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The effect of soil freezing on N cycling: comparison of two headwater subcatchments with different vegetation and snowpack conditions in the northern Hokkaido Island of Japan

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Abstract Climate change models predict that the snowpacks of temperate forests will develop later and be shallower resulting in a higher propensity for soil freezing. In the northern most island of Japan, Hokkaido, snowpack depth decreases from west to east. This snowpack depth gradient provided a unique opportunity to test the effects of variable snowpack and soil freezing on N biogeochemistry. The Shibecha Northern Catchment in Shibecha Experimental Forest, eastern Hokkaido had deciduous trees and a mean annual snowpack of 0.7 m while the M3 catchment in Uryu Experimental Forest, western Hokkaido had mixed deciduous and coniferous tree species and a mean annual snowpack of 2.0 m. We conducted a field study (October 2004–April 2005) to determine if differences in Shibecha and Uryu soil extractable N, N mineralization, and nitrification were controlled by the variability in soil freezing during winter or tree species composition that affected the quality of the forest floor. The mixed deciduous and coniferous trees forming the Uryu forest floor had a higher C:N ratio (25.0 vs. 22.4 at Shibecha), higher lignin:N ratio (15 vs. 8.8), and higher lignin concentrations (0.28 vs. 0.18 g lignin g^{-1}). These differences in forest floor quality contributed to higher net N mineralization and nitrification in Shibecha compared to Uryu. In Shibecha, soil remained frozen for the entire study. For Uryu, except for an early period with cold temperatures and no snow, the soil generally remained unfrozen. As a result of the early winter cold period and soil freezing, extractable soil NH_4^+ did not change but NO_3^- increased. Reciprocal 0–5 cm mineral soil transplants made between Shibecha and Uryu and incubated during winter at 0, 5, and 30 cm suggested that soil freezing resulted in greater net N mineralization yet lower nitrification regardless of the soil origin. The effect of soil freezing should be considered when evaluating differences in N dynamics between temperate ecosystems having a propensity for soil freezing.

Keywords Catchment · Nitrate · Soil freezing · Climate change · Tree species composition

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Introduction

Climate change may result in marked changes in the structure and function of temperate forested ecosystems including the altering of elemental cycling (Vitousek 1994; Mitchell et al. 1996; Tilman 1998).

Although climatic models of north temperate ecosystems predict greater amounts of winter precipitation in the future (Hosaka et al. 2005; Hayhoe et al. 2006), reductions in snowpack are likely to occur due to the increased importance of thaws, sleet, and rain-on-snow events (Goodrich 1982; Hayhoe et al. 2006; Huntington et al. 2004). Without an insulating snowpack, soil ice formation at the onset of winter will persist throughout the winter and/or more frequent freeze-thaw cycles will occur (Goodrich 1982; Edwards and Cresser 1992).

Despite harsh winter conditions and cold temperatures, rates of microbial activity are high in winter, comprising a significant portion of nutrient cycling and loss (Brooks et al. 1996; Hobbie and Chapin 1996; Campbell et al. 2005). According to several laboratory studies, when soils freeze, root and microbial mortality results in a release of labile organic carbon (C) and nitrogen (N) to soil (Edwards and Cresser 1992; Schimel and Clein 1996; Groffman et al. 2001a; Neilsen et al. 2001) similar to what has been observed during wetting and drying cycles of soils (Birch 1958; Soulides and Allison 1961; Lund and Goksøyr 1980; Marumoto et al. 1982; Kieft et al. 1987; Davidson et al. 1998). The majority of the initial released organic N and C upon thawing comes from cellular material released from death and lysis of microbial biomass (in the form of simple sugars and amino acids) rather than a release from disrupted organic structure (Schimel and Clein 1996; Ryan et al. 2000; Hermann and Witter 2002). Increased net mineralization and nitrification occur during thawing as surviving organisms use the killed cells as a substrate (DeLuca et al. 1992; Neilsen et al. 2001) resulting in increased leaching of NO_3^- to surface waters (Callesen et al. 2007). Increases in soil NO_3^- levels also have been shown to be linked to increased fine-root mortality, resulting in lower plant N uptake (Groffman et al. 2001b).

Rates of nitrogen deposition input to forests in the northeastern USA are among the highest in the country, far exceeding natural nitrogen inputs (Boyer et al. 2002, Driscoll et al. 2003) yet outputs of N are often much less than inputs (Likens et al. 1996; Driscoll et al. 2003; Goodale et al. 2003). Over-winter processes may influence temporal variation in N retention in forested north temperate systems (Mitchell et al. 1996; Brooks et al. 1998). Some studies have suggested that over-winter activities influence

nutrient losses during the subsequent growing season and can explain the year to year variability in NO_3^- export from catchments (Mitchell et al. 1996; Brooks et al. 1998; Williams et al. 1998; Fitzhugh et al. 2001; Callesen et al. 2007). Understanding the role of the snowpack depth and duration as a factor influencing soil freeze/thaw and soil N dynamics is critical for evaluating the effect of climate change on ecosystem N biogeochemistry. However, there have been very few measurements of in situ biogeochemical processes during winter in temperate forests (Groffman et al. 2001b) and very little analysis of the influence of soil freezing on winter N dynamics.

Recent studies also have suggested that variation in tree species composition controls the variability of litter quality, N mineralization and nitrification rates, and therefore, N retention in temperate forested systems (Christopher et al. 2006; Pastor et al. 1984; Lovett et al. 2002, 2004; Lovett and Mitchell 2004) . Tree species composition drives differences in litter quality characteristics such as C:N ratio and lignin:N ratio among sites (Lovett et al. 2002, 2004). Lower C:N and lignin:N result in higher rates of NO_3^- production (i.e. net nitrification) (Finzi et al. 1998; Gundersen et al. 1998; Lovett and Rueth 1999; Lovett et al. 2004; Melillo et al. 1982). Soil organic matter quality, which is strongly influenced by tree species composition, also has been shown to explain the variability in soil microbial response to freeze-thaw perturbations (Schimel and Clein 1996).

In Hokkaido, Japan, the climate is classified as temperate to sub-arctic with heavy snow during the winter. Snowmelt runoff in spring results in high discharge to surface waters (Shibata et al. 2002). Thus it is important to understand over-winter soil processes in Hokkaido that may affect the leaching of NO_3^- to surface water. Although temperatures are similar across Hokkaido, the snowpack decreases markedly from west to east with western Hokkaido having much deeper (2–3 m depths; Shibata et al. 1997) snow compared to eastern Hokkaido (0.5–1 m depths; Takeuchi 1980; 1981). Maximum soil freezing depths of 35–50 cm have been noted in eastern Hokkaido due to lack of snow cover (Takeuchi 1980, 1981). Thus, this east to west snowpack gradient provided a unique opportunity to conduct a field experiment testing the effects of soil freezing on N biogeochemistry. We identified two study sites in Hokkaido. The Shibecha northern catchment (SN) Catchment, located in

eastern Hokkaido (Fig. 1) is dominated by deciduous tress species while the M3 catchment, in northwestern Hokkaido, (Fig. 1) contains mixed coniferous and deciduous tree species. We conducted a field investigation to address the following questions:

1. How does forest floor and soil quality affect the response of N mineralization and nitrification rates in Uryu versus Shibecha regardless of soil freezing? Non-frozen soils buried in situ in Uryu versus soils buried in Shibecha were compared.
2. What is the effect of soil freezing on total dissolved soil nitrogen concentration (TDN, including NH_4^+, NO_3^-, and dissolved organic nitrogen-DON)? Monthly 0–5 cm soils sampled in situ in Uryu and Shibecha were compared throughout the study period.
3. What is the effect of soil freezing on N mineralization and nitrification? Uryu soil buried in situ was compared to Uryu soil buried in Shibecha, and visa versa, to examine the response of each site to freezing and non freezing environments. In addition, at each site, soils from 0–5 cm soil incubated in situ at the surface were compared with 0–5 cm soil incubated in situ at 5 and 30 cm to examine differences in freezing (0 and 5 cm) and non-freezing environments (30 cm).

Methods

Site description

The M3 Catchment (3.5 ha), located in Uryu Experimental Forest (UREF), Hokkaido University (44°21′44″ N, 142°15′55″ E), hereafter referred to as Uryu, has a mean annual stream NO_3^- concentration of 0.1 mg N l^{-1}. Precipitation and air temperature have been monitored since 1969 at a meteorological station located approximately 1 km north of the study site, at the UREF headquarters. The mean annual air temperature at UREF is 3.1°C and the mean annual precipitation is 1390 mm (1969–1998, Yoshida et al. 2005), with approximately 50 % falling as snow between late November and early May. Mean annual maximum snow depth was 2.0 m from 1970–1989.

The bedrock in Uryu is Neogene andesite of Tertiary age, and soils are Inceptisols (Typic Dystrocrepts). Vegetation consists of natural mixed hardwood and conifer species mainly represented by Sakhalin fir (*Abies sachalinensis* Masters), Glehn's spruce (*Picea glehnii* Masters), Mongolian oak (*Quercus crispula* Blume), Japanese Manchurian ash (*Fraxinus mandshurica var. japonica* Maxim.), Erman's birch (*Betula ermanii* Cham.), painted maple (*Acer mono* Maxim.) and Japanese elm (*Ulmus davidiana var. japonica* Nakai). The forest understory is almost exclusively dominated by Chishima dwarf bamboo (*Sasa kurilensis*) except for some riparian zones. A detailed description of the vegetation in each sampling plot is given in the "Results" section.

The SN Catchment, located in the Shibecha Experimental Forest, Kyoto University (43°19′ N, 144°37′ E), hereafter referred to as Shibecha, has a mean annual stream NO_3^- concentration of 2 mg N l^{-1}. The mean annual air temperature and precipitation is 5.7°C and 1157 mm (1971–2000), respectively and have been continually monitored at the Field Science Education and Research Center (FSERC), the headquarters for the Experimental Forest. Snowfall occurs from December to March, but is less than 30% of the annual precipitation. The mean maximum snow depth was 0.71 m from 1988–2005. Soil freezing has been observed from December to
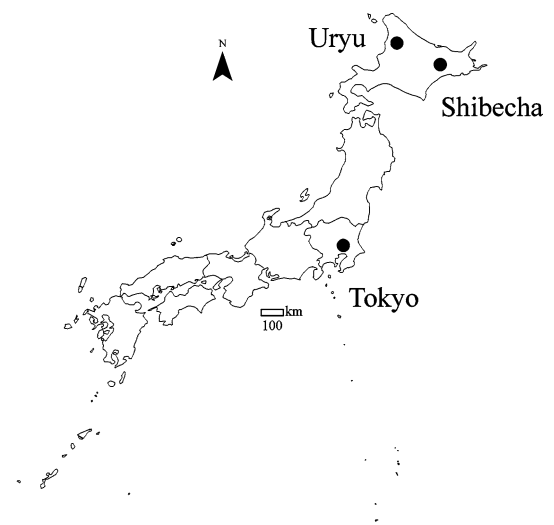

Fig. 1 Location of Uryu and Shibecha Experimental Forests in the northern Hokkaido Island of Japan.

May with maximum freezing depth varying from 35 to 50 cm and generally occurring in early March (Takeuchi 1980, 1981).

The bedrock in Shibecha is Abukuma Granitoids including basalt and chert. Soils are Humic Andosols derived from volcanic ash of Masyu (Ma-f). The deciduous broad-leaved canopy is dominated by Japanese elm, Japanese Manchurian ash, and Mongolian oak, and is discussed in more detail in the "Results" section. The understory vegetation in Shibecha is dominated also by a dwarf bamboo species (*Sasa nipponica*).

Temperature, snow depth, and soil frost

Two rectangular plots (approximately 10 m × 30 m) were established at two landscape positions (upper and lower slope) in each catchment. During the study period, October 2004-April 2005, soil temperature was measured with dataloggers at three depths (0, 5, and 30 cm) in each catchment plot at hourly intervals (the accuracy for our instruments was ± 0.4°C). Snow depth also was measured in each plot at ten locations during monthly visits and air temperature was continuously monitored by the field stations of UREF and FSERC. Frozen soil was measured using a ruler at five burial sites, described below, in each catchment plot during monthly visits.

Sampling and analyses

Soil and forest floor sampling and bulk density

In situ buried bag experiments were established at each of the two plots established in both catchments. Five, 0–5 cm mineral soil samples, weighing ∼1 kg, along a center line in each plot, were collected at approximately 5 m intervals, sieved to 5 mm, mixed, and ∼100 g of mixed soil was inserted in polyethylene bags. The polyethylene bags were then inserted into plastic bottles containing "air" holes to prevent animal chewing. We buried the 0–5 cm mineral soil samples in the plastic bottles at 0 cm, 5 cm, and 30 cm depths at five sites, approximately 5 m apart in each of the two catchment plots. At each burial site reciprocal 0–5 cm mineral soil bottle transplants were made between the Shibecha and Uryu sites at each depth. Thus, we buried 0–5 cm mineral soil at 2 plots × 5 burial sites in each plot x 3 depths at each

burial site × 2 catchments (reciprocal soil transplants for each soil bottle buried) for a total of 60 buried samples in each catchment. It is important to note that we used the same initial soil for the in situ field incubations and reciprocal soil transplants, for each catchment. Mineral soil samples were incubated for the entire winter (end of October 2005–mid-April 2006) and collected in mid April, just before spring snowmelt. Five mixed 0–5 cm mineral soil samples, in each of the two catchment plots were returned to the laboratory in coolers with ice packs for determining pre-incubation extractable NO_3^- and NH_4^+. Soil samples were stored in 1°C incubators until extractions were conducted within three days of collection.

Approximately monthly soil samples at each burial site in each catchment (2 plots × 5 burial sites = 10 total sites for each catchment) also were collected between October 2004 and April 2005 at 5 cm depth and analyzed for NO_3^-, NH_4^+, and DON. The first samples collected in October were collected on the same day that we collected the pre-incubation soil; therefore, October samples and pre-incubation soil was assumed to have similar characteristics. All soil N solute concentrations, pH, and soil moisture data reported for soil collected in Uryu on November 29, are referred to as having been collected in December to maintain consistency with Shibecha data, which was collected on December 2. During the October sampling date only, litter samples from the surface of the forest floor were collected at the soil sampling sites and analyzed for total lignin, carbon, and nitrogen. Bulk density for the 0–5 cm mineral soil was determined using the core method (Blake and Hartge 1986). Five bulk density cores (5 cm diameter) were collected from each of the two catchment plots (2 plots × 5 samples = 10 total samples for each catchment) and returned to the laboratory. Dry bulk density was calculated, after the entire cores were dried at 70°C, and corrected for root density.

Vegetation inventory

We sampled vegetation in the two plots established for each catchment. At each soil sampling site, diameter at breast height (DBH) and species of trees greater than 10 cm DBH were recorded within 5 m of the sampling site, parallel to the center line. The basal area was calculated by species and per unit catchment area ($m^2 ha^{-1}$).

Chemical and moisture determination

Soil samples were extracted with 2 M KCl. The extracts were filtered (0.7 μM pore size) and analyzed for NH_4^+, NO_3^-, and TDN using continuous flow colorimetry (AACS-4, BLTEC Co Ltd., Osaka). DON was calculated by subtracting dissolved inorganic nitrogen (NH_4^+ + NO_3^-) from TDN. Subsamples of each soil sample were oven dried for 2–3 days at 70°C, until they remained at a consistent mass, to determine the moisture content during each sampling date. Additional subsamples also were separated to analyze for pH using a ratio of 1 to 2.5 of soil to 0.01 M DI water. Net N mineralization rates during the incubation period were calculated by subtracting initial soil NH_4^+ + NO_3^- content from incubated soil NH_4^+ + NO_3^- content. Net nitrification rates were calculated by subtracting initial soil NO_3^- content from incubated soil NO_3^- content. Net mineralization and nitrification rates were converted to an areal basis (g N m^{-2}) using mineral soil depth (5 cm) and bulk density values. Litter samples were ground and analyzed for total C and N content on a Perkin-Elmer CNH autoanalyzer. An alcohol-benzene soxhlet extraction was performed on the litter samples to separate lignin compounds from other organic species. Lignin content was analyzed using the acetyl bromide method and spectrophotometry (Johnson et al. 1961).

Statistical analyses

A randomized complete analysis of variance (ANOVA) was performed to detect differences in nitrification, mineralization, and nitrification/mineralization for each landscape position and depth between catchments and switched soil within a catchment (i.e., Uryu soil buried in Uryu, Uryu soil buried in Shibecha, Shibecha soil buried in Shibecha, and Shibecha soil buried in Uryu). ANOVA also was used to assess differences in depth at each landscape position for Shibecha soil buried in Shibecha, Uryu soil buried in Uryu, Shibecha soil buried in Uryu and Uryu soil buried in Shibecha. Significant differences between means were identified using the Student–Neuman–Keuls procedure. A randomized split-plot ANOVA with repeated measures was performed to detect differences in NO_3^-, NH_4^+, DON, soil moisture, and pH by landscape position between catchments and months as well as by catchment between landscape
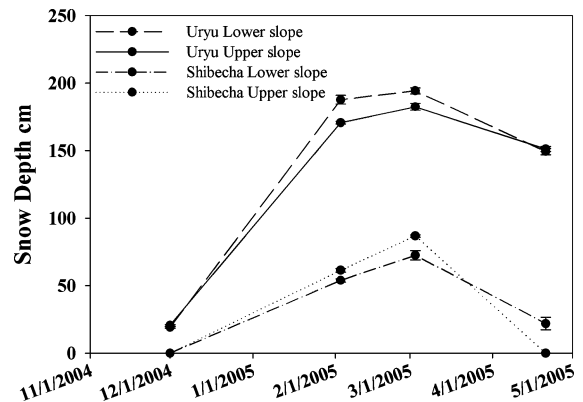

Fig. 2 Snow depth at the lower and upper slopes of the M3 Catchment (Uryu) and SN Catchment (Shibecha)

positions and months. Differences in C, N, C:N, lignin, lignin:N, and bulk density between catchments and landscape position also were assessed using a 2-way randomized complete ANOVA. Within our study, all statistical comparisons were assessed at $\alpha = 0.05$ using the Statistical Analysis System software (SAS 2004).

Results

Snow depth, soil temperature, sand soil freezing

A snowpack of ∼20 cm formed on November 29 in Uryu and increased to a maximum depth of 194 cm by early March. By late April, ∼150 cm of snow still remained at Uryu (Fig. 2). No snowpack developed in Shibecha in late November/early December; however; by February, there was ∼55 cm of snow. A maximum snow depth of 87 cm that was observed in Shibecha in early March was higher than the average maximum at this catchment. By late April, no snowpack was observed in the Shibecha upper slopes, while ∼20 cm of snow still covered Shibecha lower slopes.

The mean daily air temperature in Uryu, during the study period, was −3.1°C with a maximum daily air temperature of 19.5°C on October 7 and minimum daily air temperature of −34.3°C on January 26 (Fig. 3a). In Shibecha, the mean daily air temperature was −0.6°C during the study period. The maximum daily air temperature that occurred on October 7 was 23.7°C while the minimum daily air temperature was

Fig. 3 Mean daily air temperature in Uryu (**a**) and Shibecha (**b**); soil temperature at the lower slopes of Uryu (**c**) and Shibecha (**d**); and soil temperature at the upper slopes of Uryu (**e**) and Shibecha (**f**). The inset graphs in (**d**) and (**f**) are hourly soil temperatures during a cold snap before snowpack development in Shibecha
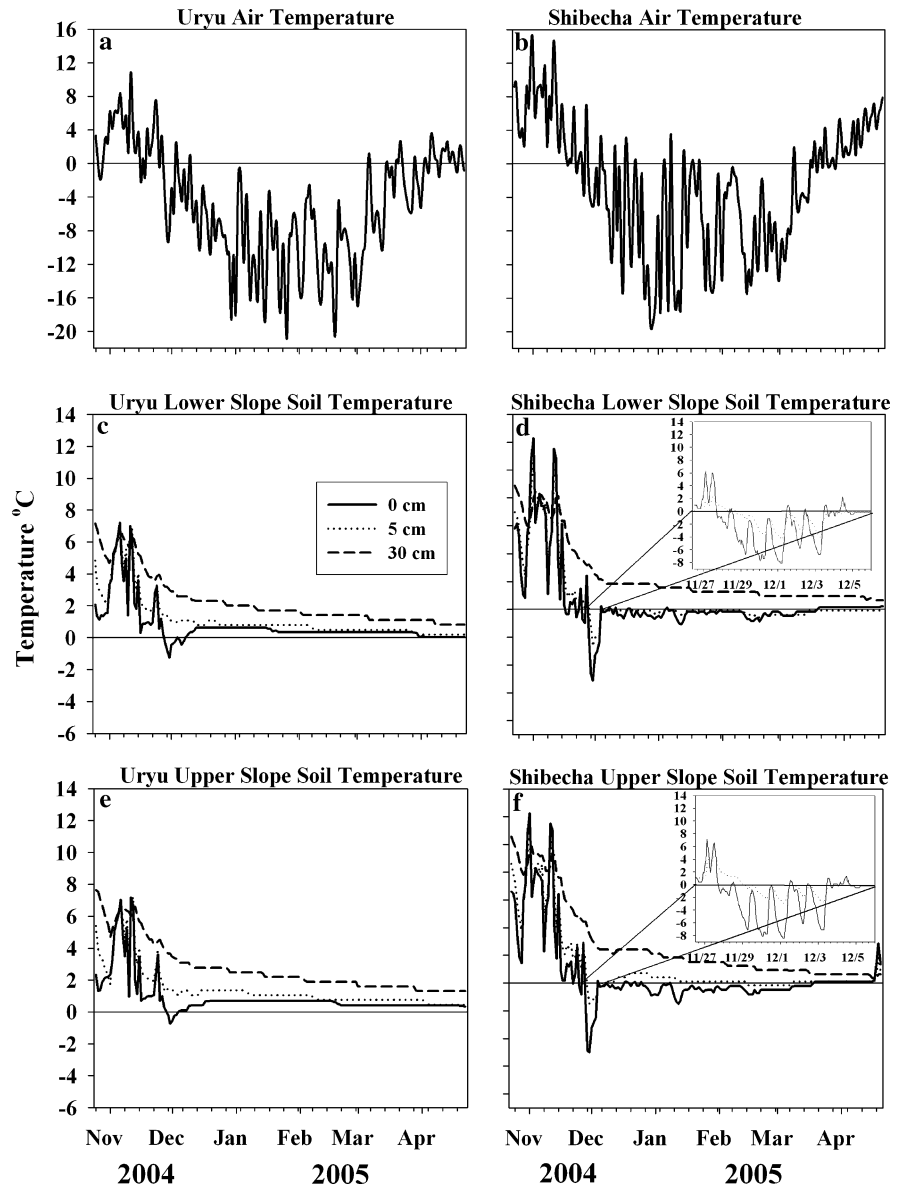
−25.9°C on March 1 (Fig. 3b). Temperature fluctuated concomitantly with air temperature in those soils without snowcover. In contrast, soils covered with snow remained at ∼0°C. In Shibecha, the sudden drop in air temperature between November 28 and December 3 resulted in diurnal soil temperature cycles at the 0 and 5 cm soil depths with lower temperature (−5 to −8°C for 0 cm and −3 to −4 for 5 cm) observed at night and temperatures closer to 0°C observed during the day (Fig. 3d, f). Soil freezing occurred in Shibecha soil during the early December

temperature drop to mean depths of 5 and 3 cm, respectively, in the lower and upper slopes (Fig. 4). Soil freezing occurred for the February, March, and April sample dates in Shibecha with deeper freezing in the upper (2–8 cm) versus the lower (2–3 cm) slopes. Soil temperatures in Uryu did not fall very far below 0°C except during the beginning of the cold period when the snowpack was just starting to form in Uryu (November 29) and air temperatures plummeted to a minimum of −17°C. There was relatively little soil freezing observed in Uryu soil (Fig. 3c, e), though we
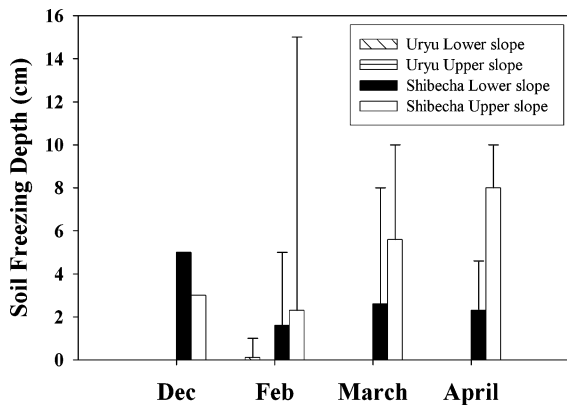
Fig. 4 Soil freezing at the lower and upper slopes of Uryu and Shibecha. Values are means with bars showing the range ($N = 5$) in values around the means

may have missed any freezing that would have occurred November 28–29, before the development of a snowpack in Uryu.

Vegetation

Tree species composition was different between the M3 catchment in Uryu and the SN catchment in Shibecha (Table 1). The Uryu catchment contained mixed deciduous species. Erman's birch and Japanese linden dominated the lower slope while Glehn's spruce dominated the upper slope. The Shibecha site contained only deciduous species with Japanese elm dominating both the lower and upper slopes.

Forest floor characteristics

There were no marked differences in total C (0.5 g C g^{-1}, $P = 0.6$) and N (0.02 and 0.02 g N g^{-1}, respectively, $P = 0.07$) between the forest floor in Uryu and Shibecha (Table 2). The C:N ratio, however, was slightly higher (25.0, $P = 0.05$) at Uryu compared to Shibecha (22.4). Lignin concentrations (0.3 and 0.2 g lignin g^{-1}, $P = 0.001$) and lignin to N ratios (15 and 8.8, $P = 0.006$) were significantly higher for Uryu compared to Shibecha, respectively.

Soil nitrogen solute concentrations, soil moisture, and pH

DON was the dominant (40–90%) N solute in both Shibecha and Uryu 5 cm soil (Fig. 5). At the lower

Table 1 Mean Basal area of each species in the Upper and Lower slopes of Uryu and Shibecha

Species	Basal area (m^2 ha^{-1})	
	Lower slope	Upper slope
Uryu		
Tilia japonica Simonk.	2.5	
Betula ermanii Cham.	4.6	
Abies sachalinensis Masters	–	6.6
Picea glehnii Masters	–	12.5
Acer mono Maxim.	–	0.4
Total	7.1	19.6
Shibecha		
Fraxinus mandshurica var. japonica Maxim.	3.0	–
Ulmus davidiana var. japonica Nakai	11.1	19.0
Syringa reticulate Hara	0.46	–
Betula platyphylla var japonica Hara	–	2.3
Populus sieboldii Miquel	–	0.7
Phellodendron amurense Rupr.	–	2.5
Ulmus hiruta	–	5.8
Total	14.5	30.3

slope, NO_3^--N concentrations were significantly greater ($P = 0.01$) in Shibecha versus Uryu. Nitrate concentrations in the upper slope of Shibecha soil were significantly greater than in Uryu soil in October ($P = 0.0003$), December ($P < 0.0001$), February ($P < 0.0001$), and March ($P < 0.0001$) though the disparity of catchment means differed among months. DON concentrations were significantly greater in Uryu versus Shibecha only in October ($P = 0.006$) and in the upper slope. There were no differences in NH_4^+-N concentrations between the catchments in the lower or upper slopes.

A marked decrease in TDN concentrations was observed from October to December in both catchments, most noticeably in the upper slopes though this shift was only significant ($P = 0.0002$) in the upper slopes of Uryu (Fig. 5, differences not shown). During this October to December shift, for Uryu and Shibecha, there was a marked decrease in DON concentrations in the lower (36.8–23.1 g N kg^{-1} and 44.1–31.6 g N kg^{-1}, respectively) and upper slopes (96.7–33.7 and 58.8–21.6 g N kg^{-1}, respectively), though only the decrease in DON in Uryu in the upper slopes was significant ($P < 0.0001$). An increase in NO_3^--N concentrations from October to December

Table 2 Summary of forest floor characteristics at Uryu and Shibecha

Site	Bulk density (g cm^{-3})	Total C (g C g^{-1})	Total N (g N g^{-1})	Lignin (g lignin g^{-1})	C:N	Lignin: N
Uryu	0.5 (0.04)	0.5 a (0.005)	0.02 a (0.0008)	0.3 a (0.02)	25.0 a (0.9)	15.0 a (1.4)
Shibecha	0.4 (0.04)	0.5 a (0.005)	0.02 a (0.0008)	0.2 b (0.02)	22.4 b (0.9)	8.8 b (1.4)

Letters within a column that are difference represent significant differences between sites at α = 0.05. Values are means with standard errors of the grouped means given in parentheses ($N = 10$)

Fig. 5 DON, NO_3^-, and NH_4^+ concentration (mg N kg^{-1}) in October, December, February, March, and April 2004–2005 in the lower slopes (**a**) and upper slopes (**b**) of Uryu and Shibecha. There was no difference in NH_4^+ between the catchments in the upper and lower slopes nor was there any difference in DON between the catchments in the lower slope. Letters that differ within each month for NO_3^--N (top row of letters for the upper slope) and DON (bottom row of letters for the upper slope) indicate significant differences between catchments at the 0.05 level
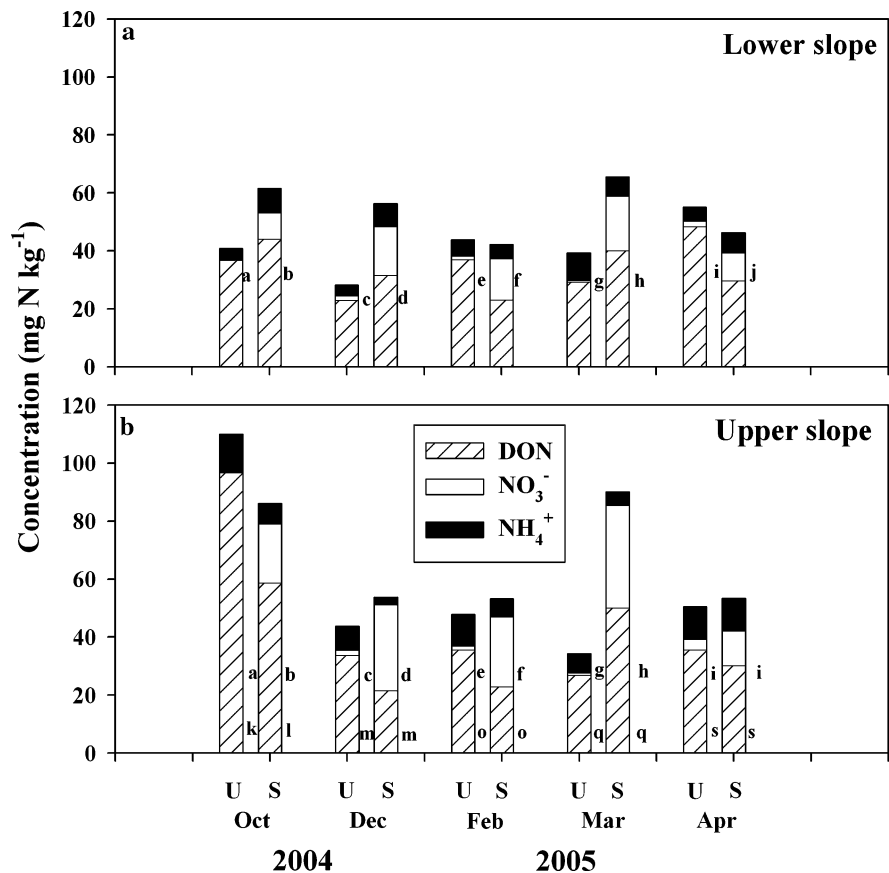
in Uryu (0.0–1.4 g N kg^{-1} in the lower slopes and 0.3–1.9 g N kg^{-1} in the upper slopes) and Shibecha (9.0–16.7 g N kg^{-1} in the lower slopes and 20.3–29.6 g N kg^{-1} in the upper slopes) also was noted, though none of these changes were significant. Ammonium concentrations remained relatively unchanged between October and December in both catchments. A marked increase in Shibecha in the upper and lower slopes in DON and NO_3^--N concentrations was observed from February to March in Shibecha though these shifts were not significant.

Shibecha soil moisture was significantly greater than Uryu only in the lower slopes ($P = 0.02$) regardless of the month (Fig. 6). In the upper slopes Shibecha soil moisture was greater than Uryu only in March ($P < 0.0001$). There were no differences in soil moisture between the upper and lower slopes in Shibecha (Table 3). In Uryu, upper slope soil moisture was greater than lower slope in October ($P = 0.002$) and December ($P = 0.01$) while lower slope soil moisture was greater than upper in March ($P = 0.04$).

Fig. 6 Mean soil moisture in October, December, February, March, and April 2004–2005 (+SE of the group means) in the lower slopes (**a**) and upper slopes (**b**) of Uryu and Shibecha. Letters that differ within each month indicate significant differences between catchments at the 0.05 level
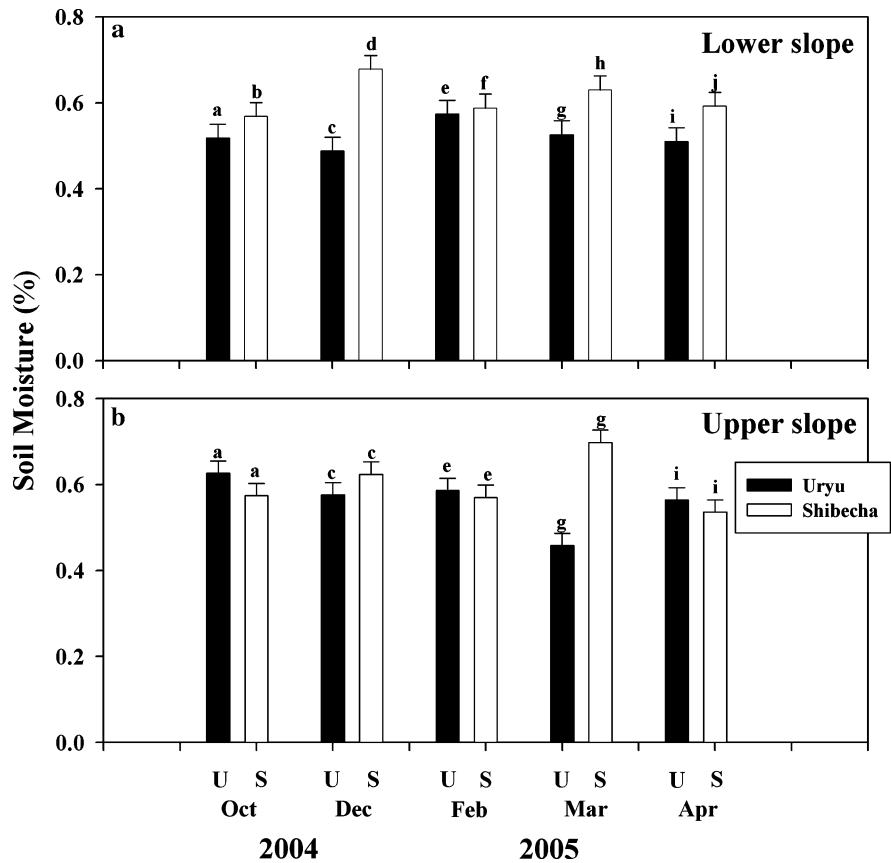

Table 3 ANOVA results for soil moisture in the upper versus lower slopes of Uryu and Shibecha

Month	Catchment			
	Uryu		Shibecha	
	LS	US	LS	US
Oct	a	b	x	x
Dec	a	b	x	x
Feb	a	a	x	x
Mar	a	b	x	x
Apr	a	a	x	x

Mean values and standard errors for each variable are given in Fig. 6. Letters that differ within a month (row) and catchment indicate a significant difference in soil moisture between the lower and upper slopes at the $\alpha = 0.05$ level

LS = Lower slope, US = Upper slope

The pH was significantly higher in Shibecha (5.4) versus Uryu (4.6) in the upper slope ($P = 0.002$, data not shown). In the lower slope, the same trend occurred (mean pH was 6.2 and 4.9 in Shibecha and Uryu, respectively) but there were differences in the magnitude of catchment differences in monthly means.

Comparison of N processes in Uryu versus Shibecha non-frozen soil

There were markedly different N mineralization and nitrification rates between Uryu versus Shibecha soil under conditions without soil freezing (soil buried at 30 cm depth). In the lower and upper slopes, net N mineralization in 30 cm soil, was significantly greater ($P < 0.0001$ for both landscape positions) in Shibecha versus Uryu (Fig. 7). Nitrification was higher than mineralization in Shibecha (104% of mineralized N was nitrified, $P = 0.002$ and 100% of mineralized N was nitrified, $P < 0.0001$, in the lower and upper slopes, respectively) versus Uryu (87% and 57% of mineralized N was nitrified in the lower and upper slopes, respectively), suggesting that a significantly greater percentage of mineralized ammonium was nitrified in Shibecha versus Uryu in both lower and upper slopes.
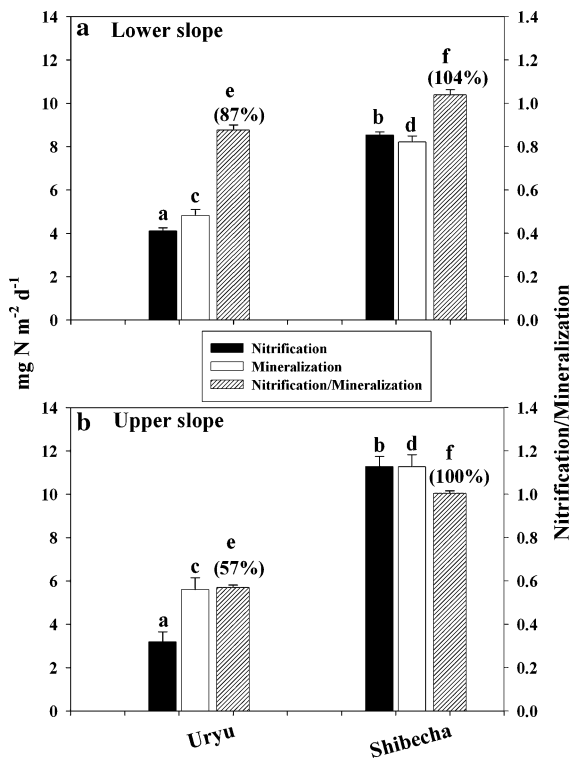
Fig. 7 Mean net nitrification and N mineralization (mg N m^{-2} d^{-1}, left axis) and nitrification/mineralization (right axis) (+SE of the grouped means) in the lower slopes (**a**) and upper slopes (**b**) of Uryu and Shibecha. Means are of catchment 0–5 cm mineral soil buried at 30 cm in situ + transplanted (N = 10). Letters that differ within each N soil process indicate significant differences between catchments at the 0.05 level

Comparison of N processes between frozen and non-frozen soil

The effects of soil freezing were most pronounced in Uryu soil buried in Shibecha at 0 cm and 5 cm depths (Fig. 8). For example, lower slope Uryu soil at 0 and 5 cm depths that was transferred to the lower slopes of Shibecha had significantly greater net N mineralization ($P = 0.0004$ and <0.0001, respectively) compared to lower slope Uryu soil buried in Uryu at the same depths (Fig. 8a). However, the fraction of N mineralization that resulted in nitrification was significantly lower in Uryu lower slope soil that was buried in Shibecha at 0 and 5 cm depths ($P < 0.001$ for both depths). Similarly, upper slope Uryu soil at 0 and 5 cm depths that was transferred to the upper slopes of Shibecha had greater net N mineralization ($P < 0.0001$) but a lower percentage of total minerali-

zation that was nitrified ($P < 0.0010$) compared to upper slope Uryu soil buried in Uryu at the same depths (Fig. 8b). Soil freezing effects on N soil cycling also were more prominent in soil buried at 0 cm versus soil buried deeper and was especially apparent in Uryu soil buried in Shibecha where 0 cm soil had greater net N mineralization yet a lower percentage of mineralized NH_4^+, which was subsequently nitrified, compared to soil buried at 5 and 30 cm (Table 4).

Discussion

How does forest floor and soil quality affect the response of net N mineralization and nitrification rates in Uryu versus Shibecha?

There were some differences in forest floor characteristics between the Uryu and Shibecha sites that could partly explain the overall greater rates of net nitrification and N mineralization in Shibecha versus Uryu. Higher rates of net nitrification and N mineralization also could explain the greater NO_3^- concentrations in soil extractions and the higher stream NO_3^- concentration in Shibecha versus Uryu. The forest floor C:N and lignin:N ratios (indicators of forest floor quality) were significantly higher in Uryu versus Shibecha. Differences in these ratios were likely driven by the differences in tree species composition between the two sites; the coniferous species in Uryu contributed to higher ratios of C:N and lignin:N. Many studies have suggested that deciduous species such as sugar maple (*Acer saccharum* Marsh.), eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), and white ash (*Fraxinus Americana* L.) are associated with soil having low C:N ratios while soil under species such as red oak (*Quercus rubra* L.), American beech, and various conifer species have higher C:N ratios in litter (Finzi et al. 1998; Lovett and Mitchell 2004; Lovett et al. 2004; Mitchell et al. 1992, 2003; Pastor et al. 1984). The relationship between vegetation and litter C:N ratios are likely driven by lignin:N ratios (Lovett and Mitchell 2004). Lower lignin:N ratios in soil often result in higher net carbon mineralization (Melillo et al. 1982; Pastor and Post 1986; McGee et al. 2007) that can result in lower C:N ratios. Lower C:N ratios and the associated higher N mineralization and nitrification rates result in elevated soil NO_3^-

Fig. 8 Mean net nitrification and N mineralization (mg N m^{-2} d^{-1}, left axis) and nitrification/mineralization (right axis) (+SE of the grouped means) in the lower slopes (**a**) and upper slopes (**b**) of Uryu and Shibecha at 0, 5, and 30 cm. Letters that differ among catchment burial sites (Uryu, Shibecha in Uryu, Uryu in Shibecha, and Shibecha) indicate significant differences at the 0.05 level
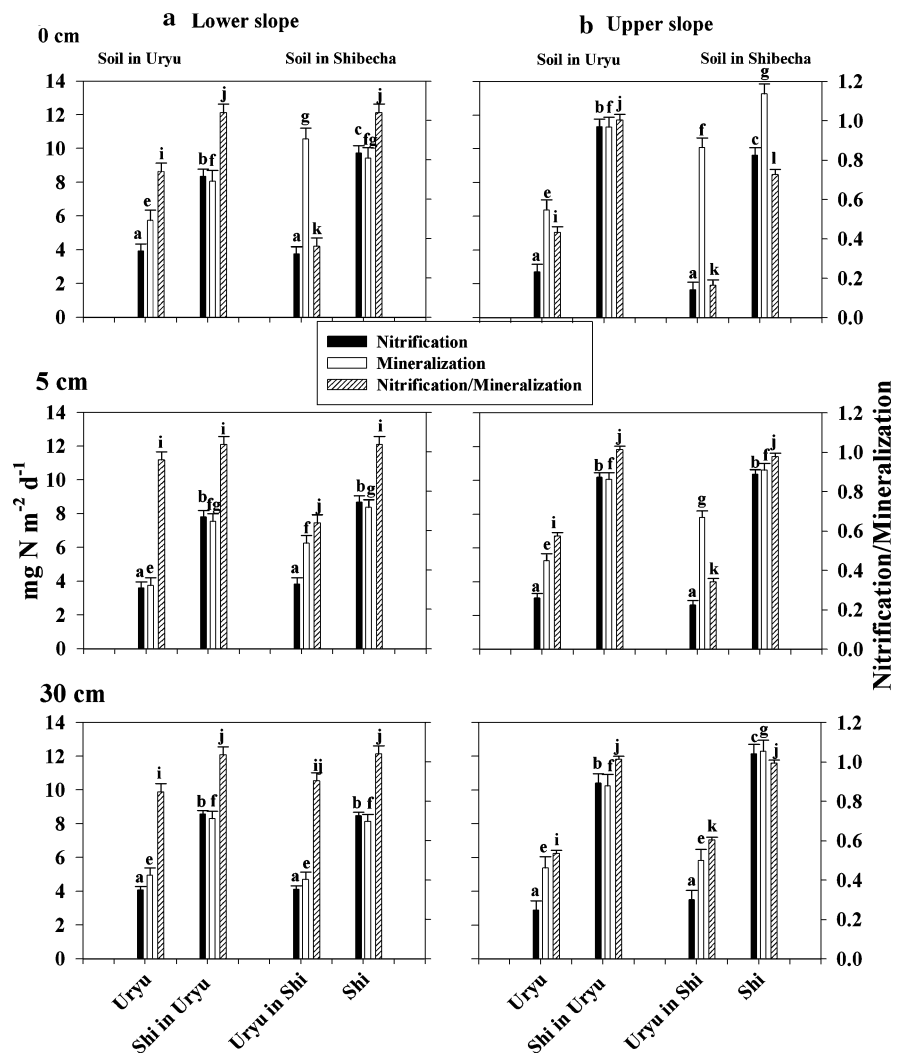
concentrations and export to surface waters (Christopher et al. 2006; Finzi et al. 1998; Gunderson et al. 1998; Lovett and Rueth 1999; Lovett et al. 2004; Melillo et al. 1982).

What is the effect of soil freezing on extractable N?

The cold period in late November/early December resulted in marked changes in soil TDN concentrations from the October to the December sampling dates, most noticeably in the upper slopes of Uryu and Shibecha. At each sampling site, there was a decrease in DON, an increase in NO_3^--N, and very little change in NH_4^+-N. Greater N mineralization likely resulted in a release of labile NH_4^+ to soil from cellular material released from death and lysis of microbial

cells (Edwards and Cresser 1992; DeLuca et al. 1992; Boutin and Robitaile 1995; Hermann and Witter 2002; Schimel and Clein 1996; Ryan et al. 2000; Neilsen et al. 2001) in these catchments that were subjected to extreme cold before a snowpack had developed. Although there were no increases in NH_4^+-N concentrations, NO_3^--N concentrations increased at both catchments possibly suggesting that decreased competition for NH_4^+-N between nitrifiers and heterotrophs and/or nitrifiers and root-mycorrhizal complexes, stimulated nitrification. In a snow manipulation experiment in Hubbard Brook, N.H., USA (Fitzhugh et al. 2001), NO_3^--N was the dominant N species in soil solution under snow-less plots containing mostly sugar maple trees (*Acer saccharum* Marsh.) and was attributed to a decreased competition

for available NH_4^+-N. Similarly, in Quebec, Canada, another snow manipulation study attributed increases in NO_3^--N concentration to lack of root uptake of NH_4^+-N thereby decreasing competition of NH_4^+-N for nitrifiers (Boutin and Robitaille 1995).

During the December and February sampling dates, TDN (including NH_4^+-N, NO_3^--N, and DON) remained relatively unchanged. In March, there was a sudden increase in TDN at Shibecha that coincided with the melting of the snowpack and the mobilization of solutes. This is further supported by the observed increase in soil moisture in Shibecha during March (Fig. 6). Mobilization of N species during snowmelt has been shown to be an important mechanism of N export in forest catchments (Hinton et al. 1997; Creed and Band 1998; Frank et al. 2000; Inamdar et al. 2006; Mitchell et al. 1996; Piatek et al. 2005).

What is the effect of soil freezing on net N mineralization and nitrification?

Rates of net N mineralization during the entire winter incubation were different for frozen soil compared to unfrozen soil. Freezing effects were most noticeable with Uryu soil buried in 0 cm and 5 cm depths in Shibecha. Greater net N mineralization (NH_4^+ production + nitrification) was found in frozen soil compared to the same soil not subjected to freezing while the fraction of mineralized N that was nitrified was smaller in frozen compared to unfrozen soils. A laboratory study conducted with soil from the Hubbard Brook Experimental Forest in N.H. suggested that increased N mineralization in the O_a and A horizons subject to low temperatures and freezing ($-13°C$) was a result of reductions of available C following freezing in these horizons (Neilsen et al. 2001). However, N mineralization was unaffected by freezing at higher temperatures (-1 to $-4°C$) in laboratory experiments (Neilsen et al. 2001) and field experiments (Groffman et al. 2001b) at Hubbard Brook. Schimel et al. (2004) suggested that increased N mineralization in arctic soils subject to freezing at moderately low temperatures ($\sim < 0°C > -7$) was a result of C limitation occurring when microbes shift their substrate use pattern from C rich material (when soils are thawed) to using more N rich material (when soils are frozen). Schimel et al. (2004) suggested there are two possible reasons why this would

occur: (1) a relative increase in the availability of N rich substrates such as from a release from organic matter (Edwards and Cresser 1992) or release from damaged or filled roots and microbes (DeLuca et al. 1992; Brooks and Williams 1999; Larsen et al. 2002) or (2) relative decrease in the availability of C rich substrate from C rich plant detritus as soils freeze (Schimel and Mikan 2005). Schimel and Mikan (2005) also observed a shift in substrate use from detrital material toward dissolved material and recycled microbial biomass at temperature just above 0°C as microbes prepare physiologically for freezing conditions.

In our study, it is uncertain why there was a net decrease in NO_3^- production in frozen versus unfrozen soils over the study period. One possibility is that soil freezing disrupts the tight coupling between NH_4^+ production and subsequent nitrification (Pawluk 1988; Miller and Jastrow 1990). Though surviving nitrifiers were able to produce NO_3^- in soil subject to the short freezing episode observed in late November/ early December, their activity was could have been depressed when soil was subjected to prolonged freezing over the entire winter, such as in Shibecha 0 and 5 cm soil depths, compared to the same soil subjected to unfrozen (e.g., at Uryu) environments. This is consistent with other studies that have suggested prolonged freeze-thaw cycles kill portions of the microbial populations (Clein and Schimel 1995; Schimel and Clein 1996; Sulkava and Huhta 2003) such that their ability to metabolize C and N is diminished. An increase in soil NH_4^+ but no increase in NO_3^- also was observed in a mesocosm study done in Swedish arctic soils frozen to ~ -4 (Grogan et al. 2004). Another possibility why there was a net decrease in NO_3^- in frozen versus unfrozen soils over the study period could have been due to losses from denitrification. Neilson et al. (2001) suggested that the observed increase in NH_4^+ following freezing in the Hubbard Brook, N.H. soils (O_a horizon) did simulate nitrification especially since they did not observe a decrease in microbial biomass. They hypothesized that denitrification also increased such that a significant portion of the excess NO_3^- produced after freezing was denitrified rather than leached. Several researchers have suggested that the increase in N_2O flux following freezing is due to increases in denitrification rates (Nyborg et al. 1997; Kaiser et al. 1998; Röver et al. 1998).

Table 4 ANOVA results for net N nitrification, mineralization, and nitrification/mineralization in the upper (a) and lower (b) slopes of Uryu and Shibecha at 0, 5, and 30 cm

| | Buried in Uryu | | | | | | Buried in Shibecha | | | | | |
| | Uryu | | | Shibecha in Uryu | | | Uryu in Shibecha | | | Shibecha | | |
Depth	N	M	N/M	N	M	N/M	N	M	N/M	N	M	N/M
(a) Lower slope												
0	a	a	a	a	a	a	a	a	a	a	a	a
5	a	b	b	a	a	a	a	b	b	a	b	a
30	a	a	ab	a	a	a	a	b	c	a	ab	a
(b) Upper slope												
0	d	d	d	d	d	d	d	d	d	d	d	d
5	d	e	e	d	d	d	d	e	e	d	e	e
30	d	de	e	d	d	d	d	f	f	e	de	e

Mean values and standard errors for each variable are given in Fig. 8. Letters that differ within a column and landscape position indicate a significant difference in depth at the α = 0.05 level

N = Nitrification, M = Mineralization, and N/M = Nitrification/Mineralization

In the current study, it is unclear why effects of soil freezing on nitrification and mineralization were more pronounced in Uryu soils both for Uryu soil buried in Shibecha (frozen) versus Uryu soil buried in situ (non-frozen) and in 0 cm Uryu soil buried in Shibecha (frozen) versus 30 cm Uryu soil buried in Shibecha (non-frozen). Shibecha soils had higher soil moisture than Uryu soils, at least in the lower slopes (Fig. 6). Soils with higher soil moisture have a higher heat capacity and therefore reduced soil thermal sensitivity. Hence, Shibecha soils were likely more buffered from the cold, resulting in less marked response in N dynamics. Similarly, in the Hubbard Brook snow manipulation study, sugar maple plots froze after yellow birch (*Betula alleghaniensis* Britt.) plots since the sugar maple soil had higher moisture content and more buffering from latent heat of fusion (Hardy et al. 2001), which partially explained the variability in N dynamics under these different tree species (Groffman et al. 2001b).

Over-winter activity and climate change

Our study raises questions concerning impacts of changes in snowpack depth and duration in affecting soil freezing and N biogeochemistry. In the current study, soil frost helped explain differences in N mineralization and nitrification rates between frozen and unfrozen soils. Our study ended before snowmelt; therefore, we did not measure N mineralization and

nitrification rates during spring/summer. We were unable to observe any changes in the net nitrification rate in soils after the over-winter period. For the snow removal experiment at Hubbard Brook (Groffman et al. 2001b) the researchers suggested that increased fine-root mortality reducing plant N uptake did not result in immediate increases in stream water NO_3^-, but rather the effect was observed later in the summer. Similarly, the snow manipulation experiment in Quebec, Canada did not observe increase in NO_3^- after plots were subjected to deep frost until the summer (Boutin and Robitaille 1995). Further evaluation of N mineralization and nitrification rates as well as soil extractable NO_3^- is needed throughout the entire year at Uryu and Shibecha.

Conclusions

There were marked differences in soil net N mineralization and nitrification rates between the M3 catchment in Uryu and the SN catchment in Shibecha. Shibecha had much greater net N mineralization, net nitrification, and stream water NO_3^- versus Uryu soil, partially a function of differences in tree species composition. A marked drop in temperature in late November/early December resulted in unchanged extractable NH_4^+ yet higher extractable NO_3^-. Prolonged soil freezing over the entire winter resulted in greater net N mineralization yet lower net nitrification.

Although this study was only conducted during winter, it raises important questions about the effect of climate change on N biogeochemistry. Soil freezing in temperate forested systems is likely to become more common if snowpacks develop later and melts occur earlier as predicted to occur as the climate warms. Several studies conducted to evaluate the effect of freezing on microbial communities and N cycling have been done in arctic and alpine soils (Brooks et al. 1997, 1998; Larsen et al. 2002; Sulkava and Huhta 2003; Grogan et al. 2004; Schimel et al. 2004; Schimel and Mikan 2005), in mostly mesocosm experiments and few in temperate soils where freezing is less severe (Groffman et al. 1999; 2001b; Neilsen et al. 2001). The effect of soil freezing should be considered when evaluating differences in N dynamics between temperate ecosystems that have different propensity for soil freezing. Furthermore, it will be important to evaluate changes in snowpack depth especially in sites such as Uryu, where soils rarely freeze, but have the potential for large changes in snowpack regimes resulting in soil freezing and marked alteration of over-winter biogeochemistry processes.

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