

NITROGEN CYCLING AT TREELINE: LATITUDINAL AND ELEVATIONAL
PATTERNS ACROSS THE BOREAL LANDSCAPE

A
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ABSTRACT

We studied spatial and temporal patterns of soil nitrogen pools and fluxes at treeline and forested sites within three Alaskan mountain ranges along a latitudinal transect of 785 km during 2001- 2002. We measured soil temperatures, pools of soil mineral (ammonium and nitrate) and organic (amino acid and microbial biomass) nitrogen, *in situ* rates of net mineralization, net nitrification, and net amino acid production, conducted a decomposition experiment at all sites using common litter, and studied soil carbon turnover in a laboratory incubation experiment. Soils at treeline were colder than forested soils, particularly during fall and over winter, and had reduced rates of nitrogen cycling and litter decomposition relative to soils in forested stands. During incubation, treeline soils had lower respiration rates per unit carbon, suggesting lower soil organic matter quality relative to forested soils. 70% of annual net nitrogen mineralization occurred from August — May, suggesting that fall and winter are critical periods for soil nitrogen transformations in forested and treeline ecosystems. Among mountain ranges, nitrogen pools and fluxes were similar, despite variation in growing season length and mean annual temperatures. Soil moisture and organic matter quality may have stronger effects on variation in nitrogen cycling than temperature at our sites.

TABLE OF CONTENTS

Signature Page	i
Title Page.....	ii
Abstract.....	iii
Table of Contents.....	iv
List of Figures.....	vi
List of Tables.....	vii
Acknowledgements.....	viii
Introduction.....	1
Methods.....	4
Study area.....	4
Nitrogen cycling.....	6
Soil organic matter decomposition.....	9
Vegetation and soil physical characteristics.....	11
Climate.....	11
Statistical analysis.....	12
Results.....	13
Vegetation description.....	13
Soils physical description.....	14
Climate.....	15
Nitrogen pools.....	16

Soil nitrogen fluxes.....	17
Decomposition.....	19
Discussion.....	21
Treeline versus forest.....	21
Seasonal patterns.....	25
Latitudinal patterns.....	28
Organic nitrogen.....	31
Conclusion.....	32
Figures.....	35
Tables.....	47
Literature Cited.....	53

LIST OF FIGURES

Figure 1. Location of study areas.....	35
Figure 2. Difference between treeline (TL) and forested (F) sites in average monthly temperatures.....	36
Figure 3. Mean air (2 m above ground) and soil (5 cm deep) temperatures (°C) by mountain range for forest and treeline sites.....	37
Figure 4. Seasonal patterns of microbial N, DIN, and AAN.....	40
Figure 5. Relationship between extractable DIN or AAN and microbial biomass N.....	41
Figure 6. Seasonal patterns of microbial biomass N (MBN) in each mountain range.....	42
Figure 7. Production of N per season in each mountain range.....	43
Figure 8. Total annual N production (mean \pm 1 SE) at A. treeline sites, and B. forested sites.....	44
Figure 9. Difference between forested and treeline sites in average respiration rate.....	45
Figure 10. Site variation in rate of C efflux.....	46

LIST OF TABLES

Table I. Description of study sites.....	47
Table II. Percent cover of growth forms and densities of white spruce.....	48
Table III. Soil physical properties.....	49
Table IV. Summary of mean soil and air temperatures.....	50
Table V. Results of Simple Linear Regression analysis on means per site.....	51
Table VI. The proportion of N mineralized or produced per season for forest and treeline sites in all mountain ranges.....	52

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INTRODUCTION

Although the ecology and distribution of treelines have been studied for more than a century, conclusive theories concerning what factors limit tree establishment and growth at treelines are still debated (Jobbagy & Jackson, 2000; Körner, 1998; Stevens & Fox, 1991; Sveinbjörnsson, 2000; Sveinbjörnsson, Hofgaard & Lloyd, 2002). Emphasis has recently focused on the response of treelines to climate fluctuations during past (MacDonald et al., 1998; MacDonald et al., 2000; Szeicz & MacDonald, 1995, Griggs 1934), present (Lloyd and Fastie, 2002; Suarez et al., 1999; Sturm, Racine & Tape, 2001; Barber, Juday & Finney, 2000), and projected future (Rupp, Chapin & Starfield, 2000, 2001; Skre et al., 2002; Starfield & Chapin, 1996) periods of warming. 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 & 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 contiguous forest in the Chugach Range, Alaska. N is often considered the most limiting nutrient to primary production in terrestrial plants (Vitousek & Howarth, 1991; Jaeger et al., 1999), especially at high latitudes, where soils are dominated by cold

temperatures and recalcitrant organic matter with low rates of decomposition (Hobbie, et al., 2000; Nadelhoffer et al., 1992). Previous studies have emphasized that estimates of 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, Stottlemyer, 2001). 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 (Schimel & Chapin, 1996; Kielland, 1994; Jones & Kielland, 2002; Näsholm et al., 1998; McFarland et al., 2002; Lipson & Näsholm, 2001). 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 (McFarland et al., 2002; Jonasson et al., 1999; Kaye & Hart, 1997), studying the temporal patterns of both organic and inorganic N availability may be relevant in describing patterns of N availability in treeline and forested systems.

Previous 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 pulse during early spring (Lipson, Schmidt & Monson, 1999; Brooks, Williams & Schmidt 1998). In N-limited systems, this over-winter sequestration of N in microbial biomass may serve to both retain N in the system during snow melt and subsequently constitute a large portion of the annual N available to plants (Lipson, Schmidt & Monson, 2000; Kielland et al., in prep). Studies on winter processes at the Niwot Ridge Long-Term Ecological Research (LTER) site in Colorado revealed that once snow depth exceeds 30 cm, subnival soils may warm significantly above ambient air temperatures to near 0 °C, allowing microbial

communities to process soil N (Brooks, Williams & Schmidt, 1998). This study and others at the Arctic LTER site at Toolik Lake, Alaska found that prolonging the period of snow cover with a snow fence significantly increased subnival microbial N transformations (Walker *et al.*, 1999; Brooks *et al.*, 1995; 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 (Grace, 1977; Sveinbjörnsson, 2000), which can compact and potentially reduce the insulative properties of the snowpack (Pomeroy & Brun, 2001), soil temperatures may be lower in treeline soils than in 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.

There are several issues that complicate our ability to make general conclusions regarding patterns of and mechanisms governing nutrient cycling processes at treeline. First, soil processes at treeline sites may be more spatially variable than at forested sites due to site history (e.g. feedback effects from past vs. present location of the treeline) and micro-site variation (Stevens & Fox, 1991; Sveinbjörnsson, 2000; Seastedt & Adams, 2001), demanding that comparisons be replicated across multiple spatial scales. Second, it is difficult to form generalizations from previous research on nutrient processes at treeline due to inconsistencies in design and methodology among projects. Overall, there

is a lack of research on annual nutrient cycling processes at treelines with large scale replication among undisturbed systems. Finally, apparent differences in N cycling rates between treeline and forests may be more closely linked to differences in soil organic matter quality than microclimate (Flanagan & Van Cleve, 1983, Michaelson & Ping, 2003; Hobbie *et al.*, 2000), requiring that studies uncouple multiple driving variables. The purpose of the present study was to seek to illustrate general patterns of N pools and fluxes distinguishing treeline and nearby forested stand types over multiple spatial and temporal scales in relatively pristine systems.

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.

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 included the Brooks Range, White Mountains, and Chugach Range (Figure 1), and varied

from a dry arctic climate to a cool interior, and wet coastal climate, respectively. Eight sites represented elevational treelines, and the northernmost site within the Brooks Range was at the circumpolar treeline. Treeline sites were established within the zone of sparse but upright trees (>3 m height) 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 (*Picea glauca*) dominated forests, although black spruce, *Picea mariana*, was also present at some sites. All nomenclature in this text follows the treatment of Flora of North America (1993+) or Hultén (1968). Aspect, elevation and vegetation varied among sites (Table I). Although the anthropogenic history of these sites is unknown, all sites appeared to be undisturbed and pristine.

The Western Regional Climate Center for individual population centers in Alaska within or near each range provides data for average climate for each region (www.wrcc.dri.edu). At Bettles in the Brooks Range, mean air temperatures for January and July are -25°C and 15°C , respectively; mean annual temperature is -6°C , and mean annual precipitation is 354 mm. At Circle City near the White Mts., mean air temperatures for January and July are -27°C and 16°C , respectively; mean annual temperature is -6°C , and mean annual precipitation is 207 mm. However, Circle City is at a low elevation, and previous research in the White Mts. demonstrates that high elevation areas are much wetter than nearby 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 , respectively; mean annual temperature is 2°C , and mean annual precipitation is 400 mm.

NITROGEN CYCLING

In order 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 or initiation of senescence) between the southernmost and northernmost sites. Sites were sampled sequentially from south to north in each time period. During the spring 2002 sampling period, soils in the Brooks Range thawed prior to those in the White Mts. and the sampling sequence was adjusted to accommodate this.

Within each treeline or forested sub-site, a 50 m transect was established parallel to the slope contour of the mountain. Six points were randomly selected along each transect, marked with a flag, and soils were sampled at these points for the entire year. Rates of net DIN mineralization and net amino acid production were measured using an *in situ* buried bag technique [(Robertson *et al.*, 1999 (LTER soil methodology))]. We used a 6.7 cm diameter 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 native litter and left to incubate. Incubation duration was

4 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 also placed into a clear plastic sleeve that was then capped on both ends, 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 backfilled with soil to minimize disturbance to adjacent samples.

In the laboratory, soils were placed into dark storage at 3 °C and processed within 30 hours. 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 for 24 hours and calculating percent water loss. A 20 g sub-sample from each core was extracted with 75 ml 0.5 M K₂SO₄ on an orbital shaker for one hour and vacuum filtered through pre-rinsed Pall Gelman Type A/E glass fiber filter paper (Pall-Gelman Sciences, Ann Arbor, Michigan) 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 autoanalyzer (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.

To determine total dissolved amino acid N content, a 5 ml sub-sample of each extract was analyzed following a ninhydrin protocol (Rosen, 1957). Sample values were determined colorimetrically with a Lambda 1 spectrophotometer (Perkin-Elmer, Oak Brook, Illinois). Net AAN production was calculated as the difference in AAN concentration between each final and initial core. All fluxes are reported per gram soil mass per day when averaged over the incubation time period.

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 hours in a moistened modified pressure cooker, extracted in 75 ml 0.5 M K₂SO₄ following the procedure detailed previously for DIN, and frozen. During the spring of 2003, frozen fumigated and non-fumigated samples were thawed, digested using a persulfate oxidation digestion (Cabrera & Beare, 1993) and analyzed for NO₃⁻-N colorimetrically using a modified Technicon system autoanalyzer (Whitledge et al., 1981). MBN was calculated as the difference in DON between fumigated and non-fumigated samples. We did not use a correction factor on the data (Ladd, Amato & vanVeen, 2004) because the efficiency of the digestion process to extract total microbial N has not been clearly defined for the soils we studied (Brookes et al., 1985).

SOIL ORGANIC MATTER DECOMPOSITION

Indices of soil organic matter decomposability, and site factors influencing soil organic matter decomposition, were assessed during 2001 and 2002. Site effects on soil organic matter decomposition were assessed by mass loss of a common substrate decaying *in situ* at all sites, and soil organic matter quality was examined in a laboratory incubation at constant temperature and moisture.

To assess the importance of site factors, we measured mass loss over 1 year at all sites using 15.2 x 1.8 cm birch wood tongue depressors (TDs) as a common litter. TDs were oven dried for 24 hours 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 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 x 10 cm) were sampled at random locations from high, mid and low elevations at each sub-site. As described above, a plastic sleeve was placed inside the soil corer to maintain structure of each core. Samples were immediately stored on ice, and, after transport to the lab, were frozen until the start of the experiment in May 2002. The exception was the site at Site Summit for reasons

mentioned above. Cores from this site were collected in May 2002 and were frozen until start of the experiment.

Half of the cores from each treeline or forested sub-site were randomly assigned to either a low (average 4.7 °C) or a high temperature (average 9.1 °C) treatment. The purpose of having 2 temperature treatments was to assess any intrinsic sensitivity in soil respiration rates to temperature.

Each core was homogenized by hand to remove rocks and roots > 2 mm diameter. We used soils only 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 2 sub-samples. Ten g was used to determine water holding capacity (WHC) by saturating soils with RO water, allowing soils to drain and then oven-drying at 65 °C to a constant weight. 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). Another 20 g sub-sample from each core was placed into an acid-washed 935 ml (Kerr brand) or 985 ml (Ball brand) glass mason jar, and adjusted to 60% WHC. Jars were covered with breathable, 1mil plastic sheeting held in place with rubber bands, and were pre-incubated in darkness at 3.5°C for 7 days. Jars were then randomly assigned to one of the two temperature treatments, and incubated in the dark for 15 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 hours 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) modified with a syringe-injection system. Soil respiration was calculated and expressed as $\mu\text{g CO}_2\text{-C g soil DWT}^{-1} \text{ d}^{-1}$ or as $\mu\text{g CO}_2\text{-C g soil C}^{-1} \text{ d}^{-1}$ after dividing by total C content.

VEGETATION AND SOIL CHARACTERISTICS

Percent cover of vegetation growth forms in the understory (excluding trees) was measured by ocular estimate for 10 1-m² plots for each treeline and forest sub-site. Tree density, tree basal diameter and height were calculated using a point-centered quarter method (Bonham, 1989). During August 2002, 5 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, 5 soil cores (6.7 cm x 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. During February 2003, we ground these samples by mortar and pestle, and analyzed for total C and N on a LECO 2000 CNS combustion analyzer.

CLIMATE

For the duration of the study, soil temperatures and moisture at 5 cm and 25 cm below the surface and air temperatures at 25 cm and 2 m above the surface were recorded

with data loggers and sensors (Campbell Scientific, Inc., Logan, Utah) 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) were used to measure soil temperatures at both 5 cm 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 years (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 trends from ranked data were compared with trends from 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 each pair of treeline and forested sites 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 pooled by site. We used a mixed-model ANOVA on mean data 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. Multiple 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 $\alpha = 0.05$ with values between 0.05 and 0.10 considered "marginally" significant. Unless otherwise stated, data reported throughout the text represent arithmetic means ± 1 standard error.

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 (Table II). 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. Cover of litter (not including standing dead material) at all sites in the Brooks Range varied from 1% to 5%, with the exception of

Gobbler's Knob forest, where litter cover was 51%, due to a greater density of alder shrubs. In the White Mts., 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 uliginòsum*, had the most cover at treeline. At 12 Mile Summit, *Salix pulchra* was also the dominant species at the forest site but the sedge *Carex bigelòwii* was dominant at treeline. At Nome Creek, *Vaccinium uliginòsum* was dominant at treeline, and Alaskan spirea, *Spirèa beauverdiàna*, was most prevalent in the forest. At these sites, litter cover varied between 1- 12%. 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*. Litter at these sites varied from 1- 23%.

SOILS PHYSICAL DESCRIPTION

When averaged across all ranges and sites, total C per gram soil averaged slightly higher at treeline sites (treeline = 22 ± 0.8 ; forest = 20 ± 0.9); however, these differences were not statistically significant ($\underline{T} = -1.19262$, $\underline{P} = 0.2672$), which most likely is a function of the large variability among sites (Table III). The coefficients of variation (CV) calculated for sites within each range varied from 11.7% (Brooks Range forest sites) to 30.1% (White Mts. forest sites). Total C on an aerial basis did not differ between treeline and forested sites ($\underline{T} = 1.0353$, $\underline{P} = 0.4889$), and ranged from $3522 \pm 315 \text{ g C m}^{-2}$

in the Brooks Range to $6646 \pm 852 \text{ g C m}^{-2}$ in the Chugach Range. Total N was similar in treeline and forested sites (treeline = $0.90 \pm 0.04\%$, forest = $0.96 \pm 0.04\%$; $\underline{T} = 0.2517$, $\underline{P} = 0.8075$), and the CV among sites was similar to that for total C. Soil C per gram was highest in the White Mts., and similar in the Brooks and Chugach Ranges (Table III). The ratio of C to N did not vary between treeline and forest sites ($\underline{T} = -2.0367$, $\underline{P} = 0.0761$) and was highest in the Chugach Range and lowest in the White Mts. 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. The volume of rocks relative to soil in the top 20 cm varied among sites and between the Brooks and Chugach Ranges, as did the depths of the layers in the soil profile (Oi; Oe + Oa) (Table III).

CLIMATE

On an annual basis, treeline soils were colder than forest soils (averaged among ranges and sites, treeline = $-0.474 \pm 0.06 \text{ }^\circ\text{C}$; forest = $1.146 \pm 0.07 \text{ }^\circ\text{C}$). This difference was, however, mainly driven by strong differences during winter (October to April; $\underline{M} = 17$, $\underline{P} < 0.0001$). During the remainder of the year, soil temperatures in treeline and forest were statistically similar (Figure 2A). Annual air (2 m height) and soil (5 cm depth) temperatures are displayed in Figure 3. Sites at treeline experienced a more variable soil temperature regime than forested sites, with greater minimum and maximum soil temperatures (Table IV), and a higher frequency of temperature fluctuation (Figure 3). Annual mean soil temperature, mean soil temperature during the growing season (Jun-

Aug), and the number of days the temperature was above 0 °C declined with increasing latitude (Table IV). In the Brooks Range, the length of the freeze-free period was equal for treeline and forest (136 days); however, the difference between stand types increased to 7 days in the White Mts. and 21 days in the Chugach Range.

The fluctuations and patterns of air temperatures were different than those for soil temperatures. There was no significant difference in average air temperatures between treeline and forested stands ($\underline{M} = 3.5$, $\underline{P} = 0.5104$), even when data were analyzed separately for the 3 mountain ranges. However, relative to forested sites, air temperatures within treeline sites were warmer in the winter and cooler in the summer (Figure 2B). Variation among ranges also had a different pattern than soil temperatures. Although mean annual air temperatures were lowest in the Brooks Range and warmest in the Chugach Range; during the growing season, the White Mts. were the coolest. The forested sites in the White Mts. experienced the most extreme low temperatures during winter, which likely is a function of the continental climate in that region.

NITROGEN POOLS

The pool size of dissolved inorganic N (DIN) in forested sites ($5.56 \pm 0.87 \mu\text{g N g}_{\text{DWT}}^{-1}$) was significantly greater than in treeline sites ($3.64 \pm 1.01 \mu\text{g N g}_{\text{DWT}}^{-1}$) (Figure 4) and was consistent across mountain ranges and sampling periods (sign test, $\underline{M} = 7.5$, $\underline{P} = 0.0167$). 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 ($5.39 \pm 0.49 \mu\text{g N g}_{\text{DWT}}^{-1}$) and treeline ($5.40 \pm 0.95 \mu\text{g N g}_{\text{DWT}}^{-1}$) sites ($\underline{P} =$

0.736, ns). The largest pool of biologically active N was found in microbial biomass, where values for forested sites ($68.41 \pm 8.27 \mu\text{g N g}_{\text{DWT}}^{-1}$) and treeline sites ($79.12 \pm 9.60 \mu\text{g N g}_{\text{DWT}}^{-1}$) were similar ($\underline{P} = 0.176$, ns). Soil DIN and AAN pools were positively correlated with total soil N (Spearman's correlation, $\rho = 0.4038$, 0.5235 , respectively, both $\underline{P} < 0.0001$) and were negatively correlated with C:N (DIN, $\rho = -0.3742$, $\underline{P} = 0.0014$; AAN, $\rho = -0.2411$, $\underline{P} = 0.04$). Mineral and amino acid pools were positively inter-correlated when examined across sites and time periods ($r^2 = 0.45$, $\underline{P} < 0.0001$), and both were positively correlated with MBN, supporting the notion that microbial biomass functions as a strong sink and source for N in soils (Figure 5).

The pattern of seasonal variation in organic and inorganic N pool sizes was strikingly similar for treeline and forest sites. DIN and AAN pool sizes varied significantly among seasons due principally to 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: $\underline{F} = 1.41$, $\underline{P} = 0.315$; treeline sites: $\underline{F} = 1.4$, $\underline{P} = 0.3168$). Amino acid pools varied slightly among ranges ($\underline{F} = 3.8$, $\underline{P} = 0.0855$), primarily due to high spring values in the White Mts. The MBN pool size was significantly greater in the White Mts. than in the Chugach and Brooks Ranges (ANOVA on range effects, $\underline{F} = 6.69$, $\underline{P} = 0.0295$), but was similar in the Chugach and Brooks Ranges. This trend was driven by high MBN pools during spring in the White Mts. (Figure 6), and may be in part due to wetter soils at these sites, given that MBN pool sizes and percent soil moisture were positively correlated ($r^2 = 0.59$, $\underline{P} < 0.0001$, Table V).

SOIL NITROGEN FLUXES

Rates of both net N mineralization and net amino acid production were higher in forested sites ($0.07 \pm 0.03 \mu\text{g N g}_{\text{DWT}}^{-1} \text{d}^{-1}$ and $-0.03 \pm 0.02 \mu\text{g N g}_{\text{DWT}}^{-1} \text{d}^{-1}$, respectively) than treeline sites ($-0.01 \pm 0.02 \mu\text{g N g}_{\text{DWT}}^{-1} \text{d}^{-1}$ and $-0.08 \pm 0.04 \mu\text{g N g}_{\text{DWT}}^{-1} \text{d}^{-1}$, respectively; mean values across ranges and time periods are reported here) (sign test, $\underline{M} = 8.5$, $\underline{P} = 0.0006$ for DIN; $\underline{M} = 7.5$, $\underline{P} = 0.0167$ for AAN). These negative rates represent net immobilization of both amino acids and inorganic N sources across all sampling locations, and result mainly from the strong sink for N during spring. Rates of net nitrification were similar for forested ($0.02 \pm 0.02 \mu\text{g N g}_{\text{DWT}}^{-1} \text{d}^{-1}$) and treeline ($0.01 \pm 0.01 \mu\text{g N g}_{\text{DWT}}^{-1} \text{d}^{-1}$) sites ($\underline{P} = 0.1214$, ns). Both net N mineralization and amino acid production rates were negatively related to the pool of microbial biomass N (Table V), although this relationship was mainly driven by high 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 amounts of immobilization in spring to positive net production values during winter (Figure 7). Similar to results for soil N pools, fluxes of N did not vary among mountain ranges [(treeline and forest analyzed separately) N mineralization: treeline, $\underline{F} = 0.40$, $\underline{P} = 0.6835$; forest, $\underline{F} = 0.39$, $\underline{P} = 0.6932$; AA production: treeline, $\underline{F} = 2.17$, $\underline{P} = 0.187$, forest, $\underline{F} = 1.18$, $\underline{P} = 0.3658$; net nitrification: treeline, $\underline{F} = 2.79$, $\underline{P} = 0.1359$, forest, $\underline{F} = 0.11$, $\underline{P} = 0.9002$].

When averaged across mountain ranges, the annual amount of net N mineralized at forested sites ($15.73 \pm 7.62 \mu\text{g N g}_{\text{DWT}}^{-1} \text{yr}^{-1}$) was nearly five times greater than at treeline sites ($3.26 \pm 2.26 \mu\text{g N g}_{\text{DWT}}^{-1} \text{yr}^{-1}$); however, this difference was not significant ($\underline{P} = 0.727$, ns). This statistical result may be a consequence of our inability to detect a difference due to the high degree of variation among sites (Figure 8). The coefficient of variation among treeline sites was 4 times greater than among forested sites. Additionally, the average difference between each paired forest and treeline site for annual net mineralization was $15.01 \mu\text{g N g}_{\text{DWT}}^{-1} \text{yr}^{-1}$, but this ranged between $-11.35 \mu\text{g N g}_{\text{DWT}}^{-1} \text{yr}^{-1}$ and $38.57 \mu\text{g N g}_{\text{DWT}}^{-1} \text{yr}^{-1}$. Annual net production of amino acids was marginally higher in forested sites ($0.20 \pm 3.44 \mu\text{g N g}_{\text{DWT}}^{-1} \text{yr}^{-1}$) than at treeline sites, due to a high degree of net immobilization measured at the latter ($-8.23 \pm 4.82 \mu\text{g N g}_{\text{DWT}}^{-1} \text{yr}^{-1}$) (sign test, $\underline{M} = 4$, $\underline{P} = 0.078$). The average difference between forested and treeline sites for AAN was much smaller than for mineral N ($2.98 \mu\text{g N g}_{\text{DWT}}^{-1} \text{yr}^{-1}$), and varied between $-2.40 \mu\text{g N g}_{\text{DWT}}^{-1} \text{yr}^{-1}$ and $17.32 \mu\text{g N g}_{\text{DWT}}^{-1} \text{yr}^{-1}$.

DECOMPOSITION

Decomposition (percent mass loss) of tongue depressors was approximately 30% greater in forest sites ($5.7 \pm 1.4\%$) than at treeline sites ($4.0 \pm 0.7\%$), but this difference was marginal statistically ($\underline{P} = 0.1202$). The lack of strong statistical evidence is driven by a minor difference between treeline and forest in the White Mts. Percent mass loss in the Chugach Range was significantly greater ($9.13 \pm 1.36\%$) than in the White Mts. ($2.62 \pm 0.17\%$) and the Brooks Range ($4.28 \pm 0.72\%$) (both $\underline{P} < 0.0001$).

During laboratory incubations, soil respiration rates did not differ among weeks 2, 6, and 11, and were still increasing linearly after 11 weeks; thus rates are reported on a daily basis averaged over this entire time period. When expressed on a per g dry weight basis, respiration rates of forested soils did not differ between soils incubated at 4.7 °C ($44.85 \pm 2.72 \mu\text{g C g}_{\text{DWT}}^{-1} \text{d}^{-1}$) and 9.1 °C ($52.43 \pm 5.50 \mu\text{g C g}_{\text{DWT}}^{-1} \text{d}^{-1}$). However, in soils from treeline sites, rates of soil respiration at the lower temperature ($55.89 \pm 4.20 \mu\text{g C g}_{\text{DWT}}^{-1} \text{d}^{-1}$) were significantly higher than at the higher temperature ($45.73 \pm 2.53 \mu\text{g C g}_{\text{DWT}}^{-1} \text{d}^{-1}$) ($F = 4.11$, $P = 0.0459$). Treeline and forested soils had similar rates of respiration (treeline: $50.81 \pm 2.49 \mu\text{g C g}_{\text{DWT}}^{-1} \text{d}^{-1}$; forest: $48.60 \pm 3.06 \mu\text{g C g}_{\text{DWT}}^{-1} \text{d}^{-1}$; $T = -0.46791$, $P = 0.6485$).

These trends were reversed when rates were expressed per g C (Figure 9). Soils from forested sites had higher respiration rates ($292.97 \pm 10.97 \mu\text{g C g C}^{-1} \text{d}^{-1}$) than those from treeline sites ($259.44 \pm 12.55 \mu\text{g C g C}^{-1} \text{d}^{-1}$) ($M = 5$, $P = 0.0309$), suggesting higher soil C quality in forested compared with treeline sites.

Although soil respiration rate did not differ among mountain ranges when averaged across sites and stand types [$F = 0.17$, $P = 0.8516$ (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 ($F = 7.52$, $P < 0.0001$) (Figure 10). 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 are consistent with a number of previous studies showing greater DIN pool sizes and higher rates of net N mineralization in forested compared with treeline sites (e.g., Sveinbjörnsson et al., 1995); although the size of the mineral N pools reported by these authors was 1-4 times greater than what we report here. This is most likely because Sveinbjörnsson et al. (1995) sampled only organic soil, whereas samples from the present study were of fixed depth and included mineral material. A study on a mountain birch treeline (*Betula pubescens* ssp. *tortuosa*) in Swedish Lapland reported soil NH_4^+ concentrations to be seventeen-fold greater in the forest than at treeline (Davis et al., 1991). Stottlemyer, Rhoades and Steltzer (2001) found net N immobilization at treeline but positive net N mineralization in forests during the growing season in northwestern Alaska, although the magnitude of the difference was about half of what we report here. These authors also reported that soil DIN pools were slightly higher in the forest than at treeline, with declining pool sizes throughout the growing season, which is similar to our results. Using a long-term buried bag incubation (1 year), Binkley et al., (1994) also found higher net N mineralization rates in a white spruce forest than in an adjacent Alaskan tundra ecosystem.

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 Mts. and Chugach Range) or similar (Brooks Range) in temperature 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 while a single event generally stimulated mineralization, multiple freeze thaws 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. The lower threshold for microbial activity is thought to be between -5 °C (Clein & Schimel, 1995; Brooks, Williams & Schmidt, 1998) and -10 °C (Michaelson & Ping, 2003), and, during winter, periods with severe freeze or a freeze of long duration have been reported to reduce CO₂ efflux from subnival soils (Walker *et al.*, 1999; Brooks, Schmidt & Williams, 1997). Our treeline sites had a greater frequency of freeze events below this threshold compared with paired forested stands, and, when coupled with the overall colder temperatures, this may explain why wintertime N mineralization at treeline was 23- 56% less than that in forested sites.

During the growing season, soil temperatures at treeline were similar to those in the forest (Figure 2A), 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). During June to September in the Brooks Range, soil temperatures at treeline sites were similar to, or warmer than, those in forest sites. In the White Mountains, soil temperatures at treeline were within 1.5 °C of soils in nearby forest stands, and were higher at treeline during June and August (the warmest month at

this site). In the Chugach Range, treeline soils were warmer during the shoulder periods of May and October. It is difficult to know whether microbial activity is insensitive to these stand type differences in soil temperature, 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 at these sites, but all N pools and fluxes measured were more tightly related to soil moisture content than to mean air and soil temperature (Table V), and decomposition of common litter was negatively correlated with soil moisture (Spearman's correlation, $P = 0.0075$). During summer, any relationship of net N mineralization, net AA production, or the size of the MBN pool to soil temperatures was restricted to treeline stands. 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 the summer period.

Common litter decayed approximately 30% slower in treeline stands compared with forested stands, but since the sampling period was over 1 year, 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, to date, no study has directly examined the difference in C quality between treeline and forested stands of white spruce at high latitudes. Reduced organic matter quality at treeline may be a result of colder temperatures, feedback effects, or differences in plant species composition relative to the forest. If colder temperatures depress rates of decomposition, microbes may primarily process labile C, resulting in an accumulation of poor quality substrates at treeline. Over time, this would tend to feedback to affect plant uptake of N, litter quality and nutrient cycling (Flanagan & VanCleve, 1983), and further reduce substrate quality. Tongue depressors are a poor quality substrate with a high C:N ratio, and therefore provide an index of N availability to microbial processes (Harmon, Nadelhoffer & Blair, 1999). If the availabilities of labile C and N for microbial growth are higher in forested soils relative to treeline soils, this may facilitate the decomposition of a recalcitrant substrate such as a tongue depressor.

Plant species are known to have strong effects on nutrient cycling, and our treeline sites had 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 was 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 clear, 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. Working in distinct tundra ecosystems on the North Slope of Alaska, Hobbie and Gough (2004) reported that site effects may be stronger than any individual species influences on litter decomposition. In addition to a colder soil environment, site effects such as variation in soil pH (Hobbie & Gough, 2004), or an interaction between site and plant species effects (Schimel, Bilbrough & Welker, 2004) most likely contribute to lower decomposition at treeline.

SEASONAL PATTERNS

We found pronounced seasonal variation in N pools and fluxes that were strikingly similar in the 3 mountain ranges, 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; Kielland *et al.*, in prep.; Schimel, Bilbrough & Welker, 2004), and at the Niwot Ridge site in the Rocky Mountains of Colorado (Lipson, Schmidt & Monson, 1999; Brooks, Williams & Schmidt, 1998). The seasonal fluctuation of microbial biomass at our sites was also similar to the pattern in a subalpine heath in Swedish Lapland (Jonasson *et al.*, 1999), and

strong net N immobilization by microbial biomass in spring has also been reported in temperate forests (Groffman et al., 1993).

Although many 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; Kielland et al., in prep). Our data show that the strongest sinks for both mineral and organic N were during spring and summer, while net mineralization mainly occurred during autumn and over winter (Table VI). 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.

The mechanisms for microbial function in subzero temperatures are still unclear, although researchers have recently sought to clarify them. Michelson and Ping (2003) reported that rates of respiration in arctic soils incubated at -2 °C were tightly linked with the amount of water soluble organic C but not to the amount of total organic C. They argued that at sub-zero temperatures, microbes are less capable of utilizing more recalcitrant forms of C. However, the soil microbial biomass in arctic tundra soils from Toolik Lake, Alaska, was found to utilize recalcitrant C compounds during sub-zero

temperatures (Loya, Johnson & Nadelhoffer, 2004). Several studies on seasonal partitioning of microbial functional groups in alpine soils report that winter communities are dominated by fungi which process complex substrates, while summer communities are dominated more by bacteria that utilize simpler substrates (Lipson, Schadt & Schmidt, 2002; Schadt *et al.*, 2003; Ley & Schmidt, 2002). Similar results have been reported for soils in the French Alps (Souto, Chiapusio & Pellissier, 2000). This suggests that at our sites, once labile C derived from the fall pulse in fine root mortality (Ruess, Hendrick & Bryant, 1998; Ruess *et al.*, 2003) has been utilized in late fall or early winter, microbial community composition may shift to one that is more fungal dominated and continue to slowly process complex components of soil organic matter throughout winter. Circumstantially, this may be supported by the observation that as snow receded from our sites, often a thick layer of mycelium growing over the ground was revealed (P. Loomis, personal observation). Although data from the present study do not pertain to rates of turnover of microbial biomass, or the fluctuations of MBN within any season, the general patterns that we observed are consistent with other research.

We hypothesize the following scenario to explain the seasonal pattern of N dynamics at high latitudes. During autumn, there is a proportional 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 winter, activity of the microbial community may be intermittent depending on temperature

thresholds; however, particularly under a deep or continuous snowpack, some activity will occur, resulting in N immobilized by the microbial pool (Lipson, Schmidt & Monson, 1999). Concomitantly, small amounts of mineralization N accumulate in the soil, leading to large pools of extractable NH_4^+ and amino acids in spring. During late winter, microbes may become C-limited (Lipson, Schmidt & Monson, 2000), but with the onset of spring, rapid environmental changes stimulate a shift in microbial functional type from fungi to bacteria (Schadt *et al.*, 2003), resulting in a large flux of labile C. This immediate energy source stimulates microbial growth, creating a strong sink for N, thus retaining N within surface soils during snowmelt. Soil N pools decrease from spring to summer, in part because of the rapidly growing microbial biomass, but also because plant demand for mineral and amino acid N increases during this time period. Additionally, drying events as summer progresses 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 possessing 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 Mts. Therefore, within and

among landscapes, there was 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 the other ranges (both $P < 0.05$), there was no variation among mountain ranges in soil respiration per unit C when soils were incubated under controlled conditions. This suggests that while 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 annual temperatures, may be more important than site differences in controlling decomposition processes. Differences in the Chugach Range may also be attributed to the maritime climate there, whereas the 2 interior ranges experienced a continental climate. 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 4 °C and 9 °C. Soils from other high latitude ecosystems have also been shown to be relatively insensitive to temperature fluctuations within this range (Nadelhoffer et al., 1991; Giblin et al., 1991; Stottleyer, 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 Mts. or Brooks Range (M. Smith &

T. Traustason, unpubl. data). This may be a function of 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 in the amount of amino acids produced annually. Soil processes can vary by an order of magnitude on a small scale (Robertson *et al.*, 1999), potentially masking variation at larger regional scales, and micro-site factors can influence macro-scale soil processes (Schimel & Bennett, 2004). 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 Mts., and found that in the last century, growth of treeline trees at Eagle Summit was positively correlated with temperature, while at Twelvemile 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 temperature 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 will directly affect 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). The factors that vary most strongly by site, such as parent material (Hobbie & Gough, 2004; Cheng *et al.*, 1998), or soil texture (Ladd, Amato & vanVeen, 2004) may be as important as climate for predicting nutrient processes. This has implications for studies that seek to model parameters relevant to vegetation and ecosystem processes at regional scales, because it demonstrates that with increasing latitude, ecological parameters do not vary directly with decreases in annual temperature.

ORGANIC NITROGEN

The present results indicate that pools, fluxes and seasonal patterns of dissolved amino acids were similar to dissolved inorganic N. This is in contrast to the work of Kielland (1995) in arctic tundra, who reported amino acid concentrations of 4 to 10 times higher than ammonium, although the range of amino acids he reported was similar (1- 8 $\mu\text{g N g}_{\text{DWT}}^{-1}$) to the average concentration reported here. This discrepancy may result from a difference in sampling methodology, since Kielland used only organic soil and we sampled both organic and mineral soil. 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 in 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, McFarland *et al.*, 2002, van Hees *et al.*, 2005), so we can only speculate about the actual amount and rate that amino acids are processed by microbes relative to inorganic N. 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 (Jones & Kielland 2002; Kielland 2001). Although we have no direct evidence to support an increased reliance on amino acid N at our sites, 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 Mts., which were the coldest and wettest sites, with strong sinks for amino acid N. Microbes may also be taking up amino acids primarily as a C source (Jones *et al.*, 2004), although if N were not retained for biosynthesis, then this should be reflected in greater amounts of total net mineralization.

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 periods for pools of N to increase in soils within these systems, and that the microbial biomass acts both as a strong sink for N, preventing 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 the 3 mountain ranges, which spanned over 6° of latitude, 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.

We also provide evidence that sinks for amino acids are strongest at treeline sites and in colder mountains ranges, suggesting that soil microbes at these sites may rely more on sources of organic N to meet their annual N demands. Schulze, Chapin & Gebauer (1994) demonstrated that under conditions of low N availability, such as in the Brooks Range, white spruce trees mainly use NH_4^+ (Kronzucker, Siddiqi & Glass, 1997) or organic N from fresh litter. Since labile nutrients in these systems primarily are derived more from fine roots than from aboveground leaf litter (Ruess *et al.*, 1996), the most important labile N source in these systems may be low molecular weight substrates, such as amino acids, from fine roots. We can further extend this scenario to suggest that

there may be reduced input of N at treeline from fine roots and therefore, a subsequent decrease in availability of organic N to both microbes and plants. We have no data to support this hypothesis, although it warrants consideration for future studies that seek to examine N limitation of white spruce at treeline.

FIGURES

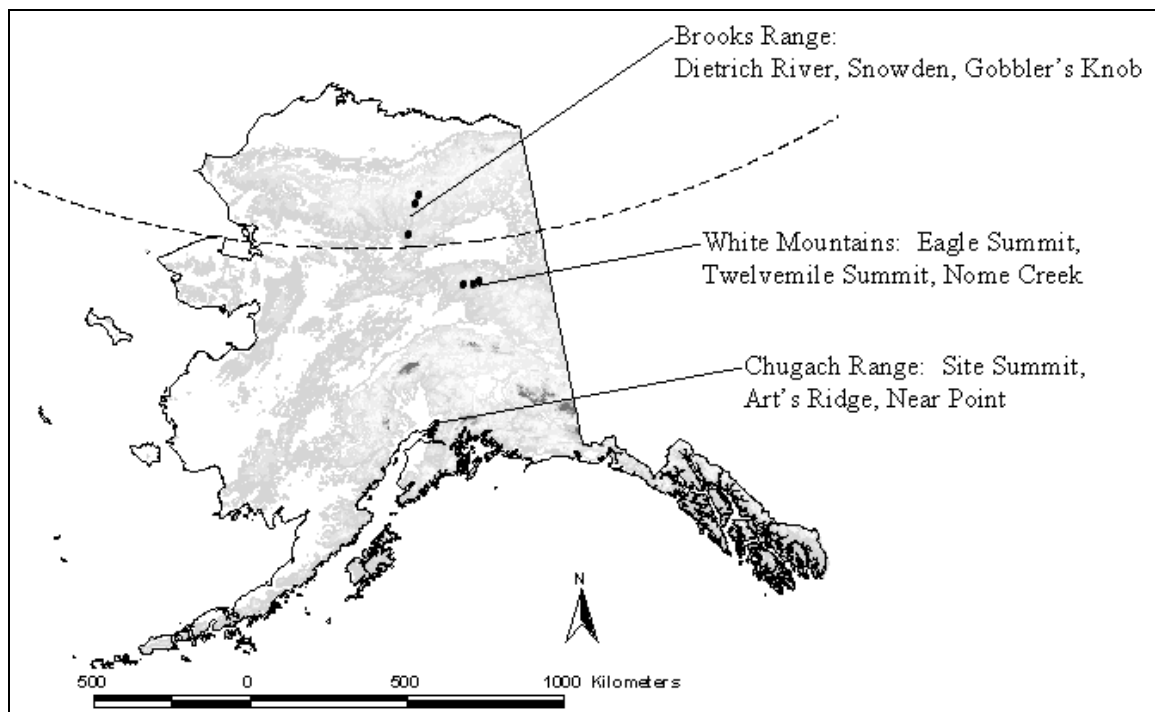


FIGURE 1. Location of study areas. Sites within each range are separated by 5- 25 km and are listed from north to south in location. Dietrich is near the circumpolar treeline, and all other sites are elevational treelines.

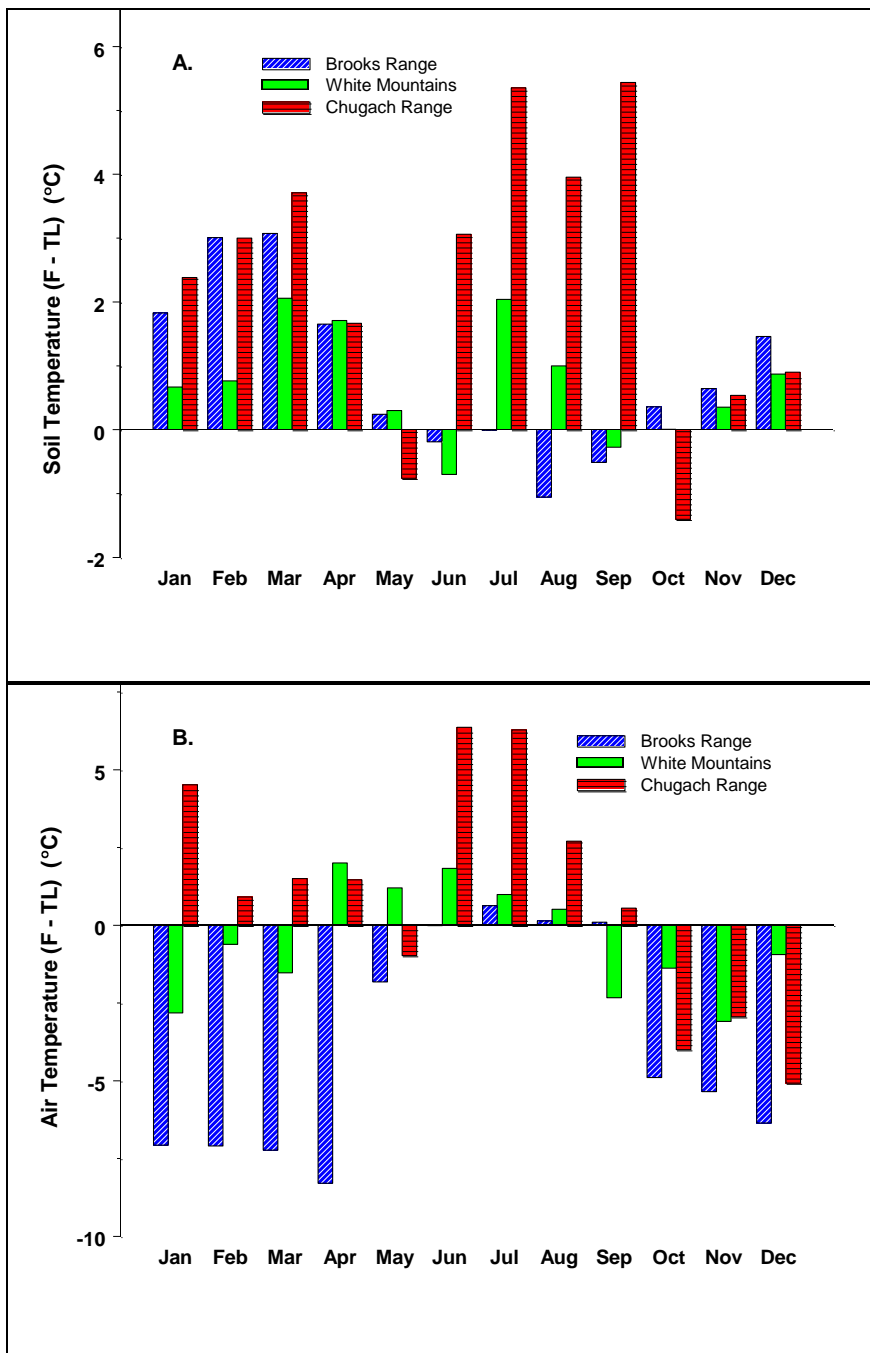


FIGURE 2. Difference between treeline (TL) and forested (F) sites in average monthly temperatures among mountain ranges. These data were compiled from 2000- 2004 for 3 sites in each range. A. Difference in soil temperatures at 5 cm below the surface. B. Difference in air temperatures at 2 m above the surface.

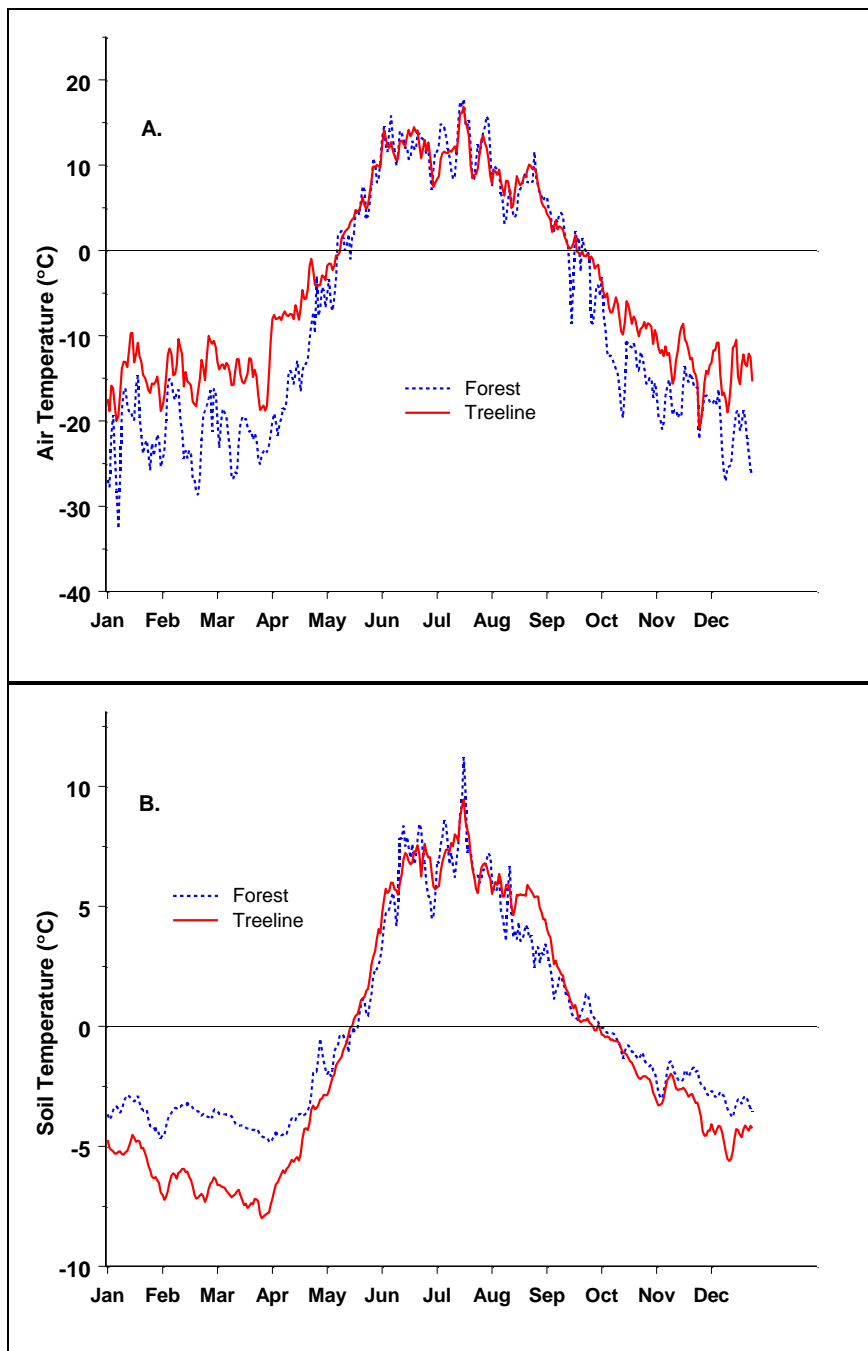


FIGURE 3. Mean air (2 m above ground) and soil (5 cm deep) temperatures (°C) by mountain range at forest and treeline sites for the Brooks Range (A, B, respectively), the White Mountains (C, D) and the Chugach Range (E, F). Data represent mean daily averages from 2000- 2004. Gaps in the data resulted from malfunctioning sensors in the Chugach Range.

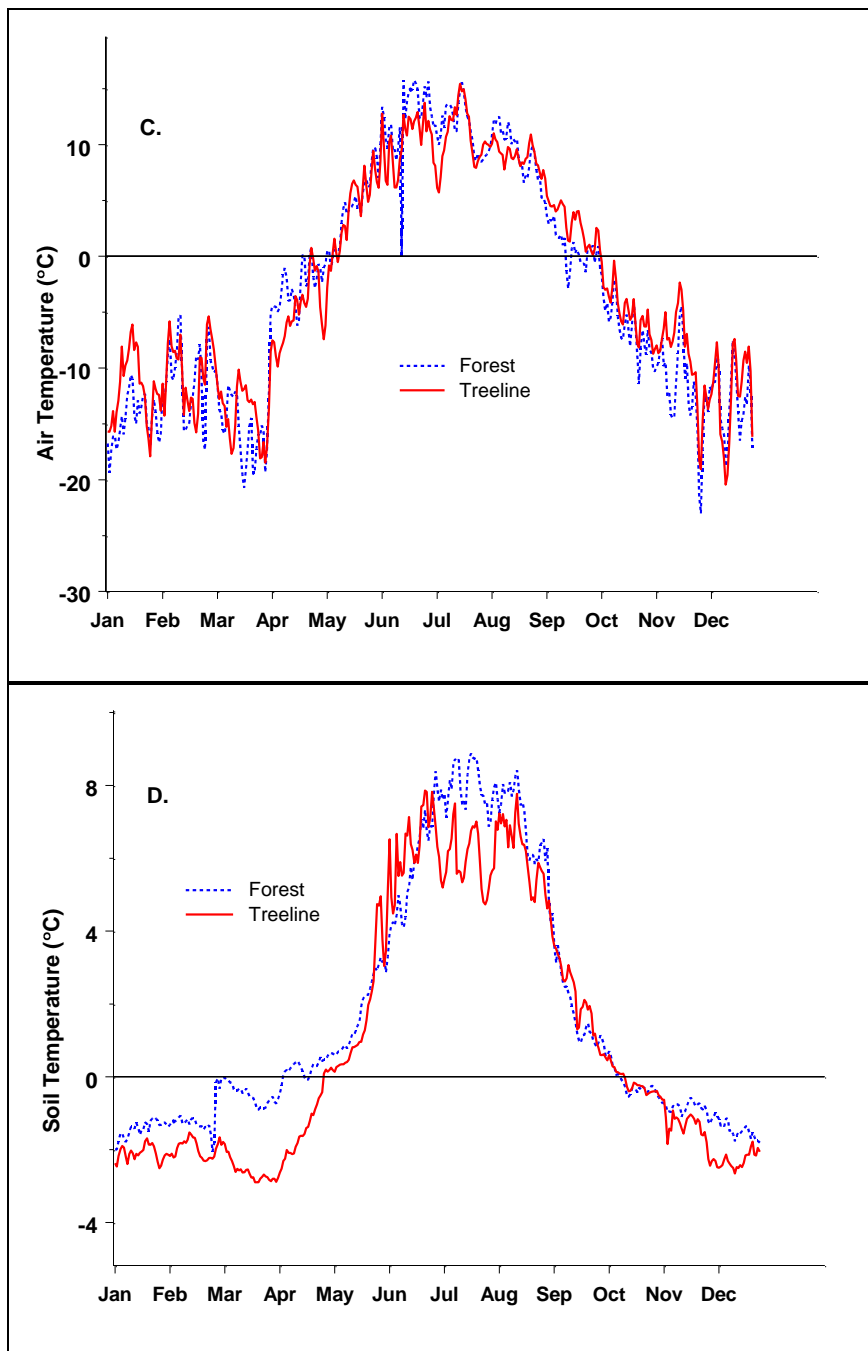


FIGURE 3 CONTINUED. Mean air (2 m above ground) and soil (5 cm deep) temperatures (°C) by mountain range at forest and treeline sites for the Brooks Range (A, B, respectively), the White Mountains (C, D) and the Chugach Range (E, F). Data represent mean daily averages from 2000- 2004. Gaps in the data resulted from malfunctioning sensors in the Chugach Range.

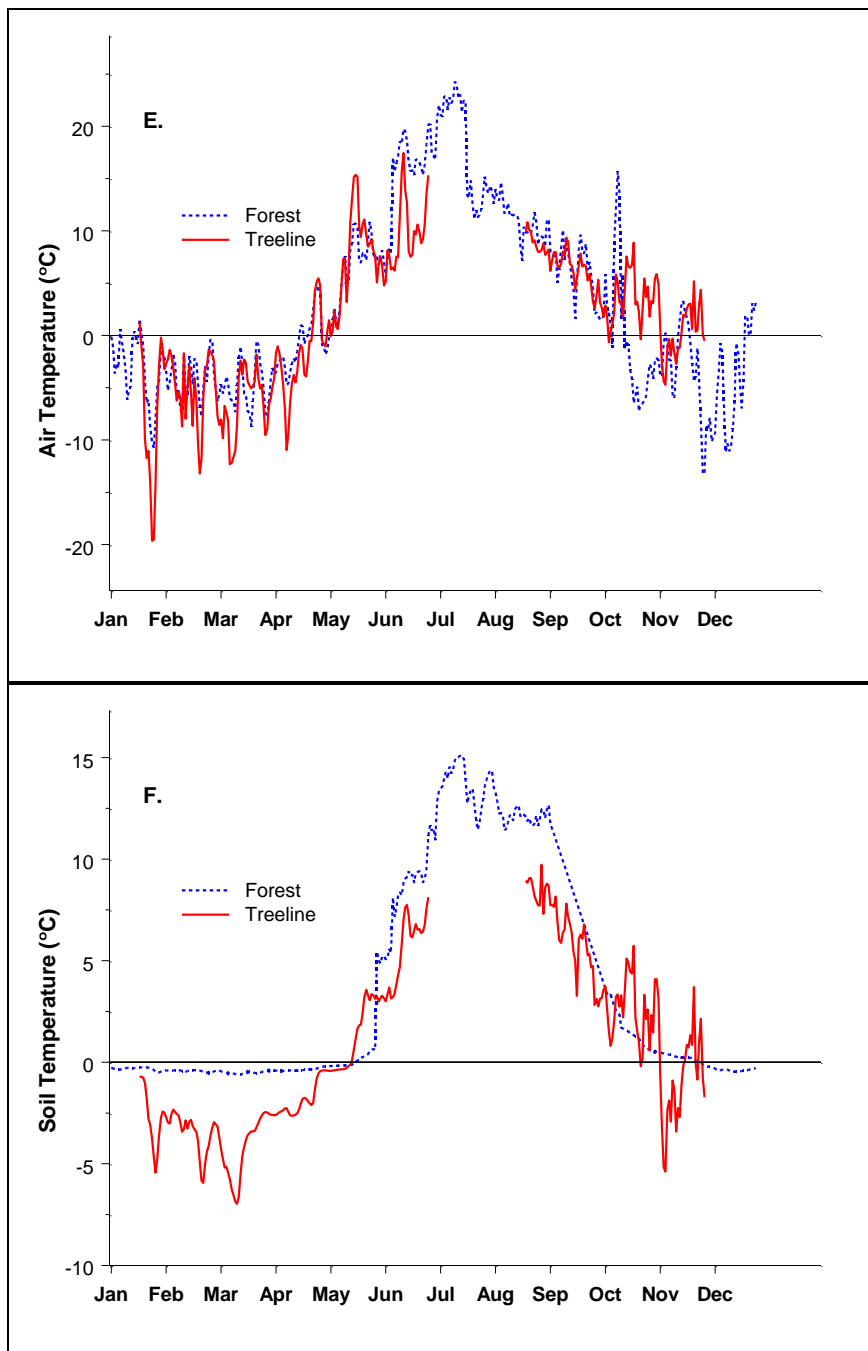


FIGURE 3 CONTINUED. Mean air (2 m above ground) and soil (5 cm deep) temperatures (°C) by mountain range at forest and treeline sites for the Brooks Range (A, B, respectively), the White Mountains (C, D) and the Chugach Range (E, F). Data represent mean daily averages from 2000- 2004. Gaps in the data resulted from malfunctioning sensors in the Chugach Range.

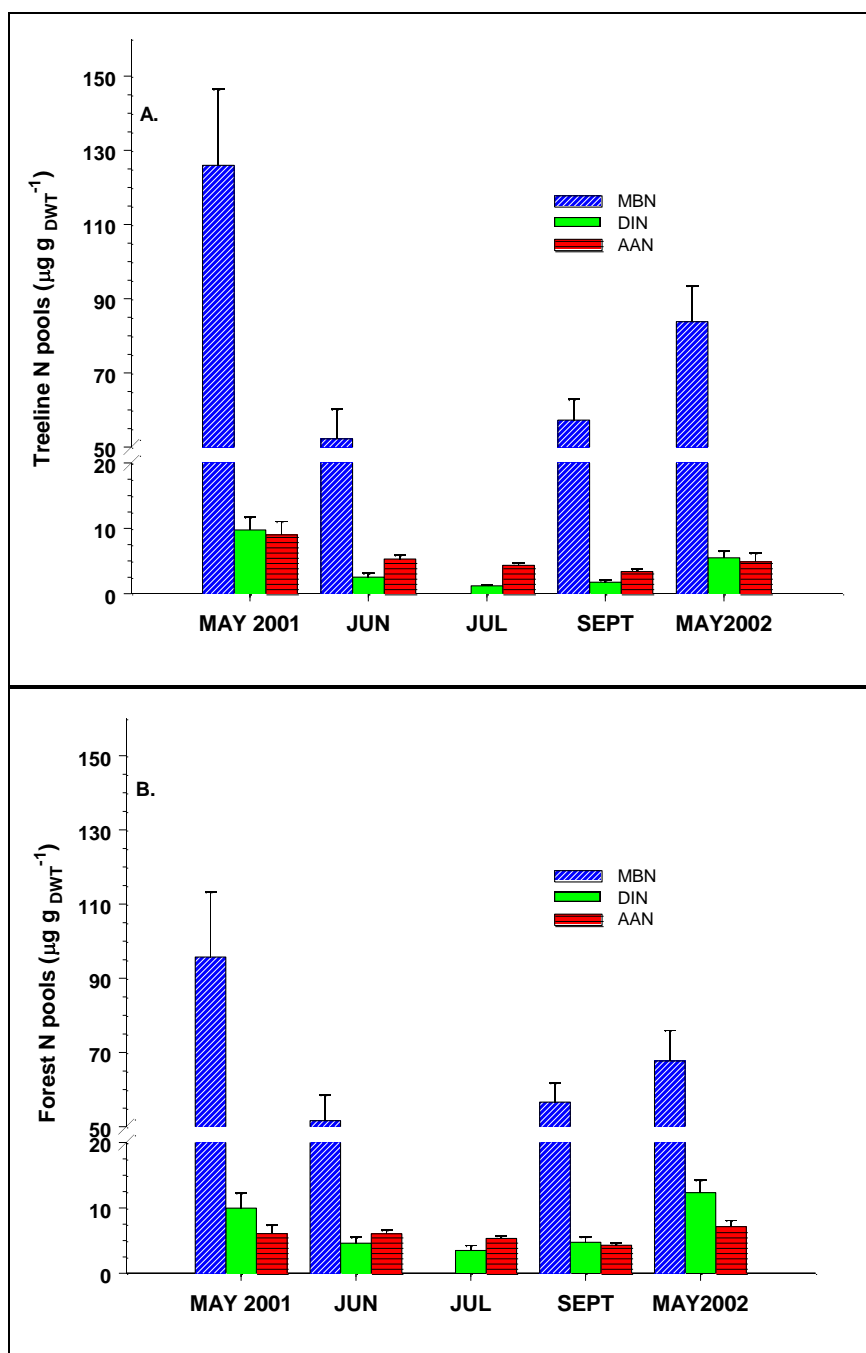


FIGURE 4. Seasonal patterns of microbial N, DIN and AAN for A. treeline sites and, B. forested sites. Means ± 1 SE are represented, n varied between 45 -52. Data were not collected for MBN during July.

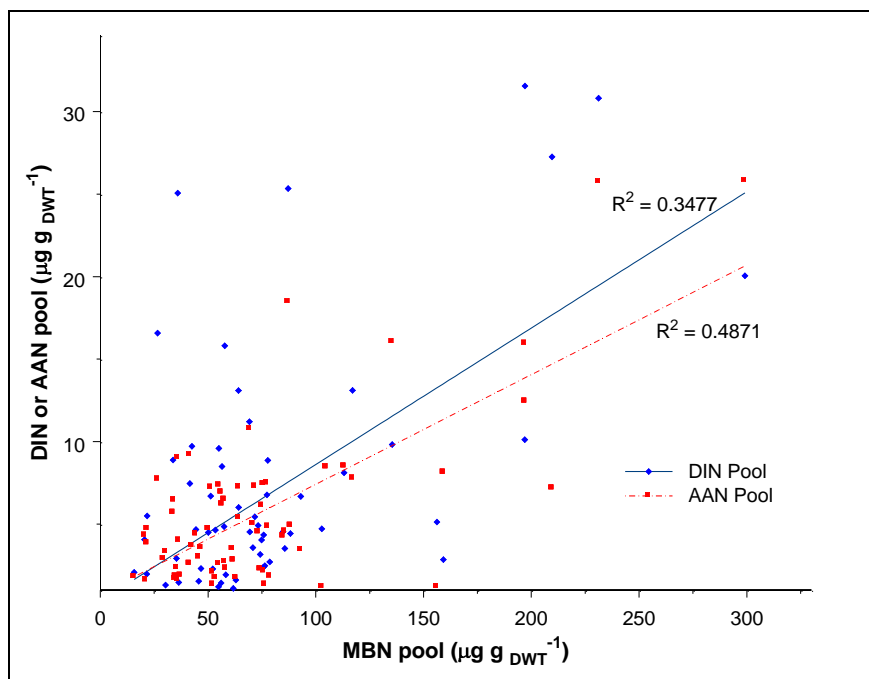


FIGURE 5. Relationship between extractable DIN or AAN and microbial biomass N. Data points represent means from each site, per season. Soil N pools are positively correlated across seasons, ranges and biome. For each variable, $n = 69$. The equation for DIN is: $y = 0.08188x + 0.048754$; the equation for AAN is: $y = 0.06602x + 0.84317$.

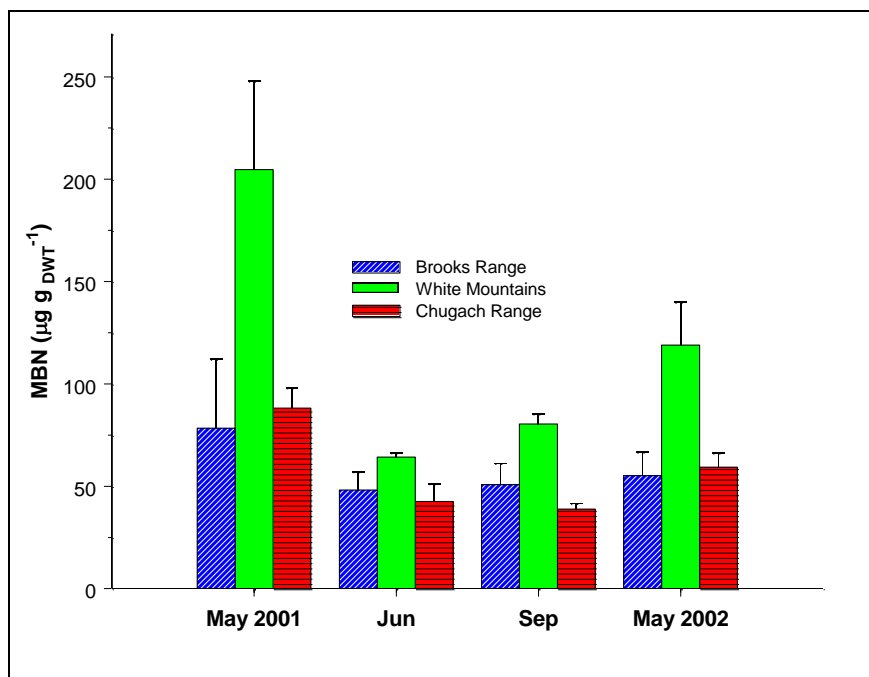


FIGURE 6. Seasonal patterns of microbial biomass N (MBN) in each mountain range. Data are means ± 1 SE for all points in each mountain range ($n = 36$).

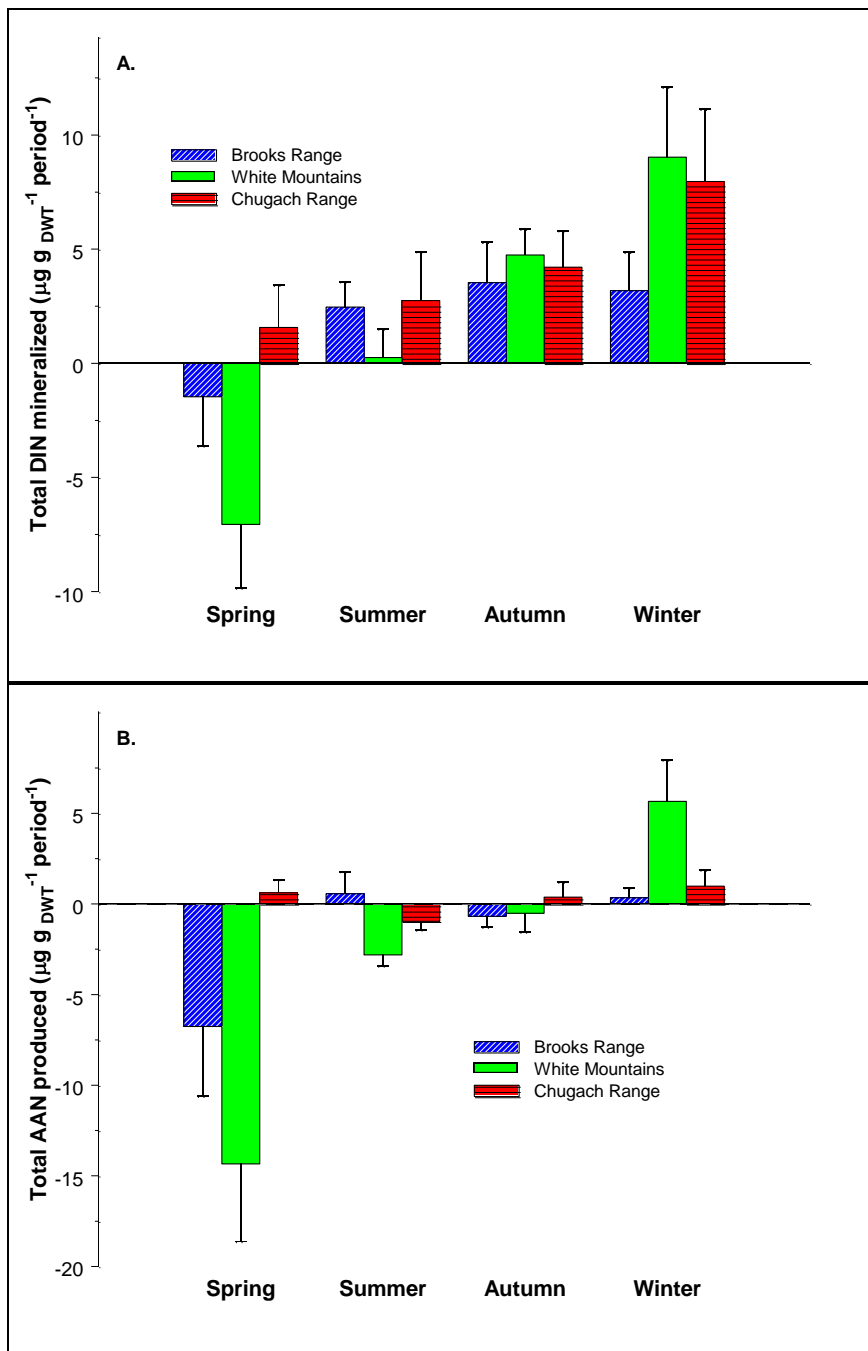


FIGURE 7. Production of N per season in each mountain range for: A. mineral N, and B. amino acid N. These values were calculated by multiplying the daily rate by number of days in each period ($\underline{n} = 36$).

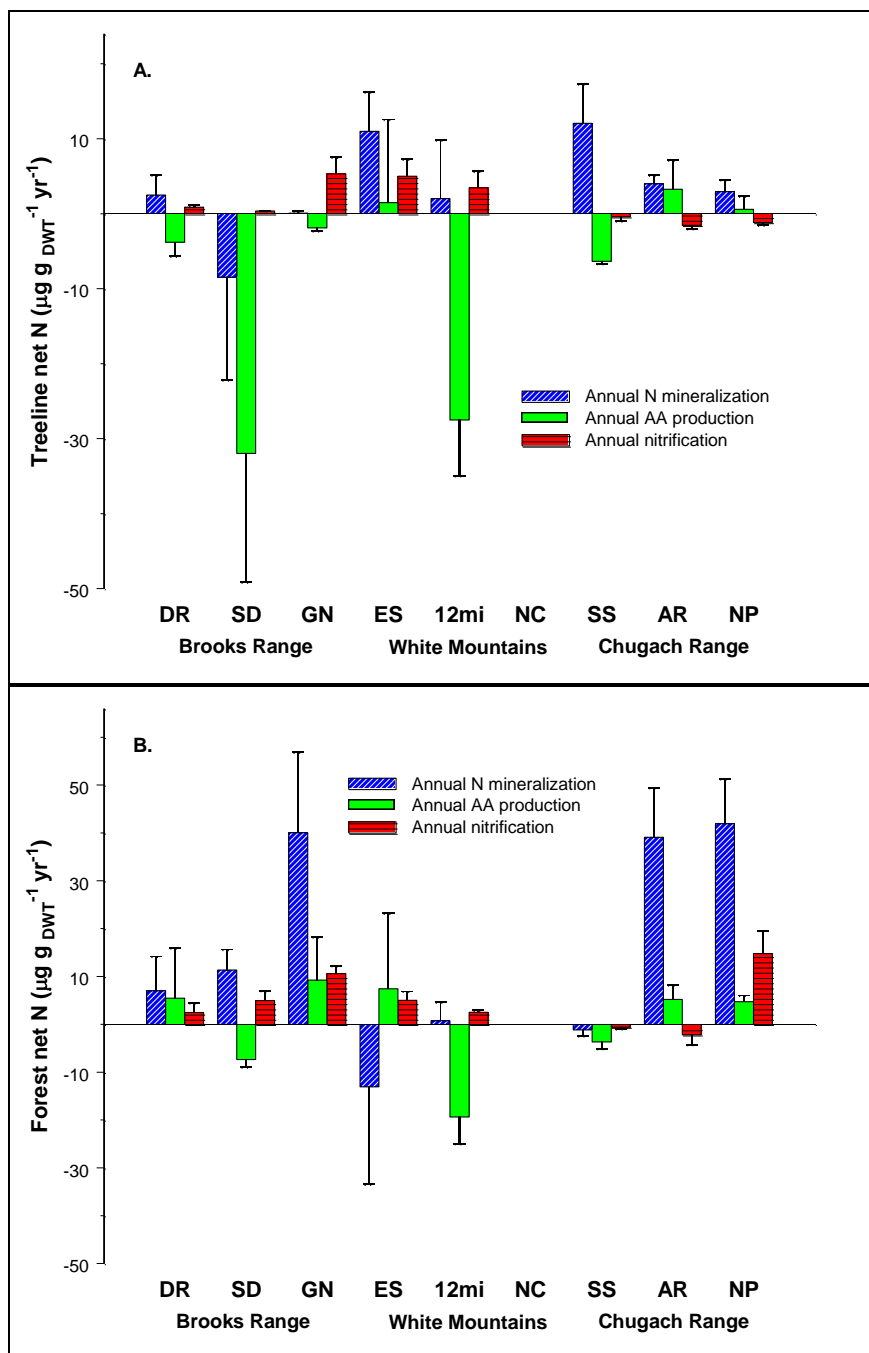


FIGURE 8: Total annual N production (mean \pm 1 SE) at A. treeline sites, and B. forested sites. Annual rates could not be calculated at Nome Creek, because we could not access the site for sampling during May 2001.

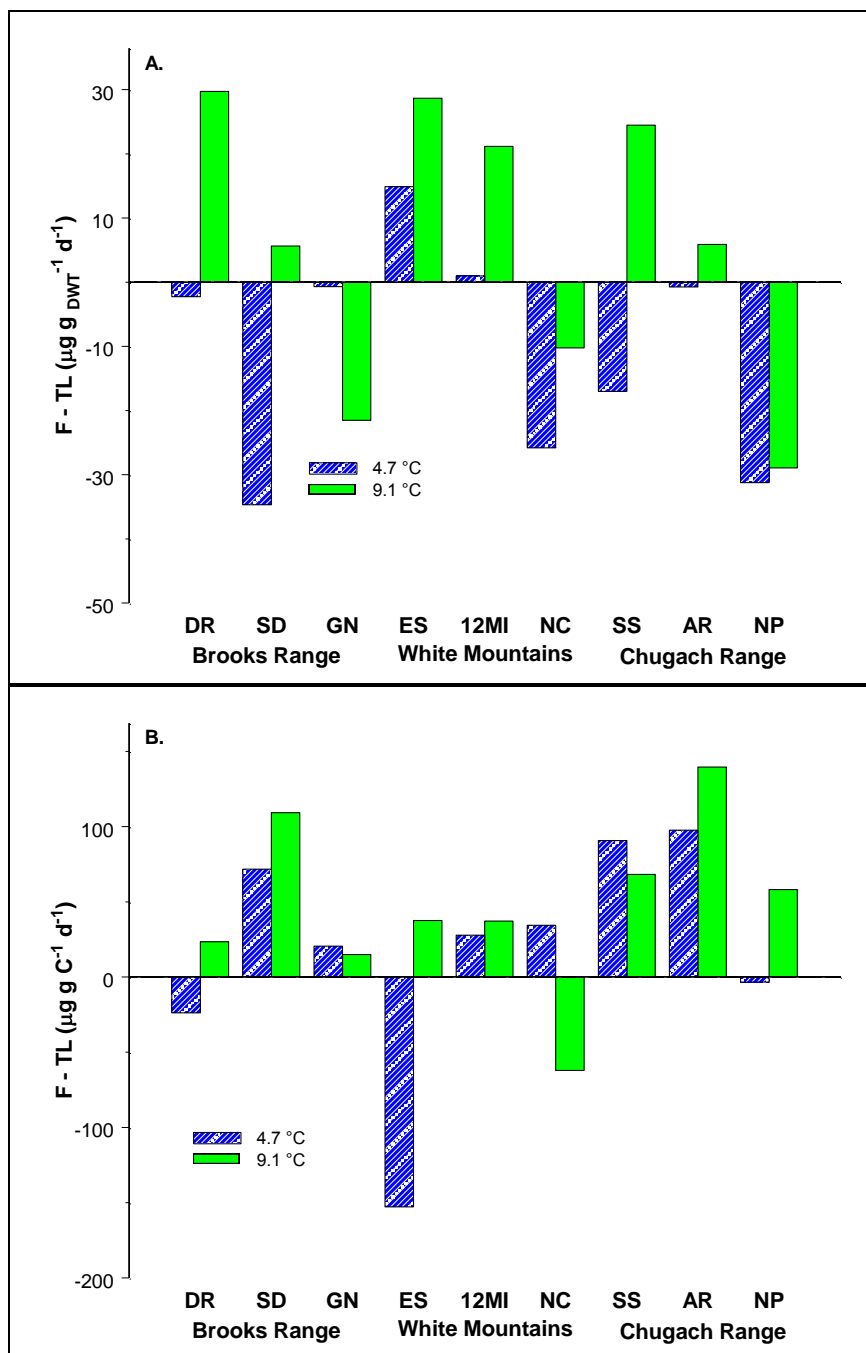


FIGURE 9. Difference between forested (F) and treeline (TL) sites in averaged respiration rate A. per gram soil, and B) per gram C. Data are shown for temperature treatments (1 = 4.69 °C, 2 = 9.11 °C), site and mountain range ($n = 5$).

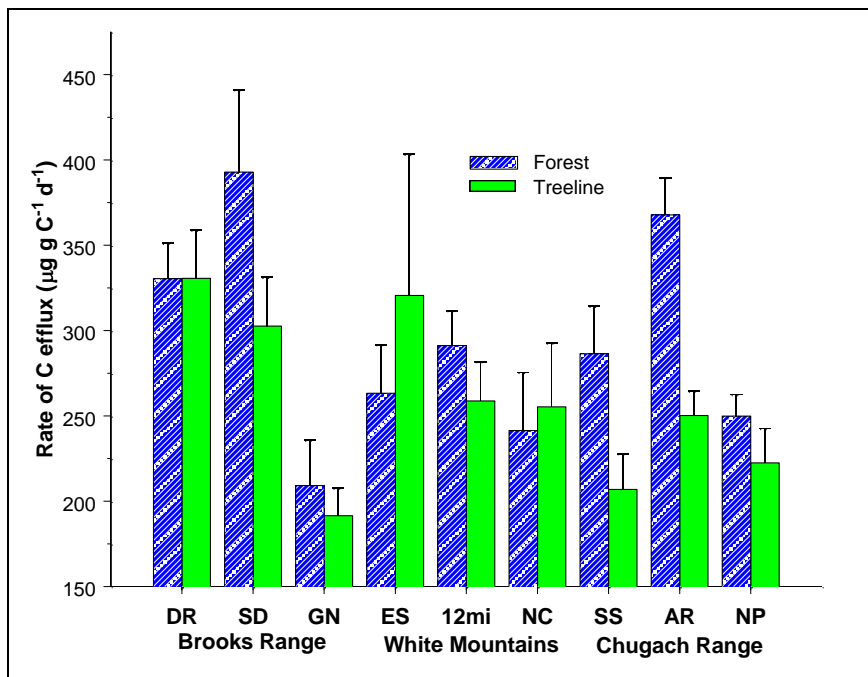


FIGURE 10. Site variation in rate of C efflux (mean \pm 1 SE) in soils from treeline and forested sites. For each observation, $n = 10$.

TABLES

TABLE I. Description of 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.

Site		Latitude/ longitude	Slope (°)	Aspect	Elevation (m)	Community description
<i>Brooks Range</i>						
Dietrich	Treeline	68° 01'N	25	SE	820	Low open shrub birch
	Forest	149° 41'W	15	SE	670	Open white spruce forest
Snowden	Treeline	67° 49'N	25	W	790	Low open shrub birch
	Forest	149° 48'W	15	W	610	Open white spruce forest
Gobbler's	Treeline	66° 44'N	2	S	620	<i>Vaccinium</i> tundra
Knob	Forest	150° 40'W	5	S	520	Open white spruce forest
<i>White Mountains</i>						
Eagle	Treeline	65° 30'N	12	S	997	Low open shrub birch
Summit	Forest	145° 21'W	15	S	936	Open white spruce forest
Twelve- mile Summit	Treeline	65° 23'N	10	NW	1010	Sedge-willow tundra
	Forest	145° 56'W	5	NW	960	Open white spruce forest
Nome	Treeline	65° 21'N	2	NW	770	<i>Vaccinium</i> tundra
Creek	Forest	146° 42'W	5	NW	715	Open white spruce forest
<i>Chugach Range</i>						
Site	Treeline	61° 15'N	10	NW	200	<i>Vaccinium</i> tundra
Summit	Forest	149° 34'W	20	N	170	Open white spruce forest
Art's	Treeline	61° 10'N	15	W	621	<i>Vaccinium</i> tundra
Ridge	Forest	149° 39'W	15	SW	492	Open white spruce forest
Near Point	Treeline	61° 9'N	15	W	590	<i>Vaccinium</i> tundra
	Forest	149° 40'W	2	W	388	Open white spruce forest

TABLE II. Percent cover of growth forms and densities of white spruce. Values in parentheses are standard errors. Tree cover other than white spruce was restricted to *Populus balsamifera*, which was present only at Art's Ridge forest site (8% cover). Abbreviations are: M = moss, L = lichens, S = shrubs, DS = dwarf shrubs, G = graminoids, F = forbs, R = rock, B = bare ground, BD = average basal diameter within a clonal group or a forked stem (cm), and H = height (m). For % cover, $\underline{n} = 10$; tree density, $\underline{n} = 7 - 10$, except Art's Ridge forest ($\underline{n} = 5$).

Site		Cover of growth forms (%)								Spruce statistics		
		M	L	S	DS	G	F	R	B	Trees (ha ⁻¹)	BD	H
Brooks Range												
Dietrich	Treeline	18	5	21	5	6	5	1	1	337 ± 72	9.6 ± 0.3	3.3 ± 0.1
	Forest	12	25	17	9	3	1	0	0	457 ± 29	15.4 ± 0.3	5.5 ± 0.1
Snowden	Treeline	35	17	1	10	3	2	1	0	302 ± 57	6.31 ± 0.2	2.5 ± 0.0
	Forest	47	5	6	3	1	2	0	1	2381 ± 275	10.3 ± 0.2	4.2 ± 0.1
Gobbler's	Treeline	1	45	27	8	1	1	1	0	16 ± 2	7.3 ± 0.1	2.1 ± 0.1
Knob	Forest	25	1	11	1	1	1	0	0	550 ± 49	13.2 ± 0.2	6.9 ± 0.1
White Mountains												
Eagle Summit	Treeline	25	4	4	9	6	1	0	0	336 ± 31	9.0 ± 0.2	2.1 ± 0.0
	Forest	71	1	9	8	1	1	0	0	863 ± 57	18.9 ± 0.3	6.5 ± 0.1
Twelvemile	Treeline	70	1	4	9	23	7	0	1	38 ± 4	9.8 ± 0.3	1.5 ± 0.0
Summit	Forest	75	3	1	5	18	4	0	0	379 ± 16	18.3 ± 0.4	4.8 ± 0.1
Nome Creek	Treeline	30	6	57	14	6	2	1	0	69 ± 4	10.6 ± 0.3	2.2 ± 0.1
	Forest	35	1	3	2	49	3	1	0	254 ± 19	25.0 ± 0.4	7.8 ± 0.1
Chugach Range												
Site Summit	Treeline	4	6	6	62	1	2	1	0	467 ± 69	12.2 ± 0.2	1.4 ± 0.0
	Forest	4	1	7	24	1	23	0	0	263 ± 19	20.4 ± 0.4	3.8 ± 0.1
Art's Ridge	Treeline	1	1	41	43	2	2	0	1	27 ± 2	25.3 ± 0.7	3.0 ± 0.1
	Forest	1	0	4	1	60	20	0	0	291 ± 79	25.6 ± 1.0	5.8 ± 0.3
Near Point	Treeline	1	1	11	37	1	2	0	0	24 ± 3	21.2 ± 0.9	2.9 ± 0.1
	Forest	27	27	4	1	11	3	0	0	71 ± 11	17.5 ± 1.2	5.6 ± 0.3

TABLE III. Soil physical properties. Percent C, N and C:N data are from organic soils ($\underline{n} = 10-14$ per site). “-“ = sites not sampled. Volumes are % of core (20 cm depth). C per m^2 (top 20 cm); $\underline{n} = 4$; rock and soil volumes: $\underline{n} = 8$; depths of live moss, dead moss and organic soil: $\underline{n} = 5$. Values in parentheses are standard deviations.

Site		C	N	C:N	C	Rock vol.	Soil vol.	Live moss	Dead moss	Organic
		%	%		g.m^2	%	%	cm	cm	cm
<i>Brooks Range</i>										
Dietrich	Treeline	16.9 ± 8.7	0.8 ± 0.4	21.3 ± 3.1	2207 ± 571	55.4 ± 6.3	44.6 ± 6.3	0 ± 0	1 ± 2	5 ± 3
	Forest	22.5 ± 13.4	0.9 ± 0.5	22.5 ± 4.5	4182 ± 998	38.5 ± 4.8	61.5 ± 4.8	0 ± 0	2 ± 3	5 ± 3
Snowden	Treeline	22.0 ± 12.4	1.1 ± 0.6	27.6 ± 3.1	4558 ± 1642	38.5 ± 7.3	61.5 ± 7.3	0 ± 0	5 ± 3	10 ± 8
	Forest	17.9 ± 12.4	0.8 ± 0.5	18.0 ± 2.6	3058 ± 1082	52.7 ± 8.0	47.3 ± 8.0	1 ± 3	3 ± 4	7 ± 6
Gobbler's	Treeline	22.0 ± 8.3	0.8 ± 0.3	21.0 ± 3.6	4047 ± 1118	46.0 ± 4.4	54.0 ± 4.4	0 ± 0	0 ± 0	10 ± 5
Knob	Forest	19.5 ± 10.3	1.1 ± 0.6	21.6 ± 4.1	3262 ± 898	44.3 ± 5.2	55.7 ± 5.2	2 ± 1	3 ± 2	5 ± 3
<i>White Mountains</i>										
Eagle	Treeline	25.0 ± 9.5	1.1 ± 0.3	17.3 ± 2.4	-	-	-	0 ± 0	8 ± 2	10 ± 3
Summit	Forest	29.3 ± 9.1	1.4 ± 0.3	17.1 ± 1.9	-	-	-	3 ± 3	10 ± 6	20 ± 8
Twelvemile	Treeline	18.8 ± 6.5	1.1 ± 0.4	22.6 ± 4.7	-	-	-	0 ± 0	7 ± 2	14 ± 5
Summit	Forest	18.0 ± 10.0	1.0 ± 0.6	21.0 ± 3.4	-	-	-	3 ± 0	10 ± 3	17 ± 3
Nome	Treeline	28.0 ± 7.9	1.3 ± 0.4	22.9 ± 3.3	-	-	-	0 ± 0	2 ± 1	24 ± 18
Creek	Forest	17.9 ± 10.6	1.0 ± 0.6	17.9 ± 4.9	-	-	-	0 ± 0	3 ± 1	11 ± 4
<i>Chugach Range</i>										
Site	Treeline	20.9 ± 6.9	0.9 ± 0.4	27.0 ± 3.5	5052 ± 1861	28.2 ± 5.5	71.8 ± 5.5	0 ± 0	1 ± 2	9 ± 3
Summit	Forest	21.6 ± 4.5	0.8 ± 0.2	18.2 ± 2.9	5036 ± 1466	30.8 ± 4.8	69.2 ± 4.8	0 ± 1	1 ± 1	11 ± 5
Art's Ridge	Treeline	19.5 ± 5.6	0.7 ± 0.2	24.9 ± 4.1	5254 ± 1990	30.8 ± 6.4	69.2 ± 6.4	0 ± 0	2 ± 1	9 ± 3
	Forest	15.9 ± 4.0	0.9 ± 0.2	27.5 ± 3.5	7414 ± 2458	15.5 ± 3.3	84.5 ± 3.3	0 ± 0	3 ± 6	8 ± 4
Near Point	Treeline	25.4 ± 6.2	0.9 ± 0.2	29.2 ± 2.1	8739 ± 3617	24.5 ± 5.9	75.5 ± 5.9	0 ± 0	2 ± 1	10 ± 3
	Forest	17.1 ± 5.8	0.8 ± 0.2	20.8 ± 2.2	7487 ± 3516	25.5 ± 4.9	74.5 ± 4.9	0 ± 0	1 ± 1	9 ± 1

TABLE IV. Summary of mean soil and air temperatures (°C). Values are means from 2000- 2004 \pm 1 SE. Date of thaw and freeze refer to the date after which soils were continuously thawed (spring) or frozen (autumn). We defined the growing season as June- August. * Warmest month was in August; † warmest month was in June; for all other groups, July was warmest.

	Annual mean	Max	Min	Date of thaw	Date of freeze	Mean temp. of growing season	Mean temp. of warmest month
Soil Temperature							
<i>Brooks Range</i>							
Forest	-0.18 \pm 0.12	14.96	-10.19	23 May	06 Oct	6.01 \pm 0.18	7.14 \pm 0.29
Treeline	-1.51 \pm 0.09	15.31	-14.24	20 May	03 Oct	6.25 \pm 0.1	7.15 \pm 0.18
<i>White Mountains</i>							
Forest	1.41 \pm 0.08	13.01	-7.38	20 Apr	14 Oct	6.9 \pm 0.12	8.01 \pm 0.17
Treeline	0.37 \pm 0.07	20.22	-11.36	29 Apr	16 Oct	6.09 \pm 0.15	6.21 \pm 0.28*
<i>Chugach Range</i>							
Forest	3.07 \pm 0.21	17.59	-0.97	18 May	30 Nov	10.53 \pm 0.28	13.45 \pm 0.31
Treeline	1.95 \pm 0.23	11.63	-6.97	16 May	07 Nov	6.12 \pm 0.33	8.46 \pm 0.19*
Air Temperature							
<i>Brooks Range</i>							
Forest	-8.31 \pm 0.45	32.48	-45.50			11.24 \pm 0.25	12.18 \pm 0.38
Treeline	-4.91 \pm 0.19	21.59	-35.84			10.84 \pm 0.16	12.18 \pm 0.21†
<i>White Mountains</i>							
Forest	-3.18 \pm 0.24	21.72	-55.64			11.17 \pm 0.21	11.93 \pm 0.27
Treeline	-3.48 \pm 0.20	21.30	-33.88			10.06 \pm 0.18	10.94 \pm 0.30
<i>Chugach Range</i>							
Forest	4.16 \pm 0.41	40.75	-43.33			16.10 \pm 0.66	19.13 \pm 1.16
Treeline	2.02 \pm 0.38	17.46	-19.63			9.42 \pm 0.46	12.84

TABLE V. Results of Simple Linear Regression analysis on means per site. Variables marked with a symbol were significant only at * treeline sites or †forest sites. When regressing variables on mean soil and air temperatures from Jun- Aug, we only used data collected during summer.

Independent variable	Dependant variable	R-Square	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 Jun-Aug	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 Jul	N mineralization	0.4720	2.11	0.0881*
	AA production	0.5134	2.30	0.0701*
	MBN pool	0.4913	-2.20	0.0794*
Mean air temp for Jun-Aug	N mineralization	0.4887	2.59	0.0361†
% 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

TABLE VI. The proportion of N mineralized or produced per season for forest and treeline sites in all mountain ranges. Units for period values are $\mu\text{g g}_{\text{DWT}}^{-1} \text{period}^{-1}$. 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	Biome	Spring	Summer	Autumn	Winter	Annual
<i>Net Mineralization</i>						
Brooks	Treeline	0	0.446	0.790	1.123	2.360
	Forest	0.978	4.485	6.268	4.876	16.607
White	Treeline	0	0.000	2.062	4.873	6.936
	Forest	3.798	5.494	6.358	10.064	25.714
Chugach	Treeline	0	0	3.700	5.695	9.396
	Forest	0	2.460	5.792	10.140	18.392
<i>Net Nitrification</i>						
Brooks	Treeline	0.669	0.380	0.527	0.673	2.249
	Forest	1.387	1.497	2.221	0.874	5.978
White	Treeline	0.148	0.695	1.416	0.714	2.973
	Forest	0.430	2.706	2.478	0.000	5.613
Chugach	Treeline	0	0	0.001	0.313	0.314
	Forest	0.533	0	1.986	3.384	5.903
<i>Net Amino Acid Production</i>						
Brooks	Treeline	0	0	0	0	0
	Forest	0	2.009	0	1.155	3.164
White	Treeline	0.264	0	0.310	0	0.574
	Forest	1.204	0	0.440	1.772	3.416
Chugach	Treeline	0	0	0	4.802	4.802
	Forest	0	0	0.313	5.794	6.107

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