Gross nitrogen transformations in soils from uncut and cut boreal upland and peatland coniferous forest stands

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Abstract. Gross and net nitrogen (N) ammonification and nitrification were measured in soils from an uncut and recently cut upland and peatland conifer stand in northwestern Ontario, Canada. Rates of gross total inorganic N immobilization were similar to gross mineralization, resulting in low net mineralization rates in soils from all four upland and peatland conifer stands. Gross ammonification rates were variable but similar in soils from uncut and cut peatland hollows (18–$19\,\mathrm{mg\,N\,kg^{-1}\,day^{-1}}$) and upland forest floor soils (14–$19\,\mathrm{mg\,N\,kg^{-1}\,day^{-1}}$). Gross ammonium ($NH_4^+$) immobilization rates were also variable but similar to ammonification rates. Median gross nitrification rates were within 0–$2\,\mathrm{mg\,N\,kg^{-1}\,day^{-1}}$ in soils from all four upland and peatland cut and uncut stands, although rates were consistently higher for the soils from the cut stands. Large variability in gross nitrification rates were observed in peatland soils, however the highest gross nitrification rates were measured in saturated peatland soils. Net rates remained low in the soils from all four stands due to high nitrate (NO_3^-) immobilization and very fast NO_3^- turnover ($<0.2\,\mathrm{day}$). Our results suggest that potential NO_3^- losses may be negated by high immobilization in uncut and cut boreal forest stands. This study reveals the potential for the interaction of N production and consumption processes in regulating N retention in upland and peatland conifer forests, and the resilience of the boreal forest to disturbance.

Introduction

The Boreal Shield region of Canada is an extensive ecosystem little studied in North America even though this system is proving sensitive to present global climate changes (Pastor and Post 1988) and is subject to considerable tree harvesting. The Boreal Shield landscape is a mosaic of coniferous uplands and peatlands. Thus, knowledge of nitrogen (N) dynamics in upland and peatland forest is essential in understanding natural variability in N cycling at the catchment-scale and the potential for N export following soil disturbance.

Field measurements of N transformations in undisturbed, boreal and arctic forest soils with similar temperatures and vegetation have shown negligible rates of net nitrification (0–$5\,\mathrm{kg\,N\,ha^{-1}\,year^{-1}}$) and relatively low rates of net N mineralization (4–$29\,\mathrm{kg\,N\,ha^{-1}\,year^{-1}}$) (Chapin 1996; Lamontagne 1998; Westbrook 2000). Similar results have been obtained in a temperate swamp (Hill and Shackleton 1989)

and in northern peatlands (Devito et al. 1999). However, net rates may underestimate gross rates and the quantity of N passing through inorganic forms due to high N immobilization (80–90%) in some ecosystems (Vitousek and Andariese 1986; Hart et al. 1994a). Whether low net mineralization and nitrification are a function of low gross rates or high immobilization is important in understanding net N cycling, and for predicting long-term forest productivity and nutrient leaching.

Recent work has demonstrated high rates of gross ammonification, gross nitrification and immobilization relative to net rates of N cycling in mature, temperate upland conifer forests (Davidson et al. 1992; Stark and Hart 1997). Low immobilization of N in peatlands has often been suggested due to small microbial populations (Jonasson and Shaver 1999); however few measurements of gross rates of ammonium (NH_4^+) and nitrate (NO_3^-) mineralization or immobilization have been made in northern peatlands. In boreal climates, lower gross N cycling may be expected due to the shorter growing season, cold temperatures, and low atmospheric N deposition. Alternatively, high rates of immobilization may be promoted in boreal systems due to a high soil C:N ratio. Detailed *in situ* studies examining the importance of N immobilization relative to gross mineralization and nitrification in determining net N cycling in northern or boreal forest ecosystems are required to better understand how these processes interact to regulate N retention in forested ecosystems.

Many tree harvesting studies in temperate and boreal–temperate transition regions have reported increased net N mineralization and nitrification rates following clearcutting of mineral upland soils, typically attributed to changes in soil temperature, moisture and C:N regimes (Munson and Timmer 1995; Paavolainen and Smolander 1998; Piatek and Allen 1999). This may have ramifications for both the export of nitrate along hydrological flowpaths (Sollins and McCorison 1981) and soil fertility for successful forest renewal (Jurgensen et al. 1997). In addition, peatlands are potentially critical interfaces regulating N export from catchments due to their relative abundance and position in the landscape (Devito and Hill 1997), but the effects of clearcutting on or adjacent to peatlands has not been well studied.

Clearcutting can influence the abiotic and biotic processes that control both the consumption and release of N within forest soils. Abiotic processes regulating immobilization of NH_4^+ include retention by 2:1 clays and chemical reactions with organic matter (Johnson et al. 2000). It has been recently proposed that abiotic immobilization of NO_3^- is the result of reduction to nitrite and subsequent reaction with organic matter to produce dissolved organic nitrogen (Davidson et al. 2003). Gross rates of N production and consumption are needed as net rates alone are inadequate to describe the actual effects of forest harvesting on soil N dynamics. It is important to distinguish between increased gross N mineralization rates or decreased gross immobilization after forest harvesting because ecosystem processes such as carbon sequestration, forest regeneration, and stream water quality are affected by the internal N production and consumption capacity. More studies incorporating the range of soil types and climates are needed to address the effects of clearcutting on immobilization of N given that it has been shown to be a key

factor regulating N loss from undisturbed forests (Davidson et al. 1992; Stottlemyer and Toczydlowski 1999).

The aim of our study is to determine the importance of N immobilization relative to gross mineralization and nitrification in uncut and cut stands to better understand how these processes interact to regulate N retention in the boreal forest. This research forms part of a larger study examining N dynamics in boreal forest soils and the potential changes to N cycling as a result of forest harvesting. Previous results from net N incubation experiments conducted from 1996 to 1998 at this site (Coldwater Lakes Experimental Watersheds, northwestern Ontario, Canada) show that these soils have a high C:N ratio and low net mineralization and nitrification rates compared to other boreal and temperate forest soils (Westbrook 2000). Net mineralization and net nitrification rates were not stimulated during the first growing season after harvesting. Data obtained using a chronosequence approach imply that forest harvesting has no long-term effect on net mineralization or nitrification (Westbrook 2000). It is thus unclear whether forest harvesting has any immediate impact on gross ammonification and nitrification rates in upland or peatland stands from this region. We present here a case study of gross rates of ammonification, nitrification and immobilization in upland and peatland soils to examine whether: (1) low net rates observed in uncut and cut stands are due to low gross N production or high immobilization rates, and (2) gross ammonification, nitrification or immobilization rates differ between recently cut and uncut stands.

Study site

This research was conducted in the Ontario Ministry of Natural Resources' Coldwater Lakes Experimental Watersheds (49°05′N and 92°10′W) (Steedman and Kushneriuk 2000) situated in the Boreal Precambrian Shield region of northwestern Ontario, Canada. The mean January and July air temperatures are −17.6 and 19.2 °C, respectively. Annual precipitation for the study year (1998) was approximately 510 mm, or 70% of normal with about 30% falling as snow (Steedman and Kushneriuk 2000). Average N deposition between 1970 and 1982 at the Experimental Lakes Area, about 350 km west of the study site, was $2.0 \pm 0.8 \, \text{kg ha}^{-1}$ of NH_4^+-N and $1.8 \pm 0.5 \, \text{kg ha}^{-1}$ of NO_3^--N (Linsey et al. 1987).

The bedrock geology of the study area is Archean granitic–gneissic and the Hartmann moraine runs along the southwest section of the study region (Zoltai 1965). Mineral soils in the study area are of glacial–fluvial origin, comprised of silty loam to coarse sand and are classified as orthic dysteric brunisols. In general, the glacial till is patchy, bouldery and thin near the top of hillslopes and up to 1 m thick at the bottom of hillslopes. The thickness of the forest floor is 3–8 cm. Organic hystols of up to 100 cm depth make up 25% of the area. These peatlands are hydrologically connected to the hillslopes primarily via subsurface flowpaths, and occasionally by channelized surface flow following precipitation events.

The forest in this study has been unburned for the last 75–120 years. The major tree species in the uncut and cut uplands were jack pine (*Pinus banksiana*) and

black spruce (*Picea mariana*), with a sparse understory of green alder (*Alnus viridis*). Black spruce with some black ash (*Fraxinus nigra*) and an understory of the shrubs *Ledum groenlandicum* and *Gaultheria hispidula* dominate the uncut and cut peatlands before harvesting. Regenerating vegetation on the logged peatland includes various graminoids, sedges and sparse *Sphagnum* spp. clumps on hummocks.

Methods

Study design

Herein we present a case study comparing gross N cycling using the ^{15}N isotope dilution technique in a cut and uncut stand of both a peatland and adjacent coniferous upland stand typical of the Coldwater Lakes Experimental Watersheds (Steedman and Kushneriuk 2000). The case study follows a three catchment replication, with a pre- and post-treatment experimental approach examining the influence of tree harvesting on net N mineralization. The present study follows the experimental cutting and no pre-treatment measurements of gross N dynamics were conducted thereby limiting interpretation of harvesting effects, as inter-stand dynamics have not been documented.

Approximately 95% of a 30 ha headwater catchment draining into Lake 39 was logged in June 1998. In August 1998, approximately 2 months following cutting, a central peatland (1 ha) and the adjacent upland forest within the Lake 39 catchment were selected for soil ^{15}N studies. These were compared to a peatland (1 ha) and adjacent upland forest selected in an uncut catchment (about 25 ha) located approximately 1 km from Lake 39. Care was taken to ensure the uncut peatland and upland stands had similar soil structure, relief, aspect and vegetation to the cut peatland and upland stands in the Lake 39 catchment.

All the trees of the cut upland and peatland stands were removed in June 1998 with chainsaws, and logs were dragged to loading docks with cable skidders. Tree harvest in the peatland occurred when the peat soils were moist causing the surface to be highly disturbed, with deep ruts occupying about 50% of the peatland surface. Standing water in these ruts became highly colored within 2 weeks of tree removal. Harvesting caused much less physical disturbance of the soils in the upland stand, leaving the soil horizons intact.

Sampling design

In each of the uncut and cut upland and peatland stands, seven sites (spaced 20 m apart) were selected. Robertson (1987) has shown that a distance of 40 m spacing can ensure spatial independence in forest soils. Semi-variograms for the net mineralization studies at this site (Westbrook 2000) and other boreal forest sites (Devito et al. 1999) indicate that 20 m was an adequate distance for spatial independence of soil N measurements.

Soil cores were taken with a 6.2 cm diameter stainless steel soil corer from the forest floor (LFH horizon) and 0–10 cm mineral (A_e, where present, and B_f horizons) in the conifer stands, and from 0–10 cm in the peatland hollows. Peatland hollows rather than hummocks were chosen as they were more likely to be affected by flowing water, permitting assessment of the potential for N export from peatlands to adjacent water bodies. Cores for estimation of net and gross rates and soil bulk density (methodology described later) were taken within 1 m of one another at each site.

Physical parameters

At each site that soil cores were collected, temperature was measured at the beginning of the soil incubation period with a thermistor probe midway at each soil depth. Soil temperatures were similar to the range of values from intensive measurements conducted concurrently in several catchments throughout the study area (Westbrook 2000). The water table was measured at the beginning of the soil incubation period in one or two wells placed within the peatland and the cut upland stands. No well was present in the uncut upland stand, so one soil pit was dug to the bedrock (35 cm) in the same week soil incubations were conducted.

Moisture was determined by oven drying (105 °C for 24 h) a sub-sample of soil from each sampling site and soil depth, with volumetric moisture as defined in Dingman (1994). Soils were dried in small batches (<30 samples) to ensure they were dry prior to measurement of dry mass. Specific density of mineral soil, organic forest soil and well-humified peat was assumed to be 2.65, 1.0 and 1.1 g m^{-3}, respectively (Brady and Weil 1999). Bulk density was calculated from the dry mass over total core volume.

Measurement of net rates

At each of the seven sites along each transect in the cut and uncut peatland and upland stands an initial (time zero) soil core was collected. Next to the initial core a second core was collected, contained in 0.025 mm thick polyethylene bag, and placed back into the soil and incubated for 24 days (Eno 1960). The thinness of the bag permitted exchange of gases between the incubated soil and the surrounding environment. The net incubations were started 1 week before the gross ammonification and nitrification incubations. Soil cores were kept on ice in the field and returned to the field laboratory where they were kept refrigerated until processing, within 12 h of sampling. Inorganic N in an approximately 5 g (dry mass) sub-sample of either the initial or incubated soil core was extracted with 50 mL 2 M KCl and shaken mechanically for 1 h to obtain equilibrium. The KCl extracts were filtered through 1 µm Fisher grade Q2 filters prerinsed with KCl, and subsequently frozen. Extractable NH_4^+-N and NO_3^--N were determined on a Technicon autoanalyzer (Technicon 1973a,b). Estimates of net nitrification rates were determined

by the difference in NO_3^--N content between the incubated and initial unlabeled cores. Net ammonification rates were estimated by the NH_4^+-N content of the incubated, unlabeled core minus that in the initial core.

Measurement of gross rates

Gross ammonification and nitrification rates were estimated at the same sites as net rates in mid-August 1998. Four soil cores were labeled with ^{15}N at each of the seven sites within each of the uncut and cut upland and peatland stands, following the methodology of Davidson et al. (1992) and Hart et al. (1994a). The cores were obtained by inserting a 0.025 mm thick polyethylene bag in a hand held soil corer and twisting down to the desired depth. Two cores were amended with $30\,mg\,N\,L^{-1}$ $(^{15}NH_4)_2SO_4$ and the remaining two with a solution containing $30\,mg\,N\,L^{-1}$ $K^{15}NO_3$. The solutions, which contained ^{15}N enriched to 98 atom percent were injected from the bottom end of the core. Each core received six 1 mL injections, made with a 1 mL syringe. A corrected volume was used for sites where the forest floor in the conifer stands was thinner than 10 cm. During depression of the plunger, the syringe was slowly lifted up while being twisted to aid in even dispersion of the N label throughout the soil core. To ensure that the soil core stayed intact during injection of the labeled N solution, injection occurred while the bag was still in the corer.

One core of each labeled pair was immediately homogenized in the plastic bag and a 10 g (peatland soils) or 15 g (upland soils) sub-sample was extracted with 50 mL (peatland soils) or 75 mL (upland soils) 2 M KCl. The other core from each pair was sealed with a twist tie, reburied and incubated *in situ* for 48 h before extraction. A 48 h incubation period was used to compensate for expected low gross mineralization rates. The thinness of the bag permitted gas exchange during the incubation period.

Use of the polyethylene bag, instead of a standard PVC cylinder (Hart et al. 1994a), was employed because Canadian Shield soils are coarse grained, making coring difficult. This method also allowed for a more accurate determination of the organic–mineral soil interface in the upland stands, and created the least soil disturbance while maintaining the structure of the soil core.

The ammonium diffusion procedure described in detail by Hart et al. (1994a) was used to prepare KCl extracts for ^{15}N analysis. When necessary, extracts were spiked with an appropriate amount of $50\,\mu g/10\,\mu L$ ^{14}N solution and/or were diluted with 2 M KCl prior to diffusion to bring the percent atom abundance down to 0.5–1.0%, and the N mass between 50 and 120 μg for more precise analysis. Direct combustion ^{15}N analysis of the glass filter disks was conducted at the Soil Biochemistry Laboratory, University of Alberta, Alberta, Canada.

Daily rates of gross ammonification, gross nitrification and ammonium and nitrate consumption were calculated using the equations developed by Kirkham and Bartholomew (1954) and presented in Hart et al. (1994a). In cases where ammonification or nitrification rates were negative, calculation of gross ammonium or nitrate consumption rates used mineralization or nitrification rates of zero. For

ecological interpretation, negative values are equivalent to negligible or zero rates. In three cases gross ammonification and NH_4^+ consumption rates were equal and in six cases gross nitrification and NO_3^- consumption rates were equal. The NH_4^+ immobilization rate was calculated by subtracting gross nitrification from gross NH_4^+ consumption. Gross NO_3^- immobilization was equivalent to gross NO_3^- consumption, as denitrification was assumed to be negligible over the short incubation period. The validity of this assumption is discussed later. Turnover time or mean residence time is the length of time an N atom resides in the N pool and is determined by dividing the pool size by the gross rate generating that pool. Turnover rates were determined by dividing the concentration of soil N by the gross rate generating that soil N.

Statistical analysis

Differences between soil type (peatland hollow, and upland forest floor, and upland mineral) were determined using nonparametric descriptive statistics owing to the lack of replication. Differences between uncut and cut stands for each soil type were assessed using the overlap of 95 percentiles about the median for each transect. A similar analysis was used to asses whether rates were different from zero.

Results

Various soil properties and water table elevations for the uncut and cut peatland and upland stands are presented in Table 1. Soil temperatures were about 2–4 °C greater in the cut compared to uncut stands (Table 1). Soil moisture in the upland stands was low ($<17\%$) and no groundwater was detected over the summer months. However, forest floor bulk density and soil moisture was lower in the forest floor of the uncut upland stand. The water table was within 30 cm of the ground surface of both the uncut and cut peatlands, and soil moisture approached saturation. The pH of the peatland and upland soils was similar, with means ranging from 3.66 ± 0.06 to 3.99 ± 0.06. Soil inorganic N content of the peatlands was generally higher than the uplands with no differences between uncut and cut stands observed (Table 1). Soil total N content, determined for replicate composite samples for each stand, were similar for uncut and cut stands. Total N content of the peatlands was 1.1–1.2%, upland forest floor soils was 0.8–1.2% and upland mineral soils was 0.1–0.2%, for uncut and cut stands, respectively.

Not all of the applied ^{15}N label could be recovered immediately after addition to the soil. Similar percent recovery of $^{15}NH_4^+$ was found for soils from the different forest stands, ranging from 29 to 73%. Percent recovery of $^{15}NO_3^-$ was consistent among soils from the different forest stands and greater than that of $^{15}NH_4^+$, ranging from 56 to 100%.

There was large within and inter-stand variability in gross ammonification rates. Averaged rates from cut and uncut stands were similar, and an order of magnitude

Table 1. Medians (5th, 95th percentile) of selected soil properties in uncut and cut upland and peatland stands.

	Bulk density, Mg/m^3	Volumetric moisture, %	Water table[1], cm	Soil temperature, °C	Soil inorganic N, mg/kg	
					NH_4^+	NO_3^-
Peatland						
Uncut	0.06 (0.04, 0.07)	48.2 (33.6, 56.8)	−25.5	15.5 (13.2, 16.4)	30.73 (13.68, 54.01)	0.22 (0.06, 0.61)
Cut	0.08 (0.03, 0.13)	49.3 (38.5, 68.8)	−0.3	17.9 (16.7, 18.6)	28.36 (4.95, 61.89)	0.06 (0.03, 0.34)
Upland forest floor						
Uncut	0.08 (0.07, 0.12)	6.0 (4.6, 14.1)	Dry to bedrock	17.3 (15.1, 18.0)	10.90 (2.34, 14.43)	0.08 (0.01, 0.14)
Cut	0.15 (0.09, 0.35)	15.4 (8.9, 39.5)	Dry to bedrock	19.1 (17.3, 20.7)	11.56 (5.23, 54.99)	0.02 (0.00, 0.39)
Upland 0–10cm mineral						
Uncut	0.42 (0.15, 0.69)	7.0 (4.4, 28.0)	Dry to bedrock	13.0 (11.8, 15.5)	1.01 (0.05, 1.33)	0.01 (0.00, 0.07)
Cut	0.45 (0.35, 0.72)	16.7 (9.8, 25.5)	Dry to bedrock	17.1 (16.2, 17.7)	2.44 (1.92, 7.50)	0.00 (0.00, 0.07)

[1]Height of water table relative to ground surface the week before soil incubation at one location within each stand.
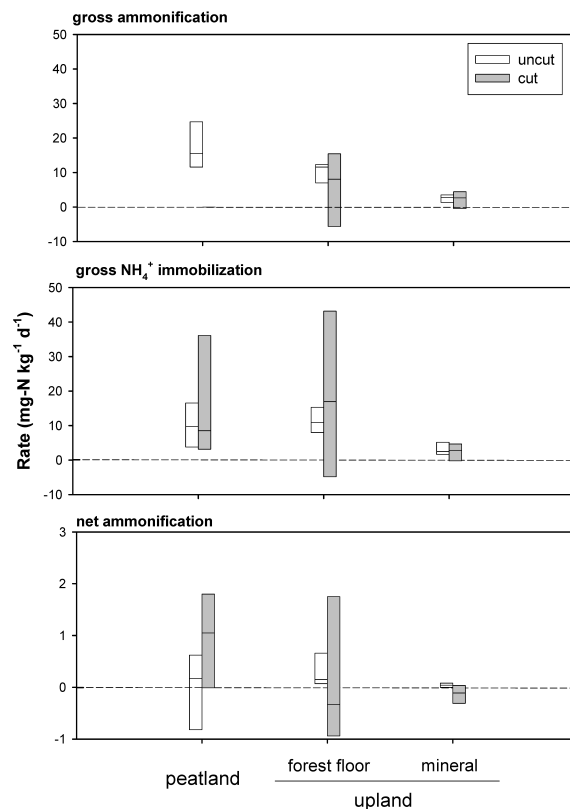
Figure 1. Rates of net ammonification, gross ammonification and gross NH_4^+ immobilization for uncut and cut peatlands and uplands, $n = 7$. Shown are medians (line), and the 5th and 95th percentiles (box). Note the scale difference between net and gross rates.

larger than net ammonification rates in all stands (Figure 1). Averages of gross ammonification rates from uncut and cut stands were similar in peatland hollows and the upland forest floor. Gross ammonification and NH_4^+ immobilization rates in the mineral soils of the upland stand were considerably lower than those in the forest floor soils of the upland stand and the peatland soils on a per gram soil basis. However, bulk densities of the upland mineral soils were much greater, and gross ammonification and NH_4^+ immobilization were similar to the peatlands and upland forest floor on an areal basis.

NH_4^+ immobilization rates in cut and uncut stands of all soil types were similar to gross mineralization rates resulting in the very low net ammonification rates (Figure 1). Net ammonification rates were low ($<1.5 \, \text{mg N kg}^{-1} \, \text{day}^{-1}$) and not different from zero in most stands. No differences in net ammonification rates among soil types were found. The similar gross ammonification and NH_4^+ immobilization rates in the uncut and cut stands within each forest type resulted in no difference in net ammonification between cut and uncut stands.
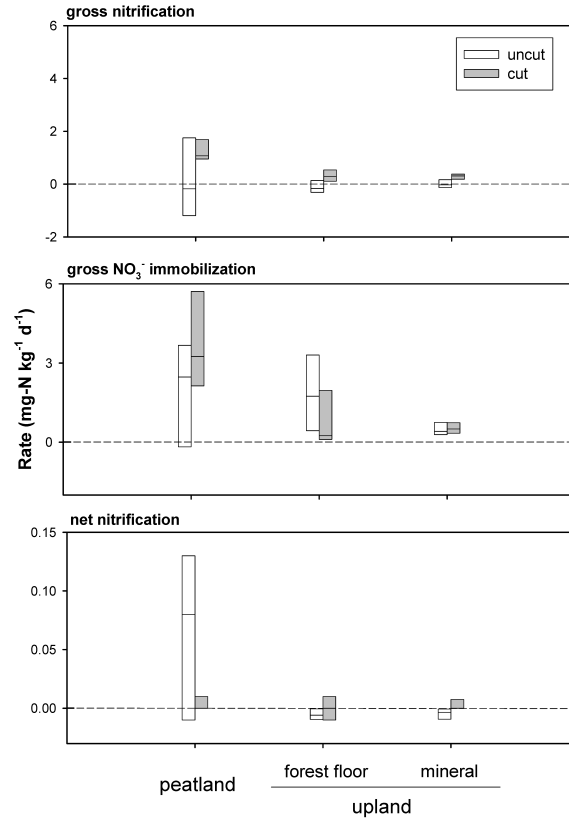
Figure 2. Rates of net nitrification, gross nitrification and gross NO_3^- immobilization for uncut and cut peatlands and uplands, $n = 7$. Shown are medians (line), and the 5th and 95th percentiles (box). One site in the uncut peatland with the highest gross nitrification ($13.1\,mg\,N\,kg^{-1}\,day^{-1}$) and nitrate immobilization ($15.8\,mg\,N\,kg^{-1}\,day^{-1}$) is not shown on the figure as it is an outlier (more than three standard deviations away from the mean). Note the scale difference between net and gross rates.

Gross nitrification rates in the all stands were an order of magnitude lower than the gross ammonification rates, with little difference among soil types (Figure 2). Gross nitrification rates were not different from zero in all uncut stands. There was large spatial variability in gross nitrification rates in the uncut peatland due to one high value ($13.1\,mg\,N\,kg^{-1}\,day^{-1}$), which was more than three standard deviations away from the mean. The other six samples ranged from -1.9 to $1.8\,mg\,N\,kg^{-1}\,day^{-1}$ and were lower than values measured in the cut peatland. In contrast, gross nitrification rates were positive at all locations in all cut stands (means ranging from 0.1 to $3.8\,mg\,N\,kg^{-1}\,day^{-1}$); with the highest rates in the peatland hollows of the cut stand.

NO_3^- immobilization rates were approximately two times greater than gross nitrification rates in all soil types, and the mineral soils of the upland stand had lower NO_3^- immobilization rates than the other two soil types (Figure 2). Peatland hollows had the greatest gross NO_3^- immobilization. The cut and uncut stands of
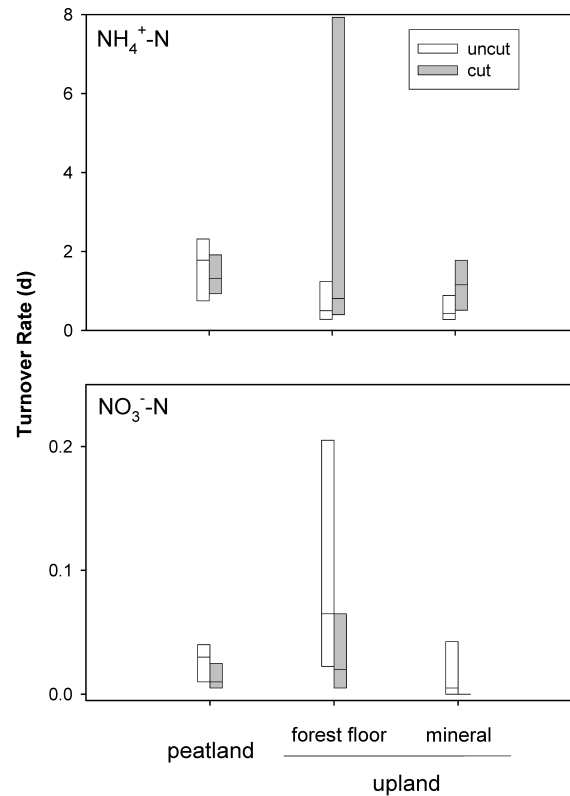
Figure 3. Length of time NH_4^+ and NO_3^- reside in the N pool, termed turnover rate, for uncut and cut peatlands and uplands, $n = 7$. Shown are medians (line), and the 5th and 95th percentiles (box).

each soil type had similar NO_3^- immobilization rates (Figure 2). The large NO_3^- immobilization rates were associated with low net nitrification rates in all stands (Figure 2). Net nitrification rates were near zero in cut stands from all soil types. Negative net nitrification rates were observed in all uncut stands.

Turnover of NH_4^+ was generally less than 2 days and no trends were observed between uncut and cut sites, nor uplands and peatlands (Figure 3). No difference in turnover of NH_4^+ was observed among soil types. Turnover of NO_3^- was very rapid, less than 0.2 day, and no trends were observed between uncut and cut sites (Figure 3). NO_3^- turnover was greater in soils from the mineral uplands than forest floor soils from the upland and peatland stands.

Discussion

Although our sampling design precluded our ability to conclusively determine the influence of forest harvesting on gross N transformation rates in this case study,

simultaneous estimates of net and gross production and immobilization of NH_4^+ and NO_3^- provide insights into the potential interactions that govern N dynamics following tree harvest and soil disturbance. Rates of N immobilization were very high ($\sim$100%) relative to gross N mineralization in all four stands. Additionally, we observed high gross nitrification rates for saturated organic soils at several locations in the cut peatland. Clearly, soil N cycling in boreal forest soils is far more dynamic than indicated by measures of net mineralization (Devito et al. 1999; Westbrook 2000). These results have important implications for retention of N in the boreal forest, especially in peatlands situated in key locations of hydrologic transport (Devito and Hill 1997).

Ammonium

Our results are one of the first to indicate that soils from upland and peatland stands in the Precambrian Shield region of the boreal forest have similar and high ammonium turnover, despite differences in the substrate, soil water content, soil total N content and vegetation cover. High NH_4^+ immobilization relative to gross ammonification in peatland soils observed here contrasts with the conclusions of Verhoeven et al. (1990), who suggested reduced or absent N immobilization in *Sphagnum*-derived organic matter, although they made no direct measurements. High ammonification rates may be expected in valley peatlands, such as these, that receive considerable runoff from adjacent uplands and high surface water flow through surface peats (Hill and Devito 1997). Furthermore, high N immobilization of produced NH_4^+ is expected with C:N ratios greater than 25 (Brady and Weil 1999), and the mean ratio in the study sites was 48.7 ± 0.04 after disturbance. While we measured gross N transformations only in the hollows of the peatlands, we expect similar processes to be occurring in the peatland hummocks as detailed comparisons of net ammonification and nitrifications rates between hummocks and hollows yielded comparable rates (C. Westbrook, unpublished data).

Rates of gross ammonification were variable but similar for uncut and cut peatland and upland stands in our study, despite differences in temperature. Comparable results have been found for other acidic boreal forest soils (Pedersen et al. 1999). However, others have shown for similar soils that gross ammonification, but not immobilization, increases with increasing temperature (Stottlemyer and Toczydlowki 1999). Studies comparing uncut and cut stands in other, more calcareous, parts of the boreal forest have shown consistently higher gross ammonification rates in cut stands (Carmosini et al. 2002). Similar findings have been documented in temperate coniferous forests (Vitousek and Andariese 1986; Davidson et al. 1992). The gross ammonification and NH_4^+ turnover rates we observed are within the range of rates for temperate and boreal forest and grassland soils (Davidson et al. 1992; Wessel and Tietema 1992; Stark and Hart 1997; Neill et al. 1999; Chen and Stark 2000), although net rates are much lower than in these studies. Our results in context of the literature indicate that further examination is needed in a wide variety of ecosystems to determine if contrasts in net ammoni-

fication rates among forest soils from different ecosystems is a function of differing percent immobilization as much as dissimilarities in gross production rates.

As we present a case study of gross N transformations from only one date and four stands, we are unable to determine conclusively the role of forest harvesting in this ecosystem. However, within the same study area, Westbrook (2000) observed no difference in net ammonification rates for coniferous upland stands 0, 1, 2, 11, 15 and 64 years old that regenerated from harvesting or fire. This suggests high immobilization may occur throughout the succession of the forest and that the tight coupling of gross ammonification and NH_4^+ immobilization found in the four stands presented here is expected to persist throughout stand succession. It however remains unclear what the long-term impacts of harvesting on gross N transformations are in the peatlands.

Nitrate

At several locations, high gross nitrification rates were measured in saturated organic soils of the cut peatland. Large spatial variability in anoxia of surface peat is to be expected in valley wetlands due to micro-topography and complex surface flow paths (Wels and Devito 1989, Devito and Dillon 1993). The high variability and lack of pre-treatment analyses did not make it possible to conclude that higher rates of gross nitrification in the cut stands were the effect of logging. However, some researchers have concluded that NO_3^- production and immobilization are prevented in peatland soils with generally anoxic conditions, low pH, low N-content and low soil temperature (e.g., Chapin 1996; Nieminen 1998). The high gross nitrification rates measured in the cut peatland are similar to those measured in the forest floor of the upland stands, and also to aerobic soils in other coniferous and some deciduous upland forests (Wessel and Tietema 1992). These results indicate that the surface peat of the cut peatland may not be uniformly anoxic, or that compaction has little effect on the aeration of the peat. Higher water table and surface water flow resulting in aeration of greater than 30 cm of the surface peat has been observed in valley peatlands on the Canadian Shield (Sparling 1966, Devito and Hill 1997), creating conditions conducive to nitrification.

Gross nitrification rates were consistently higher in soils from the cut stands, although our sampling design precluded our ability to determine conclusively the role of forest harvesting. The importance of net nitrification relative to mineralization has been shown to greatly increase following clearcutting in other upland forest soils (Pedersen et al. 1999). The exact mechanisms are not known, but studies like that of Stottlemyer and Toczydlowski (1999) suggest that interactions between temperature and moisture are important in controlling gross N transformations. We found only modest temperature differences of 2–4 °C between the uncut and cut stands. Soil moisture was two times higher in the cut upland stand compared to the uncut stand and could potentially alleviate the observed moisture deficit creating conditions more conducive to nitrification. However, it remains unclear why gross nitrification but not NO_3^- immobilization was consistently higher in the cut upland

stand, and whether this difference was indeed caused by forest harvesting. Leaching of dissolved organic carbon was observed in the standing water of the cut peatland stand. This may be providing additional substrate to stimulate microbial activity. Our results illustrate the need for further examination of the effects of forest harvesting on gross nitrification rates especially in peatlands, and the need for more complete studies that characterize the parameters (redox potential, DOC concentrations, denitrification rates) driving N transformations.

High rates of NO_3^- immobilization appear to influence net nitrification and soil NO_3^- concentrations in the peatland and upland stands. Field measurements of very low and often negative net nitrification rates throughout a 3 year period in several peatland, and conifer and aspen upland stands in the Coldwater Lakes Experimental Watersheds (Westbrook 2000) and other Precambrian Shield sites (Devito et al. 1999) support this finding. The measured turnover rates for NO_3^--N of less than 3 h in all four stands are as fast or faster than reported for other forest soils (Stark and Hart 1997), indicating rapid movement of NO_3^- through the small pool. These results suggest that the potential for leaching of NO_3^- under natural and disturbed conditions is influenced by microbial immobilization, at least in August 1998, and is very low. Concurrent studies in the Coldwater Lakes Experimental Watersheds area report very low net nitrification rates in cut coniferous upland stands 0, 1, 2, 11, 15 and 64 years following cutting (Westbrook 2000), indicating that soil NO_3^- immobilization relative to gross nitrification may remain high throughout regeneration of the harvested forests.

Measurements and errors

The occasional negative gross rates reported here are theoretically impossible, as a soil core contained in a closed polyethylene bag cannot lose N over the incubation period. The soil cores can lose N via gas loss when the bag is opened after the incubation, but that loss was not investigated here. An improved method is presented in Sala et al. (2000). When measuring gross rates of N cycling, two separate soil cores are needed – one to determine initial soil N concentration, and one to incubate. Even though soil cores are taken close together, spatial heterogeneity in soil inorganic N content is to be expected. Slightly higher inorganic N concentrations in the initial core relative to the starting concentration in the incubated core can result in a negative result if the rates are very low and less than the spatial variability in soil inorganic N content. These negative rates should be interpreted from an ecological standpoint as zero.

Nitrogen consumption may have been affected by abiotic and biotic processes. A large portion of the ^{15}N-labeled nitrate added to our soil cores was not recovered from the extractable inorganic N pool in less than 15 min. It is likely that a large portion of this lost extractable N was due to abiotic processes (Dail et al. 2001; Davidson et al. 2003), but further investigation is needed to determine the exact quantities. Nitrate immobilization may have been overestimated as denitrification is also a pathway for NO_3^- loss. This is likely of little concern in the upland stands, as

others (e.g., Stark and Hart 1997) have shown denitrification accounts for only a small portion of the NO_3^- consumed. Loss of NO_3^- via denitrification is of greater concern in the peatlands where the high water table is high and anoxic conditions can develop. However, Sparling (1966) and Devito and Hill (1997) have shown that the water movement through similar peatlands permits aeration of greater than 30 cm of the peat, and Hemmond (1983) asserts that denitrification in peat is thought to be inhibited by acidity. The validity of our assumption that denitrification was negligible and that NO_3^- consumption was primarily due to microbial immobilization requires further study.

Positive, although small, net nitrification rates were measured for sites where gross immobilization was greater than gross nitrification. Immobilization rates may be overestimated as the isotope dilution method requires the addition of inorganic N, which may enhance microbial immobilization or possibly denitrification (Hart et al. 1994b), particularly in the peatlands. This means that this method cannot be used to independently measure net ammonification and nitrification from the difference between gross mineralization and gross immobilization (Davidson et al. 1992). Nevertheless, these results demonstrate that the microbial community at this site has a greater capacity to consume NO_3^- than is produced by nitrification, and that NO_3^- assimilation is limited by NO_3^- availability.

Conclusions

Although this case study does not allow definitive testing of the influence of harvesting on gross and net N cycling, these results have implications for N retention in the boreal forest. High NH_4^+ and NO_3^- immobilization rates relative to gross mineralization rates were observed in all four cut and uncut stands. Rates of gross ammonification were similar among the three soil types, while the highest gross nitrification rates were measured in the saturated soils at sites within cut peatland. Although there was little replication within soil types, median gross nitrification rates were higher in all cut stands relative to uncut stands, indicating that tree harvesting and possibly greater soil temperatures may effect NO_3^- mobility. However, any potential increases in gross nitrification rates with harvesting were mitigated by high immobilization rates in all stands resulting in low net rates. Very rapid turnover of NH_4^+ (<2 days) and NO_3^- (<0.2 days) was observed, lending more support for a tight coupling of N production and consumptive processes in all stands. Our results suggest the importance of the interaction of N production and consumption processes in regulating N retention in uncut and cut boreal forest stands, as well as the resilience of the boreal forest N cycle to disturbance.

Acknowledgements

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