

Effects of local changes in active layer and soil climate on seasonal foliar nitrogen concentrations of three boreal forest shrubs

Jennifer K. Rohrs-Richey and Christa P.H. Mulder

Abstract: Caribou Poker Creeks Research Watershed is a boreal forest watershed in Interior Alaska that is susceptible to regional warming and permafrost thaw. We measured seasonal foliar N concentrations of the black spruce understory shrubs, *Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L., and *Ledum palustre* L. on north- and south-facing sides of the watershed. We predicted that the shrubs would respond to small-scale changes in active layer and soil climate, and we expected similar responses according to growth strategy (evergreen or deciduous). Overall, foliar N in shrubs was higher on warmer, drier soils with deep active layers: +7.9% N in *V. uliginosum*, +11.1% N in *V. vitis-idaea*, and +9.4% N in *L. palustre*. Each shrub had species-specific foliar N patterns that could not be categorized by growth strategy and were not well explained by soil climate or active layer. Leaf mineral nutrition is influenced by multiple processes, and foliar N was best explained by the combination of environmental variables operating at the study site. For Caribou Poker Creeks Research Watershed, we can expect increased N status of the black spruce understory along with continued climate warming, but changes cannot be predicted based on growth strategy.

Résumé : Le bassin expérimental de Caribou Poker Creeks qui est situé en forêt boréale à l'intérieur de l'Alaska est sujet au réchauffement régional et au dégel du pergélisol. Nous avons mesuré les concentrations saisonnières d'azote foliaire des arbustes en sous-étage de l'épinette noire : *Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L. et *Ledum palustre* L. sur les versants nord et sud du bassin. Nous avons prédit que les arbustes réagiraient à des changements à petite échelle dans le climat des horizons actifs et du sol et nous nous attendions à des réactions semblables chez les espèces qui ont la même stratégie de croissance, c.-à-d. à feuillage persistant ou caduc. Dans l'ensemble, les arbustes sur les sols plus chauds et plus secs avec un horizon actif profond avaient plus d'azote foliaire : +7,9 % N chez *V. uliginosum*, +11,1 % N chez *V. vitis-idaea* et +9,4 % N chez *L. palustre*. Chaque arbuste avait un patron d'azote foliaire spécifique qui ne pouvait pas être classé sur la base de la stratégie de croissance et qui n'était pas bien expliqué par le climat édaphique ou l'horizon actif. La nutrition minérale des feuilles est influencée par de multiples processus et le comportement d'azote foliaire était le mieux expliqué par la combinaison des variables environnementales agissant dans la station à l'étude. Dans ce bassin expérimental, nous pouvons anticiper une augmentation de l'azote dans le sous-étage de l'épinette noire avec la poursuite du réchauffement du climat mais les changements ne peuvent être prédits sur la base de la stratégie de croissance.

[Traduit par la Rédaction]

Introduction

Evergreen shrubs represent a high proportion of the understory in black spruce (*Picea mariana* (Mill.) BSP) forests of Interior Alaska, which almost exclusively occupy cold, wet sites associated with permafrost (Van Cleve et al. 1983; Viereck et al. 1983). Although evergreen shrubs dominate the black spruce understory, both deciduous and evergreen growth strategies are important to element cycling in black spruce stands, where soil N availability is severely limited by permafrost, soil climate, and litter quality (Van Cleve and Viereck 1981; Van Cleve et al. 1996). Understory

shrubs have faster leaf turnover rates than black spruce trees and a high ratio of leaf to stem biomass; therefore, the shrub layer plays a substantial role in element cycling (Chapin and Tyron 1983). The deciduous and evergreen growth strategies are also thought to have different functions in black spruce stands. Deciduous shrubs have higher tissue nutrients, dynamic seasonal movement of nutrients, and are able to take advantage of and retain nutrient pulses (Chapin et al. 1980). In contrast, the slow growth and long life span of evergreen species allows for minimum resource loss and exploitation of periods of low nutrient supply (Eckstein and Karlsson 1997).

Although evergreen and deciduous shrubs have different functional roles in black spruce stands, N acquisition in both growth strategies is limited by permafrost. Cold and frozen soils restrict root activity, nutrient uptake (Bonan and Shugart 1989), absorption (Lambers et al. 1998), and infiltration (Schimel et al. 1996). Thus, in the upland black spruce forest of Interior Alaska, understory shrubs are expected to have low concentrations of foliar N (Chapin and Tyron 1983). However, low foliar N may not be a uniform condition within black spruce stands. Permafrost is highly

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sensitive to changes in air and ground temperature, and south-facing aspects receive greater amounts of solar radiation resulting in deeper permafrost tables, warmer, drier soils (Slaughter et al. 1995), and the potential for increased N acquisition in shrubs. This study questions whether shrubs of contrasting growth strategies have a similar foliar N response to small-scale changes in soil climate and active layer within the black spruce forest. Deepening active layer and warmer, drier soils are realistic changes for the Interior of Alaska, which is at the southern limit of continuous permafrost. Permafrost melting is occurring in the Interior and further degradation is predicted with continued regional warming (Hassol 2004).

Our study is based on the sensitivity of permafrost to different aspects (north and south) of an Interior Alaskan watershed. This study area was located in a black spruce dominated watershed at Caribou Poker Creeks Research Watershed (CPCRW), where active layer depth (the top layer of permafrost that thaws during the growing season) and soil climate change with aspect and elevation of the watershed. Shallow active layers, and cold, wet soils characterized north-facing sides of the watershed, termed "high permafrost". South-facing sides, termed "low permafrost" had deeper active layers, warmer, drier soils, and a natural gradient in the permafrost table that increased with elevation. Given the very different functional roles that deciduous and evergreen shrubs play in the black spruce forest, this paper contrasts seasonal foliar N patterns of deciduous and evergreen growth strategies, including resorption in the deciduous species, with local changes in active layer and soil climate. This study also measures net N mineralization rates to address whether soil N also changes with active layer and soil climate.

Three ericaceous shrubs were chosen as focal species for this study and represent 86% of the shrub groundcover in our study area (Troth et al. 1975): the deciduous *Vaccinium uliginosum* L., and two evergreens, *Vaccinium vitis-idaea* L. and *Ledum palustre* L. The closely related *V. uliginosum* and *V. vitis-idaea* are circumpolarly distributed, co-occurring species, which grow at high altitudes and latitudes on poorly drained, acidic, soil types (Jacquemart 1996). These *Vaccinium* species are dominant vegetation in the boreal region and are often associated with *L. palustre*. Within the Caribou-3 subwatershed of CPCRW, foliar N concentrations were compared between high permafrost and low permafrost hillslopes and across an elevational gradient of increasing thaw depth. We tested three hypotheses in this study, which were formulated based on the premise that the evergreen-deciduous contrast in growth strategy would determine the overall response of foliar N to changes in active layer and soil climate. First, we hypothesized that the deciduous, more productive *V. uliginosum* would increase foliar N with deeper active layers and warmer, drier soils; therefore, we expected to find higher foliar N in *V. uliginosum* on low permafrost hillslopes and at intermediate elevations of the watershed. Our second hypothesis for both of the evergreen species, *V. vitis-idaea* and *L. palustre*, was that foliar N would not be responsive to changes in active layer or soil climate, based on the more conservative nature of this growth strategy. Therefore, we did not expect foliar N in the evergreens to differ between low or high permafrost hill-

slopes, or across the elevation gradient. Previous studies in the arctic have found that evergreen shrubs have a limited capacity for resorption (Shaver and Chapin 1991), so we limited our predictions for resorption to the deciduous *V. uliginosum*. This shrub may use resorption to recover and conserve foliar N in areas with thin active layers and cold, wet soils, and we expected increased resorption efficiency in *V. uliginosum* on the high permafrost hillslopes.

Methods

Site description

CPCRW is a 104 km² boreal forest watershed 45 km north of Fairbanks (65°10'N, 147°30'W) in the Yukon-Tanana uplands of Interior Alaska. The Yukon-Tanana uplands comprise round, steep-sided ridges that are northeast trending. Hills rise 150–500 m above the alluvial covered valley bottoms, and ridges and peaks range from 450–900 m above sea level (Haugen et al. 1982). The drainage pattern in the watershed is dendritic, and stream channels in subdrainages are generally narrow and steep, while main channels are wider (Haugen et al. 1982). CPCRW has a climate typical of Interior Alaska, characterized by the large diurnal and annual temperature variations, low annual precipitation, and low humidity. During 2003, average monthly temperature in January was –20.6 °C and average monthly temperature in July was 14.2 °C (Hinzman and Busey 2005). Annual precipitation in 2003 was 487.5 mm (National Atmospheric Deposition Program, nadp.sws.uiuc.edu), and mean snow depth in CPCRW from December through April was 304.8 mm (McClure and Avery 2003).

The research sites for this study were located in the Caribou-3 (C3) watershed, one of the four watersheds draining Caribou Creek in CPCRW. The watershed has an area of 5.7 km² (Haugen et al. 1982) with elevations in the watershed ranging from 274 to 770 m (Bredthauer and Hoch 1979). The overall aspect of the watershed is northeast and the warmest areas of the watershed are on the south-facing slopes at intermediate elevations. The watershed experiences frequent air temperature inversions during the winter, resulting in valley bottoms that are 7.2 °C colder than intermediate elevations (Haugen et al. 1982). CPCRW has never been glaciated and is underlain by mica schist of the Birch Creek Formation. Soils are thin, poorly developed silt loams within 1 m of shattered bedrock (Haugen et al. 1982). Periglacial features, such as thermokarst, are found throughout the four watersheds draining CPCRW (Kodial et al. 2005), although our research sites in the C3 watershed did not contain these features. Fifty-three percent of the C3 watershed is underlain by permafrost, and the north-facing aspect of the watershed, in combination with permafrost and topography, result in black spruce (*Picea mariana*) stands with a thick moss, lichen, and evergreen shrub understory (Haugen et al. 1982). The coniferous community of the C3 watershed has high moss and lichen cover; the dominant species are Labrador tea (*L. palustre*), bog blueberry (*V. uliginosum*), and bog cranberry (*V. vitis-idaea*) (Troth et al. 1975). Valley bottoms of the watershed are dominated by riparian communities of willow (*Salix* sp.), dwarf birch (*Betula nana* L.), and blueberry (*V. uliginosum*) (Bredthauer and Hoch 1979).

Nitrogen fixing activity of moss communities and alders

are a potentially important N input to the watershed, where low soil temperature, thick moss layer, and wet soils are responsible for N limitation in the entire CPCRW study area (Haugen et al. 1982). The widespread moss *Pleurozium schreberi* (Brid.) Mitt. may be a significant contributor of N in black spruce stands (Klingensmith and Van Cleve 1993) and has been estimated to fix between 1.5 and 2.0 kg·ha⁻¹·year⁻¹ in the boreal region of Scandinavia (DeLuca et al. 2002). Nitrogen fixing alders (*Alnus crispa* (Ait.) Pursh and *Alnus tenuifolia* Nutt.) are common species that contribute substantial amounts of N to early successional floodplain systems (Klingensmith and Van Cleve 1993), and have the potential for significant N addition to this watershed. Soils in the C3 watershed have low N content (1.2%–1.9% N vs. 46%–49% C), thick organic layers (15 to 25 cm), and low pH (3.46–4.00) (Troth et al. 1975).

Experimental design

The experimental design was developed to capture differences in foliar plant N 1) between the north-facing (high permafrost) and south-facing (low permafrost) sides of the watershed and 2) from the valley bottoms to the warmer, intermediate hillsides (411–494 m above sea level) of the watershed. All of the study sites were underlain by permafrost; however, differences in active layer, soil temperature, and soil moisture distinguished the high and low permafrost sites. In the watershed, we established ten 400 m long transects that originated in the valley bottom, and ended in the intermediate elevations (411–494 m) of the watershed (Fig. 1). Five parallel transects spaced 250 m apart were set up on the north-facing slope of the watershed and another five on the south-facing slope of the watershed. Transects were established using compass bearings, with the north-facing transects running upslope along 150° lines and the south-facing transects running upslope along 300° lines. There were five sampling points along each transect: 0 m (valley bottom, within 5 m of the stream), 20 m (toeslope region representing transition from riparian area to black spruce overstory), and 100, 300, and 400 m (Fig. 1). These were used to capture elevational differences in depth of thaw and foliar plant N. All plant samples, soil samples, and environmental data were collected at these sampling points along the transects, resulting in a total of 50 sampling points across all high and low permafrost transects. Transects on the south-facing hillslopes, designated “low permafrost”, had an average slope of 18°, and spanned elevations from 348 m (valley bottom) to 483 m (upper sampling point). The transects on the north-facing slopes were designated “high permafrost” and ranged from 340 to 494 m in elevation with an average slope of 31°.

Plant sampling and analyses

The understory plants sampled for this study were two evergreen shrubs, *V. vitis-idaea* (bog cranberry) and *L. palustre* (Labrador tea), and one deciduous shrub, *V. uliginosum* (bog blueberry). Plants were sampled at the determined points (0 m, 20 m, 100 m, 300 m, 400 m) along transects during the second to third week of June, July, and September of 2003. At each elevation, foliage was collected from a 20 m transect perpendicular to the slope and bisected by the sampling point. Foliar samples were taken at five random

points selected along the 20 m perpendicular transect, which resulted in sampling 50 individuals of each species per transect. Only foliage from the top 10 cm of each plant was collected. During the September sampling period, leaves on *V. uliginosum* (the only deciduous species) were sampled by shaking the shrub and collecting fallen leaves. This method ensured that the senesced leaves we collected had not yet experienced leaching on the forest floor.

Foliage samples were dried in an oven at 60 °C for 24 h, and leaf area was measured on a subset of 10 leaves from each sample using a CI 202 Area Meter (C.I.D., Inc., Camas, Washington). Leaf area measurements were used for resorption calculations and also to evaluate the changes in leaf morphology associated with varying tree density between the low and high permafrost hillslopes. Leaf samples were ground using small ball bearings in plastic vials on a rolling mill. Nitrogen analyses of foliage were carried out at the University of Alaska Forest Soils Laboratory, using a CNS-2000 Elemental Analyzer (LECO Corporation, Michigan).

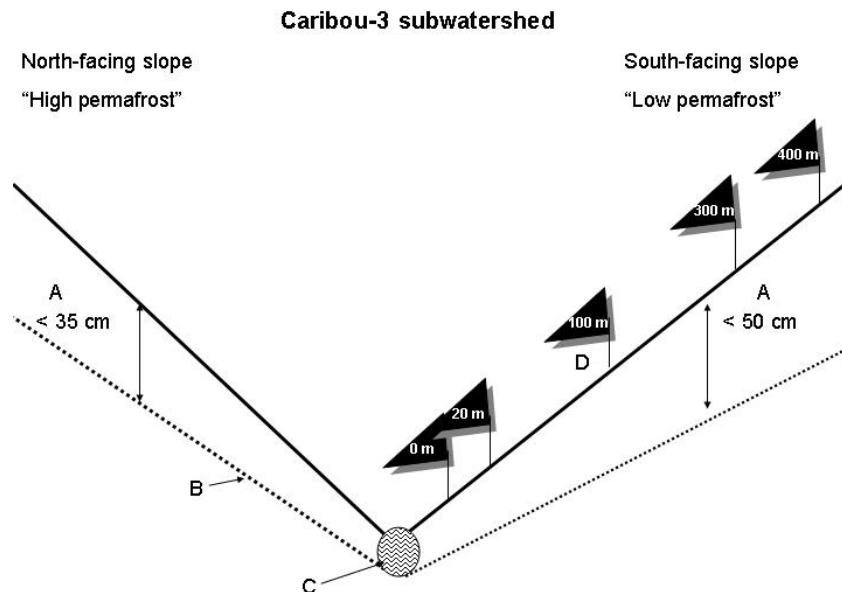
Resorption of foliar N in *V. uliginosum* was calculated on a leaf area (μg·mm⁻²) and mass basis. Resorption calculated on an area basis standardizes for the amount of photosynthetic machinery in the leaf, which may vary according to the light levels at different habitats (Eckstein et al. 1999). Resorption calculated on an area basis also reliably accounts for changes in leaf mass throughout the season, and assumes that leaf area remains fairly constant throughout the season (Killingbeck 1984, Aerts 1996). Resorption efficiency, the percentage of N removed from senescing leaves, was calculated as the difference in N (on an area basis) between peak foliar N and senesced leaves. This calculation is the most commonly used measure of nutrient resorption (Reich et al. 1995). For this equation, the term “leaf litter” represents foliage collected in mid-September

$$[1] \quad \frac{\text{maximum green leaf N} - \text{leaf litter N} \times 100\%}{\text{maximum green leaf N}}$$

Soil sampling and analyses

Net N mineralization is used as an index of N availability that measures forms of inorganic N (NH₄⁺ and NO₃⁻), which supply the majority of plant uptake (Binkley and Hart 1989). Net N mineralization does not account for organic N availability, which is also used for plant nutrition (Jones and Kielland 2002). In July and August of 2003, in situ net N mineralization was measured by the buried bag method (Robertson et al. 1999) at all ten transects (five on the low permafrost hillslope and five on the high permafrost hillslope) and all sampling points (0, 20, 100, 300, and 400 m) in the C3 watershed. At each of the 50 sampling points, a 20 m × 2 m belt transect was established perpendicular to the slope and centered on the sampling point. At three random points within this belt transect, two soil cores were taken of the top 10 cm of organic soil. One soil core was put in a cooler and taken back to the laboratory for immediate extraction. Care was taken to keep the second soil core intact; it was sealed in a ziplock bag, buried in the ground, retrieved three weeks later, and extracted at the laboratory. Three initial soil cores were taken from each elevation along

Fig. 1. The layout of one 400 m transect is illustrated. The entire study comprised ten 400 m transects, with five transects on each of the high permafrost and low permafrost hillslopes. The transects were spaced 250 m apart. A, thaw depth; B, permafrost table; C, stream bed; D, markers (0, 20, 100, 300, and 400 m) establishing the 400 m long transect.



the transect, for a total of 15 cores per transect and 150 cores per monthly sampling period. Once the soil cores were in the laboratory, the cores were measured and weighed for bulk density calculations. The soil cores were homogenized, and 10 g from each core was shaken with 75 mL of 0.5 mol·L⁻¹ K₂SO₄ for 1 h and then filtered using Buchner funnels and glass microfibre filter paper. An additional 10 g was oven dried at 60 °C for 24 h to determine soil moisture. The filtered extracts were frozen until further analysis. NH₄⁺-N was analyzed using a phenol hypochlorite assay and NO₃⁻-N using a Cd-reduction column on a Technicon Autoanalyzer (Whitledge et al. 1981).

Net mineralization calculations

The initial and final pools of extractable inorganic N were calculated on a dry soil basis. Net mineralization rates were calculated as the difference between initial and final extractable inorganic N pools over the incubation period ($\mu\text{g N}\cdot\text{g dry soil}^{-1}\cdot 21 \text{ days}^{-1}$) (Robertson et al. 1999). Bulk density calculations, based on the volume of the soil corer, were also used to convert rates to a mass per area basis ($\mu\text{g N}\cdot\text{m}^{-2}$).

Environmental and plant community measurements

At each transect and each sampling point, environmental and site variables were measured. Slope and aspect were measured using a Suunto inclinometer and compass, overstorey canopy density was measured using a convex spherical densiometer (Robert E. Lemmon, Forest Densiometers), and elevation was determined using topographic map features and a Rino 120 Garmin GPS (± 50 m above sea level). Soil temperature at the 10 cm depth was measured every two weeks from June through August with a digital soil thermometer (MULTI-thermometer) and measurements of thaw depth were taken every two weeks from July through September with a rebar thaw probe. Percent cover of understory species was measured along the transects in 2002 using the

line intercept method, and in 2003, percent cover of understory was measured at each sampling point using 1 m \times 0.5 m quadrats (Barbour et al. 1979). To estimate black spruce density, the nearest neighbour distance method was used on all points and all transects (Barbour et al. 1979).

This study also measured the density of N fixing species, which had the potential to influence inorganic soil N. Belt transects (20 m \times 2 m) centered on the sampling points were used to measure the density of alders (*Alnus* spp.), and quadrats (1 m \times 0.5 m) were used for percent cover estimates of *Pleurozium schreberi*.

Statistical analyses

Statistical analyses were performed using SAS System version 8.2 (SAS Institute Inc., Cary, North Carolina). We used analysis of variance (ANOVA) to compare means of foliar N, N resorption, tree densities, specific leaf area, and percent cover of understory species and shrubs between high and low permafrost hillslopes. We used similar ANOVA procedures to compare means of the environmental measurements, pools of inorganic N, and rates of net N mineralization between low and high permafrost hillslopes. Site designation (low or high permafrost) and sampling distance from stream (0, 20, 100, 300, and 400 m) were used as explanatory variables. We performed stepwise regression to determine which variables best explained foliar N, pools of inorganic N, and rates of net mineralization using site designation (low or high permafrost) and all possible subsets of environmental and site variables measured during the sampling months. Stepwise regression was also used to evaluate variation in percent cover using the same set of explanatory variables, with the addition of tree density. Pearson correlation was used to test for a relationship between specific leaf area and tree density, soil moisture and leaf area, alder density and net mineralization rates, and alder density and dissolved organic N.

Table 1. Stepwise regression results for soil climate variables.

Month	Distance (m)	Slope (°)	Permafrost (high/low)	Elevation (m)	Model R^2
Temperature (°C)					
June	ns	ns	$p < 0.0001$ (0.11)	$p = 0.0006$ (0.06)	0.18
July	$p = 0.0022$ (0.04)	$p = 0.0037$ (0.04)	$p < 0.0001$ (0.29)	ns	0.37
Aug.	$p = 0.004$ (0.02)	$p = 0.001$ (0.02)	$p < 0.0001$ (0.65)	ns	0.69
Sept.	$p = 0.02$ (0.01)	ns	$p < 0.0001$ (0.62)	$p < 0.0001$ (0.07)	0.71
Moisture (%)					
July	ns	$p = 0.0055$ (0.02)	$p < 0.0001$ (0.41)	$p = 0.0003$ (0.03)	0.46
Aug.	ns	ns	$p < 0.0001$ (0.35)	ns	0.35
Thaw depth (cm)					
June	ns	$p = 0.007$ (0.05)	ns	ns	0.05
July	ns	ns	$p = 0.039$ (0.01)	$p < 0.0001$ (0.22)	0.23
Aug.	$p < 0.0001$ (0.23)	ns	$p < 0.0001$ (0.18)	ns	0.42
Sept.	$p < 0.0001$ (0.19)	ns	$p < 0.0001$ (0.19)	$p < 0.0001$ (0.11)	0.49

Note: Partial R^2 values are in parentheses. Variables enter into the model at $p = 0.1$, variables stay in the model at $p = 0.05$. Soil moisture was determined from soil core samples, which were taken in July and August. Distance represents metres from the stream, along the transect sampling points (0, 20, 100, 300, and 400 m). Thaw depth was entered into the model as an explanatory variable for soil temperature and moisture, but was not retained. ns, not significant at $p > 0.05$.

Results

Seasonal and spatial changes in soil climate and thaw depth

Active layer and soil climate in the northeastern-facing C3 watershed were largely influenced by aspect: high permafrost hillslopes (north-facing) had significantly colder, wetter soils and a thinner active layer (Table 1). Although aspect explained the majority of variation in soil temperature and moisture throughout the summer, distance from the stream, slope, and elevation of the watershed were also retained in the model. Unlike soil climate, thaw depth was well explained by elevation (in July) and distance from the stream (in August) (Table 1). On low permafrost hillslopes, thaw depth was the only variable that consistently increased with distance from the stream and elevation (Table 2). On both low and high permafrost hillslopes, 300 m and 400 m sampling points had thicker active layers. The steepest gradient in active layer was on low permafrost hillslopes from the 100 m to the 400 m sampling points (Fig. 2).

Low permafrost hillslopes had considerably warmer, drier surface soils and experienced greater soil warming throughout the growing season (Table 2). Mean temperature of low permafrost soil increased about 4 °C from June to July, along with an increase in soil moisture from 57% in July to 64% in August. The active layer on low permafrost hillslopes was thicker, mean depth of 38.0 cm, and did not have significant seasonal variation (Table 2; Fig. 2). On the high permafrost hillslope, seasonal warming of the soils (5 °C by July) was followed by increased soil moisture (78% in August) and thaw depth. The active layer on high permafrost sites, mean depth of 28.8, was deepest in September (Fig. 2).

Percent cover and tree density

The percent cover of the focal shrub species, *V. uliginosum*, *V. vitis-idaea*, and *L. palustre*, was similar between the low and high permafrost hillslopes. Although horsetails

(*Equisetum* spp.) dominated a few wet areas on high permafrost slopes, there were no differences in percent cover of any other common understory species, including crowberry (*Empetrum nigrum* L.), bog rosemary (*Andromeda polifolia* L.), northern commandra (*Geocaulon lividum* (Richardson) Fernald), or dwarf birch (*B. nana*). The low permafrost hillslopes did have a denser black spruce overstory ($F_{[1,40]} = 2.74$, $p = 0.0001$) and higher cover of the *Pleurozium* moss ($F_{[1,121]} = 4.25$, $p < 0.0001$), whereas high permafrost hillslopes had more open black spruce stands with higher percent cover of *Sphagnum* moss ($F_{[1,43]} = 1.75$, $p = 0.0031$).

Foliar N

Vaccinium uliginosum

The deciduous *V. uliginosum* had the highest foliar N and the most dynamic seasonal foliar N concentrations of the focal species. Specific leaf area (SLA) measurements indicated that high N concentration in new leaves was diluted throughout the growing season with carbon gain, and N was further reduced by resorption at the end of the growing season. *Vaccinium uliginosum* had the highest N concentrations early in the growing season (June), when low permafrost sites supported higher concentrations of N in new leaves than high permafrost sites (Fig. 3). In June, peak N concentrations at high and low permafrost sites differed significantly (2.34% N vs. 2.68% N), and aspect was the only variable that explained foliar N (Table 2). The high concentration of foliar N in June was reduced in July, when leaf thickness typically increases with carbon gain. Foliar N concentrations were not significantly different between low and high permafrost sites in September, when resorption reduced foliar leaf N to approximately 1% N (Fig. 3).

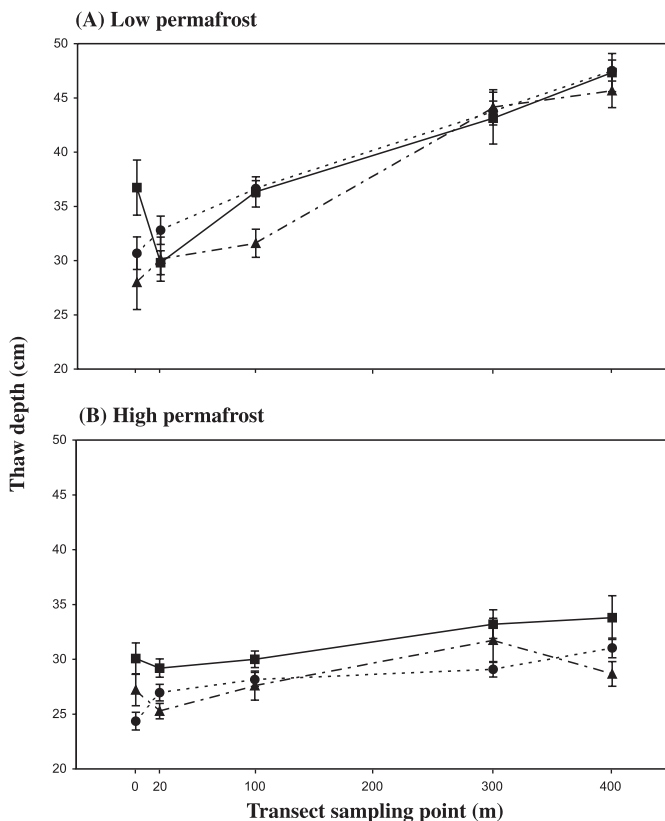
One objective of our study was to compare N resorption efficiency in the deciduous *V. uliginosum* between high and low permafrost hillslopes, as N resorption may be an important nutrient conservation mechanism on high permafrost

Table 2. Soil climate and thaw depth on high and low permafrost hillslopes.

Sampling distance from stream (m)	Low permafrost (south-facing aspect)	High permafrost (north-facing aspect)
Thaw depth (cm)		
0	30.31±6.65a	32.14±6.69
20	47.44±7.40a	33.33±6.24
100	39.59±4.91a	37.78±3.85
300	44.07±5.44b	33.33±6.25
400	49.67±9.63b	33.82±3.65
Soil temperature (°C)		
0	4.78±0.89	2.39±0.35
20	5.84±1.49	4.56±0.43
100	6.00±1.26	4.23±1.15
300	6.11±0.86	4.32±1.07
400	6.86±0.55	5.08±1.45
Soil moisture (%)		
0	57.81±1.86	72.61±2.23
20	62.59±1.87	77.43±1.85
100	60.30±1.65	75.74±1.72
300	59.04±1.67	76.69±1.59
400	60.88±2.18	74.25±1.76

Note: Values are mean ± SE. At each sampling distance, sample sizes are: thaw depth $n = 45$, soil temperature $n = 45$, and soil moisture $n = 30$. Only thaw depth differed between sampling points on the low permafrost hillslope. Thaw depth values within the low permafrost column followed by the same letter are not significantly different ($p = 0.05$, Tukey's HSD test).

Fig. 2. Thaw depth ($n = 15$, mean ± SE) is reported along sampling points in July (●), August (▲), and September (■). Different letters indicate significant differences between months determined by Tukey's HSD test ($p = 0.05$).



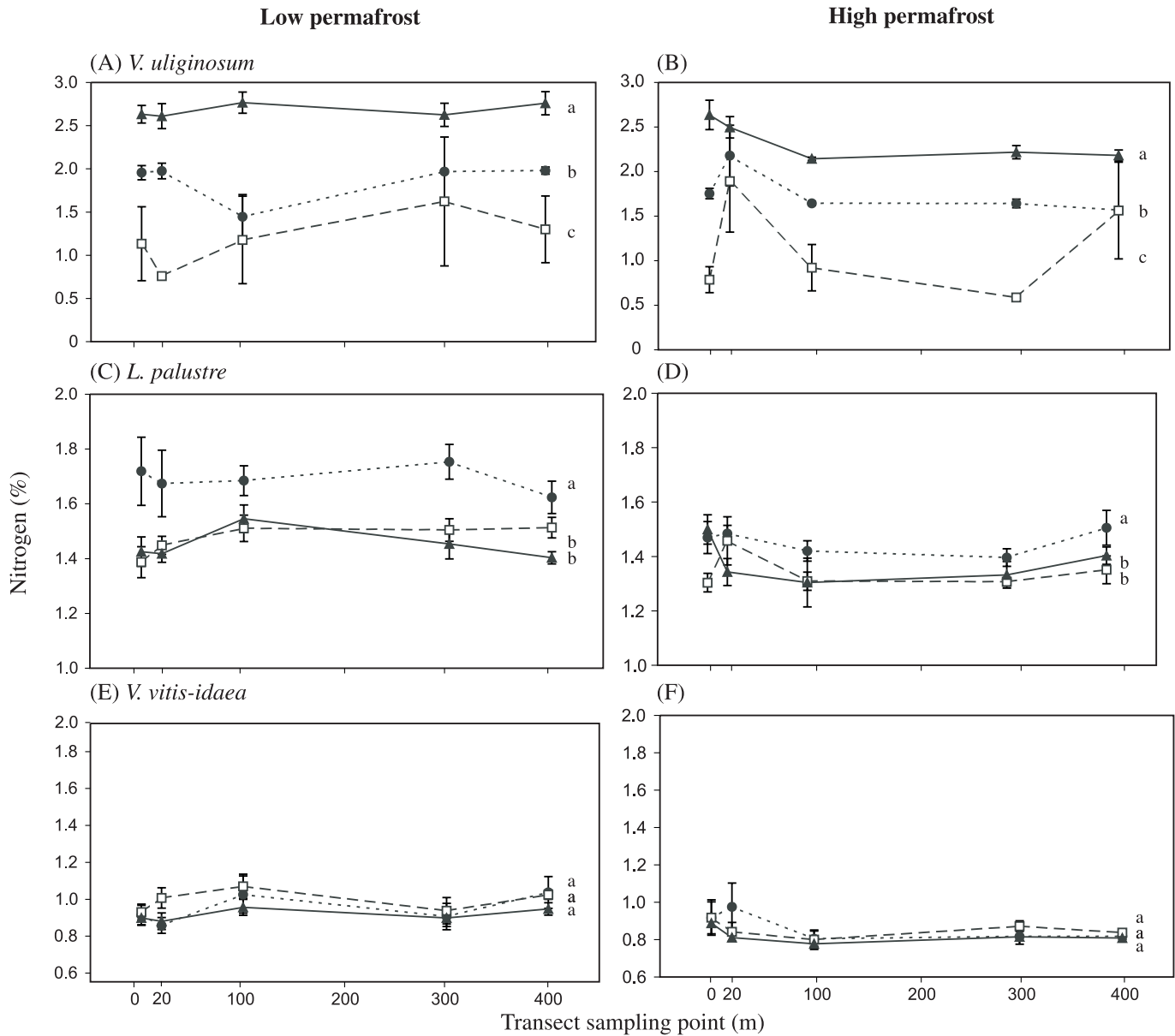
hillslopes. Calculated on a leaf area basis, *V. uliginosum* had higher N resorption at low permafrost sites ($F_{[1,33]} = 2.25$, $p = 0.016$), which had an overall mean N resorption of $67.18\% \pm 5.16\%$ N, compared with $36.27\% \pm 12.19\%$ N at high permafrost sites. Although differences were in the same direction when calculated on a mass basis ($63.6\% \pm 5.10\%$ N in the low permafrost site and $49.86\% \pm 8.54\%$ N on high permafrost sites) resorption was not significantly different. Specific leaf area (SLA) was correlated with tree density ($r^2 = 0.43$, $p < 0.0001$) and low permafrost sites had higher SLA (thinner leaves with more surface area); however, neither leaf weight nor SLA explained resorption efficiency.

Ledum palustre

The evergreen *L. palustre* was the only species that had higher foliar N concentrations on low permafrost hillslopes throughout the growing season (Table 3). *Ledum palustre* reached its peak seasonal N concentration in July at both high and low permafrost hillslopes; however, foliar N increased 15% from June to July at low permafrost sites, while *L. palustre* on high permafrost sites only experienced a 5% increase in foliar N (Fig. 3). At the end of the growing season in September, foliar N in *L. palustre* was reduced to June levels at both low and high permafrost sites.

Ledum palustre was the only species to have consistently higher concentrations of leaf N at the 300 m to 400 m sampling points on low permafrost hillslopes (Fig. 3). Therefore *L. palustre* was also the only species in which thaw depth or distance from the stream were significant explanatory variables, and in September we were able to explain 52% variation in foliar N (Table 3).

Fig. 3. Percent N ($n = 5$, mean \pm SE) is reported along sampling points in June (\blacktriangle), July (\bullet), and September (\square). Different letters indicate significant differences between months, determined by Tukey's HSD Test ($p = 0.05$). Note that the figures for the evergreens (*Ledum palustre*, *Vaccinium vitis-idaea*) are scaled differently than the figure for the deciduous *Vaccinium uliginosum*.



Vaccinium vitis-idaea

Among the three focal shrubs, *V. vitis-idaea* had the lowest foliar % N, the least seasonal variation in foliar N, and the smallest changes in leaf N along the elevation transect (Fig. 3). *Vaccinium vitis-idaea* had higher leaf N at low permafrost sites in June and September, when leaf N was explained by site (high or low permafrost) rather than by soil climate or active layer (Table 3). *Vaccinium vitis-idaea* was the only species that had little change in foliar N throughout the growing season: changes in overall percent N from June to September were less than 1% N at low and high permafrost sites.

Net N mineralization rates

The low permafrost hillslope, with warmer, drier soil and deeper active layer, did not support higher net mineraliza-

tion rates than the high permafrost hillslope, nor did net N mineralization rates increase upslope from the stream. In fact, net mineralization rates were higher on north-facing hillslopes in July (Table 4).

Although soil moisture and temperature are typical controls of net mineralization, soil climate and thaw depth did not explain much variation in net mineralization rate (Table 5). Soil moisture was the only soil climate variable retained in the model in August. Only 13% variation in net mineralization rate was explained in July and August: slope and nitrate were retained in the model in July, whereas elevation, soil moisture, and nitrate were retained in the model in August.

Foliar N and N-fixing species

Nitrogen-fixing species may be an important source of in-

Table 3. Stepwise selection results for percent foliar N.

Month	Permafrost (high/low)	Thaw depth (cm)	Distance (m)	Temperature (°C)	Moisture (%)	Model R^2
<i>Vaccinium uliginosum</i>						
June	$p < 0.0001$	ns	ns	ns	ns	0.27
July	ns	ns	ns	ns	ns	—
Sept.	ns	ns	ns	ns	ns	—
<i>Vaccinium vitis-idaea</i>						
June	$p = 0.0004$	ns	ns	ns	ns	0.24
July	ns	ns	ns	ns	ns	—
Sept.	$p < 0.0001$	ns	ns	ns	ns	0.37
<i>Ledum palustre</i>						
June	ns	$p = 0.029$ (0.10)	$p = 0.031$ (0.19)	ns	ns	0.29
July	$p < 0.0001$	ns	ns	ns	ns	0.44
Sept.	$p < 0.0001$ (0.44)	ns	$p = 0.017$ (0.08)	ns	ns	0.52

Note: Partial R^2 values are in parentheses. All significant relationships were positive. Variables enter into the model at $p = 0.1$, variables stay in the model at $p = 0.05$. Temperature and moisture are soil variables. Distance represents the distance from stream along transects (0, 20, 100, 300, and 400 m). ns, not significant at $p > 0.05$.

Table 4. Results for ANOVA of inorganic N pools and net N mineralization rates.

Form of N	Inorganic N pools and net mineralization rates		Explanatory variable, Type III SS	p
	High permafrost	Low permafrost		
July				
NH ₄	3.12±0.30	1.37±0.17	Perm, 112.32 Dist, 52.31	<0.0001 0.015
NO ₃	0.155±0.06	0.09±0.04	Dist, 1.84	0.0266
Net mineralization	3.1±0.66	0.7±0.32	Perm, 208.59	0.001
August				
NH ₄	2.64±0.40	0.91±0.18	Perm, 116.77	<0.0001
NO ₃	0.14±0.05	0.02±0.001	Perm, 0.878 Dist, 0.182 Perm × Dist, 0.853	0.0004 0.0177 0.0143
Net mineralization	2.6±0.73	1.4±0.3		ns

Note: Explanatory variables included in the model were high or low permafrost (Perm), distance from stream (Dist) as a categorical variable (0, 20, 100, 300, and 400 m), and a permafrost × distance interaction (Perm × Dist). ns, not significant at $p > 0.05$. Units for NH₄ and NO₃ are $\mu\text{g N}\cdot\text{g}^{-1}$ and values are the initial concentrations used for net mineralization calculations. Units for net mineralization rates are $\mu\text{g N}\cdot\text{g}^{-1}\cdot 21 \text{ days}^{-1}$.

organic soil N to the C3 watershed. We regressed inorganic N pools and net N mineralization rates on the densities of *Alnus* spp. and *Pleurozium schreberi*. Across all sites and all months, the correlation was positive between mean alder density and mean initial NH₄⁺ pools ($p < 0.0001$, $r^2 = 0.47$). Alder densities were higher at all sampling points on high permafrost hillslopes ($F_{[1,24]} = 1.44$, $p = 0.0152$) and alder density was positively correlated with initial pools of NH₄⁺ in July ($R^2 = 0.27$), although the relationship was weak in August. We also found positive correlations found between NH₄⁺ and foliar N at low permafrost sites in July for *V. vitis-idaea* ($r^2 = 0.64$, $p = 0.002$) and at low permafrost sites in September for *L. palustre* ($r^2 = 0.46$, $p = 0.03$).

Discussion

Both evergreen and deciduous shrubs in our study had

lower overall percent foliar N at the high permafrost sites (−7.96% N in *V. uliginosum*, −11.12% N in *V. vitis-idaea*, and −9.4% N in *L. palustre*). In the C3 watershed, active layer and soil climate did not consistently explain variation in foliar N. The only consistent and significant explanatory variable for foliar N throughout the entire growing season was site designation (high or low permafrost), which represented the combination of all environmental variables operating at that site. On the north-facing sides of the watershed, these variables (low soil temperature, thick moss layer, and wet soils) are all associated with permafrost and contribute to N limitation in the entire CPCRW study area (Haugen et al. 1982). These cold, wet conditions are integral for maintaining permafrost and comprise a feedback loop which is so closely connected that it may be difficult to distinguish which variables are responsible for N limitation in these shrubs (Camill 1999). Although our study hypothesized that

Table 5. Stepwise selection results for net mineralization rates and inorganic N.

Form of N	Permafrost (high/low)	Slope (°)	Elevation (m)	Moisture (%)	NO ₃	NH ₄	Model R ²
July							
NH ₄	<i>p</i> < 0.0001 (0.13)	<i>p</i> = 0.017 (0.02)	<i>p</i> = 0.0031 (0.03)	ns	<i>p</i> < 0.0001 (0.09)	ns	0.26
NO ₃	ns	ns	<i>p</i> = 0.0028 (0.03)	ns	ns	<i>p</i> < 0.0001 (0.09)	0.12
NMin	ns	<i>p</i> < 0.0001 (0.08)	ns	ns	<i>p</i> = 0.0003 (0.05)	ns	0.13
August							
NH ₄	<i>p</i> < 0.0001 (0.06)	ns	ns	ns	<i>p</i> < 0.0001 (0.16)	ns	0.19
NO ₃	ns	ns	ns	ns	ns	<i>p</i> < 0.0001	0.14
NMin	ns	ns	<i>p</i> = 0.04 (0.04)	<i>p</i> = 0.0239 (0.04)	<i>p</i> < 0.0001 (0.06)	ns	0.13

Note: Response variable NMin represents net mineralization rate. Partial R² is in parentheses. Variables enter into the model at *p* = 0.1, variables stay in the model at *p* = 0.05. Units for NH₄ and NO₃ are µg N·g⁻¹ and units for net mineralization are µg N·g⁻¹·21 days⁻¹. Moss layer, thaw depth, temperature, distance from the stream, and bulk density of soil were not retained in the model for any response variable. ns, not significant at *p* > 0.05.

active layer and soil climate would be the primary explanatory variables for foliar N, our data suggest that it is unlikely that two or three variables can adequately explain variation in foliar N. Leaf mineral nutrition is influenced by multiple processes (Welker et al. 2005), and it is necessary to consider the combination and interaction of environmental variables for predicting seasonal N concentrations.

Our hypotheses for foliar N response in the shrubs were based on the different functional roles of the evergreen and deciduous growth strategies. Given that deciduous species have faster growth rates and higher turnover rates, we predicted that *V. uliginosum* would reflect small-scale changes in active layer and soil climate. However, we found that *Ledum* was the only shrub that had consistently higher foliar N at low permafrost sites throughout the entire growing season. *Ledum* was also the only shrub for which foliar N was explained by thaw depth. Despite the more conservative growth strategy, *Ledum* has a shallow, lateral rooting system which may be advantageous earlier in the spring when root growth and activity allows nutrient and water to be accessed from freshly thawed, organic soils (Schimel et al. 1996). Higher values of leaf N in *Ledum* have also been observed in the arctic shortly after emergence from snowpack, suggesting use of soil resources during the later stages of snowmelt (Welker et al. 2005). Root growth in *V. uliginosum* doesn't peak until later in the growing season when flower buds are formed (Jacquemart 1996) and may be at a competitive disadvantage during the early nutrient flush when it has only a fraction of the number of new fine roots as *Ledum* (Kummerow et al. 1983). Although *V. uliginosum* did not demonstrate a foliar N response to increased active layer, it may have had other positive responses that we did not measure, such as longer leaf life span (Suzuki and Kudo 2000) and increased aboveground biomass (Press et al. 1998).

Throughout the growing season, *L. palustre* also had higher N concentrations and greater changes in seasonal N than the evergreen *V. vitis-idaea*. Although the two evergreen shrubs generally moved N into leaves slowly throughout the growing season, the shrubs had unique temporal and

spatial patterns of foliar N. While *V. vitis-idaea* had minimal changes in foliar N, higher foliar N concentrations in *Ledum* were found in July at higher elevations in the watershed and on low permafrost sites (Fig. 3). These species-specific patterns of foliar N suggest that different mechanisms determine seasonal courses of N in these evergreen understory shrubs. These mechanisms may be related to the inherent differences in stature and physiology of each shrub. *Ledum* is larger, often dominates the shrub canopy to reach higher light levels, has shown positive growth responses to increased air temperature and light (Chapin and Shaver 1985), and has higher leaf production (Shaver 1986). *V. vitis-idaea* is a smaller, shade-adapted shrub that grows low to the ground, may be limited by interspecific competition for soil nutrients (Shevtsova et al. 1995), and responds positively to increased fertilizer and temperature (Parsons et al. 1994). Previous studies in the Alaskan Arctic and subarctic Sweden have concluded that despite the similarity in growth strategy, *V. vitis-idaea* and *Ledum* have individualistic responses to similar regimes of light, nutrients, and temperature (Press et al. 1998; Leith et al. 1999), and it is likely that these co-occurring species are limited by different environmental variables (Chapin and Shaver 1985).

Although the contrast in growth strategies was the basis for our predictions of foliar N response, differences in foliar N were not defined by growth strategy. Is there a life history trait that can be used to predict foliar N responses to varying environmental conditions? Leaf life span is an important life history trait that is responsive to environmental and nutrient conditions and may explain variation in seasonal N courses. Reich et al. (1992) suggests that although the deciduous–evergreen contrast is useful, variation in leaf life span within each growth strategy may be just as important. For example, Suzuki and Kudo (2000) reported that an effect of experimental warming in open top chambers is increased leaf life span for *Ledum* and *V. vitis-idaea*, as well as earlier leaf emergence and later leaf senescence in *V. uliginosum*. Although it may be appropriate to categorize species by growth strategy across large-scale studies that include dra-

matic differences in leaf life span, predictions based on leaf longevity may have been useful for our smaller scale study within one community type.

Resorption

In this study, we anticipated that active layer and soil climate would affect N resorption in *V. uliginosum*. We measured resorption in only *V. uliginosum*, because previous studies in the Arctic have found that evergreen growth forms have a limited capacity for nutrient resorption (Chapin et al. 1980; Shaver and Chapin 1991). Efficient resorption of nutrients may be an important conservation strategy for plants living in low nutrient environments (Chapin and Kedrowski 1983) by reducing demand for nutrient uptake (Reich et al. 1995) and effectively minimizing resource loss prior to senescence (Eckstein and Karlsson 1997). We did not find evidence that *V. uliginosum* adjusted resorption efficiency according to variation in active layer or soil climate. Contrary to our hypothesis, we found higher resorption efficiencies in *V. uliginosum* (on an area basis) on low permafrost sites. The overall mean resorption per unit area on low permafrost hillslopes was 67%, which is comparable to previously measured N resorption in *V. uliginosum* at different arctic community types (60% for a tussock site, 62.1% for a heath site, and 70.1% for a shrub site; Chapin and Shaver 1991). Although it has been previously found that higher leaf N per unit area is correlated with higher resorption efficiency (Eckstein et al. 1999), no clear ecological controls over resorption have been established (Lambers et al. 1998). Our data gives no evidence for resorption as a conservation mechanism and suggests that shrubs with higher foliar N are simply resorbing more of that N at the end of the growing season.

Nitrogen fixers

The N-fixing species at our study sites, *Pleurozium schreberi* and *Alnus* spp., may be important sources of NH_4 addition to the N-limited watershed and may also account for variation in pools of dissolved inorganic N. We found that NH_4 concentrations were positively correlated with the density of *Alnus* spp. across study sites (*Alnus* spp. density was 65% greater on high permafrost hillslopes) and may account for the greater net N mineralization rates at the high permafrost sites. Although the potential N addition from alders may be a critical input for this watershed, lower foliar N at high permafrost sites indicates that *Alnus* spp. did not compensate for the overall nutrient limiting conditions.

Soil N availability

Compared with other habitat types within Interior Alaska, black and white spruce communities have very low net N mineralization rates. For example, rates in poplar–alder stands can be as high as $16 \mu\text{g N}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ (Van Cleve et al. 1993); in our study, rates were comparable to previously measured rates in black spruce stands, $<1 \mu\text{g N}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ (Van Cleve et al. 1993). Large-scale studies have determined that the typical controls on N cycling are soil temperature and moisture (Schimel et al. 1996), and in the Alaskan Interior, N cycling is also affected by permafrost and litter quality (Van Cleve et al. 1996). In our study area, the environmental conditions on south-facing slopes were more fa-

vorable for these typical controls of net mineralization. Contrary to expectations, and contradicting the pattern for foliar N, the north-facing hillslopes had higher net N mineralization rates and pools of inorganic N than south-facing hillslopes. When we used site characteristics (slope, elevation) in addition to soil temperature, soil moisture, thaw depth, and moss layer to explain net mineralization rates, we were only able to explain 13% of the variation. This suggests that other variables, perhaps related to organic matter quality of associated vegetation or the distribution of N fixers, plays a larger role in affecting net N mineralization at this smaller scale. In our study, net mineralization is used as an indicator of soil N availability and does not include the role that soluble organic N may have in nutrient cycling (Jones and Kielland 2002).

Conclusions on foliar N and low resource environments

Although we measured foliar N concentrations, not total plant N, we have good reason to believe that the lower levels of foliar N on the higher permafrost slopes are not a dilution effect (i.e., increased biomass in response to higher N availability (Shaver and Chapin 1980)) but do reflect total plant N. Studies in several ecosystems have found that the potential of a species to increase biomass depends on its ability to compete for N and use it for biomass production (Nordin et al. 1998). Plants from low resource environments, such as our focal species, may not have this competitive ability because they chronically experience a limitation, and nutrient-limited plants tend to exploit a temporarily favorable environment through nutrient storage rather than immediate growth (Bloom et al. 1985). In this subarctic plant community, growth may be additionally constrained by abiotic factors such as low air temperature, low light intensity, short growing season, and frozen soil. Therefore, in these low-resource environments, species have inherently low growth rates and are more likely to respond to temporarily favourable resources by storing nutrients (luxury consumption) rather than growing rapidly (Chapin et al. 1990).

Implications for CPRW

In our study, the effect of aspect (low or high permafrost) on N status of the dominant understory shrubs suggests that the impact of regional warming on active layer and soil climate would result in the transition to a more N-rich black spruce understory. Although both evergreen and deciduous growth strategies have the potential for increased N status, shrubs may have individualistic responses to warmer, drier conditions which cannot be categorized by growth strategy.

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