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Nutrient Control of Microbial Carbon Cycling Along an Ombrotrophicminerotrophic Peatland Gradient

Nutrient control of microbial carbon cycling along an ombrotrophic-minerotrophic peatland gradient

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[1] Future climate change and other anthropogenic activities are likely to increase nutrient availability in many peatlands, and it is important to understand how these additional nutrients will influence peatland carbon cycling. We investigated the effects of nitrogen and phosphorus on aerobic CH_4 oxidation, anaerobic carbon mineralization (as CO_2 and CH_4 production), and anaerobic nutrient mineralization in a bog, an intermediate fen, and a rich fen in the Upper Peninsula of Michigan. We utilized a 5-week laboratory nutrient amendment experiment in conjunction with a 6-year field nutrient fertilization experiment to consider how the relative response to nitrogen and phosphorus differed among these wetlands over the short and long term. Field fertilizations generally increased nutrient availability in the upper 15 cm of peat and resulted in shifts in the vegetation community in each peatland. High nitrogen concentrations inhibited CH_4 oxidation in bog peat during short-term incubations; however, long-term fertilization with lower concentrations of nitrogen stimulated rates of CH_4 oxidation in bog peat. In contrast, no nitrogen effects on CH_4 oxidation were observed in the intermediate or rich fen peat. Anaerobic carbon mineralization in bog peat was consistently inhibited by increased phosphorus availability, but similar phosphorus additions had few effects in the intermediate fen and stimulated CH_4 production and nutrient mineralization in the rich fen. Our results demonstrate that nitrogen and phosphorus are important controls of peatland microbial carbon cycling; however, the role of these nutrients can differ over the short and long term and is strongly mediated by peatland type.

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1. Introduction

[2] Over the past ~10,000 years, many northern wetlands have accumulated deep organic soils (i.e., peat) owing to an imbalance between plant production and decomposition. Despite covering <3% of the terrestrial land surface, peatlands currently store an estimated 460×10^{15} g of carbon, approximately one third of the terrestrial soil carbon pool [*Maltby and Immirzi*, 1993; *Gorham*, 1995]. In response to future global change, peatlands may release this large store of carbon as methane (CH_4) and/or carbon dioxide (CO_2), augmenting anthropogenic emissions of these important greenhouse gases. Microbial processes, including the mineralization of organic carbon to CO_2 and CH_4 and the aerobic oxidation of CH_4 to CO_2, are key regulators of the CH_4 and CO_2 flux from peatlands [*Blodau*, 2002]. Understanding the controls of peatland microbial carbon cycling is therefore crucial to understanding the carbon balance of these ecosystems and has important implications for global climate change [*Gorham*, 1995; *Bridgham et al.*, 1995; *Moore et al.*, 1998].

[3] Similar to other natural ecosystems, peatlands are experiencing increased nutrient (especially nitrogen and phosphorus) loading due to agricultural inputs, atmospheric deposition, and other anthropogenic activities [*Vitousek et al.*, 1997; *Richardson and Qian*, 1999; *Tilman*, 1999; *Tilman et al.*, 2001; *Galloway et al.*, 2003]. Future nutrient dynamics in peatlands (e.g., mineralization) are likely to be further altered in response to climate change [*Bridgham et al.*, 1995; *Updegraff et al.*, 1995; *Keller et al.*, 2004]. Thus it is likely that nitrogen and phosphorus will become increasingly important controls of microbial activities in peatland ecosystems.

[4] Understanding the impact of nutrients on microbial carbon cycling is complicated in part because nutrients can act over a wide range of temporal scales [*Schimel*, 2000]. Over very rapid timescales, nitrogen (as NH_4) can inhibit

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CH_4 oxidation by competing for methane monooxygenase, the enzyme used by methanotrophs to oxidize CH_4 [*Hanson and Hanson*, 1996]. Nutrients can also directly influence microbial communities at timescales reflecting the turnover of microbial populations. For example, high concentrations of CH_4 can counter balance the potentially negative effects of NH_4 at an enzyme level, allowing nitrogen-limited methanotroph populations to increase in response to nitrogen fertilization [*Bodelier et al.*, 2000a, 2000b; *Chan and Parkin*, 2001; *Bodelier and Laanbroek*, 2004].

[5] Over longer timescales, nutrients can also impact microbial activities through ecosystem feedbacks associated with the vegetation community. Nutrient-mediated changes in vegetation productivity can alter CH_4 and oxygen transport through plant arenchyma [*Schütz et al.*, 1991; *Whiting and Chanton*, 1993], with important consequences for CH_4 oxidation and net CH_4 flux. Shifts in plant community composition and/or productivity can also alter soil carbon quality and quantity through altered litter inputs to the peat [*Chapin et al.*, 1995; *Moore and Dalva*, 1997; *Bridgham and Richardson*, 2003] and labile root exudates dynamics [*Hutchin et al.*, 1995; *Joabsson et al.*, 1999; *Megonigal et al.*, 1999; *Updegraff et al.*, 2001; *King et al.*, 2002]. Although the carbon in peatland soils has typically been accumulating for centuries, shifts in soil carbon quality resulting from comparably rapid changes in vegetation dynamics can occur by influencing small labile carbon pools which have a large influence on carbon mineralization in peatlands [*Chanton et al.*, 1995; *Updegraff et al.*, 1995; *Bridgham et al.*, 1998; *Keller et al.*, 2004]. Such ecosystem-mediated shifts in soil carbon quality will likely influence the anaerobic production of CO_2 and CH_4 in peatlands. While the short- and long-term impacts of nutrients on peatland microbial carbon cycling may differ considerably, these potential differences are not well studied.

[6] The influence of nutrients on microbial carbon cycling in peatlands is further complicated by differences in nutrient dynamics among peatland types. Northern peatlands represent a diverse group of wetlands that are often described as a gradient from precipitation-fed (ombrotrophic) bogs to predominantly groundwater-fed (minerotrophic) fens. Although primarily defined by degree of groundwater influence, such factors as plant community structure and productivity, aboveground-belowground plant allocation, soil carbon quality, pH, alkalinity, and nutrient availability change dramatically along this gradient [e.g., *Szumigalski and Bayley*, 1996; *Thormann et al.*, 1999; *Bridgham et al.*, 1996, 1998, 2001; *Weltzin et al.*, 2000]. Soil nitrogen availability generally increases along the ombrotrophic-minerotrophic gradient, while changes in phosphorus availability are more complex and variable [*Verhoeven et al.*, 1990; *Bridgham et al.*, 1998, 2001; *Chapin et al.*, 2003; *Bragazza and Gerdol*, 2002; *Kellogg and Bridgham*, 2003]. Plant productivity in peatlands is often limited by phosphorus, nitrogen, or a combination of nitrogen and phosphorus [*Bridgham et al.*, 1996; *Bedford et al.*, 1999], although responses to fertilization are often species-specific [*Thormann and Bayley*, 1997; *Chapin et al.*, 2004] and vary among peatland types [*Verhoeven and Schmitz*, 1991; *Aerts et al.*, 1992, 1999]. Therefore it is likely that the response of microbial carbon cycling to changes in nutrient status will be strongly mediated by peatland type.

[7] A number of previous studies have contributed to our understanding of the role of nitrogen and phosphorus in controlling microbial carbon cycling in peatlands [e.g., *Crill et al.*, 1994; *Aerts and Toet*, 1997; *Aerts and de Caluwe*, 1999; *Saarnio and Silvola*, 1999; *Saarnio et al.*, 2000; *Granberg et al.*, 2001]. A few multiyear studies have considered the importance of nutrient-mediated shifts in vegetation communities [*Nykänen et al.*, 2002; *Keller et al.*, 2005], but most studies have utilized short-term (<1 year) nutrient amendments which cannot capture potential long-term effects owing to ecosystem feedbacks. Further, these studies were often carried out in only one peatland type and thus did not investigate differential responses along the peatland gradient to similar nutrient loads.

[8] We utilized a 5-week laboratory nutrient amendment experiment, in combination with a 6-year field nutrient fertilization experiment, to investigate the effects of nitrogen and phosphorus on aerobic CH_4 oxidation, anaerobic carbon mineralization (as CO_2 and CH_4 production), and anaerobic nutrient (nitrogen and phosphorus) mineralization in three different peatlands (a bog, an intermediate fen, and a rich fen) in the Upper Peninsula of Michigan. This project allowed a unique comparison of the relative response of microbial carbon cycling to similar nutrient loads in three peatlands representing an ombrotrophic-minerotrophic gradient. Further, this approach allowed us to compare the short-term effects of nutrients (in the laboratory amendment experiment where ecosystem feedbacks were not possible) to the long-term ecosystem feedbacks of nutrients (which were possible in the field fertilization experiment) in these peatland ecosystems.

2. Site Descriptions

[9] The bog, intermediate fen, and rich fen used in this study were located at the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan in Gogebic County (46°N, 89°W). These sites are representative of peatlands in the area which have been described elsewhere [*Kellogg and Bridgham*, 2003; *Iversen*, 2004; *Kellogg*, 2004]. Briefly, the vegetation in the bog was dominated by *Sphagnum* spp. bryophytes and woody ericaceous shrubs such as *Vaccinium oxycoccus* (L.), *Rhododendron groenlandicum* (Oeder) Kron and Judd, and *Chamaedaphne calyculata* (L.). Graminoids including *Carex oligosperma* Michx and *Scheuchzeria palustris* (L.) were also present in the bog. The intermediate fen was dominated by the graminoids *Carex* spp., *Eriophorum vaginatum* (L.), and *E. virginicum* (L.). A partial ground cover of *Sphagnum* spp. bryophytes and woody shrubs including *R. groelandicum*, *C. calyculata*, and alder, *Alnus incana rugosa* (Du Roi) R. T. Clausen (henceforth, *A. rugosa*), were also present in the intermediate fen. The graminoids *Calamagrostis canadensis* (Michx.) P. Beauv. and *Carex* spp. were dominant in the rich fen, although scattered woody shrubs (*A. rugosa* and *Salix* spp.) were also present. Soil characteristics and vegetation community parameters were measured using

Table 1. Mean (±1 SE) Extractable N (as NH_4^+ + NO_3^-), Extractable P, Total N, Total P, Total C, and pH of Peatland Soils at Two Depths[a]

	Surface			Subsurface		
	Bog	Intermediate Fen	Rich Fen	Bog	Intermediate Fen	Rich Fen
Extractable N, μmol N g dry peat^{-1}	0.89 ± 0.19 a	2.27 ± 0.61 ab	3.12 ± 0.75 b	1.19 ± 0.61 a	4.42 ± 0.51 b	2.28 ± 0.86 a
Extractable P, μmol P g dry peat^{-1}	1.06 ± 0.66	0.66 ± 0.08	0.14 ± 0.02	0.21 ± 0.04 b	0.34 ± 0.04 c	0.06 ± 0.02 a
Total N, %	0.94 ± 0.05 a	1.39 ± 0.05 b	2.29 ± 0.07 c	1.30 ± 0.05 a	2.82 ± 0.04 c	2.05 ± 0.02 b
Total P, %	0.040 ± 0.002 a	0.055 ± 0.002 b	0.079 ± 0.002 c	0.043 ± 0.001 a	0.082 ± 0.001 c	0.066 ± 0.001 b
Total C, %	43.61 ± 0.09 b	42.55 ± 0.13 a	45.69 ± 0.19 c	45.23 ± 0.08 b	44.54 ± 0.13 a	45.56 ± 0.12 b
pH	3.80 ± 0.01 a	4.62 ± 0.02 b	5.59 ± 0.01 c	3.70 ± 0.02 a	4.66 ± 0.02 b	5.60 ± 0.03 c

[a]Within each depth, means with the same letter are not significantly different (Fisher's LSD test; $P > 0.05$). Letters later in the alphabet correspond to higher values. "Surface" and "Subsurface" represent the depth intervals from 0–5 cm and 15–20 cm below the peat surface, respectively. All measurements were made on homogenized peat that had been processed aerobically for the short-term amendment experiment.

the methods described below and are summarized in Tables 1 and 2.

3. Methods

3.1. Methane Oxidation

3.1.1. Laboratory Amendment Experiment

[10] To examine the short-term effects of nutrient additions on aerobic CH_4 oxidation, five randomly chosen peat cores were removed from each peatland (in areas that had not been previously fertilized in the long-term experiment described below) in July of 2002. Cores were located at least several meters apart and were collected with PVC pipes (10 cm diameter, ~25 cm depth), using a sharp, serrated knife to guide the PVC into the peat. Upon removal, the cores were immediately capped on the bottom to maintain water table levels and minimize oxygen leakage into the core. In the laboratory, the peat cores were separated into 0–5 cm ("Surface") and 15–20 cm ("Subsurface") depth increments, which represent depths above and below the water table levels typically measured during sampling in these sites in the summers of 2002 and 2003. As such these depths were typically exposed to aerobic ("Surface") and anaerobic ("Subsurface") conditions in the field. Woody material, green vegetation, and large roots were quickly removed by hand and peat from each depth increment was homogenized in the laboratory. Thus, for each peatland, there was one homogenized sample for each depth increment.

[11] To measure rates of potential CH_4 oxidation, 10 g of field moist peat were added to 120-mL serum bottles, and nutrient amendments were added as 1 mL of concentrated nutrient stock followed by vigorous shaking. There were five nutrient treatments utilized in this experiment: control ("C," 1 mL of deionized water with no nutrients added); low nitrogen ("LN," the equivalent of 1 g N m^{-2} as NH_4Cl); high nitrogen ("HN," the equivalent of 10 g N m^{-2} as NH_4Cl); phosphorus ("P," the equivalent of 2 g P m^{-2} as a combination of NaH_2PO_4 and Na_2HPO_4); and salt ("S"). Our salt treatment represents the molar-equivalent of the HN treatment as NaCl and provides a control for potential effects of the Cl^- ion added as a part of the HN amendment. There were five replicates of each nutrient amendment treatment. The pH of all treatments was corrected to the average control treatment value using 0.1M NaOH or HCl as necessary.

[12] The phosphorus amendment was designed to be equivalent to the field fertilization phosphorus treatment (described below). The high and low nitrogen treatments

Table 2. Mean (±1 SE) Extractable Nitrogen (as NH_4^+ + NO_3^-); Extractable Phosphorus; Forb, Graminoid, and Shrub ANPP; Total Bryophyte Cover; and Community BNPP in a Bog, an Intermediate Fen, and a Rich Fen Which Have Been Fertilized With Four Treatments[a]

	Treatment	Extractable Nitrogen, μmol N g^{-1}	Extractable Phosphorus, μmol P g^{-1}	Forbs ANPP, g m^{-2} yr^{-1}	Graminoids ANPP, g m^{-2} yr^{-1}	Shrubs ANPP, g m^{-2} yr^{-1}	Bryophytes, % Cover	Root BNPP, mg cm^{-3}
Bog	C	1.59 ± 0.33	0.40 ± 0.06 B	0.2 ± 0.2 A	85.2 ± 16.3 A	8.1 ± 1.1 AB	100 C	0.55 ± 0.04 A
	N	2.29 ± 0.43	0.29 ± 0.10	2.5 ± 2.2	116.3 ± 25.7[b]	23.7 ± 6.9[c]	23.0 ± 9.2[c]	0.65 ± 0.15
	P	1.65 ± 0.20	0.68 ± 0.11[c]	1.5 ± 0.4	75.4 ± 10.5	34.0 ± 8.0[c]	99.5 ± 0.5	0.50 ± 0.06
	NP	1.67 ± 0.63	1.47 ± 0.40[b]	0[c]	216.7 ± 56.7	62.9 ± 7.7	49.0 ± 11.7 [b]	0.58 ± 0.08
Intermediate Fen	C	1.84 ± 0.33	0.62 ± 0.08 C	106.7 ± 40.3 C	93.7 ± 25.2 A	66.9 ± 33.0 B	39.0 ± 0.7 B	2.61 ± 0.81 B
	N	4.35 ± 0.97[c]	0.47 ± 0.03	258.0 ± 112.6[c]	273.5 ± 97.8[b]	48.7 ± 32.7	6.0 ± 4.8[c]	1.59 ± 0.36
	P	3.43 ± 1.46[b]	1.33 ± 0.27[b]	110.4 ± 27.6[c]	29.5 ± 10.6	173.7 ± 36.8[c]	28.8 ± 7.4	2.48 ± 0.25
	NP	7.65 ± 1.47	0.99 ± 0.58	9.2 ± 4.6[c]	331.6 ± 132.9	386.3 ± 97.3	4.0 ± 2.74	2.81 ± 0.85
Rich Fen	C	1.02 ± 0.13	0.15 ± 0.13 A	38.2 ± 18.3 B	602.6 ± 46.5 B	12.3 ± 12.3 A	0.2 ± 0.2 A	1.25 ± 0.50 AB
	N	4.75 ± 1.25[c]	0.33 ± 0.06	15.4 ± 4.2[b]	476.3 ± 70.4[c]	61.4 ± 57.0	0.2 ± 0.2[c]	1.24 ± 0.25
	P	1.05 ± 0.20	2.52 ± 0.87[c]	74.0 ± 29.8	473.8 ± 37.3[c]	10.9 ± 6.6	0.2 ± 0.2[c]	1.10 ± 0.26
	NP	2.74 ± 0.74	1.54 ± 0.25	54.5 ± 51.9	213.7 ± 78.7[b]	11.5 ± 3.5	8.0 ± 4.2[c]	1.53 ± 0.27

[a]Treatments are: control (C), nitrogen alone (N), phosphorus alone (P), and nitrogen and phosphorus in combination (NP). Upper case letters signify significant differences among peatlands in the unfertilized control treatments only. Peatlands with higher extractable nutrients, productivity, or bryophyte cover have letters later in the alphabet. Within each peatland type, significant nitrogen and phosphorus effects are indicated in the N and P rows. Significant interactions between nitrogen and phosphorus are indicated in the NP row for each peatland type. ANPP, aboveground net primary productivity; BNPP, belowground net primary productivity.

[b]$P < 0.10$.

[c]$P < 0.05$.

bracket the nitrogen level used in the field fertilization experiment (described below) to consider potential differential effects of high and low nitrogen additions. For consistency with field fertilizations, these nutrient treatments were defined as the equivalent of "g nutrient m^{-2}." Calculations for these nutrient treatments assumed a homogenous distribution of nutrients over 20 cm depth of peat and were corrected for bulk density at each site. Bulk densities were measured on bulk peat samples (roots removed by hand) in 1998 prior to initiating the long-term fertilization treatments. Bulk densities for the bog, intermediate fen, and rich fen were 0.09, 0.21, and 0.21 g soil cm^{-3}, respectively (L. E. Kellogg and S. D. Bridgham, unpublished data, 1998), and are comparable to measurements of other peatlands in the area [*Kellogg and Bridgham*, 2003].

[13] The serum bottles were sealed with gray butyl septa, and the headspace CH_4 concentrations were adjusted to 10,000 ppm. CH_4 oxidation samples were incubated at 15°C (an average field temperature during the growing season) in the dark. To ensure that headspace oxygen was not depleted, the serum bottles were opened every 2 days and allowed to equilibrate with the ambient atmosphere for 1 hour before being resealed and returning the headspace CH_4 concentration to 10,000 ppm. Rates of CH_4 oxidation are expressed as positive values calculated as the linear decrease in headspace CH_4 concentrations over ~24 hours. Rates were measured using a Varian 3600 gas chromatograph equipped with a flame ionization detector (FID) following 1 week of incubation after the nutrient additions. Subsamples of homogenized peat were used to determine the percent moisture of each core by drying at 60°C for at least 48 hours, and all rates are expressed per gram dry peat (g^{-1}).

3.1.2. Field Fertilization Experiment

[14] Beginning in 1998, four 32-m^2 plots in each peatland received one of the following fertilization treatments: control ("C"), nitrogen ("N," 6 g N m^{-2} yr^{-1} in the form of urea ($CO(NH_2)_2$)), phosphorus ("P," 2 g P m^{-2} yr^{-1} as triple superphosphate ($Ca(H_2PO_4)_2$), or nitrogen and phosphorus in combination ("NP"). Fertilization treatments were applied with hand spreaders in the spring of each year through 2002, but no fertilizer was applied in 2003. Within each peatland, fertilization plots were located at least 5 m apart (often much farther) to minimize potential hydrological exchange of nutrients.

[15] The nutrient levels used in these experiments were initially selected to alleviate potential nutrient limitation of peatland vegetation communities. For comparison, total atmospheric inorganic nitrogen wet deposition in this area is currently ~0.4 g N m^{-2} yr^{-1} [*National Atmospheric Deposition Program*, 2005]. Our treatment levels represent the upper range of atmospheric nitrogen deposition to peatlands. For example, nitrogen deposition ranges from 0.5 to 2.5 g m^{-2} yr^{-1} in the eastern United States and from 0.5 to 6.0 g N m^{-2} yr^{-1} in northern Europe [*Wedin and Tilman*, 1996].

[16] Smaller replicate plots were not established in each peatland because these sites were part of a larger experiment focusing on fertilization effects on vegetation and included multiple peatlands of each type [*Kellogg and Bridgham*, 2003; *Kellogg*, 2004]. For logistical reasons, our experiment utilized only one representative site from each peatland type (i.e., bog, intermediate fen, and rich fen), and multiple cores taken from each fertilization plot were treated as replicates for statistical analyses. This statistical shortcoming was a necessary trade off of utilizing this unique long-term field fertilization experiment. Owing to the small spatial scale of microbial processes, it is likely that the microbial communities in each core were ecologically independent of each other, further justifying our approach.

[17] In August 2003 (6 years after the initiation of the fertilization treatments), five peat cores (10 cm diameter, ~25 cm depth) were randomly collected, as described above, from a central portion of each long-term fertilization plot in the bog, intermediate fen, and rich fen to measure rates of potential CH_4 oxidation. A subsection of the surface 0–5 cm depth increment from each core was placed in a Mason jar, with roots intact. The headspace CH_4 concentration was adjusted to 10,000 ppm, and the jars were allowed to incubate at 15°C for 3 days. Following this incubation period, the samples were opened and allowed to equilibrate with the ambient atmosphere for 1 hour. The jars were resealed and the headspace CH_4 concentration was readjusted to 10,000 ppm. Rates of CH_4 oxidation was calculated as the linear decline of headspace CH_4 concentrations over ~32 hours.

3.2. Anaerobic CO_2 and CH_4 Production

3.2.1. Laboratory Amendment Experiment

[18] To examine the effects of short-term nutrient amendments on potential anaerobic CO_2 and CH_4 production, an additional five peat cores were collected from unfertilized areas of the bog, intermediate fen, and rich fen. They were processed as described above, except all processing was done in a glove box with a N_2 atmosphere to maintain anaerobic conditions. Rates of anaerobic CO_2 and CH_4 production were measured in 120-mL serum bottles containing 10–20 g of field-moist peat slurried in a 1:1 ratio with stock nutrient solutions to create the same nutrient amendment treatments described above. The slurries were bubbled vigorously with N_2 to ensure anaerobic conditions, and the serum bottles were subsequently sealed with gray butyl caps.

[19] Samples were incubated at 15°C in the dark for 5 weeks. After approximately 1, 3, and 5 weeks of incubation, the headspace of all samples were analyzed for CH_4 and CO_2 simultaneously using a Varian 3600 gas chromatograph equipped with a thermal conductivity detector and a FID for CO_2 and CH_4, respectively. Each sample was shaken vigorously prior to injection to remove gas bubbles trapped within the peat slurry. Following each sampling, headspace pressure was measured using an Omega HHP 520 pressure meter (Omega Engineering, Stamford, Connecticut). On each sampling date, the serum bottles were opened briefly, pH was measured and the slurry was bubbled again with N_2 for 5 min, resealed, and returned to the 15°C incubator. Dissolved CH_4 and CO_2 were calculated using Henry's Law, adjusting for solubility, temperature, and pH [*Stumm and Morgan*, 1995]. Headspace CH_4 and CO_2 concentrations were corrected for pressure. Cumulative carbon mineralization represents the sum of CO_2 or CH_4 produced on all sampling dates.

3.2.2. Field Fertilization Experiment

[20] To examine the long-term effects of nutrient additions on carbon and nutrient mineralization, an additional

five peat cores (10 cm diameter, ~25 cm depth) were removed from each field fertilization plot. The peat cores were returned to the laboratory where woody material, green (i.e., living) bryophytes, and large roots were quickly removed from the top 15 cm of the peat by hand. All peat processing was done in the ambient atmosphere. Thirty grams of field-moist peat were placed in 120-mL serum bottles, slurried with 30 mL of deionized water, and bubbled with N_2 to ensure anaerobic conditions. The serum bubbles were then sealed and incubated in the dark at 15°C. After approximately 1, 2, 4, 8, and 12 weeks of incubation, the samples were analyzed for CH_4 and CO_2 simultaneously (using the methods described above), opened briefly to allow accumulated gas to escape and measure pH, and rebubbled with N_2. Cumulative production was calculated as the sum of CO_2 or CH_4 production on all sampling dates. Processing samples in the ambient atmosphere temporarily introduced oxygen into the peat and despite bubbling with N_2, it is possible that trace amounts of oxygen were initially present in our anaerobic slurries. Given the long duration of our incubations (12 weeks), we suggest that any remaining oxygen would have been quickly depleted and would not have affected our overall mineralization results.

3.2.3. Cumulative Nutrient Mineralization

[21] Anaerobic samples from the long-term fertilization experiment were used to calculate cumulative net nitrogen and phosphorus mineralization potentials. Nutrient mineralization was calculated as the difference in extractable nitrogen (as NH_4^+ and NO_3^-) or phosphorus (PO_4^{3-}) in the peat before and after the 12-week anaerobic incubations. Nitrogen (as NH_4^+ and NO_3^-) was extracted with 2 M KCl and phosphorus was extracted with acid fluoride [*Kuo*, 1996; *Mulvaney*, 1996]. Extracts were analyzed for PO_4^{3-}, NO_3^-, and NH_4^+ by standard spectrophotometric methods with a Lachat Quickchem 8000 autoanalyzer (Hach Corporation, Loveland, Colorado). Extractable NO_3^- and NH_4^+ were summed to calculate extractable nitrogen (although NH_4^+ accounted for at least 95% (average >98%) of the total mineralized nitrogen).

3.2.4. Soil Characteristics

[22] Subsamples of homogenized peat (n = 5) that had been processed aerobically for the short-term amendment experiment were used to measure a number of soil characteristics (Table 1). Soil pH was measured in a slurry of 10-g field-moist peat and 10 mL of deionized water, which was allowed to equilibrate for 30 min. Additional subsamples of homogenized peat from each depth were used to estimate extractable nutrient content using the methods described above. Dried homogenized subsamples were ground to pass a 2-mm sieve (Udy Mill, Udy Corporation, Fort Collins, Colorado) to determine total carbon, nitrogen, and phosphorus content of peat. Phosphorus content was determined by digestion with concentrated H_2SO_4 and 30% H_2O_2 [*Allen*, 1989] followed by spectrophotometric analysis on a Lachat Quickchem 8000 autoanalyzer. Carbon and nitrogen content were determined using a Costech 4010 Elemental Combustion System (Costech Analytical Technologies, Inc., Valencia, California).

3.2.5. Plant Responses to Long-Term Fertilization

[23] The fertilization treatments utilized in this project have led to shifts in the vegetation communities in these peatlands [*Iversen*, 2004; S. D. Bridgham et al., unpublished data, 2005]. A detailed description and thorough discussion of the vegetation responses to these fertilization treatments is beyond the scope of this paper. Nonetheless, we summarize the results from 2002, one year before our microbial carbon cycling sampling regime, to demonstrate that nutrient effects on microbial carbon cycling are potentially mediated by shifts in carbon quality due to changes in the vegetation community. The methods used to characterize the vegetation response are described in detail elsewhere [*Iversen*, 2004] and are briefly summarized below.

[24] Percent cover by bryophytes was estimated using the point intercept method in five 1-m^2 subplots randomly placed in each treatment plot (40 points per plot; 20 plots per peatland). When bryophytes covered $\geq$5% of the subplot, *Sphagnum* spp. were dominant and were responsible for at least 84.0% of the total cover (98.8% average). The remaining bryophyte cover was primarily *Polytricum* spp. Aboveground net primary productivity (ANPP) was determined by clipping vegetation from all fertilization treatment plots in each peatland during the peak of the growth season, but after estimates of bryophyte cover, in August 2002. All vegetation was clipped to the peat surface in each of four randomly placed 20-cm^2 squares in the five 1-m^2 subplots within each fertilization treatment plot. The vegetation which had been produced during the current growing season (ANPP) was separated from older biomass and dried at 60°C for at least 48 hours. ANPP values were measured for the dominant functional groups present at each site (forbs, graminoids, and shrubs). Trees represented a minimal component of aboveground productivity and were excluded from subsequent analyses.

[25] Community belowground net primary productivity (BNPP) was determined using in-growth root cores filled with homogenized, root-free peat from the same wetland type [*Weltzin et al.*, 2000]. Four in-growth cores were placed in each fertilization treatment to a 25-cm depth from May through October 2002. After the in-growth cores were removed, live roots longer than 1 cm were separated by hand from the peat and dried at 60°C for at least 48 hours.

[26] Extractable nutrient values from before the 12-week anaerobic incubation provide an estimate of the impact of these fertilization treatments on nutrient availability in these peatland (summarized in Table 2).

3.2.6. Statistical Analyses

[27] In the aerobic and anaerobic laboratory amendment experiments, there were numerous interactions among peat type, depth increment, and nutrient treatment. Thus we investigated the effect of short-term nutrient amendments on rates of CH_4 oxidation, cumulative CH_4 production, and cumulative CO_2 production in a single-factor ANOVA framework (with nutrient treatment as the main factor) for each peatland depth increment (GLM procedure (SAS Institute, SAS OnlineDoc®, version 8, 1999; version 9 is now available at http://support.sas.com/onlinedoc/913/docMainpage.jsp)). Following significant ANOVAs ($P < 0.05$), Fisher's Least-Significant Differences (LSD) tests were used to analyze pairwise comparisons among nutrient amendments. Rates of CH_4 oxidation and cumulative anaerobic CH_4 and CO_2 production were log-transformed prior to analysis to improve overall data distribution. Differences in physical characteristics among peatlands were analyzed in a similar manner.

[28] In the field fertilization experiments, there were significant differences among peat types and significant interactions between peat type and fertilization treatments. Therefore we investigated the effects of nitrogen, phosphorus, and their interaction, on rates of CH_4 oxidation, cumulative anaerobic CO_2 and CH_4 production, and cumulative nitrogen and phosphorus mineralization in a two-factor ANOVA framework (GLM procedure (SAS Institute, SAS OnlineDoc®, version 8, 1999; version 9 is now available at http://support.sas.com/onlinedoc/913/docMainpage.jsp)). Rates of CH_4 oxidation were log-transformed prior to analysis to meets assumptions of normality. The effects of long-term fertilization on extractable nitrogen and phosphorus, as well as responses of ANPP, moss cover, and belowground biomass, were analyzed in the same manner. A single-factor ANOVA was used to investigate differences in initial values of extractable nitrogen and phosphorus, as well as vegetation variables, in the unfertilized control treatment plots. Following significant ANOVAs ($P < 0.05$), significant differences among peatland types were determined with Fisher's LSD tests.

4. Results

4.1. Soil Characteristics

[29] In surface peat (0–5 cm depth) from the short-term amendment experiment, extractable nitrogen, total nitrogen, total phosphorus, and pH increased along the ombrotrophic-minerotrophic peatland gradient (Table 1). Total carbon was lowest in the intermediate fen peat and highest in the rich fen peat, and there was no difference in extractable phosphorus among peatland types in the shallow depth increment (Table 1).

[30] Nutrient patterns in the subsurface peat (15–20 cm depth) were less clear. Extractable nitrogen, total nitrogen, and total phosphorus were highest in peat from the intermediate fen and lowest in peat from the bog. Extractable phosphorus was also highest in peat from the intermediate fen, but was lowest in peat from the rich fen (Table 1). As in the surface peat, pH in subsurface peat increased along the ombrotrophic-minerotrophic gradient. Total carbon content in the subsurface peat was lowest in the intermediate fen and did not differ in the bog and rich fen peat (Table 1).

[31] The control plots in the long-term fertilization experiment also provided estimates of nutrient availability (Table 2). Extractable nitrogen did not differ significantly among peatland types, and extractable phosphorus was lowest in the rich fen peat and highest in the intermediate fen peat. Extractable nitrogen increased in response to nitrogen fertilization in peat from the intermediate fen and the rich fen, but not in the bog (Table 2). Extractable phosphorus increased in response to phosphorus fertilization in all peatland types, although this increase was greater when phosphorus was added in combination with nitrogen in the bog (Table 2).

4.2. Plant Responses to Long-Term Fertilization

[32] Peatland vegetation also responded to long-term fertilization with nitrogen and phosphorus. In the bog, nitrogen fertilization stimulated graminoid and shrub ANPP, but bryophyte cover decreased by 77% in response to fertilization with nitrogen alone. The inhibitory effect of nitrogen on bryophyte cover was diminished (51% reduction in cover) when added in combination with phosphorus as indicated by the significant interaction between nitrogen and phosphorus. Shrub ANPP in the bog was also stimulated by phosphorus fertilization (Table 2). In the intermediate fen, graminoid ANPP was stimulated by nitrogen fertilization, whereas shrub ANPP was stimulated by phosphorus fertilization. Forb ANPP was stimulated when nitrogen and phosphorus were added alone in the intermediate fen, but when added in combination forb productivity declined dramatically. Similar to the bog, bryophyte cover in the intermediate fen decreased in response to nitrogen fertilization (Table 2). Graminoid ANPP in the rich fen was reduced by both nitrogen and phosphorus fertilization, especially when added in combination. Bryophyte cover was generally low in the rich fen and increased when nitrogen and phosphorus were added in combination, but not when added alone (Table 2). Despite clear shifts in the aboveground community productivity patterns, there were no significant fertilization effects on belowground productivity (Table 2) or community belowground biomass (data not shown) in any peatland.

4.3. Methane Oxidation

[33] Short-term laboratory nutrient amendments did not have consistent effects on rates of CH_4 oxidation among different peatland types (Figure 1). In the bog surface peat, the high nitrogen, salt, and phosphorus treatments inhibited CH_4 oxidation compared to the control; however, the inhibition by the salt treatment was more severe than the inhibition from the high nitrogen treatment. Both the high nitrogen and salt treatments inhibited CH_4 oxidation in the subsurface bog peat, while the low nitrogen treatment stimulated CH_4 oxidation. In the intermediate fen surface peat, the phosphorus treatment inhibited rates of CH_4 oxidation, but there were no nutrient effects in the intermediate fen subsurface peat. The phosphorus and salt treatment inhibited CH_4 oxidation in the rich fen surface peat, and there were no nutrient effect in the rich fen subsurface peat.

[34] Long-term fertilization with nitrogen alone, phosphorus alone, and nitrogen and phosphorus in combination had no effect on potential CH_4 oxidation, except for a significant positive effect of nitrogen fertilization in bog peat (Figure 2). The effect of nitrogen was not mediated by phosphorus fertilization (i.e., the interaction between nitrogen and phosphorus was not significant, Figure 2) in any peat type. It should be noted that statistical analyses were performed on log-transformed data to meet assumptions of normality; however, we present the actual (i.e., nontransformed) rates of CH_4 oxidation in Figure 2. This convention tends to overemphasize the interaction term in peat from the bog which was not significant in the log-transformed data.

4.4. Anaerobic CO_2 and CH_4 Production

[35] Potential anaerobic CH_4 and CO_2 production were generally higher in the shallow depth increment (especially in the intermediate and rich fen peat) over the course of the laboratory nutrient amendment experiment (Figure 3). The salt and phosphorus amendments increased cumulative CH_4 production in 5-week incubations in surface peat from the rich fen. The nutrient amendments did not influence cumulative CH_4 production in any other surface peat

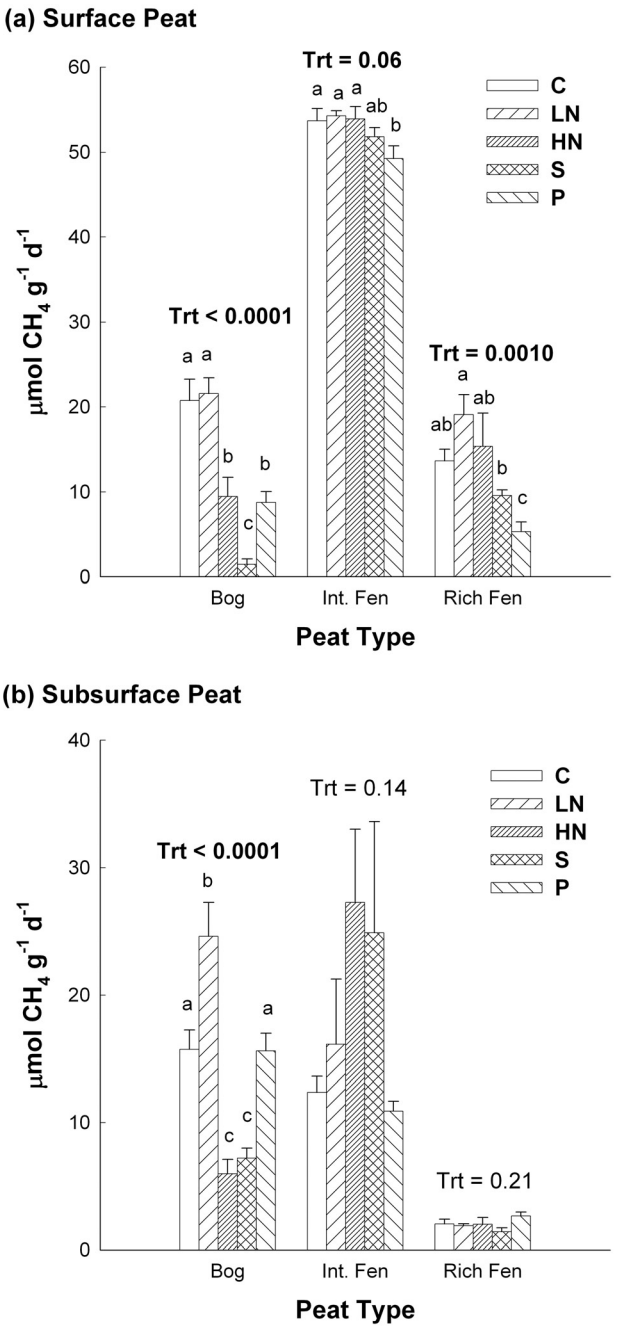

Figure 1. Rates of CH_4 oxidation (±1 SE) measured over ~24 hours in bog, intermediate fen, and rich fen peat. Control (C), low nitrogen (LN), high nitrogen (HN), phosphorus (P), and salt (S) amended peats were incubated at 15°C for 1 week. "Surface" and "Subsurface" represent the depth intervals from 0–5 cm and 15–20 cm below the peat surface, respectively. "Trt" refers to the ANOVA main effect of nutrient treatment. Within each peat type, treatment means with the same letter are not significantly different (Fisher's LSD test; $P > 0.05$).

type (Figure 3). Rates of cumulative CO_2 production were inhibited by the high nitrogen, phosphorus, and salt amendments in the surface bog peat. There were no nutrient effects in the surface peat from the intermediate fen or rich fen (Figure 3). In the subsurface bog peat, both the low and high nitrogen amendments stimulated CO_2 production, while the phosphorus amendment inhibited CO_2 production. The salt and phosphorus amendments also inhibited cumulative CO_2 production in subsurface peat from the intermediate fen. CO_2 production did not differ among nutrient amendments in subsurface peat from the rich fen (Figure 3). We also analyzed the effects of these nutrient amendments on rates of CH_4 and CO_2 production on individual sampling dates during the 5-week incubations (i.e., at 1, 3, and 5 weeks). While there were differences among sampling dates in many cases, no clear temporal patterns emerged from these analyses (data not shown).

[36] In the 6-year fertilization experiment, cumulative CH_4 and CO_2 production were inhibited by long-term phosphorus fertilization in peat from the bog (Figure 4). There were no effects of nitrogen or phosphorus fertilization on cumulative CO_2 or CH_4 production in peat from the intermediate fen. Cumulative CH_4 production in the rich fen peat appeared to be stimulated by phosphorus fertilization ($p = 0.08$, Figure 4). Cumulative CO_2 production in the rich fen peat was not influenced by nitrogen or phosphorus fertilization (Figure 4). Interactions between nitrogen and phosphorus fertilization treatments were not important in any peat type (Figure 4).

[37] Similar patterns emerged in all peat types when rates of CH_4 and CO_2 production were analyzed at individual

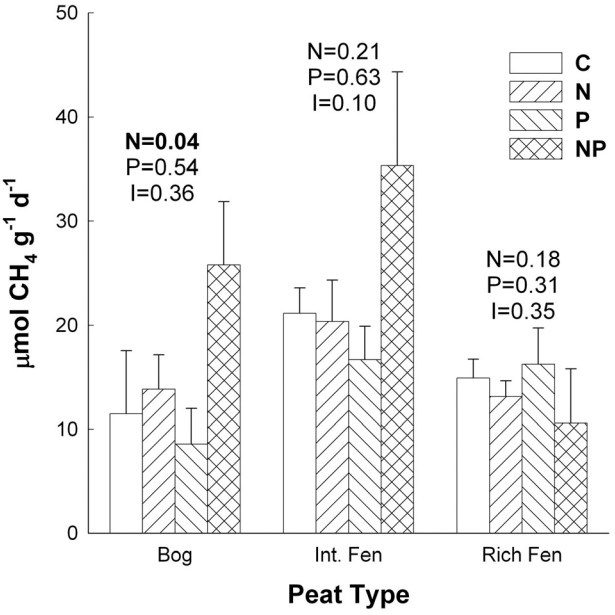

Figure 2. Rates of CH_4 oxidation measured over ~32 hours in bog, intermediate fen, and rich fen peat fertilized for 6 years with four nutrient treatments: control (C), nitrogen alone (N), phosphorus alone (P), and nitrogen and phosphorus added together (NP). CH_4 oxidation was measured following 3-day laboratory incubations at 15°C. Means ±1 SE are shown. Within each peat type, the P values for nitrogen ("N") and phosphorus ("P") treatment effects, and their interaction ("I"), were determined using two-factor ANOVAs. Significant treatment effects ($P < 0.05$) are indicated with bold text.

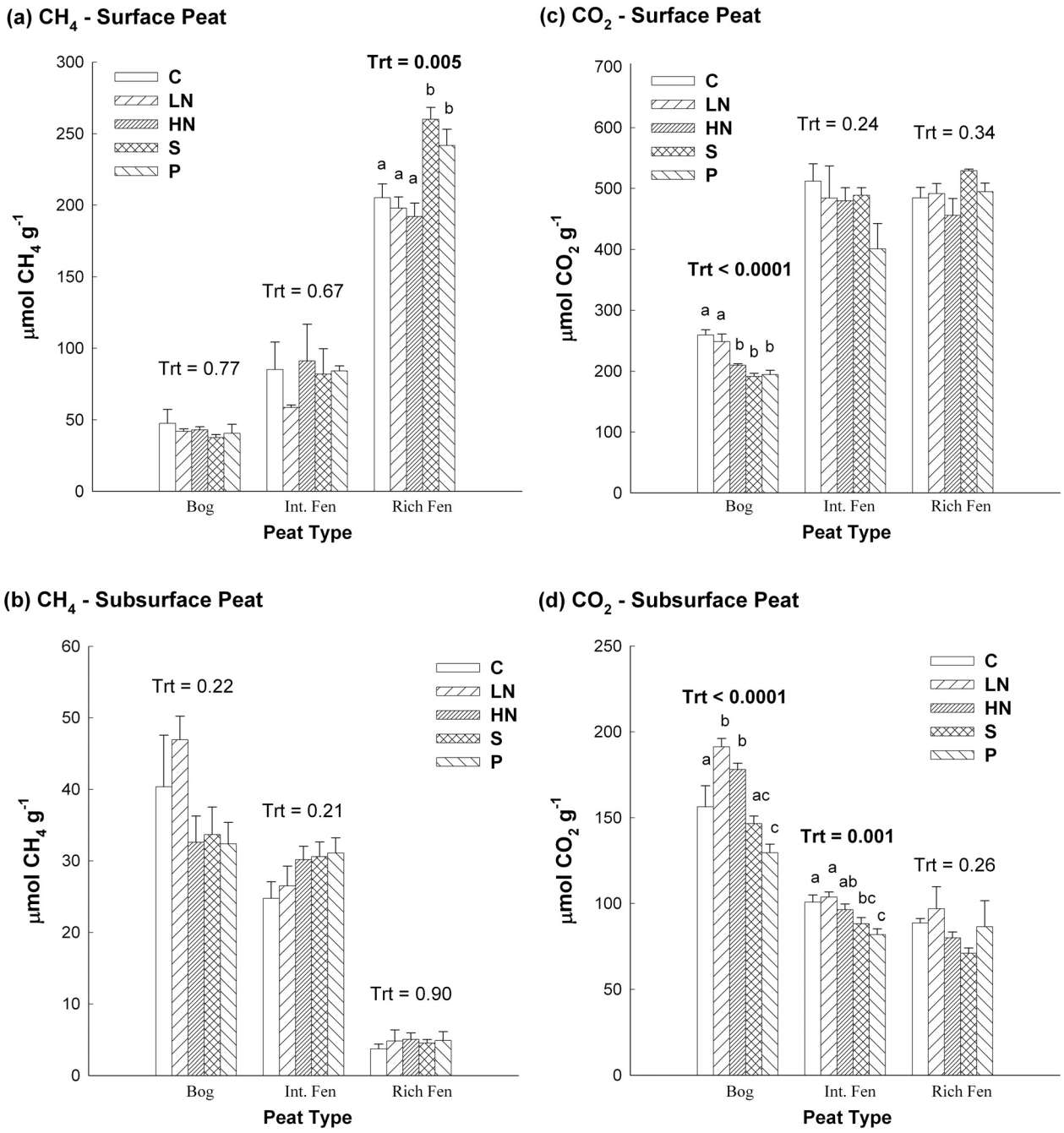

Figure 3. Mean (±1 SE) cumulative (a, b) CH_4 production and (c, d) CO_2 production in bog, intermediate fen, and rich fen peat. Control (C), low nitrogen (LN), high nitrogen (HN), phosphorus (P), and salt (S) amended peats were incubated at 15°C for 5 weeks. "Surface" and "Subsurface" represent the depth intervals from 0–5 cm and 15–20 cm below the peat surface, respectively. "Trt" refers to the ANOVA main effect of nutrient treatment. Within each peat type, treatment means with the same letter are not significantly different (Fisher's LSD test; $P > 0.05$).

time points during the 12-week incubation (i.e., at 1, 2, 4, 8, and 12 weeks; data not shown). Specifically, phosphorus significantly inhibited CH_4 and CO_2 production in the bog peat on all sampling dates. Nitrogen also significantly inhibited CH_4 and CO_2 production initially in the bog peat, but this effect disappeared by the second week of the incubation. There were no significant nutrient effects on CO_2 or CH_4 production in the intermediate fen peat on any sampling date. Phosphorus stimulated CH_4 production in the rich fen peat on all but the final sampling date (at 12 weeks), and there were no nutrient effects on CO_2 production in the rich fen peat.

4.5. Cumulative Nutrient Mineralization

[38] In peat fertilized for 6 years, anaerobic nitrogen mineralization was stimulated by phosphorus fertilization

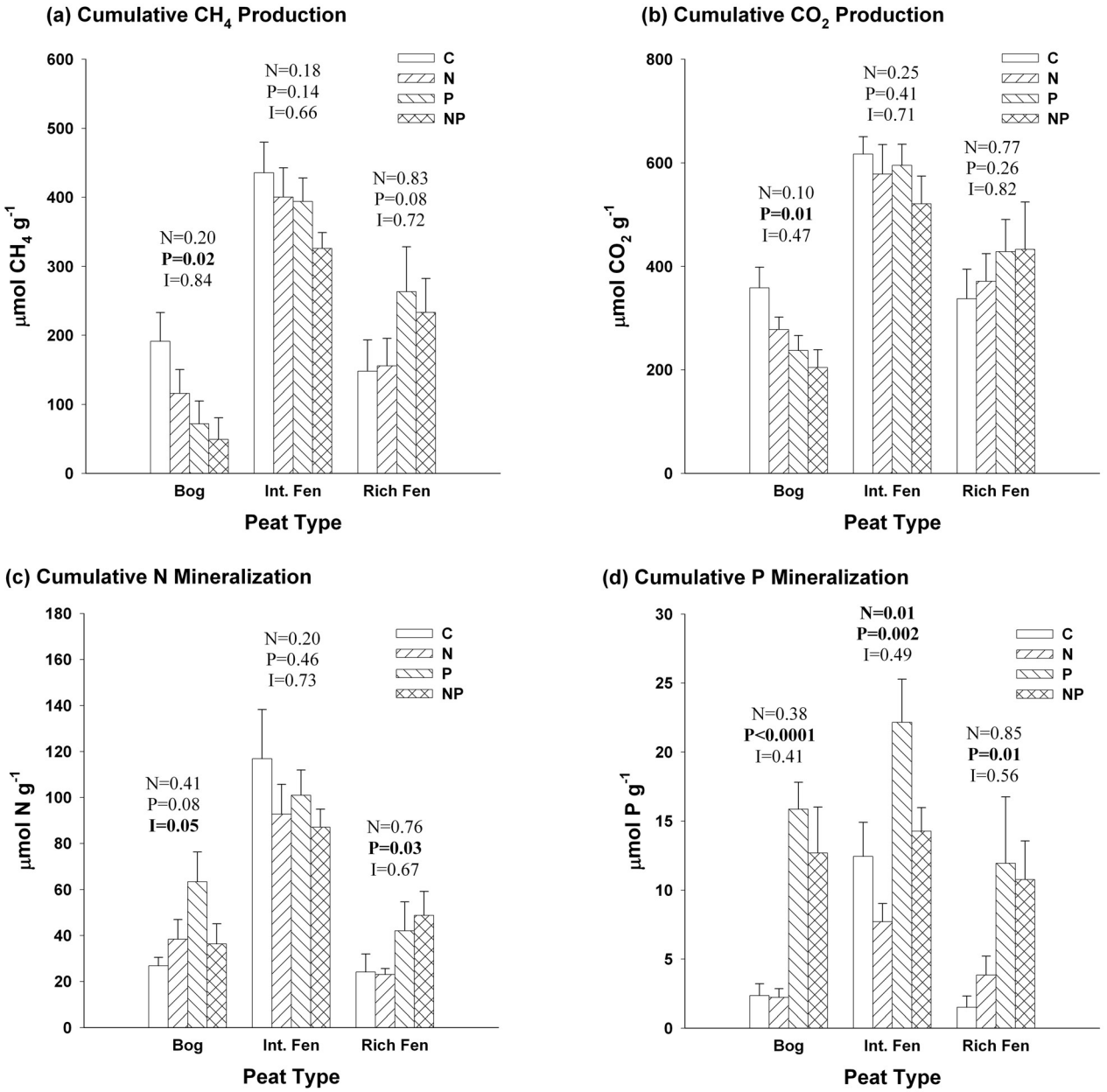

Figure 4. Mean (±1 SE) cumulative (a) CH_4 production, (b) CO_2 production, (c) nitrogen mineralization, and (d) phosphorus mineralization in bog, intermediate fen, and rich fen peat fertilized for 6 years with four treatments: control (C), nitrogen along (N), phosphorus alone (P), and nitrogen and phosphorus in combination (NP). Mineralization was measured in anaerobic peat slurries incubated in the laboratory for 12 weeks at 15°C. Within each peat type, the P values for nitrogen ("N") and phosphorus ("P") treatment effects, and their interaction ("I") were determined using a two-factor ANOVA. Significant treatment effects ($P < 0.05$) are indicated with bold text.

in the bog and rich fen peat (Figure 4). However, in peat from the bog, there was a significant interaction between nitrogen and phosphorus and the stimulatory effect of phosphorus fertilization was greater when phosphorus was added alone than when it was added in combination with nitrogen (Figure 4). There were no effects of nitrogen or phosphorus fertilization on nitrogen mineralization in peat from the intermediate fen. Long-term fertilization with phosphorus stimulated phosphorus mineralization in all peat types (Figure 4). In peat from the intermediate fen, anaerobic phosphorus mineralization was inhibited by nitrogen fertilization (Figure 4).

5. Discussion

[39] Our primary goal was to investigate the impacts of increased nitrogen and phosphorus availability on microbial carbon cycling in three peatlands. By comparing the effects of short-term nutrient amendments with the effects of long-term (6-year) nutrient fertilizations, we hoped to gain

insights into the importance of nutrient control at multiple spatial and temporal scales [*Schimel*, 2000]. For example, consistent effects of short- and long-term nutrient additions may suggest a direct impact of nutrient availability at the level of microbial metabolism or microbial growth. In contrast, responses only to long-term nutrient fertilizations suggest that nutrient effects through ecosystem feedbacks (e.g., through shifts in the vegetation community) may be particularly important. Finally, we examined the relative response of microbial carbon cycling to similar nutrient loads along an ombrotrophic-minerotrophic peatland gradient; i.e., were patterns of stimulation, or inhibition, by nutrients consistent among different peatland types?

[40] Owing to logistical limitations, we utilized a single bog, intermediate fen and rich fen in this experiment. Physical peat characteristics and vegetation patterns suggest that these three peatlands represent an ombrotrophic-minerotrophic gradient defined primarily by increased pH and extractable nitrogen (Table 1). Patterns of nitrogen availability among peatlands were less clear when measured in the field (Table 2, control treatments); however, the peat used for nutrient estimates was not homogenized and within site variability may have masked differences among peatlands. As in other peatlands, changes in chemical parameters coincide with shifts in the dominant vegetation community [*Heinselman*, 1970; *Vitt et al.*, 1990; *Gorham and Janssens*, 1992; *Bridgham et al.*, 1996]. Specifically, *Sphagnum* bryophytes were an important component of the bog ecosystem, while graminoids dominated in the rich fen (Table 2, control treatments). Thus, while generalization of our results to other peatlands should be cautioned, these three wetlands are typical of other northern peatlands found in the region [*Dise*, 1993; *Bridgham et al.*, 1998; *Chapin et al.*, 2003; *Kellogg and Bridgham*, 2003] and represent an ombrotrophic-minerotrophic gradient.

5.1. Methane Oxidation

[41] Previous peatland studies have demonstrated an increase in net CH_4 flux in response to nitrogen fertilization [*Aerts and Toet*, 1997; *Aerts and de Caluwe*, 1999; *Saarnio and Silvola*, 1999], likely as a result of an inhibition of CH_4 oxidation by biochemical competition for the methane monooxygenase enzyme [*Hanson and Hanson*, 1996]. A number of laboratory studies have supported the hypothesis that nitrogen inhibits CH_4 oxidation in peatlands [*Crill et al.*, 1994; *Kravchenko*, 1999a, 1999b, 2002] and several other ecosystems [*Steudler et al.*, 1989; *Adamsen and King*, 1993; *Mancinelli*, 1995; *van der Nat et al.*, 1997; *Whalen*, 2000; *Chan and Parkin*, 2001]. However, *Updegraff et al.* [2001] observed a negative relationship between CH_4 flux and pore water NH_4 concentrations in bog and fen plots receiving several heating and water table treatments. They hypothesized that one likely mechanism for this relationship was a stimulation of a nitrogen-limited methanotrophic community, as has been observed in other ecosystems with high concentrations of CH_4 [*Bodelier and Laanbroek*, 2004, and references therein]. In this experiment, we initially hypothesized that such stimulatory effects of nitrogen would occur relatively rapidly in response to the short-term amendment experiment, especially in the more ombrotrophic bog where nitrogen availability is typically low.

[42] In contrast to our hypothesis, CH_4 oxidation in our laboratory amendment experiment was only stimulated by the low nitrogen treatment in the subsurface bog peat. This suggests that the methanotroph communities in these peatlands are not nitrogen limited or were unable to respond to increased nitrogen availability during the time frame of this experiment. There were significant inhibitory effects of the high nitrogen amendment on potential CH_4 oxidation in the surface and subsurface bog peat (Figure 1). It is possible that these reduced rates of CH_4 oxidation represent a biochemical inhibition through competitive binding of methane monooxygenase, especially at high nitrogen concentrations. Overall, the lack of a consistent inhibition or stimulation of CH_4 oxidation by nitrogen in the short-term amendment experiment demonstrates that many peatland methanotroph communities are tolerant of a wide range of nitrogen availability, as has been suggested previously [*Saarnio and Silvola*, 1999; *Nykänen et al.*, 2002; *Keller et al.*, 2004].

[43] In this project, we focus on comparisons between nutrient amendment treatments and the unamended control treatment; however, it is important to acknowledge that these responses could result from "salt effects" associated with our nutrient amendments, specifically the Cl^- ion added in our nitrogen treatments [*Crill et al.*, 1994; *Gulledge and Schimel*, 1998; *Whalen*, 2000]. Our salt treatment provides a control for these effects relative to the high nitrogen amendment. In cases where the high nitrogen treatment did inhibit rates of CH_4 oxidation compared to the control treatment, there was often a greater inhibition observed in the salt treatment (e.g., surface peat of the bog and rich fen; Figure 1). This suggests that in many cases, increased nitrogen availability counterbalanced the negative salt effects associated with increased ion concentrations. In other words, nitrogen may be stimulating rates of CH_4 oxidation even though rates were lower than the control treatment. As our salt treatment represented the molar equivalent of the high nitrogen treatment, we are limited in our ability to partition between nutrient and salt effects in the other nutrient amendment treatments. Many previous studies that have examined the effects of nutrient additions on microbial carbon cycling in peatlands (and other ecosystems) failed to incorporate salt controls, and our results suggest that more effort needs to be focused on separating out ionic (i.e., salt) and nonionic effects of nutrients.

[44] Long-term fertilization with nitrogen stimulated potential rates of CH_4 oxidation in peat from the bog (Figure 2). It is possible that methanotrophs in the bog were, in fact, nitrogen-limited, but were only able to respond to increases in nitrogen availability over longer time frames. However, it is also possible that this stimulation takes place through an indirect ecosystem pathway. Specifically, nitrogen fertilization in the bog resulted in an increase in aboveground shrub and graminoid productivity and a concomitant decrease in bryophyte cover (Table 2). While belowground productivity in the bog was not affected by nitrogen fertilization (Table 2), increases in aboveground productivity may have resulted in increased radial oxygen loss within the rhizosphere, with an associated positive effect on rates of CH_4 oxidation.

[45] Short-term amendments with phosphorus inhibited rates of CH_4 oxidation compared to the control treatment in surface peat from all peat types (Figure 1). This pattern of

low tolerance to increased phosphorus availability by peatland microbial communities is also seen in a number of anaerobic carbon processes and is discussed in more detail below.

5.2. Anaerobic Carbon Mineralization

[46] We initially hypothesized that anaerobic carbon mineralization would be stimulated by phosphorus fertilization due to increases in vegetation productivity, which is often phosphorus-limited in peatland ecosystems [*Bedford et al.*, 1999; *Chapin et al.*, 2004], and subsequent shifts in soil carbon quality. Thus we predicted minimal impacts of short-term nutrient amendments on anaerobic mineralization as these treatments did not allow for long-term ecosystem level effects to occur.

[47] In accordance with this hypothesis, there were limited effects of short-term nutrient amendments on CH_4 production, although there was a stimulatory effect of phosphorus on cumulative CH_4 production in surface peat from the rich fen (Figure 3). The effects of short-term nutrient amendments on anaerobic CO_2 production were not always straightforward (Figure 3); however, there was an inhibition of CO_2 production by short-term phosphorus amendments in the bog peat and in the intermediate fen subsurface peat (Figure 3). This inhibition by phosphorus in the ombrotrophic bog was also present in response to long-term fertilizations, where phosphorus fertilization (alone or in combination with nitrogen) inhibited cumulative CO_2 and CH_4 production (Figure 4). This consistent inhibition of anaerobic carbon mineralization by phosphorus suggest that the microbial community in the bog may be directly inhibited by phosphorus availability (i.e., this inhibition is not mediated by ecosystem level shifts in carbon quality).

[48] *Amador and Jones* [1995] observed that phosphorus addition inhibited carbon mineralization (as CO_2 and CH_4 evolution) from added carbon substrates in peat from the Florida Everglades which had been subjected to long-term phosphorus pollution. A similar inhibition of acetoclastic methanogenesis by phosphorus has been observed in rice paddy roots, although the mechanism of inhibition was unknown [*Conrad et al.*, 2000]. Fertilization with single superphosphate (SSP) inhibited CH_4 emission from a flooded rice paddy soil, although this apparent phosphorus inhibition was likely due to sulfate content of the SSP fertilizer [*Adhya et al.*, 1998]. We can not exclude the possibility that sulfur contamination of our fertilizer inhibited CH_4 production in bog peat from the field fertilization experiment (Figure 4). However, the triple superphosphate (TSP) we used in our study likely had minimal sulfur contamination. Currently The Mosaic Company is the only U.S. company to manufacture TSP (Bill Herz, The Fertilizer Institute, personal communication, 2006), and their TSP has $\sim$1.3% SO_4-S (Granular triple superphosphate spec sheet, 1995, available at http://www.mosaicco.com/stellent7/groups/public/documents/mosaic_ss_web_resources/spec_gstp_0-45-0.pdf). Further, the inhibition of anaerobic carbon mineralization in bog peat from the short-term laboratory amendment experiment (Figure 3) suggests that phosphorus is likely involved in the observed inhibition.

[49] Methanogenesis can also be limited by the availability of trace metals, for example Fe, Ni, and Co [*Speece et al.*, 1983; *Jarrell and Kalmokoff*, 1988]. This trace metal limitation may be especially important in mineral-poor (i.e., ombrotrophic) peatlands which generally have lower concentrations of these metals [*Basiliko and Yavitt*, 2001; *Bragazza and Gerdol*, 2002]. If the addition of phosphorus resulted in a decrease in the availability of these trace metals through the many complicated biogeochemical interactions between phosphorus and trace metals (e.g., through the formation of metal-phosphorus complexes), an indirect limitation of methanogenesis by trace metals in response to phosphorus addition is possible. The microbial processes responsible for anaerobic CO_2 production could also be inhibited through indirect limitation by trace metals.

[50] Interestingly, long-term phosphorus fertilization had the opposite result in peat from the rich fen where cumulative CH_4 production was stimulated in response to long-term phosphorus fertilization (Figure 4). The short-term phosphorus amendment also stimulated CH_4 production in the rich fen surface peat (Figure 3). Taken together, these results suggest that the methanogen community in the rich fen may be phosphorus limited. The dominant pathway of CH_4 production (i.e., acetoclastic versus autotrophic methanogenesis) may differ among peatlands [*Shannon and White*, 1996; *Chasar et al.*, 2000; *Hines et al.*, 2001; J. K. Keller and S. D. Bridgham, unpublished data, 2006], and this could, in part, explain the opposing responses to long-term phosphorus fertilization in the bog and the rich fen.

5.3. Cumulative Nutrient Mineralization

[51] Our estimates of cumulative mineralization were based on preincubation and postincubation extractions of nitrogen and phosphorus. This approach represents a net cumulative mineralization of these nutrients, but does not capture potentially important mechanisms such as changes in microbial immobilization and sorption reactions. Further, extraction efficiencies often differ among soil types, particularly for phosphorus [*Bridgham et al.*, 1998]. However, we stress fertilization effects within a peatland type where differences in extraction efficiencies among samples should be minor.

[52] Phosphorus availability appears to be an important control of cumulative nutrient mineralization in peatlands, but once again, the role of phosphorus differs among peatland types. Long-term phosphorus fertilization stimulated nitrogen and phosphorus mineralization, as well as cumulative CH_4 production in the rich fen (Figure 4). These results suggest that overall anaerobic microbial activity in the rich fen may be phosphorus limited.

[53] In the bog, there were differential responses of nutrient and carbon mineralization to phosphorus fertilization. While phosphorus inhibited cumulative CO_2 and CH_4 production in the bog, phosphorus stimulated rates of phosphorus and nitrogen mineralization in the same bog (Figure 4). The decoupling between carbon and nutrient mineralization in this experiment is surprising because it is commonly thought that nutrient, especially nitrogen, mineralization is linked to carbon mineralization in decomposition of organic matter [*Chapin et al.*, 2002].

[54] However, *Verhoeven et al.* [1990] also noted an inverse relationship between net nutrient mineralization and cellulose decomposition (measured with cotton strips) in *Sphagnum*-dominated mires in the Netherlands. They

hypothesized that nitrogen-rich organic compounds were selectively decomposed by a sparse microbial community in these systems. This pattern of microbial activity would leave a majority of carbon hardly decomposed (low rates of carbon mineralization) and would have minimal nutrient requirements. Thus limited microbial immobilization could explain high rates of net nutrient mineralization in these systems, although patterns in phosphorus mineralization would be further complicated by geochemical processes.

6. Conclusions and Implications

[55] The present study is unique in addressing two key themes critical to understanding the response of microbial carbon cycling to nitrogen and phosphorus in peatland ecosystems. First, we demonstrate that nutrients can have different short-term (e.g., through direct stimulation or inhibition of microbial communities) and long-term impacts (e.g., through long-term changes in soil carbon quality resulting from altered plant community dynamics). For example, high nitrogen concentrations inhibited CH_4 oxidation in bog peat in the 5-week laboratory amendment experiment, but lower nitrogen concentrations stimulated CH_4 oxidation in the 6-year field fertilization experiment possibly through an increase in vascular plant productivity. In contrast, the effects of phosphorus fertilization on anaerobic CO_2 and CH_4 production in bog and rich fen peat were qualitatively similar over both the short and long term. Thus it appears that ecosystem-level shifts in carbon quality in response to 6 years of phosphorus fertilization were not important controls of anaerobic carbon mineralization in these peatlands. Although our 6-year fertilization treatments represent a long-term nutrient addition compared to our laboratory amendments, they are still relatively short in terms of peatland carbon accumulation which takes place over centuries. Thus it is possible that over longer periods of time, changes in vegetation community structure related to nutrient fertilization will translate into shifts in soil carbon quality with the potential to alter CH_4 and CO_2 fluxes from peatlands.

[56] Second, the role of nutrients in controlling peatland microbial carbon cycling is strongly mediated by peatland type, with different peatlands responding differently, or even oppositely, to similar nutrient additions. For example, increased phosphorus availability inhibited CH_4 production in peat from a bog. In contrast, the same phosphorus levels did not affect CH_4 production in peat from an intermediate fen, and stimulated CH_4 production in peat from a rich fen. Similarly, high nitrogen concentrations had an inhibitory effect on CH_4 oxidation, possibly due to a salt effect, in only bog peat. While we utilized only a single representative of each peatland type, our results suggest that differential effects of nutrients on microbial carbon cycling among peatland types will be a key determinant of how peatland CO_2 and CH_4 dynamics will respond to increased nutrients in the future.

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