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The seasonal dynamics of amino acids and other nutrients in Alaskan Arctic tundra soils

MICHAEL N. WEINTRAUB* and JOSHUA P. SCHIMEL
*Department of Ecology, Evolution, and Marine Biology University of California, Santa Barbara Santa Barbara, CA 93106, USA; *Author for correspondence (e-mail: weintrau@lifesci.ucsb.edu; phone: +1-805-451-2566; fax: +1-240-358-6080)*

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Abstract. Past research strongly indicates the importance of amino acids in the N economy of the Arctic tundra, but little is known about the seasonal dynamics of amino acids in tundra soils. We repeatedly sampled soils from tussock, shrub, and wet sedge tundra communities in the summers of 2000 and 2001 and extracted them with water (H_2O) and potassium sulfate (K_2SO_4) to determine the seasonal dynamics of soil amino acids, ammonium (NH_4^+), nitrate (NO_3^-), dissolved organic nitrogen (DON), dissolved organic carbon (DOC), and phosphate (PO_4^{2-}). In the H_2O extractions mean concentrations of total free amino acids (TFAA) were higher than NH_4^+ in all soils but shrub. TFAA and NH_4^+ were highest in wet sedge and tussock soils and lowest in shrub soil. The most predominant amino acids were alanine, arginine, glycine, serine, and threonine. None of the highest amino acids were significantly different than NH_4^+ in any soil but shrub, in which NH_4^+ was significantly higher than all of the highest individual amino acids. Mean NO_3^- concentrations were not significantly different from mean TFAA and NH_4^+ concentrations in any soil but tussock, where NO_3^- was significantly higher than NH_4^+. In all soils amino acid and NH_4^+ concentrations dropped to barely detectable levels in the middle of July, suggesting intense competition for N at the height of the growing season. In all soils but tussock, amino acid and NH_4^+ concentrations rebounded in August as the end of the Arctic growing season approached and plant N demand decreased. This pattern suggests that low N concentrations in tundra soils at the height of the growing season are likely the result of an increase in soil N uptake associated with the peak in plant growth, either directly by roots or indirectly by microbes fueled by increased root C inputs in mid-July. As N availability decreased in July, PO_4^{2-} concentrations in the K_2SO_4 extractions increased dramatically in all soils but shrub, where there was a comparable increase in PO_4^{2-} later in the growing season. Previous research suggests that these increases in PO_4^{2-} concentrations are due to the mineralization of organic phosphorus by phosphatase enzymes associated with soil microbes and plant roots, and that they may have been caused by an increase in organic P availability.

Abbreviations: TFAA – Total free amino acids; DOC – Dissolved organic carbon; DON – Dissolved organic nitrogen; NH_4^+ – Ammonium; NO_3^- – Nitrate; PO_4^{2-} – Phosphate; DIN – Dissolved inorganic nitrogen: ammonium + nitrate; N – Nitrogen; C – Carbon

Introduction

Plant growth in the Arctic tundra of Alaska is limited by N availability, especially in tussock tundra (Shaver and Chapin 1980, 1986; Shaver et al. 1986;

Shaver and Kummerow 1992; Schimel et al. 1996). While net N mineralization has been considered to define the amount of plant available N (Vitousek et al. 1979; Schimel and Bennet 2003), previous research has shown that it cannot meet the total N requirements of tundra plants (Giblin et al. 1991; Nadelhoffer et al. 1991). As a result, N availability to plants in the Arctic tundra is still poorly understood. Several studies have shown that tundra plants can take up amino acids (Chapin et al. 1993; Kielland 1994; Schimel and Chapin 1996; Kielland 1997), but the role of amino acids as a component of the soil N cycle and as an N source to plants has not been well quantified. In part, this is because little is known about the seasonal dynamics of soil amino acids and dissolved organic N (DON), and how they relate to the dynamics of dissolved inorganic N (DIN) and plant growth. One study measuring soil amino acids in the Alaskan Arctic tundra found total free amino acids (TFAA) to be seven times higher than NH_4^+ in tundra soils, on average (Kielland 1995), while another study found TFAA to be consistently lower than NH_4^+ in tundra soils (Nordin et al. 2003). In both of these studies, samples were only collected three times in a growing season, too few to resolve the seasonal dynamics of these N forms. Because of this, and the lack of agreement between prior studies, we are still left with a poor understanding of how soil TFAA and DIN change across the growing season in tundra soils.

Concentrations of soil nutrients are controlled by their relative production and consumption rates. The extremely rapid turnover of soil amino acids (Kielland 1995; Lipson et al. 2001; Weintraub, unpublished data) suggests that extractable concentrations are a snapshot of the relative difference between production and consumption at any given time, and are therefore a short-term measure of nutrient availability. In the case of amino acids, production is controlled by the activities of exoenzymes, particularly proteases, which break down proteins into soluble peptides and individual amino acids, and by direct release from soil microbes in response to osmotic changes or as a result of cell lysis (Lipson and Nasholm 2001). The death of microbial cells and the input of fresh plant detritus are also likely to increase the production of amino acids by providing proteins to proteases.

For both plants and soil microbes, N uptake rates at any given time depend on both the organisms' physiological capacity to take up DIN and amino acids, and on the concentrations of these compounds available in the soil. The controls on the timing and magnitude of nutrient uptake in soil are poorly understood, but microbial N demand is likely to be stimulated by high C availability, while nutrient uptake by plants is likely to be controlled by growth form and phenology. Plant uptake from the soil can act as a direct sink for soil N, while inputs of C rich plant detritus to the soil can also stimulate microbial N immobilization. As a result, plant species-specific patterns in the timing and magnitude of both nutrient uptake and detritus inputs to the soil have the potential to create different patterns of nutrient availability in different plant communities.

Previously observed differences between the different tundra communities in soil DIN concentrations and net N mineralization rates suggest that N

availability varies considerably across them (Giblin et al. 1991; Nadelhoffer et al. 1991; Weintraub and Schimel 2003). Other studies have found that extractable NH_4^+, NO_3^-, and amino acid concentrations are lower in shrub tundra soil than in tussock soil (Giblin et al. 1991; Kielland 1995), suggesting that either N consumption rates are relatively high or that N production rates are relatively low in shrub soil. In a laboratory incubation of tundra soils, N mineralization rates in shrub soil were dramatically higher than in tussock soil (Weintraub and Schimel 2003), suggesting that there is a larger pool of potentially available N in shrub soil, but that more soil N is also taken up.

While nutrient availability is the principal factor limiting plant productivity in the Arctic (Billings et al. 1984; Schimel et al. 1996), plant growth often does not depend on nutrient uptake from the soil in the first half of the growing season. Instead, it depends on nutrients stored in plant tissues (Mckendrick et al. 1978; Chapin et al. 1980; Chapin et al. 1986a, b; Shaver et al. 1986; Shaver and Kummerow 1992). This is a necessary adaptation for growth in the tundra, since soils remain frozen for several weeks after air temperatures are above freezing, during the time of year when solar radiation is highest (Shaver and Kummerow 1992). The most intensive period of root growth in deciduous tundra plants generally does not start until after leaf expansion is well underway (Shaver and Kummerow 1992). Leaf expansion begins when air temperatures rise above freezing, but before the soil historically thaws (Shaver and Kummerow 1992). Historically, these soils thawed later in the spring, but the extent of spring snow cover has been decreasing as spring temperatures have been increasing due to climate warming, resulting in an earlier thaw (Serreze et al. 2000).

Plant community composition in the Arctic tundra is already changing in response to warming, with the predominance of the deciduous shrub *Betula nana* increasing, especially in the tussock community (Hobbie 1996; Hobbie and Chapin 1998). Strong differences in N availability between tussock and shrub soils suggest that the increasing predominance of *Betula nana*, the dominant shrub where we sampled, has the potential to change N cycling dynamics in tussock soil. However, the seasonal N dynamics of these tundra communities are not well enough understood to predict how they will change with the increasing predominance of deciduous shrubs.

To help understand how patterns of N availability vary over the growing season in different tundra communities, and how patterns of organic and inorganic N availability vary with respect to one another, we sampled and extracted tundra soils every 1–2 weeks through the summer of 2000 and twice in the summer of 2001, and analyzed the extracts for amino acids, NH_4^+, NO_3^-, DON and DOC, and PO_4^{2-} to determine the seasonal time-courses of these nutrients. The goals of this research were to determine which amino acids predominate throughout the growing season, and whether changes in TFAA or individual amino acid concentrations are associated with changes in soil DON and DIN concentrations; and to provide an accurate, fine scale time-course of soil solution composition over the course of the entire growing season. We hypothesized that the early part of the growing season, when plant nutrient

uptake rates are low, and late in the growing season, after plant senescence begins and plant nutrient demand decreases, would be the times when soil nutrient concentrations are highest.

Materials and methods

Study site

This research was conducted at the Toolik Field Station (Lat. 68°38′N, Long. 149°38′W), on the north slope of the Brooks Range in Alaska. We worked in three tundra communities at Toolik Lake: tussock tundra, shrub tundra, and wet sedge tundra (Table 1).

Table 1. Soil classifications (from C.L. Ping pers. comm.), and mean N and C contents

Soil type	Soil classification	%N	%C
Intertussock	Loamy, mixed, typic aquaturbel	0.5	42
Shrub	Loamy-skeletal, mixed, active, gelic aquic umbrorthel	1.3	38
Tussock	Loamy, mixed, typic aquaturbel	1.6	33
Wet sedge	Dysic, typic hemistel	2.0	37

In the northern foothills of the Brooks Range tussock tundra is the most common vegetation type. Tussock tundra is a mesic, or moist, tundra form, and usually occurs on moderately hilly topography with silty to gravelly soils (Shaver and Chapin 1991). It is dominated by *Eriophorum vaginatum*, a tussock forming sedge, interspersed with a mix of scattered shrubs (*Salix* spp., *Betula nana, Vaccinium vitis-idaea*), *Sphagnum rubellum*, and feather mosses (e.g. *Hylocomium splendens*and *Dicranum elongatum*) (Shaver and Chapin 1980; Shaver et al. 1986; Shaver and Chapin 1991). The mosses and shrubs grow predominately in the spaces between the 10 and 30 cm tussocks, which we call 'intertussock.' There is an uneven cover of organic soil 0–20 cm thick in tussock tundra, and the soil is always moist (Shaver and Chapin 1991). All of our soil samples in tussock tundra were collected from the organic layer directly underneath *Eriophorum vaginatum* plants to a depth of approximately 15 cm. This soil consists primarily of decaying roots of *Eriophorum vaginatum*. Intertussock soil was sampled underneath the mosses and shrubs between *Eriophorum vaginatum* tussocks. This organic soil is comprised of decomposing mosses, shrub fine roots and leaf litter.

Wet sedge tundra occurs in flat low-lying areas where low stature (< 20–30 cm) rhizomatous sedges such as *Carex aquatilis* and *Eriophorum angustifolium* predominate, with some *Eriophorum scheuchzeri* (Shaver and Chapin 1991). Further north on the Arctic coastal plain where the soil is typically wet, it becomes the dominant plant community. Areas where this community occurs are usually flat, and are characterized by standing water throughout much of

the summer, resulting in high water contents and anaerobic soil conditions (Shaver and Chapin 1991). Wet sedge soils are relatively thick peats (typically >30 cm) with a shallow thaw depth (25–30 cm; Shaver and Chapin 1991). Permafrost prevents the deep drainage of water, isolates plants from mineral soil, and keeps the soil flooded and cold. All of the samples we collected in wet sedge were from the top 15 cm of the peat layer.

The shrub tundra community is another mesic tundra form, found in upland sites and along water tracks (Shaver and Chapin 1991). In other regions of the Arctic shrub tundra is more common than tussock (Bliss and Matveyeva 1992). The relatively high stature (<1–2 m) shrubs *Salix pulchra* and *Betula nana* predominate in shrub tundra, with several other shrubs as lesser components (e.g. *Vaccinium vitis-idaea*). Shrub tundra often occurs on well-drained, gravelly soils, which are typically covered with a thin moss/organic mat 2–10 cm thick (Shaver and Chapin 1991). The organic surface soil just beneath the litter layer is what we call shrub soil. It appears similar to intertussock soil, but is dominated less by decaying mosses and more by shrub derived organic matter. In shrub soils we sampled from the soil surface to the bottom of the organic horizon, approximately 5–10 cm.

Sampling

In the summer of 2000 sample collection began with spring thaw in June, and continued every one to two weeks through August. Samples were collected on two dates in July 2001, as well. Values from the sampling dates in 2001 are included in the averages shown, but are not shown in the seasonal time-courses.

One area was sampled for each of the community types described. Each time soil was collected three cores were taken at random locations within a predefined area in each community. All samples were collected within 100 m of one another. Only organic soil was sampled – mineral soil was intentionally excluded to avoid the influence of mineral type or parent material. Inter-tussock samples were collected adjacent to sampled tussocks. Upon collection, samples were immediately hand sorted to remove live plant material and other debris. The soils were then mixed by hand for several minutes to homogenize them. Once homogenized, three 10 g (wet weight) sub-samples of each soil were shaken with either 50 ml de-ionized H_2O, or 0.5 M K_2SO_4 in 100 ml specimen containers on an orbital shaker table at $\sim$120 rpm for 1 h and were then vacuum filtered through Whatman GMF 2 μm filters. The extracts were then frozen until analysis.

Analyses

Soil C and N contents (Table 2) were analyzed using a Fisons element analyzer (Fisons, Inc., Beverly, MA). For the means presented in Table 2, $n = 15$ in tussock and intertussock, $n = 22$ in shrub, and $n = 24$ in shrub soil. Total

Table 2. The amino acids we measured, their abbreviations, and charge classes

Amino acids analyzed		Charge class	Amino acids analyzed		Charge class
Aspartic acid	Asp	Acidic	Leucine	Leu	Neutral
Glutamic acid	Glu	Acidic	Methionine	Met	Neutral
Arginine	Arg	Basic	Phenylalanine	Phe	Neutral
Histidine	His	Basic	Proline	Pro	Neutral
Lysine	Lys	Basic	Serine	Ser	Neutral
Alanine	Ala	Neutral	Threonine	Thr	Neutral
Cysteine	Cys	Neutral	Tyrosine	Tyr	Neutral
Glycine	Gly	Neutral	Valine	Val	Neutral
Isoleucine	Ile	Neutral			

DOC and DON were analyzed by persulfate digestion and flow injection analysis (Doyle et al. 2004). NH_4^+, NO_3^-, and PO_4^{2-}, and persulfate C and N (as CO_2 and NO_3^-) were all analyzed using a Lachat AE flow injection auto analyzer (Lachat Instruments, Milwaukee, WI). Amino acids were analyzed by reverse phase high performance liquid chromatography (HPLC) on a Waters HPLC with a Waters fluorescence detector using the Waters AccQ-Tag amino acid analysis system (Waters, Milford, MA).

Statistics

Statistical analyses were conducted on untransformed data using Systat version 10 (Systat Software Inc., Richmond, CA). To compare the overall means of the different variables we measured, or to compare the overall means of the same variable by soil type, we used *T*-tests for two variables; for comparisons of more than two variables we used analysis of variance (ANOVA), followed by Tukey's multiple comparisons test when a significant result was obtained from the ANOVA. To test the strength of the relationship between two variables we used regression analysis. For regressions across the different soils, we used the mean value for each soil type. When mean values for the different soils were correlated with one another we found similar, but stronger patterns than we did when using individual sample values. Using mean values in the regressions prevents the introduction of bias into the analyses caused by having different sample sizes for the different sites. This method also helps to reduce the influence of extreme values from individual sample replicates. As a result, the correlations across the soil types contain only one mean value per soil type, and four points total, per regression. The regressions for each individual soil type were calculated using replicate means from each of the sampling dates, and contain eight to ten points. For all statistical tests $p < 0.05$ unless otherwise noted. In these statistical analyses, $n = 10$ in tussock and intertussock, 8 in shrub, and 9 in wet sedge soils. Each n represents one date and is a mean of values from typically three sample replicates collected on that date. This was

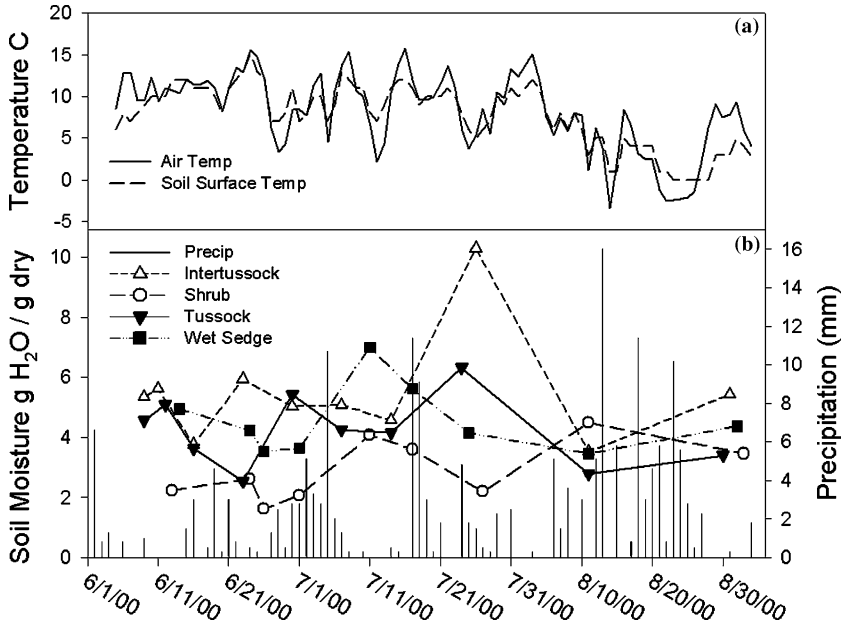

Figure 1. Seasonal air and soil temperatures (a), and rainfall and soil moisture (b).

done to ensure that the statistical analyses would not contain different numbers of points for different dates. The seasonal time-courses all show the sample replicate mean for any given time-point. Error bars in the graphs all show the standard error of the mean.

Results

Seasonal weather patterns

Soil surface temperatures consistently varied between 5 and 10 °C from the beginning of June to the beginning of August, when they started to decline (Figure 1; Toolik LTER weather station data). Mean soil surface temperatures in tussock tundra were 9.0 °C in June, and 9.4 °C in July, but dropped to 4.3 °C in August. Precipitation, on the other hand, increased over the summer, with rainfall totals of 32 mm in June, 69 mm in July, and 89 mm in August. Precipitation exceeded 10 mm on five days during this three-month period: 7/5, 7/17, 8/13, 8/18, and 8/23. Daily precipitation did not exceed 5 mm on any days in June, but it did on four days in July, and on eight days in August, indicating that smaller rainfall events, as well as larger ones, were more common in August.

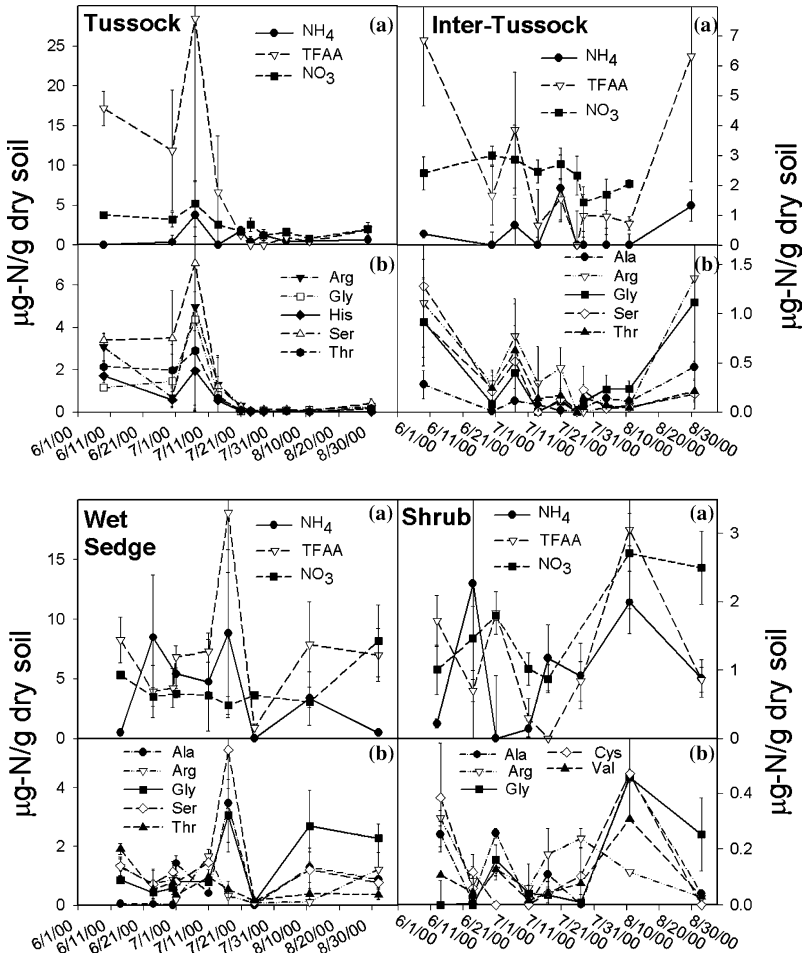

Figure 2. Seasonal dynamics of TFAA, NH_4^+, and NO_3^- (a), and of the five highest individual amino acids (b) from H_2O extractions in the summer of 2000. Note that the *Y* axes have different scales.

Seasonal patterns of amino acids and DIN in the H_2O extractions

Tussock

In the H_2O extractions, tussock soil was characterized by generally low NH_4^+ and NO_3^-, relatively high amino acids from snowmelt to the middle of July, and extremely low amino acid concentrations after that, when extractable N concentrations crashed Figure 2). The individual amino acids, NH_4^+, and NO_3^- generally did not exceed 5 μg N/g soil. NH_4^+ concentrations were low even when TFAA was relatively high. This, along with previously observed low N mineralization rates (Giblin et al. 1991; Nadelhoffer et al. 1991; Weintraub

and Schimel 2003), suggests that NH_4^+ is not the predominant form of available N in tussock soil, but does not indicate whether or not this is due to high demand for, or low production rates of NH_4^+.

The five highest overall individual amino acids were serine, arginine, glycine, threonine, and histidine. They all closely tracked one another, and DIN, for the most part. At the beginning of June, immediately after snowmelt, amino acid concentrations in tussock soil were among the highest we measured that summer, in any soil, while NH_4^+ was below detection and NO_3^- was below 5 μg N/g soil. The highest TFAA concentration we observed during the growing season, 28 μg N/g soil, was on July 7, 2000, when there was a large peak in amino acids and smaller peaks in NH_4^+ and NO_3^-. After this, the declines in concentrations were rapid, and none went above 2 μg N/g soil after July 14. On July 24 and 28 no amino acids were detected whatsoever .

Intertussock

Overall N availability was consistently low throughout the growing season in intertussock soil, although, amino acids were higher at the shoulders of the growing season (Figure 2). Mean TFAA and NO_3^- were both significantly higher than NH_4^+. For most of the growing season, NO_3^- concentrations were higher than both TFAA and NH_4^+, but were still low relative to the other soils (< 5 μg N/g soil; Figure 3).

The five highest amino acids in intertussock soil were arginine, glycine, serine, threonine, and alanine. As in tussock soil, they tended to track one another fairly closely (Figure 2). While the highest individual amino acids typically were higher than NH_4^+, their average concentrations were all less than 1 μg N/g soil, and none of them exceeded 2 μg N/g dry. TFAA was usually under 2 μg N/g soil, but exceeded 6 μg N/g soil at the beginning and end of the 2000 growing season, in early June and late August. Both TFAA and NH_4^+ dropped to their lowest levels of the season on July 26. On that date, only three of the 17 different amino acids were detected – alanine, isoleucine, and valine. Typically at least 13 were detected. This drop in the number of amino acids highlights the lack of available nitrogen at this time.

Wet sedge

Wet sedge had the highest overall TFAA, NH_4^+ and NO_3^- concentrations of any of the soils (Figure 2). TFAA was significantly higher than NH_4^+, on average (Figure 2). NH_4^+ ranged from below detection to 9 μg N/g soil. After the beginning of July, NH_4^+ started to track amino acids, peaking and crashing at the same times, but was lower (Figure 2). NH_4^+ did not rebound as strongly as amino acids at the end of the growing season, though. The seasonal dynamics of NO_3^- in wet sedge soil were distinctly different from amino acids and NH_4^+. NO_3^- was highest in the last extraction of the growing season, when it reached 8 μg N/g dry. Until then, concentrations were variable, but consistently between 2 and 5 μg N/g soil (Figure 2). NO_3^- was not significantly different from either TFAA or NH_4^+.

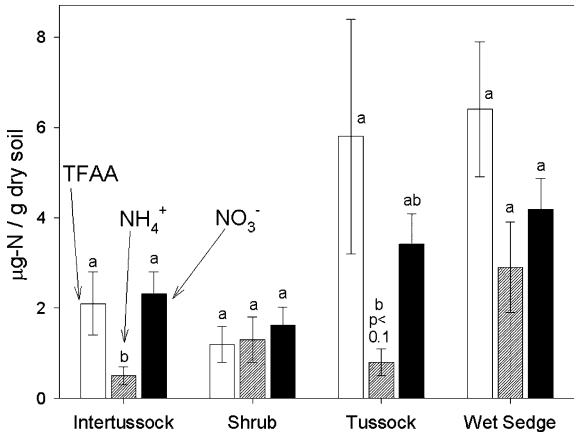

Figure 3. Means of TFAA, NH_4^+, and NO_3^- from H_2O extractions in the summers of 2000 and 2001. Within a soil type, bars marked with the same letters are not significantly different from one another (one way ANOVA followed by Tukey's multiple comparison test).

The five highest individual amino acids in wet sedge soil, on average, were serine, glycine, alanine, arginine, and threonine. Their concentrations ranged from below detection to over 5 μg N/g soil, and tended to track one another, and NH_4^+. From our first sampling date in mid-June 2000, just after the ground thawed, TFAA was variable, but relatively high (>8 μg N/g soil) until July 17, when TFAA peaked at almost 20 μg N/g soil. On our next sampling date, July 25, TFAA had crashed to less than 1 μg N/g dry. After that drop in concentrations, amino acids then rebounded to early season levels for the rest of the growing season.

Shrub

In general, shrub soil was characterized by low extractable N concentrations, especially in the first half of the growing season, followed by a rebound starting in late July (Figure 2). Mean TFAA and NO_3^- were both the lowest of any of the soils in our study (Figure 3), and were typically <3 μg N/g soil. However, mean NH_4^+ and TFAA concentrations were both lower than NO_3^-. The highest concentrations that we observed were on July 28, 2001 (data not shown), when TFAA exceeded 3.5 μg N/g soil and NH_4^+ exceeded 5 μg N/g soil. Similarly high values were not observed at the same time in 2000. In the summer of 2000 NH_4^+ was barely detectable (<0.5 μg N/g soil) until July 17, and then rebounded, reaching its seasonal high on August 11, which was still less than 2 μg N/g soil.

Shrub was the only soil in which TFAA was not significantly higher than either NH_4^+ or NO_3^- (Figure 3). The five highest amino acids – glycine, cysteine, alanine, arginine, and valine were significantly lower than both NH_4^+ and NO_3^-. Amino acids hit a low in mid-July, and then rebounded somewhat by our sampling on August 11, the only time during the 2000 growing season

when TFAA exceeded 3 μg N/g dry (Figure 2). All of the individual amino acids had average concentrations below 0.5 μg N/g soil, and only glycine, in our two 2001 samples, ever exceeded this low level. NH_4^+ did not track the individual amino acids in shrub soil, as it did in tussock and intertussock.

H_2O extractions comparisons between the soils

Overall, no significant differences between the different soils in either TFAA or NH_4^+ were detected, but wet sedge NO_3^- was significantly higher than shrub NO_3^- (Figure 3). While there was a relatively large difference in TFAA between wet meadow and shrub soils, it was not statistically significant. Wet sedge and tussock soils had the highest concentrations of the amino acids and DIN, on average, followed by intertussock and shrub soils. The pool of available N was dominated by DIN in shrub soil, and to a lesser extent in wet sedge soil, while amino acids predominated in tussock and intertussock soils. Across all soils, TFAA and NO_3^- were both significantly higher than NH_4^+.

NO_3^- was actually the principal form of DIN, and in all soils it was higher than NH_4^+, which was the lowest of the available N forms (Figures 2 and 3). NO_3^- was also the measure of DIN that was best correlated with amino acids, overall ($R^2 = 0.65$ with TFAA, $R^2 = 0.94$ with neutral amino acids).

DIN, DON, DOC, and PO_4^{2-} in the K_2SO_4 extractions

DIN

K_2SO_4–NH_4^+ tracked H_2O–NH_4^+ but was often 5–10 μg N/g soil higher, and they were significantly different, both by individual soil, and across soils (Figure 4), although they were well correlated with one another ($R^2 = 0.82$). For the most part, K_2SO_4–NH_4^+, TFAA, and H_2O–NH_4^+ all tracked one another. In tussock and intertussock soils, K_2SO_4–NH_4^+ approached H_2O–NH_4^+ concentrations at times when N availability was lowest in these soils, suggesting that the pool of NH_4^+ held on soil cation exchange complexes gets consumed under N limited conditions. In shrub soil K_2SO_4 and H_2O–NH_4^+ diverged in the latter part of the growing season, suggesting that the exchangeable pool was being replenished by net N mineralization.

NO_3^- concentrations in the two extractions were not significantly different from one another in any soil but intertussock, in which K_2SO_4–NO_3^- was briefly higher than H_2O–NO_3^- in mid-July (data not shown). The fact that NO_3^- concentrations in the two different extractions were closer to one another than NH_4^+ indicates lower anion than cation exchange capacity in these tundra soils, as we would expect.

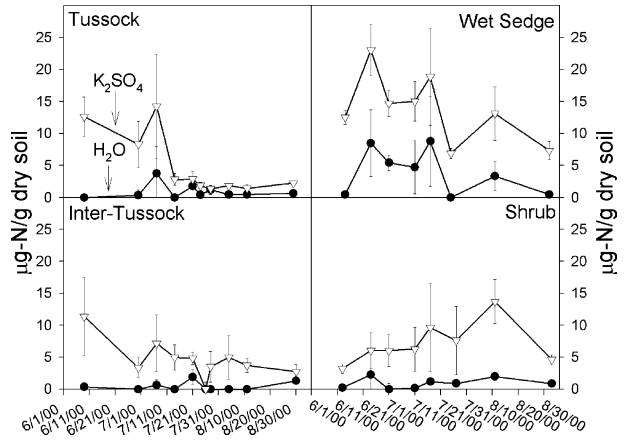

Figure 4. Seasonal dynamics of NH_4^+ in H_2O and K_2SO_4 extractions from the summer of 2000.

DOC and DON

DON was often more than order of magnitude higher than amino acids, NH_4^+, and NO_3^-. Tussock and intertussock had the highest, and most variable DOC and DON concentrations, while wet sedge had the lowest, and most stable concentrations (Figure 5). The overall DOC:DON ratio ranged from 8 to 10 in wet meadow, shrub, and intertussock soils, but was 17 in tussock. Typically, DON did not track the other forms of soluble N. However, in tussock and intertussock soils, DON dropped to its lowest concentration of the

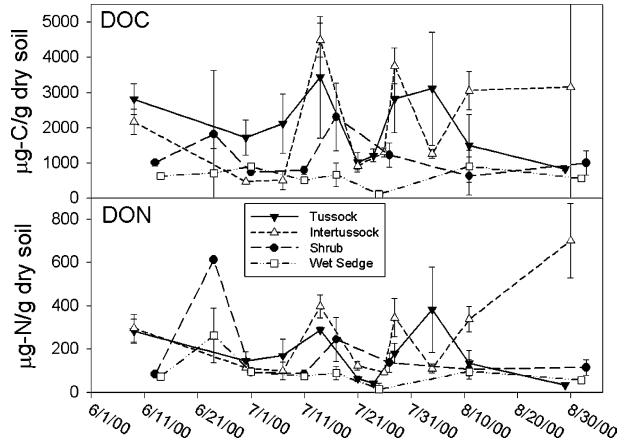

Figure 5. Seasonal dynamics of DOC and DON in K_2SO_4 extractions from the summer of 2000.

growing season in the second half of July, like amino acids and NH_4^+. DOC typically tracked DON closely. There was no significant difference between any of the soils in mean DON, but intertussock and tussock soils had significantly higher DOC than wet sedge.

DON had strong negative correlations with both H_2O–NH_4^+ ($R^2 = 0.98$) and K_2SO_4–NH_4^+ ($R^2 = 0.72$). DON was also negatively correlated with neutral amino acids ($R^2 = 0.61$) and every other measure of dissolved nitrogen, although the correlations were not as strong. However, in wet sedge soil there was a strong positive correlation between DON and K_2SO_4–NH_4^+ ($R^2 = 0.73$).

PO_4^{2-}

There were no significant differences in mean PO_4^{2-} between any of the soils. After starting out extremely low (< 5 μg P/g soil), both tussock and intertussock PO_4^{2-} rose over 100 μg P/g soil, then rapidly declined again, going back down to barely detectable levels within a month (Figure 6). Both soils also experienced second, smaller peaks in PO_4^{2-} in our last sampling of 2000. Wet sedge PO_4^{2-} followed a similar pattern to tussock and intertussock, but had an earlier and smaller peak of 51 μg P/g soil on July 17, and then declined earlier, and not as sharply. Wet sedge PO_4^{2-} also increased again in August. The highest concentration we observed in that soil, > 70 μg P/g soil, was in our last extraction of the growing season, on September 1. Shrub PO_4^{2-} started out the 2000 growing season low and began to increase in mid-July, slowly rising through the remainder of the growing season. By our last sampling date shrub PO_4^{2-} was the highest of any soil, 118 μg P/g soil.

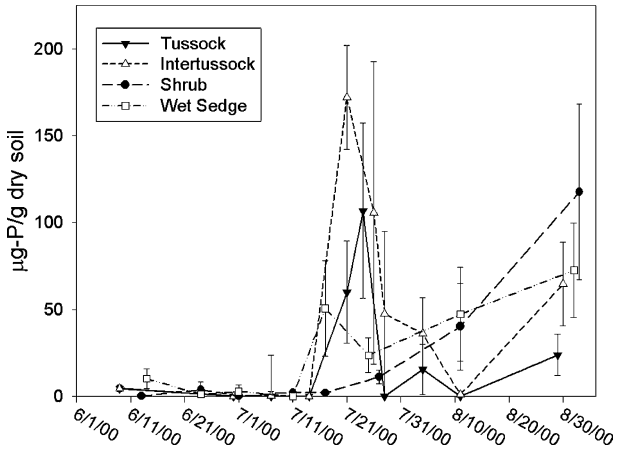

Figure 6. Seasonal dynamics of K_2SO_4–PO_4^{2-} from the summer of 2000.

Discussion

Amino acids

Across all soils and dates, the highest individual amino acids in our extractions were serine, glycine, arginine, threonine, and alanine. Our results were similar to those of other studies, but we detected lower concentrations of acidic amino acids (Kielland 1995; Raab et al. 1999). There were many strong correlations among the five highest amino acids and among the three charge classes of amino acids, and between these measures of amino acids and TFAA (data not shown). The sum of the individual amino acid concentrations was not overly dominated by any of the highest individual amino acids in each soil, and the highest amino acids usually tracked one another. This makes sense when the sources of amino acids are considered, since both proteolysis and direct release from cells release a mix of amino acids (Schulten and Schnitzer 1998; Lipson and Nasholm 2001).

As in other studies (Stevenson 1994; Schulten and Schnitzer 1998), we encountered some amino acids in our HPLC analyses that are not typical protein constituents. In every chromatogram there were several unidentifiable amino acid peaks, often higher in magnitude than the peaks of the known amino acids. The presence of these unknown amino acids indicates that the TFAA pool is actually larger than the sum of the known amino acids. As a result, a measure of amino N that includes all amino acids, not just the 20 or so typically identified on an HPLC, may provide a more accurate estimate of the extractable amino N pool. Amino acid composition also varies little between soils (Schulten and Schnitzer 1998), further suggesting that measuring individual amino acids is unnecessary when assessing amino N pools, unless hypotheses about specific amino acids are being tested.

Seasonal patterns of amino acids and DIN

Tussock

Extractable N concentrations were relatively high in the first half of the growing season. We were surprised that TFAA and DIN were as high as they were at this time, considering the extremely high N immobilization and low N mineralization potential of tussock soil (Giblin et al. 1991; Schimel and Chapin 1996; Weintraub and Schimel 2003). In mid-July, TFAA and DIN plummeted down to barely detectable levels, and remained extremely low until the beginning of September, the last time we sampled. Giblin et al. (1991) also observed declining DIN in tussock soil in the second half of the growing season, while Kielland (1995) observed a decline in tussock TFAA in the month of July, as we did. Nordin et al. (2003) also observed declines in TFAA concentrations across the growing season in both acidic and non-acidic tussock tundra soils.

One possible explanation for the crash in N concentrations in tussock would be rainfall related soil leaching. However, the decline in soil N availability occurred after July 7 and before July 14, while the biggest rainstorms that month were on the 5th and 17th. Furthermore, this decline in N concentrations persisted for the remainder of the growing season. While rainfall did increase in the second half of the growing season, it was not consistent enough to continuously leach the soil. Additionally, tussock soil moisture actually went down in the second half of the growing season, despite increased rainfall (Figure 1). Thus, we think that leaching is an unlikely explanation for the decreases in available N forms in mid-July. That suggests that the reductions are due to biotic processes, either reduced production or increased uptake of bioavailable N forms.

Decreased production of bioavailable N also seems somewhat unlikely as an explanation. Since microbial activity is responsible for supplying bioavailable N, there would have to be either a major reduction in substrate availability or a change in environmental conditions that would reduce decomposition rates. Substrate pools are extremely large in tussock tundra (Weintraub and Schimel 2003), and there is no obvious reason why microbial activity would decrease in mid-July. Both soil moisture and soil temperature were relatively constant through this period (Figure 1). Thus, the most likely explanation for the reduction in available N is an increase in biotic uptake, either directly by roots or indirectly by microbes fueled by increased root C inputs in mid-July.

The most intensive period of root growth in *Eriophorum vaginatum*, the dominant plant in tussock, is known to be in mid-July, coincident with the decline in soil N availability we observed (Kummerow and Russell 1980; Chapin et al. 1986b; Shaver et al. 1986). This increase in root production occurs after leaf expansion is already well underway. This is because early season growth is fueled by N stored in the plant from the previous year, mostly in the form of amino acids (Mckendrick et al. 1978; Chapin et al. 1980, 1986a, b; Shaver et al. 1986). As stored nitrogen is used up in the construction of new plant biomass, internal plant amino acid and organic phosphorus concentrations drop dramatically from May to July (Chapin et al. 1986b). Once internal nutrient stores are depleted, plant growth slows or ceases and root uptake begins to replenish internal nutrient stocks to fuel growth in the following year (Chapin et al. 1986b). At this time, allocation of nutrients goes to storage for the following year's growth first, and to the current year's growth second (Shaver et al. 1986). As a result, there is a change from the breakdown of soluble organic nitrogen in tissues of *Eriophorum vaginatum* to nutrient uptake and synthesis of these compounds in late July. Nutrient uptake continues through September, and there is a late season increase in root growth at the end of the August (Shaver et al. 1986), which has the potential to increase direct root uptake and to stimulate microbial N immobilization late in the growing season.

Thus, the available data and literature suggest that the reductions in available N we observed were largely due to plant-driven processes. This is

actually somewhat surprising, as *Eriophorum vaginatum* competes poorly for N, taking up only a few percent of ^{15}N labeled compounds that are added to intact tussock cores (Schimel and Chapin 1996; Nordin et al. 2003). This would suggest the hypothesis that the reduction in N concentrations is due to plant-mediated microbial processes, rather than direct plant uptake. However, without a better understanding of how N partitioning between plants and soil microbes changes as a result of increased soil C inputs from root growth, we cannot say how much of the decrease in N availability we observed was due plant versus microbial uptake, or whether there was any change in microbial N release.

Intertussock

In intertussock soil, N availability dropped down to its lowest level of the growing season at the end of July, and was generally lower in the second half of the growing season, as was the case in tussock soil. Thus, it seems likely that the same mechanism was responsible for the decrease – increased root growth, with the associated increased plant and microbial nutrient uptake. Seasonal patterns of nutrient uptake have not been well studied for the plants growing in the intertussock community, but plant growth on stored nutrients during the first part of the growing season is considered to be a necessary adaptation in tundra communities (Shaver and Kummerow 1992). Thus, it seems likely that plant uptake could explain the decrease in N availability we observed in the middle of the growing season.

Wet sedge

As in tussock soil, wet sedge TFAA and NH_4^+ concentrations peaked in mid-July and then declined rapidly. After this drop in available nitrogen, late season concentrations rebounded more strongly in wet sedge than they did in tussock soil. The peak in amino acids and NH_4^+ that we observed occurred at the same time as the mid-July rains, and may have been the result of runoff related N inputs to this low lying community. However, we did not see a similar effect from larger rainfall events at other times, which suggests that the changes in concentrations were not runoff related.

The fact that the seasonal dynamics of N availability in wet sedge soil were so similar to those in tussock soil suggests that root growth and N uptake by *Eriophorum angustifolium* and *Carex aquatilus*, the dominant sedges in the wet sedge community, may control N availability in the same manner as *Eriophorum vaginatum*, but that soil N uptake happens later, and does not persist for as long in wet sedge.

Unlike the other soils, there was a large increase in late season NO_3^- concentrations in wet sedge soil. This may indicate a relative decrease in demand for soil N and an increase in nitrification in response to higher soil N availability. Previous research has shown microbial NH_4^+ uptake rates are relatively low in wet sedge soil (Schimel 1995), suggesting that NH_4^+ may be relatively available to nitrifying bacteria.

Shrub

Despite having the highest net N mineralization rates of any of the soils in our study (Weintraub and Schimel 2003), shrub had the lowest extractable N concentrations, suggesting high rates of N uptake. Shrub soil also showed a distinctly different pattern of nutrient dynamics that the other three soils, with the dominant pattern being a relatively large increase in the second half of the season. While TFAA and DIN concentrations were generally low in shrub soil, there was a decline in N availability in early July 2000. NH_4^+ dropped first, followed by TFAA and NO_3^-. There were no major rainstorms during the period when NH_4^+ fell, but the fall in TFAA and NO_3^- did coincide with a period of relatively high rainfall. DIN and TFAA concentrations then increased in late July and August, during the period of highest rainfall, suggesting that the changes in concentrations are due to biological rather than physical processes.

One possible reason for the increase in available N forms late in the season is that there was a decrease in plant nutrient consumption. The fact that the decrease in N availability occurred earlier in shrub than in the other soils, and that the highest concentrations of amino acids and NH_4^+ we observed were at the end of the growing season suggest that the period of nutrient uptake in the deciduous shrub *Betula nana*, the dominant species where we sampled the shrub tundra community, begins and ends relatively early in the growing season.

Another possible explanation for the increase in soil N availability late in the season is increased N mineralization rates. Unlike the other tundra types, shrub soil contains a small active pool of organic matter that can be consumed in a moderate amount of time, causing substantial net mineralization (Weintraub and Schimel 2003). If this pool is resupplied by detritus inputs each fall, it may be consumed over the growing season, supporting net N mineralization during the latter part of the growing season.

Betula nana is spreading in the Alaskan tundra in response to rising temperatures (Hobbie 1996; Hobbie and Chapin 1998), especially in tussock communities. Warming has been shown to decrease *Eriophorum vaginatum* biomass as *Betula nana* biomass increases (Chapin et al. 1995; Hobbie et al. 1999). *Betula nana's* bud break has been shown to occur earlier in response to warming (Pop et al. 2000). Since bud break is the critical event that determines growth and development during the growing season for winter deciduous plants (Pop et al. 2000), this confirms that *Betula nana* responds favorably to increasing spring temperatures. Warming also increases early season photosynthesis rates in *Betula nana* (Hobbie and Chapin 1998). Earlier bud break and higher early season photosynthesis rates are likely to increase its N demand in the early part of the growing season. Since the early season growth of many other tundra plants, including *Eriophorum vaginatum*, is dependent on stored nutrient reserves, this may allow *Betula nana* to take advantage of a period of relatively low competition for soil nutrients, after the soil thaws, but before most plants are taking up nutrients from the soil.

Seasonal dynamics of DOC and DON

DON was by far the highest measure of dissolved nitrogen in our study. DOC and DON were at least 2 and 1 order of magnitude higher, respectively, than NH_4^+ and TFAA. Jones and Kielland (2002) found TFAA to range from 4 to 20% of DON in taiga soils. In our study TFAA ranged from less than 1% of DON in intertussock and shrub soils, to ~6% in tussock and wet sedge soils.

While most of the N in DON is in the amino form, much of it is in recalcitrant protein/peptide–polyphenol complexes or amino compounds associated with humic substances that may have relatively low biological availabilities (Yu et al. 2002). In a mass fractionation of DON in taiga soils, the bulk of DON was in molecules larger than 1 kilodalton (kd), often with more than half of it in compounds larger than 10 kd (Smolander and Kitunen 2002). While some dinoflagellates have been shown to take up compounds as large as 2 kd (Legrand and Carlsson 1998), much of DON may be in molecules too large for soil microbes to take up without prior extra-cellular decomposition. However, the fact that DON was usually poorly or negatively correlated with amino acids, NH_4^+, and NO_3^- suggests that DON may be consumed during the production of more labile N forms. DON also sharply decreased in tussock and intertussock soils in late July, when N demand was at its peak, further suggesting DON utilization.

Seasonal dynamics of PO_4^{2-}

PO_4^{2-} was an order of magnitude or more higher than NH_4^+, NO_3^-, and amino acids, indicating that P availability is high relative to N in these tundra soils. Nadelhoffer et al. (1991) concluded that wet sedge soils may be phosphorus limited, but we observed high PO_4^{2-} concentrations in wet sedge soil, particularly in late July, when there were large spikes in PO_4^{2-} in all soils but shrub (Figure 6). PO_4^{2-} in shrub soil began to gradually rise in late July, roughly paralleling changes in N, except that PO_4^{2-} concentrations continued to increase through the end of August. By the end of the growing season shrub had the highest PO_4^{2-} of any soil.

Giblin et al. (1991) found that the weathering of mineral P is not a major source of P to plants in any of the tundra soils in our study. They concluded that most of the P required by plants in these soils comes from soil organic matter decomposition. Most P is bound in insoluble organic forms that require extra-cellular breakdown by enzymes to make it available (Giblin et al. 1991). These enzymes are considered to be widely associated with roots, mycorrhizae, and soil microbes in tundra ecosystems (Moorhead and Linkins 1997). Living *Eriophorum vaginatum* roots have been shown to have phosphatases on their root surfaces (Moorhead et al. 1993). Moorhead et al. (1993) estimated that on an annual basis, *Eriophorum vaginatum* root surface phosphatases mineralize almost twice as much P as is required for plant growth, and concluded that

Eriophorum vaginatum may meet much of its P demand from the activities of root surface phosphatases. They also concluded that about 28% of total annual tussock phosphatase activity (plants and soil combined) occurs during a brief period of high organic P availability relatively late in the growing season, resulting in a late season pulse in soil PO_4^{2-} (Moorhead et al. 1993). As a result, they suggested that the majority of P uptake in *Eriophorum vaginatum* occurs late in the growing season, after the period of growth, as is also the case for N. However, our results showing peaks in PO_4^{2-} starting in mid July suggest that this pulse of P availability may occur somewhat earlier than suggested by Moorhead et al. (1993).

Conclusions

Somewhat surprisingly, we found that both N and P concentrations were extremely dynamic in Arctic tundra soils. Nutrient pools can both spike and crash in periods as short as a week. For example in tussock soils, TFAA spiked at over 25 μg N/g soil in mid-July, declined by a factor of 5 within a week, and within a short time was non-detectable. Extractable PO_4^{2-} was extremely low until mid-July and then within a week or two increased to more than 150 μg P/g soil. These fluctuations were not random, but rather appeared to be seasonally driven. The major transitions in both N and P pool dynamics happened at the same time during mid-July. The most likely explanation for the rapid shifts in soil nutrient concentrations is that the changes are driven by the onset of rapid root growth, with associated nutrient depletion of available N, and a spike in phosphatase activity and in extractable P concentrations. Thus, this study suggests that nutrient pool size dynamics are driven more by sink than by source processes. As a result, changes in plant communities should have the potential to rapidly change the dynamics of soil nutrient pools.

A second finding that further develops this conclusion is the difference between the nutrient dynamics in shrub compared to the other communities, which are dominated by graminoids and mosses. In graminoid/moss soils, soil nutrient pools were generally high during the early season, and then crashed in mid-July. This was the case despite the fact that tussock soil does not readily mineralize N when incubated – rather microbes appear to be N limited (Weintraub and Schimel 2003). Shrub soils on the other hand, mineralize the most N in lab incubations, but have the lowest concentrations in the field, and have the lowest concentrations early in the growing season. This is likely at least partially a function of *Betula nana's* ability to take up nutrients early in the season. This ability may partially explain *Betula's* recent expansion – it may be able to take advantage of the relatively large available nutrient pools present in tussock tundra early in the year. The presence of *Betula nana* in intertussock may also help to explain the relatively low N concentrations we observed there in the first half of the growing season.

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