

Nitrogen cycling at treeline: Latitudinal and elevational patterns across a boreal landscape¹

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Abstract: We studied spatial and temporal patterns of nitrogen pools and fluxes in soils at treeline and forested sites within three mountain ranges across a 785-km transect in Alaska during 2001–2002. We measured pools of soil mineral (ammonium and nitrate) and organic (amino acid and microbial biomass) nitrogen, *in situ* rates of net mineralization, net nitrification, net amino acid production, and decomposition, as well as soil carbon turnover in a laboratory incubation experiment. Soils at treeline were mostly colder than forested soils, particularly during fall and over winter, and had reduced rates of nitrogen cycling and litter decomposition relative to forested stands. Treeline soils also had lower rates of potential respiration per unit carbon, suggesting reduced soil organic matter quality relative to forest soils. Therefore, effects of both colder temperatures and poorer substrate quality appeared to suppress rates of nitrogen turnover at treeline. Seasonal patterns of nitrogen turnover were similar across latitudes (*i.e.*, mountain ranges). On average, 70% of total annual net nitrogen mineralization occurred from August through May, suggesting that fall and winter are critical periods for soil nitrogen transformations in both forested and treeline ecosystems. Among mountain ranges, pool sizes and fluxes of nitrogen were similar despite significant variation in growing season length and mean annual temperatures. Soil moisture and soil organic matter quality may have stronger effects on variation in nitrogen cycling than temperature at our sites.

Keywords: amino acids, mineralization, nitrogen cycling, seasonal patterns, treeline, winter.

Résumé : Nous avons étudié les patrons temporels et spatiaux du contenu et des flux d'azote dans le sol à la limite des arbres et dans des sites forestiers dans trois chaînes de montagnes le long d'un transect de 785 km en Alaska en 2001-2002. Nous avons mesuré le contenu du sol en azote minéral (ammonium et nitrate) et en azote organique (acides aminés et biomasse microbienne), les taux *in situ* de minéralisation nette, de nitrification nette, de production nette d'acide et de décomposition ainsi que le renouvellement du carbone du sol dans une expérience d'incubation en laboratoire. Les sols à la limite des arbres étaient en général plus froids que les sols forestiers, particulièrement durant l'automne et au cours de l'hiver et ils avaient des taux de cyclage d'azote et de décomposition de litière plus faibles que ceux des sites forestiers. Les sols à la limite des arbres avaient aussi des taux plus faibles de respiration potentielle par unité de carbone ce qui suggère que la matière organique des ces sols est de moins bonne qualité que celle des sols forestiers. Par conséquent, l'effet combiné de températures plus froides et d'un substrat de moins bonne qualité semble réduire les taux de renouvellement de l'azote à la limite des arbres. Les patrons saisonniers du renouvellement de l'azote étaient similaires à toutes les latitudes (*i.e.*, entre les chaînes de montagnes). En moyenne, 70% de la minéralisation nette annuelle totale de l'azote se produisait de août à mai suggérant que l'automne et l'hiver sont des périodes critiques pour la transformation de l'azote du sol dans les écosystèmes forestiers et de la limite des arbres. Le contenu et les flux d'azote dans le sol étaient similaires entre les différentes chaînes de montagnes malgré des variations significatives dans la longueur de la saison de croissance et dans les températures moyennes annuelles. Il se peut donc que dans nos sites, l'humidité du sol et la qualité de la matière organique aient des effets plus importants que la température sur les variations du cycle de l'azote.

Mots-clés : acides aminés, cyclage de l'azote, hiver, limite des arbres, minéralisation, patrons saisonniers.

Nomenclature: Flora of North America, 1993-; Hulten, 1968.

Introduction

Although the ecology and distribution of treelines have been studied for more than a century, the factors that limit tree establishment and growth at treelines are still debated (Stevens & Fox, 1991; Körner, 1998; Jobbagy & Jackson, 2000; Sveinbjörnsson, 2000; Sveinbjörnsson, Hofgaard & Lloyd, 2002). In this study, we define treeline as the zone or

ecotone containing upright trees > 3 m tall between a forest ecosystem and an alpine or arctic ecosystem.

Nutrient limitation has often been considered one factor restricting plant growth at treeline; however, evidence that treeline stands have a greater degree of nutrient limitation than forested stands has been challenged. For example, Schulze, Chapin, and Gebauer (1994) reported nitrogen (N) to be the nutrient most limiting to white spruce (*Picea glauca*) near circumpolar treeline in the Brooks Range, Alaska; however, Sveinbjörnsson (2000) found no differential limitation of N in white spruce between the treeline and

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contiguous forest in the Chugach Range, Alaska. Nitrogen is often considered the most limiting nutrient to primary production in terrestrial plants (Vitousek & Howarth, 1991), especially at high latitudes, where soils are dominated by cold temperatures and recalcitrant organic matter with low rates of decomposition (Nadelhoffer *et al.*, 1992; Hobbie *et al.*, 2000). Previous studies have emphasized that net rates of annual N mineralization fail to account for the annual N demand by plants in both boreal forest (Ruess *et al.*, 1996) and arctic tundra ecosystems (Kielland, 1994; Schimel & Chapin, 1996). Current research indicates that organic N, particularly dissolved amino acids, constitutes a large portion of the N budget of plants in these high latitude ecosystems (Kielland, 1994; Lipson & Näsholm, 2001; McFarland *et al.*, 2002). It follows that organic N may play a prominent role in the N economy of treeline plants. Because competition between plants and soil microorganisms for amino acids is high during the growing season (Kaye & Hart, 1997; Jonasson *et al.*, 1999; McFarland *et al.*, 2002), studying the temporal patterns of both organic and inorganic N availability may be relevant in describing patterns of N availability between treeline and forested systems.

Research on the seasonal patterns of N cycling has shown that N sequestered in soil microbial biomass over winter can be released as a large flush during early spring (Brooks, Williams & Schmidt, 1998; Lipson, Schmidt & Monson, 1999). In N-limited systems, this over-winter sequestration of N in microbial biomass may serve to retain N in the system during snow melt and may subsequently constitute a large portion of the annual N available to plants (Brooks, Williams & Schmidt, 1998; Lipson, Schmidt & Monson, 2000). Moreover, prolonging the period of snow cover with a snow fence significantly increased subnival microbial N transformations (Brooks *et al.*, 1995; Walker *et al.*, 1999; Schimel, Bilbrough & Welker, 2004). The lower threshold for microbial activity in arctic soils is thought to be between -5°C (Clein & Schimel, 1995) and -10°C (Michaelson & Ping, 2003). Because the treeline ecotone is characterized by frequent high winds that can compact and potentially reduce the insulative properties of the snowpack (Pomeroy & Brun, 2001), soil temperatures may be lower in treeline soils compared with forested stands. Treelines may thus be subjected to a more variable climatic regime, with greater frequencies of freeze–thaw and/or wet–dry cycles than forested areas. These disturbances may result in reduced N accumulation within microbial biomass during winter and lower N availability at treeline throughout the growing season relative to forested areas.

We studied pools and fluxes of mineral, amino acid, and microbial biomass N at treeline and forested sites in three mountain ranges in Alaska for one year. Concurrently, we assessed site effects on decomposition with a common litter experiment. We also assessed intrinsic soil effects on decomposition with an incubation experiment in the laboratory. Our objective was to characterize general spatial and temporal patterns of N cycling within treeline and forested landscapes across a latitudinal transect of mountain ranges and to identify any commonalities in soil N cycling at multiple scales. We hypothesized that both N mineralization and soil organic matter quality would be lower at treeline sites

relative to forested sites, and would decrease with increasing latitude, due to direct and indirect effects of colder and more variable soil temperatures on these parameters.

Methods

STUDY AREA

Study areas were located at three paired treeline and forest sites within each of three mountain ranges along a 785-km latitudinal transect in Alaska. Regions of study (Figure 1) included a dry arctic climate (Brooks Range), a cool interior (White Mountains), and a wet coastal climate (Chugach Range). One site within the Brooks Range was at circumpolar treeline, while the remaining sites were at elevational treeline. Treeline sites were established within the zone of sparse but upright trees ($> 3\text{ m}$) below the krummholz zone, when present. Each forested site was established within the forest, 0.5 to 1 km down-slope from the associated treeline site. All sites were located in white spruce-dominated forests, although black spruce, *Picea mariana*, was present at some sites. Aspect, elevation, and vegetation varied among sites (Table I).

The Western Regional Climate Center for individual population centres in Alaska, within or near each range, provided data for average climate for each region (<http://www.wrcc.dri.edu>). At Bettles in the Brooks Range, mean air temperatures for January and July are -25°C and 15°C , respectively, and mean annual precipitation is 354 mm. At Circle City near the White Mountains, mean air temperatures for January and July are -27°C and 16°C , respectively, and mean annual precipitation is 207 mm. However, Circle City is at a low elevation, and previous research in the White Mountains demonstrated that high-elevation areas are much wetter than low-elevation areas (Lloyd & Fastie, 2002). In Anchorage, near but lower in elevation than our sites in the Chugach Range, mean air temperatures for January and July are -10°C and 15°C , and mean annual precipitation is 400 mm.

NITROGEN CYCLING

To assess spatial and seasonal patterns of pools and fluxes of dissolved inorganic N (DIN), amino acid N (AAN), and microbial biomass N (MBN), we conducted *in situ* soil incubations at four time periods during May 2001–May 2002: spring thaw, peak growing season, fall senescence, and over-winter. The goal was to be consistent in sampling each of these time periods within each mountain range, which was possible due to the 3–4 week lag in phenology (*e.g.*, budbreak) between the southernmost and northernmost sites. Sites were sampled in order from south to north. During the spring 2002 sampling period, soils in the Brooks Range thawed prior to those in the White Mountains and the sampling sequence was adjusted to accommodate this.

Within each treeline or forested sub-site, a 50-m transect was established parallel with the slope contour of the mountain. Six points were randomly selected along each transect, and soils were sampled near these points for the entire year. Rates of net DIN mineralization and net AAN production were measured using an *in situ* buried bag technique (Robertson *et al.*, 1999). We used a 6.7-cm-diameter

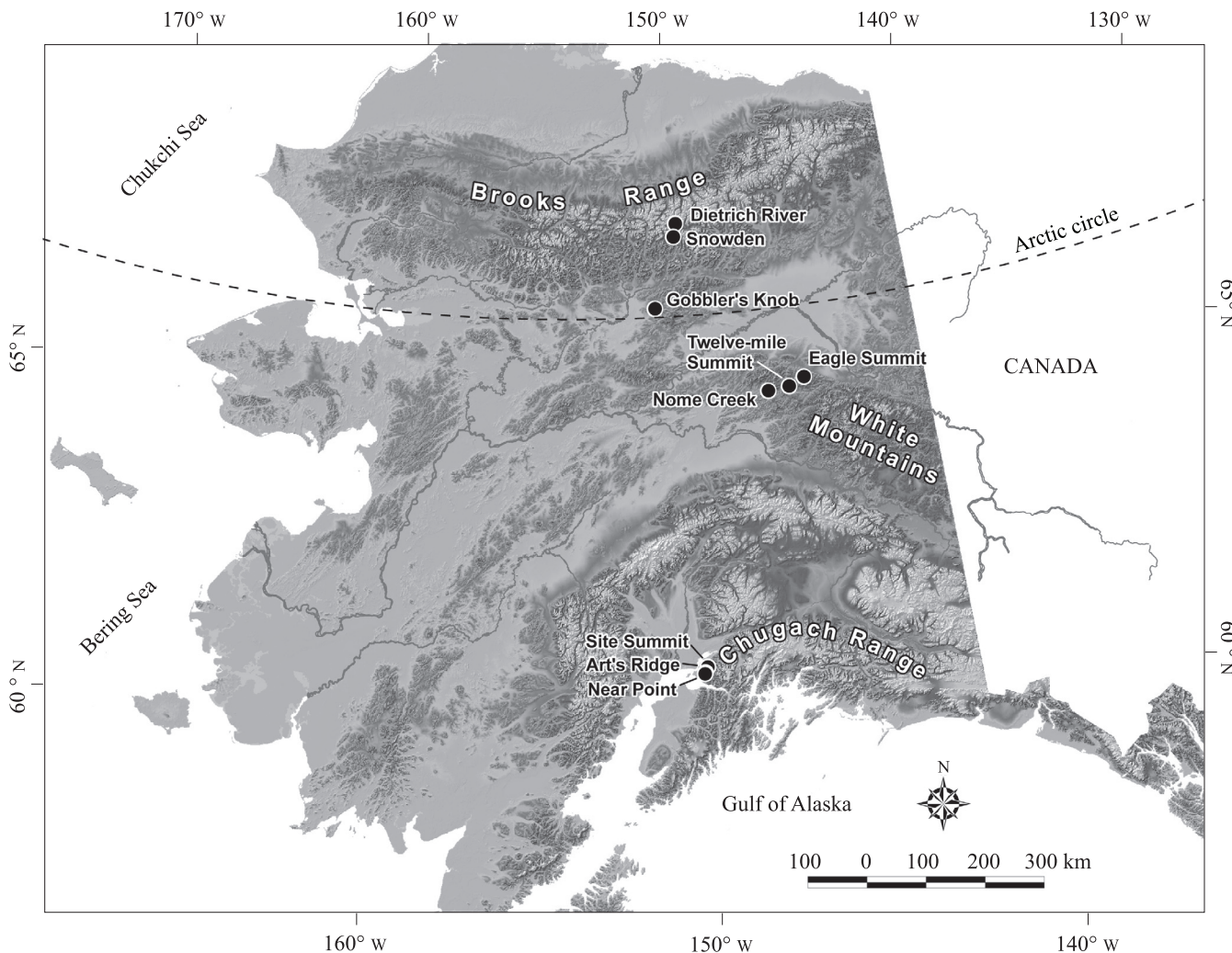


FIGURE 1. Location of study areas. Sites within each range are separated by 5–25 km and are listed from north to south in location. Dietrich River is near the circumpolar treeline, and all other sites are elevational treelines.

TABLE I. Study sites. Community description is based on Viereck *et al.* (1992). All treeline sites have less than 10% cover of trees and therefore are classified based on shrub vegetation. Tree density is the density of white spruce trees per ha.

Site		Latitude/ longitude	Slope (°)	Aspect	Elevation (m)	Tree density	Community description
BROOKS RANGE							
Dietrich River	Treeline	68° 01' N / 149° 41' W	25	SE	820	337 ± 72	Low open shrub birch
	Forest		15	SE	670	457 ± 29	Open white spruce forest
Snowden	Treeline	67° 49' N / 149° 48' W	25	W	790	302 ± 57	Low open shrub birch
	Forest		15	W	610	2381 ± 275	Open white spruce forest
Gobbler's Knob	Treeline	66° 44' N / 150° 40' W	2	S	620	16 ± 2	<i>Vaccinium</i> tundra
	Forest		5	S	520	550 ± 49	Open white spruce forest
WHITE MOUNTAINS							
Eagle Summit	Treeline	65° 30' N / 145° 21' W	12	S	997	336 ± 31	Low open shrub birch
	Forest		15	S	936	863 ± 57	Open white spruce forest
Twelve-mile Summit	Treeline	65° 23' N / 145° 56' W	10	NW	1010	38 ± 4	Sedge–willow tundra
	Forest		5	NW	960	379 ± 16	Open white spruce forest
Nome Creek	Treeline	65° 21' N / 146° 42' W	2	NW	770	69 ± 4	<i>Vaccinium</i> tundra
	Forest		5	NW	715	254 ± 19	Open white spruce forest
CHUGACH RANGE							
Site Summit	Treeline	61° 15' N / 149° 34' W	10	NW	200	467 ± 69	<i>Vaccinium</i> tundra
	Forest		20	N	170	263 ± 19	Open white spruce forest
Art's Ridge	Treeline	61° 10' N / 149° 39' W	15	W	621	27 ± 2	<i>Vaccinium</i> tundra
	Forest		15	SW	492	291 ± 79	Open white spruce forest
Near Point	Treeline	61° 9' N / 149° 40' W	15	W	590	24 ± 3	<i>Vaccinium</i> tundra
	Forest		2	W	388	71 ± 11	Open white spruce forest

steel corer fitted with a perforated plastic sleeve to collect paired adjacent soil cores and sampled below the live moss and detritus layers to a depth of 20 cm. The function of the perforated sleeve was to maintain structural integrity of the soil core during sampling. The perforated sleeve containing the intact core was then placed in a 1-mil breathable polyethylene bag followed by a fine mesh bag, gently returned to the original location, covered with litter and left to incubate. Incubation length was four weeks for the spring, growing season, and senescence sampling periods and from September 2001 to early June 2002 for the over-winter sampling period. The second core in each pair was stored on ice and transported to the laboratory in Fairbanks. Soils were rocky at some sites and sampling to 20 cm was not possible; for these samples, the minimum depth of coring was 10 cm. After harvesting each core, the subsequent pit was back-filled with soil to minimize disturbance to adjacent samples.

In the laboratory, soils were placed in dark storage at 3 °C and processed within 30 h. Each core was weighed and homogenized by hand. Rocks and roots > 2 mm diameter were removed. Soil moisture was determined gravimetrically for each core by oven drying a 5–7 g sub-sample at 65 °C to a constant weight. A 20-g sub-sample from each core was extracted with 75 mL 0.5 M K₂SO₄ on an orbital shaker for 1 h and vacuum filtered through pre-rinsed Pall Gelman Type A/E glass fibre filter paper (Pall-Gelman Sciences, Ann Arbor, Michigan, USA) into 50-mL centrifuge tubes. This extract was used for analysis of DIN, AAN, and MBN concentrations. After collection, the incubated cores were processed similarly.

NO₃⁻-N and NH₄⁺-N concentrations were determined colorimetrically using a modified Technicon system auto-analyzer (Whitledge *et al.*, 1981). Net DIN mineralization was calculated for each soil core pair as the difference in NO₃⁻-N plus NH₄⁺-N in excess of initial concentrations. Net nitrification was calculated as the difference between NO₃⁻-N concentrations for each pair.

Total dissolved amino acid N was determined using the ninhydrin method (Rosen, 1957). Net AAN production was calculated as the difference in AAN concentration between each final and initial core. All fluxes are reported per gram dry soil per day.

Microbial biomass N concentrations were analyzed from extracts of field fresh cores sampled in May, June, and September 2001 and from over-winter incubated cores in May 2002. MBN was determined using the chloroform fumigation-extraction method (Brookes *et al.*, 1985). A 20-g sub-sample from each soil sample was fumigated with ethanol-free chloroform for 24 h in a moistened modified pressure cooker, extracted in 75 mL 0.5 M K₂SO₄ following the procedure detailed for DIN, and frozen. Frozen samples were later thawed, digested using a persulfate oxidation digestion (Cabrera & Beare, 1993), and analyzed for NO₃⁻-N colorimetrically using a modified Technicon system auto-analyzer (Whitledge *et al.*, 1981). MBN was calculated as the difference in dissolved organic nitrogen (DON) between fumigated and non-fumigated samples.

SOIL ORGANIC MATTER DECOMPOSITION

We examined the decomposability of soil organic matter by measuring mass loss over 1 y at all sites using

15.2- × 1.8-cm birch wood tongue depressors (TDs) as a common litter. TDs were oven dried for 24 h and weighed before placement in the field. During September 2001, three 20-m transects were randomly established at high, mid, and low elevations (spaced 10 m apart) at each forest and treeline sub-site. Five TDs were inserted vertically into the soil profile until flush with the surface of the organic layer at 5-m intervals along each transect. In September 2002, TDs were carefully collected, transported to the laboratory in Fairbanks, rinsed, oven-dried, and reweighed. Percent mass loss was calculated. The site at Site Summit on Fort Richardson Military Base was closed during fall 2001 and was not sampled.

Soil organic matter quality was assessed by measuring soil respiration in the laboratory. During September 2001, 10 cores (6.7 × 10 cm) were sampled at random locations from high, mid, and low elevations at each sub-site. Samples were immediately stored on ice and frozen in the laboratory until the start of the experiment in May 2002. The exception was the site at Site Summit for reasons mentioned above, where cores were collected in May 2002 and were frozen until the start of the experiment.

Half the cores from each treeline and forested sub-site were randomly assigned to either a low (5 °C) or a high temperature (9 °C) treatment. The purpose of having two temperature treatments was to assess any intrinsic temperature sensitivity in soil respiration rates.

Each core was homogenized by hand as previously described. We used soils from the organic horizon unless the core contained less than 25 g organic soil, in which case soil from the mineral horizon was added to achieve a mass of 25 g. Soils were then split into two sub-samples. We determined water-holding capacity (WHC) with one sub-sample. These soils were then ground in a steel ball mill and analyzed for total carbon (C) & N on a LECO CNS 2000 (Leco Corporation, St. Joseph, Michigan, USA). Another 20-g sub-sample from each core was placed into an acid-washed glass mason jar (985 mL) and adjusted to 60% WHC. Jars were covered with breathable 1-mil plastic wrap held in place with rubber bands and pre-incubated in darkness at 3.5 °C for 7 d. Jars were then randomly assigned to one of the two temperature treatments and incubated in the dark for 11 weeks. Ten empty jars were also incubated as controls. Jars were sampled for respiration rate at 1, 2, 6, and 11 weeks. Jars were flushed with ambient air and readjusted to 60% WHC on a balance 24 h prior to sampling and capped with a tight-fitting metal lid equipped with a rubber sampling septa. A 15-mL gas sample was withdrawn by syringe from the headspace of each jar and analyzed for CO₂ concentration using a LI-COR 6200 (LI-COR Corp., Lincoln, Nebraska, USA) modified with a syringe-injection system. Soil respiration was calculated and expressed as μg CO₂-C·g soil_{DWT}⁻¹·d⁻¹ or as μg CO₂-C·g soil C⁻¹·d⁻¹.

VEGETATION AND SOIL CHARACTERISTICS

Percent cover of vegetation growth forms in the understory (excluding trees) was measured by ocular estimate for ten 1-m² plots for each treeline and forest sub-site. Tree density, tree basal diameter, and height were calculated using a point-centred quarter method (Bonham, 1989). During

August 2002, five soil pits were dug to a depth of 30–50 cm at each sub-site to describe average depth of soil horizons. To determine average bulk density, soil C and N stocks, and average rockiness of the soil, five soil cores (6.7×20 cm) were collected in random locations. These procedures were not performed on soils from sites in the White Mountains due to logistical constraints. In the laboratory, we separated the cores by horizon, measured the mass of rocks in each horizon, homogenized the soil through a 4-mm sieve, and dried it. These samples were ground by mortar and pestle and analyzed for total C and N on a LECO CNS 2000 combustion analyzer.

CLIMATE

Soil temperatures at 5 and 25 cm below the surface and air temperatures at 25 cm and 2 m above the surface were recorded hourly throughout the study with Campbell data loggers and thermistors (Campbell Scientific, Inc., Logan, Utah, USA) at both the treeline and forest stands in one site per mountain range. At the remainder of the sites, HOBO data loggers (Onset Computer Corp., Bourne, Massachusetts, USA) were used to record soil temperatures at both 5 and 25 cm and air temperatures at 25 cm and 2 m above the surface. Although we measured N indices only during 2001–2002, we used climate data averaged across 4 y (2000–2004) in order to account for gaps in the climate data that resulted from malfunctioning sensors.

STATISTICAL ANALYSIS

We used SAS 8.2 (SAS Institute, 1999) to analyze data and test for normality; where necessary, either log transformed or ranked data were analyzed. All significant statistical results from ranked data were compared with the analysis of the raw data, and unless divergent, results of the raw analysis are reported here. To determine differences between treeline and forest, data were analyzed with a paired design by calculating a difference between means of each paired treeline and forested site and using those values in the analysis. Data with both high skewness and kurtosis were analyzed with sign tests in PROC UNIVARIATE; otherwise, paired Student's *T*-tests were used to determine any overall difference between treeline and forested sites. Analysis of variance (PROC GLM) was used to determine if the difference between treeline and forest varied among mountain ranges or seasons.

When testing for temporal and spatial patterns, variables with a significant difference between treeline and forested sites were analyzed separately by stand type (treeline or forest) to separate the analysis from the paired aspect of the design, and variables with no significant stand-type effect were compiled by site. We used ANOVA on mean data for each site with season, and range and as classes and as independent effects in the model. To test for differences in total soil C and N, we used a mixed-model ANOVA on replicates for each site with season, range, and site nested within range as classes and as independent effects in the model. Any significant effects were subsequently examined with a Tukey's HSD test. Regression analysis (PROC REG) was used to describe relationships between N fluxes, N pools, temperature, or soil moisture. We used Spearman's correlation (PROC CORR) to examine any

possible correlation between any of the measured variables. Statistical significance was determined at $\alpha = 0.05$. Unless otherwise stated, data reported throughout the text represent means ± 1 SE.

Results

VEGETATION DESCRIPTION

Percent cover of vegetation growth forms in the understory and the density of white spruce varied between stand types and among ranges. In the Brooks Range, dwarf birch, *Betula nana*, was the dominant vascular species at most sites (both treeline and forest), excluding the Snowden forest site, where Labrador tea, *Ledum palustre* ssp. *decumbens*, was dominant, and the Gobbler's Knob forest site, where alder, *Alnus viridis* ssp. *fruticosa*, was dominant. In the White Mountains, the most common vascular species varied among sites. At Eagle Summit, diamond leaf willow, *Salix pulchra*, had the most cover in the forest, whereas blueberry, *Vaccinium uliginosum*, had the most cover at treeline. At Twelve-Mile Summit, *Salix pulchra* was also the dominant species at the forest site, but the sedge *Carex bigelowii* was dominant at treeline. At Nome Creek, *Vaccinium uliginosum* was dominant at treeline, and Alaskan spirea, *Spirea beaverdiana*, was most prevalent in the forest. In the Chugach Range, the vascular species with the highest cover was the same at all treeline sites: the crowberry, *Empetrum nigrum* ssp. *hermaphroditum*, which was also dominant in the forest site at Site Summit. At Art's Ridge, the dominant species in the forested site was the bluejoint grass, *Calamagrostis canadensis*. At Near Point forest, the most common understory species was *Alnus viridis*.

SOILS PHYSICAL PROPERTIES

Total soil C was slightly greater at treeline sites (treeline = $22 \pm 0.8\%$; forest = $20 \pm 0.9\%$); however, these differences were not statistically significant ($T = -1.19262$, $df = 8$, $P = 0.2672$), which most likely is a function of the large variability among sites (Table II). The coefficients of variation (CV) calculated for sites within each range varied from 11.7% (Brooks Range forest sites) to 30.1% (White Mountains forest sites). Total C on an aerial basis did not differ between treeline and forested sites ($T = 1.0353$, $df = 1$, $P = 0.4889$), and ranged from 3522 ± 315 g C·m⁻² in the Brooks Range to 6646 ± 852 g C·m⁻² in the Chugach Range. Total N was similar in treeline and forested sites (treeline = $0.90 \pm 0.04\%$, forest = $0.96 \pm 0.04\%$; $T = 0.2517$, $df = 8$, $P = 0.8075$). Total soil C was highest in the White Mountains, and similar in the Brooks and Chugach Ranges (Table II). The ratio of C to N did not vary between treeline and forest sites ($T = -2.0367$, $df = 8$, $P = 0.0761$) and was highest in the Chugach Range and lowest in the White Mountains. There was greater variability in total soil C and C:N ratio among sites within ranges than among ranges, and CVs were two times greater among sites within ranges than among mountain ranges.

CLIMATE

Overall, soils at treeline were colder than soils in the forest, particularly during winter (October to April; $M = 17$, $P < 0.0001$; Figure 2). During the remainder of the year, soil

TABLE II. Soil physical properties. Percent C, percent N, and C:N data are from organic soils ($n = 10\text{--}14$ per site). “-” = sites not sampled. C ($\text{g C}\cdot\text{m}^{-2}$) (top 20 cm); $n = 4$. Values are mean \pm standard deviations.

Site		C (%)	N (%)	C:N	C ($\text{g C}\cdot\text{m}^{-2}$)
BROOKS RANGE					
Dietrich	Forest	22.5 \pm 13.4	0.9 \pm 0.5	22.5 \pm 4.5	4182 \pm 998
River	Treeline	16.9 \pm 8.70	0.8 \pm 0.4	21.3 \pm 3.1	2207 \pm 571
Snowden	Forest	17.9 \pm 12.4	0.8 \pm 0.5	18.0 \pm 2.6	3058 \pm 1082
	Treeline	22.0 \pm 12.4	1.1 \pm 0.6	27.6 \pm 3.1	4558 \pm 1642
Gobbler’s	Forest	19.5 \pm 10.3	1.1 \pm 0.6	21.6 \pm 4.1	3262 \pm 898
Knob	Treeline	22.0 \pm 8.30	0.8 \pm 0.3	21.0 \pm 3.6	4047 \pm 1118
WHITE MOUNTAINS					
Eagle	Forest	29.3 \pm 9.10	1.4 \pm 0.3	17.1 \pm 1.9	-
Summit	Treeline	25.0 \pm 9.50	1.1 \pm 0.3	17.3 \pm 2.4	-
Twelve-mile	Forest	18.0 \pm 10.0	1.0 \pm 0.6	21.0 \pm 3.4	-
Summit	Treeline	18.8 \pm 6.50	1.1 \pm 0.4	22.6 \pm 4.7	-
Nome	Forest	17.9 \pm 10.6	1.0 \pm 0.6	17.9 \pm 4.9	-
Creek	Treeline	28.0 \pm 7.90	1.3 \pm 0.4	22.9 \pm 3.3	-
CHUGACH RANGE					
Site Summit	Forest	21.6 \pm 4.5	0.8 \pm 0.2	18.2 \pm 2.9	5036 \pm 1466
	Treeline	20.9 \pm 6.9	0.9 \pm 0.4	27.0 \pm 3.5	5052 \pm 1861
Art’s Ridge	Forest	15.9 \pm 4.0	0.9 \pm 0.2	27.5 \pm 3.5	7414 \pm 2458
	Treeline	19.5 \pm 5.6	0.7 \pm 0.2	24.9 \pm 4.1	5254 \pm 1990
Near Point	Forest	17.1 \pm 5.8	0.8 \pm 0.2	20.8 \pm 2.2	7487 \pm 3516
	Treeline	25.4 \pm 6.2	0.9 \pm 0.2	29.2 \pm 2.1	8739 \pm 3617

TABLE III. Summary of soil and air temperatures ($^{\circ}\text{C}$). Values are means from 2000–2004 \pm 1 SE. Frost-free days refers to the number of days that soils were continuously thawed (spring) or frozen (autumn). We defined the growing season as June–August.

	Annual mean	Max	Min	Frost-free days	Mean temp.
					of growing season
SOIL TEMPERATURE					
Brooks Range					
Forest	-0.18 \pm 0.12	14.96	-10.19	136	6.01 \pm 0.18
Treeline	-1.51 \pm 0.09	15.31	-14.24	136	6.25 \pm 0.10
White Mountains					
Forest	1.41 \pm 0.08	13.01	-7.38	179	6.9 \pm 0.12
Treeline	0.37 \pm 0.07	20.22	-11.36	172	6.09 \pm 0.15
Chugach Range					
Forest	3.07 \pm 0.21	17.59	-0.97	197	10.53 \pm 0.28
Treeline	1.95 \pm 0.23	11.63	-6.97	176	6.12 \pm 0.33
AIR TEMPERATURE					
Brooks Range					
Forest	-8.31 \pm 0.45	32.48	-45.50		11.24 \pm 0.25
Treeline	-4.91 \pm 0.19	21.59	-35.84		10.84 \pm 0.16
White Mountains					
Forest	-3.18 \pm 0.24	21.72	-55.64		11.17 \pm 0.21
Treeline	-3.48 \pm 0.20	21.30	-33.88		10.06 \pm 0.18
Chugach Range					
Forest	4.16 \pm 0.41	40.75	-43.33		16.10 \pm 0.66
Treeline	2.02 \pm 0.38	17.46	-19.63		9.42 \pm 0.46

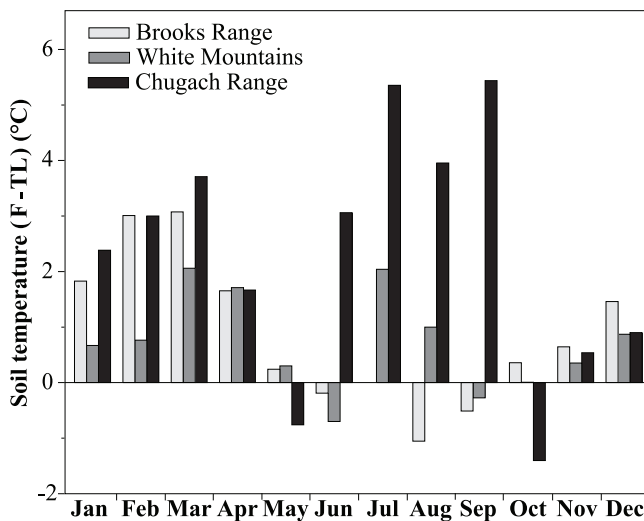


FIGURE 2. Difference between treeline (TL) and forested (F) sites in average monthly soil temperatures among mountain ranges. Soil temperatures were measured at 5 cm below the surface. These data were compiled from 2000–2004 for three sites in each range.

temperatures at treeline and in the forest were very similar. Sites at treeline experienced a more variable soil temperature regime than forested sites, with greater minimum and maximum soil temperatures (Table III) and a higher frequency of temperature fluctuation (Figure 3). In the Brooks Range, the length of the frost-free period was equal for treeline and forest (136 d); the difference between stand types increased to 7 d in the White Mountains and 21 d in the Chugach Range.

NITROGEN POOLS

The pool size of dissolved inorganic N (DIN) in forested sites ($5.56 \pm 0.87 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}$) was significantly

greater than that of treeline sites ($3.64 \pm 1.01 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}$) (Figure 4) and was consistent across mountain ranges and sampling periods (sign test, $M = 7.5$, $P = 0.0167$). Values reported here are means of all sampling points. The average pool size of free amino acids was of similar magnitude to that of DIN, but did not differ between forested ($5.39 \pm 0.49 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}$) and treeline ($5.40 \pm 0.95 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}$) sites ($M = 1.5$, $P = 0.736$, ns). The largest pool of biologically active N was found in microbial biomass, where values for forested sites ($68.41 \pm 8.27 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}$) and treeline sites ($79.12 \pm 9.60 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}$) were not statistically different ($M = -4.5$, $P = 0.176$). Soil DIN and AAN pools were positively correlated with total soil N, but were negatively correlated with C:N (DIN, $\rho = -0.3742$, $P = 0.0014$; AAN, $\rho = -0.2411$, $P = 0.04$). Mineral and amino acid pools were positively correlated when examined across sites and time periods ($r^2 = 0.45$, $P < 0.0001$), and both were positively correlated with MBN, supporting the notion that microbial biomass functions as a strong sink and source for N in soils.

The pattern of seasonal variation in organic and inorganic N pool sizes was similar for treeline and forest sites; pools had high values during spring and very low values during peak growing season (Figure 4). In contrast to this seasonal pattern, there were no differences among mountain ranges in soil DIN (forest sites: $F = 1.41$, $df = 2$, $P = 0.315$; treeline sites: $F = 1.4$, $df = 2$, $P = 0.3168$). Amino acid pools varied slightly among ranges ($F = 3.8$, $df = 2$, $P = 0.0855$), primarily due to high spring values in the White Mountains. The MBN pool size was significantly greater in the White Mountains than in the Chugach and Brooks Ranges (ANOVA on range effects, $F = 6.69$, $df = 2$, $P = 0.0295$), but was of similar size in the Chugach and Brooks Ranges. This trend was driven by high MBN pools during spring in the White Mountains (Figure 5) and may have been due to wetter soils at these sites, given that MBN pool sizes and

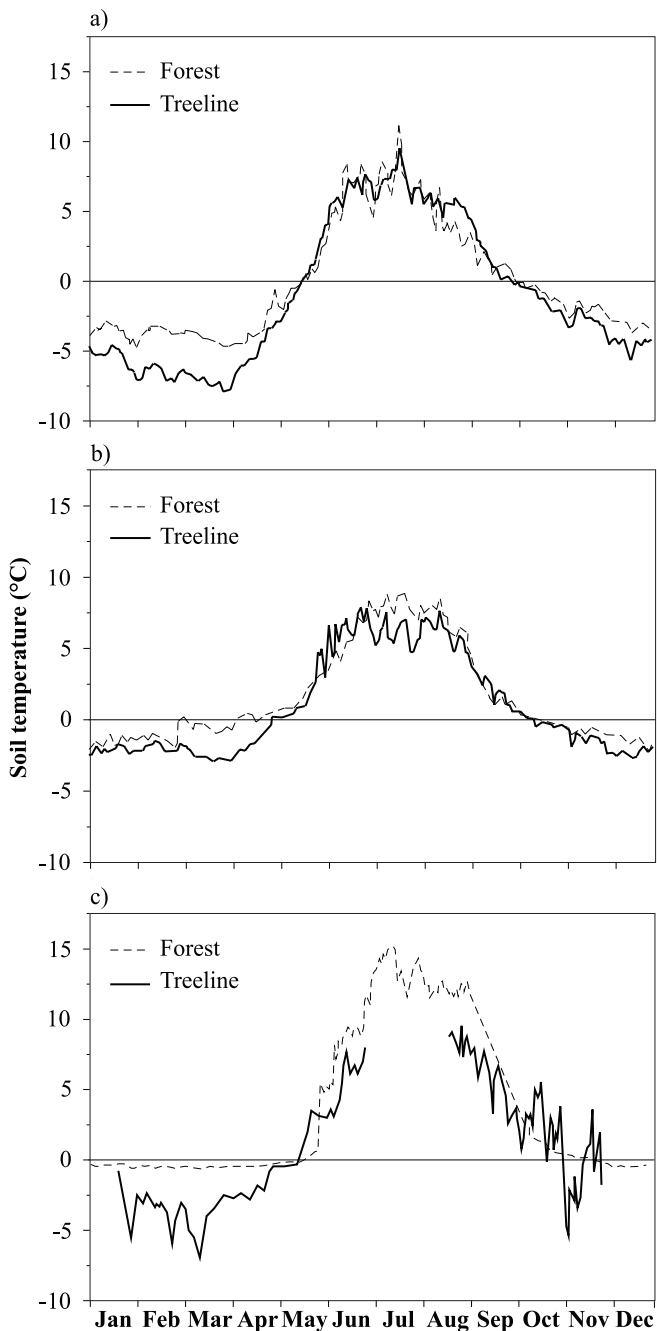


FIGURE 3. Mean soil (5 cm deep) temperatures (°C) by mountain range at forest and treeline sites for the Brooks Range (a), the White Mountains (b), and the Chugach Range (c). Data represent mean daily averages from 2000–2004.

percent soil moisture were positively correlated ($r^2 = 0.59$, $P < 0.0001$, Table IV).

NITROGEN FLUXES

Rates of both net N mineralization and net amino acid production were higher in forested sites (0.07 ± 0.03 and $-0.03 \pm 0.02 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{d}^{-1}$, respectively) compared with treeline sites (-0.01 ± 0.02 and $-0.08 \pm 0.04 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{d}^{-1}$, respectively; mean values across ranges and time periods are reported here) (sign test, $M = 8.5$, $P = 0.0006$ for

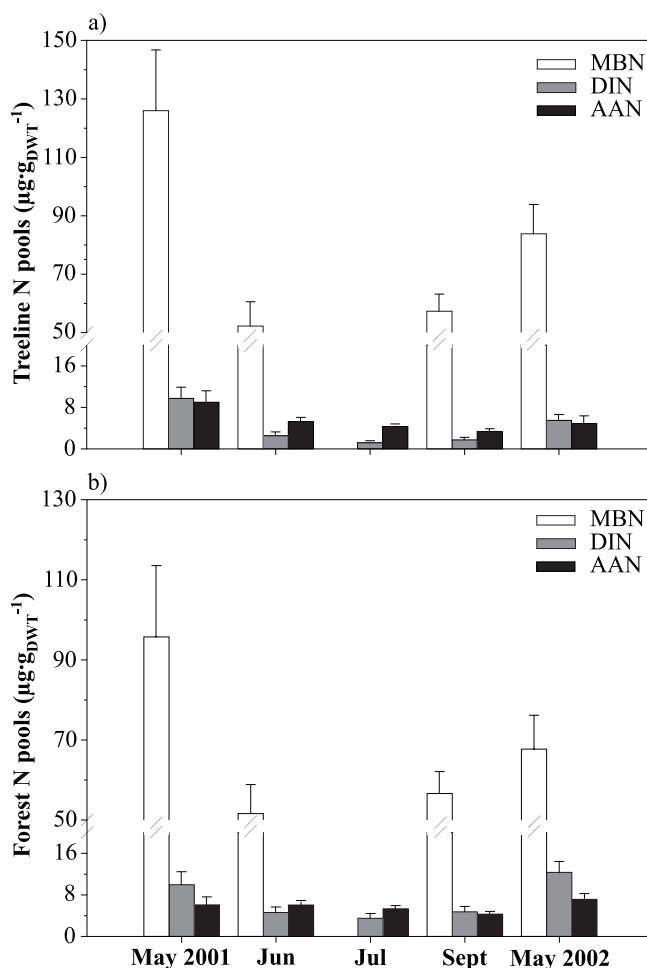


FIGURE 4. Seasonal patterns of microbial N, DIN, and AAN concentrations for (a) treeline sites and (b) forested sites. Means + 1 SE are represented, $n = 45\text{--}52$. Data were not collected for MBN during July.

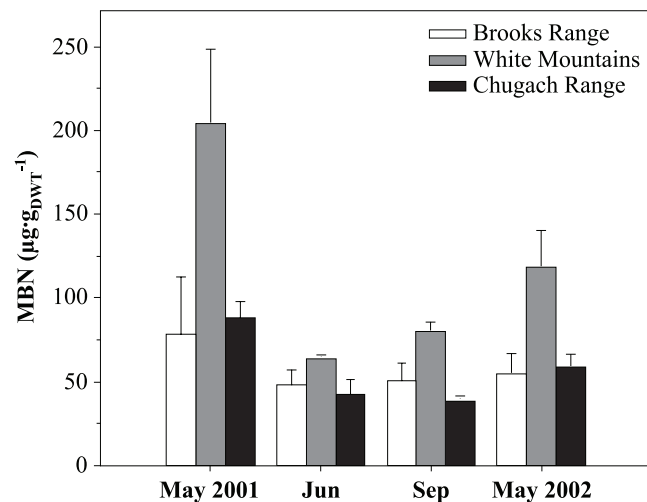


FIGURE 5. Seasonal patterns of microbial biomass N (MBN) in each mountain range. Data are means + 1 SE for all points in each mountain range ($n = 36$).

DIN; $M = 7.5$, $P = 0.0167$ for AAN). These negative rates represent net immobilization of both amino acids and inorganic N sources across all data points and result mainly

TABLE IV. Results of Single Linear Regression analysis of means of subplots (per site). “*” = significant at treeline sites only. When regressing variables on mean soil temperatures from June–August, we used only data collected during summer.

Independent variable	Dependant variable	r ²	T-statistic	P-value
MBN pool	N mineralization	0.4038	-5.82	< 0.0001
	AA production	0.6276	-9.18	< 0.0001
	DIN pool	0.3477	6.02	< 0.0001
	AAN pool	0.4871	8.04	< 0.0001
Mean soil temp for June–August	N mineralization	0.5477	2.46	0.0572*
	AA production	0.5099	2.28	0.0711
	MBN pool	0.3169	3.52	0.0170*
Mean soil temp during July	N mineralization	0.472	2.11	0.0881
	AA production	0.5134	2.30	0.0701
	MBN pool	0.4913	-2.20	0.0794
% Soil moisture	MBN pool	0.5851	9.79	< 0.0001
	AAN pool	0.3007	5.41	< 0.0001
	DIN pool	0.3787	6.44	< 0.0001
	N mineralization	0.2313	-3.88	0.0003
	AA production	0.2707	-4.31	< 0.0001
DIN pool	N mineralization	0.2698	-4.30	< 0.0001
AAN pool	N mineralization	0.1419	-2.88	0.0059
AAN pool	DIN pool	0.4542	7.52	< 0.0001
AA production	N mineralization	0.4018	5.80	< 0.0001
N mineralization	DIN pool	0.2698	-4.30	< 0.0001

from the high rates of N immobilization during spring. Rates of net nitrification were similar for forested ($0.02 \pm 0.02 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{d}^{-1}$) and treeline ($0.01 \pm 0.01 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{d}^{-1}$) sites ($M = 5, P = 0.1214, \text{ns}$). Both net N mineralization and amino acid production rates were negatively correlated with the pool of microbial biomass N (Table IV), although this relationship was mainly driven by strong immobilization of N during spring.

There were significant seasonal differences in rates of net N mineralization, net nitrification, and net amino acid production. The amount of both inorganic and organic N mineralized per season increased steadily from high rates of immobilization in spring to positive net production values during winter (Figure 6). Similar to the results for soil N pools, fluxes of N did not vary among mountain ranges ([treeline and forest analyzed separately] N mineralization: treeline, $F = 0.40, \text{df} = 2, P = 0.6835$; forest, $F = 0.39, \text{df} = 2, P = 0.6932$; AA production: treeline; $F = 2.17, \text{df} = 2, P = 0.187$, forest, $F = 1.18, \text{df} = 2, P = 0.3658$; net nitrification: treeline, $F = 2.79, \text{df} = 2, P = 0.1359$, forest, $F = 0.11, \text{df} = 2, P = 0.9002$).

When averaged across mountain ranges, the annual amount of net N mineralized at forested sites ($15.73 \pm 7.62 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{y}^{-1}$) was nearly five times greater than at treeline sites ($3.26 \pm 2.26 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{y}^{-1}$); however, this difference was not significant ($M = 1, P = 0.727, \text{ns}$). This statistical result may be a consequence of our inability to detect a difference due to the high degree of variation among sites. Additionally, the average difference between each paired forest and treeline site for annual net mineralization was $15.01 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{y}^{-1}$, but this ranged between -11.35 and $38.57 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{y}^{-1}$. Annual net production of amino acids was marginally higher in forested sites ($0.20 \pm 3.44 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{y}^{-1}$) than at treeline sites, due

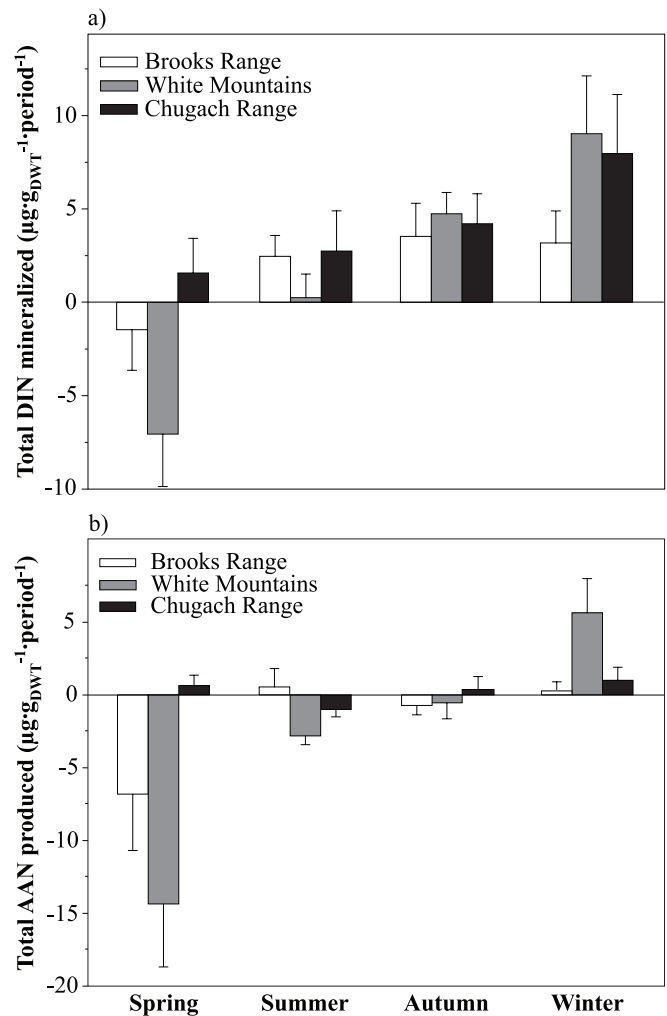


FIGURE 6. Net mineralization or production of N per season in each mountain range for (a) mineral N and (b) amino acid N. These values were calculated by multiplying the daily rate by number of days in each period ($n = 36$).

to a high degree of net immobilization measured at the latter ($-8.23 \pm 4.82 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{y}^{-1}$) (sign test, $M = 4, P = 0.078$). The average difference between forested and treeline sites for AAN was much smaller than for mineral N ($2.98 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{y}^{-1}$), and varied between -2.40 and $17.32 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{y}^{-1}$.

DECOMPOSITION

Decomposition (percent mass loss) of tongue depressors was approximately 43% greater in forest sites ($5.7 \pm 1.4\%$) relative to treeline sites ($4.0 \pm 0.7\%$), but this difference was marginal statistically ($T = 1.77, \text{df} = 7, P = 0.1202$). The lack of strong statistical evidence is driven by a minor difference between treeline and forest in the White Mountains. Percent mass loss in the Chugach Range was significantly greater ($9.1 \pm 1.4\%$) than in the White Mountains ($2.6 \pm 0.2\%$) and the Brooks Range ($4.3 \pm 0.7\%$) (both $P < 0.0001$).

When expressed on a per g dry weight basis, respiration rates of forested soils did not differ between soils incubated at 5°C ($44.9 \pm 2.7 \mu\text{g C}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{d}^{-1}$) and 9°C ($52.4 \pm 5.5 \mu\text{g C}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{d}^{-1}$). However, in soils from

treeline sites, soil respiration rates at the lower temperature ($55.9 \pm 4.2 \mu\text{g C}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{d}^{-1}$) were significantly greater than at the higher temperature ($45.7 \pm 2.5 \mu\text{g C}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{d}^{-1}$) ($F = 4.11$, $\text{df} = 1$, $P = 0.0459$). Treeline soils had similar rates ($50.8 \pm 2.5 \mu\text{g C}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{d}^{-1}$) of respiration relative to soils from forested sites ($48.6 \pm 3.1 \mu\text{g C}\cdot\text{g}_{\text{DWT}}^{-1}\cdot\text{d}^{-1}$) ($T = -0.46791$, $\text{df} = 8$, $P = 0.6485$). These trends were reversed when rates were expressed per g C. Soils from forested sites had higher respiration rates ($293.0 \pm 11.0 \mu\text{g C}\cdot\text{g C}^{-1}\cdot\text{d}^{-1}$) than those from treeline sites ($259.4 \pm 12.6 \mu\text{g C}\cdot\text{g C}^{-1}\cdot\text{d}^{-1}$) ($M = 5$, $P = 0.0309$), suggesting higher soil C quality in forested compared with treeline sites.

Although soil respiration rate did not differ among mountain ranges ($F = 0.17$, $\text{df} = 2$, $P = 0.8516$ [from analysis of per unit C, all other groups had similar values]), there were large differences in soil respiration rates among sites within ranges when averaged across stand types ($F = 7.52$, $\text{df} = 6$, $P < 0.0001$) (Figure 7). This suggests that variability in the effects of C quality on soil respiration rates may be greater at landscape than regional scales.

Discussion

TREELINE VERSUS FOREST

Our findings showing greater DIN pool sizes and higher rates of net N mineralization in forested compared with treeline sites are consistent with a number of previous studies (Sveinbjörnsson *et al.*, 1995). Our data indicate that both site-factor effects and soil organic matter quality contribute to lower rates of decomposition and net N production in treeline stands relative to forested stands. Site effects, mainly low soil temperatures, appear to depress nutrient cycling rates at treeline. Treeline soils were colder 7–8 months of the year and were either cooler (White Mountains and Chugach Range) or similar (Brooks Range) in temperature

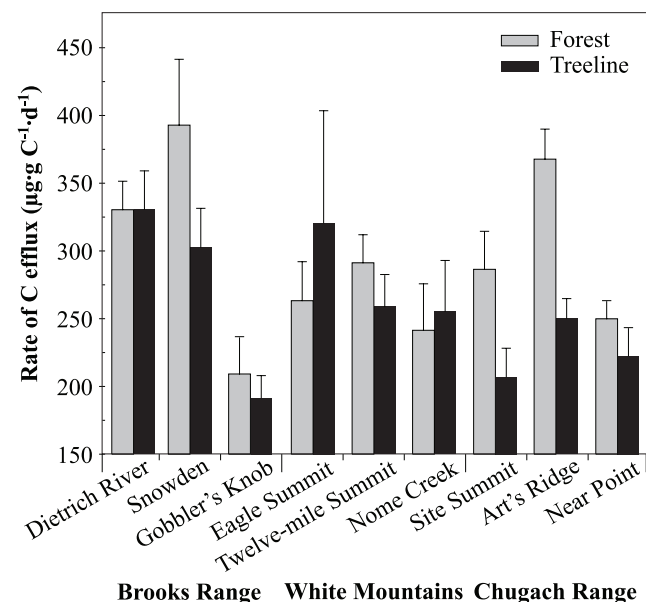


FIGURE 7. Potential soil respiration rate (mean + 1 SE) in soils from treeline and forested sites. For each observation, $n = 10$. Data from the temperature treatments were combined.

to forested soils during July. In addition to being colder, treeline soils also experienced greater fluctuations in soil temperatures. At least one study on repeated freeze–thaw events in soils reported that although mineralization was generally stimulated after a single event, multiple freeze–thaws caused reduced net mineralization by reducing the ability of microbes to process soil N (Schimel & Clein, 1996); however, this effect did vary among soils from different vegetation types.

During the growing season, soil temperatures at treeline were similar to those in the forest (Figure 2), and in some cases, soils were warmer in treeline stands; however, this did not translate to equal or higher N mineralization rates or greater rates of decomposition of common litter. It is difficult to know whether microbial activity is unresponsive to soil temperature for these stand type differences or if other environmental factors are more important or are masking temperature effects on N mineralization. We did not directly assess any measure of drought stress, but all N pools and fluxes measured were more tightly related to soil moisture content than to mean air and soil temperature (Table IV), and decomposition of common litter was negatively correlated with soil moisture (Spearman's correlation, $P = 0.0075$). Given the lack of a direct response of N cycling to increased soil temperatures during the growing season, other factors must be more important in explaining differences in soil N cycling rates between treeline and forest stands during this time period.

Common litter decayed approximately 30% slower in treeline stands compared with forested stands, but since the sampling period was 1 y, it is difficult to determine whether reduced decay at treeline is due to colder temperatures during winter or to factors other than soil temperature, such as soil organic matter quality. However, the laboratory decomposition study showed lower respiration rates per unit soil C in treeline sites compared with forested sites, suggesting that organic matter quality may contribute to reduced rates of N mineralization at treeline. In interior Alaskan boreal forests, soil organic matter quality decreases throughout succession (Flanagan & VanCleve, 1983), and in arctic tundra, C quality varies strongly among ecosystem types (Nadelhoffer *et al.*, 1991). A study from Swedish Lapland reported higher C quality in a mountain birch forest than in the adjacent tundra (Sjögersten & Wookey, 2002), but we are not aware of any study that has directly examined the difference in C quality between treeline and forested stands of white spruce at high latitudes.

Plant species are known to have strong effects on nutrient cycling, and our treeline sites have a greater abundance of shrubs than forested sites (Student's T -test, $T = -2.792$, $P = 0.0235$). In particular, shrubs such as *Betula nana* and *Ledum palustre*, both of which have high phenol and lignin contents (Hobbie, 1996; Castells, Penñelas & Valentine, 2003), may negatively affect soil organic matter quality at sites where they dominate. Furthermore, crowberry, *Empetrum nigrum*, which is dominant at the treeline sites in the Chugach Range, is an allelopathic species (Nilsson, 1994), as are several ericaceous species (Mallik & Pellissier, 2000). The input of these chemicals from plants may depress

rates of N cycling (Wardle *et al.*, 1998). Species effects, however, are rarely simple, and direct effects of species on litter quality may differ from direct effects on rates of soil N turnover. The forested sites had a slightly higher percentage of moss cover (Student's *T*-test, $T = 2.249$, $P = 0.0546$), which is known to decompose very slowly (Hobbie, 1996). However, given the presence of other more decomposable litter types such as spruce and alder at these forested stands, moss likely contributes less to total litterfall at forested compared to treeline sites. We did not directly examine specific species effects and can only infer that shrub or moss composition may affect N cycling.

SEASONAL PATTERNS

We found pronounced seasonal variation in N pools and fluxes that were strikingly similar across the 785-km latitudinal transect regardless of variation among sites, between treeline and forested stands, and in climate. These seasonal patterns are consistent with patterns described by other high-latitude studies (Giblin *et al.*, 1991; Schimel, Bilbrough & Welker, 2004) and at the Niwot Ridge site in the Rocky Mountains of Colorado (Brooks, Williams & Schmidt, 1998; Lipson, Schmidt & Monson, 1999). The seasonal fluctuation of microbial biomass at our sites is also similar to the pattern in a subalpine heath in Swedish Lapland (Jonasson *et al.*, 1999).

Although the majority of previous studies have focused primarily on processes that occur during the growing season, data from the present study support the increasing emphasis that recent research has placed on both the autumn and the over-winter period for N processing (Hobbie & Chapin, 1996; Schadt *et al.*, 2003; Schimel, Bilbrough & Welker, 2004). Our data show that the strongest sinks for both mineral and organic N were during spring and summer,

TABLE V. The proportion of N mineralized or produced per season for forest and treeline sites in all mountain ranges. All negative values (indicating net immobilization) were replaced with a zero for the purpose of calculating the percent each season contributes to the annual amount produced.

Range	Stand type	Spring	Summer	Autumn	Winter
NET MINERALIZATION					
Brooks	Treeline	0	0.189	0.335	0.476
	Forest	0.058	0.270	0.377	0.294
White	Treeline	0	0	0.297	0.703
	Forest	0.148	0.214	0.247	0.391
Chugach	Treeline	0	0	0.394	0.606
	Forest	0	0.134	0.315	0.551
NET NITRIFICATION					
Brooks	Treeline	0.298	0.169	0.234	0.299
	Forest	0.232	0.250	0.372	0.146
White	Treeline	0.050	0.234	0.476	0.240
	Forest	0.077	0.482	0.441	0
Chugach	Treeline	0	0	0.003	0.997
	Forest	0.090	0	0.336	0.573
NET AMINO ACID PRODUCTION					
Brooks	Treeline	0	0	0	0
	Forest	0	0.635	0	0.365
White	Treeline	0.460	0	0.540	0
	Forest	0.352	0	0.129	0.519
Chugach	Treeline	0	0	0	1
	Forest	0	0	0.051	0.949

while net mineralization mainly occurred during autumn and over winter (Table V). Averaged across all sites, 70% of the annual net N mineralization and net amino acid production occurred during the coldest months. The only exception was in the Brooks Range, where in the forested sites, amino acid production during winter was 37% of the total annual production, and at treeline, where net immobilization of amino acids occurred during all seasons. These data, however, strongly support the idea that autumn and winter are active periods for net production of both mineral and amino acid N within high-latitude systems.

We hypothesize the following scenario to explain the seasonal pattern of N dynamics in the sub-arctic. During autumn, there is an increase in the amount of root exudates into the soil matrix (Olsrud & Christensen, 2004) and an increase in fine root mortality and decomposition (Ruess, Hendrick & Bryant, 1998; Ruess *et al.*, 2003). These relatively labile C and N inputs at a time of low plant nutrient uptake are rapidly utilized by soil microbial biomass during fall and early winter. Throughout the remainder of winter, activity of the microbial community may be intermittent depending on temperature thresholds; however, some activity will occur under the snowpack (Lipson, Schmidt & Monson, 1999). This results in accumulation of mineralized N in the soil and leads to pools of extractable NH_4^+ and amino acids in spring. The microbial population transitions from fungal-dominated to bacterial-dominated (Ley & Schmidt, 2002; Lipson, Schadt & Schmidt, 2002; Schadt *et al.*, 2003) during spring as plants come out of dormancy, resulting in a flush of N that is rapidly taken up by plants and microbes (Lipson, Schmidt & Monson, 1999). Plant uptake subsequently leads to lower N pools during spring and summer, although there is enough substrate available for N mineralization to also occur. Additionally, drying events throughout summer may reduce the size or activity of the microbial community. These patterns of seasonal dynamics are important for understanding the variation in the underlying controls on microbial possession and retention of N in these Alaskan treeline and forested ecosystems.

LATITUDINAL PATTERNS

Although soil and air temperatures varied with latitude, indices of N cycling did not. Rates and patterns of net N mineralization, amino acid production, and nitrification were similar even though the mountain ranges spanned greater than 6° latitude. Decay of a common substrate was substantially greater in the Chugach Range compared with the other two ranges, but similar in the Brooks Range and White Mountains. Therefore, within and among landscapes, there is a disconnect between the factors regulating the decomposition of complex substrates and the turnover of N observed, since decomposition of common litter varied with climate among ranges, but N pools and flux rates varied within landscapes. Although the C:N ratio of soil in the Chugach Range was significantly higher than in the other ranges (both $P < 0.05$), we did not detect significant variation among mountain ranges in soil respiration per unit C when soils were incubated under controlled conditions. This suggests that whereas soils in the Chugach Range are not of different organic matter quality than soils in the other ranges, fundamental distinctions among mountain ranges,

such as the length of the growing season and warmer temperatures, may be more important than site differences in controlling decomposition processes. During the growing season, the average soil temperatures among mountain ranges varied within a few degrees. Most likely, variation in temperature within this narrow span does not limit the physiological capacity of microbes to process soil organic matter, which could explain why indices of N cycling did not change with increasing latitude. This is supported by the lack of a difference in respiration per gram C between soils incubated at 5 and 9 °C. Soils from other high-latitude ecosystems have also been shown to be relatively insensitive to temperature fluctuations within this range (Giblin *et al.*, 1991; Nadelhoffer *et al.*, 1991; Stottlemyer, Rhoades & Steltzer, 2001). Although soil N processes were similar across latitudes, branch growth of white spruce was almost three times greater in the Chugach Range than in the White Mountains or Brooks Range (M. Smith & T. Traustason, unpubl. data). This may be a function of the maritime climate, the longer growing season, and higher temperatures during both summer and winter in the Chugach Range.

We found more variation among sites within ranges than among ranges when averaged across sites and stand types in soil percent C, soil moisture content, flux of C in the lab incubation, and amount of amino acids produced annually. Two studies analyzing trends of tree-ring growth in Alaska also report substantial regional and site variability in the response of white spruce to climate (Lloyd & Fastie, 2002; Wilmking *et al.*, 2004). Lloyd and Fastie (2002) correlated the width of tree rings to climate for white spruce growing at similar sites in the White Mountains and found that in the last century, growth of treeline trees at Eagle Summit was positively correlated with temperature, while at Twelve-mile Summit growth was not, but growth of treeline trees at Nome Creek exhibited a negative temperature response. Treeline trees at all these sites also exhibited greater growth than trees in the forest during the last quarter century. A differential response of growth between treeline and forested stands was not found in the Brooks Range or the Alaska Range, although white spruce responded both positively and negatively to climate in both ranges (Wilmking *et al.*, 2004). The authors of both studies attributed the reduced growth response to warming temperatures over the past century to drought stress. Drought stress varies substantially among sites due to differences in topography, hydrological regimes, and proximity to permafrost, and it directly affects nutrient cycling and nutrient uptake by plants. At our sites, all pools and rates of N turnover were highly correlated to soil moisture, which is consistent with other studies in arctic and alpine ecosystems (Binkley *et al.*, 1994; Fisk, Schmidt & Seastedt, 1998).

ORGANIC N

The present results indicate that pools, fluxes, and seasonal patterns of dissolved amino acids are similar to dissolved inorganic N. This is in contrast to the work of Kielland (1995) in arctic tundra, who reported amino acid concentrations 4 to 10 times higher than ammonium, although the range of amino acids he reported was similar ($1\text{--}8 \mu\text{g N}\cdot\text{g}_{\text{DWT}}^{-1}$) to the average concentration reported

here. This discrepancy may result from either a difference in sampling methodology or sample processing. Our data on the size and proportion of mineral to amino acid N are similar to those reported for a boreal forest gradient in northern Sweden (Nordin, Högberg & Näsholm, 2001).

The microbial sink for amino acid N was stronger than the sink for mineral N at both treeline and forested sites. At treeline, there was reduced net production of amino acids, but this was not reflected by reduced N in the microbial biomass or by lower pools of dissolved AAN in soils. This suggests that the N taken up by microbes may support functions other than growth (*e.g.*, the amount of N in microbial biomass) (Vance & Chapin, 2001), although we have no data on the turnover rates of the microbial community. Amino acids cycle rapidly through microbes on the scale of hours, not months (Lipson *et al.*, 2001; Jones & Kielland, 2002; McFarland *et al.*, 2002; van Hees *et al.*, 2005), so we can only speculate about the actual amount and rate of amino acids that are processed by microbes relative to inorganic N. Additionally, an unknown amount of amino acids taken up by microbes is further mineralized into DIN, which may lead to stronger microbial immobilization of AAN relative to DIN. In N-limited systems, microbes are predicted to rely more strongly on organic N than mineral N to meet functional needs (Schimel & Bennett, 2004), especially at high latitudes (Kielland, 2001; Jones & Kielland, 2002). The fact that we observed stronger sinks for amino acids than mineral N may support this hypothesis. In particular, microbes may rely more strongly on organic N in the White Mountains, which were the coldest and wettest sites, with strong sinks for amino acid N.

Conclusion

We have presented evidence that both soil pools and fluxes of organic and mineral N forms, and the ability of microbes to decay substrates, are reduced at treeline sites relative to contiguous forests over large spatial scales in Alaska. This pattern does not vary with broad changes in climate and most likely is due to differences in organic matter quality, reduced temperatures during winter, and increased disturbance (frequency of freeze–thaw and dry–rewet cycles) at treeline sites. The pattern of seasonal N dynamics described here is consistent across latitudes regardless of varying site factors. We suggest that the fall and over-winter periods are both critical to prevent N loss from the ecosystem by soil microbial activity, which acts to prevent N loss from the ecosystem and as a strong source for N for both plants and microbes. We observed greater variation in N processes within landscapes between treeline and forested stands than among mountain ranges along a 785-km latitudinal transect, suggesting that studies on local-scale controls over the N cycle may be more critical for calibrating ecosystem models than studies on broad-scale controls on N cycling, such as mean annual temperature.

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