Nitrogen dynamics in floating and non-floating peatlands in the Western Boreal Plain

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Wray, H. E. and Bayley, S. E. 2008. **Nitrogen dynamics in floating and non-floating peatlands in the Western Boreal Plain**. Can. J. Soil Sci. **88**: 697–708. The overall objective of this study was to measure the major nitrogen pools and fluxes in nutrient- and peat-rich, vegetated marshes and fens surrounding shallow ponds in the Western Boreal Plain (WBP) of Canada. Within the same peatland-pond complex, marshes and fens did not differ from each other in major N fluxes and pool sizes; however, significant differences in N dynamics were measured between different peatland-ponds. Specifically, N cycling rates (gross and net mineralization) were much greater in a floating peatland than in a non-floating peatland. Gross N mineralization rates were 59 and 453 mg N m^{-2} d^{-1} in the non-floating and floating peatlands, respectively. Gross ammonification rates were approximately 4–10 times net rates while gross nitrification rates were 500–800 times net rates, indicating rapid turnover of extractable inorganic N pools. Increased moisture and carbon in the floating peat supported higher microbial biomass and activity, however net primary production values were lower, presumably due to competition by microbes for available inorganic N. Monthly measurements of N fluxes were combined to provide an estimate of annual internal N cycling within marshes and fens surrounding shallow ponds in the WBP.

Key words: Gross mineralization, microbial biomass, nitrogen, peatland

Wray, H. E. et Bayley, S. E. 2008. **Dynamique de l'azote dans les tourbières émergées et immergées de la plaine boréale de l'Ouest**. Can. J. Soil Sci. **88**: 697–708. L'étude devait préciser les principaux bassins et flux d'azote dans les marécages et les marais à carex riches en éléments nutritifs et en sphaigne qui entourent les étangs superficiels de la plaine boréale de l'Ouest (PBO), au Canada. Les principaux flux de N et la taille des bassins de N ne varient pas entre les marécages et les marais à carex du même complexe étang-tourbière; cependant, les auteurs ont observé d'importantes fluctuations dans la dynamique du N entre des complexes distincts. Plus précisément, le cycle du N (minéralisation brute et nette) est beaucoup plus rapide dans les tourbières émergées que dans les tourbières immergées. Le taux de minéralisation brute du N s'établit respectivement à 59 et à 453 mg de N par mètre carré et par jour dans les tourbières immergées et les tourbières émergées. Le taux d'ammonisation brute dépasse 4 à 10 fois le taux net, alors que le taux de nitrification brute dépasse le taux net de 500 à 800 fois, signe que les bassins de N inorganique utilisable se renouvellent rapidement. La plus grande quantité d'eau et de carbone dans les tourbières immergées favorisent une activité accrue de la microflore et une plus grande biomasse unicellulaire, cependant la production primaire nette demeure faible, sans doute parce que les microorganismes se livrent concurrence pour le N inorganique disponible. Les auteurs ont combiné les relevés mensuels des flux de N pour estimer le cycle interne annuel du N dans les marécages et les marais à carex entourant les étangs peu profonds de la PBO.

Mots clés: Minéralisation brute, biomasse unicellulaire, azote, tourbière

There has been growing interest in peatland biogeochemistry because peat can be an important site of nutrient transformations on a global scale. Many peatlands are active carbon sinks (Gorham 1991) and may also be important for nitrogen removal via denitrification (Saunders and Kalff 2001). Internal N fluxes in peatlands are also important because N is often limiting to plant productivity (Moore 2002) and internal cycling of N is often 10–20 times greater than the amount received from outside the system (Schlesinger 1991; Paul and Clark 1996).

Nitrogen biogeochemistry in peat is poorly understood, in part because most studies have focused on nutrient poor systems with emphasis on bogs and fens (Updegraff et al. 1995; Bridgham et al. 1998). In the Western Boreal Plain (WBP) of Canada, peatlands cover up to 50% of the land area (Vitt et al. 1995) and are often found surrounding shallow ponds in small basins, forming peatland-pond complexes (National Wetlands Working Group 1997). Bogs, fens and marshes commonly surround these ponds (Whitehouse and Bayley 2005) and all three types of peatlands are relatively nutrient rich (Vitt et al. 1995) and can accumulate peat (Bayley and Mewhort 2004).

In most boreal peatlands, slow decomposition of dead plant material returns organic N to the soil and is responsible for peat accumulation (Clymo 1965; Szumigalski and Bayley 1996; Jonasson and Shaver 1999; Moore 2002). Mineralization of organic N to inorganic

Abbreviations: **DOC,** dissolved organic carbon; **DON,** dissolved organic nitrogen; **DDW,** distilled deionized water; **TN,** total nitrogen; **WBP,** Western Boreal Plain

N [ammonium (NH_4^+) and nitrate (NO_3^-)] is often measured as a net rate i.e., production of ammonium and/or nitrate in excess of denitrification and microbial uptake (Schlesinger 1991). Ammonium and nitrate have several fates in soil, including biotic uptake (Vitousek et al. 1979) and nitrogen availability to plants is often controlled by the partitioning of inorganic N between plants and soil microorganisms (Jackson et al. 1989).

Microbial uptake is estimated using gross and net rates of mineralization. Measurements of gross N mineralization rates i.e., the total amount of N mineralized, are therefore very useful when simultaneously measured with net N mineralization. Comparisons of gross and net N mineralization rates have been conducted extensively in forest, grassland and agricultural systems (Booth et al. 2005). In boreal peatlands, due to difficulties in measuring gross rates of N transformation, net rates have been most commonly measured (Humphrey and Pluth 1996; Bayley et al. 2005). Simultaneous measurements of gross and net N transformation in peat or boreal systems are valuable because they provide a more complete picture of nitrogen cycling in any system, yet these studies are scarce and are mainly conducted in relatively nutrient-poor systems (Potila and Sarjala 2004; Westbrook and Devito 2004).

The specific objectives of this study were: (1) to measure rates of gross and net N mineralization in the marsh and fen vegetation zones of two peatland-pond sites, one a floating peatland and the other non-floating, (2) to determine the size of the microbial biomass pool and estimate microbial N uptake in the peatlands, and (3) to integrate major fluxes of N with N pool sizes into an annual internal N budget for marsh and fen peatlands of the WBP.

MATERIALS AND METHODS

Site Descriptions

This study was performed in 2004 in two peatland-pond complexes in the mid-boreal ecoclimatic zone of northern Alberta (National Ecoregions Working Group 1989) near the Utikuma Lake Area (56°52′N, 115°27′W), approximately 300 km north of Edmonton, AB. The area was characterized by short warm summers (mean July 2004 temperature of 17.5°C) and long cold winters (mean January 2004 temperature of −20.6°C) with a mean annual temperature of 0.8°C in 2004 (Environment Canada 2005). The two peatland-pond sites chosen for this study were both in depressions with clay-till basins. Both sites consisted of a shallow pond (<2 m depth) surrounded by a marsh fringe at the pond edge and an open fen vegetation zone surrounding the marsh. The fens were adjacent to bogs and aspen (*Populus tremuloides*) dominated uplands. One site was a floating peatland (i.e., the marsh and fen were on a floating mat of peat above the water surface) and the other site was a non-floating peatland.

The pond surface water at the non-floating peatland site averaged a pH of 9.1 over the course of the study. The marsh peat was humic and mucky and vegetation was dominated by common cattail (*Typha latifolia*). Water levels in the marsh fluctuated throughout this study from 9 to 16 cm above the peat surface. The open fen at the non-floating site was composed of humic peat and dominated by hairy-fruited sedge (*Carex lasiocarpa*). Water levels in the fen fluctuated slightly over the study from 0 cm (at the peat surface) to 2 cm above the peat surface.

The pond at the floating peatland site had an average surface water pH of 8.4 during this study and was surrounded by a floating peatland, defined as a thick mat of peat floating above the water surface (National Wetlands Working Group 1997). The peatland had a narrow marsh fringe around the entire pond dominated by *Carex* species and smaller emergent macrophytes including water arum (*Calla palustris*) and buckbean (*Menyanthes trifoliata*). Water levels in the marsh fluctuated from 5 cm to 13 cm. The open fen at the floating site was dominated by two-stamened sedge (*Carex diandra*). The peat was very fibrous and water levels fluctuated slightly throughout the study from 0 to 2 cm above the peat surface.

Experimental Approach

This study estimated nitrogen stocks/pools as well as fluxes of recycled N that are available to plants or microbes. We also estimated uptake and loss of N by the dominant vegetation in the two peatland complexes (both of which have a marsh and a fen vegetation zone). Flux estimates included total inorganic N released (gross mineralization), N mineralized in excess of that consumed by denitrification and microbial uptake (net mineralization) as well as mineralized N that is assimilated by microbes (microbial uptake). Mass loss of decomposing litter as well as peak vegetative biomass allowed estimates of litter N inputs to the peat as well as plant N uptake. Surface water, peat and microbial pools of N were also measured. A summary of definitions and methods used is in Table 1.

All major internal nitrogen pools and fluxes were estimated from May through August 2004 in the fen and marsh vegetation zones of the two sites. Over-winter rates of net mineralization and decomposition were also measured from October 2003 until May 2004. Inputs of nitrogen to the sites were not measured however N fixation and precipitation values were estimated based on values in the literature. Therefore, information presented here describes the internal N budget and limited external fluxes.

Net Mineralization

Field Procedures

Net nitrogen mineralization was measured monthly from May through August using the buried bag method

Table 1. Definitions of N fluxes and pools measured in this study with methods used in parentheses

N flux or pool	Definition (and method used)
Pools	
Extractable NH_4^+	Estimate of readily available NH_4^+ in peat (extracted with KCl)
Extractable NO_3^-	Estimate of readily available NO_3^- in peat (extracted with DDW)
Inorganic N	Readily available $NH_4^+ + NO_3^-$ in peat
Microbial biomass N	Total Organic N in microbes (fumigation-extraction)
Organic N	Total N in the peat excluding extractable NH_4^+ and NO_3^- [TN–($NH_4^+ + NO_3^-$)]
Plant biomas	Total N in above-ground, vascular plant biomass (harvest)
Fluxes	
Decomposition	Total N added to peat as organic N through decomposition of above-ground vascular plant biomass (mass loss × TN in plant biomass)
Denitrification	Flux of N_2 gas to the atmosphere from peat (N_2-flux technique)
Gross ammonification	Actual rate of NH_4^+ production in peat (^{15}N isotope dilution)
Gross nitrification	Actual rate of NO_3^- production in peat (^{15}N isotope dilution)
Gross N mineralization	Gross ammonification + gross nitrification
Net ammonification	Production of NH_4^+ minus nitrification and microbial uptake (buried bag incubation)
Net nitrification	Production of NO_3^- minus denitrification and microbial uptake (buried bag incubation)
Net N mineralization	Net ammonification + net nitrification
Gross N consumption	Actual rate of N consumption (of NH_4^+ and NO_3^-) by all consumptive processes including microbial uptake and denitrification
Microbial uptake	Amount of NH_4^+ and NO_3^- assimilated by microbes in the peat (estimated as gross–net mineralization)
Plant uptake	Total N assimilated by above ground vascular vegetation during the growing season (assumed equivalent to plant biomass N in August)

described by Eno (1960). Peat cores were taken with a sheet metal corer 15 cm in diameter. The surface litter layer (and moss layer, if present) was removed; cores were cut to 10 cm depth and then cut in half vertically. The core halves were sealed in polyethylene bags. One half was returned to the original hole and re-covered with the litter layer and left in the field for approximately 30 d before collection and transport back to the lab (Final core), and the other half of the core was transported back to the lab on ice (Initial core). Cores were extracted in the lab within 72 h of collection.

Laboratory Procedures

All cores were weighed and mixed thoroughly before extraction for ammonium and nitrate. Ammonium was extracted from the peat using 1 N KCl (100 mL per 10 g of wet soil) and nitrate and phosphorus were extracted using distilled deionized water (DDW) (100 mL per 10 g of wet soil) as previous studies have shown nitrate addition in peat extracted with reagent grade KCl (Bayley, unpublished data). Samples were shaken for 60 min and centrifuged. Nitrate samples were filtered through Whatman GF/F glass microfibre filters (1.0 μm pore size) and ammonium samples were unfiltered. Analysis of NH_4-N and NO_3-N was performed on a Technicon TM Autoanalyzer II.

Concentrations of NH_4^+ and NO_3^- taken in the initial cores were assumed to be equivalent to extractable NH_4^+ and NO_3^- in the peat. Net mineralization rates were calculated by subtracting the concentrations of NH_4^+ or NO_3^- in the initial core from the concentrations in the incubated core (on a per volume basis). Monthly values were divided by the number of days the sample was incubated in the field to give units of mg NH_4^+-N or NO_3^--N m^{-2} d^{-1} (to 10 cm peat depth).

Gross Nitrogen Mineralization

Field Procedures

Gross nitrogen mineralization was measured using ^{15}N isotope dilution methods as outlined by Hart et al. (1994b). Twelve cores 5 cm in diameter and 10 cm deep were taken monthly from May through August in each of the two fens and two marshes. Cores were taken in groups of four, of which two cores were used to measure gross nitrification and two were used to measure gross ammonification. Nitrification cores were injected with 6 mL of $K^{15}NO_3$ solution (98% enrichment, 35 μg^{15}N L^{-1}) and ammonification cores were injected with 6 mL of $(^{15}NH_4)_2SO_4$ (98% enrichment, 35 μg^{15}N L^{-1}). One NO_3^- and one NH_4^+ core were immediately extracted with DDW and 1 N KCl, respectively. The remaining cores were left in the coring tubes, capped, placed in sealed plastic bags to prevent leakage, and placed in their original holes for 24 h. After the incubation, the cores were collected and extracted as above.

Laboratory Procedures

Subsamples of soil from each core were used to determine the gravimetric moisture content of each sample. Subsamples of soil extracts were used to determine the concentration of NH_4^+ and NO_3^- in the soil using methods described above.

Diffusion procedures for trapping $^{15}NH_4$-N and $^{15}NO_3$-N follow those outlined by Hart et al. (1994b) for direct combustion ^{15}N analysis. Thirty-five milliliters of extract solution was placed into plastic 50-mL specimen vials. NO_3^- cups received a scoop of MgO powder (approximately 0.2 g), which causes NH_3 vapor to be released. Vials were left open for 6 d and then one scoop of Devarda's alloy (approximately 0.4 g) was added to reduce NO_3^- to NH_4^+. Filter discs acidified with 2.5 M K_2HSO_4 were suspended above the solution and the vial capped for a further 6 d to allow the discs to trap released NH_4^+. Ammonium extract samples received a scoop of MgO powder, followed immediately by addition of the

acidified filter disc to trap NH_4^+ and capping of the vial for 6 d. After incubation, filter disks were dried in a desiccator overnight and placed in tin capsules for direct combustion ^{15}N mass spectrometry analysis. Analysis of ^{15}N samples were performed using a continuous flow isotope ratio mass spectrometer consisting of a NA 1500 Carlo Erba Instrument (Milan, Italy) for sample combustion and a SIRA 10 VG ISOGAS mass spectrometer (Middlewich, Cheshire England) for isotope ratio analysis. Rates of gross ammonification and nitrification as well as gross ammonium and nitrate consumption were calculated using equations developed by Kirkham and Bartholomew (1954).

Gross consumption of N is not to be confused with microbial immobilization of N, which is only one consumptive process. In addition to microbial uptake, NH_4^+ can also be consumed via volatilization, leaching, mineral fixation and nitrification while NO_3^- can be consumed via leaching, denitrification and dissimilatory nitrate reduction (Hart et al. 1994b). Many of these other processes are often assumed to be insignificant over the small incubation period (Hart et al. 1994b), although high denitrification rates have been measured in the peatlands studied in this experiment (Wray and Bayley 2007). Denitrification was measured as part of a companion study using the N-flux technique, which involves incubating cores in gas-tight chambers, flushing out nitrogen and measuring flux of N from the soil to the headspace. For a more detailed description of these methods see Wray and Bayley (2007). Therefore, we estimated daily microbial immobilization using isotope dilution studies according to the following equations:

$$\text{Microbial uptake of } NH_4^+ = \text{gross } NH_4^+ \text{ consumption} - \text{gross nitrification}$$

$$\text{Microbial uptake of } NO_3^- = \text{gross } NO_3^- \text{ consumption} - \text{mean denitrification}$$

where all values are in mg N m^{-2} d^{-1}. Immobilization was estimated by subtracting net rates of mineralization from gross rates for both ammonium and nitrate.

Decomposition

In mid-October 2003, standing dead *Carex diandra* was collected from fen and marsh vegetation zones in the floating peatland. *Carex diandra* was not present at the non-floating peatland in 2003;therefore,litter from the marsh and fen of the floating peatland was used for decomposition studies in the non-floating peatland as well. The same species was used because decomposition rates vary between different species (Thormann and Bayley 1997c) and we wanted to compare decomposition rates in marshes vs. fens in the two peatland-ponds. The plants were clipped at ground level and dried for 48 h at 60°C. Approximately 1 to 2 g of the plant material was added to pre-weighed mesh litter bags (3 cm × 6 cm, 1-mm mesh gauge). Twenty-four litter bags were deployed in each of the two sites (12 in each marsh and fen) in late October 2003. Bags were sewn shut, and placed horizontally just below the peat surface and left over winter. After 211, 241, 263 and 291 d (collections made monthly from May to August 2004), three bags were collected from each zone in both sites. Bags were cleaned of roots and other debris and then dried at 60°C for 48 h and weighed. The percent of plant mass remaining was calculated as follows:

$$\text{Mass remaining } (\%) = 100 - [(X_o - X)/X_o] \times 100$$

where X_o represents the initial mass of litter in the bag and X represents the final mass after field incubation (Reader and Stewart 1972;Bartsch and Moore 1985). Litter inputs of N into the peat during decomposition were estimated by multiplying the amount of N in the plants at peak biomass by the proportion of the litter that was lost via decomposition.

Production

Aboveground biomass was measured in late August 2004 (peak biomass). Ten 0.5 × 0.5 m (0.25 m^2) quadrats were harvested in each of the marsh and fen vegetation zones of both sites. Quadrats were placed randomly in the vegetation zone, and all live vascular vegetation was clipped at ground level. Plants were separated by genus, dried at 60°C for 1 wk and weighed. Aboveground biomass values are expressed as g m^{-2} and are used as an index of annual aboveground production. We realize that peak aboveground biomass is an underestimate of total production due to nonvascular productivity, belowground structures (root production), leaf mortality and herbivory; however, because we are trying to compare between sites and vegetation zones using the same technique, aboveground vascular production is used as an index of primary production.

Whole plants of *Carex diandra* from the peak production harvest in August 2004 were selected from each marsh and fen for analysis of tissue nitrogen, phosphorus and carbon content. Total carbon and nitrogen content of the plants was determined upon combustion using a Control Equipment Corporation 440 element analyzer. Ground plants were analyzed for total phosphorus using a peroxide/sulfuric acid digest following Parkinson and Allen (1975). Plant biomass N at peak harvest was estimated by multiplying tissue N concentrations by total NPP (to give g N m^{-2}). This value was used as an index of annual plant uptake of N.

Microbial Biomass

Microbial biomass C and N were measured following the chloroform fumigation extraction method outlined by Horwath and Paul (1994). Pairs of subsamples (approximately 10 g dry weight) of initial cores taken for net mineralization measurements were used to

measure microbial biomass C and N. Of each subsample pair, one was left unfumigated and the other was fumigated with chloroform in a sealed desiccator for 24 h. Fumigated and unfumigated soil samples were extracted for both dissolved organic carbon (DOC) and total nitrogen (TN) with 0.5 M K_2SO_4 (50 mL of K_2SO_4 per soil sample), shaken for 1 h, filtered through Whatman No. 1 filter paper and stored at 4°C until analysis. Microbial DOC and TN were analyzed directly on a Shimadzu TOC-VTN (Mandel Scientific Company Inc). Dissolved organic nitrogen (DON) was calculated as:

$$\mathrm{DON} = \mathrm{TN} - (\mathrm{NO_3^-} + \mathrm{NH_4^+}).$$

Microbial biomass DOC and DON were calculated using the following formulas:

$$\text{Microbial biomass C} = (\mathrm{DOC_{fumigated}} - \mathrm{DOC_{unfumigated}})/\mathrm{K_c}$$

$$\text{Microbial biomass N} = (\mathrm{DOC_{fumigated}} - \mathrm{DOC_{unfumigated}})/\mathrm{K_n}$$

where K_c and $K_n = 0.45$ (Jenkinson et al. 2004) and are correction factors that represent the efficiency of the extraction.

Environmental Variables

Peat temperature (to 5 cm depth) and water depth were measured monthly in the field at the same time as core collection. Porewater pH was measured in the field using an Accumet pH meter. Gravimetric soil moisture content and bulk density were measured by drying known volumes of soil at 105°C and measuring mass loss. Surface water samples were analyzed for ammonium (NH_4^+) and nitrate (NO_3^- and NO_2^-). Nitrate samples were filtered using Whatman GF/F filters (1.0 μm pore size), while ammonium samples were not filtered. Both nitrate and ammonium were analyzed on a Technicon Autoanalyser II. Subsamples of peat from monthly initial net mineralization cores (May through August) in both marshes and fens were dried at 105°C for nutrient analysis. Peat samples were ground and analyzed for total phosphorus using a peroxide/sulfuric acid digest (Parkinson and Allen 1975). Total C and N content of the peat was determined upon combustion using a Control Equipment Corporation 440 element analyzer.

Statistical Procedures

Nitrogen flux rates and pool sizes were analyzed using repeated measures ANOVA for differences between months, sites and vegetation zones. Primary production data were analyzed using a nested ANOVA for differences between sites and vegetation zones. Relationships between N fluxes and pools and environmental variables were investigated using Pearson correlations. All statistical procedures were performed using SPSS 12.0 software.

RESULTS

There were no significant differences ($P > 0.05$) between marshes and fens within the same peatland-pond complex in any of the major N fluxes or pools measured, except for total N concentration in the peat (Table 2). Therefore, results were pooled (marshes and fens) within the same peatland-pond complex for comparisons

Table 2. Nutrient concentrations (±SE) in *Carex* (in August) and mean monthly nutrient concentration in peat and microbes for May through August, 2004

	Floating peatland		Non-floating peatland	
	Fen	Marsh	Fen	Marsh
TC Peat,b*	47.15 (0.34)	48.20 (0.35)	19.75 (1.18)	24.36 (1.34)
TN Peat,a*	2.23 (0.10)	2.98 (0.08)	1.41 (0.09)	1.67 (0.09)
*TP Peat**	0.18 (0.02)	0.24 (0.02)	0.14 (0.01)	0.13 (0.02)
N:P Peat	12.4	12.4	10.1	12.8
Extractable NH_4^+	0.023 (0.004)	0.018 (0.004)	0.0069 (0.002)	0.019 (0.004)
Extractable NO_3^-	0.0017 (0.0003)	0.0022 (0.0007)	0.00024 (0.00007)	0.0072 (0.0005)
TC Carex	45.96 (0.10)	45.81 (0.10)	44.79 (0.10)	45.64 (0.10)
TN Carex	1.50 (0.01)	1.20 (0.01)	1.08 (0.01)	1.36 (0.01)
TP Carex	0.18 (0.01)	0.16 (0.01)	0.15 (0.01)	0.14 (0.01)
N:P Carex	8.3	7.5	7.2	9.7
*TC Microbes**	7.03 (0.29)	5.65 (0.25)	0.57 (0.03)	0.44 (0.01)
*TN Microbes**	20.12 (0.83)	11.38 (0.13)	0.39 (0.02)	0.64 (0.02)
C:N Microbes	9.8	9.5	22.5	9.6
Surface Water NH_4^+	48.4 (11.4)		23.7 (4.6)	
Surface Water NO_3^-	4.37 (1.1)		2.15 (0.5)	

*denotes significance between sites ($P<0.005$). Significant differences between marshes and fens denoted by *a* ($P<0.05$) and *b* ($P<0.005$). Peat nutrients are expressed as percentage of peat dry weight, *Carex* as percentage of dry biomass and microbes as a percentage of the peat Total C or N. Surface water N concentrations are expressed in μg L^{-1}

Table 3. Net vs. gross mineralization rates in two boreal peatlands expressed as mg N m^{-2} d^{-1}. Data are the mean of all measurements (± SE) from May through August 2004 ($n = 24$ for each site)

	Floating peatland	Non-floating peatland
Gross mineralization		
NH_4^+	202.37 (45.4)	27.72 (4.6)
NO_3^-	250.89 (66.0)	31.65 (7.07)
Net mineralization		
NH_4^+	18.12 (2.6)	8.05 (1.55)
NO_3^-	0.31 (0.4)	−0.059 (0.2)
NO_3^- *	157.22 (29.1)	85.36 (32.1)

*Indicates an estimate of net nitrate mineralization assuming that all N released via denitrification was derived from mineralized nitrate.

between sites (floating vs. non-floating). Large differences in N cycling were found between the two peatland-pond sites and results will therefore focus on these differences.

Comparison of Net and Gross Mineralization Rates

Net mineralization of N was dominated by ammonification, whereas net nitrification rates were very low or negative. Net ammonification was significantly higher in the floating peatland than in the non-floating peatland. On average, net nitrification rates were positive in the floating peatland and were negative in the non-floating peatland; however, these differences were not significant (Table 3). Because high denitrification rates were also measured in these sites (Wray and Bayley 2007), estimates of net nitrification rates were also calculated assuming that all N released via denitrification was derived from the nitrate produced via nitrification in the cores (Table 3).

Net ammonification and net nitrification were not different between months in both the floating and non-floating peatlands (seasonal data not shown). In general, ammonification was lowest over winter (4.98 to 9.48 mg NH_4-N m^{-2} d^{-1}) and highest in July (9.81 to 22.28 mg NH_4-N m^{-2} d^{-1}). Net nitrification was highest in July (0.59 to 1.71 mg NO_3-N m^{-2} d^{-1}) and lowest in May (−0.37 to −1.01 mg NO_3-N m^{-2} d^{-1}). Gross ammonification and nitrification rates were both significantly higher in the floating peatland than in the non-floating peatland (Table 3).

Microbial Biomass and Gross N Consumption

Microbial biomass C and N pools were significantly higher in the floating peatland than in the non-floating peatland ($P < 0.001$) (Table 2). In addition, total carbon, nitrogen and phosphorus and extractable N concentrations in the peat were also significantly higher in the floating peatland (Table 2). Gross rates of NH_4^+ and NO_3^- consumption were significantly higher in the floating peatland than the non-floating peatland ($P = 0.029$ and $P = 0.008$, respectively) (Table 4).

Table 4. Estimates of gross N consumption and microbial uptake in two boreal peatlands (mg N m^{-2} d^{-1}) for May through August 2004 ($n = 24$). Microbial uptake estimates from isotope dilutions are calculated as: NH_4^+ microbial uptake = gross NH_4^+ consumption − gross nitrification, and NO_3^- microbial uptake = gross NO_3^- consumption − denitrification.

	Floating peatland	Non-floating peatland
Gross consumption		
NH_4^+	308.30 (105.6)	30.58 (4.4)
NO_3^-	404.08 (108.1)	33.92 (7.0)
Microbial uptake estimate (isotope dilution)		
NH_4^+	57.41 (111.7)	−1.07 (6.87)
NO_3^-	249.84 (111.6)	−52.16 (27.9)
Microbial uptake estimate (gross − net mineralization)		
NH_4^+	184.97 (43.7)	19.67 (4.6)
NO_3^-	250.58 (63.3)	31.76 (6.9)
NO_3^- *	104.42 (73.4)	−41.96 (29.2)

*indicates an estimate of microbial uptake using net NO_3^- mineralization values that assume all N released via denitrification was produced from mineralized nitrate.

Plant Dynamics

Peak aboveground biomass in August 2004 was significantly higher ($P < 0.001$) in the non-floating peatland than the floating peatland and in both sites plant biomass was inversely related to microbial biomass (Fig. 1). Total nutrients (carbon, nitrogen and phosphorus) in *Carex diandra* tissues from the August harvest were not significantly different between the two peatlands (Table 2). *Carex* N:P ratios ranged from 7:1 to 10:1 suggesting that vegetation in both the floating and non-floating peatlands is N limited (Koerselman and Mueleman 1996). Estimates of plant biomass N (assumed equivalent to annual plant N uptake)

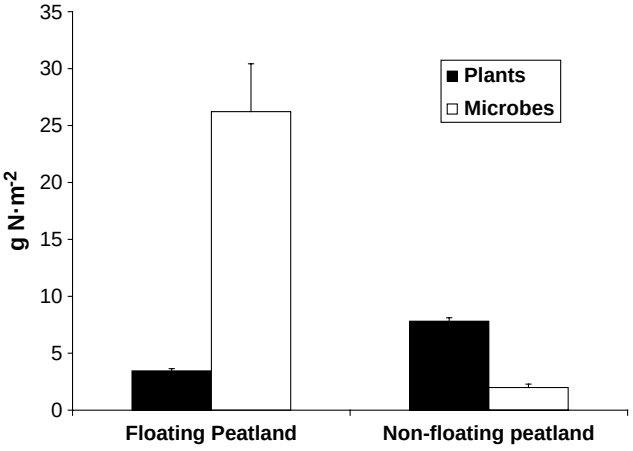

Fig. 1. Comparison of plant and microbial biomass N in a floating and non-floating peatland. Plant nitrogen represents g N m^{-2} of aboveground tissues; microbial nitrogen represents g N m^{-2} of peat to 10 cm peat depth. Bars represent standard error of the mean.

Table 5. Environmental variables in the floating and non-floating peatland

Floating peatland	Non-floating peatland	
Bulk density *a*(g cm^{-3})	0.068 (0.002)	0.26 (0.01)
Moisture content *a*(g water/g peat)	12.84 (0.5)	3.21 (0.2)
Water Level (cm) *b*		
Fen	1.79 (0.6)	1.75 (0.6)
Marsh	8.00 (1.1)	10.87 (2.1)
pH porewater	5.38 (0.1)	5.84 (0.3)
Soil temperature (°C)	12.25 (1.2)	8.85 (1.6)

a denotes a significant difference between the two peatlands at $P<0.05$; *b* denotes a significant difference between marshes and fens within the same peatland ($P<0.001$). Values are means ($\pm$SE) for measurements taken from May through August. $n=24$ for all except water level, where $n=12$.

were 3.45 g N m^{-2} in the floating peatland and 7.82 g N m^{-2} in the non-floating peatland (Fig. 1).

Decomposition of *Carex diandra* litter was not significantly different between the two peatlands. Total mass loss in the floating and non-floating peatlands was 46.05 and 54.69%, respectively, after 291 d in the field. There were significant differences in mass loss between months ($P<0.001$) with greatest mass loss occurring over winter and significant losses between May and June and July and August. Estimates of N inputs into the peat via decomposition after 291 d are 1.59 g N m^{-2} in the floating peatland and 4.28 g N m^{-2} in the non-floating peatland.

Environmental Variables and N Fluxes and Pools

Major differences in physical and environmental parameters were measured between the two sites (Table 5). In general, peat bulk density was highest in the non-floating peatland, and moisture was highest in the floating peatland. Water level relative to the peat surface was not different between sites ($P=0.292$); however it was significantly higher in marshes than in fens ($P<0.001$). Peat porewater pH and mean soil temperature were not different between the two peatlands.

Integrated Internal N Budget

Annual rates of major nitrogen flux rates and pool sizes were estimated for both the floating and non-floating peatland (Fig. 2a and b, Table 6). No significant differences between monthly N pool sizes were measured and therefore annual pool sizes were estimated by averaging monthly pool sizes. Annual flux rates of N were estimated by extrapolating daily means into monthly rates and adding monthly rates together (May through August). This annual estimate assumes that there is no major N flux over winter from September through April when the peat is frozen.

In general, the floating peatland has a larger microbial pool that is much more active (as indicated by the much higher N flux rates) than the non-floating peatland. The extractable ammonium pool turns over four times daily in the floating peatland and every 3 d in the non-floating peatland. Nitrate turnover was much faster in both sites, calculated to be 12 times daily in the floating peatland and 7 times daily in the non-floating peatland.

DISCUSSION

The lack of difference between the marsh and fen community within each site can be attributed to location of the peatlands in fairly small peatland basins, adjacent to ponds where both marshes and fens can be affected by the surface water of the pond. Differences in the vegetation communities between marshes and fens are attributed to water level differences and not nutrient differences (Whitehouse and Bayley 2005).

Comparison of Net and Gross Mineralization Rates

Net nitrification in this study was either negative (net consumption) or only slightly above zero. This corresponds to findings from other western boreal peatlands (Humphrey and Pluth 1996; Mewhort 2000; Bayley et al. 2005). Net nitrification in the incubated bags was low due to its rapid reduction to N_2 in the process of denitrification (Wray and Bayley 2007). Net ammonification rates are comparable to other studies in peatlands using the buried bag technique (Devito et al. 1999; Mewhort 2000; Bayley et al. 2005) and using resin bags (Bridgham et al. 2001).

Gross ammonification in the floating peatland and gross nitrification in the non-floating peatland were higher than estimates from boreal shield peatland soils (Westbrook and Devito 2004). Gross ammonification values in the floating peatland are more similar to those measured in a mature coniferous forest (Davidson et al. 1992). Nitrification rates were especially high compared with net rates. We presume that this is due to the nature of peatlands saturated with oxygen-rich surface waters and an aerobic surface layer of soil where nitrification can occur. Very high gross rates (vs. net rates) of mineralization indicate that nitrate and ammonium are rapidly consumed in the system and therefore turn over quickly. This highlights the limitations of measuring only net rates as a measure of mineralization.

Site differences in gross N mineralization are most likely due to differences in microbial biomass and soil moisture between the two sites. Gross ammonification rates were positively correlated with moisture content of the peat in the floating peatland and with microbial biomass C in the non-floating peatland. Microbial biomass was much higher in the floating peatland, and is an important regulator of mineralization rates because microbes are mediating the entire process and are responsible for transforming organic N to ammonium and nitrate. Soil moisture content has been shown to be positively related to gross mineralization rates (Puri and Ashman 1998) and nitrification can be enhanced with increasing available phosphorus (Bowden 1986), both of

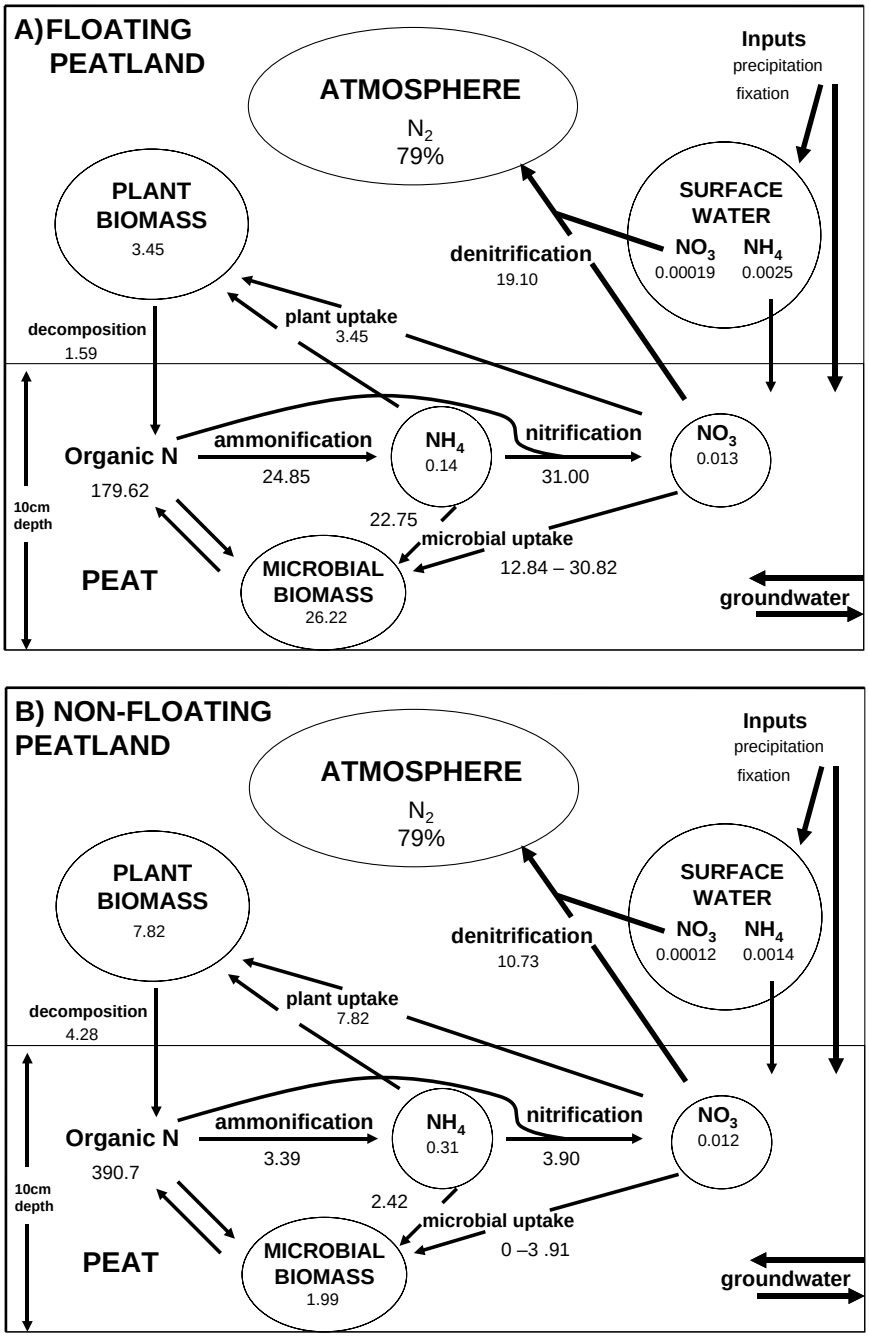

Fig. 2. Estimated annual N fluxes and pool sizes in (A) a floating peatland and (B) a non-floating peatland. All measurements are to 10 cm peat depth and were taken from May through August 2004. Ammonification and nitrification rates are gross rates. All fluxes are expressed as g N m^{-2} yr^{-1} and all pools are expressed as g N m^{-2}.

which are higher in the floating peatland and may explain higher N mineralization rates in that site.

Microbial Biomass and Gross N Consumption

Microbial biomass C and N were higher in the floating peatland than in the non-floating peatland and also remained relatively stable throughout the season, a finding which corresponds to other studies (Puri and Ashman 1998). The size of the soil microbial biomass pool increases with increasing C content of the soil (Anderson and Domsch 1985) and increasing moisture content of the soil (Mitchell et al. 2003); in this study microbial N is positively correlated with moisture content of the soil. Both peat TC and moisture content

Table 6. Estimated annual inputs and outputs of inorganic N in a non-floating and floating peatland. All values are expressed as g N m^{-2} peat to 10 cm depth based on measurements from a 123-d season (May through August 2004). Literature values are used for estimates of fixation (Amon et al. 2005) and precipitation (Schindler et al. 2006). Microbial uptake values are based on estimates of gross – net mineralization of NH_4^+ and NO_3^-. The range of microbial uptake of NO_3^- represents a range of net nitrification estimates based on maximum potential denitrification occurring in buried cores (in this case we assume that all N that is denitrified is derived from mineralized nitrate which amplifies net rates) to no denitrification in buried cores

Floating peatland	Non-floating peatland	
Inputs		
Fixation	1.43	1.43
Precipitation	4	4
Groundwater	No estimate	No estimate
Litter	1.59	4.28
Surface water	No estimate	No estimate
Gross ammonification	24.85	3.39
Gross nitrification	31.00	3.90
Total	61.07	17.00
Outputs		
Denitrification	19.10	10.73
Groundwater	No estimate	No estimate
Plant Uptake	3.45	7.82
NH_4 consumption	31.00	3.90
Microbial uptake:		
NH_4^+	22.75	2.42
NO_3^-	12.84–30.82	0–3.91
Total	89.14–107.12	24.87–28.78

were significantly higher in the floating peatland, which may explain the higher microbial biomass.

Microbial biomass C and N in the non-floating peatland (28.18 and 1.99 g m^{-2}, respectively) are within the same range as microbial pools in southern wetlands (Wright and Reddy 2001), forests (Davidson et al. 1992) and *Sphagnum* peatlands (Williams and Silcock 2000) whereas microbial C and N pool sizes in the floating peatland are much larger (202.0 and 26.2 g m^{-2}, respectively). Microbial C:N ratios are higher than those measured in forests (Davidson et al. 1992) and are closer to C:N ratios in Alaskan boreal soils (Vance and Chapin 2001), European peatlands (Francez et al. 2000), sub-arctic ecosystems (Schmidt et al. 1999) and northern forests (Fisk and Fahey 2001). Higher microbial C:N ratios have been associated with high proportions of fungi relative to bacteria (Tate 1995). Most microbes mediating N cycling are bacteria (Tate 1995); therefore we would expect greater N fluxes in sites with a lower proportion of fungi comprising the microbial biomass. We hypothesize that the higher C:N ratio may be due to a larger fungal community.

Peat TC, TN and TP were all significantly higher in the floating peatland when expressed as a percent of peat dry weight. Peat TC in the floating peatland is higher than that measured in other boreal fens, while peat TC in the non-floating peatland is lower than that measured in other studies (Bridgham et al. 1998; Bayley et al. 2005). Peat TN is roughly within the same range as that measured in other boreal fens (Bridgham et al. 1998; Bayley et al. 2005) and marshes (Bedford et al. 1999). Higher nutrients in marshes could be related to movement of nutrients from N and P-rich water above the peat. Increased peat carbon content in the floating peatland is most likely due to the less decomposed peat (as indicated by the fibrous nature and low bulk density), because slower rates of decomposition conserve C in peatlands (Moore 2002).

The pool of extractable ammonium in the peat is similar to that in other northern wetlands, while extractable nitrate in this study is much higher (Bridgham et al. 2001). Extractable nitrate concentration was almost identical in both sites, whereas the extractable ammonium concentration was higher in the non-floating peatland. Given the higher rates of N fluxes between these pools within the floating peatland it is surprising that extractable NH_4^+ concentrations are higher in the non-floating peatland. Inorganic nutrients can be turned over rapidly and concentration does not necessarily correspond with supply rates because demand by microbes and/or primary producers could leave small labile pools (Dodds 2003). Sizes of the extractable N pools are therefore not necessarily an accurate indication of mineralization rates between these pools. High rates of N mineralization can correspond to low accumulation of inorganic N provided that consumption rates are also high.

Gross N Consumption and Estimates of Microbial Uptake

Gross consumption of both NH_4^+ and NO_3^- was significantly higher in the floating peatland than the non-floating peatland and boreal shield peatlands (Westbrook and Devito 2004). This is not surprising since the majority of N is consumed via microbial immobilization (Schlesinger 1991) and there is a much higher microbial biomass in the floating peatland. Besides microbial immobilization, ammonium is also consumed by nitrification and nitrate is consumed via denitrification (Schlesinger 1991). Both gross nitrification and denitrification rates are much higher in the floating peatland, which would also account for the high rates of N consumption. In this study, consumption rates are consistently higher than gross mineralization rates, a finding that corresponds to those of Davidson et al. (1992). Gross consumption measurements using isotope dilution are often overestimated due to enrichment of the substrate pool (Hart et al. 1994a) and where consumption is higher than mineralization it indicates that N addition rapidly stimulated microbial assimilation of N, a process that is further enhanced by the lack of opportunity for plant uptake in the cores.

Plant Dynamics

Net primary production in the floating peatland is lower than other values in the literature from western boreal

fens and marshes; however, it follows the same trend in that marshes are more productive than fens (Thormann and Bayley 1997a, b; Mewhort 2000; Vitt et al. 2001). Higher plant biomass in the non-floating peatland was surprising, since this is the site with the lowest N pool sizes and cycling rates. Production differences may not be due to differences in N mineralization rates, but may be more closely related to the actual availability of inorganic N to plants (Verhoeven et al. 1988). NH_4^+ is the preferred inorganic N form for microbes as well as grasses and sedges (Jackson et al. 1989). Nitrogen availability for plant uptake in N-limited systems such as the ones in this study is controlled by partitioning of inorganic nitrogen between the microbes and plants (Jackson et al. 1989). It is generally believed that microbes are superior competitors for bioavailable N because they are responsible for converting organic N to inorganic N and thus should have first access (Schimel and Bennett 2004). High microbial demand for inorganic N can limit N availability to plants (Nadelhoffer et al. 1991) and larger microbial pool sizes have been measured in boreal soils that support less vegetative biomass than those with smaller microbial populations (Vance and Chapin 2001); our study sites show the same pattern.

Decomposition rates after 291 d in the field were also not significantly different between the two sites. A difference in decomposition rates between the sites was not seen, possibly because the same type of plant material was used in both sites. Decreased peat humification in the floating peatland may be due to the presence of a significant moss stratum that was not present in the non-floating peatland. Mosses, relative to graminoids such as Carex species, have higher concentrations of "decay-resistant" polymers (Bayley et al. 2005). Decomposition measurements and nutrient analysis of decomposing litter were further limited in this study since plants may resorb nutrients during decomposition due to microbial activity (Berg and Soderstrom 1979). Despite these limitations, we feel our measurements are a useful index of decomposition and suit our purposes for comparing patterns among sites.

Environmental Variables and N Fluxes and Pools

Sites differed in several physical and environmental parameters, which may be related to the differences seen in N fluxes and pool sizes between the two sites (namely, larger N pools and cycling rates in the floating peatland than in the non-floating peatland). In the floating site, the peat is very fibrous with a low bulk density. This is in direct contrast to the non-floating peatland where the peat is not floating and is very humic with a significantly higher bulk density. This higher level of humification in the non-floating peatland is probably directly related to long-term water level fluctuations with drought cycles, which are much greater than those in the floating fen/marsh, which would not be as susceptible to water level changes. Greater water level fluctuations can lead to increased decomposition of peat and increased bulk density. Increased bulk density of the peat results in lower soil moisture and increased anoxic conditions due to fewer pore spaces within the peat, which limits microbial activity (Brinson et al. 1981) and could therefore limit N cycling in the non-floating peatland.

Integrated Internal N Budget

Although nutrient pools remain relatively stable over the course of the season, internal cycling of N between these pools is high (Fig. 2).

Inputs of N into these peatlands was not measured as part of this study; however, estimates based on literature values were made. Nitrogen fixation in temperate Midwestern USA fens was measured as 11.6mg N m^{-2} d^{-1} (Amon et al. 2005) and precipitation inputs are approximately 4 g N m^{-2} yr^{-1} in north-central Alberta (Schindler et al. 2006).

The largest nitrogen pool is in the peat. Gross ammonification and nitrification released large amounts of N in the floating peatland. Gross nitrification rates were high, and in many cases were higher than gross ammonification rates; this indicates that nitrate may not always be mineralized from ammonium and that some nitrate may be mineralized directly from organic N (heterotrophic nitrification). Extractable nutrient pools are very small and turnover rapidly to accommodate high rates of N cycling.

Both sites have a deficit of inorganic N in the peat (Table 6) i.e. mineralization and other inputs are not high enough to accommodate rates of nitrification, denitrification, and microbial and plant uptake. It is possible that plants and microbes are able to assimilate organic N (Tate 1995; Persson and Näsholm 2001; Henry and Jefferies 2002) in addition to ammonium and nitrate. Also, heterotrophic nitrification from organic N may also play a role in these peatlands, as autotrophic nitrification activity has been found to be low in some western North American (forest) ecosystems (Jordan et al. 2005) and heterotrophic nitrification is higher than autotrophic nitrification in some wetlands (Matheson et al. 2003). It is also possible that surface water nitrate is an important substrate for denitrification in the non-floating peatland and the pool turns over rapidly (Christensen et al. 1990; Venterink et al. 2003) and groundwater inflow may be an important source of nitrate (Ferone and Devito 2004).

In conclusion, internal nitrogen cycling within peatlands of the western boreal plain can be high. Although marsh and fen peatland types surrounding the same shallow nutrient-rich ponds do not differ in major N fluxes rates and pool sizes, significant differences in N cycling can occur between different peatland-pond complexes (sites). Differences in N cycling between sites is strongly influenced by physical and environmental characteristics site including bulk density and moisture content of the peat and surface water level fluctuations.

These factors affect the microbial community of the peat which in turn mediates all major N cycles. The non-floating peatland had higher plant productivity and lower N cycling, presumably due to reduced competition for inorganic N by microbes.

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