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Phosphorus retention and movement across an ombrotrophic-minerotrophic peatland gradient

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Abstract. An understanding of the mechanisms controlling nutrient availability and retention in and across ecosystems allows for a greater understanding of the role of nutrients in maintaining ecosystem structure and function. To examine the underlying mechanisms of phosphorus (P) cycling in northern peatlands, we compared the retention and movement of P across a natural hydrologic/pH gradient in nine peatlands by applying as a light rain an *in situ* tracer amount of $^{32}PO_4^{-3}$ to track changes in P pools (vegetation, soil, microbial) over 30 days. The ^{31}P concentrations of available P, microbial P, and the root P at 10–20 cm did not differ across the gradient, although total soil P and aboveground vegetation P content (μg m^{-2}) increased from bog to rich fen. Total retention of ^{32}P in the first 24 hours of application was greatest in the bogs and intermediate fens (90–100%) and was very low (20–50%) in the rich fens. Retention of P in the different pools was dependent on the type of peatland and changed with time. In the first 24 hours in the bogs and intermediate fens, the microbial pool contained the largest amount of ^{32}P, but by the seventh day, the aboveground vegetation contained the largest amount. In the rich fen, the recovered ^{32}P was almost equally divided between the aboveground vegetation and the litter layer with very little in other pools. Therefore, although bogs and intermediate fens have a small total P pool, they have similar P availability to rich fens because of rapid cycling and efficient retention of P.

Introduction

The most limiting nutrient to ecosystem production is theorized to be tightly controlled and retained in order to maintain ecosystem stability (Aerts 1999). However, increasing anthropogenic nutrient loading directly affects ecosystems through alterations in primary production (Davis 1989; Berg and Tamm 1991; Chapin 1998), nutrient cycling, nutrient retention (Richardson and Qian 1999), and plant community dynamics (Craft and Richardson 1997; Jonasson et al. 1999). A knowledge of mechanisms and interactions governing nutrient cycling and retention within a system can lead to better predictions of consequences to anthropogenic disturbances and potential extrapolation to a more general theory (Hedin et al. 1995; Jonasson et al. 1999). Greater clarification of ecosystem nutrient cycling will be gained through the analysis of the least impacted sites and utilizing this as a reference point to further study (Hedin et al. 1995).

Most nutrient cycling and retention studies in wetlands have focused on the role of nitrogen (Bowden 1987; Golterman 1995; Hedin et al. 1998). Although nitrogen limits ecosystem production in most terrestrial (Vitousek and Howarth 1991) and some wetland ecosystems (Bedford et al. 1999), primary production in many wetlands, including peatlands, in North America has been found to be limited by phosphorus availability (Bridgham et al. 1996; Chapin 1998; Bedford et al. 1999). However, the mechanisms that control the cycling of P, and therefore the availability of P, within peatlands are still poorly understood. For example, in a fertilization study in the Everglades, Chiang et al. (2000) found that increasing P input did not necessarily significantly increase easily exchangeable phosphorus. As in all ecosystems, this is primarily due to the complex interactions between geochemical and biological processes that control the cycling of P (Chapin et al. 1978; Walbridge 1991; Walbridge and Struthers 1993; Bridgham et al. 2001).

Peatlands are a diverse group of ecosystems structured by the amount and source of hydrologic inputs (Moore and Bellamy 1974; Bridgham et al. 1996). Ombrotrophic bogs receive only atmospheric inputs of nutrients, basic cations, and water and consequently have poorly buffered, low pH soils. They are dominated by plant species typically thought to reflect nutrient poor conditions, e.g., *Sphagnum* mosses, ericaceous shrubs and *Picea mariana*. Minerotrophic fens receive ground water and/or surface flow from the surrounding watershed, maintaining a higher pH and receiving a much higher input of nutrients than bogs. Because nutrient inputs are less in ombrotrophic bogs, the assumption has been that nutrient retention should be higher in bogs than fens (Damman 1988). Retention of nutrients is controlled by geochemical, microbial, and vegetative interactions (Pomeroy 1970; Richardson and Marshall 1986; Walbridge 1991; Walbridge and Struthers 1993; van Breemen and Finzi 1998); therefore the expectation is that these interactions would more tightly control nutrients within the bog ecosystem.

Since increased ground-water inputs must be accompanied by increased nutrient inputs, it has been assumed that availability of nutrients to vegetation and microbial communities is much higher in minerotrophic peatlands (cf. Damman (1986) and Bridgham et al. (1996)). Some studies have found that total soil nutrients pools are smaller in ombrotrophic bogs than in minerotrophic fens (Vermeer and Berendse 1983; Bridgham et al. (1998, 2001)), whereas other studies have found no difference (Vitt 1990). However, mineralization rates and soil extractions show that nutrient availability in bogs can be as high as or higher than in rich fens (Verhoeven et al. 1990; Walbridge 1991; Bridgham et al. 1998; Chapin 1998). A comparison of a large number of different nutrient availability indices in a variety of wetlands found consistently higher N availability in minerotrophic peatlands, but results for P were contradictory and depended strongly on the method used (Bridgham et al. 2001). Thus, the assumption that availability of nutrients correlates with hydrologic inputs is a more complex issue than originally thought and remains in dispute, particularly for P.

We used *in situ* applications of $^{32}PO_4^{-2}$ to: 1) quantify the retention and partitioning of P within different peatland types, and 2) compare changes in P availability across the ombrotrophic-minerotrophic gradient. In this experiment, we tested three major hypotheses: 1) ombrotrophic bogs, with their lower nutrient inputs, have higher retention of P; 2) biotic components, such as vegetation and microorganisms, are more important in P retention in bogs than in fens because of bogs' lower mineral content; and 3) P availability is higher in bogs than in fens because of less geochemical control in the bogs and high microbial turnover.

Methods

Site description

Sites were located in the Upper Peninsula of Michigan in Gogebic County (46° N, 89° W) at the University of Notre Dame Environmental Research Center (UNDERC) and the Ottawa National Forest. In May of 1997, based on plant communities and pH, we selected three rich fens, three intermediate fens and three bogs (Table 1). The vegetation in the rich fens ($pH = 6.0$) was dominated by *Carex* spp., *Calamagrostis canadensis* and scattered *Alder rubrus* and *Salix* spp. Water levels in the rich fen remained above the surface of the peat for the duration of this study (June 1 to July 15, 1998). The dominant vegetation in the intermediate fens ($pH = 4.9$) was *Carex* spp., *Eriophorum vaginatum*, *E. virginicum*, and *Sphagnum* spp. mosses. Ericaceous shrubs such as *Ledum palustre* and *Chamaedaphne calyculata* were also present. In June the water levels in the intermediate fens were above the surface of the peat, but by July 15 the water levels had dropped to the surface. The dominant vegetation in the bogs ($pH = 3.8$) was *Sphagnum* spp. and ericaceous shrubs such as *Vaccinium* spp., *Ledum palustre*, and *Chamaedaphne calyculata*. In June the water level in the bogs was at the surface of the *Sphagnum* carpet but was 5 to 10 cm below the surface by the end of July.

^{32}P application and sample collection

We chose a 4-m^2 treeless plot within each peatland. The plot was enclosed with galvanized steel roofing sheets that spanned 0.5 m above and below the surface of the soil. These remained in place for the duration of the growing season to minimize horizontal movement of the radiotracer, but they did not impede vertical water flux. Although retention time of water within these wetlands was not measured, there was no discernable surface flow even within the rich fens. In mid-June, we applied 9.25×10^4 MBq m^{-2} of carrier-free $KH^{32}PO_3$ (<3.0 mM) as a radioactive tracer dissolved in 2 l of filtered water from the site. The mixture was sprayed onto the plot with a pump sprayer simulating a light rain.

At 1, 7, 14, and 30 days after ^{32}P application, we collected soil and plant samples. Also at each sampling period we measured radioactivity outside of the plots with a Geiger counter and did not have detectable radioactivity. At each time period we collected three soil cores from each plot to a depth of 20 cm using 7-cm diameter PVC pipes. These cores were then cut into two 10-cm sections. The sec-

Table 1. Mean soil site characteristics. All except microbial P are averaged over the two depths (0–10, 10–20 cm). Soil depth interacted with site for microbial P biomass in the repeated measures ANOVA and therefore was separated. Letters indicate significant difference among the peatland types ($p < 0.05$). Numbers indicate significant differences within peatlands between the two depths ($p < 0.05$). Numbers in the parentheses are standard error.

Peatland Type	pH	Bulk Density (g soil cm^{-3})	Total C (g cm^{-3})	Total N (mg cm^{-3})	Total P (ug cm^{-3})	Microbial P (ug cm^{-3})	
						0–10 cm	10–20 cm
Bog	3.8 (0.03)^{A}	0.09 (0.008)^{A}	0.089 (0.003)^{A}	1.40 (0.17)^{A}	44.5 (3.3)^{A}	12.5 (1.6)^{1}	11.6 (1.4)^{1}
Int. Fen	4.9 (0.05)^{B}	0.13 (0.011)^{B}	0.114 (0.004)^{B}	3.25 (0.52)^{B}	75.9 (8.0)^{B}	21.7 (11.7)^{1}	11.7 (1.4)^{2}
Rich Fen	6.0 (0.05)^{C}	0.21 (0.018)^{C}	0.181 (0.002)^{C}	9.29 (0.45)^{C}	147.6 (17.4)^{C}	19.1 (11.1)^{1}	11.1 (1.7)^{2}

tions were placed on ice and processed within 24 hours. Total aboveground vegetation was clipped to ground level in three 49-cm^2 subplots within each main plot. The litter layer was also collected within the 49-cm^2 subplots.

Sample analysis

Living roots were handpicked from each core section, and roots and aboveground vegetation were dried at 65 °C for 24 hours to determine belowground and aboveground biomass. Subsamples of the root-free soil were dried at 65 °C for 48 hours to determine moisture content and bulk density. A subsample of roots, root-free soil, and aboveground vegetation were ground using a Udy mill to pass a 2-mm sieve (Udy Corporation, Fort Collins, Colorado). The ground subsamples were then digested using a sulfuric acid/hydrogen peroxide solution (Lowther 1980) and analyzed for total P.

We determined available soil PO_4-P for each 10-cm depth using a dilute acid-fluoride (AF) extraction on 5-g wet-weight subsamples (Olsen and Sommers 1982). Microbial P was calculated as the increase in AF-extractable P after chloroform-fumigation of subsamples using an efficiency factor (k_p) of 0.4 to correct for incomplete recovery of the microbial biomass (Brookes et al. 1984; Walbridge 1991). Fifteen grams of wet-weight soil was sealed in a vacuum desiccator with chloroform and incubated for 24 hours (Brookes et al. 1984).

A molybdate colorimetric method was used on a Lachat QuikChem 8000 Autoanalyzer to analyze all phosphorus fractions (Lachat #10–465, Milwaukee, WI). Nitrogen and carbon concentrations for soil, plant and root solid samples were determined on a Carlo-Erba CHN elemental analyzer/mass spectrophotometer. We determined ^{32}P contents of all P fractions using Cerenkov liquid scintillation. Before radioactive analysis for the AF-extractable P, we partitioned the dissolved organic ^{32}P from the inorganic ^{32}P using a butanol/molybdate separation and counted only the inorganic P fraction (Jayachandran et al. 1992).

Statistical analysis

For ^{31}P and ^{32}P concentrations within the aboveground vegetation and the litter layer, we used repeated measures analysis of variance (ANOVAR) to test for interactions between time and peatland type. For analyses with a significant interaction between peatland type and time ($p < 0.05$), we examined the differences among the peatland types within each time period and then determined the differences across time for each peatland type (Zar 1996). For ^{31}P and ^{32}P concentrations within the root and soil fractions, we used ANOVAR to test for interactions between time, depth, and peatland type. For analyses with a significant interaction ($p < 0.05$), we determined depth and time differences within each peatland type and then examined the differences among peatland types within each depth and time period (Zar 1996). To determine pairwise comparisons, we used a Tukey post hoc test.

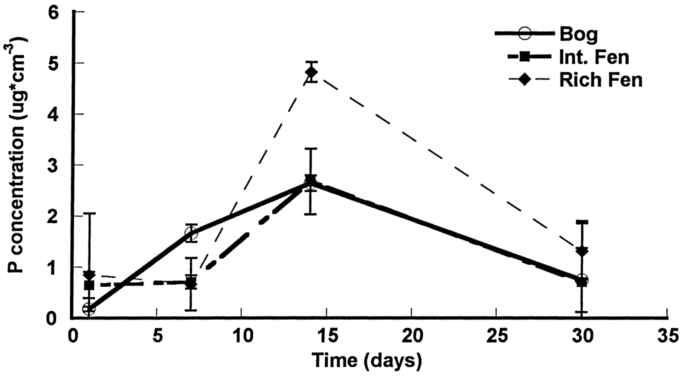

Figure 1. Available P (μg*cm^{-3}) pool across time. Day 14 was significantly higher in all peatland types ($p < 0.05$). Error bars are 1 standard error.

Results

^{31}P pools

Neither available soil P (Figure 1) nor microbial soil P pool sizes (Table 1) differed across the gradient, although the total soil P concentration increased from bog to fen (ANOVAR $p = 0.001$, Table 1). Within the intermediate fens and the rich fens, the microbial soil P pool was larger in the 0–10 cm depth than in the 10–20 cm depth (ANOVAR 0.029, Table 1) but there was no depth effect for the bogs.

Although total aboveground vegetation ^{31}P concentration (mg g^{-1} of vegetation) and biomass did not significantly differ across the gradient, total aboveground vegetation ^{31}P content (g m^{-2}) doubled from bog to rich fen and remained consistent through time (ANOVAR 0.025, Table 2). The same pattern occurred in the litter, with litter ^{31}P concentration (mg g^{-1}) equivalent across the gradient, but biomass and ^{31}P content (g m^{-2}) increasing from bog to rich fen (Table 2).

Differences in root biomass depended on both peatland type and depth (ANOVAR type × depth interaction $p = 0.027$, Table 2). Root biomass was higher in the 0–10 cm depth than in the 10–20 cm depth in the intermediate and rich fens (ANOVA $p = 0.015$, 0.001 respectively). Conversely, bogs had higher root biomass in the 10–20 cm depth than the 0–10 cm depth (Tukey $p = 0.025$). In the 0–10 cm depth, root biomass was lowest in the bog and similar in the intermediate and rich fens (Table 2). Root biomass in the 10–20 cm depth in the bog and intermediate fen was more than twice that of the rich fen.

Belowground ^{31}P concentration (mg g^{-1} root) across the gradient interacted with depth (ANOVAR peatland type × depth $p = 0.001$, Table 2), with no difference among peatland types in the 0–10 cm depth but greater ^{31}P concentration in the rich fen in the 10–20 cm depth (Tukey $p = 0.01$). Root ^{31}P content (g m^{-2}) differed based on depth and site (ANOVAR type × depth interaction $p = 0.001$, Table 2). In the 0–10 cm depth, the intermediate and rich fens were higher than the bog (Tukey

Table 2. Living and dead vegetation for each peatland type. The letters denote significant differences among the peatland types ($p < 0.05$) and numbers denote significant differences within peatlands between depths. Numbers in parentheses are one standard error.

	Peatland Type		
	Bog	Int. Fen	Rich Fen
Above ground plant			
Biomass (kg m^{-2})	0.563 (0.0046)	0.775 (0.119)	0.820 (0.188)
P (g m^{-2})	0.503 (0.051)^{A}	0.905 (0.100)^{B}	1.002 (0.058)^{C}
P (mg g^{-1} of veg)	1.01 (0.194)	1.39 (0.253)	1.34 (0.248)
^{32}P (MBq m^{-2})	4471.2 (600)^{A}	3335.9 (320)^{A}	1348.5 (235)^{B}
Belowground plant 0–10 cm			
Biomass (kg m^{-2})	0.770 (0.15)^{A1}	3.110 (0.60)^{B1}	3.398 (1.35)^{B1}
P (g m^{-2})	0.479 (0.017)^{A}	1.884 (0.057)^{B}	2.249 (0.103)^{B}
P (mg g^{-1} of veg)	0.623 (0.115)^{1}	0.606 (0.095)^{1}	0.662 (0.077)^{1}
^{32}P (MBq m^{-2})	0	0	0
Belowground plant 10–20 cm			
Biomass (kg m^{-2})	1.458 (0.34)^{A2}	1.656 (0.26)^{A2}	0.688 (0.12)^{B2}
P (g m^{-2})	0.589 (0.013)	0.763 (0.010)	0.353 (0.012)
P (mg g^{-1} of veg)	0.404 (0.04)^{A2}	0.461 (0.039)^{A2}	0.746 (0.101)^{B2}
^{32}P (MBq m^{-2})	0	0	0
Total Living Plant			
Biomass (kg m^{-2})	2.791 (0.494)^{A}	5.541 (0.979)^{B}	4.906 (1.658)^{B}
P (g m^{-2})	1.571 (0.018)^{A}	3.552 (0.167)^{B}	3.604 (0.173)^{B}
P (mg g^{-1} of veg)	2.118 (0.713)	2.457 (0.387)	2.748 (0.426)
^{32}P (MBq m^{-2})	4471.2 (600)^{A}	3335.9 (320)^{A}	1348.5 (235)^{B}
Litter			
Biomass (kg m^{-2})	0.0087 (0.004)^{A}	0.0047 (0.003)^{A}	0.2372 (0.137)^{B}
P (g m^{-2})	0.0049 (0.003)^{A}	0.0214 (0.009)^{B}	0.1195 (0.074)^{B}
P (mg g^{-1} of veg)	0.462 (0.048)	0.521 (0.033)	0.473 (0.052)
^{32}P (MBq m^{-2})	109.3 (45.7)^{A}	352.6 (112.3)^{B}	1253.8 (662.9)^{C}

$p = 0.042$, 0.015 respectively). In the 10–20 cm depth, the sites did not significantly differ.

Bulk density and total soil carbon more than doubled from bog to rich fen (ANOVA $p \leqslant 0.001$, Table 1). One of the more dramatic differences was in total soil nitrogen, which was almost nine times higher in the rich fen than in the bog (ANOVA $p = 0.013$, Table 1). Bulk density, total soil carbon, and total soil nitrogen did not differ over the incubation period.

^{32}P dynamics

The total retention of ^{32}P was higher in the bogs and intermediate fens than in the rich fens over the entire 30-day incubation period, but there was no difference in retention between the bogs and intermediate fens (Figure 2). However, retention

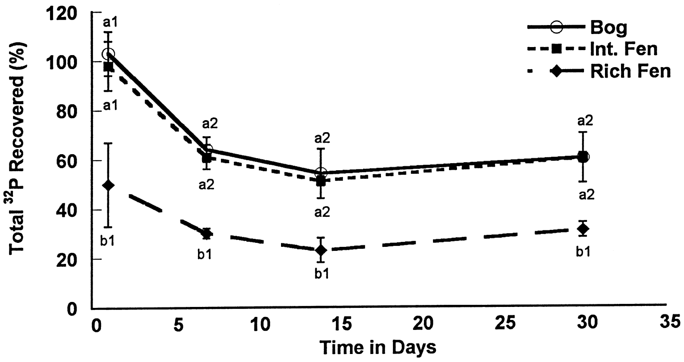

Figure 2. Percentage of the total added ^{32}P recovered within each peatland type. In all peatlands, total recovered ^{32}P decreases after the first day and becomes relatively stable by day seven. Letters denote statistical difference among the peatland types within a sampling period ($p \leqslant 0.05$). Numbers denote statistical difference within peatland types across time ($p \leqslant 0.05$). Error bars represent ± 1 standard error.

decreased between Day 1 and Day 7 in the bog and intermediate fen sites but not in the rich fen sites (ANOVAR type × time interaction $p = 0.001$). Retention in the bog and intermediate fen was close to 100% at Day 1 but fell to 63% by Day 7 and remained relatively constant thereafter (Figure 2). The total percentage of recovered ^{32}P in the rich fen was relatively constant over the 30-day sampling period at 30–45% (Figure 2).

The distribution of recovered ^{32}P among the pools varied over time within the bogs and intermediate fens (ANOVAR pool × time interaction $p = 0.001$, 0.042 respectively). However, there was no corresponding change over time in the distribution of ^{32}P in the rich fens. In the bogs and intermediate fens on Day 1, 65% of the total recovered ^{32}P was found in the microbial pool, but recovery in the microbial pool decreased to 25–30% by Day 7 (Fig. 3a). In contrast, the vegetation contained the largest percentage of the total recovered ^{32}P by Day 7 (ANOVA $p = 0.01$) (Fig. 3b). In the bogs, there was a significant decrease in the available ^{32}P pool at Day 14 (ANOVA $p = 0.01$). The intermediate fens showed the same trend as the bogs with two exceptions. First, there was an increase in the available ^{32}P pool at Day 14, rather than a decrease (Fig. 3c). Second, by Day 30 the microbial biomass again contained the highest percentage of recovered ^{32}P (Fig. 3a, b). The rich fen ^{32}P distribution remained equally divided between the microbial and vegetation pools over time, even though the available ^{32}P pool increased at Day 14 (Fig. 3a, b, c).

Total ^{32}P amounts within the different pools differed based on peatland type over time. Microbial ^{32}P decreased in all peatland types in the 0–10 cm depth between Day 1 and Day 7 (ANOVAR $p = 0.042$) and increased between Day 14 and Day 30 (ANOVAR $p = 0.032$, Fig. 4a), but remained relatively stable over time in the 10–20 cm depth (Fig. 4b). Total microbial ^{32}P activity was consistently greater in the bogs and intermediate fens than in the rich fens in the 0–10 cm depth with the exception of Day 30, but there were no differences in microbial ^{32}P activity among the peat-

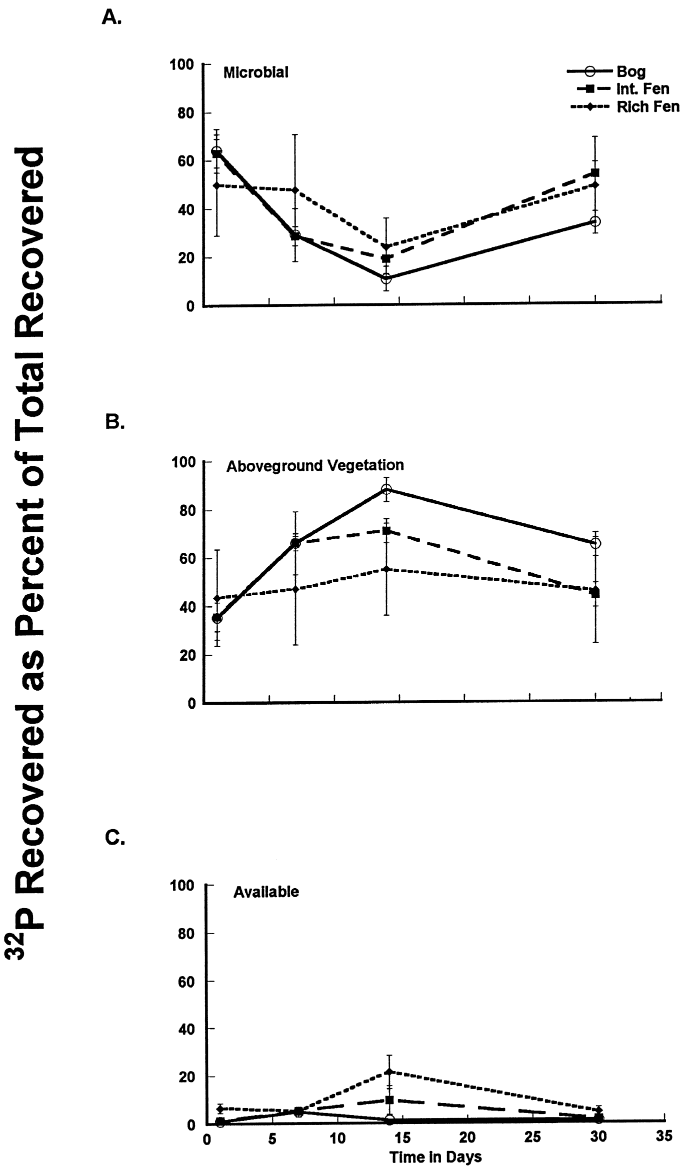

Figure 3. Percentage of the recovered ^{32}P found in the different P pools. The microbial pool for the rich fen includes the litter layer. The soil fractions are summed over both depths. Error bars represent ± 1 standard error.

land types in the 10–20 cm depth. Total ^{32}P activity in the available P pool did not vary with depth, but peatland type and time interacted because of an increase in this pool in the intermediate and rich fens at Day 14 (ANOVAR type × time inter-

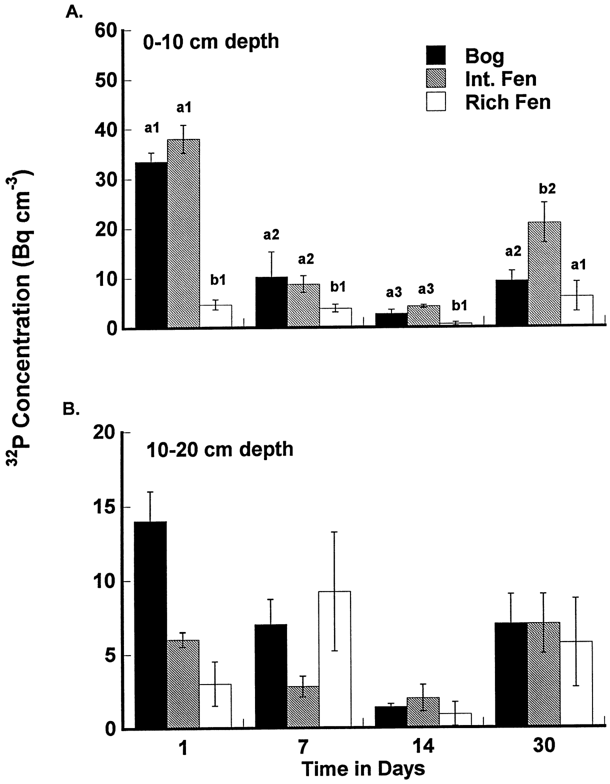

Figure 4. Microbial Biomass ^{32}P. Microbial ^{32}P in the (a) 0–10 cm depth was greatest in the bogs and intermediate fens, with the exception of Day 30. Microbial ^{32}P in the (b) 10–20 cm depth did not follow this pattern. Letters denote statistical differences within a sampling period ($p < 0.05$). Numbers denote statistical differences among time periods within a peatlands type ($p < 0.05$). Error bars are ± 1 standard error.

action $p = 0.001$; Tukey $p = 0.01, 0.001$ respectively, Figure 5). No ^{32}P activity was found in the total soil P pool at any time period.

The aboveground vegetation pool content (MBq m^{-2}) did not differ over time, although the bogs and intermediate fens were higher than the rich fens (Tukey $p = 0.045, 0.042$ respectively). No detectable ^{32}P was found in the belowground vegetation at any time period.

Discussion

^{31}P pools

With increasing minerotrophy, there was a distinct change in the type of vegetation found — a switch from primarily evergreen species to deciduous species (personal

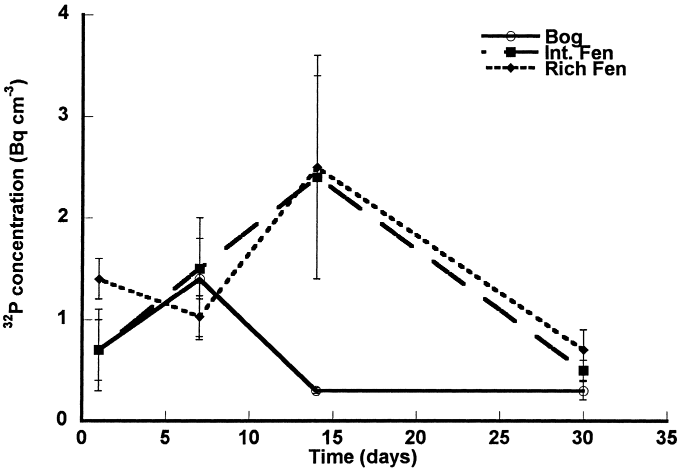

Figure 5. ^{32}P found in the available P pool. Day 14 was significantly higher in the intermediate and rich fens ($p < 0.05$). Error bars are ± 1 standard error.

observation) corresponding to a hypothesized change in nutrient uptake from low to high nutrient availability (Small 1972). However, we found no statistical difference in aboveground vegetation biomass or P concentration (P mg g^{-1} vegetation) across the gradient. Nor did we find a difference among the peatland types with total vegetation P concentration (P mg g^{-1} vegetation). By using the vegetation nutrient concentration as an indicator for nutrient availability (Chapin and Van Cleve 1994) this demonstrates that available P is as high in the bog as the rich fen. Furthermore, the measured available ^{31}P pool did not differ across the gradient. These two lines of evidence confirm that despite P inputs being larger in rich fens, bogs do not necessarily have lower P availability.

Nevertheless, the P content (P mg m^{-2}) of the aboveground vegetation increased from bog to rich fen. This indicates that statistically insignificant differences in the biomass ($p = 0.095$) of the aboveground vegetation combined with the P concentration produced differences large enough to be statistically significant for the P content (P mg m^{-2}). Therefore, the trend of increasing biomass from bog to rich fen, though not statistically significant, is most likely real and is similar to results found in other peatland studies of aboveground vegetation biomass (Szumigalsky and Bayley 1996).

We found in intermediate and rich fens that root biomass decreased with depth, which corresponded to a decrease in the microbial ^{31}P biomass. A combination of decreasing nutrient availability with peat depth (e.g. Updegraff et al. (1995)) and increasing anoxia associated with prolonged waterlogging (e.g. Megonigal and Day (1992)) will likely restrict root biomass to the more actively decomposing peat, as we see in this study. As the root biomass in peatlands diminishes with depth, the microorganisms associated with the rhizosphere would also be expected to decrease. Recently, data has shown that the population distribution of soil microorganisms follows the growth pattern of roots, primarily due to the root exudates (van

Bruggen et al. 2000). Further, with increasing depth, peat becomes more recalcitrant (Hogg 1993; Updegraff et al. 1995). This combination of decreasing root biomass and more recalcitrant carbon in the peat depth would be expected to cause a decrease in microbial ^{31}P biomass, which we see in the intermediate and rich fens.

Conversely, in bogs, root biomass doubled with increasing depth, which has also been seen in pine bogs (Håland and Brække 1989). In contrast, the ^{31}P concentration (mg g^{-1} vegetation) decreased. Furthermore, unlike the intermediate and rich fens, the bog microbial ^{31}P biomass did not decrease with depth. Because root biomass provides soil microorganisms labile carbon and nutrients in the form of root exudates and habitats through the alteration of the soil medium, the increase in roots at 10–20 cm depth in the bogs may have maintained the microbial biomass, even though decomposition and nutrients decrease with depth (Vitt 1990; Hogg 1993). However, the decreased nutrient concentration of the belowground vegetation combined with increasing recalcitrant material may limit microbial ^{31}P biomass. The equivalent microbial ^{31}P pools with depth demonstrate that there are limitations other than belowground vegetation restricting microorganism growth.

^{32}P dynamics

In this study, the short-term retention of P was mediated in all peatland types primarily by biotic components. As in other studies in peatlands (Richardson and Marshall 1986; Walbridge 1991), the microbial pool was important for initial uptake of P, in some cases accounting for up to 75% of the total added ^{32}P (Fig. 3a). However, microbial retention and its importance depended on peatland type. If we assume that ^{32}P recovered in the litter layer was primarily associated with attached microbial biomass (cf. Richardson and Marshall (1986)), then the soil microbial pool constituted half of the recovered ^{32}P in the rich fens even though the ^{31}P microbial pool represented only 9–13% of the total soil ^{31}P pool. Our results imply that microbial P uptake in minerotrophic wetlands is more important than previously believed (Walbridge 1991; Walbridge and Struthers 1993).

However, the low recovery (<50% in most cases, Figure 2) of ^{32}P in the rich fens indicates either a loss from the system or adsorption to physical exchange sites, both of which could be geochemically driven. Although ^{32}P was below our detection limit in total soil P, we cannot rule out that some of the missing ^{32}P in the minerotrophic peatlands may have been due to soil adsorption. The dilution caused by the digestion for total soil P combined with the disintegration of ^{32}P before counting limited our ability to detect low levels of adsorbed ^{32}P and could correspond to up to 15% of the original addition of ^{32}P. Furthermore, the ^{31}P pool in the rich fen sites is three times higher than bogs and double the amount in the intermediate fens; therefore, we are confident that geochemical controls are active in the rich fens. However, acid-fluoride promotes dissolution of aluminum phosphates (Susuki et al. 1963), and the low levels of ^{32}P in this fraction suggests that aluminum phosphates, even in the rich fens, were not a dominant geochemical P sink over the 30 day incubation period.

The microbial pool was the dominant pool in the bog and intermediate fen sites for uptake and retention of P. Unlike the rich fens, the bog and intermediate fen sites had very little surface litter. The behavior of the microbial pool has major implications for the maintenance of available P at higher than expected levels in the more ombrotrophic sites. This is illustrated by the high rate of initial microbial uptake, subsequent turnover, and reuptake that occurred in both the bogs and intermediate fens (Fig. 3a).

As in other studies in peatlands, the microbial pool in the bog and intermediate fen sites rapidly sequestered a large majority of the added ^{32}P (Richardson and Marshall 1986; Walbridge and Vitousek 1987; Walbridge 1991). However, this initial uptake was quickly (7 days) followed by a large release of ^{32}P, which by Day 30 had begun to be taken up again (Fig. 3a). Microbial activity has long been assumed to be lower in bogs than in the more minerotrophic systems due to pH restrictions (Waughman 1980; Runge 1983), low nutrient levels (Fauci and Dick 1994), and recalcitrant carbon (Clymo and Hayward 1982; Wilson and Fitter 1984; Bridgham et al. 1998; Chapin 1998). In this study, we have shown not only that microbial biomass ^{31}P was similar across the gradient, but also, microbial activity as P uptake was higher in the more ombrotrophic sites. Higher net mineralization of P has also been found in peat from ombrotrophic peatlands (Verhoeven et al. 1990; Bridgham et al. 1998). This high turnover rate insures greater than expected values of available P in the soil solution within the more ombrotrophic sites even though P inputs may be low.

Aboveground vegetation also proved to be an important sink, which was consistent across the gradient. The percentage of the recovered ^{32}P found in the vegetation was approximately 50%, although in the bog this rose to 80% by Day 14 (Fig. 3b) while the ^{31}P vegetation pool was the second largest pool in all sites (total soil ^{31}P being the largest). In all peatland types, we found no evidence that P was translocated from the aboveground plant parts to the roots or soil during the study period that encompassed the early part of the growing season (June 1 to July 15). The initial uptake of the aerially applied ^{32}P by aboveground vegetation was high in all the sites. Although uptake of aerially introduced nutrients is hypothesized to be limited to the moss functional group (Malmer 1993; Bridgham et al. 1996), because mosses were either absent or limited in the rich fens, we have shown that the vascular plants play a substantial role in aerial uptake.

Richardson and Marshall (1986) found that although under natural conditions plants played an important role in P retention, microorganisms and adsorption were more important. These findings contrast with this study in which the plant and microorganisms appear to play equally important parts in uptake. However, the vegetation may provide a stronger sink when P is introduced aerially by potentially alleviating competition between roots and microorganisms. This is especially important in areas where dry and wet deposition of P may be a significant input in regions with oceanic aerosols, intense agricultural, wind-blown erosion, and burning (Redfield 1998).

The function of the vegetation in bogs and intermediate fens in retention of P was both direct and indirect. The absolute amount of ^{32}P found in the vegetation did not change; therefore the vegetation effectively absorbed and retained the applied ^{32}P. However, due to changes in other pools, the percentage of the total recovered ^{32}P in vegetation differed with time. In the bog and intermediate fen sites, the percentage of the total recovered ^{32}P found in the vegetation increased over time until Day 14, after which there was a decrease caused by increasing uptake in microbial biomass (Figure 3). Thus, during our study, the vegetation tightly held the applied ^{32}P, but the microbial pool was much more dynamic temporally.

Conclusions

From the results of this study, we conclude that the mechanisms controlling P availability and cycling do not necessarily respond to pH and hydrologic changes along a gradient in a coordinated way. In agreement with our first hypothesis, we found that P retention was greatest in sites with less input, although the intermediate fens in this study acted similar to the bogs. This similarity may be caused by the similarity of vegetation between the bog and intermediate fen sites. We demonstrated that retention is controlled primarily by vegetation and microorganisms in the bogs and intermediate fens, which correspond to the largest ^{31}P pools also.

Our second hypothesis was partially confirmed in that we demonstrated that P cycling in the bogs and intermediate fens is a closed cycle with primarily biotic retention mechanisms, as suggested by Richardson and Marshall (1986). However, retention of P in the rich fen was also greatly affected by the vegetation and microbial pools. As percentages of the total recovered ^{32}P, the vegetation and microbial pools in the rich fens were in the same range as the intermediate fens and bogs. But the rich fens seem to be responding to different mechanisms as shown by the overall lower P retention. However, we may have underestimated phosphate adsorption to soil particles in the rich fens because of methodological limitations (i.e., sample dilution and isotope disintegration), but at the maximum it would have represented 15% of the added ^{32}P. If this had been the case with the maximum amount added into our findings, then retention of P within the rich fens would then have been divided equally among the total soil, vegetation, and microbial P pools, demonstrating that biotic control is still important in the more minerotrophic wetlands.

Finally, our third hypothesis of greater P availability in the more ombrotrophic sites was not supported in this study. The availability of P did not differ across the gradient, despite the larger P pools in the more minerotrophic sites. We found that microbial biomass was highly dynamic within bogs and intermediate fens. Because of this constant turnover, P mineralization of microbial biomass is likely to be high, maintaining the observed availability of P. In conclusion, the P cycle in these peatlands is controlled by factors that are not easily predicted from the hydrogeochemical gradient of ombrotrophy to minerotrophy, but instead are controlled by subtle differences in biota among the sites.

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