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Nitrogen additions to pristine, high-latitude, forest ecosystems: consequences for soil nitrogen transformations and retention in mid and late succession

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Abstract. We hypothesized that differences in microbial and plant N demand in balsam poplar and white spruce stands would control *in situ* net N transformation and retention following N additions. Throughout the study, N fertilizer (NH_4NO_3) was added in three increments during the growing season, giving an annual N addition of 100 kg ha^{-1} yr^{-1}. In balsam poplar, fertilization induced a large (~285%) increase in annual net nitrification but tended to reduce net ammonification. In white spruce, fertilization generally stimulated net N mineralization (via higher net ammonification) while net nitrification increased only slightly or remained unchanged. For 0–20 cm soil cores of both stand types, fertilization rapidly increased extractable DIN pools; however, the absolute amount of this increase was significantly larger in white spruce than in balsam poplar. In both stands, extractable NO_3^-–N in 20–30 cm mineral cores increased within the first year following N additions, indicating that leaching of NO_3^-–N was fairly rapid. Fertilization did not significantly alter microbial biomass N or C. After four years of fertilizer additions there were slight but insignificant changes in fine-root C:N and % N. The immediate alteration of N transformation rates and extractable DIN pools, notably the higher NO_3^-–N at the 20–30 cm depth, may indicate that this ecosystem is sensitive to atmospheric N deposition. However, we also theorize that plants and microbes in this ecosystem, in which the extractable DIN pool is dominated by NH_4^+(NH_4^+–N: NO_3^-–N = 18–30), might be poorly adapted or physiologically unable to assimilate significant quantities of NO_3^-.

Introduction

Prompted by concern for the large increase in human-derived nitrogen (N) inputs into terrestrial ecosystems during the past several decades (Galloway et al. 1995; Vitousek et al. 1997; Asman et al. 1998; Fowler et al. 1998; Mosier et al. 2001), a number of studies in recent years have examined the consequences of experimental N additions to soil nutrient and carbon (C) cycling in temperate and boreal forest ecosystems (Aber et al. 1998; Wright and Rasmussen 1998). These experiments have provided insights into factors

regulating nutrient cycling and retention in forest soils and have helped increase our knowledge of the consequences of human-alterations to the global N and C cycles. These studies have shown that forest soils often respond to such additions with increased leaching of nitrate (Tietema et al. 1997; de Schrijver et al. 2000) and base cations (Adams et al. 2000; Hruska et al. 2001), soil acidification (Fenn et al. 1998; Bergholm and Majdi 2001), and increases in N transformation rates, notably net nitrification (Aber et al. 1995; Gundersen et al. 1998; Tietema 1998; Andersson et al. 2001).

Nearly all studies which have simulated N deposition in temperate and subarctic forest ecosystems, or which have examined increasing ambient N deposition, have taken place in the northeastern US and Europe where the deposition of N, sulfur and acid rain have been substantial for several decades and also where humans otherwise have altered the landscape for centuries and sometimes longer. Thus, there is the potential that forest research sites experimentally amended with N were adversely affected by one or more anthropogenic disturbances prior to the start of the N additions (Emmett et al. 1998a). Additionally, some N-amended sites are on previously agricultural landscapes that were once fertilized with inorganic and/or manure N. Therefore, despite controls on the amounts of N applied and, to a lesser degree on land-use history (Aber and Driscoll 1997), it has not always been clear to what extent plants and soils responded to the experimental N additions alone versus those plus the combination of long-term atmospheric pollutants, prior fertilization, and land-use change.

Forests in interior Alaska are part of a pristine landscape in a region which has been minimally impacted by logging (Van Cleve and Viereck 1981) and which has very low background levels of ambient wet N deposition averaging approximately 0.21 kg N ha^{-1} yr^{-1} (NADP unpublished). This rate is similar to that reported by Perez et al. (1998) for an unpolluted temperate forest in southern Chile (0.1 kg N ha^{-1} yr^{-1}) but is substantially smaller than values reported for forests of western Europe and Scandinavia (2.6–59 kg N ha^{-1} yr^{-1}; wet + dry) (Emmett et al. 1998a; Wright and Rasmussen 1998), and the northeastern US (5–19 kg N ha^{-1} yr^{-1}; wet + dry) (Ollinger et al. 1993; Likens and Bormann 1995; Magill et al. 2000) where most experimental N-deposition studies have taken place. Low ambient N deposition and a historic lack of disturbance from pollution or land clearing make Alaska's interior forests an ideal location to investigate the consequences of N additions to soil nutrient cycling in high-latitude forest ecosystems.

In this study, we examined the influence of experimental N additions to deciduous and coniferous forest stands which represent mid and late stages of a primary successional sequence along the Tanana River floodplain in interior Alaska. Primary succession in the floodplain ecosystem is initiated by the deposition of glacially derived silt loam alluvium, on which the early succession plant communities (e.g., willow (*Salix* spp.) and thin-leaf alder (*Alnus tenuifolia*)) are established. The continued addition of mineral alluvium during flooding events builds terraces several meters above the river on which suc-

cessive plant communities develop. During early succession the N cycle is relatively open, with large amounts of soil N accretion (up to 164 kg N ha^{-1} yr^{-1}) due to N_2-fixation by thin-leaf alder (Van Cleve 1971; Klingensmith and Van Cleve 1993a). Although, N inputs into this system have been shown to rapidly enter a stable organic matter pool and are not immediately available for microbial processing (Kaye et al. 2003). Balsam poplar (*Populus balsamifera* L.) replaces thin-leaf alder to begin the mid-successional period 20–30 years after initial alluvium deposition, though alder remains a significant component of the understory. Soil N cycling slows during this stage with much reduced rates of N_2-fixation (avg. 38 kg N ha^{-1} yr^{-1}; Uliassi and Ruess 2002) and soil N accumulation, and vegetation that is thought to be increasingly N limited (Van Cleve and Viereck 1981; Flanagan and Van Cleve 1983). These deciduous stands are eventually dominated by white spruce (*Picea glauca* (Moench) Voss) after approximately 150 years (Van Cleve et al. 1996).

The transition from balsam poplar to mature white spruce is characterized by significant changes in nutrient cycling processes that are induced by changes in vegetation, notably the formation of a substantial moss layer (Van Cleve et al. 1991; Viereck et al. 1993a). Accompanying this transition there is a general decline in average soil temperatures, primary productivity, soil organic matter decomposability (Flanagan and Van Cleve 1983; Van Cleve et al. 1991) and net soil N transformation rates (Klingensmith and Van Cleve 1993b; Van Cleve et al. 1993b). While primary productivity of both balsam poplar and white spruce may be limited by soil N or P availability, soil microbial communities in white spruce stands are likely limited by labile C due to inputs of recalcitrant litter with a high lignin:N ratio (Flanagan and Van Cleve 1983). In contrast, the soil of balsam poplar stands contains a large pool of labile C from low-molecular weight phenolics, and heterotrophic microbes in this stand type have been theorized to be N limited (Clein and Schimel 1995; Schimel et al. 1998). Thus, within the span of 50–150 years there may be a shift from N-limited to C-limited soil microbes corresponding to changes in aboveground plant community structure.

The objective of this study was to examine the initial effects of approximately 3.5 years of experimental N additions (100 kg N ha^{-1} yr^{-1}) to stands of balsam poplar and white spruce in order to determine how major differences in plant species composition and associated soil properties affect soil N transformations and retention. Specifically, we hypothesized that soil microbes in late-successional stands of white spruce (C limited) would be ineffective at immobilizing added N, and would rapidly exhibit characteristics of 'N saturation' (Aber et al. 1989, 1998), including an increase in the pool size of nitrate at depth, an increase in net mineralization and net nitrification, and a decrease in soil pH. In contrast, we hypothesized that stands of balsam poplar, in which soil heterotrophs are thought to be N limited and plants have higher rates of net primary productivity (higher N demand), would readily accommodate N additions through N immobilization and increased microbial biomass with lesser changes to soil N transformations or evidence of N leaching losses than in white spruce.

Materials and methods

Study site

This study took place within the Bonanza Creek Long Term Ecological Research Site (BNZ-LTER) located along the Tanana River in interior Alaska, approximately 30 km south of Fairbanks (64 °45′ N, 148 °18′ W). Annual precipitation in this region is very low, averaging only 269 mm, and is exceeded by potential evapotranspiration of 466 mm. The mean annual air temperature is −3.7 °C with extremes ranging from −50 °C in winter to 35 °C in summer (Viereck et al. 1993b). Our research sites were in stands of balsam poplar and white spruce located on terraces >3 m above average river height on islands within the active portion of the floodplain. All sites had frozen soil throughout a significant portion of the growing season; however, balsam poplar sites became ice-free by early August while white spruce sites generally contained frozen soil until at least early October (Figure 1). The soils in these sites are classified as Typic Cryofluvents (Viereck et al. 1983; Van Cleve et al. 1993a) and consist of silt with occasional pockets of sand. Mineral soils on the floodplain are alkaline (pH >7) due to the high concentrations of $CaCO_3$ from the weathering of carbonate rock by glaciers in the Alaska Range (Marion et al. 1993a, b). As a result of flooding events all sites contained multiple buried organic layers, although the number, depth and thickness of these vary among sites.

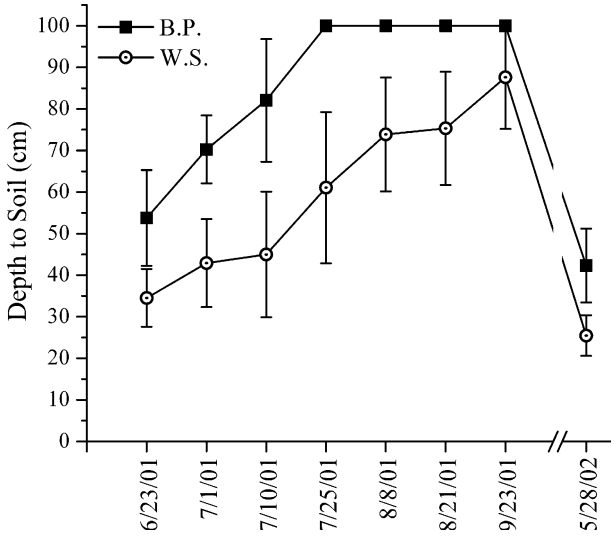

Figure 1. Growing season depth-of-thaw for stands of balsam poplar (BP) and white spruce (WS). Measurements were taken between June 2001 and May 2002 using a 1 m frost probe. Values are mean (±1S.E.), $n = 3$ plots per stand type.

Balsam poplar sites (LTER sites BP1, BP2 and BP3) consisted of mature, uneven stands with some individuals exceeding 100 years of age and a dense understory dominated by thin-leaf alder, rose (*Rosa acicularis*) and intermittent white spruce. White spruce sites (4A, 4B and 4C) consisted of both mature and senescing stands 200+ years in age with an understory of thin-leaf alder, rose and feather mosses (*Hylocomium splendens* and *Pleurozium schreberi*). Alder (*Alnus crispa* and *A. tenuifolia*) was a much smaller component of the understory in white spruce sites than in balsam poplar and was nearly absent at the 4C site. Table 1 lists above- and belowground biomass and productivity for these sites. A complete description of plant and soil characteristics for the floodplain successional sequences can be found in Viereck et al. (1983) and on the Bonanza Creek LTER website (LTER unpublished – See References Section).

N-fertilized (30 × 30 m) and control plots (30 × 30 m) were established at each site (n = 3 sites per successional stage) when fertilizer additions began during the summer of 1998. Ammonium nitrate (NH_4NO_3) as dry pellets was applied by hand spreader to fertilized plots in three equal portions over the course of the growing season (June–August) at a rate of 100 kg N ha^{-1} yr^{-1}. Fertilizer was applied each summer during this study and was ongoing as of 2003.

Net nitrogen transformations

Net rates of nitrogen (N) mineralization, nitrification and dissolved organic N production were assessed *in situ* from August 1999 to August of 2001 (except for September of 1999) with a modified intact-core incubation technique (Raison et al. 1987). In our view, it was not possible or practical to separate organic and mineral horizons without causing a major disturbance to the physical characteristics of the soil due to the high degree of integration between forest floor, buried organic horizons and mineral soil. Thus, pool sizes, net transformation rates and other dependent variables measured in this study were obtained from intact soil cores consisting of both organic and mineral soil and are presented on an area basis.

At the beginning of each incubation period five pairs of soil cores at the 0–20 cm depth were randomly collected from each plot with a 5.8 cm ID steel hand corer fitted with a 0.5 mm thick plastic sleeve. Cores started at approximately the interface of the Oi and Oa layers and included highly decomposed leaf litter in balsam poplar plots and dead moss in white spruce plots. One core from each pair was immediately brought to the laboratory for processing. The other core, collected within a sleeve pre-drilled with approximately 30, 0.5 cm-diameter holes, was placed in a 0.025 mm (1 mil) plastic bag within a fiberglass 'mosquito mesh' bag, then re-inserted into the soil and covered with surface litter. This procedure was designed to keep cores intact and allow the free exchange of air while keeping soil moisture constant. Cores remained in the soil for approximately 30 days during the growing season (June–October) but were

Table 1. Stand structure and biomass production for balsam poplar and white spruce stands on the Tanana River floodplain ($n = 6$ for each stand type)

Stand Type	Species	[1]Stem Density (stems ha^{-1})	[1]Basal Area (m^2 ha^{-1})	[1]Aboveground Tree Biomass (kg ha^{-1})	[2]Aboveground Production (kg ha^{-1} yr^{-1})	[1,3]Fine Litterfall (kg ha^{-1} yr^{-1})	[4]Fine Root Production (kg ha^{-1} yr^{-1})
Balsam poplar	*Populus balsamifera*	763 ± 93	36.7 ± 2.9	170411 ± 14079	5236 ± 355	2585 ± 202	3036 ± 428
	Alnus tenuifolia	485 ± 77	1.8 ± 0.3				
White spruce	*Picea glauca*	518 ± 36	38.9 ± 5.5	203089 ± 26837	4541 ± 833	1020 ± 311	1814 ± 605
	Alnus crispa/tenuifolia	148 ± 158	0.6 ± 0.7				

Biomass, production and litterfall values are expressed as kg oven-dry (65 °C) mass.
[1]Ruess, unpublished data.
[2]Includes trees, shrubs and bryophytes (Ruess et al. *in review*).
[3]Litterfall includes leaves and needles, fine wood (< 10 cm) and reproductive litter.
[4]Stand-level estimates of fine root production derived from minirhizotrons (Ruess et al. *in review*).

incubated from October to late-May during the winter. All cores were kept cool during transport to Fairbanks where they were sieved (to 5.6 mm) and homogenized within 24–48 h of collection. A 10 g sample of homogenized field-moist soil from each core was extracted with 75 ml of 0.5 M K_2SO_4 for 24 h before vacuum-filtration through a 1-μm pore diameter glass fiber filter. Subsamples from each core were taken for determination of gravimetric water content. Four times during the study (July 1999, July 2000, August 2000 and September 2000) we also incubated soil from the 20–30 cm depth of the soil profile *in situ* in order to examine net N transformations and extractable N within the deeper mineral soil.

Soil extracts were analyzed for ammonium and nitrate + nitrite with an API 300 segmented flow autoanalyzer (Astoria-Pacific Inc., Clackamas Oregon, USA). Dissolved organic nitrogen (DON) in extracts was determined by digestion with a buffered potassium persulfate solution (Cabrera and Beare 1993) followed by nitrate analysis.

Net mineral N production was calculated as the total change in extractable NH_4^+–N + NO_3^-–N per incubation period while net production of ammonium (ammonification) and nitrate (nitrification) were separately determined from the change in NH_4^+–N or NO_3^-–N, respectively, during the incubation period. Net DON production was calculated as the net change in DON per incubation period. Annual net N transformations were calculated for the complete 1 yr period (June 2000-June 2001) and the 2 yr period from August 1999-August 2001 (excluding September-October 1999) by summing N production across incubation periods within each plot and – in the case of the 2 yr data set – adjusting for the total number of incubation days. Mean annual net N transformation rates from individual plots were then used as replicates in the split–plot ANOVA (see *Statistical Analysis* below).

Microbial biomass

Microbial biomass in soil samples taken from initial cores in June of 2001 was determined using chloroform fumigation–extraction (CFE) (Horwath and Paul 1994). Fumigated and non-fumigated extracts were digested with potassium persulfate as described for DON except that the digestion took place in serum vials fit with rubber septa which were crimp-capped. Solutions containing 0–150 mg C l^{-1} phenylalanine were used as internal digestion standards. Phenylalanine was chosen as a standard because it contains an aromatic ring and was thought to provide a good comparison to the types of complex molecules (e.g., humics and phenolics) found in soil solution.

Following digestion, serum vials were cooled to room temperature and the pressure inside each vial was measured using a pressure transducer (Soil Measurement Systems, Tucson, Arizona, USA). A 10–15 cc headspace sample was then drawn into a syringe and immediately analyzed for CO_2 using a LICOR 6200 (LICOR, Lincoln, Nebraska, USA) modified with a syringe–

injection system. In order to determine an approximate digestion efficiency of samples, the predicted amount of CO_2 in the headspace of the phenylalanine standards was calculated using a pressure–volume equation and compared to linear curves of the actual CO_2 in the headspace of the standards measured with the LICOR. The digestion efficiency of the phenylalanine standards was determined to be >90%, and the amount of dissolved C in the samples was subsequently determined using the linear regressions from these standards. Digestion efficiency was based on C rather than N because it is 10 or more times more prevalent than N in the extraction solution and requires the largest portion of oxidizing power from the potassium persulfate. After headspace sampling, the solution in each serum vial was removed and analyzed for nitrate as for soil extracts. We did not use a conversion factor to correct for extraction efficiency of C (K_c) or N (K_n). A conversion factor is dependent upon soil properties (e.g., organic matter content) and is likely highly variable among floodplain forests due to stand and plot-level variation in buried organic horizons and, perhaps, associated differences in microbial community composition.

Soil and fine-root C, N and pH

Total soil C and N were determined for subsamples of homogenized soil cores collected throughout the course of the study. Total C and N of live fine roots (<0.5 mm), removed from soil cores collected in August 2001, were determined using a LECO CNS 2000 autoanalyzer (LECO, St. Joseph, Michigan, USA). Soil pH from 0–20 cm soil was determined on field-fresh samples collected in October 2000 (Robertson et al. 1999). All pools of C and N in the soil were first calculated per g 105 °C oven-dry soil and then converted to an area basis using plot-level estimates of bulk density.

Statistical Analysis

Comparisons of N transformation rates and pool sizes between individual incubation periods were done with a restrictive maximum likelihood (REML) technique (Littell et al. 2002) using PROC MIXED in SAS (SAS 1999). Models with appropriate covariance structures (first-order autoregressive, unstructured and Toeplitz) were compared, and the model with the lowest Akaike Information Criterion (AIC) value was used for further analyses. Standard errors and degrees of freedom were obtained using a Kenward and Roger correction (Littell et al. 2002).

Pool size and N transformation rate data from individual soil cores collected within each of the 12 research plots were averaged so that each plot represented a single replicate. Data that were not collected over several time periods (e.g., fine-roots, microbial C and N, soil pH) or that were obtained by averaging

values across time (e.g., DIN pools and yearly N transformation rates) were analyzed using a split–plot ANOVA design with the GLM module of Statistica (Statsoft 2003) or with PROC MIXED in SAS. Stand type was the between-subject (whole plot) factor, and treatment the within-subject (split–plot) factor. Significant effects for planned tests were further analyzed using paired contrasts, and Satterthwaite's approximation was implemented when exact F-tests were not possible. Both linear and non-linear regressions were used to explore relationships between microbial C and N and soluble N pools. For all analyses the homogeneity of variance assumption was tested using Levene's test. When there were significant deviations from this assumption, data were square-root transformed (Zar 1999), and an additional analysis was performed. Data presented in tables and figures are means ± 1 standard error (SE) from untransformed data. Significance for all tests was established at the $p \leq 0.05$ level; however, we classify as 'marginally significant' values ≤ 0.10.

Results

Extractable N pools

Fertilization significantly increased 0–20 cm extractable DIN pools within the first year (1999) following N additions (Figure 2; $F_{1,4} = 8.8$; $p = 0.04$); however, there was not a consistent increase in soil DIN over time for either stand type. When averaged across all sampling periods, pools of extractable NH_4^+–N and NO_3^-–N (mg N m^{-2}) were significantly larger in fertilized plots compared to control plots for both stand types (Table 2). Although pool sizes of extractable NH_4^+–N and NO_3^-–N were similar for the fertilized plots of both stand types, there was a significant and much larger absolute increase in DIN following fertilization in white spruce compared to balsam poplar ($F_{1,4} = 14.7$, $p = 0.02$), due primarily to an increase in NH_4^+–N (Figure 2, Table 2). During July 2001, the last measurement period, there was a spike in NO_3^-–N in fertilized white spruce which was significantly larger (Figure 2b; $F_{1,4} = 15.4$; $p = 0.02$) than extractable NO_3^-–N pools during all other periods. For 0–20 cm soil control plots, extractable NH_4^+–N made up the vast majority of DIN in both stands types; however, the pool size of NH_4^+–N was over twice as large ($F_{1,4.7} = 8.3$; $p = 0.04$) in control plots of balsam poplar compared to white spruce. Pools of extractable NO_3^-–N in control plots were quite low (<0.04 g N m^{-2}) and not significantly different between stand types (Table 2a; $F_{1,7.98} = 0.03$; $p = 0.86$).

Dissolved organic nitrogen (DON) made up the largest pool of soluble N (mg N m^{-2}) for 0–20 cm soil (Table 2). The pool size of DON was not affected by N fertilization but was significantly larger for balsam poplar compared to white spruce (Table 2a; $F_{1,8} = 7.1$; $p = 0.03$), averaging 3733 ± 309 mg N m^{-2} for balsam poplar and 2571 ± 254 mg N $^{-2}$ for white spruce when control and fertilized plots were considered together.

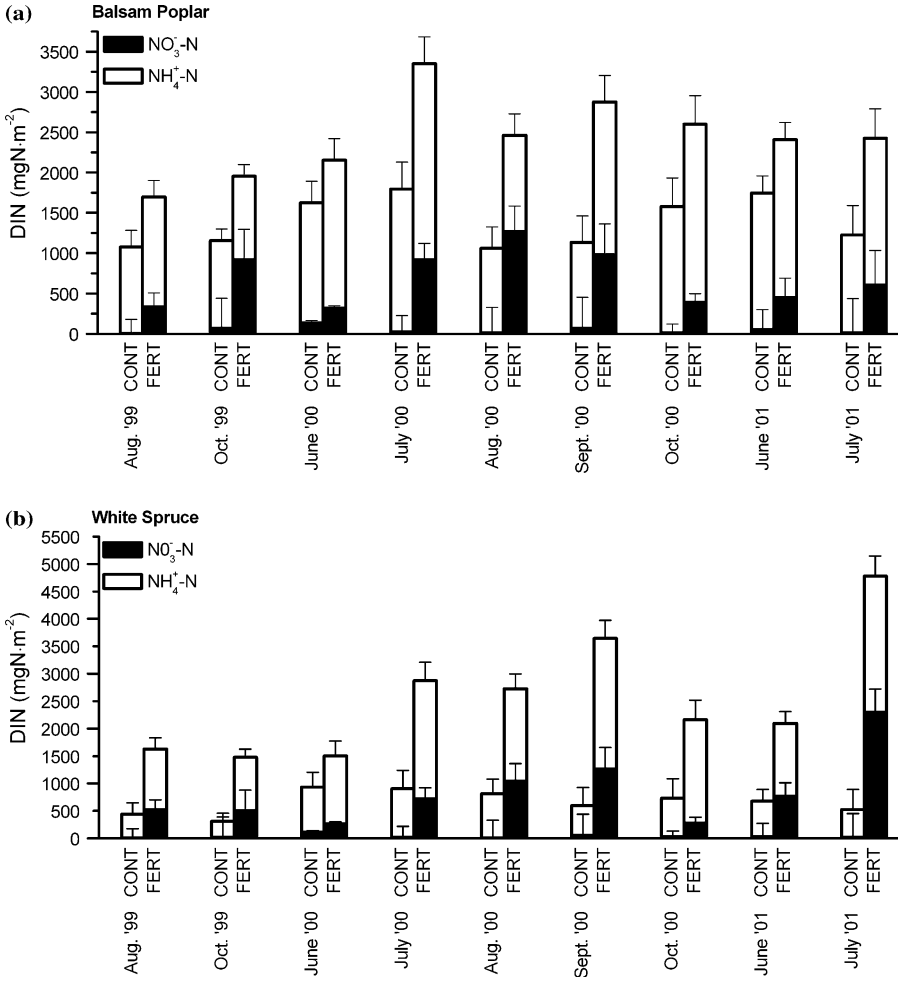

Figure 2. Pool size (mg N m^{-2}) of 0.5 M K_2SO_4-extractable inorganic N for 0–20 cm soil cores at each of the nine incubation periods for control (CONT) and fertilized (FERT) plots of (a) balsam poplar and (b) white spruce. Ammonium-N begins at the top of the NO_3^-–N bar, thus bar height indicates total the sum of NO_3^-–N + NH_4^+–N or DIN. Values are means (+1S.E.; $n = 3$ for each stand × treatment combination).

Fertilization significantly increased average extractable pools of NO_3^-–N in 20–30 cm mineral soil cores for both stand types when averaged across all time periods (Table 2b). In September 2000 (Figure 3), the last time mineral soil cores from the 20–30 cm depth interval were collected, NO_3^-–N concentrations were significantly elevated in fertilized white spruce ($F_{1,4} = 15.2$; $p = 0.02$) and balsam poplar ($F_{1,4} = 8.9$; $p = 0.04$), compared to those collected during all other time periods. In contrast, NH_4^+–N concentrations in 20–30 cm cores were not significantly different for control and fertilized plots within either

Table 2. Soil C and N content and pH for a) 0–20 cm soil and b) 20–30 cm soil in control (CONT) and N fertilized (FERT) plots of balsam poplar and white spruce (n = 3 replicate sites for each stand × treatment combination)

Stand	Treatment	pH	Soil C ($gC \cdot m^{-2}$)	Soil N ($gN \cdot m^{-2}$)	C:N	NH_4–N ($mgN \cdot m^{-2}$)	NO_3–N ($mgN \cdot m^{-2}$)	DON ($mgN \cdot m^{-2}$)
a) 0–20 cm soil								
Poplar	CONT	7.62	5174	298	17.36	1333	44	3910
	(± S.E.)	(0.22)	(367)	(25)	(0.37)	(58)	(5)	(319)
						**	**	
	FERT	7.06	5220	289	18.06	1749	687	3556
	(± S.E.)	(0.34)	(330)	(23)	(0.43)	(66)	(262)	(587)
		p = 0.06		*	**			*
Spruce	CONT	6.43	4569	193	23.67	626	34	2499
	(± S.E.)	(0.49)	(784)	(41)	(1.31)	(166)	(2)	(502)
						***	**	
	FERT	6.18	3997	174	22.97	1690	853	2642
	(± S.E.)	(0.12)	(412)	(18)	(0.09)	(291)	(220)	(256)
b) 20–30 cm soil								
Poplar	CONT	7.71	959	61	15.72	225	28	869
	(± S.E.)	(0.28)	(178)	(11.5)	(0.75)	(44)	(6)	(125)
							*	
	FERT	7.70	1881	94	20.01	157	264	945
	(± S.E.)	(0.22)	(749)	(29)	(2.95)	(13)	(64)	(201)
Spruce	CONT	7.14	1181	67	17.63	302	31	836
	(± S.E.)	(0.34)	(311)	(20)	(0.56)	(89)	(9)	(240)
							*	
	FERT	6.51	1220	72	16.94	220	407	736
	(± S.E.)	(0.42)	(647)	(29)	(2.15)	(51)	(232)	(370)

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.
Values are means (±1S.E.) of nine sampling events spanning a two-year time period (August 99–July 01). Asterisks between stands indicate significance of stand-level effects, those between treatments indicate significant contrasts.

stand type (Table 2b) and did not increase over time (data not shown). As in 0–20 cm cores, the majority of soluble N for the 20–30 cm cores consisted of DON (Table 2b). DON at this depth did not differ significantly by stand or treatment type.

Net N Transformations

Across stand types, fertilized plots had significantly higher annual rates of net N mineralization (0–20 cm soil depth, Table 3) when calculated for the entire two-year study. Relative to control plots, annual net production of DIN was 62% higher in the fertilized plots of balsam poplar ($F_{1,4}$ = 12.5; p = 0.02) and 77% higher in white spruce (marginally significant, $F_{1,4}$ = 4.3; p = 0.10). Annual net N mineralization was also higher for control plots of balsam poplar than white spruce, although not significantly ($F_{1,5.76}$ = 3.6; p = 0.11).

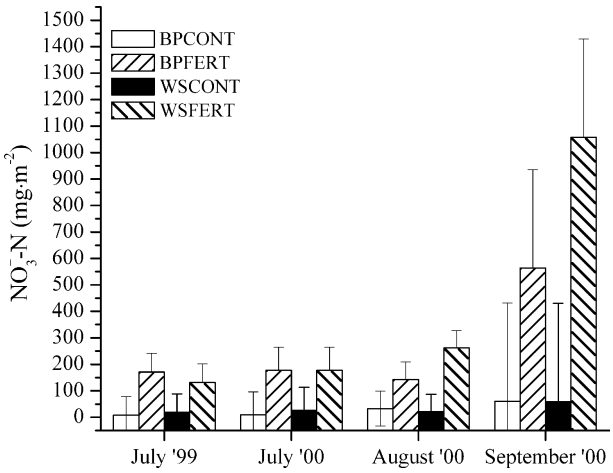

Figure 3. Pool size (mg m^{-2}) of 0.5 M K_2SO_4-extractable NO_3^-–N from 20–30 cm soil depth collected from control (CONT) and fertilized (FERT) plots of balsam poplar (BP) and white spruce (WS) at four times during the two year study. Values are means (+1S.E.), $n = 3$ for each stand × treatment combination). Graph is from untransformed data.

When considering just the 2000–2001 period, fertilization increased annual net mineralization in white spruce but not balsam poplar stands (Table 3). Control plots of balsam poplar had significantly higher annual net mineralization than white spruce control plots during this period ($F_{1,7.81} = 6.4$; $p = 0.04$).

For the two-year study period, fertilization increased annual net nitrification rates (mg NO_3^-–N m^{-2} yr^{-1}), but only in balsam poplar (Table 3), where net nitrification was higher than in control plots during eight of the nine incubation periods (Table 4). Although fertilization did not increase average net nitrification in white spruce for the two-year period, this was largely due to unusually high net immobilization of NO_3^-–N during July–August 2001 (Table 4) which offset the majority of incubation periods in which nitrification was either marginally higher or not statistically different in fertilized plots. For the 2000–2001 period fertilization significantly increased annual net nitrification across stand types (Table 3), but this was due principally to a fertilization response in balsam poplar (marginally significant, $F_{1,4} = 4.7$; $p = 0.10$) as white spruce stands did not have significantly higher nitrification during this period ($F_{1,4} = 3.9$; $p = 0.12$).

Fertilization tended to increase ammonification rates in white spruce, but lowered them in balsam poplar (Table 3, Table 4). This created a significant stand × treatment interaction for the one-year (2000–2001) incubation period and a marginally significant interaction effect for the two-year incubation period.

There was a large amount of variation in net N transformations during the two overwinter incubation periods (Table 4). In the winter of 1999–2000,

Table 3. Annual net of net N mineralization, nitrification, ammonification and DON production (mg N m^{-2} yr^{-1}) for 0–20 cm depth soil based on the entire 2 years of the buried-bag study and on the complete 1 year period from June 2000-June 2001 (±1S.E.; $n = 3$ experimental plots for each stand × treatment combination)

Stand	Treat.	Net Min. (2-year)	Net Min. (2000–2001)	Net Nit. (2-year)	Net Nit. (2000–2001)	Net Ammon. (2-year)	Net Ammon. (2000–2001)	Net DON Prod. (2-year)	Net DON Prod. (2000–2001)
p-values for ANOVA	Stand	**0.06**	0.21	**0.03**	**0.07**	0.75	0.49	**0.03**	**0.09**
	Fert.	**0.02**	**0.07**	**0.05**	**0.04**	0.63	0.83	0.16	**0.06**
	Stand×Fert	0.36	**0.10**	**0.07**	0.90	**0.09**	**0.02**	0.33	0.15
B. Poplar	CONT	2972 (± 733)	3210 (± 1220)	849 (± 570)	999 (± 670)	2123 (± 179)	2212 (± 551)	1104 (± 371)	−377 (± 582)
	Contrast *p*-values	**0.02**	0.84	**0.02**	**0.10**	0.34	**0.05**	N/A	0.58
	FERT	4824 (± 791)	3222 (± 587)	3266 (± 488)	2548 (± 742)	1558 (± 480)	675 (± 239)	289 (± 162)	−651 (± 437)
W. Spruce	CONT	1365 (± 373)	933 (± 280)	138 (± 113)	24 (± 107)	1227 (± 344)	908 (± 229)	−586 (± 406)	−1288 (± 712)
	Contrast *p*-values	**0.10**	**0.03**	0.9	0.12	0.13	**0.04**	N/A	**0.04**
	FERT	2453 (± 385)	3455 (± 532)	262 (± 249)	828 (± 234)	2191 (± 512)	2627 (± 528)	−774 (± 462)	−2693 (± 225)

Estimates were calculated by summing plot-level production of individual N species during either the one-year period from June 2000 to June 2001 or the two-year period from August 1999 to July 2001. *p*-Values between control (CONT) and N-fertilized (FERT) means are for contrasts, *p*-values at the top of the table are from the split–plot ANOVA with 1 and 4 degrees of freedom. Significant, $p < 0.05$, and marginally significant, $p < 0.10$, *p*-values are in bold.

Table 4. Total N produced (Prod.) (mg N m^{-2}) during each incubation period from (a) mineralization, (b) nitrification and (c) ammonification (0–20 cm soil depth) for control (CONT) and fertilized (FERT) plots of balsam poplar (BP) and white spruce (WS)

Net DIN production/ mineralization		Aug–Sept.'99	Oct.'99–June'00	June–July'00	July–Aug.'00	Aug.–Sept.'00	Sept.–Oct.'00	Oct.'00–June'01	June–July'01	July–Aug.'01
	Length of incubation (days)	38–39	235–236	28–29	29	25–26	39–40	232–233	33	29
BPCONT	Prod.	753.6	1054.7	1345.9	−42.9	1113.8	999.4	−206.3	13.0	595.1
	(±SE)	(154.2)	(204.0)	(259.4)	(342.8)	(467.7)	(71.8)	(227.1)	(127.2)	(129.0)
BPFERT	Prod.	1643.1	2507.0	1031.3	−769.8	2320.1	882.3	−241.6	598.6	1160.8
	(±SE)	(180.4)	(774.7)	(362.4)	(309.3)	(220.8)	(263.7)	(280.1)	(605.5)	(111.2)
WSCONT	Prod.	395.2	676.6	81.5	−90.9	390.6	631.5	−80.2	−7.8	588.0
	(±SE)	(113.5)	(147.5)	(22.3)	(56.4)	(256.3)	(205.5)	(161.8)	(113.8)	(136.1)
WSFERT	Prod.	1130.4	857.1	495.0	204.4	2074.3	90.3	590.9	146.4	−944.2
	(±SE)	(417.1)	(308.3)	(74.2)	(434.8)	(764.5)	(731.3)	(283.1)	(983.0)	(1058.3)
Net NO^{-}_{3}–N production/nitrification										
BPCONT	Prod.	399.2	29.1	364.9	192.8	157.0	197.1	86.6	59.8	120.2
	(±SE)	(244.6)	(59.3)	(238.6)	(118.8)	(107.1)	(138.7)	(70.3)	(68.8)	(61.6)
BPFERT	Prod.	888.3	895.4	550.1	−93.9	1006.9	835.4	249.3	851.8	998.9
	(±SE)	(111.6)	(651.6)	(270.1)	(236.1)	(290.6)	(180.5)	(193.4)	(373.9)	(450.2)
WSCONT	Prod.	130.9	19.0	−73.5	36.5	25.4	4.5	31.2	21.3	66.1
	(±SE)	(8.8)	(25.9)	(18.2)	(19.3)	(17.8)	(21.5)	(47.4)	(34.5)	(43.5)

WSFERT	Prod.	105.7	37.4	36.5	123.2	534.8	−214.7	348.4	276.1	−751.0
	(±SE)	(168.5)	(149.9)	(80.7)	(180.3)	(383.6)	(433.8)	(161.4)	(770.8)	(514.1)
Net NH^+_4–N production/ammonification										
BPCONT	Prod.	354.4	1025.7	981.0	−235.7	956.8	802.3	−292.9	−46.8	474.9
	(±SE)	(93.3)	(262.8)	(158.0)	(232.9)	(379.1)	(68.0)	(161.3)	(62.0)	(99.7)
BPFERT	Prod.	754.8	1611.6	481.2	−675.9	1313.2	46.9	−490.9	−253.3	161.9
	(±SE)	(182.0)	(248.0)	(351.5)	(78.4)	(144.8)	(201.3)	(105.0)	(385.2)	(351.7)
WSCONT	Prod.	264.3	657.6	155.0	−127.5	365.3	627.0	−111.4	−29.1	522.0
	(±SE)	(110.0)	(146.5)	(17.3)	(71.7)	(239.6)	(193.9)	(143.7)	(140.2)	(107.3)
WSFERT	Prod.	1024.7	819.7	458.5	81.2	1539.6	305.0	242.5	−129.7	−193.1
	(±SE)	(264.1)	(164.8)	(107.9)	(292.3)	(587.7)	(403.8)	(337.7)	(261.8)	(551.9)

The parameters (mg N m^{-2}) are expressed as cumulative values for each incubation period. Daily rates can be calculated by dividing production estimates by the number of days in the incubation period. Values are means (±1S.E.) and $n = 3$ plots for each stand×treatment combination.

net N ammonification tended to be positive and accounted for a large portion of the yearly net N mineralization rate, but in 2000–2001 net N ammonification tended to be negative except in white spruce fertilized plots where it was positive. Net nitrification rates were also highly variable but were positive for all stand × treatment combinations during both overwinter periods.

Net rates of DON production were strongly positive for balsam poplar (697 ± 257 mg DON m^{-2} yr^{-1}) but strongly negative for white spruce (-680 ± 278 mg DON m^{-2} yr^{-1}) when computed for the two-year time period (Table 3; $F_{1,4} = 10.01$; $p = 0.03$). Fertilization did not significantly affect net DON production rates over this period for either stand type, although rates were somewhat lower in fertilized stands of balsam poplar relative to controls. A similar trend existed during the 2000–2001 period when there was a marginally significant effect from stand type on net DON production and a marginally significant effect due to fertilization. During this period white spruce control plots had significantly higher net DON production than fertilized plots Table 3; $F_{1,4} = 9.8$; $p = 0.03$).

There were no significant stand or treatment effects on net N mineralization rates (mg DIN m^{-2} day^{-1}) for the 20–30 cm mineral soil cores (data not shown). Net N mineralization rates were very low during the four periods measured, and average net mineralization for this soil depth was not significantly different from zero for any stand × treatment combination.

Microbial biomass C & N

Fertilization did not have a significant effect on either microbial biomass C or N within either stand type (Figure 4); however, slightly larger pools of microbial N and slightly smaller pools of microbial C resulted in significantly lower microbial C:N in fertilized stands relative to control stands ($F_{1,4} = 10.2$; $p = 0.03$) (9.4 ± 0.4 for control plots versus 7.9 ± 0.4 for fertilized plots). There was no difference in microbial C:N between stand types ($F_{1,4} = 0.4$; $p = 0.56$). When averaged across control and fertilized plots, balsam poplar stands had 88% higher microbial biomass C (Figure 4; $F_{1,4} = 36.7$; $p = 0.004$), and 93% higher microbial biomass N, than white spruce ($F_{1,4} = 203.5$; $p < 0.0001$).

Soil and fine-root C & N and Soil pH

Fertilization did not have a significant influence on either fine-root C:N ($F_{1,4} = 2.5$; $p = 0.19$) or %N ($F_{1,4} = 2.2$; $p = 0.23$) (Figure 4b). Fine-root C:N was significantly lower ($F_{1,4} = 18.2$; $p = 0.01$; Figure 4b), and fine-root %N significantly higher ($F_{1,4} = 29.2$; $p = 0.006$), in balsam poplar stands compared to white spruce. The 0–20 cm soil C:N (Table 2) was also signifi-

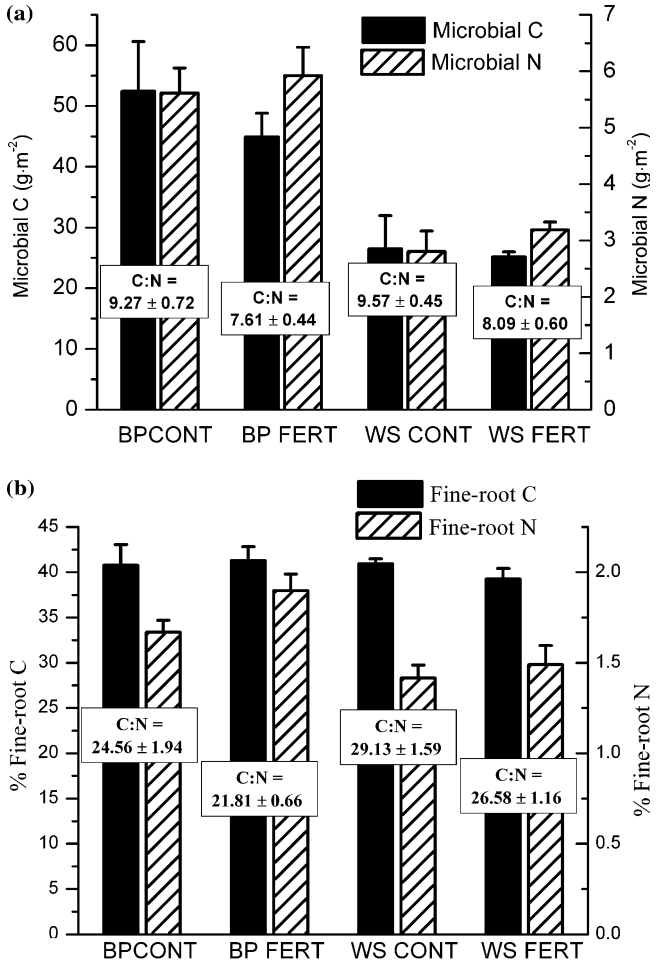

Figure 4. (a) Microbial biomass C, N (g m^{-2}) and C:N; and (b) Fine root (<0.5 mm) %:C, % N and C:N for 0–20 cm depth soil in control (CONT) and fertilized (FERT) plots of balsam poplar (BP) and white spruce (WS). Balsam poplar stands had significantly higher microbial biomass C, N, fine-root % N and significantly lower fine-root C:N than white spruce, but only microbial C:N was significantly affected (reduced) by N fertilization. Values are means, (+1S.E.), and $n = 3$ plots for each stand × treatment combination.

cantly lower in balsam poplar compared to white spruce ($F_{1,4} = 53.96$; $p = 0.002$) but was unaffected by fertilization ($F_{1,4} = 0.17$; $p = 0.7$). Soil pH (Table 2) was generally lower in the fertilized plots of both stand types, but this difference was not significant ($F_{1,4} = 3.4$; $p = 0.13$). Across control and fertilized plots, stand type had a marginally significant effect on 0–20 cm soil pH ($F_{1,4} = 6.7$; $p = 0.06$) which was higher in balsam poplar than white spruce (Table 2).

Discussion

N transformations and pool sizes from intact cores

Results from this study do not support our hypothesis that balsam poplar would be minimally impacted by N fertilization. Fertilizer additions brought about significant alterations to soil N transformations in balsam poplar by decreasing net ammonification and substantially increasing both annual net nitrification as well as pools of DIN (0–20-cm depth) and NO_3^-–N (20–30 cm depth). Given our assumption that soil microbes (Clein and Schimel 1995; Schimel et al. 1996, 1998) and perhaps plants in balsam poplar stands were N limited, and would quickly immobilize fertilizer additions, we were surprised by the speed and magnitude of response in this stand type. By 1999, just one year after initial fertilizer additions, the pool size of extractable NO_3^-–N in balsam poplar was already appreciably higher in fertilized balsam poplar plots than in control plots for the 0–20 cm (Figure 2a) and 20–30 cm cores (Figure 3). Because negligible root biomass was observed at the 20–30 cm soil depth, we believe that an increase in NO_3^-–N following fertilization is indicative of N leaching. Thus, it would appear that large-scale net immobilization of added N may not have occurred as we had anticipated or that the added N simply overwhelmed plant and microbial uptake.

Soil microbes in the balsam poplar stands of this study may not have been as N limited as we had originally thought or may have had very different soil characteristics than those from the Clein and Schimel (1995) study. For example, their soil contained only forest floor organic material that likely had a much higher proportion of phenolic-rich leaf litter and could very well have been N limited. In contrast, we purposefully excluded the prior season of leaf litter from our 0–20 cm intact cores, but our soil did include several buried organic horizons. We suspect that our soil consisted of older, more highly decomposed organic material which had reduced heterotrophic N demand and, perhaps, also contained a higher density of N-fixing nodules.

An overall annual net nitrification rate that was dramatically higher in fertilized balsam poplar plots (Table 3) is consistent with previous suggestions that nitrification in poplar is primarily controlled by soil N availability rather than allelopathic inhibition from the large amount of secondary metabolites produced by this species (Clein and Schimel 1995; Schimel et al. 1996; Uliassi et al. 2000). We believe that fertilizer additions produced an immediate increase in overall N availability such that soil nitrifiers could more successfully compete with heterotrophic microbes (and perhaps plants) for NH_4^+–N. This reasoning may seem counterintuitive given that control plots of balsam poplar already had a higher NH_4^+–N supply than white spruce; however, it is important to note that net nitrification was also substantially higher in control plots of balsam poplar compared to white spruce (Table 3). Thus, nitrification may already have been stimulated in balsam poplar prior to N additions. The much larger pool size of NH_4^+–N in balsam poplar control

plots may be a function of the microbial biomass (larger in balsam poplar, Figure 4a) involved in N transformations combined with the temporal gap between NH_4^+–N production and immobilization – a 'snapshot' of a flux. Thus, NH_4^+–N pool size may be less representative of N demand than it is of NH_4^+–N flow between pools. Long-term measurements of *in situ* gross N mineralization and nitrification and the microbial pool size would be needed to resolve this issue.

Arguably, fertilization produced an even greater change to soil N cycling and DIN pool sizes in white spruce. Annual rates of net N mineralization, driven by elevated ammonification (Tables 3 and 4), consistently increased with fertilization in white spruce plots but were only occasionally higher following fertilization in balsam poplar. This would indicate that N additions overwhelmed the ability of soil heterotrophs in white spruce to immobilize excess N. There was also a significantly larger absolute increase in the average pool size of DIN for 0–20 cm soil and NO_3^-–N for 20–30 cm soil (though not significant) in white spruce compared to balsam poplar. Although, it is unclear if such stand-level differences were due to dissimilar plant or microbial N demand or were the result of contrasting patterns of N losses such as leaching or denitrification. The large spikes in NO_3^-–N for 0–20 cm during July 2001 (Figure 2b) and 20–30 cm soil during September 2000 (Figure 3) in fertilized white spruce – the last time these depths were sampled – may indicate that NO_3^- leaching was increasing dramatically. In contrast, *in situ* denitrification has previously been shown to be negligible in these stands (Klingensmith and Van Cleve 1993a) and suggests that this process was not responsible for controlling DIN pool sizes following fertilization. However, that study only measured denitrification from July–September during a single growing season. We believe that denitrification may be an important source of ecosystem N losses during the spring (mid-May to mid-June) when soil is at or near saturation following snowmelt.

Our results, which show that white spruce soils in interior Alaska responded quickly to fertilizer additions, with NO_3^-–N leaching and increases in net N mineralization, are similar to other studies of northern coniferous forests exposed to long term N additions (Emmett et al. 1998b; Gundersen 1998). However, our study sites did not exhibit the consistent increases in nitrification or a drop in soil pH often associated with 'N saturation' in coniferous stands. This may be due to the relatively recent nature of N additions in this study (<4 years) and because the alkaline soils of the floodplain served to buffer the effects of N additions.

The measurement of net DON production during soil incubation experiments is not one that has been used widely in the literature (but see Neff and Hooper 2002) and may not be particularly meaningful to specific aspects of plant or microbial N demand. However, we presented measurements of DON production here in order to stimulate discussion of what is, increasingly, regarded as an important component of plant and microbial N uptake in the boreal forest (Nasholm et al. 1998; McFarland et al. 2002) and to highlight the

higher DON production in balsam poplar relative to white spruce (Table 3). We speculate that input to the DON pool is tied to the heterotrophic breakdown of soil detritus as well as the release of organic leachates from decomposing leaves and roots. Thus, the measurement of net DON production may be an index of inputs into the soluble pool and indicate a larger or more active pool of detritus in balsam poplar compared to white spruce.

Plant N demand

The lack of significant change in fine-root %N or C:N following several years of N additions (Figure 4b) mirrors results by Pregitzer et al. (2002) who measured fine roots from these same plots shortly after the initiation of fertilization in 1998 and 1999. Since roots from our study were collected in August 2001, after two additional years of N additions, our results might indicate that the C:N of these roots is relatively fixed or indicate that plant N demand was not as high as we had originally anticipated. It is also probable that some component of these stands (e.g., alder) is limited by phosphorus rather than N (Uliassi et al. 2000; Uliassi and Ruess 2002).

Perhaps a more meaningful indication of plant N limitations will come not from changes to tissue N concentrations but rather from ongoing studies of belowground processes examining the response of fine-root production and turnover to increases in soil N availability. Minirhizotron-based estimates from control plots show that fine-root production was 67% higher in balsam poplar than white spruce (Table 1) and likely play a large, albeit unknown, role in determining microbial N and C demand in these stands. A large portion of fine roots in this system die and decompose within a year of being produced (Ruess et al. *in review*). Fine roots have low C:N ratios, and may account for a substantial source of actively cycled soil N; however, there is uncertainty regarding how much fine root N may be re-translocated prior to root death or senescence (Gordon and Jackson 2000), and the amount of plant N retranslocation may vary widely depending upon plant and soil nutrient status (Salifu and Timmer 2001). The answer to this problem has large implications for microbial C and N demand: If much of the N in fine roots is re-translocated prior to senescence then soil microbes should have a large N demand as they decompose a labile source of C; however, if much of the N remains in senesced roots then soil microbes should cycle a substantial portion of this back into soil during decomposition.

Ecosystem NO_3^- Utilization

Could there be a common factor responsible for the immediate increase in extractable NO_3^-–N pools observed following fertilization in both stand types for 20–30 cm soil? A plant and/or microbial preference for NH_4^+ over NO_3^- (or

inability to utilize NO_3^-) could be the answer. Ammonium, which dominates the salt-extractable DIN pool in these stands (NH_4^+–N:NO_3^-–N = 18.2 in white spruce and 30.3 in balsam poplar; Table 2), is known to inhibit nitrate reductase activity in both plants (Larcher 1995) and microbes (Atlas and Bartha 1993; Myrold 1999). It has also been suggested that plants and microbes exposed to increased N deposition have a reduced ability to absorb NO_3^- (Kjonaas et al. 1998), and Tietema (1998) reported no immobilization of NO_3^- by soil microbes in sites with substantial N deposition in northwestern Europe. White spruce in particular is known to have a very limited capacity to utilize NO_3^- (Kronzucker et al. 1995a, b; 1997), while field and laboratory studies have shown that Norway spruce (*Picea abies*) and beech (*Fagus sylvatica*) have a reduced or complete inability to take up NO_3^- when exposed to N fertilizer or when grown in soil with a high NH_4:NO_3 ratio (Gessler et al. 1998; Rennenberg et al. 1998). Several other studies (Chapin et al. 1986; Hangs et al. 2003; Yarie 1993) also report low or negligible uptake of NO_3^-, but substantial uptake of NH_4^+ by balsam poplar, aspen (*Populus tremuloides*), green alder (*Alnus crispa*), paper birch (*Betula papyrifera*) and jack pine (*Pinus banksiana* Lamb.).

Thus, many coniferous and deciduous trees in the boreal forest generally may have a limited ability to utilize NO_3^-, especially in the presence of larger amounts of DIN or NH_4^+, which may inhibit the uptake of NO_3^- and/or suppress nitrate reductase. While the leaching of NO_3^- to the 20–30 cm soil depth in this study could, in part, be attributed to the high mobility of NO_3^- in the soil profile relative to NH_4^+, this may not fully explain why NO_3^- was able to move through multiple buried organic horizons within a year after initial fertilizer additions.

Microbial C and N

Contrary to our prediction, N fertilization did not increase microbial biomass in balsam poplar stands; rather, biomass remained unchanged in both stand types after more than 3 years of N fertilization while microbial C:N was significantly lower across both stand types. Although we are skeptical that microbial C:N was actually reduced in response to fertilization, rather than changed by slight differences between control and fertilized plots, Tietema (1998) also observed lower microbial C:N ratios following N additions and found that microbial biomass C remained unchanged across a wide gradient of N deposition in coniferous forests across Europe. Aber et al. (1995, 1998) (hardwoods and conifers) and Gundersen (1998) (conifers) also concluded that microbial biomass did not change following large-scale N addition, while Fisk and Fahey (2001) and Corre et al. (2003) (hardwoods) showed a significant decrease in chloroform-extractable biomass in N fertilized stands. Thus, the response of soil microbial biomass to long-term N additions would appear to be variable across forest ecosystems.

The much larger pool of microbial biomass in balsam poplar compared to white spruce (Figure 4a), but lack of change following fertilization, suggests that factors associated with plant composition and inputs (fine-root and litter quality) have a much stronger influence on microbial biomass in this ecosystem than short-term N inputs and availability. In this regard we reiterate our view that the production and turnover of labile fine roots plays a major role in belowground carbon and nutrient cycling and, almost certainly, microbial biomass in the boreal forest where the ratio of belowground production to aboveground litter fall inputs is high relative to temperate forests (Ruess et al. 1996, 2003). We predict that, with longer- term N additions in these stands, the degree to which plant belowground production and turnover may be altered with increased N availability will ultimately determine whether or not there are significant changes in microbial biomass.

Conclusions

The results from this study help to elucidate controls on successional patterns of ecosystem N cycling as well as the types of responses that could be expected as pristine high-latitude forests experience increased deposition of human-derived reactive N. Though current N deposition in Alaska's interior boreal forest is exceptionally low, N deposition is already elevated beyond pre-industrial levels in parts of the boreal forests in Canada and Russia (Holland et al. 1999), and global N deposition is predicted to increase substantially during the next several decades (Galloway et al. 1994, 1995). The 100 kg N ha^{-1} yr^{-1} applied during this study is in excess of any conceivable near-term increase in human-induced N deposition to interior Alaska; however, primary productivity in these stands is at the extreme upper range relative to other plant communities (e.g., black spruce) in this region. Thus, the responses of soil N cycling observed here (e.g., the leaching of NO_3^- and the alteration of N mineralization and nitrification) could occur with substantially smaller inputs of N in other pristine boreal communities which have much lower N demand. We believe that both deciduous and coniferous high-latitude forests, in which state factors such as light and temperature play a critical role in limiting nutrient cycling and primary production during a brief growing season, are particularly vulnerable to the effects of N deposition compared to temperate systems with higher overall ecosystem N demand.

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