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Contribution of winter processes to soil nitrogen flux in taiga forest ecosystems

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Abstract We measured annual net nitrogen (N) mineralization, nitrification, and amino acid production in situ across a primary successional sequence in interior Alaska, USA. Net N mineralization per gram dry soil increased across the successional sequence, but with a sharp decline in the oldest stage (black spruce). Net N mineralization expressed per gram soil organic matter exhibited the opposite pattern, suggesting that soil organic matter quality decreases significantly across succession. Net N mineralization rates during the growing season from green-up (early May) through freeze-up (late September–early October) accounted for approximately 60% of the annual inorganic N flux, whereas the remaining N was released during the apparent dormant season. Nitrogen release during winter occurred primarily during October–January with only negligible N mineralization during early spring in stands of willow, alder, balsam poplar and white spruce. By contrast, black spruce stands exhibited substantial mineralization after snow melt during early spring. The high rates of N mineralization in late autumn through early winter coincide with high turnover of fine root biomass in these stands, suggesting that labile substrate production, rather than temperature, is a major controlling factor over N release in these ecosystems. We suggest that the convention of restricting measurements of soil processes to the growing season greatly underestimate annual flux rates of inorganic nitrogen in these high-latitude ecosystems.

Keywords Alaska · Biogeochemistry · Boreal forests · Nitrogen mineralization · Nitrogen cycling · Subarctic ecosystems

Introduction

Terrestrial ecological investigations dealing with plant and soil processes in high-latitude environments have largely been conducted during the summer months, under the reasonable assumption that low temperatures (near, at, or below 0°C) severely curtail the enzymatic machinery driving photosynthesis, soil nitrogen mineralization and other biochemical processes. However, the progression of freeze-up during autumn can be a prolonged affair, even in arctic and sub-arctic systems. High soil moisture, and thus increased soil heat capacity, coupled with an increasingly insulating snow cover often leaves the top 10 cm of the soil, where most of the biological activity is

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concentrated, unfrozen for many weeks after "freeze-up" has occurred.

Reports of high efflux of decomposition products such as CO_2 and CH_4 during winter (Brooks et al. 1996; Zimov et al. 1996) strongly suggest that microbes can sustain significant activity during this "dormant" period (Schadt et al. 2003). In high-latitude ecosystems, such as taiga forests, the transitional seasons (late fall–early winter and late winter–early spring) exceed the length of the vegetation growing season. Because of the potential uncoupling of plant growth and microbial processes during these time periods, the flux of nutrients is likely to be altered among these pools resulting in nitrogen losses or intensifying the competition between plant and microbes for soil N.

Microbial activity in apparently frozen soils over winter has been inferred from measurements of soil respiration (Flanagan and Bunnell 1980; Welker et al. 2000), litter decomposition (Moore 1983; Hobbie and Chapin 1996), and N mineralization (Brooks et al. 1996; Schimel et al. 2004). Low processing rates during winter are counteracted by the long duration of this period in arctic and sub-arctic soils, resulting in the potential for substantial flux of carbon (Clein and Schimel 1995), and presumably nitrogen. Moreover, the insulating effect of early-winter snow pack keeps the soils up to 50°C warmer than the ambient air temperature and could allow for considerable microbial activity when air temperatures are far below freezing (Taylor and Jones 1990; Sommerfeld et al. 1993).

Temperature and organic matter quality have been postulated as the primary drivers of nitrogen flux in taiga forest soils (Van Cleve et al. 1981; Flanagan and Van Cleve 1983). Here we examine nitrogen dynamics across a primary successional sequence on the Tanana River floodplain, interior Alaska. The successional sequence represents an approximately 350-year chronosequence (Viereck et al. 1993) that spans deciduous vegetation on newly formed alluvium to coniferous forests with well developed organic soils. We hypothesized that N mineralization would be inversely related to successional age due to warmer temperatures and higher organic matter quality of early successional soils compared to soils of coniferous forest types in the latter part of succession. Further, we hypothesized that the extremely low ambient temperatures during winter coupled with light snowfall typical of interior Alaska, would render the soils too cold for any significant microbial activity after senescence in the autumn until snowmelt the following spring. However, if mineralization of soil N occurred during winter, we expected it to happen primarily during the transitional seasons; in late autumn when soils are still unfrozen and the soil microbes still active, but the plants are largely dormant. This could also occur in deeper soil horizons during early spring under the same prevailing soil–plant–microbe conditions.

Methods

Study sites

We conducted the study at the Bonanza Creek Taiga Long Term Ecological Research (LTER) sites approximately 20 km SW of Fairbanks, Alaska (65°45′ N, 148°15′ W). These sites comprise a primary successional sequence along the Tanana River that includes five stages of floodplain forest succession (Willow, Alder, Balsam Poplar, White Spruce, and Black Spruce). Each successional stage is replicated three times and each replicate is separated by up to several km.

The general pattern of primary succession starts on newly formed silt bars that are colonized by light-seeded willows, particularly *Salix interior*, as well as horsetail (*Equisetum* sp.) and herbs such as *Hedysarum alpinum* and *Castilleja caudata* (Viereck et al. 1993). Thin-leaf alder (*Alnus tenuifolia*) typically dominates the site after 10–20 years and is associated with large changes in soil chemistry and primary productivity (Viereck et al. 1993; Kielland et al. 1997). Balsam poplar (*Populus balsamifera*) forests predominate 60–100 years following initial colonization, and after approximately 200 years the forest is an even-aged stand of white spruce (*Picea glauca*). Depending on the fire regime and other disturbances such as channel avulsion into peat lands adjacent to the river, black spruce (*Picea mariana*) forests predominate after approximately 300–500 years (Mann et al. 1995).

The climate is strongly continental, and the area lies within a rain shadow created by the Alaska Range approximately 100 km to the south. Temperature extremes range from – 50°C in winter to >+ 30°C during the summer with an annual average of –3.3°C. Average annual precipitation is 269 mm, 37% of which falls as snow. Snow covers the ground 6–7 months of the year. Maximum snow depth is generally less than 60 cm (National Resource Conservation Service Alaska Snow Programs, http://www.ambcs.org/pub/sc_sum_ak/SNOWCOURSE.HTM). Soil temper atures during our study were obtained from the Bonanza Creek LTER data base. Surface temperatures refer to the surface of the alluvium in early successional soils and the surface of litter or moss layer in mid to late successional soils. Complete site descriptions regarding climate, vegetation, and soils can be found at the web site for the Bonanza Creek LTER Program: http://www.lter.uaf.edu/.

Sampling methods

Nitrogen mineralization measurements were carried out employing the buried bag method (Robertson et al. 1999) using gas-permeable polyethylene bags (Gordon et al. 1987). Soils were sampled to a depth of 10 cm (below live moss and recent litter fall) with a 6 cm diameter stainless steel corer at six random intervals along randomly oriented 50 m transects in each stand type. Six intact soil cores per stand replicate per time period were incubated sequentially for 30 days between approximately 1 June and 1 October, 2001. On 10 October we started winter incubations using the same number of stand * site replicates. The concentrations of free amino acid-N, ammonium, and nitrate at this date were used as time zero values for measuring net amino acid production and net N mineralization through mid-winter (January) and spring (May). To estimate the relative importance of early versus late winter processes, we retrieved half the samples ($n = 45$) on 25 January 2002 (when air temperature was –38°C), and the remaining samples 1 week after breakup on 19 May 2002. (Logistic constraints pertaining to travel by river boat to our field sites during ice-out prevented us from retrieving the soil cores during snowmelt).

Laboratory methods

In the laboratory individual soil cores were manually homogenized, and any coarse debris (>1 mm) and stones were removed. Sub-samples were saved for moisture determinations, after which 10 g fresh weight soil were extracted with 75 ml 0.5 M K_2SO_4 over-night, filtered under vacuum through 50-mm glass fiber filters (Gelman Laboratory A/E Glass Fiber Filters), and frozen for later analysis. Filtered extracts were analyzed for NH_4^+ using a phenol hypochlorite assay and for NO_3^- using the Griess-Illosway procedure in combination with a Cadmium-reduction column on a modified Technicon autoanalyzer II (Whitledge et al. 1981). Mineralization and nitrification rates were calculated as the change in inorganic N (NH_4^+ + NO_3^-) and changes in nitrate concentration, respectively, over the incubation period (Robertson et al. 1999). Site-specific soil/air temperatures and snow fall data were obtained from the Bonanza Creek LTER data base (http://www.lter.uaf.edu/).

Amino acid analysis

Soil samples were extracted and vacuum filtered using Type A/E glass fiber filters as explained above. Samples were refrigerated at 4°C and analyzed the next day for total amino acid concentrations using a modified ninhydrin reaction (Rosen 1957; Moore 1968). Absorbance at 570 nm was measured on a Perkin-Elmer UV/Vis Lambda 25 spectrometer. Amino acid concentrations were determined by comparison to a leucine standard analyzed at the same time. After subtraction of T_0 values net amino acid production rates were determined per gram soil dry weight.

Statistical analyses

Data were analyzed using a nested analysis of variance by the GLM procedure in the Statistical Analysis System (SAS Systems 1998; SAS Institute, Gary, NC, USA), with successional stage and date as fixed effects. Tukey's test was used to examine treatment means after performing the ANOVA.

Results

Snow depth and temperature

Snow depth increased fairly steadily over the winter at an average rate of approximately 5 cm per month reaching a maximum (33 cm) in late February through mid-April and declining thereafter (Fig. 1). The sites were completely snow-free on 10 May 2002.

Air temperatures (1.5 m above ground) did not differ greatly among successional stages throughout the year (Fig. 2a), despite substantial differences in canopy characteristics and stand density (Viereck et al. 1993). However, seasonal soil surface (ground) temperature patterns differed markedly across successional stages. Black spruce stands exhibited the highest surface (top of the moss layer) temperatures during summer, but were coldest in the winter (Fig. 2b). By contrast, surface temperatures in the willow stages (top of mineral soil) were coolest from May through mid-July, but warmest during the winter compared with the other successional stands. We also found surprising dissimilarities in soil temperatures (5 cm depth) across the successional sequence. Willow stands were comparatively the warmest during both winter and summer (Fig. 2c). Moreover, soil temperatures increased faster as summer progressed in the early successional stands (Willow and Alder), than in later successional stands. With the exception of willow, all soils reached their maximum temperatures in mid-August. General soil characeristics are presented in Table 1.

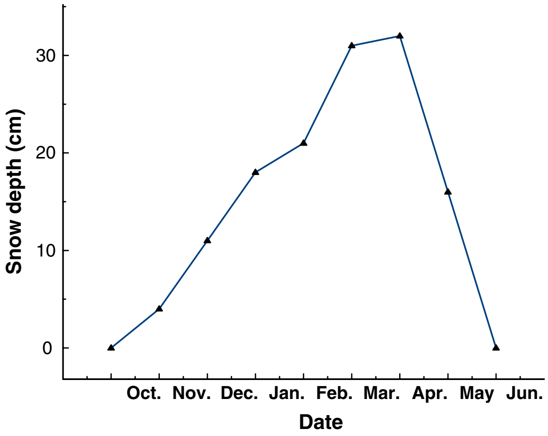


Fig. 1 Snow depth at the main Bonanza Creek LTER site weather station during the winter of this study (http://www.lter.uaf.edu/)

Growing season N dynamics

Rates of net nitrogen mineralization during the growing season (June–September) varied substantially across the successional sequence ($F_{4,11} = 6.45$, $P = 0.0068$), with the stage effect explaining about 34% of the variance. We also observed high fluctuations across the season within stands ($F_{3,11} = 8.73$, $P < 0.001$), which explained about 20% of the variation. The highest rates of N mineralization (μg g^{-1}) were found in balsam poplar and white spruce soils, and the lowest in soils from the willow stands (Fig. 3a). The seasonal pattern of net N mineralization tended to be highest early in the season (June) and lowest in the autumn (September). Post hoc multiple comparisons testing (Tukey's test) showed that cumulative net N mineralization was lowest in willow stands and highest in Balsam Poplar and White spruce stands. Alder and Black spruce were intermediate; higher than Willow, but not significantly different from one another.

Table 1 Selected physical and chemical parameters of soils across a primary successional sequence on the Tanana River floodplain. The temperature sum (Σ°C) refers to soil temperatures at 10-cm depth during the growing season 2001 (June–September), and gravimetric moisture content (θ_g) the average season value over the same time period (Mean ± S.E., $n = 15$)

Soil parameter	Willow	Alder	Balsam poplar	White spruce	Black spruce
Carbon (%)	1.5 (0.1)	2.6 (0.4)	6.9 (1.3)	10.5 (1.2)	25.5 (2.4)
Nitrogen (%)	0.07 (0.0)	0.14 (0.0)	0.39 (0.1)	0.43 (0.1)	0.85 (0.1)
% H_2O (θ_g)	47.1(1.3)	47.1 (0.3)	40.9 (0.4)	53.9 (0.2)	127.3 (0.7)
pH	8.1 (0.0)	8.2 (0.1)	6.7 (0.1)	6.1 (0.2)	5.1 (0.1)
$\Sigma°C_{soil}$	1206	841	633	664	427

Fig. 2 Seasonal temperature profiles during the period of this study for (**a**) air, (**b**) soil surface, and (**c**) at 5 cm depth of soil. Data from Bonanza Creek LTER (http://www.lter.uaf.edu/)

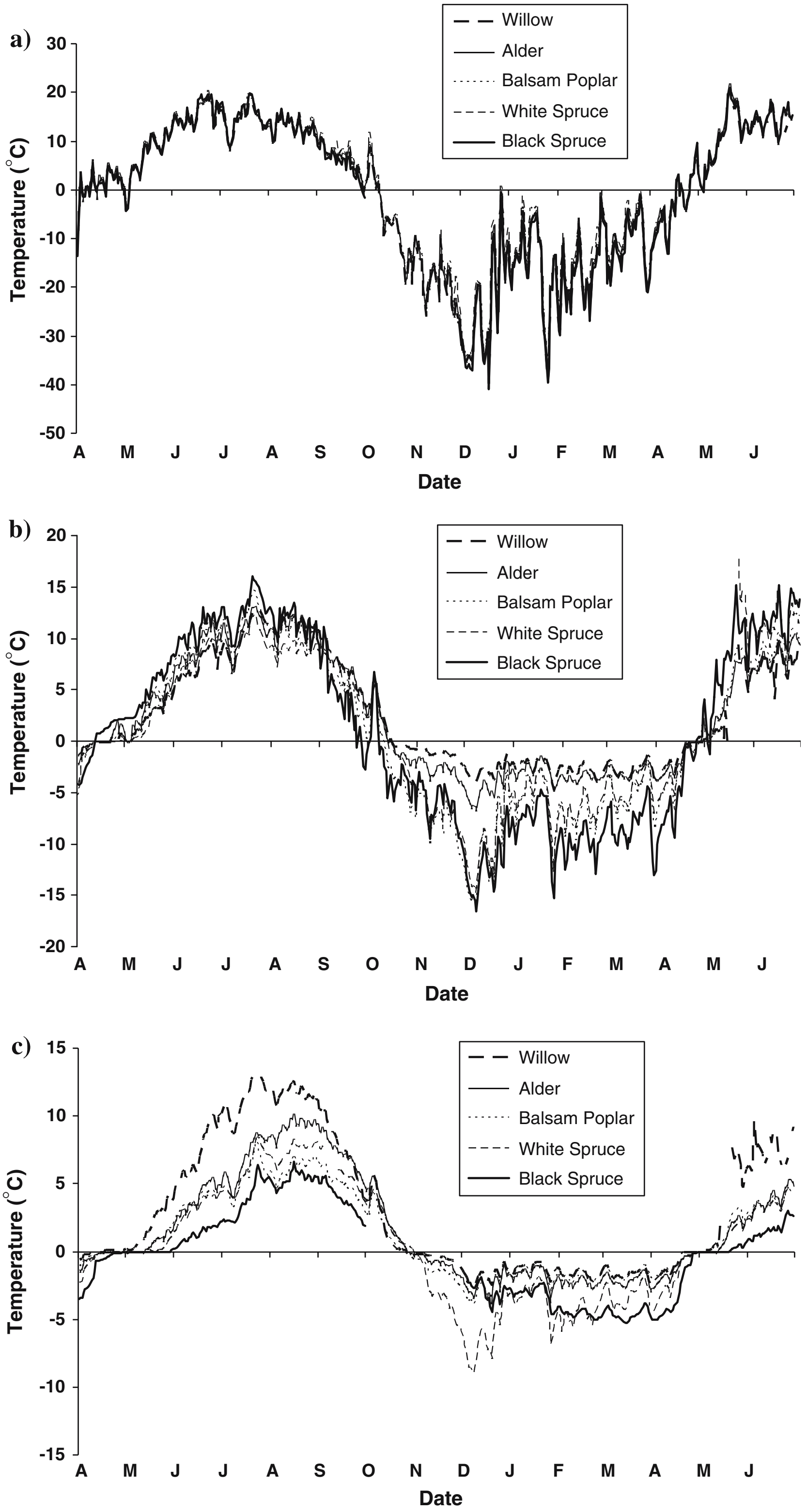
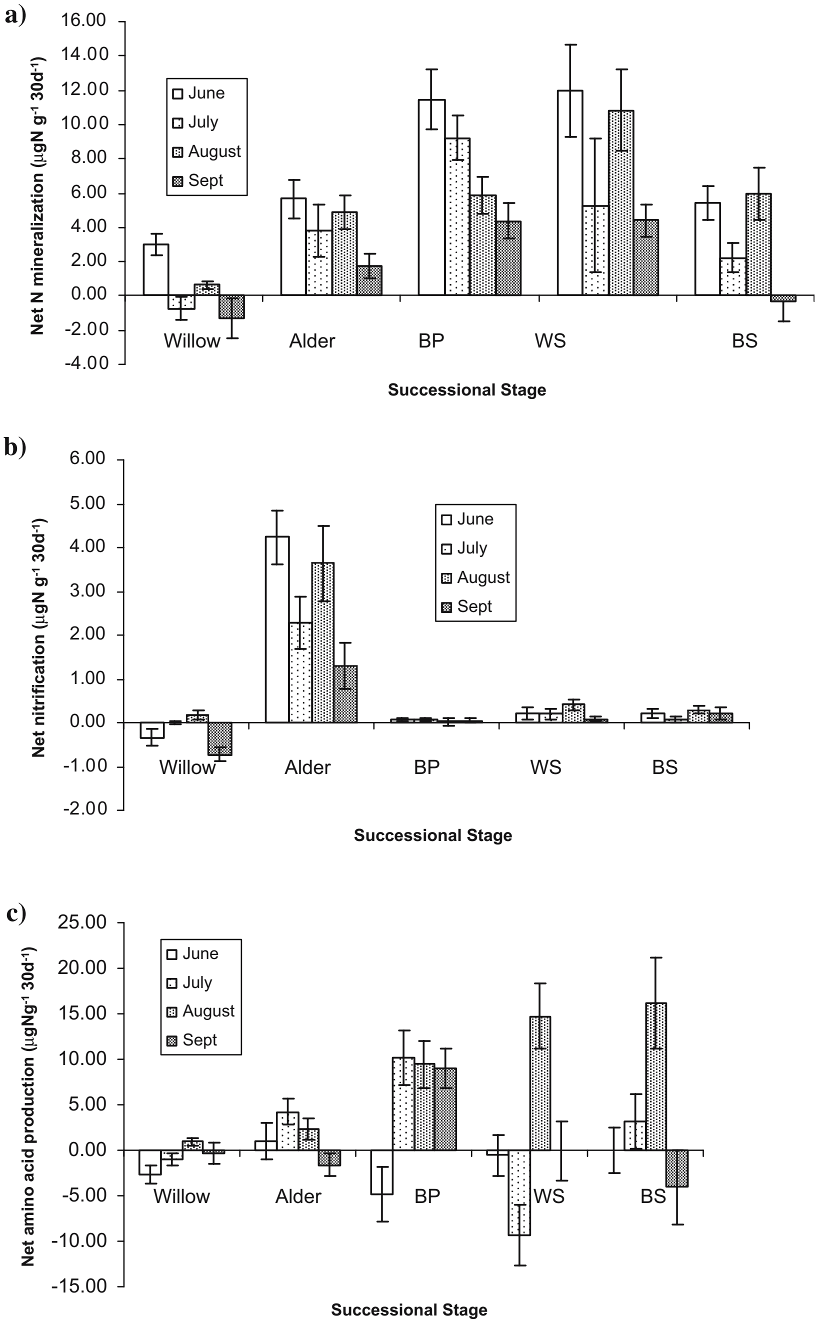


Fig. 3 Net rates of (**a**) N mineralization, (**b**) nitrification, and (**c**) amino acid production over the growing season (June–October) across a primary successional sequence on the Tanana River floodplain, interior Alaska. Mean ± S.E., $n = 3$



Rates of net nitrification during growing season were very low in all soils except in alder stands, where net nitrification represented a large fraction (approximately 80%) of net mineralization (Fig. 3b). Net amino acid production exhibited significant temporal variation within a given successional stage, as well as a considerable range among stages, as has been found in similar kinds of studies in the Arctic (Kielland 1995). Generally the seasonal pattern of net amino acid production was different from net nitrogen mineralization, i.e., relatively low rates early in the season and higher rates mid to late in the season (Fig. 3c). Maximum rates of either net amino acid production or consumption were over twice as high as net nitrogen mineralization, suggesting a weak quantitative coupling of nitrogen from organic to inorganic form when expressed as net rates.

We found no clear temporal relationships, however, among net nitrification, mineralization and amino acid production (e.g., high net amino acid production followed by high mineralization, followed by increased nitrification). Nor did we observe a simple relationship between soil temperatures and N mineralization across these successional soils. When we plotted monthly rates of net N mineralization against monthly soil temperature sums for each successional stage from June through September, some soils exhibited a weak positive relationship while others showed a negative relationship. None of the relationships were significant, however. (Coefficient of determination ranged from 0.03 to 0.22 and P values from 0.86 to 0.51).

When we examined summer time net N mineralization per growing degree day (GDD) (cumulative N mineralization over the summer divided by number of growing degree days at 10 cm soil depth, designated K_T), we found large differences across the successional soils. K_T varied from about 5.5 ng g^{-1} GDD^{-1} in Willow to 62.0 ng g^{-1} GDD^{-1} in White Spruce (Fig. 4). This 11-fold variation contrasts to the 6-fold stage variation of net N mineralization rates over the summer, and suggest that the colder, late successional soils have higher ‘‘thermal efficiency’’ for net N production.

The pattern of cumulative N mineralization over the growing season exhibited opposite patterns in relation to successional stage when expressed per unit SOM versus per gram dry soil (Fig. 5). The strong, inverse relationship between N mineralization and successional stage of the latter suggests that organic matter quality decreases across succession along with an increasing soil C:N ratio, and that this parameter exerted a stronger control over net N mineralization in the field than did temperature.

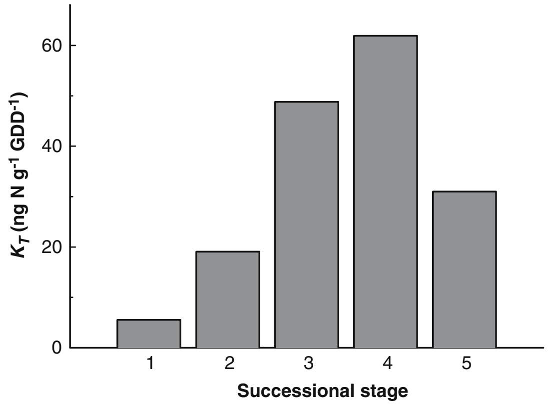


Fig. 4 Cumulative net soil nitrogen mineralization (ng N g^{-1}) per growing degree day (K_T) over the growing season across succession on the Tanana River floodplain. Stage 1 represents Willow, 2 – Alder, 3 – Balsam poplar, 4 – White spruce, and 5 – Black spruce

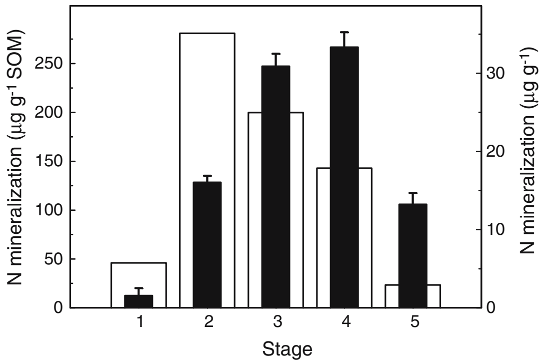


Fig. 5 Cumulative net N mineralization per gram soil dry weight (filled bars) and per gram soil organic matter – SOM (open bars) across a primary successional sequence on the Tanana River, interior Alaska. Mean ± S.E., n = 3. Stage designations as in Fig. 4

Winter N dynamics

Soils from all successional stages exhibited significant mineralization between freeze-up (October) and mid-winter (January) with approximately a doubling of the soil ammonium concentration during this time interval (Fig. 6a). Only the black spruce soils showed evidence of ammonification and nitrification in late winter to early spring (May). Net amino acid production showed a similar pattern to ammonium in early winter, but in contrast tended to decrease between January and late winter/early spring (Fig. 6c). Nitrate pools were very low and the most variable soil N parameter during winter. Soils from willow and white spruce stands exhibited positive nitrification prior to the mid-winter sampling, whereas soil from stands of alder, poplar, and particularly,

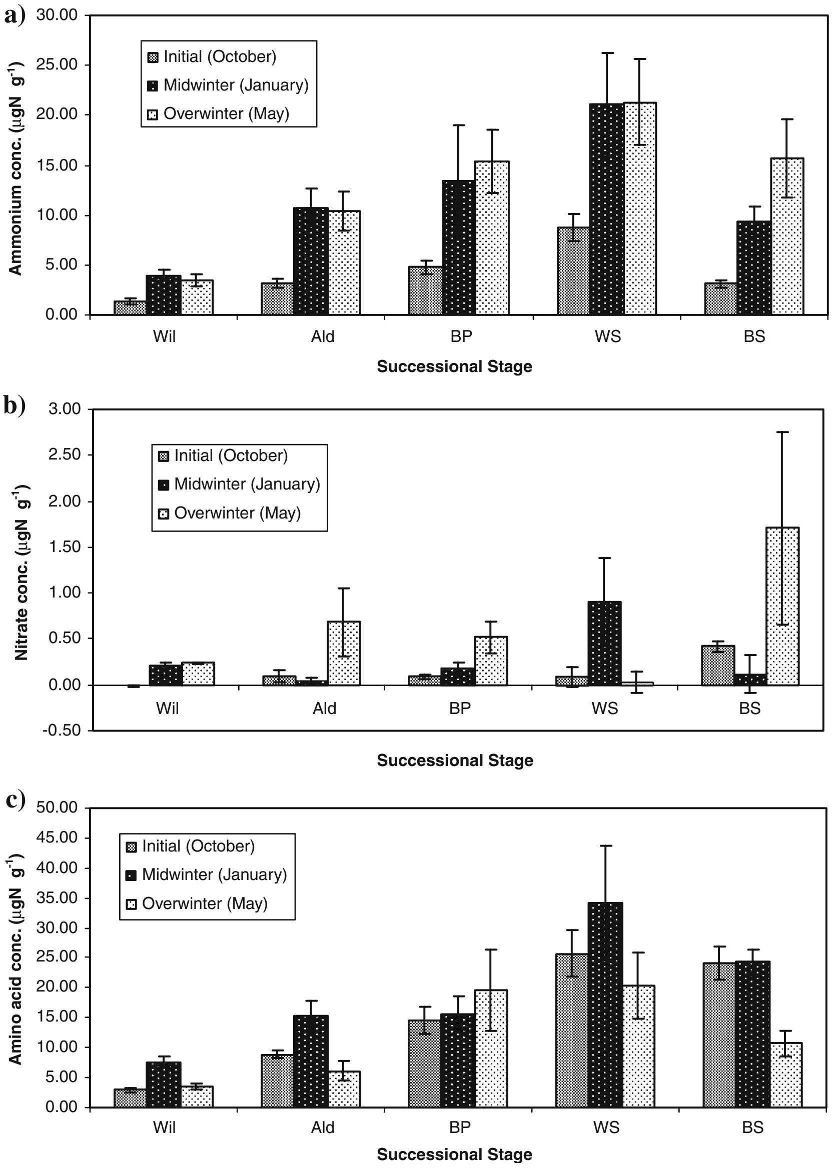


Fig. 6 Soil concentrations of (**a**) ammonium, (**b**) nitrate and (**c**) total free amino acids in over-winter incubations; initial concentrations in late autumn (October), mid-winter (January) and Spring (May). Mean ± S.E., $n = 3$

black spruce exhibited significant nitrification in the spring (Fig. 6b). The importance of cumulative N mineralization during winter varied significantly ($F = 2.48$, $DF = 44$, $P = 0.03$) across successional stands. Soils from alder, balsam poplar and white spruce all mineralized less than half as much nitrogen during winter as during summer. By contrast, in willow and black spruce stands cumulative N mineralization was divided approximately evenly between these periods (Fig. 7). Thus, the contribution of winter-time N mineralization (freeze-up through spring) to the annual inorganic nitrogen flux varied from approximately 30% in white spruce to over 50% in willow and black spruce. The average (across ecosystems) contribution of cumulative N mineralization in winter to the total annual flux (mg N m^{-2} $year^{-1}$) was approximately 41%, underscoring the importance of winter processes in controlling this ecological parameter (Fig. 7).

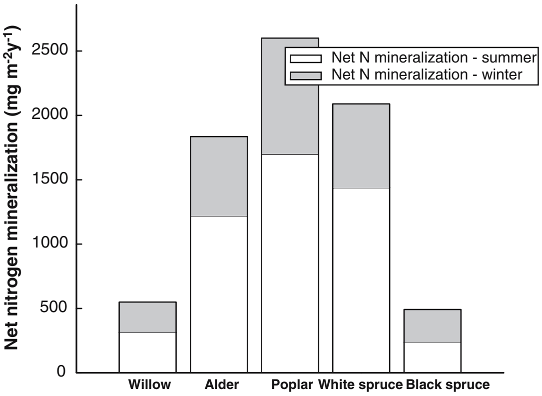


Fig. 7 Annual net flux of inorganic nitrogen (mg N m^{-2}) across the Tanana River successional sequence depicting the contribution of N flux during winter

Discussion

The present data set represents the first measurements of net mineralization, nitrification, and net amino acid production for the entire primary successional sequence on the Tanana River, and the net flux rates of inorganic N estimated here were very similar to those obtained previously during the growing season for selected stages such as willow, balsam poplar, and white spruce (Van Cleve et al. 1993), and annual fluxes (including over-winter) in balsam poplar and white spruce (Brenner et al. 2005). Net N mineralization from the most productive stands in these forests (balsam poplar and white spruce) are nevertheless much lower (approximately 3–5 ×) than rates obtained in temperate forests (e.g., Groffman et al. 2001), but much higher than those reported from subarctic sites in northern Sweden (Schmidt et al. 1999). Our results pertaining to net nitrification suggest that these soils are strongly ammonium dominated, though we recognize that measurements of gross nitrification might have yielded a different interpretation (cf. Stark and Hart 1997).

Our results demonstrate that taiga forest soils have a substantial capacity for net nitrogen production during winter, a time of presumed biological inactivity. The rates of net N mineralization during winter were substantially greater in soils where the annual N flux is very low as has been observed in other subarctic ecosystems (Schmidt et al. 1999). Under-snow microbial metabolism may represent an important sink for nitrogen, but during winter the apparent gross N release exceeded microbial nitrogen demand. The accumulation of mineralized N during winter may be used by plants and microbes during the transitional seasons if soil temperatures remain close to 0°C (Andresen and Michelsen 2005), or be lost from the system through denitrification, leaching, and runoff. The recent observation that some taiga ecosystems appear to lose more nitrogen than is produced during the growing season (Jones et al. 2005), may in part be explained by these winter processes.

We also show that temporal differences in net N mineralization and nitrification within successional stands were nearly as great as inter-stand differences averaged across time periods, suggesting that the large differences in soil temperatures among stand types did not translate into proportional differences in nitrogen flux. Rates of N mineralization increased across the successional sequence both during summer and over winter, with the exception of black spruce. This low response to temperature is consistent with other studies of arctic and sub-arctic soils in both the field (e.g., Giblin et al. 1991; Van Cleve et al. 1993) and the laboratory (e.g., Marion and Miller 1982; Klingensmith and Van Cleve 1993), but some important exceptions to this pattern have also been observed (Nadelhoffer et al. 1991). The apparent differences in K_T (“thermal efficiency”) among early and late successional soils are somewhat analogous to the kind of temperature compensation observed for other physiological systems (Chapin 1974). Because oscillations in soil temperatures are dampened in late-successional, moist organic soils, the resident microbial communities may be more sensitive to small physical changes than microbial populations occupying warmer, drier, early-successional soils. Moreover, this response of net N mineralization to temperature could be related to increased Q_{10} of soil respiration in colder soils (Kirschbaum 2004).

Differences in ground temperature profiles among successional stands are likely a consequence of how each ecosystem type partitions incoming solar radiation. The open willow stands have a higher albedo, as well as a thin boundary layer contributing to the cool temperatures of the soil surface early in the season. By mid-season these sites are covered by growth of horsetails (*Equisetum* sp.) which lowers the albedo and increases the boundary layer, thus increasing surface temperatures. By contrast, the black spruce stands have lower albedo than broadleaved deciduous vegetation (Baldocchi et al. 2000) and thicker boundary layer due to higher stem density and canopy height. Interestingly, the forest stands (Black Spruce) with the lowest thawing degree days (Σ°C > 0° at –20 cm) had the highest soil surface temperatures from June through mid-August.

Nitrification rates over winter exhibited the same low and variable patterns that we observed during the growing season. However, three successional stages (Alder, Balsam Poplar, and Black Spruce) showed a spike in nitrate concentrations from mid-winter (January) to spring (May), suggesting increased nitrifier activity despite no apparent change in net ammonification during this time period of increased soil temperatures. By contrast, net amino acid production was negative in all forest stands between sampling in mid-winter and spring. With the exception of black spruce soils, amino acid concentrations in spring returned to the approximate values exhibited during the previous autumn (October).

Our finding that time of the year explains almost as much of the variation in nitrogen mineralization as did successional stage suggests that physical and biological drivers of this ecological process may be temporally coupled across succession. We surmise there is a flush of net N mineralization in spring due to soil thaw, followed by a decline in net N release as plants start competing with soil microbes in early May–June. The second flush of net N release in August we ascribe principally to root mortality, an event that appears to be fairly synchronous across successional stages (Ruess et al. 2003). Nearly all carbon allocated to fine roots turns over within a year (Ruess et al. 2003), and a large proportion of root mortality occurs at the end of the growing season. This input of nitrogen from decaying roots alone ([root mortality * root nitrogen concentration]; Ruess et al. 2003) can account for the entire nitrogen flux during the growing season. For example, in black spruce stands on the Tanana River floodplain, fine root mortality during the month of August (averaged over 2 years) equates to a flux of 0.80 g N m^{-2}. The fate of this fine root N is of course unknown. However, we believe it is a relatively labile pool, given the fact that during the growing season, fine roots in these stands decompose in approximately 50 days (Ruess et al. 2003). Further, we suggest that the possible effects of low soil temperatures on net nitrogen mineralization during early winter are in part offset by the large input of readily mineralizable substrate during late autumn. Thus, in addition to leaf litter fall, these taiga soils experience a large flush of energy and nutrients derived from rapidly decaying fine roots at the end of the growing season. The final decline in net N mineralization during September we attribute to reduced soil temperatures.

We suggest that winter-time biogeochemical processes represent a significant component of annual N flux in taiga forests. Our average estimate placing winter-time net N mineralization as approximately 40% of the annual flux is much higher than similar estimates (≈15%) from temperate forests (calculated from Groffman et al. 2001). Even though air temperatures in taiga forests during winter typically reach below – 40°C, the modulating thermal effect of an early snow pack coupled to unfrozen water in the soil, despite negative soil temperatures, allow microbial activity to continue during this presumed dormant season.

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References

Andresen L, Michelsen A (2005) Off-season uptake of nitrogen in temperate heath vegetation. Oecologia 155:585–597

Baldocchi D, Finnigan J, Wilson K, Paw UKT, Falge E (2000) On measuring net ecosystem carbon exchange over tall vegetation on complex terrain. Boundary-Layer Meteorol 96:257–291

Brenner RE, Boone RD, Ruess RW (2005) Nitrogen additions to pristine, high-latitude, forest ecosystems: consequences for soil nitrogen transformations and retention in mid and late succession. Biogeochemistry 72:257–282

Brooks PD, Williams MW, Schmidt SK (1996) Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. Biogeochemistry 32:93–113

Chapin FS III (1974) Morphological and physiological mechanisms of temperature compensation in phosphate absorption along a latitudinal gradient. Ecology 55:1180–1198

Clein JS, Schimel JP (1995) Microbial activity of tundra and taiga soils at sub-zero temperatures. Soil Biol Biochem 27:1231–1234

Flanagan PW, Bunnell FL (1980) Microfloral activities and decomposition. In: Brown J, Miller PC, Tiezen LL, Bunnell FL (eds) An Arctic ecosystem: the coastal Tundra of Barrow, Alaska. Van Norstrand Reinhold, New York, pp 291–334

Flanagan PW, Van Cleve K (1983) Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Can J Forest Res 13:795–817

Giblin AE, Nadelhoffer KJ, Shaver GR, Laundre JA, McKerrow AJ (1991) Biogeochemical diversity along a riverside toposequence in arctic Alaska. Ecol Monogr 61:415–435

Gordon AM, Tallas M, Van Cleve K (1987) Soil incubations in polyethelene bags: effect of bag thickness and temperature on nitrogen transformations and CO2 permeability. Can J Soil Sci 67:65–75

Groffman PM, Driscoll CT, Fahey TJ, Hardy JP, Fitzhugh RD, Tierney GL (2001) Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest. Biogeochemistry 56:191–213

Hobbie SE, Chapin FS III (1996) Winter regulation of tundra litter carbon and nitrogen dynamics. Biogeochemistry 35:327–338

Jones JB Jr, Petrone KC, Finlay JC, Hinzman LD, Bolton WR (2005) Nitrogen loss from watersheds of interior Alaska underlain with discontinuous permafrost. Geophys Res Lett 32:L02401

Kielland K (1995) Landscape patterns of free amino acids in arctic tundra soils. Biogeochemistry 31:85–98

Kielland K, Bryant JP, Ruess RW (1997) Moose herbivory and carbon turnover of early successional stands in interior Alaska. Oikos 80:25–30

Kirschbaum MU (2004) Soil respiration under prolonged soil warming: are rate reduction caused by acclimation or substrate loss? Global Change Biol 10:1870–1877

Klingensmith KM, Van Cleve K (1993) Denitrification and nitrogen fixation in floodplain successional soils along the Tanana River, interior Alaska. Can J Forest Res 23:956–963

Mann DH, Fastie CL, Bigelow NH (1995) Spruce succession, disturbance and geomorphology on the Tanana River floodplain, Alaska. Ecoscience 2:184–199

Marion GM, Miller PC (1982) Nitrogen mineralizationin a tussock tundra soil. Arctic Alpine Res 14:287–293

Moore S (1968) Amino acid analysis: aqueous dimethyl sulfoxide as solvent for the ninhydrin reaction. J Biol Chem 243:6281–6283

Moore TR (1983) Winter-time litter decomposition in a subarctic woodland. Arctic Alpine Res 15:413–418

Nadelhoffer KJ, Giblin AE, Shaver GR, Laundre JA (1991) Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology 72:242–253

Robertson GP, Wedin DA, Groffman PM, Blair JM, Halland EA, Nadelhoffer KJ, Harris D (1999) Soil carbon and nitrogen availability: nitrogen mineralization, nitrification, and soil respiration potentials. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P (eds) Standard soil methods for long-term ecological research. Oxford University Press, New York, pp 258–271

Rosen H (1957) A modified ninhydrin colorimetric analysis for amino acids. Arch Biochem Biophys 67:10–15

Ruess RW, Hendrick RL, Burton AJ, Pregitzer KS, Sveinbjörnsson B, Allen MF, Maurer G (2003) Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol Monog 74:643–662

Schadt CW, Martin AP, Lipson DA, Schmidt SK (2003) Seasonal dynamics of priviously unknown fungal lineages. Science 301:1359–1361

Schimel JP, Bilbrough C, Welker JM (2004) Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. Soil Biol Biochem 36:217–227

Schmidt IK, Jonasson S, Michelsen A (1999) Mineralization and microbial immobilization of N and P in arctic soils in relation to season, temperature and nutrient amendment. Appl Soil Ecol 11:147–160

Sommerfeld RA, Mosier AR, Musselman RC (1993) CO_2, CH_4, and N_2O flux through a Wyoming snowpack and implications for global budgets. Nature 361:140–142

Stark JM, Hart SC (1997) High rates of nitrification and nitrate turnover in undisturbed coniferous forests. Nature 385:61–64

Taylor BR, Jones HG (1990) Litter decomposition under snow cover in balsam fir forest. Can J Bot 68:112–120

Van Cleve K, Barney R, Schlentner RE (1981) Evidence of temperature control of production and nutrient cycling in two interior Alaska black spruce ecosystems. Can J Forest Res 11:258–273

Van Cleve K, Viereck LA, Marion GM (1993) Introduction and overview of a study dealing with the role of salt-affected soils in primary succession on the Tanana River floodplain, interior Alaska. Can J Forest Res 23:879–888

Viereck LA, Dyrness CT, Foote MJ (1993) An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. Can J Forest Res 23:889–898

Welker JM, Fahnestock JT, Jones MH (2000) Annual CO2 flux in dry and moist arctic tundra: field responses to increases in summer temperatures and winter snow depth. Clim Change 44:139–150

Whitledge TE, Mallow SC, Patton CJ, Wirick CD (1981) Automated nutrient analysis in seawater. Technical Report Ocean Science Division, Brookhaven National Laboratory, Upton, NewYork, USA

Zimov SA, Davidov SP, Voropaev YV, Prosiannikov SF, Semiletov IP, Chapin MC, Chapin FS, III (1996) Siberian CO_2 efflux in winter as a CO_2 source and cause of seasonality in atmospheric CO_2. Clim Change 33:111–120