University of Alberta

Nitrogen dynamics in two peatland-pond complexes in the mid-boreal plain, Alberta

by

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Abstract

Major nitrogen flux rates and pool sizes were measured in two peatland-pond complexes (one floating and one non-floating) in the Western Boreal Plain of Alberta, both consisting of a marsh and fen vegetation zone. Denitrification rates were substantial in both peatland sites (up to 24 g $N \cdot m^{-2} \cdot yr^{-1}$); the predominant product was N_2. In contrast N_2O production was less than 2% of the denitrification product in the floating peatland while the non-floating peatland was a sink for N_2O. Internal N fluxes and pools were significantly higher in the floating peatland, presumably due to increased moisture and carbon content in the peat supporting greater microbial biomass and activity. Plant biomass was lower in this site, possibly due to competition by microbes for available inorganic N. Monthly measurements of N fluxes and pools were combined to provide an estimate of internal N cycling within marshes and fens surrounding shallow ponds in the boreal plain.

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1. Introduction

Peatlands are important to nutrient cycles on a global scale. Many peatlands are active carbon sinks (Gorham 1991) and may also be important to nitrogen biogeochemistry as transformation sites (Schlesinger 1991) and removal sites (Saunders and Kalff 2001) via biological denitrification, which is the primary mechanism for N loss from wet soils (Kadlec and Knight 1996). Although outputs and inputs of N to peat systems can be large, internal cycling of N is often 10-20 times greater than external inputs and outputs (Schlesinger 1991, Paul and Clark 1996). Dynamics of the nitrogen cycle in peat are poorly understood, especially in western boreal peatlands. In Alberta, peatlands of the Western Boreal Plain (WBP) are unique from other northern peatlands because they are naturally nutrient rich and thus have potential for increased cycling of N including N removal.

In the WBP, peatlands are commonly found surrounding shallow ponds in small basins (National Wetlands Working Group 1997). A variety of peatland types (bogs, fens and marshes) surrounding these ponds have been classified according to vegetation (Whitehouse and Bayley in press). While bogs are ombotrophic and nutrient poor, marshes and fens receive nutrients from precipitation as well as surface and ground water flow and are therefore more nutrient rich (Mitsch and Gosselink 2000). Thus, denitrification in marshes and fens could be an important removal mechanism for increased inflows of N from activities in the watershed. Furthermore, waterlogged conditions of marsh and fen peat provide an ideal environment for biological denitrification (Knowles 1982).

Despite the potential importance of denitrification in boreal Alberta peatlands, there are little data in this area that give an accurate estimate of potential denitrification rates. The predominant product of denitrification is N_2 gas (Knowles 1982), however N_2O, which is a powerful greenhouse gas (Crutzen 1970) may also be produced during denitrification. Due to the difficulty of measuring denitrification against the atmospheric background concentration of N_2, denitrification studies have focused on measurements of N_2O using the acetylene block technique (Urban and Bayley 1988, Robertson et al 1988, Davidsson and Leonardson 1997), which underestimates denitrification rates (Seitzinger et al. 1993). Direct measurements of N_2 flux from soil are becoming more common, however few studies that measure direct N fluxes from peat soils have examined the relative importance of N_2 vs. N_2O as an end product of denitrification (Mewhort 2000).

Cycling of N within the peat is also important as it provides the substrate needed for denitrification and also N is often limiting to plant growth in peatlands (Moore 2002). Nutrient availability in wetlands is often determined by internal nutrient cycles (Verhoeven et al. 1990) i.e., mineralization, which replenishes inorganic (NH_4^+ and NO_3^-) pools in the soil (Bridgham et al. 2001). Nitrogen mineralization is often measured as a net rate which does not give an indication of N turnover rates or consumption by microbes as gross rates of mineralization do. Very few studies have measured gross N transformations in peatlands (Westbrook and Devito 2004, Potila and Sarjala 2004), and these studies have been performed in more nutrient poor systems than peatlands of the WBP. The role of microbes in N transformations is also important as they mediate all N cycling, yet studies of microbial pool sizes in peat are not common (Williams and Silcock 2000, Francez et al. 2000, Potila and Sarjala 2004).

The overall objective of this study was to quantify denitrification rates and internal N fluxes and pool sizes in two boreal peatland-pond complexes, each with a marsh and fen vegetation zone. This thesis is organized so that one data chapter examines the loss of N from peatlands via denitrification and the other chapter examines the other aspects of nitrogen cycling in the peat complex.

Chapter Two provides an estimate of potential denitrification rates from WBP marsh and fen peat. We hypothesized that denitrification rates would be high in peat of the WBP based on previous studies measuring high denitrification in a different part of boreal Alberta (Mewhort 2000). We also hypothesized that denitrification rates would be higher in marshes than fens due to higher water levels in marshes (Whitehouse and Bayley in press) leading to increased anoxia which promotes denitrification, as well as increased NO_3^- in marsh surface water (Bayley and Mewhort 2004) providing a substrate for denitrification. We further hypothesized that seasonal denitrification rates would vary with temperature (i.e., higher denitrification with higher air and soil temperatures) since increasing temperature increases microbial activity and denitrification rates (Knowles 1982, Tiedje 1988). Although peatlands can possibly be important sources of atmospheric N_2O (Regina et al. 1996, 1998), N_2O becomes a greater product of denitrification in soils with low pH (Wolf and Brumme 2003) and increasing oxygen availability (Firestone et al. 1980), environmental conditions that are characteristic of bogs, although not fens and marshes (Mitsch and Gosselink 2000). Therefore, in our study sites, we hypothesized that N_2 would be the predominant denitrification product.

Denitrification rates were compared between peatland types and sites and also between different months to quantify seasonal variations in N flux. Data from July through September 2003 and May through August 2004 were combined to estimate an annual rate of denitrification from boreal marshes and fens surrounding shallow ponds. Denitrification rates were also examined in relation to physical, environmental and nutrient parameters in the peatlands.

Chapter Three examines internal N cycling rates and pool sizes within the same boreal marshes and fens from May through August 2004. As many northern wetlands are nutrient poor, (Jonasson and Shaver 1999) most studies of nutrient cycling in boreal peatlands are performed in nutrient poor systems (Updegraff et al. 1995, Bridgham et al. 1998). In contrast, many ponds and associated peatlands in the WBP are more nutrient rich, therefore we hypothesized increased N cycling in our study sites relative to other boreal peatlands. We hypothesized that net and gross mineralization rates, as well as the size of microbial biomass and microbial uptake of N would be higher in marshes than fens due to increased nutrients at the edges of nutrient-rich ponds and higher water levels in marshes stimulating microbial activity (Bayley and Mewhort 2004). We further hypothesized increased nutrient availability would be reflected in higher plant biomass in marshes.

Gross and net NH_4^+ and NO_3^- mineralization rates were measured and compared with each other. Furthermore, internal N pools (microbial, plant, peat and surface water) were quantified. Plant uptake and litter return of N to the peat were estimated based on net primary productivity and decomposition studies. These rates and pool sizes were integrated with input estimates from the literature and losses via denitrification to estimate annual N cycling in boreal peatland-pond complexes.

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2. Potential denitrification rates in two marshes and fens in boreal Alberta, Canada

Introduction

Nitrogen inputs into many watersheds have increased due to human activities such as agriculture and fossil fuel burning (Vitousek et al. 1997). In boreal Alberta, background nitrogen deposition is low except in selected areas associated with disturbances to the landscape by the oil and gas industries. In the Western Boreal Plain (WBP) of Alberta, peatlands, predominately fens and bogs, cover 20-50% of the land area (Vitt et al. 1995). Peatlands are important to the global N cycle because they can remove, via denitrification, N loaded into the system. The peatlands of the WBP in Alberta are naturally nutrient rich and thus have potential for increased cycling of N, including N removal.

Nitrogen can be retained in aquatic systems via biological denitrification, sedimentation and assimilation by plants (Saunders and Kalff 2001). Of these, denitrification is considered the only permanent mechanism for nitrogen loss, since it completely removes nitrogen from the system and returns it to the atmosphere in a form (N_2) that is not readily available to organisms (Vitousek et al. 1997, Laursen and Seitzinger 2002). Denitrification is the reduction of nitrate (NO_3^-) and/or nitrite (NO_2^-) by anaerobic bacteria, releasing nitrous oxide (N_2O) and/or dinitrogen (N_2) gases as products (Knowles 1982, Tiedje 1988). The predominant product is N_2 (Knowles 1982, Kadlec and Knight 1996, Seitzinger et al. 1993), however N_2O is a powerful greenhouse gas and ozone degrader (Crutzen 1970, Wang et al. 1976) and there have been concerns that peatlands can contribute significantly to N_2O concentrations in the atmosphere (Regina et al. 1996, 1998). Nitrous oxide becomes a more important product of denitrification in soils with low pH (Wolf and Brumme 2003) and increasing oxygen availability (Firestone et al. 1980), environmental conditions that are characteristic of ombotrophic bogs, although not fens and marshes (Mitsch and Gosselink 2000).

Despite the potential importance of denitrification for nitrogen flux in boreal Alberta, there are little data in this area that give an accurate estimate of potential denitrification rates. Difficulties with the measurements of denitrification may have contributed to this scarcity of data. The popular acetylene block technique (Sørensen 1978) has been shown to underestimate denitrification rates due to the inhibition of nitrification by acetylene (Knowles 1982, Seitzinger et al. 1993, Watts and Seitzinger 2000). Use of ^{15}N tracers can be problematic because of possible fertilizer effects due to substrate addition (Nishio et al. 1983). Direct measurements of denitrification are ideal; however this is difficult due to the high background concentration of the end product i.e., N_2, which is in the atmosphere. The N_2-flux technique directly measures denitrification from intact soil cores in N-free, sealed chambers (Seitzinger et al 1980, Seitzinger 1988, 1993). The method is labour-intensive, and results are comparable to those obtained by using ^{15}N tracers (Seitzinger et al. 1993).

In freshwater systems, denitrification is the main mechanism for N removal (Seitzinger 1988, Saunders and Kalff 2001). This is especially evident in wetlands, as they provide ideal conditions for coupled nitrification-denitrification due to waterlogged soil, anoxic conditions, and a thin oxidized layer at the soil surface (Knowles 1982). Nitrate from the oxidized zone of soil can diffuse into the anaerobic soil layer and be denitrified (Delaune et al. 1998). Furthermore, wetland vegetation creates air spaces in the rhizosphere as well as slows water discharge rates which allowa greater soil-water contact time, and enhances denitrification rates (Reddy et al. 1989, Saunders and Kalff 2001). Denitrification rates in wetlands are regulated by environmental conditions as well as by the rate of nitrate production i.e., nitrification (Patrick and Reddy 1976), but net nitrification rates (the most common measurement of nitrification) are often low or negative in aquatic systems due to the high mobility of nitrate (Schlesinger 1991) and its rapid denitrification (Reddy et al.1989), a phenomenon that has been measured in boreal Alberta soils (Mewhort 2000). Few studies have examined gross nitrification rates in peatlands or compared net and gross nitrification rates (Westbrook and Devito 2004).

In boreal Alberta, wetlands, most of which are peatlands, cover up to 50% of the land area (Zoltai 1988). Peatlands accumulate nutrients in the form of partially decayed plant material (peat) and are thus important to global nutrient cycles as they can act as sources, sinks and transformation sites for several elements. They are potentially important sites of denitrification due to the high carbon content and waterlogged conditions.

In boreal Alberta, peatlands commonly occur in landscape depressions (Zoltai 1988) and many surround shallow water ponds. Whitehouse and Bayley (in press) identified these unique peatland-pond complexes as a common feature on the landscape and classified five distinct peatland vegetation communities surrounding these ponds. The two communities occurring closest to the pond are a marsh fringe along the water edge surrounded by an open (non-forested) fen. Marshes are characterized as wetlands with fluctuating water levels and vegetation dominated by emergent aquatic macrophytes (National Wetlands Working Group 1997), often cattails and tall *Carex* species, and have accumulated significant peat deposits at the edge of depressional ponds (Bayley and

Mewhort 2004). Fens are defined as peatlands with more than 40 cm of accumulated peat, characterized by vegetation cover dominated by graminoid species and brown mosses (National Wetlands Working Group 1997). Marshes and fens are relatively 'open' systems and receive nutrients from inflows of surface water and groundwater (Mitsch and Gosselink 2000). Thus, denitrification in marshes and fens could be important for removal of N from increased inflows due to activities in the watershed.

In northern peatlands, denitrification is thought to be unimportant (Etherington 1983) since denitrification rates decrease with decreasing temperatures (Knowles 1982). However, most studies have been done in nutrient-poor peatlands and use the acetylene block method (Urban and Bayley 1988, Davidsson and Leonardson 1998).

High rates of denitrification have been measured in some wetlands using the N_2 flux technique (maximum of approximately 2-7 mg $N \cdot m^{-2} \cdot hr^{-1}$) (Seitzinger et al. 1993, Seitzinger 1994) and ^{15}N methods (maximum of approximately 3-5 mg $N \cdot m^{-2} \cdot hr^{-1}$) (Reddy et al. 1989, Seitzinger et al. 1993, Delaune et al. 1998). These results are surprising since most wetlands are limited by available nitrogen in the soil (Bowden 1987, Mewhort 2000, Bayley et al. in press), however high rates of denitrification may be supported by diffusion of nitrate from surface water (Seitzinger 1994, Delaune et al. 1998). A study by Mewhort (2000) using the N_2-flux technique measured very high rates of denitrification (4.2 – 4.6 mg $N \cdot m^{-2} \cdot hr^{-1}$) in N-limited boreal marshes and fens in Alberta. Net nitrification rates in the soil were near zero and surface water did not appear to provide significant amounts of NO_3 for denitrification, therefore the mechanism for high denitrification rates was believed to be high rates of nitrification within the soil with fast turnover times (Mewhort 2000); however gross nitrification rates were not measured.

We hypothesized that denitrification rates would be high in peatland-pond complexes in the WBP based on previous studies measuring direct fluxes (Mewhort 2000) and that denitrification would be higher in marshes than in fens due to higher water levels leading to increased water saturation of the peat and increased anaerobic conditions as well as higher nitrate concentrations from the pond surface water. We further hypothesized that seasonal denitrification rates would vary with temperature (i.e., higher denitrification with higher air and soil temperatures) and that the predominant product of denitrification would be N_2 since marsh and fen soils are minerotrophic with circumneutral pH and anoxic due to water saturation.

The major objectives of this study were:

1. To determine the denitrification rates in different peatland vegetation communities (marsh and fen) surrounding shallow ponds in two different peatland-pond complexes.
2. To determine the seasonal denitrification rates in these boreal peatlands.
3. To determine the relative importance of the two gases (N_2 and N_2O) as the end product of denitrification.

Site descriptions

This study was performed in two peatland-pond complexes in the Mid Boreal ecoclimatic zone of northern Alberta (National Ecoregions Working Group 1989) in the Utikuma Lake Area (56°52' N, 115°27' W), approximately 300 km north of Edmonton, Alberta. This area is characterized by short warm summers and long cold winters with a mean annual temperature of 0.9°C over the two year study period (Environment Canada, 2005).

The two peatland-pond sites (Site 118 and Site 171) chosen for this study are both in depressions with clay till basins. Both sites consist of a shallow pond (<2 m depth) surrounded by a marsh fringe on the pond edge and an open fen vegetation zone surrounding the marsh, and the fen grades into bogs and aspen (*Populus tremuloides*) dominated uplands.

Site171 has an extensive marsh fringe located on the south side of the pond (where the study was done) and an average pond surface water pH of 9.1 over the course of the study. Mean porewater pH in the peatland was 5.8 (6.1 in marsh and 5.4 in fen). Marsh peat was very humic and mucky and vegetation was dominated by large emergent macrophytes including marsh ragwort (*Senecio congestus*) in 2003 and common cattail (*Typha latifolia*) in 2004. Water levels in the marsh fluctuated throughout this study from 9 cm to 16 cm above the peat surface. The open fen at Site 171 was composed of humic peat and dominated by common reed grass (*Phragmites australis*) in 2003 and by hairy-fruited sedge (*Carex lasiocarpa*) in 2004. Water levels in the fen fluctuated slightly over the study from 0 cm (at the peat surface) to 2 cm above the peat surface.

Site 118 has a narrow marsh fringe around the entire pond and an average surface water pH of 8.4. Mean porewater pH was 5.4 (5.4 in both marsh and fen). Both the marsh fringe surrounding the pond and the open fen are on a floating mat of peat above the water surface. The marsh fringe is 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 above the peat surface. The open fen is dominated by two-stamened sedge (*Carex diandra*). The peat is very fibrous and water levels fluctuated slightly throughout the study from 0 cm to 2 cm above the peat surface.

Methods

Techniques to estimate denitrification rates

Fluxes of N_2 and N_2O were measured from peat using two different techniques. Direct measurements of N_2 flux were taken in the laboratory from intact peat cores in gas tight chambers. Cores were collected monthly in marshes and fens from July through September in 2003 and from May through August in 2004. The upper 20-30 cm of soil is the site of the majority of microbial activity and N cycling (Schlesinger 1991), however it has been shown that this activity is significantly decreased below 10 cm depth in boreal peat (Humphrey and Pluth 1996) therefore all N_2 fluxes were measured from 0-10 cm peat depth, which we assume to be the depth of the active layer.

Nitrous oxide fluxes from soils were measured in the two fens from May through August in 2004 using *in situ* chambers to determine the relative importance of N_2O as a denitrification product.

N_2 flux - Field procedures

Three 7.5 cm diameter cores were taken in the fen and marsh vegetation zones of the two sites using a metal corer, for a total of 12 cores studied monthly. Cores were collected to approximately 15 cm depth, sealed in Ziploc bags and stored on ice until further processing. Twenty litres of surface water from the pond was collected at the same time as core collection each month.

N_2 Flux - Laboratory procedures

Denitrification (as N_2 flux) was measured following the methods of Seitzinger (1993) and modified by Nowicki (1994) to include controls. Peat cores were cut to 10 cm depth and sealed intact into gas-tight incubation chambers within 24 hours of field collection (Day 0). Chambers were constructed out of two pieces of glass pipe joint and sealed together with a rubber O-ring and metal clamp (see Seitzinger (1993) for further description). In each set of three cores (for each marsh and fen), one core was incubated without oxygen to serve as a control for sediment degassing (Nowicki 1994). Surface water from the site was flushed for at least 30 minutes with a mixture of 21% O_2 and 79% He gas for aerobic cores and He gas for anoxic cores to remove nitrogen gas from the water. Nitrogen gas-free water was then siphoned into the chambers until full (approximately 500 mL of water per chamber). Excess water was poured from the chambers until water depth over the core was the same as field water depth. The volume of water displaced was used as the value for the chamber headspace volume. The headspace was then flushed with the He/O_2 gas mixture (aerobic cores) or He (anaerobic cores) and the chambers sealed. Anoxic cores serve as a control because in the absence of oxygen, nitrification ceases thereby eliminating the NO_3 needed for denitrification (Nowicki 1994). Any N flux measured from anoxic cores we assumed to be due to out-gassing of pore space in the peat and not due to biological denitrification. Water over the cores was replaced every 48 hours, following the same flushing procedures. Cores were incubated in a growth chamber kept at average field soil temperature (taken at 5 cm depth). Measurements of N in the headspace began on Day 4 (initial N values) after flushing the chambers and water. Four days of incubation were used before measurements of denitrification to allow for depletion of background atmospheric N_2 from the cores (Seitzinger 1993). Final measurements were taken after 48 hours (Day 6); the chambers were flushed out and initial measurements taken again. This process was repeated for 14 days. Headspace samples (75 μL volume) were taken from the chambers using a gas-tight syringe that was kept in a stream of He at all times during sampling to avoid N contamination from the atmosphere. Headspace concentrations of N_2 and O_2 were analyzed using a Hewlett-Packard 5890 Series II gas chromatograph using a molecular sieve 5A 200cm × 0.318 cm o.d. with 45/60 mesh stainless steel column and a thermal conductivity detector. Standards of nitrogen and oxygen of known concentrations were run at the same time as samples to provide a regression curve from which we calculate the concentrations of N_2 and O_2 in our samples. Each chamber was sampled until three runs within approximately 10% of each other were recorded. Nitrogen flux from the cores was calculated as Final N concentration – Initial N concentration. The N flux from the anoxic cores (assumed to not be due to biological denitrification) was subtracted from the average of the two aerobic cores taken from the same site and vegetation zone.

Nitrous oxide – Field procedures

Nitrous oxide fluxes from peat in the fen vegetation zone were measured monthly from May through August, 2004 in the two sites. Nitrous oxide flux from the marsh vegetation zone was not measured. In each fen, ten fiberglass soil collars 27cm in diameter were driven into the peat to 15 cm depth so that the top of the collar was level with the peat surface. Boardwalks were built around the collars so that the peat would not be disturbed when samples were taken. The boardwalks and collars were left for 24 hours to allow for equilibration.

Plastic chambers made from 10 L water-cooler jugs with the bottoms cut off were placed in the water-filled grooves in the collars. The tops of the chambers were sealed with rubber stoppers and rubber stopcocks were placed in the chambers to act as a sampling port. Chambers were covered with tin foil to prevent heating within the chamber. A needle attached to approximately 50 cm of tygon hose was inserted into the chamber sampling port. A 20 mL syringe was attached to the hose using a three-way valve and pumped a few times to mix around the sample in the chamber. An air sample was taken from the chamber and injected into a 10 mL Exetainer vial (Labco). A subsequent sample was taken after 20 minutes to get an estimate of N_2O flux over time from the peat. Samples were transported back to the lab, stored at 4°C and analyzed for N_2O concentrations within one week of collection.

Nitrous Oxide - Laboratory Procedures

Samples were analyzed using a Varian Star 3400 gas chromatograph equipped with a Flame Ionization Detector (FID) operating at 300°C with a Poropak Q 80/100 366 cm × 0.32 cm column. Carrier gas used was 5% methane and 95% argon.

Environmental variables

Peat temperature (to 5 cm depth) was measured and water depth were measured monthly in the field (three replicates per vegetation zone) 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 10 cm^3 subsamples of peat at 105 °C for 48 hours and measuring mass loss. This dried peat was ground and analyzed for total carbon using a Control Equipment Corporation 440 element analyzer. Extractable nitrate in the peat was measured in summer 2004. Three separate peat cores 15 cm in diameter were taken in each marsh and fen to 10 cm depth extracted for NO_3 using distilled deionized water (DDW), 100 mL of DDW per 10 g of peat. Surface water NO_3 concentrations in the pond surface water was measured monthly over the course of the study and NO_3 in chamber surface water was measured in August, 2004. All nitrate samples were filtered through Whatman GF/F filters (1.0 µm pore size) and analyzed on a Technicon Autoanalyzer II.

Statistical Procedures

N_2 and N_2O flux data were analyzed with repeated measures ANOVA using SPSS 12.0 software with site and zone as between-subject factors and time (month) as the within-subjects factor. Pearson correlations were performed to compare environmental variables with N_2 flux.

Results

N_2 flux in different vegetation zones and peatland-pond sites

Directly measured hourly flux rates ranged from 0 -17 mg $N \cdot m^{-2} \cdot hr^{-1}$. Potential mean hourly denitrification rates were not significantly different ($p > 0.05$) (Table 2-1) between years for months in common, between the two peatland sites or between the two peatland vegetation zones (Table 2-1). In general, mean hourly denitrification rates were higher at Site 118 than at Site 171 and higher in fens than marshes. Differences were not statistically significant due to the high range of variation in all measurements taken. Coefficients of variation for hourly fluxes ranged from 90 – 120%.

Seasonal N_2 flux rates

N_2 flux rates were not significantly different between months (May through September) ($p = 0.543$) due to high variation between samples. In general, measured denitrification rates were highest in May (mean 11.22 mg $N \cdot m^{-2} \cdot hr^{-1}$), then dropped to near zero in June but increased through July and August (mean 5.32 and 7.36 mg $N \cdot m^{-2} \cdot hr^{-1}$, respectively), and then dropped near zero again in September (Figure 2-1).

Relative importance of N_2O as a product of denitrification

Seasonal differences in fluxes of nitrous oxide from fens did not differ significantly, however there was a significant difference in nitrous oxide flux between the two peatland-pond sites ($p < 0.001$) (Figure 2-2). The open fen at Site 118 was a net source of N_2O (up to 0.025 mg $N \cdot m^{-2} \cdot hr^{-1}$); while the fen at Pond 171 was a net sink of N_2O (up to -0.032 mg $N/m^2/hr$). Therefore, in the fen at Site 171, nitrous oxide was not a product of denitrification. At Site 118, if we assume that all nitrous oxide measured is a product of denitrification, it accounts for less than 2 % of N released from denitrification and therefore is not a significant product compared to N_2 released (Table 2-2).

Environmental variables

Obvious differences in environmental variables were measured between the two different peatland-pond sites (Table 2-3). Moisture, extractable NO_3-N and total carbon in the peat were significantly higher at Site 118 than at Site 171 in both fens and marshes. Low moisture levels at Site 171 corresponded to a significantly higher bulk density of the peat. Peat temperature was not different between the two sites (mean 11.8 °C at Site 118 and 9.7 °C at Site 171) and was not different between fens and marshes (10.2 and 11.3 °C, respectively). Water depth was not significantly different between the two peatland-pond sites, however was significantly higher in marshes (mean 9.9 cm above the peat surface) than in fens (mean 1.0 cm above the peat surface). Porewater pH was also not different between sites (mean 5.4 at Site 118 and 5.8 at Site 171) or between fens and marshes (mean 5.5 and 5.8, respectively). Surface water NO_3 concentrations were higher at Site 118 (mean 4.37 μg/L) than at Site 171 (mean 2.15 μg/L) though the difference was not significant.

N_2 flux was significantly correlated with air temperature ($p = 0.029$) (Figure 2-3), mean monthly water depth ($p = 0.001$) (Figure 2-4) and mean monthly extractable nitrate in the peat ($p = 0.027$) (Figure 2-5). There was no correlation between denitrification rates and surface water NO_3^- in the chambers in measurements taken over the same 48 hour period ($p = 0.772$) or between denitrification and pond surface water NO_3^- concentrations ($p = 0.323$). This suggests that NO_3-N in the peat is a more important substrate for denitrification than NO_3-N in the surface water.

Discussion

N_2 flux in different vegetation zones and peatland-pond sites

Mean hourly denitrification rates were 5.13 and 4.41 $mg \cdot m^{-2} \cdot hr^{-1}$ in the peatlands at Site 118 and Site 171, respectively. Larger differences were seen between the two peatland vegetation zones. Mean hourly denitrification rates were 6.41 and 3.12 $mg \cdot m^{-2} \cdot hr^{-1}$ in fens and marshes, respectively. Despite these obvious differences in potential denitrification rates between marshes and fens, variation among the samples was so high that no significant differences were found in the analyses. Higher measured annual denitrification rates in fens can be attributed to very high denitrification rates in fens in May; these high rates were not seen in marshes at the same time. The high flux rates in May in fens may be due to a rapid recent thaw in the peat. Average depth to frost in the fen when cores were taken in May was 21 cm, while average depth to frost in the marshes was 64 cm. The marshes were flooded earlier which probably thawed the peat earlier.

Freeze-thaw cycles in soil increase the amount of N available in the soil (Herrmann and Witter 2002, Koerselman et al. 1993) because ammonium can build up under the ice of northern wetlands over winter (Kadlec and Knight 1996). This ammonium can be oxidized, resulting in pulses of NO_3-N release in spring (Stoddard 1994), which can subsequently be denitrified upon thawing. We see evidence of this pulsed flux just after the thaw in fens, and it is likely that we missed this event in the marshes (if it occurred).

We hypothesized that denitrification rates would be higher in marshes than fens due to higher water levels leading to increased anoxic conditions as well as nitrate supply from surface water increasing denitrification rates. The fact that we did not observe the expected differences between the two vegetation zones may be due to the above mentioned spring pulse in fens, the nature of our study sites, and the high amount of variation in denitrification measurements. In these two peatland-pond complexes, the marsh is only a narrow fringe along the pond edge and is surrounded by the open fen. Because the marsh and fen vegetation zones are so narrow and close together, fewer differences between the two vegetation zones were found in this study as compared to other studies of open expanses of separate marshes and fens (Bayley and Mewhort 2004).

Coefficients of variation (COV) in this study ranged from 90-120%. A similarly high range of variation among measurements is common in many denitrification studies (Robertson et al. 1988, Davidsson and Leonardson 1998, Mewhort 2000) and variation among denitrification rates is higher than variation among other soil properties (Robertson et al. 1988).

Despite the high variation of the samples, our results clearly indicate high levels of potential denitrification in boreal peatland complexes. Comparison to other studies is difficult due to the wide variety of methods used to measure denitrification; Table 2-4 summarizes denitrification rates from other studies. This study directly measured rates of denitrification at 6.2 - 6.8 mg $N \cdot m^{-2} \cdot hr^{-1}$ in fens and 2.1 – 4.2 mg $N \cdot m^{-2} \cdot hr^{-1}$ in marshes. These values are similar to those obtained in a study of denitrification using the N_2 flux technique in other boreal Alberta peatlands from July through October which measured denitrification rates of 4.22 mg $N \cdot m^{-2} \cdot hr^{-1}$ in fens and 4.55 mg $N \cdot m^{-2} \cdot hr^{-1}$ in marshes (Mewhort 2000). Our estimates of denitrification rates are higher than those obtained using the N_2 flux technique in mineral wetlands (0.28 – 3.64 mg $N \cdot m^{-2} \cdot hr^{-1}$) (Seitzinger 1994), lake sediments (0.92 – 6.0 mg $N \cdot m^{-2} \cdot hr^{-1}$) (Tomaszek et al. 1997), estuaries (0 – 2.73 mg $N \cdot m^{-2} \cdot hr^{-1}$) (Nowicki 1994) and rivers (0.004 – 0.22 mg $N \cdot m^{-2} \cdot hr^{-1}$) (Laursen and Seitzinger 2002).

Values of potential denitrification rates from the N_2 flux chambers in this study (6.2 - 6.8 mg $N \cdot m^{-2} \cdot hr^{-1}$ in fens and 2.1 – 4.2 mg $N \cdot m^{-2} \cdot hr^{-1}$ in marshes) are similar to those estimating denitrification using ^{15}N in wetlands (4.25 – 5.08 mg $N \cdot m^{-2} \cdot hr^{-1}$) (Reddy et al. 1989), swamps (1.11 – 3.42 mg $N \cdot m^{-2} \cdot hr^{-1}$) (Delaune et al. 1998) and lake sediments (1.08 – 4.06 mg $N \cdot m^{-2} \cdot hr^{-1}$) (Seitzinger et al. 1993). Studies using ^{15}N may be an overestimate due to addition of nitrate or ammonium as tracers to the cores (Cornwell et al. 1999). ^{15}N studies show that enrichment of the core with nitrate leads to higher denitrification rates than enrichment with ammonium (Seitzinger et al. 1993, Delaune et al. 1998) and nitrate availability is known to be one of the most important factors regulating denitrification (Tiedje 1988).

Seasonal N_2 flux rates

No significant difference in denitrification rates was found between the two years of the study (2003 and 2004). In general, rates were high in May, very low in June, higher in July and August and low in September, however due to high variation these differences between months were not significant. These general seasonal trends may be affected by two contrasting factors which peak at different times. Peat temperature, which enhances microbial processes such as denitrification (Kadlec and Knight 1996) was lowest in May and September and peaked in July. Pulsed release of N from denitrification after spring melt can be high (Lemke et al. 1998), thus we saw a negative correlation between denitrification rates and air temperature due to low temperatures in May corresponding with high rates of denitrification upon peat thawing. Throughout the rest of the season, it appears that denitrification rates are responding to air temperature, as denitrification was highest during months with highest soil and air temperature (i.e., July and August).

Relative importance of N_2O as a product of denitrification

Nitrous oxide flux from the soil was measured only in the fen vegetation zone from May through August, 2004. All nitrous oxide emitted from soil is not necessarily a product of denitrification since nitrous oxide is also produced in soils as a by-product of the oxidation of ammonium (nitrification) (Groffman 1991, Knowles 1982). Because both processes occur simultaneously, it can be difficult to determine the process responsible for N_2O production (Arah 1997), however denitrification is considered to be the main source of N_2O from soils (Azarn et al. 2002), including peat (Pihlatie et al. 2004).

In this study, nitrous oxide fluxes ranged from -0.032 to 0.025 mg $N{\cdot}m^{-2}{\cdot}hr^{-1}$ while N_2 fluxes in fens were 6.2 - 6.8 mg $N{\cdot}m^{-2}{\cdot}hr^{-1}$. Assuming that all N_2O release measured in our study is a product of denitrification, it is either a very small fraction (less than 2 %) of the denitrification product or not a product of denitrification at all in these peatlands. Relatively small amounts of N_2O vs. N_2 as denitrification products has also been measured in other wetland studies (Reddy et al. 1989, Delaune et al. 1998, Ruckauf et al. 2004). Measured fluxes of nitrous oxide from our fen soils is similar to rates measured in upland boreal soils (Hendzel et al. in press), swamps (Delaune et al. 1998), and forests (Wolf and Brumme 2003). Measurements using *in situ* chambers also provide comparable results measured in peat soils using acetylene inhibition (Urban and Bayley 1988, Davidsson and Leonardson 1998, Dowrick et al. 1999).

Peatland-ponds as N_2O sources and sinks

There were obvious differences in nitrous oxide fluxes from peat between the two study sites. The fen at Site 118 was a net source of nitrous oxide, and at Site 171 was a net sink. Fluxes of nitrous oxide from soil vary widely (Lemke et al. 1998) and range from net consumption to net production in several studies (Davidsson and Leonardson 1997, Hendzel et al. in press). The fact that one of the peatlands in this study was a net N_2O source while the other was a net sink may be due to differences in peat carbon, nitrate and moisture content in the two sites. Carbon is an important regulating factor of denitrification because it provides the substrate for growth of denitrifying organisms (Knowles 1982). Hendzel (pers. comm.) found high carbon boreal upland soils were net N_2O sources and low carbon sites were N_2O sinks. Denitrification is an anaerobic process (Knowles 1982), therefore increased soil moisture can also increase N_2O production (Azarn et al. 2002, Pihlatie et al. 2004), due to anoxic conditions in flooded soil. An available supply of nitrate is needed, as denitrifiers use this as the terminal electron acceptor in the absence of oxygen (Kadlec and Knight 1996), thus producing N_2O and N_2. Freshwater lake sediments are a source of N_2O when nitrate was added but a sink in absence of nitrate (Chan and Knowles 1979). The peat in the fen at Site 171 (a net N_2O sink) had lower total carbon, soil moisture and extractable nitrate than the peat at Site 118 (a net N_2O source). All nitrous oxide in the fen at Site 171 is apparently reduced to dinitrogen gas, while at Site 118 N_2O is a small fraction of the product of denitrification (less than 2 %). It is also possible that the soils of the two sites harbour different microbial denitrifier communities; not all denitrifiers have the ability to reduce N_2O to N_2 (Stevenson 1986) and those that do can have differing efficiencies at reducing nitrate all the way to N_2 (Holtan-Hartwig et al. 2000).

Environmental variables

All denitrification, whether of N_2 or N_2O, is regulated by three main environmental factors: a carbon source, available nitrate and anoxic conditions in the soil (Knowles 1982, Tiedje 1988, Groffman 1994). Although differences in these regulating factors were measured between the two peatland-pond complexes, in general both sites had substantial carbon, nitrate, and anoxia to support high rates of denitrification (as N_2 flux).

Oxygen limitation in the soil is often thought to be the most important mechanism regulating denitrification (Tiedje 1988). In general, both marshes and fens were continually saturated with water (i.e., water levels at or above the peat surface) therefore anaerobic conditions were present in the soil below a thin aerobic layer near the surface. Degree of anoxia in these sites may have changed seasonally as water levels fluctuated. Monthly mean water depths are positively correlated with monthly rates of denitrification, possibly due to increased soil anoxia with increased flooding.

Nitrate availability is also known to be an important factor regulating denitrification (Tiedje 1988). Mean monthly denitrification rates were positively correlated with mean monthly extractable nitrate in the peat. Net nitrification rates in these sites was negligible, however gross nitrification rates are higher and correspond seasonally with higher denitrification rates, i.e. highest in May (Chapter 3). In general, gross nitrification rates were higher in marshes and fens at Site 118 than at Site 171. Low rates of net nitrification coupled with high rates of gross nitrification suggest that the nitrate pool is denitrified very rapidly once it is produced and turns over very quickly.

Nitrate from the surface water can also be a potentially important substrate for denitrification (Venterink et al. 2003, Christensen et al. 1990) as it can diffuse into the sediment and be denitrified (Delaune et al. 1998). Nitrate in surface waters of the chambers did not appear to be a significant source of nitrate for denitrification. This corresponds to findings by Mewhort (2000) but not Seitzinger (1994).

There was also no correlation between monthly pond surface water NO_3^- concentrations and monthly denitrification rates. This suggests that nitrate produced in the soil by nitrification is an important source of N for denitrification, whereas surface water nitrate is either an unimportant N source for denitrification, or it is very important and is turned over rapidly. Rapid turnover of surface water nitrate may be important at Site 171 which had significantly lower gross rates of soil nitrification but only slightly lower rates of denitrification than the peatlands at Site 118.

Annual denitrification estimates and limitations of study

Annual potential denitrification estimates were obtained by extrapolating measured hourly denitrification rates to daily and monthly rates and adding mean monthly denitrification rates from May through September. Total potential annual denitrification rates are estimated at 24 g $N \cdot m^{-2} \cdot yr^{-1}$ in fens and 11 g $N \cdot m^{-2} \cdot yr^{-1}$ in marshes. These values are comparable to those measured in similar study sites in a different part of boreal Alberta (Mewhort 2000) and are estimated to 10 cm peat depth and assume that no denitrification occurs in the soil from October through April when the peat is frozen. Soil temperatures below freezing result in significant declines of microbial communities (Biederbeck and Campbell 1971) due to the lack of free water (Tate 1995) and hence denitrification rates are decreased at low temperatures (Knowles 1982). Low rates of denitrification have been measured in frozen soils, however the N gas generally remains trapped in the frozen soil and is released upon spring thaw (Hatch et al. 2000), although a spring pulse of denitrification was measured in fens but not in marshes in this study.

The annual values of denitrification in marshes and fens are estimates only. Extrapolation from small cores to a large aerial basis and from daily and weekly to monthly rates is difficult, especially in a system where variation is so high. Actual direct measurements of fluxes of N_2 from soil cores may be overestimated because plants are removed from the cores and nitrate that would be taken up by plants would be denitrified instead in the chamber (Schimel and Bennett 2004). In addition, coring disturbs the soil which can stimulate nitrification (Ross and Hales 2003) and increase subsequent denitrification rates.

Annual estimates in marshes may be underestimated since we may have missed the spring pulse of denitrification after thaw. Freezing and thawing of soil increases soil available N (Herrmann and Witter 2002) and C (McGarity 1962) which are released upon lysis of microbes (Kadlec and Knight 1996).

Freeze-thaw cycles are especially important in mid latitudes (Herrmann and Witter 2002) and repeated freezing and thawing of the peat in April and October (not sampled in this study) when temperatures fluctuate around zero could lead to increased denitrification potential

Conclusions

Despite high variability of measurements, it is apparent that denitrification removes substantial amounts of nitrogen from marshes and fens in WBP peatland-pond complexes (11 -24 g $N \cdot m^{-2} \cdot yr^{-1}$). N_2 was the predominant product of denitrification and N_2O fractions were minimal in a carbon rich site and no N_2O was produced in a more carbon-poor site. Denitrification rates in these peatlands are high due to high rates of nitrate supply via gross nitrification in the peat and possibly surface water nitrate, as well as continually water-saturated soil leading to anoxic conditions.

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Table 2-1: Mean hourly denitrification rates (± SE) compared between A) the two peatland-pond complexes (sites), B) the two years of the study for months in common and C) the two peatland vegetation zones. All means are in mg $N \cdot m^{-2} \cdot hr^{-1}$ to 10 cm peat depth.

A. SITE	**Site 118**	**Site 171**	**p-value**
	5.13 (5.1)	4.41 (2.4)	0.320

B. YEAR	**2003**	**2004**	**p-value**
	7.82 (1.6)	6.35 (3.0)	0.477

C. VEGETATION ZONE	**Fen**	**Marsh**	**p-value**
	6.41 (3.3)	3.12 (1.3)	0.482

Table 2-2: Mean hourly denitrification rates (±SE) of N_2 and N_2O in two peatland-pond sites for May through August, 2004. Nitrous oxide was not measured in marshes.

	Site 118		**Site 171**	
	Fen	Marsh	Fen	Marsh
N_2 ($mg \cdot m^{-2} \cdot hr^{-1}$)	6.10 (3.2)	4.16 (1.3)	6.72 (3.4)	2.09 (1.6)
N_2O ($mg \cdot m^{-2} \cdot hr^{-1}$)	0.024 (0.008)	----	-0.040 (0.004)	----

Table 2-3: Selected physical and chemical parameters of the peat compared between the two peatland-ponds (sites) and the two vegetation zones (marshes and fens). Values are means (±SE) from monthly measurements taken from July through September 2003 and May through August 2004. Extractable nitrate values are monthly means from May through August 2004 only since cores were frozen in 2003 (see Appendix A).

	Site 118			**Site 171**		
	Fen	Marsh	Site Mean	Fen	Marsh	Site Mean
Moisture content (g water/g dry peat)	12.77 (0.8)	11.60 (0.5)	12.18 (0.5)	2.75 (0.2)	3.90 (0.1)	3.32 (0.2)
Bulk density (g/cm^3)	0.067 (0.003)	0.073 (0.002)	0.070 (0.002)	0.23 (0.009)	0.27 (0.013)	0.25 (0.009)
Extractable NO_3 (µg NO_3-N/g peat)	1.66 (0.3)	2.02 (0.7)	1.84 (0.4)	0.22 (0.06)	0.72 (0.5)	0.47 (0.2)
Total Carbon (%)	47.04 (0.3)	48.18 (0.3)	47.61 (0.2)	20.54 (1.1)	24.46 (1.1)	22.50 (0.8)

Table 2-4: Comparison of potential denitrification rates using three methods (N_2-flux, ^{15}N and acetylene inhibition) for different ecosystems.

Method	**Study site**	**Denitrification rate (mg $N \cdot m^{-2} \cdot hr^{-1}$)**	**Reference**
N_2 – Flux	Wetland	0.28 – 3.64	Seitzinger 1994
	Wetland	0.14 – 3.43	Watts and Seitzinger 2000
	Lake sediments	3.64 – 6.86	Seitzinger et al. 1993
	Rivers	0.004 – 0.22	Laursen and Seitzinger 2002
	Estuarine sediments	0 – 2.73	Nowicki 1994
	Lake sediments	0.66 – 0.70	Gardner et al. 1987
	Estuarine sediments	0.92 – 6.00	Tomaszek et al. 1997
	River floodplain	0.625	Venterink et al. 2003
	Boreal marshes	4.55	Mewhort 2000
	Boreal fens	4.22	Mewhort 2000
	Boreal marshes	2.14 – 4.19	This study
	Boreal fens	6.19 – 6.81	This study
^{15}N	Lake sediments	1.08 – 4.06	Seitzinger et al. 1993
	Wetland	4.25 – 5.08	Reddy et al. 1989
	Wetland	1.11 - 3.41	Delaune et al. 1998
	Forest soils	0.006 – 0.008	Wolf and Brumme 2003
	Rice paddies	0.063 – 14.25	Lindau et al. 1990
Acetylene	Wetland	0.003 – 0.14	Watts and Seitzinger 2000
	Peat meadow	2.51	Davidsson and Leonardson 1998
	Coniferous forest	0.00114	Gundersen 1991
	Temperate forests	0.006 – 1.154	Robertson and Tiedje 1984
	Tropical forests	0.047 – 0.22	Robertson and Tiedje 1988
	Crop soil	0.0024 – 0.0052	Mosier et al. 1986
	Bogs	0.0002 – 0.002	Urban and Bayley 1988

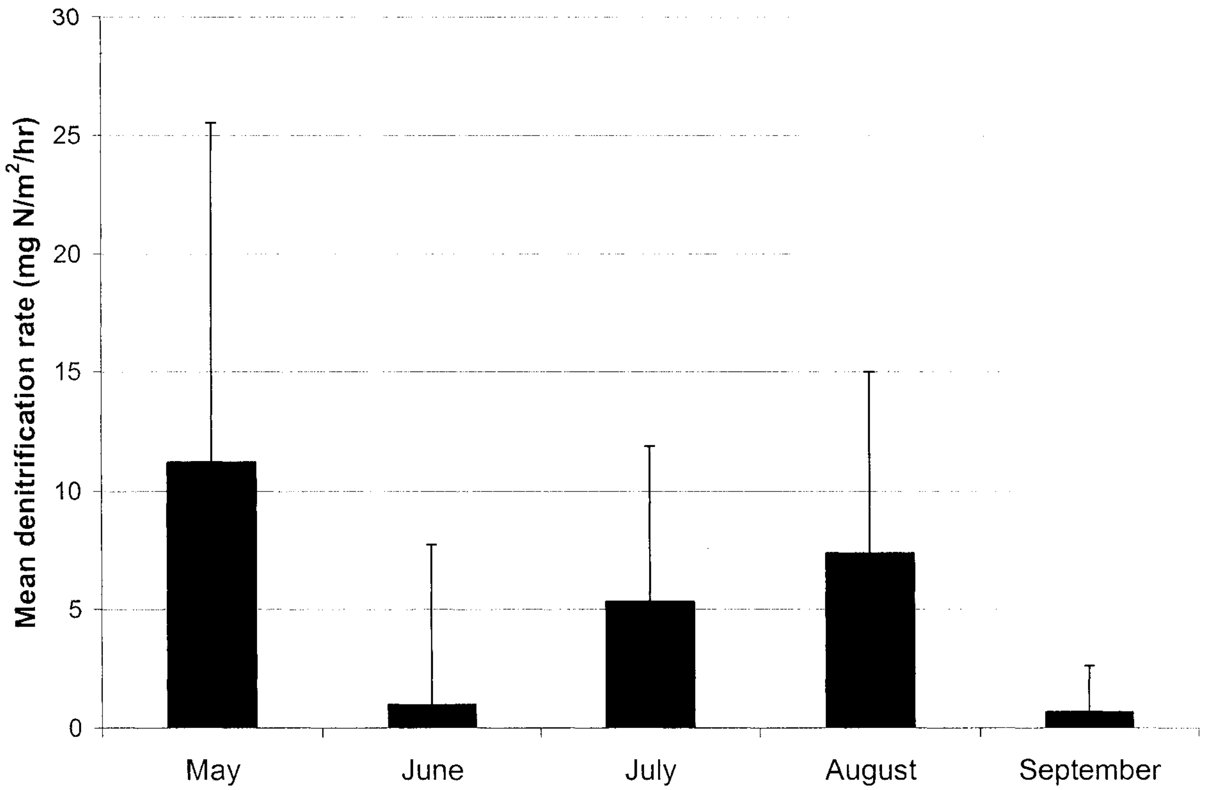

Figure 2-1: Mean seasonal denitrification rates as N_2 flux. Rates are directly measured using the N_2-flux technique and are the means of marshes and fens in both peatland-pond sites. Error bars represent standard error of the mean.

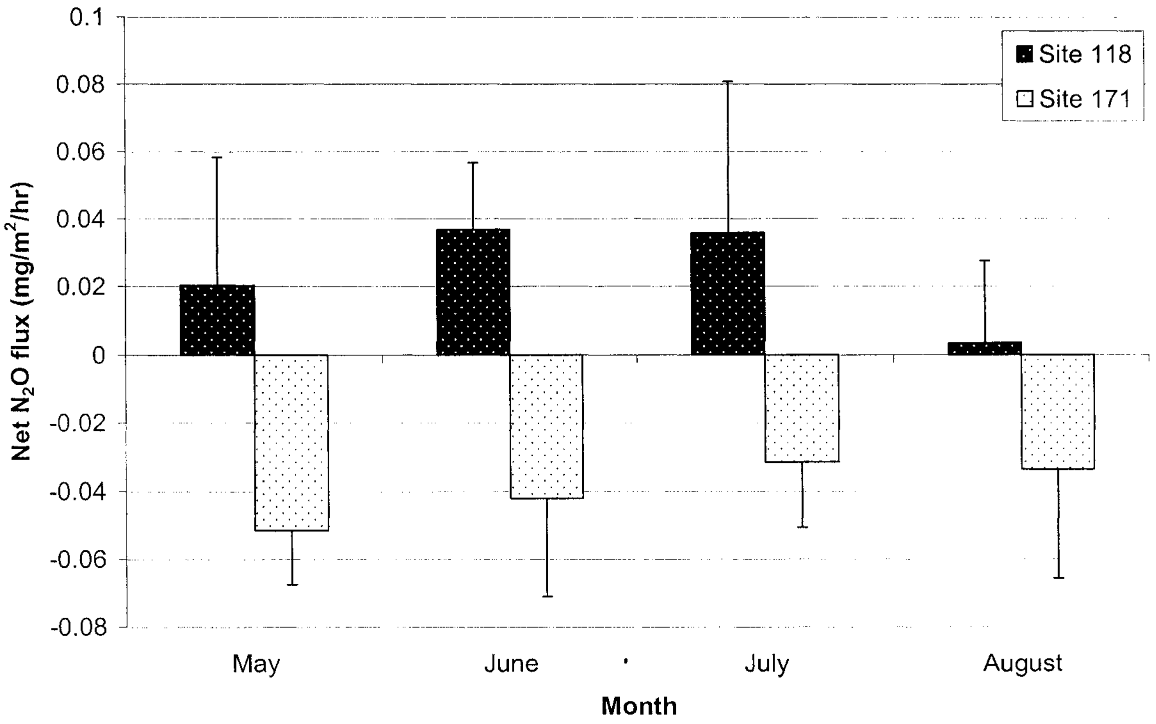

Figure 2-2: Mean seasonal N_2O fluxes from fen soils in both peatland-pond sites in 2004. Error bars represent standard error of the mean.

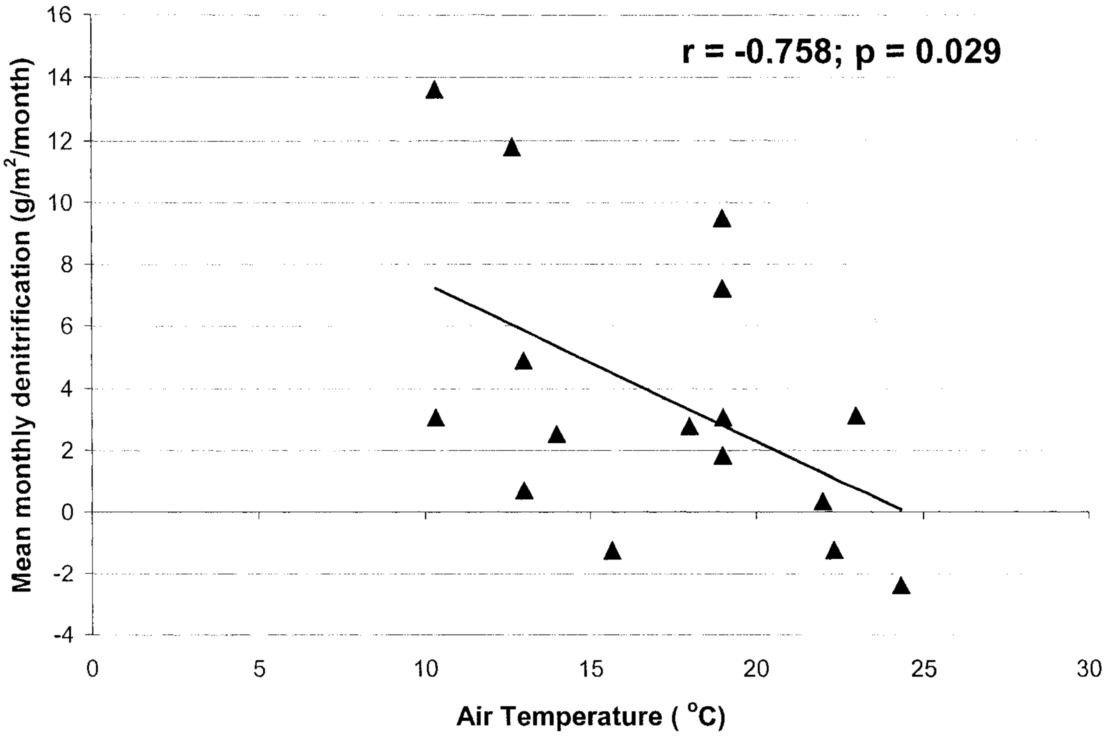

Figure 2-3: Correlation between mean monthly denitrification rates and air temperature (taken at time of core collection).

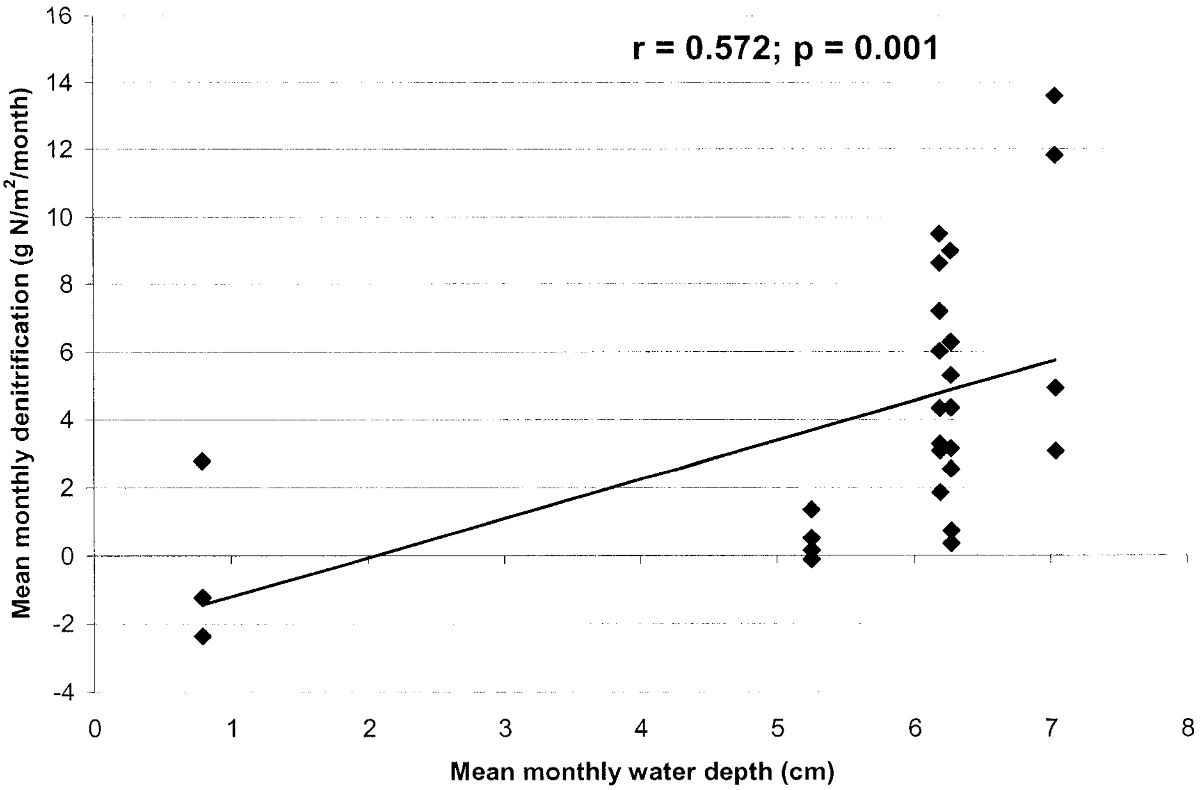

Figure 2-4: Correlation between mean monthly denitrification rates and mean monthly water depth relative to the peat surface.

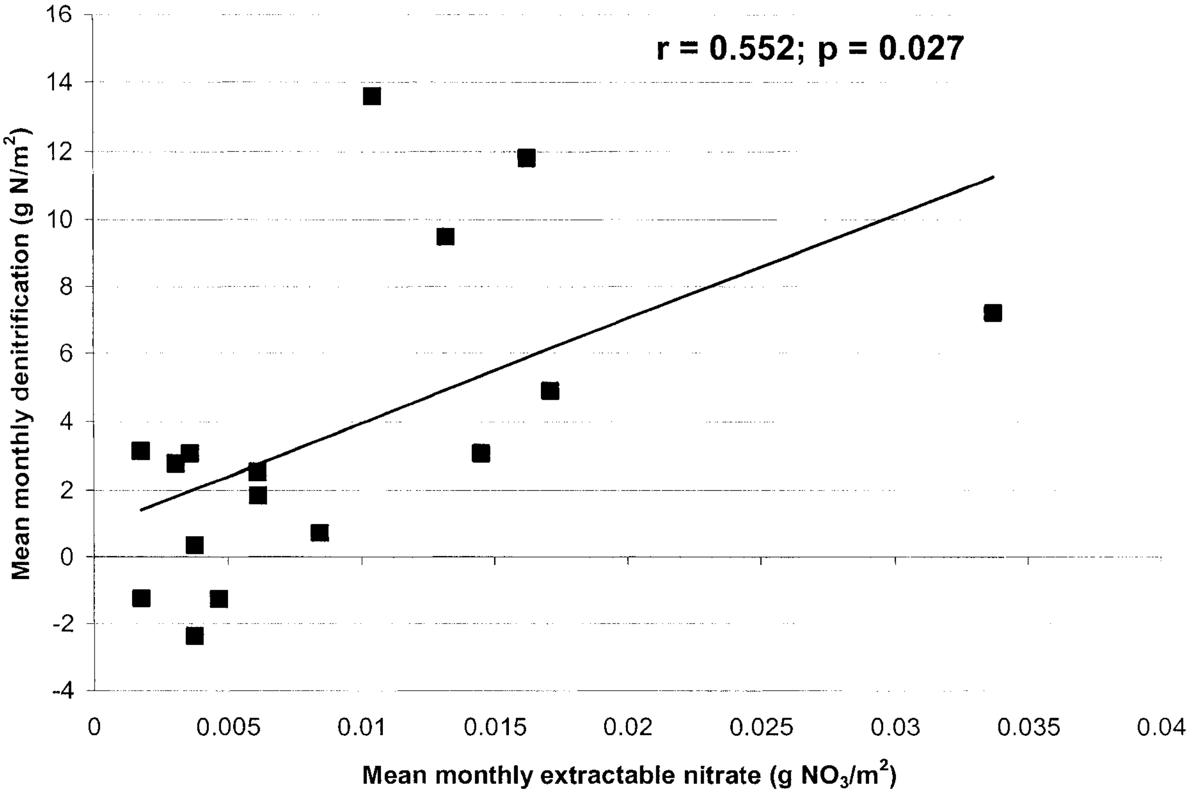

Figure 2-5: Correlation between mean monthly denitrification rates and mean monthly extractable nitrate in the peat (all values to 10cm depth).

3. Internal nitrogen cycling in two marsh and fen peatlands in the Western Boreal Plain of Alberta, Canada

Introduction

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 (Saunders and Kalff 2001, Chapter Two). Nitrogen biogeochemistry in peatlands is also important because N is often limiting to plant productivity (Moore 2002). Many peatlands get the nitrogen needed for plant growth from recycled nitrogen, however the dynamics of the nitrogen cycle in peat is poorly understood, especially in western boreal peatlands. Plants can receive nitrogen from sources external to the system (fixation, precipitation, and groundwater) or from recycling within the system (decomposition of litter, and mineralization). Although inputs and outputs of N to soil systems can be large, internal cycling of N is often 10-20 times greater than the amount received from outside the system (Schlesinger 1991, Paul and Clark 1996). This internal nutrient cycling maintains soil fertility by continuously replenishing inorganic nutrient pools within the soil (Bridgham et al. 2001).

Peatlands are important to N biogeochemistry because they accumulate nutrients in the form of partially-decayed organic matter (peat). In the Western Boreal Plain (WBP) of Alberta, peatlands, predominately fens, cover 20-50% 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). Whitehouse and Bayley (in press) identified distinct peatland vegetation communities surrounding these shallow ponds, with marshes next to the open water, fens adjacent to the marsh and bogs at the upland boundary. These peatland-pond systems are nutrient rich, with surface water TP concentrations up to 150 μg/L and TN up to 3500 μg/L (Bayley and Prather 2003). Many northern wetlands are nutrient poor (Jonasson and Shaver 1999) and thus many studies of nutrient cycling in boreal peatlands are performed in more nutrient poor systems, with emphasis on studies of bogs and fens (Updegraff et al. 1995, Bridgham et al. 1998). There are fewer studies on marshes or comparisons of marshes and fens in the nutrient rich Western Boreal Plain (Bayley and Mewhort 2004).

In boreal peatlands, slow decomposition, not high production, is responsible for peat accumulation (Clymo 1965, Szumigalski and Bayley 1996, Jonasson and Shaver 1999, Moore 2002). Decomposition of dead vegetation determines nutrient availability in these peatlands (Bridgham and Richardson 2003) because it returns organic N to the soil. Organic N in the peat is mineralized to inorganic N (ammonium (NH_4^+) and nitrate (NO_3^-)) and nitrogen mineralization is often expressed as a net rate i.e., production of ammonium and/or nitrate in excess of denitrification and uptake by microbes (Schlesinger 1991).

Measurements of gross N mineralization rates i.e., the total amount of N mineralized, are useful when simultaneously measured with net N mineralization because they give an indication of N turnover rates and microbial uptake of N (i.e., the difference between gross and net mineralization). Comparisons of gross and net N mineralization rates have mostly been conducted in forest ecosystems (Davidson et al. 1992, Hart et al. 1994a, Verchot et al. 2001, Carmosini et al. 2002, Ross et al. 2004). In boreal peatlands, due to difficulties in measuring gross rates of N transformation, net rates have been most commonly measured (Humphrey and Pluth 1996, Mewhort 2000; Bayley et al. in press).

Simultaneous measurements of gross and net N transformation in peat or boreal systems are scarce and are mainly conducted in relatively nutrient poor systems (Westbrook and Devito 2004, Potila and Sarjala 2004).

Ammonium and nitrate both 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). Plant demand for N is considered equivalent to the N content of tissues at peak biomass (Schlesinger 1991), however microbial demand for N is more difficult to measure and microbial uptake is estimated using gross and net rates of mineralization. In peatlands, the microbial community is dominated by heterotrophic organisms, primarily bacteria and secondarily fungi (Mitchell et al. 2003) and generally comprise up to 3 % of total soil C and 5 % of total soil N (Smith and Paul 1990). Because soil microorganisms mediate the conversion of organic matter into inorganic forms (Rosswall 1982, Horwath and Paul 1994), it is believed that they should have first access to bioavailable inorganic N and are therefore superior competitors to plants for ammonium and nitrate (Schimel and Bennett 2004). Measurement of microbial pool sizes (microbial biomass) is therefore important to determine a complete picture of nutrient fluxes in any system, however measurements of microbial biomass in peatlands of the WBP have not been conducted.

Studies of internal nitrogen cycling in boreal peatlands of Alberta have focused mainly on net mineralization rates (Szumigalski and Bayley 1996, Humphrey and Pluth 1996, Bayley and Mewhort 2004, Bayley et al. in press), with no studies estimating gross rates of mineralization. Previous research has indicated that N mineralization increases along the ombotrophic-minerotrophic gradient in northern wetlands (Bridgham et al.

1998) i.e., from fens to marshes (Mewhort 2000). We hypothesized that net and gross mineralization rates, as well as the size of microbial biomass and microbial uptake rates would be higher in marshes than fens due to increased nutrients at the edge of nutrient-rich ponds and higher water levels in marshes stimulating microbial activity. We also hypothesized that this increased nutrient availability would be reflected in higher primary production in marshes.

The overall objective of this study was to measure the nitrogen dynamics (major pools and fluxes) in peat-rich, vegetated marshes and fens surrounding shallow ponds in the western boreal plain of Alberta. We have previously described denitrification, the major mechanism of N loss, from these marshes and fens (Chapter Two). In this chapter our goal is to describe how much N is recycled internally in the peat-plant complex. The specific objectives of this study were:

1. To compare rates of gross N mineralization with rates of net N mineralization in two different peatland-pond complexes, both of which have a marsh and a fen vegetation zone.
2. To determine the size of the microbial biomass pool in the peat and to estimate microbial uptake of N in the two peatlands.
3. To estimate N uptake by plants (net primary production) and N returned to the peat in litter (decomposition).
4. To determine seasonal trends in N dynamics in the peatlands and to integrate the above findings to estimate an annual internal N budget.

Site descriptions

This study was performed in two peatland-pond complexes in the Mid Boreal ecoclimatic zone of northern Alberta (National Ecoregions Working Group 1989) in the Utikuma Lake Area (56°52' N, 115°27' W), approximately 300 km north of Edmonton, Alberta. This area is 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). Total precipitation in 2004 was 408.2 mm, with a total of 182.2 mm over the course of this study (May through August 2004).

The two peatland-pond sites (Site 118 and Site 171) chosen for this study are both in depressions with clay till basins. Both sites consist 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 with the fen adjacent to bogs and aspen (*Populus tremuloides*) dominated uplands. Separate marsh and fen vegetation communities had been previously classified in peatland-pond sites in the same area based on a wet to dry and bare to vegetated gradient (Whitehouse and Bayley in press).

Site 171 is surrounded by a non-floating or "fixed" peatland and has an extensive marsh fringe located on the south side of the pond (where the study was done). The pond surface water pH averaged 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 cm to 16 cm above the peat surface. The open fen at Site 171 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 Site 118 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 has 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 Site 118 is dominated by two-stamened sedge (*Carex diandra*). The peat is very fibrous and water levels fluctuated slightly throughout the study from 0 cm to 2 cm above the peat surface.

Experimental Approach

This study estimates nitrogen stocks/pools as well as recycled N that is made available to plants or microbes, and uptake and loss of N by the dominant vegetation in two peatland complexes (both of which have a marsh and a fen vegetation zone). Flux estimates include 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 allow 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 for all major N fluxes and pools measured as part of this study is in Table 3-8.

All major internal nitrogen pools (peat, plants, microbial biomass, and surface water) and internal nitrogen fluxes (net and gross mineralization, microbial uptake, plant uptake) 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. The main nitrogen removal mechanism, denitrification, was estimated (Chapter Two) at the same time as internal flux rates. Inputs of nitrogen to the sites (i.e., groundwater inflow and runoff) were not estimated as part of this study, however N fixation and precipitation values were estimated based on values in the literature. Therefore, information presented here describes the internal N budget and only limited inputs and outputs from the system. Furthermore, all measurements in this study were taken in the surface layer of peat only. The upper 20-30 cm of soil contains the majority of plant roots and is the site of most microbial activity and N cycling (Schlesinger 1991), however it has been shown that this activity is significantly decreased below 10 cm depth in boreal peat (Humphrey and Pluth 1996) therefore all measurements in this study were taken from 0-10 cm peat depth, which we assume to be the depth of the active layer.

Methods

Net mineralization

Field Procedures

Net nitrogen and phosphorus mineralization were measured using the buried bag method described by Eno (1960). Peat cores were taken with a sheet metal corer 15 cm in diameter. The litter layer on the top of the core was removed; cores were cut to 10 cm depth and then cut in half vertically. The core halves were sealed in Ziploc bags. One half was returned to the original hole and re-covered with the litter layer and left in the field for approximately 30 days 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 hours of collection.

Laboratory Procedures

All cores were weighed and mixed thoroughly before extraction for ammonium and nitrate. Ammonium was extracted from the peat using 1N 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). Nitrate samples were extracted with DDW as previous work showed nitrate addition in peat extracted with reagent grade KCl (Bayley unpublished). Samples were shaken for 60 minutes and centrifuged to remove suspended soil. Nitrate samples were filtered through Whatman GF/F glass microfibre filters (1.0 μm pore size) and ammonium samples were unfiltered. Nitrogen samples were stored in plastic scintillation vials with polypropylene cone-lined caps and frozen until analysis. Analysis of NH_4-N and NO_3-N was performed on a Technicon Autoanalyzer II. Extracted phosphorus samples were filtered through HAWP Millipore 0.45 μm filters and analyzed for soluble reactive phosphorus according to Menzel and Corwin (1965).

Concentrations of NH_4^+, NO_3^- and SRP taken in the initial cores were assumed to be equivalent to extractable NH_4^+, NO_3^- and SRP in the peat. Net mineralization rates were calculated by subtracting the concentrations of NH_4^+, NO_3^- or P in the initial core from the concentrations in the incubated core. Monthly values were divided by the number of days the sample was incubated in the field to give units of mg NH_4^+ or NO_3^- or SRP $\cdot m^{-2} \cdot day^{-1}$ (to 10cm peat depth).

Gross Nitrogen Mineralization

Field Procedures

Gross nitrogen mineralization was measured using ^{15}N isotope dilution methods outlined by Hart et al. (1994b). Twelve cores 5 cm in diameter and 10 cm deep were taken monthly from May through August, 2004 in 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 $\mu g^{15}N/L$) and ammonification cores were injected with 6 mL of $(^{15}NH_4)_2SO_4$ (98% enrichment, 35 $\mu g^{15}N/L$). Two cores were immediately extracted (one for NO_3 and one for NH_4) by mixing the peat thoroughly in a plastic bag. Subsamples of mixed peat were placed in vials of distilled deionized water (DDW) (NO_3 cores) or 1N KCl (NH_4 cores) for extraction. 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 hours. 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 extracts from the soil were used to determine the concentration of NH_4 and NO_3 in the soil. Nitrate samples were filtered through Whatman GF/F filter paper (1.0 μm pore size) and ammonium samples were not filtered. Concentrations of NH_4 and NO_3 were determined using a Technicon Autoanalyzer II.

Diffusions

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. Extracts for nitrate received a scoop of MgO powder (approximately 0.2g), which causes NH_3 vapour to be released. Vials were left open for 6 days and then 1 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 six days 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 days. After incubation, filter disks were dried in a dessicator overnight and placed in tin capsules for direct combustion ^{15}N mass spectrometry analysis. Analysis of ^{15}N samples was 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). A schematic of methods used to estimate gross mineralization and consumption as well as equations for the calculations can be found in Appendix B.

Gross consumption of N is not to be confused with microbial uptake of N, which is only one consumptive process. In addition to microbial immobilization, 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 in these peatlands we have measured high daily rates of nitrification and denitrification. Therefore, we estimated microbial uptake using isotope dilution according to the following equations:

Microbial uptake of NH_4^+ = gross NH_4^+ consumption – gross nitrification

Microbial uptake of NO_3^- = gross NO_3^- consumption – mean daily denitrification

where all values are in mg $N \cdot m^{-2} \cdot d^{-1}$. We also estimated microbial uptake 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 peatland at Site 118 (the floating peatland). *C. diandra* was not present at Site 171 (the fixed peatland) in 2003. Therefore, *C. diandra* litter from the marsh and fen of the floating peatland was used for decomposition studies in the fixed 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-pond sites. The plants were clipped at ground level and dried for 48 hours at 60°C. Approximately 1 to 2g of the plant material was added to pre-weighed mesh litter bags (3 cm × 6cm, 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 days (collections made monthly from May through 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 hours and weighed. The percent of plant mass remaining was calculated as follows:

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

where Xo 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). Organic N inputs into the peat through 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

Net primary production 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 one week and weighed. Primary production values are expressed as g/m^2 and are assumed to be equivalent to annual above- ground production. Although peak aboveground biomass is an underestimate of total production due to nonvascular productivity, belowground structures, leaf mortality and herbivory, because we are trying to compare between sites and vegetation zones using the same technique, aboveground vascular production is a reasonable approximation 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, carbon and phosphorus content. Total carbon and nitrogen content of the plants was determined upon combustion of dried, ground samples using a Control Equipment Corporation 440 element analyzer. Dried, ground plants were analyzed for total phosphorus using a peroxide/sulfuric acid digest following Parkinson and Allen (1975). Plant biomass N and P at peak harvest was estimated by multiplying tissue N (or P) concentrations by total NPP (to give g N/m^2 or g P/m^2. This value was assumed to be equivalent to annual plant uptake of N or P.

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. One subsample was left unfumigated and the other was fumigated. Peat samples to be fumigated were placed in 50 mL beakers and, along with a separate beaker of chloroform, were placed in a sealed dessicator. A vacuum was applied to make the chloroform boil and distribute to all samples, followed by incubation of the samples in the dessicator. After 24 hours, chloroform was removed from the soil via a vacuum pump. Both fumigated and unfumigated soil samples were extracted for both dissolved organic carbon (DOC) and total nitrogen (TN) with 0.5 M K_2SO_4 (50mL of K_2SO_4 per soil sample), shaken for one hour, 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 instrument

(Mandel Scientific Company Inc). Dissolved organic nitrogen (DON) was calculated as $DON = TN - (NO_3^- + NH_4^+)$.

Microbial biomass dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) was calculated using the following formulas:

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

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

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 5cm depth) and surface 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 was 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 glassfibre 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 P 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.

Turnover times of major N pools were estimated by dividing the concentration of the N pool (assumed to be at a steady state) by the gross N cycle rate supplying that pool.

Statistical Procedures

Nitrogen flux rates and pool sizes were analyzed using repeated measures ANOVA for differences between months (within-subjects factor) and differences between sites and vegetation zones (between-subjects factors). Primary productivity data was 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

We hypothesized that N cycling and pool sizes would be higher in marshes than in fens due to higher nutrient concentrations and water levels at closer proximity to the pond water. However, we did not find marshes to have significantly higher concentrations of N or faster N cycling relative to fens. There was no significant difference ($p > 0.05$) between marshes and fens within the same peatland-pond complex in any of the major N fluxes or pools measured, except for total N in peat (Table 3-2). Because of the similarity of marshes and fens, results were pooled within the same peatland-pond complex for comparisons between sites (Site 171 vs. Site 118). Large differences in N measurements were found between the two peatland-pond complexes and results will therefore focus on these differences. The marsh and fen at Site 118 will be referred to collectively as the “floating peatland” and the marsh and fen at Site 171 will be referred to as the “fixed peatland”.

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 fixed peatland, while there was no significant difference in net nitrification rates between the two peatlands. On average, net nitrification rates were positive in the floating peatland and were negative in the fixed peatland (Table 3-1). Because high denitrification rates were also measured in these sites (Chapter Two), estimates of net nitrification rates were also calculated assuming that all N released via denitrification was derived from nitrate produced via nitrification in the cores (Table 3-1). Net P mineralization was significantly different between sites ($p < 0.001$), with net mineralization of P occurring in the floating peatland and net consumption of P occurring in the fixed peatland (Table 3-1).

Net ammonification was not different between months in both the floating and fixed peatlands. In general, ammonification was lowest over winter (4.98 – 9.48 mg $NH_4\text{-}N \cdot m^{-2} \cdot d^{-1}$) and highest in July (9.81 – 22.28 mg $NH_4\text{-}N \cdot m^{-2} \cdot d^{-1}$) (Figure 3-1a). Net nitrification was not significantly different between months ($p = 0.126$). Net nitrate consumption was measured in May (-0.37 to -1.01 mg $NO_3\text{-}N \cdot m^{-2} \cdot d^{-1}$) and net nitrification was measured in July (0.59 – 1.71 mg $NO_3\text{-}N \cdot m^{-2} \cdot d^{-1}$) (Figure 3-1b).

Net P mineralization was not significantly different ($p = 0.399$) between months in the floating and fixed peatland (Figure 3-1c).

Gross ammonification and nitrification rates were both significantly higher in the floating peatland than in the fixed peatland (Table 3-1). In general, gross rates of nitrogen mineralization are much higher than net rates. This highlights the limitations of measuring only net rates as a measure of mineralization and further indicates that nitrate and ammonium are rapidly consumed in the system and therefore turn over quickly. Gross ammonification was significantly different between months ($p = 0.031$) as was gross nitrification ($p = 0.001$). In general, gross mineralization rates were higher in spring and lower at the end of the summer (Figure 3-2).

Microbial biomass and gross N consumption

Microbial biomass C and N were significantly larger in the floating peatland than in the fixed peatland ($p < 0.001$). In addition, total carbon, nitrogen and phosphorus and extractable N in the peat were also significantly higher in the floating peatland (Table 3-2). Gross rates of NH_4 and NO_3 consumption were significantly higher ($p = 0.029$ and $p = 0.008$, respectively) in the floating peatland than the fixed peatland (Table 3-3).

Plant dynamics

Peak above ground biomass in August 2004 was significantly higher ($p < 0.001$) in the fixed peatland than the floating peatland. Within the fixed peatland, above ground biomass was higher in the fen than in the marsh ($p = 0.005$) while in the floating peatland, above ground biomass was higher in the marsh, however the difference was not significant (Figure 3-3).

Total nutrients (carbon, nitrogen and phosphorus) in *Carex diandra* tissues from the August harvest were not significantly different between the two peatland sites (Table 3-2). *Carex* N:P ratios are very similar in both sites and in marshes and fens and range from 7:1 to 10:1, suggesting that vegetation in both the floating and fixed peatlands is N limited (Koerselman and Mueleman 1996). Estimates of plant biomass N (assumed equivalent to annual plant N uptake) are 3.45 g $N \cdot m^{-2}$ in the floating peatland and 7.82 g $N \cdot m^{-2}$ in the fixed peatland.

Decomposition of *Carex diandra* litter was not significantly different between the two peatland sites ($p = 0.125$). Total mass loss in the floating and fixed peatlands was 46.05 and 54.69 %, respectively, after 291 days 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 (Figure 3-4). Estimates of N inputs into the peat via decomposition after 291 days are 1.59 g $N \cdot m^{-2}$ in the floating peatland and 4.28 g $N \cdot m^{-2}$ in the fixed peatland.

Environmental variables and N fluxes and pools

Major differences in physical and environmental parameters were measured between the two sites (Table 3-4). In general, peat bulk density was highest in the fixed peatland, and moisture content 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. Correlations between major N fluxes and pools and environmental variables within each peatland are presented in Table 3-5.

Integrated internal N budget

Annual rates of major nitrogen flux rates and pool sizes were estimated for both the floating and fixed peatland (Figure 3-5). No major differences between monthly N pool sizes were measured, 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 had a larger microbial pool that was much more active, (as indicated by the much higher N flux rates) than the fixed peatland. Turnover times in the floating peatland were also much faster than in the fixed peatland (Table 3-6). Internal N cycling in both peatlands is unbalanced i.e., inputs of N to the system (relative to the plants) via decomposition and mineralization are smaller than outputs via plant uptake, microbial uptake and denitrification (Table 3-7).

Discussion

Differences between marshes and fens and peatland types (floating vs. fixed)

The lack of difference between the two vegetation zones within each site can be attributed to the nature of the sites themselves. The marshes and fens were located 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 hydrologic differences and not nutrient differences (Whitehouse and Bayley in press).

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 studies of peatlands in western boreal Alberta, where net nitrification rates were negligible compared to net ammonification (Humphrey and Pluth 1996, Mewhort 2000, Bayley et al. in press). Net nitrification in the incubated bags was low due to the high mobility of nitrate (Rosswall 1982) and its rapid reduction to N_2 in the process of denitrification (Chapter Two). Net ammonification rates ranged from 7.44 to 16.26 mg NH_4-N·m^{-2}·d^{-1}. This is comparable to other studies in peatlands using the buried bag technique (Devito et al. 1999, Mewhort 2000, Bayley et al. in press) and using resin cores (Brigham et al. 2001).

Net phosphorus mineralization was not different between marshes and fens and rates were very low (-0.09 to 2.29 mg SRP·m^{-2}·d^{-1}). This is similar to findings in other western boreal marshes and fens in Alberta (Mewhort 2000). Phosphorus was mineralized in the floating peatland and was immobilized in the fixed peatland. Net immobilization of P in this site is mostly likely related to the binding of P in iron and/or mineral complexes (Bridgham et al. 1996, Schlesinger 1991). Mineral content in the fixed peat is most likely higher than the floating peat due to the lower carbon (and organic) content of the peat. Furthermore, iron oxides were visually observed in the peat at this site. High amounts of TP in the fixed peatland relative to low SRP mineralization rates also indicate high amounts of adsorbed P (Schlesinger 1991) and adsorption tests on this peat indicate potential for high P adsorption (Ferone 2001).

Gross N mineralization rates were higher than net rates. Substantially higher rates of gross vs. net nitrification have also been measured in forest ecosystems (Davidson et al. 1992, Hart et al. 1994a, Verchot et al. 2001, Carmosini et al. 2002) and peat ecosystems (Westbrook and Devito 2004). Higher gross rates (vs. net rates) of mineralization indicate that there is substantial and rapid turnover of nitrate and ammonium. Comparisons of gross rates of mineralization with other boreal peatland studies are difficult as there have been very few studies of gross N transformations in peatlands (Westbrook and Devito 2004, Potila and Sarjala 2004). Gross ammonification in the floating peatland and gross nitrification in the fixed 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).

Gross mineralization of N was much higher in the floating peatland. 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 fixed peatland. Microbial biomass was much higher in the floating peatland, and is an important regulator of mineralization rates because microbes mediate 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 which are higher in the floating peatland and would help explain the higher N mineralization rates in that site.

Over winter, net ammonification and net consumption of nitrate occurred. Ammonification and nitrification have been measured at temperatures near 0°C

(Nadelhoffer et al. 1991, Koerselman et al. 1993), however most of the net fluxes of N measured in this study probably occurred in early spring since over winter the peat was frozen solid. Jonasson and Shaver (1999) detected a decline of microbial populations over the winter with a flush of N after the spring thaw of soil (Herrmann and Witter 2002). Gross nitrification rates in early spring are high as are denitrification rates (Chapter Two), therefore it is likely that net rates are negative due to the denitrification of nitrate by microbes after the thaw of peat.

Microbial biomass and gross N consumption

Microbial biomass C and N were higher in the floating peatland than in the fixed peatland and also remained relatively stable throughout the season, a finding which corresponds to other studies (Puri and Ashman 1998). Size of the soil microbial biomass pool increased with increasing C content of the soil (Anderson and Domsch 1985, Strauss and Lamberti 2000) and increased moisture content of the soil (Mitchell et al 2003); in this study microbial N was positively correlated with moisture content of the soil. Both peat TC and moisture content were significantly higher in the floating peatland, which may be responsible for the higher microbial biomass.

Microbial biomass C and N in the fixed peatland (28.18 and 1.99 $g{\cdot}m^{-2}$ respectively) were 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 $g{\cdot}m^{-2}$, respectively). Microbial C:N ratios are higher in the fixed peatland (mean 16.05) than the floating peatland (mean 9.65). These 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), subarctic ecosystems (Schmidt et al. 1999) and northern forests (Fisk and Fahey 2001). Scandinavian peatlands have much higher microbial C:N ratios, frequently above 20 (Potila and Sarjala 2004). 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.

Peat TC, TN and TP were all significantly higher in the floating peatland when expressed as a percent of peat dry weight. On an aerial basis, there were more total nutrients in the fixed peatland due to the higher bulk density of the peat. In addition, TN and TC were also higher in marsh vs. fen peat in both sites which corresponds to results of a study of boreal Alberta marshes and fens (Bayley and Mewhort 2004). Peat TC in the floating peatland is higher than that measured in other boreal fens while peat TC in the fixed peatland is lower than that measured in other studies (Bridgham et al 1998, Bayley et al. in press). Peat TN is roughly within the same range as that measured in other boreal fens (Bridgham et al. 1998, Bayley et al. in press) and marshes (Bedford et al. 1999); however peat TP in both sites in this study is approximately two times higher than TP in other fens and marshes (Bedford et al. 1999). Higher nutrients in marshes could be related to diffusion of nutrients from N and P-rich surface water into 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 northern wetlands, while extractable nitrate in this study is much higher (Bridgham et al. 2001). Extractable nitrate was almost identical in both sites whereas the extractable ammonium pool was higher in the fixed peatland. Given the higher rates of N flux between pools in the floating wetland, it is surprising that extractable NH_4 concentration is higher in the fixed 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 consumption of both NH_4 and NO_3 was significantly higher in the floating peatland than the fixed peatland and in boreal shield peatlands (Westbrook and Devito, 2004). This is not surprising since the majority of N is consumed via microbial uptake (Schlesinger 1991) and there is a much higher microbial biomass in the floating peatland. Besides microbial uptake, 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 Davidson et al. (1992). Gross consumption measurements using isotope dilution are often overestimated due to enrichment of the substrate pool (Hart et al. 1994b) 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.

Estimates of microbial uptake of ammonium and nitrate calculated by subtracting net mineralization rates from gross mineralization rates are somewhat similar to gross consumption rates; this has also been found in other northern peatlands (Westbrook and Devito 2004). Gross consumption is often considered to be equivalent to microbial uptake because other consumptive processes (i.e. plant uptake, denitrification, volatilization, leaching) are considered to be negligible during short incubations (Hart et al. 1994b). While this may be true for most consumptive processes, we cannot definitively say that gross consumption rates are equivalent to microbial uptake in these peatlands because significant daily consumption of NH_4^+ via nitrification and of NO_3^- via denitrification were measured (Chapter Two).

Plant dynamics

Net primary production in the floating peatland is lower than other values in the literature from western boreal fens and marshes, however they follow the same trend in that marshes are more productive than fens (Thormann and Bayley 1997a and b, Mewhort 2000, Vitt et al. 2001). In the fixed peatland, high production values in the fen and marsh are more similar to marsh NPP values in other western boreal peatlands (Thormann and Bayley 1997a and b, Vitt et al. 2001). Lower values of NPP in the floating peatland may be attributed to the fact that only vascular vegetation was harvested. This site had a substantial moss layer in the fen which was not measured as part of the total aboveground NPP. Moss production in a floating fen contributed a mean of 170 $g \cdot m^{-2} \cdot yr^{-1}$ to NPP over a two year study in western boreal Alberta (Thormann and

Bayley 1997a). We most likely underestimated total NPP in the floating peatland by excluding non-vascular plants. If we estimate a value of moss NPP of 170 $g{\cdot}m^{-2}{\cdot}yr^{-1}$, total production is still greater in the fixed peatland, a surprising result since this is the site with the lowest nutrient pool sizes and cycling rates. Production differences are not always readily explained by mineralization rates of N and P, but may be more closely related to the actual availability of these nutrients 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) because it is more easily assimilated than NO_3 (Schlesinger 1991). Nitrogen availability for plant uptake in an N-limited system 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 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).

Decreased microbial activity and smaller microbial pool sizes in the fixed peatland would result in less competition with plants for available inorganic N and thus more nutrients would be assimilated into plant tissues allowing for greater NPP. In addition, the extractable pool of NH_4 in the fixed peatland was higher than that in the floating peatland, again due to lower consumption rates, specifically lower nitrification and assimilation by microbes. Bulk density may also be responsible for differences in NPP observed between the two sites. Lower bulk density of peat in the floating site could have had a negative effect on plant growth due to increased diffusion distances through the peat to the plant roots (Barko and Smart 1986).

Decomposition in general was higher in marshes than fens, although the difference was not significant. Marshes generally have greater decomposition rates than fens (Davis and van der Valk 1978, Bayley and Mewhort 2004) however there are exceptions where decomposition rates are the same in both peatland types (Thormann and Bayley 1997a). Decomposition rates after 291 days in the field were also not significantly different between the two sites. Mass loss in this study (45 – 54%) was higher than mass loss of *Carex aquatilus* leaves (38%) in boreal peatlands of Alberta (Thormann et al 2001).

Because of all the other site differences, we expected that decomposition rates would be much slower in the floating peatland, due to the lower degree of peat humification and higher C content of the peat (Humphrey and Pluth 1996). Differences in decomposition rates between the sites was not seen in this study however because the same type of plant material (i.e., *Carex*) was used in both sites. *Carex* litter has fast decay rates (Szumigalski and Bayley 1996) and differences in decomposition rates among *Carex* species have shown *C. diandra* decomposes faster than some other species (Aerts and de Caluwe 1997). Peatlands that have a significant moss stratum, such as the floating peatland in this study, accumulate more peat than those dominated by graminoids such as *Carex* spp. (Thormann et al. 1999). This is because *Carex* species have lower concentrations of "decay-resistant" polymers such as lignins (Bayley et al. in press). Therefore, litter quality is an important predictor of the rate of decomposition (Szumigalski and Bayley 1996) and higher litter quality may result in increased decomposition rates and therefore decreased peat accumulation (Thormann et al. 1999) because higher quality litter is more easily used by microorganisms (Schlesinger 1991).

Water levels are also important (Thormann et al 1999, Bridgham and Richardson 2003) because higher water levels lead to increased anoxic conditions in the peat which may limit microbial activity and therefore decomposition (Bridgham and Richardson 1992). This would explain the increased mass loss observed in marshes than fens. Nitrogen fluxes were not directly related to decomposition rates as has been found in another study in boreal Alberta (Bayley et al. in press).

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 fixed peatland). In the floating site, the marsh and fen vegetation communities are on a mat of peat above the water surface. This floating peatland may be more nutrient rich than non-floating peatlands because the rooting zone of plants could be affected by pond water below the peat mat (National Wetlands Working Group 1997). In addition, the peat in the floating peatland is very fibrous with a low bulk density. This is in direct contrast to the fixed peatland where the peat is not floating and is humic with a significantly higher bulk density. This higher level of humification in the fixed 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 humification/decomposition and increased bulk density due to aeration upon water level drawdowns. 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 fixed peatland.

Integrated internal N budget

Although nutrient pools remain relatively stable over the course of the ice-free season, internal N cycling rates between these pools is high (Figure 3-5). Turnover times of the extractable inorganic pools were rapid (Table 3-6). Turnover times for extractable nitrate were similar to those measured in boreal shield peatlands (Westbrook and Devito 2004) and were much faster than nitrate turnover in forests (Davidson et al. 1992, Verchot et al. 2001). Ammonium turnover in the floating peatland was similar to other boreal peatlands (Westbrook and Devito 2004) and was slower in the fixed peatland than in forest ecosystems (Davidson et al. 1992).

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 freshwater wetlands is often around 1g $N \cdot m^{-2} \cdot yr^{-1}$ and precipitation inputs range from 1 – 2 g $N \cdot m^{-2} \cdot yr^{-1}$ (Bowden 1987).

The largest nitrogen pool is in the peat, however only a small fraction is available for decomposition by microbes so plant litter is usually considered the main source of N for decomposing microbes (Bowden 1987). Gross ammonification and nitrification release 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 is not always mineralized from ammonium and that some nitrate is mineralized directly from organic N (heterotrophic nitrification), although we did not estimate how much. Extractable nutrient pools are very small and turnover rapidly to accommodate high rates of N cycling.

Inorganic N inputs (relative to the plants) are less than outputs in both peatlands (Table 3-7). Microbial uptake estimates were based on calculations of gross – net mineralization rates. Net nitrification values used in this calculation were estimated assuming that all N released via denitrification was derived from nitrate in the peat. Calculations of outputs and inputs assume that all nitrification is a product of ammonium; that plants and microbes only assimilate inorganic N and that denitrification substrate is from nitrification in the soil only. This leads to a deficit of inorganic N in the peatlands (Table 3-7) i.e., mineralization and other inputs are not high enough to accommodate rates of nitrification, denitrification, and microbial and plant uptake. It is known that some 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. Heterotrophic nitrification from organic N may also play a role in these peatlands, as autotrophic nitrification activity can 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 fixed peatland and the pool turns over rapidly (Christensen et al.1990, Venterink et al. 2003) and that groundwater inflow could be an important source of nitrate (Ferone and Devito 2004). The inputs and outputs of N could be balanced if there is substantial surface and ground water inputs to the system and if organic N is an important N source for microbes and plants.

These annual internal N pools and fluxes should only be considered estimates as it is difficult to extrapolate from small cores to a larger aerial basis and from daily and monthly rates to annual rates. We may have missed N cycling in April and September when temperatures drop and soil is undergoing freeze-thaw cycles which are known to increase N availability in soils (Appendix A, Koerselman et al. 1993).

Conclusions

Internal nitrogen cycling within peatlands of the western boreal plain is high (Figure 3-5). Marsh and fen peatland types surrounding the same shallow nutrient-rich ponds do not differ in major N flux rates and pool sizes, however significant differences in N cycling can occur between different peatland-pond complexes (sites). Differences in N cycling between sites appears to be strongly influenced by physical and environmental characteristics including bulk density and moisture content of the peat and water level fluctuations of the surface water. These factors affect the microbial community of the peat which in turn mediates all major N cycles. The fixed peatland had higher plant productivity and lower N cycling due to reduced competition for inorganic N by microbes.

Denitrification rates are substantial in both the floating and fixed peatlands. It appears that when mineralization rates are lower, surface water may be an important source of nitrate for denitrification. Use of isotope tracers would be useful to partition the consumption of NH_4 and NO_3 between microbial and plant pools and determine the relative importance of surface water nitrate as a substrate for denitrification.

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Table 3-1: Net vs. gross mineralization rates in two boreal peatlands expressed as mg $N \cdot m^{-2} \cdot d^{-1}$. Data are the mean of all measurements (±SE) from May through August 2004 (n = 24 for each site). * indicates an estimate of net nitrate mineralization assuming that all N released via denitrification was derived from mineralized nitrate.

	Floating Peatland	**Fixed Peatland**
Gross Mineralization		
NH_4^+	202.37 (45.4)	27.72 (4.6)
NO_3^-	250.89 (66.0)	31.65 (7.07)
SRP	----	----
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)
SRP	2.29 (0.7)	-0.067 (0.1)

Table 3-2: Nutrient concentrations (±SE) in *Carex* (in August) and mean monthly nutrient concentration in peat and microbes for May through August, 2004; * denotes significance between sites at $p<0.005$; significant differences between marshes and fens denoted by a = $p<0.05$, 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.

	Floating Peatland		**Fixed 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
C:P Peat	261.9	200.8	141.1	187.4
C:N Peat	21.1	16.2	14	14.6
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
C:P Carex	255.3	286.3	298.6	326.0
C:N Carex	30.6	38.2	41.5	33.6
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)	

Table 3-3: Estimates of mean consumption and immobilization of inorganic N in two boreal peatlands (mg $N \cdot m^{-2} \cdot d^{-1}$) for May through August, 2004 (n = 24). Immobilization estimates from isotope dilutions are calculated as:

NH_4^+ immobilization = gross NH_4^+ consumption – gross nitrification, and

NO_3^- immobilization = gross NO_3^-consumption – denitrification.

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

	Floating Peatland	**Fixed Peatland**
Gross Consumption		
NH_4^+	308.30 (105.6)	30.58 (4.4)
NO_3^-	404.08 (108.1)	33.92 (7.0)
Immobilization estimate (isotope dilution)		
NH_4^+	57.41 (111.7)	-1.07 (6.87)
NO_3^-	249.84 (111.6)	-52.16 (27.9)
Immobilization 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)

Table 3-4: Environmental variables in the floating and fixed peatland;* denotes a significant difference between the two peatlands at $p<0.05$; ** denotes a significant difference between marshes and fens within the same peatland ($p < 0.001$). Values are means (±SE) for measurements taken from May through August. n = 24 for all except water level, where n = 12.

	Floating Peatland	**Fixed Peatland**
Bulk density* **(g/cm^3)**	0.068 (0.002)	0.26 (0.01)
Moisture content* **(g water/g peat)**	12.84 (0.5)	3.21 (0.2)
Water Level (cm)**		
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)

Table 3-5: Significant correlations ($p < 0.05$) for major N fluxes and pools in two boreal peatland-pond complexes from May through August.

Compared variables	R-value	p-value
Floating peatland		
Net nitrification and:		
Net ammonification	0.823	0.012
Surface water [NH_4^+]	0.747	0.033
Gross ammonification and:		
Moisture content	0.751	0.032
Net P mineralization	0.908	0.002
TC in peat	0.712	0.048
Gross NH_4^+ consumption	0.911	0.002
Gross nitrification and:		
Gross NO_3^- consumption	0.861	0.006
Microbial biomass DON and:		
Moisture content	0.713	0.047
pH of porewater	0.892	0.017
Fixed peatland		
Net nitrification and:		
Surface water [NO_3^-]	0.745	0.034
Gross nitrification	-0.720	0.044
Extractable NO_3^-	-0.902	0.002
Gross ammonification and		
Microbial biomass DOC	0.851	0.007
Gross nitrification and:		
Surface water [NO_3^-]	-0.938	0.001
Gross NO_3^- consumption	0.887	0.003

Table 3-6: Estimated turnover times for major inorganic N pools in the peat. Extractable NH_4 turnover assumes NH_4 is used by plants, microbial uptake and gross nitrification. Extractable NO_3 turnover assumes NO_3 is consumed by denitrification only. Daily turnover rates are based on measurements from the 123 days of this study (May through August, 2004).

	Floating Peatland	**Fixed Peatland**
Extractable NH_4^+		
Daily	0.25	3.20
Extractable NO_3^-		
Daily	0.08	0.14

Table 3-7: Estimated annual inputs and outputs of inorganic N from a fixed and floating peatland. All values are expressed as g N·m^{-2} peat to 10cm depth based on measurements from a 123 day season (May through August, 2004). Estimates for fixation and precipitation inputs are based on values in Bowden (1987). 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 assumptions of maximum potential denitrification in buried bag cores to no denitrification in buried bag cores.

Inputs	**Floating Peatland**	**Fixed Peatland**
Fixation	1	1
Precipitation	1	1
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	**57.64**	**13.57**

Outputs	**Floating Peatland**	**Fixed Peatland**
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**

Table 3-8: 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 biomass	Total N in above-ground, vascular plant biomass (harvest)
Fluxes	
Decomposition	Total N added to peat 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
Microbial Uptake	Amount of NH_4^+ and NO_3^- taken up by microbes in the peat (estimated as gross – net mineralization)
Plant Uptake	Total N taken up by above ground vascular vegetation during the growing season (assumed equivalent to plant biomass N)

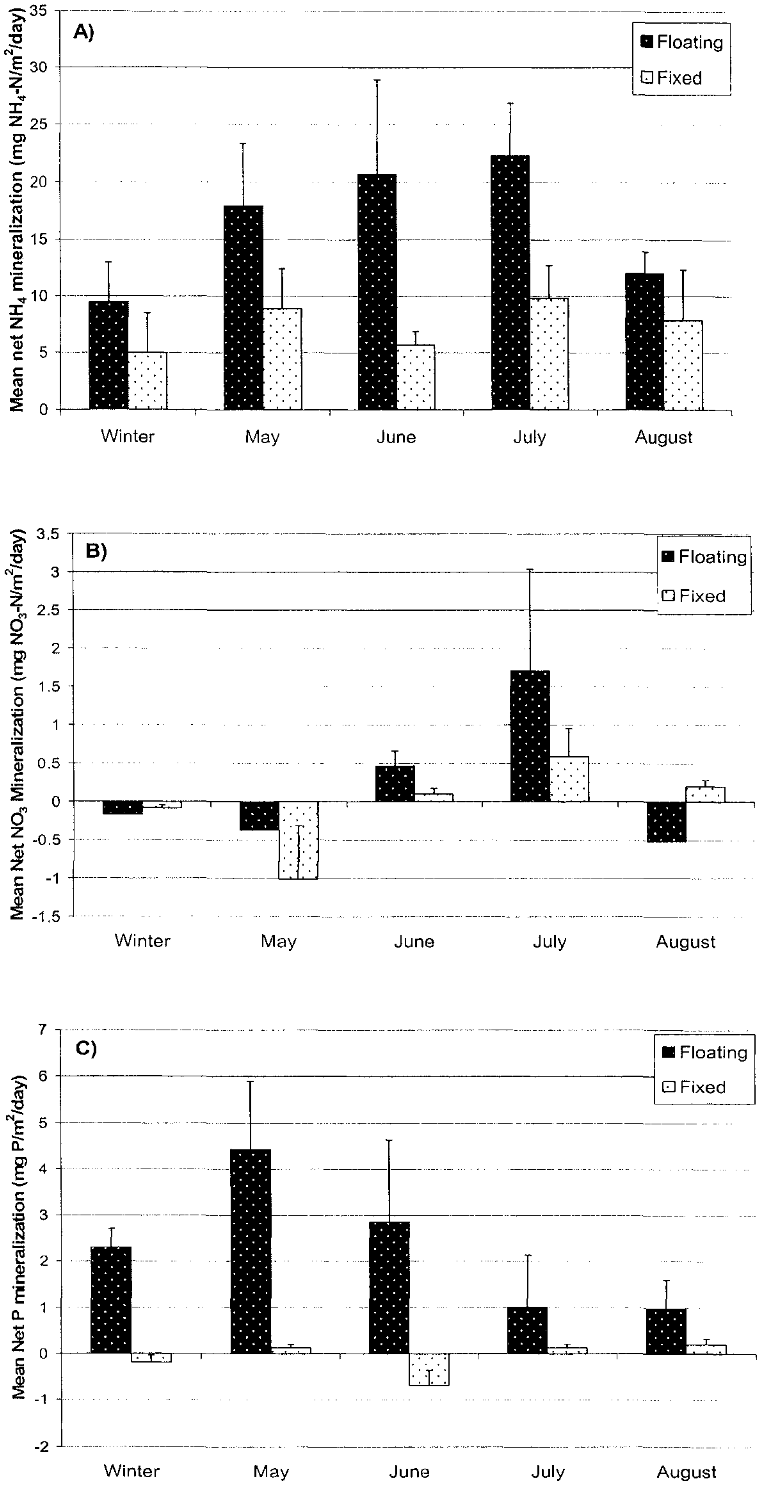

Figure 3-1: Mean net mineralization of A) ammonification, B) nitrification and C) soluble reactive phosphorus. Error bars represent standard error of the mean. All values are to 10 cm peat depth.

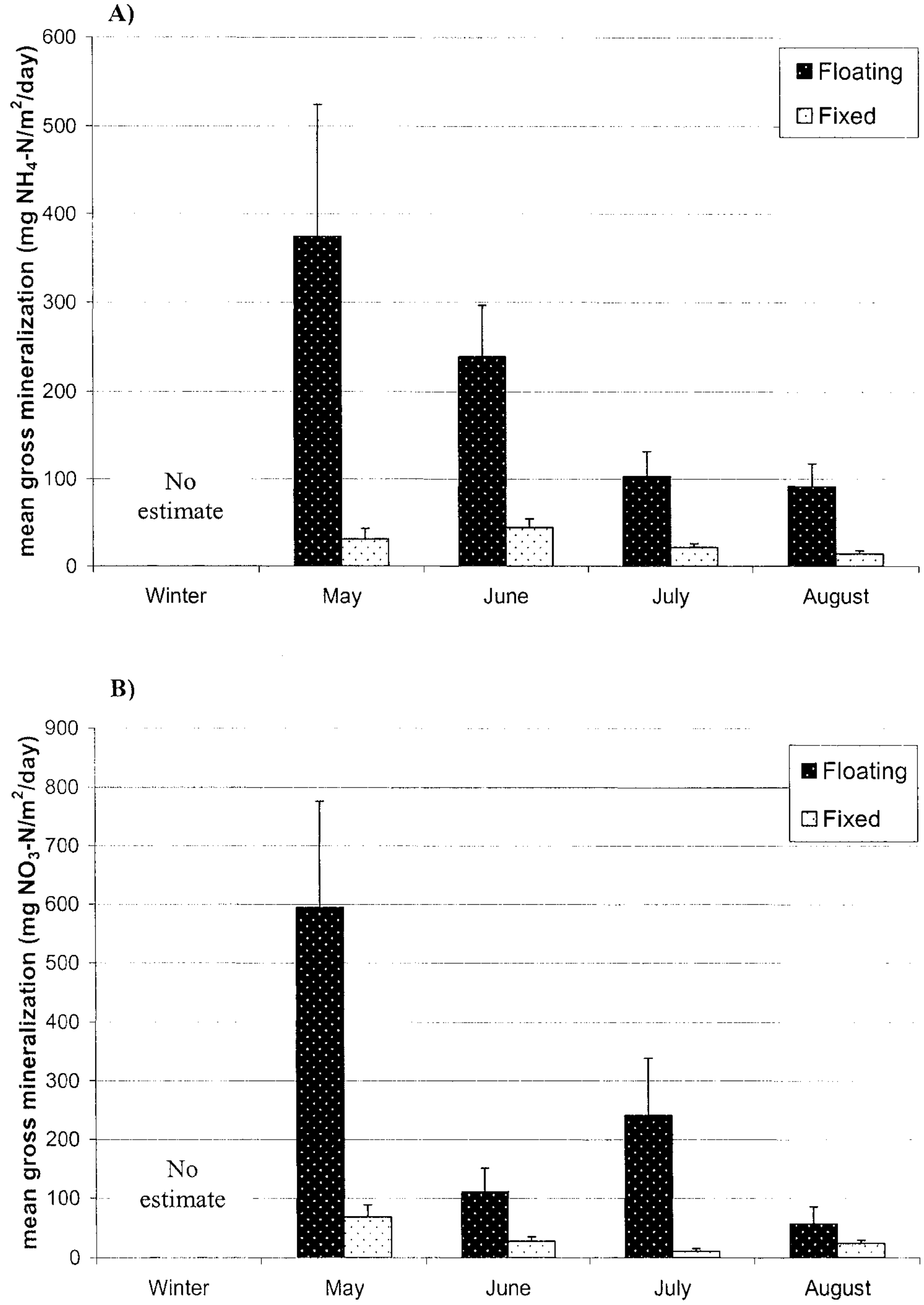

Figure 3-2: Mean gross mineralization over the season in the floating and fixed peatland A) ammonification and B) nitrification. Error bars represent standard error of the mean. All values are to 10 cm peat depth.

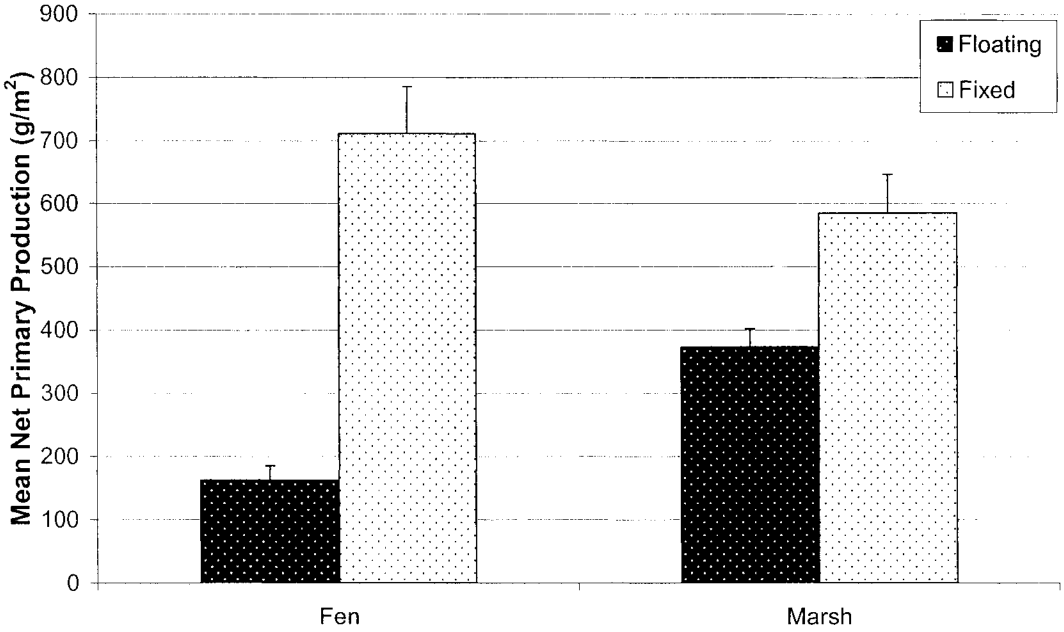

Figure 3-3: Mean peak biomass of aboveground vascular vegetation in the fen and marsh of a floating and fixed peatland. Error bars represent standard error of the mean.

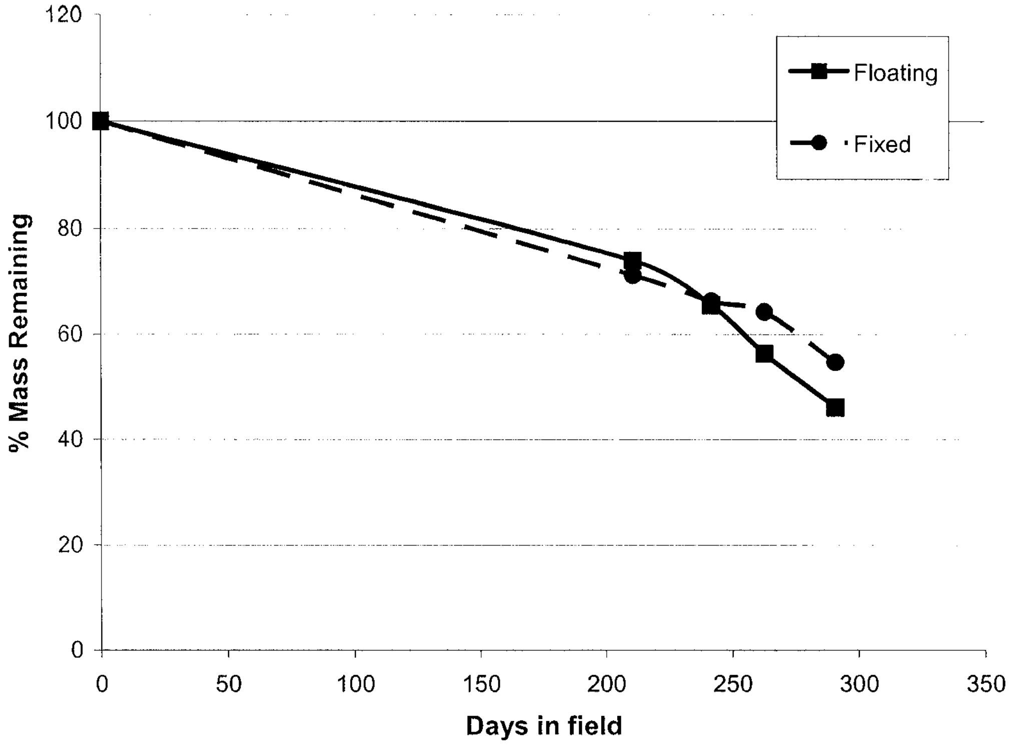

Figure 3-4: Mean decomposition rates of *Carex diandra* in the floating and fixed peatlands over a 291 day study period (October 2003 through August 2004).

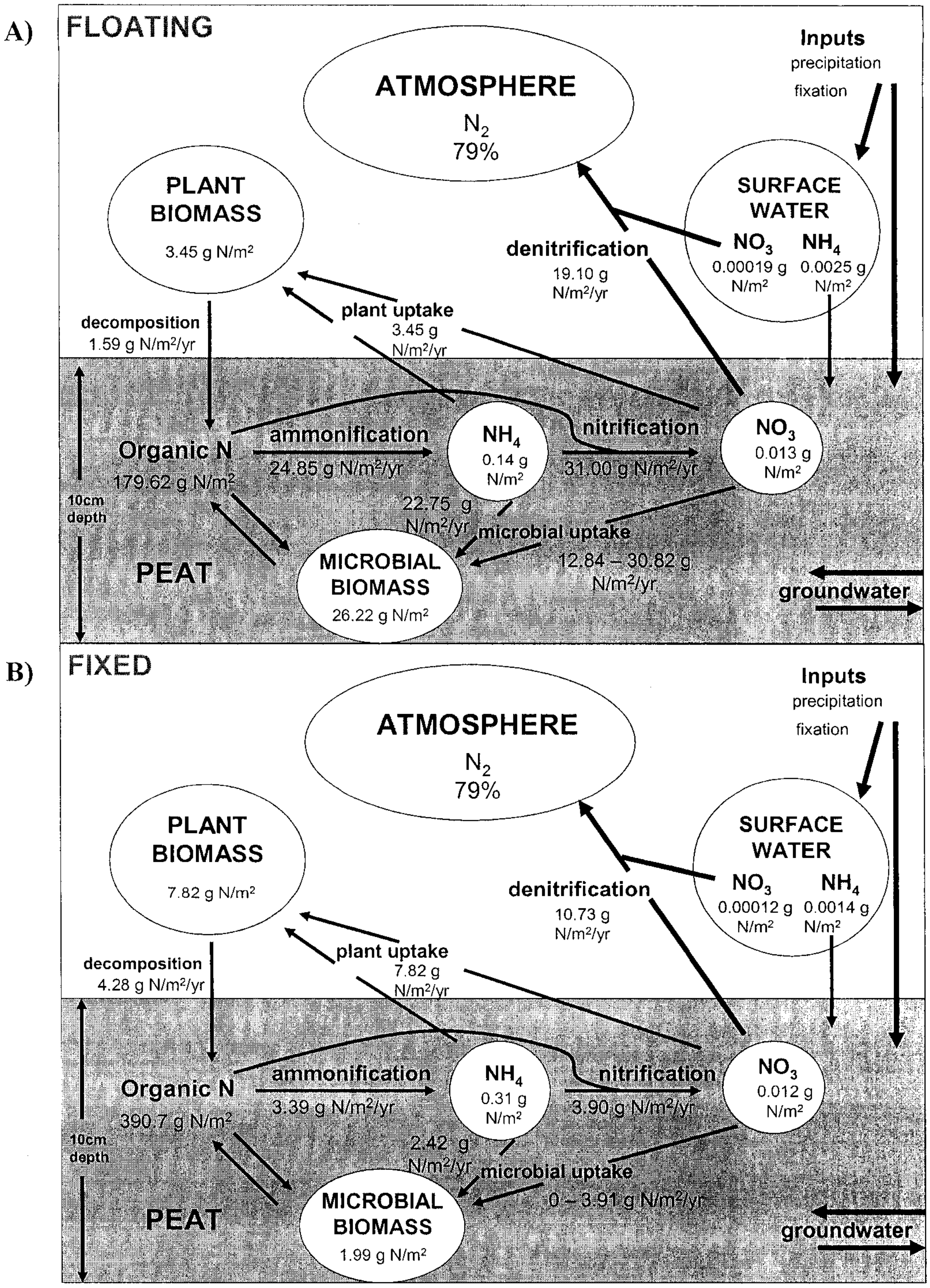

Figure 3-5: Estimated annual N fluxes and pool sizes in A) a floating peatland and B) a fixed peatland. All measurements are to 10cm peat depth and were taken from May through August 2004. Ammonification and nitrification rates are gross rates.

4. Conclusions

Two peatland-pond complexes in the Western Boreal Plain of Alberta, Canada were studied to compare internal N cycling and N removal via denitrification from marsh and fen vegetation zones within each peatland. This study was performed because peatland-ponds in the WBP are relatively nutrient rich, and few studies of N cycling have been performed in western peatlands. Previous estimates of nutrient dynamics in Alberta boreal peatlands have focused on net mineralization rates (Humphrey and Pluth 1996, Mewhort 2000, Bayley et al in press), with few studies examining differences between marshes and fens (Thormann and Bayley 1997, Bayley and Mewhort 2004). Direct measurements of denitrification are rare due to the complexity of methods, and very few studies measuring direct gas flux have been employed in boreal peatlands (Mewhort 2000). Measurements of gross rates of N transformations in Alberta boreal peatlands have not been done, and measurements of gross N cycling in other peatlands are rare (Westbrook and Devito 2004, Potila and Sarjala 2004).

Chapter Two examined potential rates of denitrification in the marsh and fen vegetation zones of two peatland-pond complexes. It was hypothesized that marshes would have significantly higher denitrification rates (as N_2) than fens however no significant differences were found between vegetation classes and between the two peatland-pond sites. Nitrogen fluxes from soils were highly variable; however results still show that potential denitrification rates in these study peatlands were very high and were estimated at 24 g $N \cdot m^{-2} \cdot yr^{-1}$ in fens and 11 g $N \cdot m^{-2} \cdot yr^{-1}$ in marshes. The relative contribution of N_2O as an end-product of denitrification was also examined in the fen vegetation zone of both peatland sites. It was hypothesized that N_2O fluxes would be relatively small since N_2 flux was so high, however any flux of N_2O would be important because it is a powerful greenhouse gas (Crutzen 1970) and wetlands are thought to be an important source of atmospheric N_2O (Bowden 1987). Nitrous oxide flux from fen soils was measured monthly in the summer of 2004. Results indicate that N_2O is only a very small product of denitrification (2%) in a floating nutrient-rich peatland. Peat was a sink for N_2O (i.e. N_2 appeared to be the only product of denitrification) in a fixed peatland with lower %C, higher bulk density and lower soil moisture content.

Chapter Three measured monthly internal N cycling and pools in marshes and fens in the same two peatland-pond complexes. Net and gross ammonification and nitrification rates and gross N consumption rates as well as major internal N pools (peat, plant biomass, microbial biomass) were measured from May through August 2004. Decomposition rates of *Carex diandra* litter were also measured from October 2003 until August 2004. Net primary production was measured by harvesting peak biomass in August 2004. No differences in major N fluxes were found between marshes and fens within the same peatland-pond complexes, however significant differences were found between the two sites. Both sites had similar extractable NO_3 and NH_4 concentrations, although cycling of N and the microbial pool differed substantially. Site 118 (a floating fen and marsh), with higher peat %C, lower bulk density and higher soil moisture, had significantly higher gross and net mineralization and consumption rates as well as a significantly higher microbial biomass. Site 171 (a 'fixed' marsh and fen), with lower %C, higher bulk density and lower moisture had lower N cycling rates, however had higher net primary production, presumably due to decreased competition with microbes for available inorganic N.

Results of this study do not agree with Bayley and Mewhort (2004) that marshes and fens are different in chemistry and N cycling. This may be due in part to the nature of our study sites, which consisted of small, narrow adjacent marsh and fen zones surrounding a pond. Vegetation differences between marshes and fens in these peatland-pond sites is due to hydrologic differences (Whitehouse and Bayley in press) whereas N cycling and the amount of N cycling appear to be related to the physical characteristics of the peatlands i.e., floating vs. fixed. This could be related to long term drought cycles; fixed peatlands will show greater water level fluctuations with droughts and re-wetting and increased wet-dry cycles over time could lead to increased peat humification (due to increased decomposition in dry periods) and therefore increased bulk density and decreased moisture content of soils. These factors affect the microbial community, and in turn all N cycling.

Internal budgets of inorganic nitrogen for both peatland sites show inputs (relative to the plants) are lower than measured outputs. These budgets could be balanced if there are inputs of N via ground and surface water as well as use of organic N by microbes in and plants (these fluxes were not measured as part of this study).

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Appendix A

Comparison of using fresh vs. frozen soil cores for mineralization studies

Previous studies of net mineralization in northern forests (Groffman et al. 2001) and nutrient-poor peatlands (Bayley unpublished) have not found significant differences in rates estimated using fresh soil cores and cores that are frozen prior to extraction. Freezing soil cores is advantageous in terms of time constraints because it allows more time in the field and less rush to do extractions upon return of samples to the lab. In more mineral rich sites or sites with higher microbial activity, freezing of soil cores may lead to overestimates of mineralization rates due to a flush in nutrient availability (Koerselman et al. 1993) released in part from the lysis of microorganisms (Herrmann and Witter 2002).

To test the effects of freezing peat cores on net mineralization rates, soil cores were collected in October 2003 in two peatland-ponds, one floating and one fixed, each with a fen and marsh vegetation zone. Twelve peat cores were taken to 10cm depth in each marsh and fen. Cores were divided in half length-wise and placed into plastic bags for incubation. One half of each core was placed in the original hole for incubation and the other half was returned to the lab. For each vegetation zone in each peatland-pond, six cores were returned to the lab and six remained in the field. Of the six returned to the lab, three were extracted immediately for NH_4-N and NO_3-N (initial extractable N) and the other three were frozen for extraction at a later date. Cores were incubated in the field over winter and removed in early spring 2004 after the peat had thawed. Again, half of the cores were extracted immediately for NH_4-N and NO_3-N and the others were frozen.

In the floating peatland, freezing treatments significantly affected extractable NH_4-N and NO_3-N as well as net ammonification and nitrification rates. There was no effect of freezing on extractable N or net N mineralization rates in the fixed peatland (Table 1). In general, freezing the peat increased extractable N concentrations and, where freezing had a significant effect, decreased net mineralization rates of both ammonium and nitrate.

The floating peatland has a significantly larger microbial biomass pool than the fixed peatland (Chapter Two), therefore it is not surprising that we see a larger increase in extractable N released upon freezing and thawing. A change in the net mineralization rates was unexpected since initial and final cores were treated the same way, therefore we would expect the same elevation in extractable nutrients in both samples and the difference between them (i.e., the net mineralization rate) would not change, provided there was no change in the soil microbial biomass pool over the same time period. Extractable nutrients in the final cores were not significantly elevated in frozen vs. fresh cores, most likely because of natural freeze thaw cycles occurring in the soil in the spring.

Freezing does significantly increase extractable nutrient concentrations in sites with large microbial populations therefore fresh cores must be used in order to get an accurate estimate. Because extractable nutrients are analyzed as the initial concentrations in mineralization estimates, final concentrations must also be extracted from fresh cores. Freezing may also affect net mineralization rates, therefore it is recommended that fresh cores are used whenever possible in sites that have large microbial biomass.

	Floating Peatland			Fixed Peatland		
	Fresh peat	Frozen peat	p-value	Fresh peat	Frozen peat	p-value
Net NH_4-N mineralization (mg NH_4-N·m^{-2}·day^{-1})	0.85 (0.2)	0.12 (0.05)	0.026	-0.06 (0.03)	1.24 (0.8)	0.181
Net NO_3-N mineralization (mg NO_3-N·m^{-2}·day^{-1})	0.50 (0.3)	-0.02 (0.002)	0.022	-0.02 (0.01)	-0.02 (0.01)	0.547
Extractable NH_4-N (ug·cm^{-3})	0.06 (0.01)	0.13 (0.03)	0.011	0.40 (0.07)	0.61 (0.17)	0.352
Extractable NO_3-N (ug·cm^{-3})	0.05 (0.004)	0.13 (0.03)	0.022	0.04 (0.01)	0.06 (0.02)	0.327

Table A-1: Means (±SE) of net N mineralization rates and initial extractable N in both fresh and frozen peat cores and associated p-values of comparisons of fresh and frozen peat.

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Appendix B

Gross mineralization estimates using ^{15}N isotope dilution

Gross rates of NH_4^+ and NO_3^- mineralization and consumption were estimated based on methods outlined by Hart et al. (1994) for direct combustion ^{15}N analysis (Figure B-1).

Gross rates of NH_4^+ mineralization (m) and consumption (c_A) were calculated from equations developed by Kirkham and Bartholomew (1954):

$$m = \frac{[NH_4^+]_o - [NH_4^+]_t}{t} * \frac{\log(APE_o/APE_t)}{\log([NH_4^+]_o/[NH_4^+]_t)}$$

$$c_A = m - \frac{[NH_4^+]_o - [NH_4^+]_t}{t}$$

where

m = gross NH_4^+ mineralization rate (mg $N \cdot kg^{-1}$ soil$\cdot$day^{-1})
c_A = NH_4^+ consumption rate (mg $N \cdot kg^{-1}$ soil$\cdot$day^{-1})
t = time (days)
APE_o = atom % ^{15}N excess of NH_4^+ pool at time 0
APE_t = atom % ^{15}N excess of NH_4^+ pool at time t
where APE = the atom % ^{15}N enrichment of an enriched pool minus the atom % ^{15}N enrichment of the pool prior to ^{15}N addition (background)
$[NH_4^+]_o$ = total NH_4^+ concentration (mg$\cdot$kg^{-1}) at time 0
$[NH_4^+]_t$ = total NH_4^+ concentration (mg$\cdot$kg^{-1}) at time t

Background ^{15}N enrichments are assumed to be 0.37 atom % ^{15}N

Gross rates of nitrification (n) and nitrate consumption (c_N) were calculated using the above equations, substituting n for m and c_N for c_A.

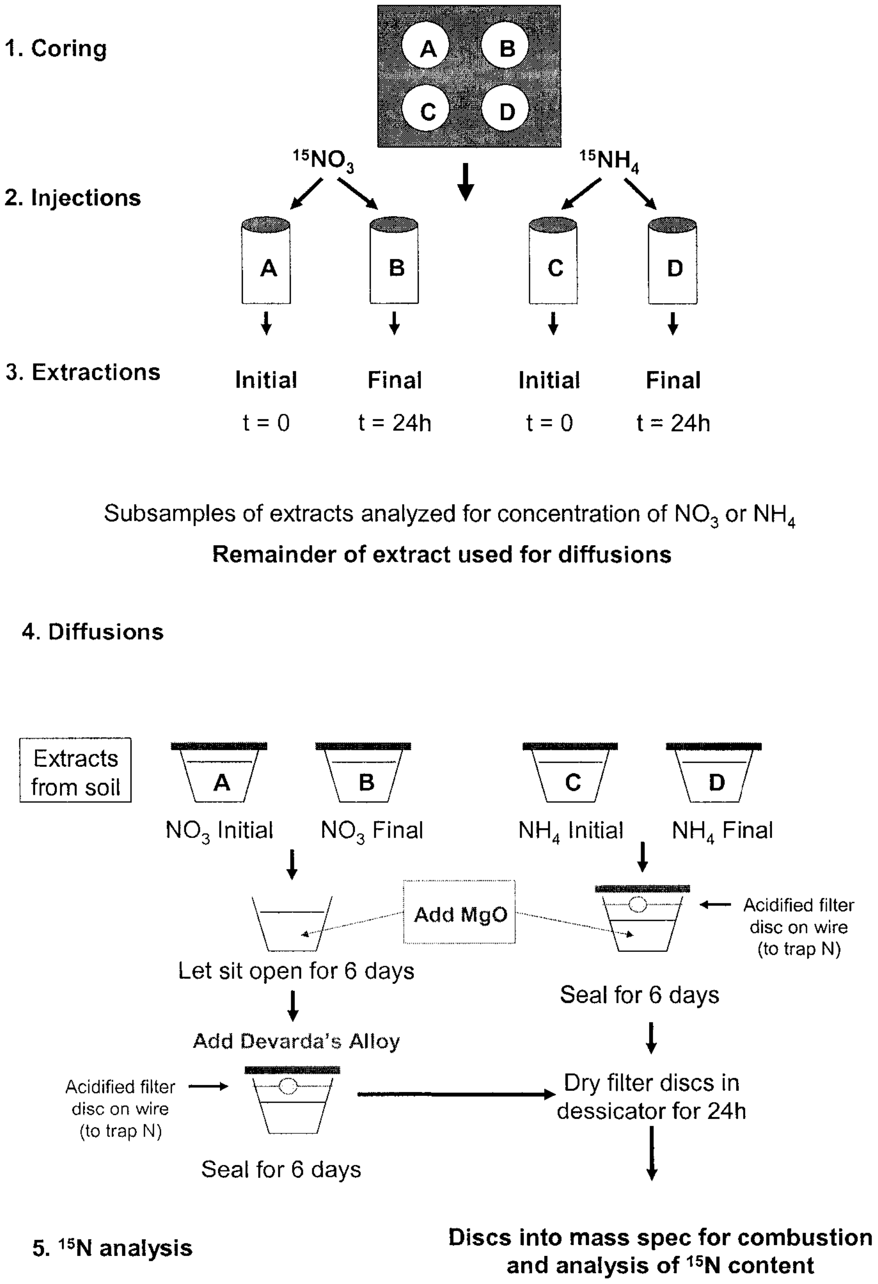

Figure B-1: Gross mineralization methods as outlined by Hart et al (1994). Ammonium samples were extracted using 1N KCl and nitrate samples were extracted using distilled deionized water (DDW). Magnesium oxide (MgO) powder makes the solution basic and causes NH_3 vapour to be released; Devarda's Alloy reduces NO_3^- to NH_4^+. Released ammonium vapour is trapped on the acidified filter discs.

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