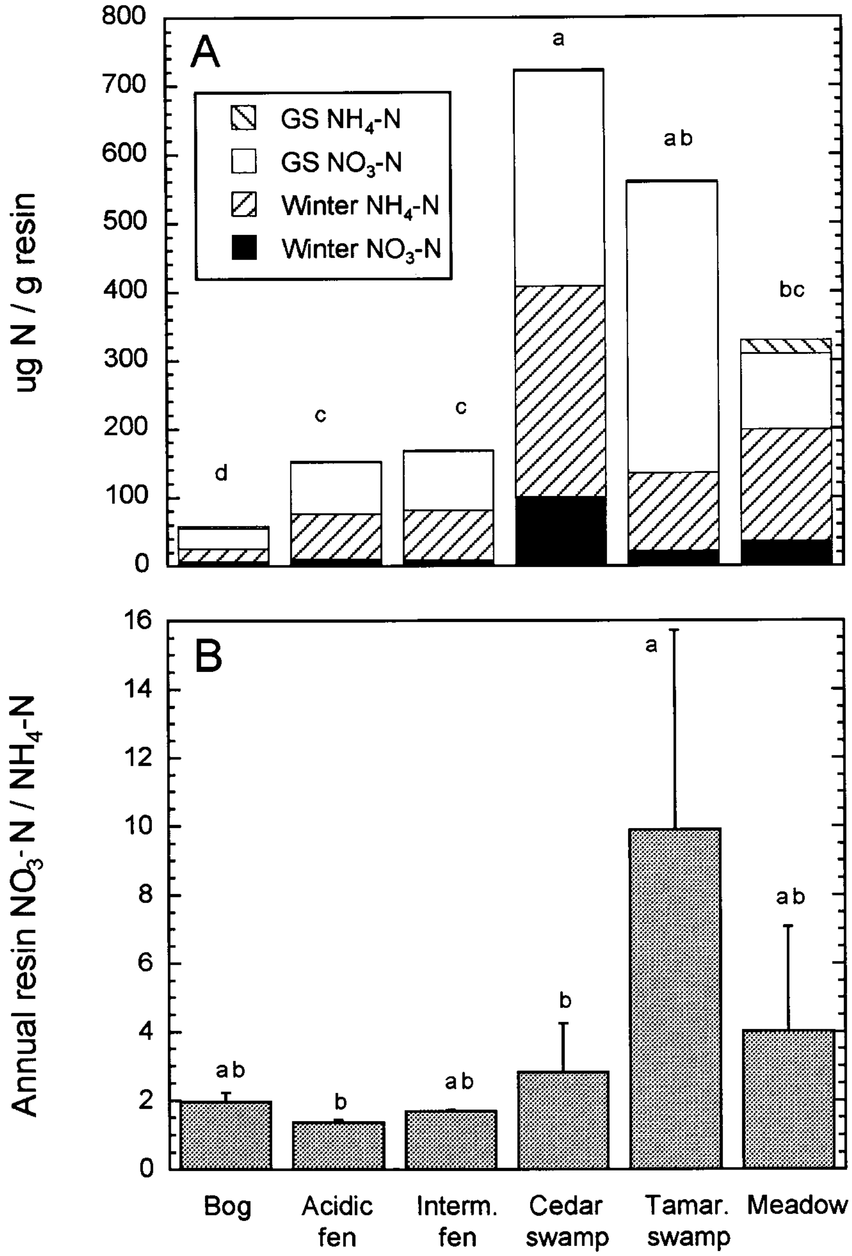

Fig. 1. (A) NH_4–N and NO_3–N on H–OH resins in during the growing season (GS) and winter months. (B) The ratio NO_3–N to NH_4–N on the resins when summed over 1 yr. Mean ± 1 SE (error bars in B only). Columns with differing letters are significantly different at $P \leq 0.05$. Interm. = intermediate, Tamar. = tamarack.

N availability increases with a greater degree of minerotrophy, at least among Histosols. Other soil N availability indices reported previously from the same sites in Bridgham et al. (1998) generally support this trend (Table 1). However, it is not clear that N availability is higher in wetlands with mineral soils than in minerotrophic Histosols. The two beaver meadows were the most minerotrophic sites and were the only sites with soils that were not Histosols. They had the highest potential N mineralization rates, soil N content, and extractable N concentrations. In contrast, plant N concentrations and resin N had only intermediate values in the beaver meadows.

Among the sites with Histosols, the cedar and tamarack swamp forest sites had the highest potential N mineralization rates, soil N content, plant N concentration, and resin N. Clearly, minerotrophic Histosols have higher N availability than more ombrotrophic Histosols. However, the small total soil N pool in ombrotrophic Histosols turns over comparatively rapidly, as indicated by their relatively high N_0 values (Table 1, Bridgham et al., 1998). Thus, higher N availability in minerotrophic sites is due to a larger soil N pool rather than an increase in the lability of that pool. As differences in N concentration (on a dry mass basis) are small across the gradient, the larger soil N pool in minerotrophic sites is largely

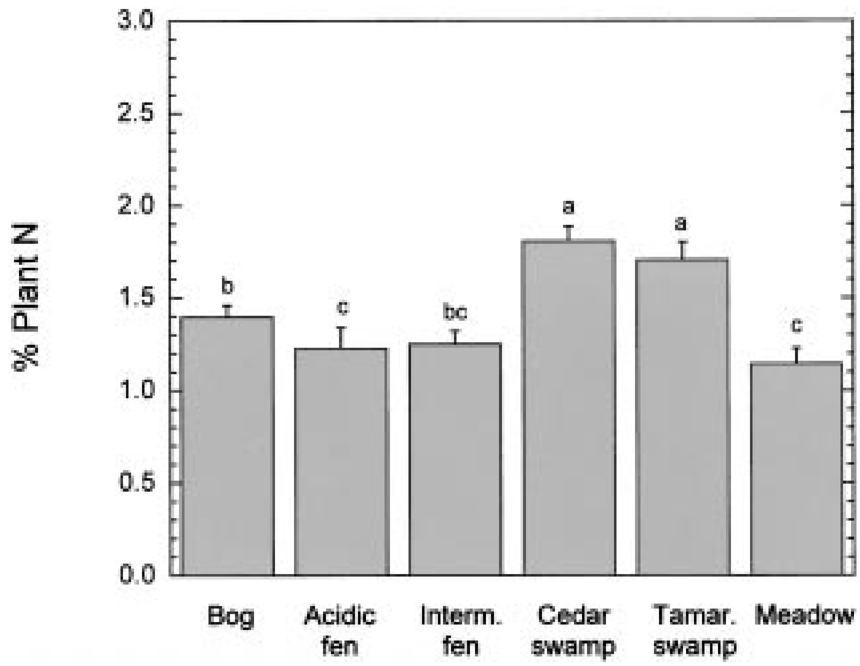

Fig. 2. Plant N concentration along an ombrotrophic–minerotrophic gradient in Minnesota wetlands. Mean ± 1 SE. Columns with differing letters are significantly different at $P \leq 0.05$. Interm. = intermediate, Tamar. = tamarack.

due to the 12-fold increase in soil bulk density (Bridgham et al. 1998).

Nitrate

The high percentage of NO_3–N on the H–OH resins in the growing season in the low pH, more ombrotrophic soils was surprising as others have found that NO_3–N levels are near detection limits in porewater (Hemond, 1983; Gorham et al., 1985; Vitt and Chee, 1990) and soil from Histosols (Waughman, 1980; Bridgham and Richardson, 1993). Nitrification rates in low pH organic soils have been found to be very low (Martin and Holding, 1978; Rosswall and Granhall, 1980; Rangeley and Knowles, 1988; Regina et al., 1996).

We can compare the recovery of NO_3–N on resins with extractable NO_3–N concentrations and potential nitrification rates from these same sites (Table 1, Bridgham et al., 1998). The potential N mineralization and extractable N data support the generalization that nitrification is severely inhibited in low pH, ombrotrophic soils. Only the beaver meadows had substantial extractable NO_3–N, and the percentage conversion of mineralized N to NO_3–N increased along the ombrotrophic–minerotrophic gradient and was positively correlated with soil pH ($r^2 = 0.90$). Resin data gave a more complicated result, with a switch from dominance of NO_3–N in the growing season to dominance by NH_4–N in the winter, suggesting a strong temperature dependence of nitrifying bacteria. Also, NO_3–N was a much larger percentage of resin N annually in the tamarack swamps, which are among the most minerotrophic Histosol sites. The high NO_3–N loading on the resins in the growing season in the low pH soils may also reflect the greater mobility of NO_3–N as compared to NH_4–N (Binkley, 1984).

The Ombrotrophic—Minerotrophic Gradient: Soil Phosphorus

Although both HCO_3^- and H–OH resin P differed among communities in both the growing and winter seasons (Fig. 3, $P < 0.001$ for community effect), they gave quite different relative responses across the gradient. HCO_3^- resin P increased along the ombrotrophic–minerotrophic gradient, with highest availability in cedar swamps and the beaver meadows and lowest availability in fens and bogs. In contrast, there was no clear trend in H–OH resin P along the community gradient, with highest availability in acidic fens and beaver meadows and lowest availability in the intermediate fens. Moreover, there was more than an order of magnitude difference among community types in the ratio of HCO_3^- resin P/H–OH resin P (Fig. 3C). Much more P was sorbed on the HCO_3^- resins than on the H–OH resins in more minerotrophic, higher pH wetlands, suggesting a direct pH or cation affect on their activities.

Plant P concentrations showed a more complex response (Fig. 4, $P < 0.001$ for community effect). The herbaceous layer in the minerotrophic swamp forests had the highest concentrations, the beaver meadow, bog, and acidic fen sites had intermediate concentrations, and the intermediate fens had the lowest concentrations.

We can compare these results with other indices of P availability previously published by Bridgham et al. (1998, Table 2). Different methods of determining soil P availability gave disparate results across the ombro-

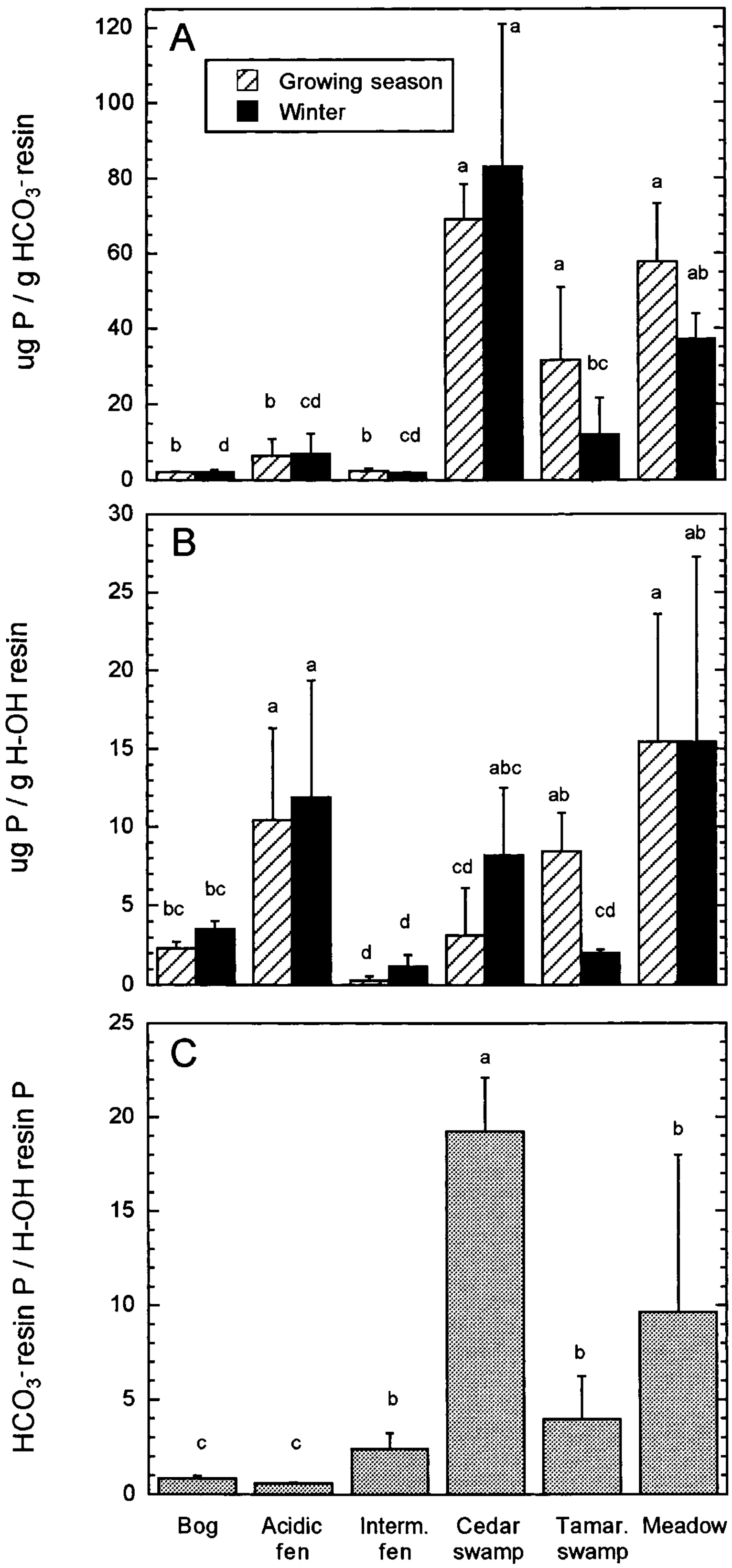

Fig. 3. Phosphorus retained on (A) HCO_3^- and (B) H–OH charged resins during the growing season and winter. (C) Ratio of HCO_3^- resin P to H–OH resin P when summed over 1 yr. Mean ± 1 SE. Columns with differing letters are significantly different at P ± 0.05. Interm. = intermediate, Tamar. = tamarack.

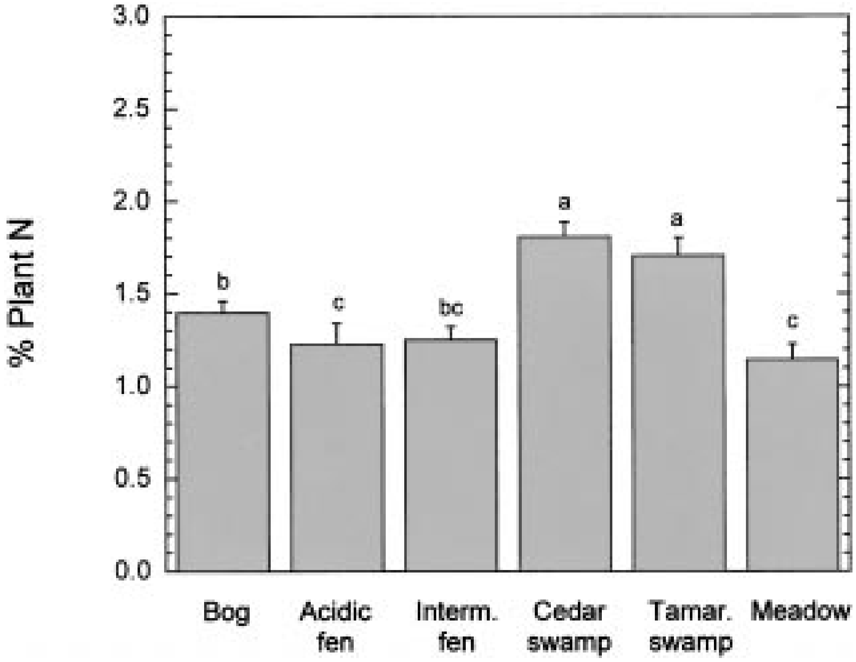

Fig. 4. Plant P concentration along an ombrotrophic–minerotrophic gradient in Minnesota wetlands. Mean ± 1 SE. Columns with differing letters are significantly different at $P \leq 0.05$. Interm. = intermediate, Tamar. = tamarack.

trophic–minerotrophic gradient, although all methods showed large differences among communities. As with total soil N content, total soil P content increased in a consistent manner across the gradient, but the small total soil P pool in more ombrotrophic sites was relatively labile and turned over quickly. Higher total soil P content in more minerotrophic sites were offset by lower concentrations of labile P (P_o), so there was no clear trend in potential P mineralization rates across the gradient. Net P mineralization also includes geochemical sorption of biologically mineralized P, and this appears to have been much greater in more minerotrophic sites.

The two soil extractants (Table 2) and the two resin types (Fig. 3) also gave contradictory results. The acid-fluoride extract and the HCO_3^- resins suggested that more minerotrophic sites have greater P availability, but the $CaCl_2$ extracts and the H–OH resins did not show a consistent change across the gradient, although there were large differences among communities. Overall, the majority of the methods (i.e., HCO_3^- resins, total soil P content, acid-fluoride P, plant P) suggest that P availability is higher in minerotrophic swamp forests or beaver meadows, but P availability appears to be low in bogs and fens.

A Comparison of Methods

Soils

This study provides a useful opportunity to compare the relative results of a large number of commonly used indices of soil nutrient availability in a diverse group of organic soils. Despite the fact that each method measures a somewhat different soil nutrient pool (Binkley and Hart, 1989), it is reasonable to assume that they should provide similar predictive trends in widely differing soils. Although we have focused here on organic soils, the results are probably translatable to mineral soils. Many studies have used the same or similar methods to compare nutrient availability among diverse natural ecosystems with widely varying soil characteristics (Pastor et al., 1984; Hart and Firestone, 1989; Zak et al., 1989; Giblin et al., 1991; Walbridge, 1991; Bridgham and Richardson, 1993). Spearman rank-order correlations among the N–availability indices measured in this study are presented in Table 3. any indices are highly positively correlated, suggesting that most N–availability indices do indeed effectively measure components of a common available pool.

There were several exceptions to this generalization. NH_4–N on the H–OH resins during the growing season was not highly correlated with any other N index, but this probably simply reflects the predominance of NO_3–N on the resins during the growing season (Fig. 1). The aerobic 2-wk potential mineralization results were poorly correlated with other N indices, as opposed to the 59-wk aerobic potential mineralization results, suggesting that a 2-wk incubation time is insufficient to determine potential N availability. However, anaerobic 2-wk, anaerobic 59-wk, and aerobic 59-wk potential mineralization results generally gave similar correlations to the other N indices, with anaerobic 59-wk mineralization giving the highest correlation in almost all cases. Aerobic N_o was negatively correlated with most other N indices. Differences in N content among soils overwhelmed trends in N_o across the ombrotrophic–minerotrophic gradient, yielding an opposite trend to N_o in other availability indices. Anaerobic N_o was poorly correlated with almost all other N indices.

In contrast to the N results, the different methods of determining soil P availability were generally poorly correlated (Table 4). In particular, there were no consistent relationships between resin P or extractable P and

Table 3. Spearman correlations ($r \geq 0.50$) for N related variables measured in sites across an ombrotrophic-minerotrophic gradient.

	GS NH_4–N resin†	GS NO_3–N resin	GS total resin N	W NH_4–N resin	W NO_3–N resin	W total resin N	Yr NH_4–N resin	Yr NO_3–N resin	Yr total resin N	$CaCl_2$–N	Plant N	Total soil N cm^{-3}	Aer 59-wk Min	An 59-wk Min	Aer 2-wk Min	An 2-wk Min	Aer N_0
GS NO_3–N resin																	
GS total resin N		0.99															
W NH_4–N resin		0.89	0.92														
W NO_3–N resin																	
W total resin N		0.73	0.80	0.89	0.61												
Yr NH_4–N resin		0.89	0.92	1.00		0.89											
Yr NO_3–N resin		0.84	0.89	0.84	0.60	0.93	0.84										
Yr total resin N		0.86	0.91	0.89	0.58	0.95	0.89	0.99									
$CaCl_2$–N		0.64	0.72	0.69	0.76	0.81	0.69	0.83	0.83								
Plant N																	
Total soil N cm^{-3}					0.67	0.62		0.67	0.63	0.76							
Aer 59-wk Min		0.55	0.60	0.54	0.54	0.61	0.54	0.66	0.67	0.82		0.88					
An 59-wk Min		0.62	0.66	0.62	0.68	0.68	0.62	0.72	0.73	0.87		0.95	0.93				
Aer 2-wk Min													0.56				
An 2-wk Min			0.52	0.54	0.50	0.59	0.54	0.59	0.61	0.68		0.84	0.89	0.89	0.63	−0.52	
Aer N_o		−0.73	−0.69	−0.59	−0.60	−0.59	−0.59	−0.69	−0.65	−0.72		−0.62	−0.65	−0.67			
An N_o																	

† GS = growing season; W = winter; Yr = annual; $CaCl_2$–N = 0.01 *M* $CaCl_2$–extractable N; Aer = aerobic; An = anaerobic; Min = laboratory mineralization potentials.

mineralized P. Acid-fluoride P was positively correlated with resin P and total soil P. Additionally, total soil P was correlated with HCO_3^- resin P.

It is particularly problematic that closely related methods were often poorly correlated. For example, the correlations between H–OH and HCO_3^- resin P in the two seasons was <0.46. The results from the HCO_3^- resins suggested higher available P in the minerotrophic sites, but the H–OH resins gave relatively high available P in the acidic fens (Fig. 3). Additionally, the ratio of HCO_3^- resin P to H–OH resin P increased dramatically across the ombrotrophic–minerotrophic gradient (Fig. 3C). Thus, these two resins seem to be measuring different P pools, with much greater P sorption on the HCO_3^- resins in soils with higher pH and cation content. Sen Tran et al. (1992) examined correlations in P availability among resins charged with HCO_3^-, F^-, Cl^-, and H–OH in mineral soils that varied greatly in acidity and found Pearson $r \geq 0.68$ among the different resins. The correlation between HCO_3^- and H–OH charged resins was even higher $r = 0.82$). These authors cautioned against using H–OH resins for P because of pH changes in the soil–solution matrix, but they used small volume containers in the laboratory. Potentially, the H–OH resins may also cause acidity changes in their immediate surroundings when deployed in the field, which may explain the changes seen in the ratio of HCO_3^- resin P/H–OH resin P across sites (Fig. 3C). However, H–OH resins have long been successfully used to measure N availability, were relatively successful in this regard in this study, and have the advantage of allowing for simultaneous measurement of NH_4–N, NO_3–N, and PO_4–P availability.

Acid-fluoride extractable P and $CaCl_2$-extractable P were also not particularly well correlated ($r = 0.51$). The acid-fluoride extract removes easily acid-soluble P forms, largely Ca–phosphates and a portion of the Al– and Fe–phosphates (Stevenson, 1986). The weak salt solution of $CaCl_2$ would measure porewater P and only the most weakly bound soil P pools. The two extractants gave similar pool sizes in all but the minerotrophic tamarack swamps and beaver meadows, where the acid-fluoride extract suggested much greater available P. This probably reflects more Ca-, Fe-, and Al-bound P in these higher pH, less organic soils.

Overall, these contradictory results suggest that either, (i) the various methods of determining P availability are characterizing different soil pools that do not

Table 4. Spearman correlations ($r \geq 0.50$) for P related variables measured in sites across an ombrotrophic-minerotrophic gradient.

	GS HCO_3^- resin†	GS H–OH resin	W HCO_3^- resin	W H–OH resin	Yr HCO_3^- resin	Yr H–OH resin	AF–P	$CaCl_2$–P	Plant P	Total soil P cm^{-3}	Aer 59-wk Min	An 59-wk Min	Aer 2-wk Min	An 2-wk Min	Aer P_0
GS H–OH resin															
W HCO_3^- resin	0.75														
W H–OH resin															
Yr HCO_3^- resin	0.85		0.96												
Yr H–OH resin		0.92		0.66											
AF–P	0.75	0.54	0.64		0.65	0.63									
$CaCl_2$–P		0.54				0.57	0.51								
Plant P	0.75		0.62		0.74		0.61								
Total soil P cm^{-3}	0.72		0.53		0.61		0.77		0.58						
Aer 59-wk Min															
An 59-wk Min	0.54								0.63	0.50	0.54				
Aer 2-wk Min		0.67		0.66		0.76		0.77							
An 2-wk Min											0.72	0.76			
Aer P_o			−0.59								0.73				
An P_o										−0.64	0.78			0.63	0.78

† Variables as in Table 3, except AF–P = acid-fluoride extractable P and $CaCl_2$–P = 0.01 *M* $CaCl_2$-extractable P.

change in a concerted manner across the ombrotrophic–minerotrophic gradient, or (ii) the large number of standard methodologies that we used are inadequate to determine differences in P availability in a wide range of organic soils. Although we did not determine different soil P pools, it is reasonable to assume that they would change in the variety of soils used in this study. Thus, the differences among P–availability methods could be real and biologically meaningful. Other studies have found better correlations among P–availability indices in mineral soils (Sharpley et al., 1984; Schoenau and Huang, 1991; Sen Tran et al., 1992), which would support the first possibility.

These common methods all have limitations for the measurement of P availability. In particular, geochemical sorption of P places severe methodological limitations on common measurements of biologically available P. Isotopic techniques such as isotopically exchangeable P (White, 1976) may give more meaningful results, although they do not inherently separate out biological mineralization, geochemical sorption, and resultant biological availability. Isotopic gross P mineralization techniques hold promise (Walbridge and Vitousek, 1987; Frossard et al., 1996; Lopez-Hernandez et al., 1998), but they are less developed than gross N mineralization techniques, are quite time consuming, and have been problematic to interpret in some instances. Characterization of P pools in soils is common as an index of availability (Stevenson, 1986), but the results reflect static pools unless placed within an experimental context.

Plant N and P Concentrations

Plant N concentrations were not well correlated with any soil N availability index (Table 3). In contrast, plant P concentrations were positively correlated with HCO_3^- resin P, acid-fluoride extractable P, total soil P content, and anaerobic 59-wk mineralization potentials (Table 4). These results suggest that either, (i) soil N availability indices do not adequately reflect plant N availability, (ii) N does not limit plant growth, or (iii) our sampling scheme for plants was inadequate to capture changes in nutrient availability across the ombrotrophic–minerotrophic gradient. Concerning the first possibility, numerous studies have examined the relationship between plant–nutrient uptake in nutrient-limited vegetation and many of the soil nutrient availability indices, and they have generally shown a good correlation among them (Binkley and Hart, 1989). Additionally, the soil N availability indices tended to give consistent relative results across the gradient, in contrast to the soil P availability indices. Thus, we conclude that it is unlikely that the low correlation between plant N concentration and the soil N indices is because these soil indices are inherently poor at predicting plant nutrient availability.

One way to examine the second possibility (i.e., N does not limit plant growth) is to consider the stoichiometry of nutrient concentrations in leaf tissue. Koerselman and Meuleman (1996) suggested that N/P ratios >16 indicate P limitation, ratios <14 indicate N limitation, and intermediate ratios indicate colimitation by N and P. In our study, the highest N/P ratios in plant tissue occurred in intermediate fens ($\bar{x}$ = 30.4, SE = 0.5), the lowest ratios occurred in cedar swamps ($\bar{x}$ = 12.0, SE = 0.7) and beaver meadows ($\bar{x}$ = 12.3, SE = 0.9), and intermediate ratios occurred in tamarack swamps ($\bar{x}$ = 14.5, SE = 3.5), bogs ($\bar{x}$ = 16.6, SE = 0.7), and acidic fens ($\bar{x}$ = 17.5, SE = 2.8) (Fig. 5, $P < 0.001$ for community effect on N/P ratio). Nutrient stoichiometry suggests N limitation of minerotrophic cedar swamps and beaver meadows, P limitation of intermediate fens, and colimi-

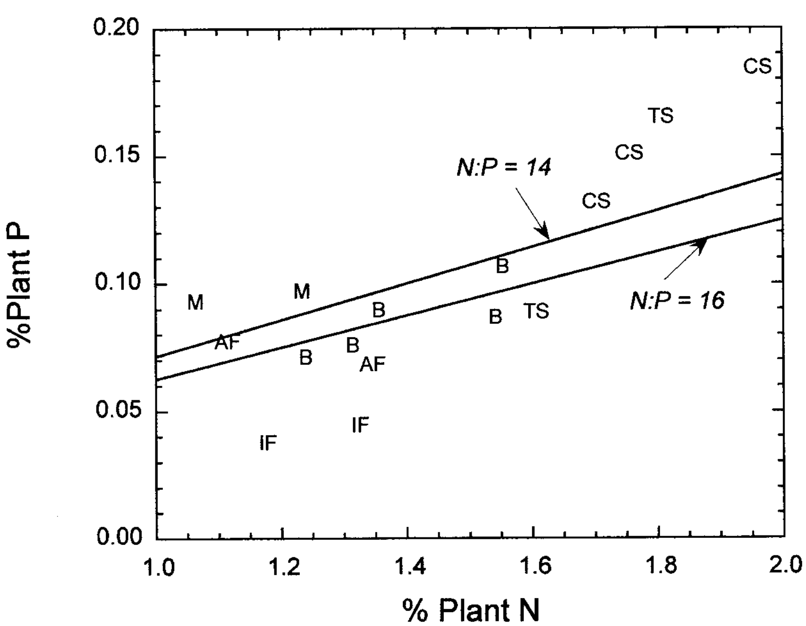

Fig. 5. Nitrogen concentration relative to P concentration in plant tissue across an ombrotrophic–minerotrophic gradient in Minnesota wetlands. According to Koerselman and Meuleman (1996), a N/P ratio <14 indicates N limitation, whereas a N/P ratio >16 indicates P limitation. B = bog, AF = acidic fen, IF = intermediate fen, CS = cedar swamp, TS = tamarack swamp, M = beaver meadow.

tation by N and P in tamarack swamps, bogs, and acidic fens.

Fertilization experiments are a more direct test of plant nutrient limitation. A review of nutrient fertilization studies in peatlands showed that N, P, or K were limiting plant growth, or there was no nutrient limitation, depending on the particular study (Bridgham et al., 1996). Additionally, we and our colleagues have carried out fertilization studies with N and P in one of the bog and intermediate fen sites and both of the beaver meadows included in this study. Overall net primary production (NPP) in the bog showed N toxicity with an addition of only 6 g N m^{-2} yr^{-1} and no effect of P fertilization, whereas P fertilization increased NPP in the fen (Chapin, 1998). Nitrogen and P were colimiting in one of the beaver meadows, but the other meadow showed no significant response to fertilization (Erickson, 1994). In both of these studies, nutrient additions tended to cause higher nutrient concentrations in above ground vegetation, even when there was no increase in NPP, demonstrating luxury nutrient uptake. However, in the bog and fen examined by Chapin (1998), the effect of fertilization on tissue nutrient concentrations varied among species, and there was no increase in N concentration in the overall fen community. Thus, experimental data show that nutrient effects on NPP and tissue nutrient concentrations in wetlands depend on plant community composition and do not necessarily change in a concerted manner across the ombrotrophic–minerotrophic gradient, suggesting that this is a reasonable explanation for the lack of correlation of plant N concentration with the soil N availability indices. Others have suggested that nutrient supply rate (as measured by soil nutrient availability indices) and plant nutrient limitation may be decoupled in natural communities growing in low nutrient environments (Chapin et al., 1986; Binkley and Vitousek, 1989).

Two recent reviews examined changes in nutrient concentrations in plant tissue across the ombrotrophic–minerotrophic gradient, with each using a somewhat different group of published and unpublished studies. Using only North American data, N and P concentrations in plants increased along the ombrotrophic–minerotrophic gradient (Bedford et al., 1999). Based upon N/P ratios of plants and soils, they suggested that North American wetland vegetation was limited by P or showed colimitation by N and P, with the exception that marsh vegetation (qualitatively similar to our beaver meadow vegetation) showed N limitation. In contrast, Aerts et al. (1999) used a global data set and found no difference in the N concentration of plants in bogs and fens, but fen species had a higher P concentration than bog species. In the present study, we found that plant N concentrations were highest in minerotrophic swamp forests and lowest in fens and beaver meadows (Fig. 2), and that plant P concentrations were highest in the swamp forests and lowest in the intermediate fens (Fig. 4). Thus, our data and other studies present somewhat conflicting findings on whether nutrient concentrations increase in plant tissue across the ombrotrophic–minerotrophic gradient.

Concerning the third possibility (i.e., our sampling scheme for plants was inadequate to capture changes in nutrient availability), we picked two plant life forms, graminoids and bryophytes, to examine tissue N concentrations, but species within these life forms varied greatly among sites. Individual species within these life forms may respond very differently to nutrient limitation (Chapin and Shaver, 1985; Chapin, 1998). Additionally, we sampled the vegetation in October when nutrient concentrations were probably at a seasonal low. It is quite possible that individual species were nutrient limited, but our sampling scheme and the lack of common species across the gradient limited our ability to detect these limitations.

In conclusion, most soil N availability indices increased along the ombrotrophic–minerotrophic gradient. Additionally, there was a high degree of correspondence among soil N availability indices along this gradient, indicating that they may be used somewhat interchangeably despite measuring different pools and fluxes. In contrast, P availability indices were poorly correlated and gave contrasting results across the ombrotrophic–minerotrophic gradient. However, there was an overall suggestion that soil P availability was greatest in minerotrophic swamp forests and/or beaver meadows and low in bogs and fens. We suggest that current P–availability methods may give highly contradictory results and more research is necessary in developing techniques that give straightforward biological interpretation. Plant nutrient concentrations did not show clear relationships with soil nutrient indices, particularly for N, which probably reflects the complicated relationship between soil nutrient availability and plant response in natural wetlands.

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