

Amino acid uptake in deciduous and coniferous taiga ecosystems

Knut Kielland · Jack McFarland · Karl Olson

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Abstract We measured in situ uptake of amino acids and ammonium across deciduous and coniferous taiga forest ecosystems in interior Alaska to examine the idea that late successional (coniferous) forests rely more heavily on dissolved organic nitrogen (DON), than do early successional (deciduous) ecosystems. We traced $^{15}\text{N-NH}_4^+$ and $^{13}\text{C-}^{15}\text{N}$ -amino acids from the soil solution into plant roots and soil pools over a 24 h period in stands of early successional willow and late successional black spruce. Late successional soils have much higher concentrations of amino acid in soil solution and a greater ratio of DON to dissolved inorganic N (DIN) (ammonium plus nitrate) than do early successional soils. Moreover, late successional coniferous forests exhibit higher rates of soil proteolytic activity, but lower rates of inorganic N turnover. Differences in ammonium and amino acid uptake by early successional willow stands were insignificant. By contrast, the in situ uptake of amino acid by late successional black spruce forests were approximately 4-fold greater than ammonium uptake.

The relative difference in uptake of ammonium and amino acids in these forests was approximately proportional to the relative difference of these N forms in the soil solution. Thus, we suggest that differences in uptake of different N forms across succession in these boreal forests largely reflect edaphic variation in available soil N (composition), rather than any apparent physiological specialization to absorb particular forms of N. These findings are relevant to our understanding of how taiga ecosystems may respond to increases in temperature, fire frequency, N deposition, and other potential consequences of global change.

Keywords Amino acids · Boreal ecosystems · N cycling · Nutrient uptake · Taiga forests

Introduction

Plant communities dominated by willows (*Salix* sp.) and black spruce (*Picea mariana*) represent, respectively, the start and end point of primary succession on the Tanana River floodplain in interior Alaska (Viereck et al. 1993). This chronosequence represents approximately 300–400 years of ecosystem development during which large biogeochemical changes occur. These changes include order-of-magnitude increases in soil carbon and N stocks, but marked decreases in growing-degree days (3×) and soil pH. Annual

K. Kielland (✉) · K. Olson
Institute of Arctic Biology, University of Alaska,
Fairbanks, AK 99775, USA
e-mail: ffk@uaf.edu

J. McFarland
Department of Biology and Wildlife, University of
Alaska, Fairbanks, AK 99775, USA

rates of soil N mineralization increase through mid-succession, but return to approximate initial levels by the time black spruce is the dominant tree species (Kielland et al. in press a). In contrast, the concentrations of both soil free amino acids and protein increase about 10-fold with successional time, and potential rates of soil proteolytic activity also increase across succession at a similar magnitude (Kielland et al., in press a). Thus, taiga forest ecosystems exhibit substantial variation in structural properties (soil characteristics, species composition and plant growth forms) as well as large functional variation in many ecosystem processes (net primary productivity and N turnover). The diversity of soil chemical environments between early successional deciduous vegetation and late successional coniferous forests suggests that the species have been subjected to different patterns of N cycling which in turn may contribute to different physiological characteristics among these species. Whereas the concentrations of ammonium and amino acids are near unity in early successional soils, concentrations of free amino acids are approximately 5-fold greater than ammonium in late successional soils (Kielland et al. in press a). In light of this dominance of soluble organic N in black spruce soils, coupled with high protease activity and rapid amino acid turnover (Jones and Kielland 2002), we hypothesized that black spruce ecosystems would exhibit a greater preference for absorption of amino acid relative to ammonium in the field than would early successional willow communities in which amino acids appear to be a less dominant component of the N cycle. Here we examine the relative in situ uptake of amino acids and ammonium by deciduous and coniferous forests in interior Alaska that differ radically in soil N composition and N turnover characteristics.

Methods

Study sites

We conducted the study at the Bonanza Creek Taiga Long Term Ecological Research (LTER) sites approximately 20 km SW of Fairbanks, Alaska (65°45'N, 148°15'W). The LTER sites

along the Tanana River comprise a primary successional sequence that includes five stages of floodplain forest succession (Willow, Alder, Balsam Poplar, White Spruce, and Black Spruce). Each successional stage is replicated three times, and each replicate is separated by up to several kilometers to avoid pseudoreplication (Hurlburt 1984). The general pattern of primary succession starts on newly formed silt bars that are colonized by light-seeded willows, particularly *Salix interior* and *Salix alaxensis* as well as horsetail (*Equisetum* sp.) and herbs such as *Hedysarum alpinum* and *Castilleja caudata* (Viereck et al. 1993). Thin-leaf alder (*Alnus tenuifolia*) typically dominates the site after 10–20 years and is associated with large changes in primary productivity and soil chemistry (Viereck et al. 1993; Kielland et al. 1997). Balsam poplar (*Populus balsamifera*) forests predominate 60–100 years following initial colonization, and after approximately 200 years the forest is an even-aged stand of white spruce (*Picea glauca*). Depending on the fire regime and other disturbances such as channel avulsion into peat lands adjacent to the river, black spruce (*Picea mariana*) forests predominate after approximately 300–500 years (Mann et al. 1995).

The climate is strongly continental and the area lies within a rain shadow created by the Alaska Range approximately 100 km to the south. Temperature extremes range from -50°C in winter to $>+30^{\circ}\text{C}$ during the summer with an average of -3.3°C . Average annual precipitation is 269 mm, 37% of which falls as snow. Snow covers the ground 6–7 months of the year. Maximum snow depth is generally <60 cm (National Resource Conservation Service Alaska Snow Programs, http://www.ambcs.org/pub/sc_sum_ak/SNOWCOURSE.HTM). We measured soil temperatures at all sites during the course of our field experiments. Other pertinent environmental data on general environmental conditions and soil characteristics were obtained from the Bonanza Creek LTER data base. Complete site descriptions regarding climate, vegetation, and soils can be found through the web address for the Bonanza Creek LTER Program: <http://www.lter.uaf.edu/>. Contrasting soil characteristics pertinent to N cycling processes in these forests are presented in Table 1.

Amino acid uptake

Beginning in July 2002 we set up three 9 m² subplots within three previously established black spruce sites. These sites represent permanent research locations within the Bonanza Creek LTER and all are separated by several kilometers. Simultaneously, we established two subplots within each of three early successional willow communities. These sites were several 100 m apart and separated by natural transitions in the vegetative community that included either relatively pure stands of alder (*Alnus tenuifolia*) or occluded river channels containing horsetail (*Equisetum spp.*) and mixed herbaceous species. Each subplot contained three randomly placed injection grids, one for each of three treatments as described below.

Injection grids measured 81 × 15 cm and consisted of six identical templates with 37 holes each (222 total/grid). Grids were injected with one of three treatment solutions in the upper 10 cm of soil. The treatment solutions were as follows: (a) 134 μM ¹⁵NH₄⁺ (ammonium treatment), (b) a cocktail of 88 μM U-¹³C¹⁵N-glycine, 88 μM U-¹³C¹⁵N-aspartic acid, and 88 μM U-¹³C¹⁵N-alanine (amino acid treatment), or (c) distilled water (control). Using doubly labeled amino acids in the second treatment allowed us to evaluate the root uptake of intact

amino acids by comparing the molar ratio of ¹⁵N and ¹³C found within fine-root tissue (Näsholm et al. 1998). Thus, a ¹³C:¹⁵N molar ratio of 3:1 (average of glycine, 2:1; alanine, 3:1; and aspartic acid, 4:1) in roots would indicate that the amino acids were on the average taken up in intact form. Unlabeled ammonium and unlabeled amino acids (glycine, alanine, and aspartic acid) were added to the amino acid and ammonium treatments respectively. Total N added in the form of labeled and unlabeled solution represented approximately 2.5 and 11 μg N g⁻¹ in the willow stands and black spruce forest, respectively. The rationale behind adding unlabeled substrate was to minimize the bias of uptake of the labeled N form (e.g. amino acids) against a smaller pool of an unlabeled N form (e.g. ammonium).

Our injection volume was 2 ml. Each 2-ml aliquot was delivered by inserting the needle to a 10-cm depth and emptying the repeating pipette as the needle was withdrawn. In using this technique, we assumed an even distribution of labeled solution throughout the vertical profile of the soil. Coring grids consisted of six holes large enough to allow a soil corer with an inside diameter of 5.5 cm to pass through unobstructed (McFarland et al. 2002). The center of each coring hole exactly matched the center of its respective injection template. Therefore we used the surface area ratio of the injection template to the coring template to estimate the fraction of label that was injected into each treatment core. Theoretically, this permitted us to remove a soil core 12 cm in depth with a known amount of added label (296 μg ¹⁵N and 766 μg ¹³C core⁻¹).

Both the injection grids and the coring grids were constructed of 32-mm thick Lexan sheets, which were flexible enough to mold to the surface of the forest floor. Grids were held in position by four steel pins buried to a depth of 20 cm, which made it easy to properly align the coring grids over the respective injection grids. Injecting a subplot with all three treatment solutions took approximately 30 min, after which we began harvesting the first in a series of cores for each treatment. For our short term observations of root uptake, cores within each grid were harvested at 45 min; 2, 12, and 24 h.

Table 1 Ecosystem characteristics and biogeochemical properties (seasonal averages) of willow and black spruce stands on the Tanana River floodplain, interior Alaska.

Parameter	Willow	Black spruce
Age (years)	5–20	300–400
Soil C (%)	1.54 (0.01)	25.45 (2.45)
Soil N (%)	0.01 (0.001)	0.85 (0.08)
pH	8.01 (0.03)	5.10 (0.12)
Soil ammonium concentration (μg N g ⁻¹)*	2.30 (0.29)	4.44 (0.49)
Soil free amino acid concentration (μg N g ⁻¹)	2.77 (0.26)	24.02 (1.76)

* Average nitrate concentrations not presented, but represented less 5% of the ammonium pool

Means ± SE, n = 15

Immediately after sampling, we conducted preliminary processing of our soil cores in an on-site tent laboratory. Each core was split vertically into two equal halves. One half was used for sorting and freezing roots for ^{13}C and ^{15}N analysis; the other half was used for ^{13}C and ^{15}N analysis of total soil C and N and extractable dissolved inorganic N (DIN). In willow stands, soils had to be hand-sorted and mixed due to the high moisture and silt content of the soil. Soil samples from black spruce stands were sieved to ensure complete homogenization. Once initial processing was complete, all root and soil samples were frozen with liquid N_2 in the field and transported on ice to our laboratory facilities.

In the lab root samples were thawed and all remaining soil organic matter was removed. We separated roots into two broad size classes. Roots over 1 mm diameter were classified as coarse roots, while those 1 mm or less were classified as fine roots. Fine roots were oven-dried at 45°C , manually crushed, and ground for 24 h using a modified roller mill to ensure complete homogenization within each sample. Soil moisture content was determined by drying subsamples at 70°C for 48 h. Both roots and soils were then analyzed for C, N, ^{13}C , and ^{15}N using a Europa Scientific continuous flow mass spectrometer (PDZ Europa, Inc.).

To determine the amount of label recovered as DIN, we extracted approximately 10 g of wet soil with 75 ml of 0.5 M K_2SO_4 containing 5 ppm phenyl mercuric acetate for 1 h. Extractions were filtered through Whatman glass fiber filter paper and analyzed for NH_4^+ and NO_3^- by flow injection colorimetry using a Lachat autoanalyzer (Keeney and Nelson 1982). Following colorimetric analysis, samples were assessed for ^{15}N content by a diffusion procedure (Khan et al. 1998). Briefly, 20 ml of the sample were pipetted into 500 ml mason jar fitted with a lid modified to suspend two quartz fiber disks above the sample solution. Each disk was acidified with 10–15 μl of 1.0 M H_2SO_4 . Five acid-washed glass beads were added to the container along with 0.2 g of Devarda's alloy to reduce and collect nitrate- ^{15}N . We volatilized the dissolved ammonium by adding approximately 0.2 g of MgO to each jar just prior to sealing it. After 5 days at room temperature, the disks were removed, vacuum dried, and

digested with concentrated HF prior in preparation for mass spectrometer analysis. Standards with a known atom% ^{15}N were analyzed along with the samples to evaluate diffusion efficiency.

Calculations

Isotope values are reported in delta notation using standard formulae for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ where the stable isotope composition of the element under study is expressed as,

$$\delta^{XX}E = 1000 \cdot \left[\left(R_{\text{sample}}/R_{\text{standard}} \right) - 1 \right],$$

Where E is the element under study (e.g. ^{15}N , ^{13}C), " XX " is the mass of the heaviest isotope in the abundance ratio, and R is the abundance ratio of those isotopes, e.g. $^{15}\text{N}/^{14}\text{N}$ (Dawson et al. 2002).

To estimate the uptake of ammonium and amino acids we fitted first-order rate equations to the data of isotopic enrichment in the roots, using non-linear regression in the curve-fitting program Axum[®] 7.0 (MathSoft, Cambridge, MA 2001). These equations take the following general form,

$$E_t = E_0 * (1 - e^{-k*t}), \quad (1)$$

where E_t is the cumulative isotopic value of roots ($\delta^{15}\text{N}$) for a given N form within a successional stage, E_0 is maximum enrichment over the experimental period, k is the rate constant, and t is time. To account for differential isotope dilution between N forms we estimated the relative uptake of ammonium versus amino acids by multiplying the individual rate constants by the respective soil N pool (after tracer additions) to derive the total flux into roots of a given N form. The ratio of these fluxes thus represents the relative uptake of ammonium versus amino acids in each successional stage.

Statistical analysis

Differences in ^{15}N recovery in plant and soil pools were analyzed using analysis of variance (ANOVA) by Statistix 8 (Analytical Software, 2003),

with subplots nested within stands. Treatment differences in isotopic enrichment were analyzed by 2-sample *t*-tests, and normality and homogeneity of variances were determined from Shapiro–Wilks statistics and Bartlett’s test, respectively.

Results

Enrichment of ^{15}N in willow roots (Fig. 1a) was approximately 3-fold greater than in roots of black spruce (Fig. 1b), reflecting in part the

higher nutrient absorption capacity of deciduous species, relative to the slow-growing black spruce (Chapin et al. 1986). Enrichment of root ^{15}N from ammonium uptake in willow stands increased over time more strongly than did amino acid uptake, but this difference was only significant after 24 h (*t*-test, $P = 0.013$). Isotopic enrichment of ^{15}N in black spruce roots was also quite similar between the ammonium and the amino-acid treatment throughout the experimental period, differing only in the third sampling period (Fig. 1b). The rate equations of change in isotopic

Fig. 1 In situ recovery of ^{15}N -ammonium (solid) and ^{15}N -amino acids (stippled) in roots of (a) willow and (b) black spruce. Mean \pm SE, $n = 6\text{--}9$

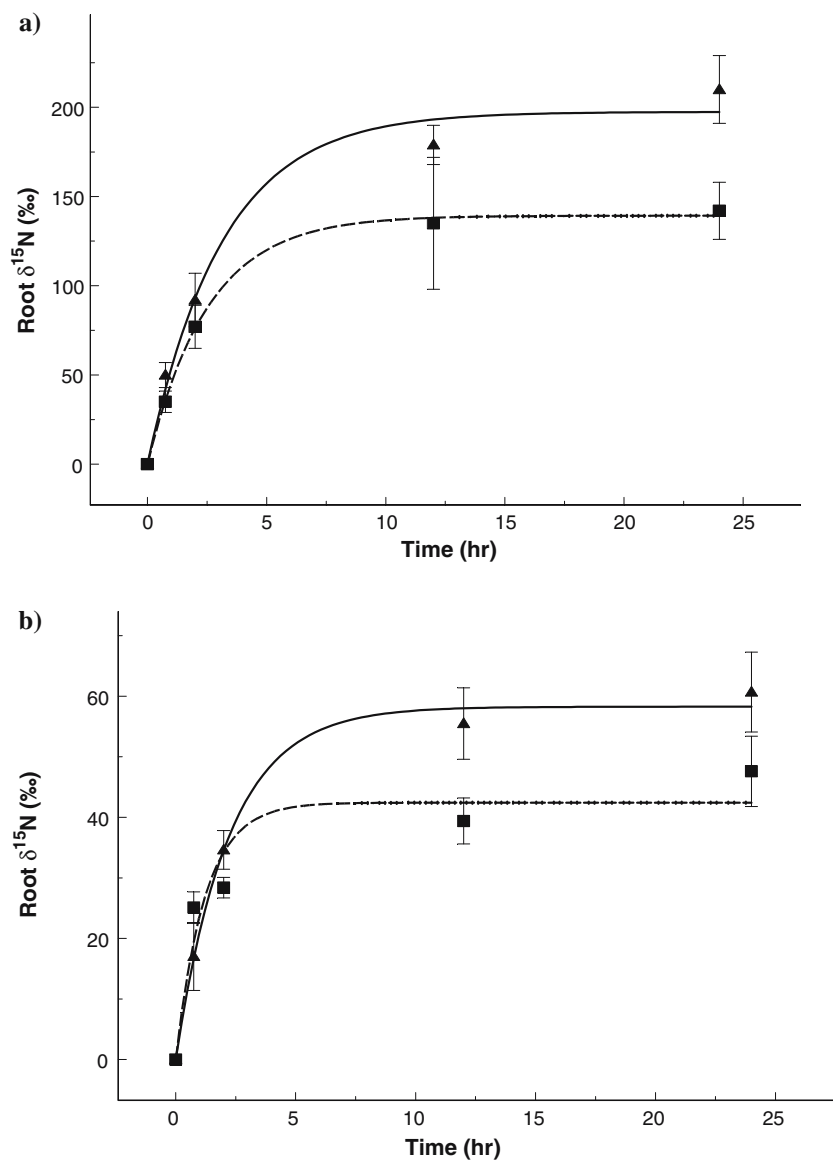


Table 2 Rate equations for isotopic enrichment of roots following in situ ^{15}N , $^{13}\text{C}^{15}\text{N}$ labeling, and concentrations of amino acids and ammonium ($\mu\text{g-N core}^{-1}$) in soils after

N additions, from early (Willow) and late successional (Black Spruce) forests along the Tanana River, in interior Alaska

Rate equation	Soil N concentration ($\mu\text{g N core}^{-1}$)	
	Amino acid	Ammonium
Willow (ammonium) = $197.43 (1 - e^{-0.319t})$	n.a.	356
Willow (amino acid) = $139.24 (1 - e^{-0.396t})$	398	n.a.
Black spruce (ammonium) = $55.72 (1 - e^{-0.481t})$	n.a.	457
Black spruce (amino acid) = $42.43 (1 - e^{-0.813t})$	1115	n.a.

All regressions were highly significant ($P < 0.01$)

enrichment over the experimental period for each N form and forest type are given in Table 2. We derived estimates of uptake of each N form from the product of the rate constants and the concentration of each N form in the soil after adding the label to account for the differential isotopic dilution between each soil. The relative uptake of amino acids versus ammonium (expressed as a ratio) was approximately 1.4 in willow and 4.0 in black spruce (Fig. 2). This finding suggests that plant acquisition of DIN versus DON may vary across ecosystems, and consequently that the ecological importance of proteolysis (amino acid production) and mineralization (ammonium production), and the controls thereof, may change as well.

We conclude from analyses of the $^{13}\text{C}:^{15}\text{N}$ ratios in the roots of black spruce that the amino acids were absorbed intact (Fig. 3). The regression relationship was strongest for the first sampling period (45 min, $r^2 = 0.56$, $P = 0.012$) and weakest for the 24 h sampling period ($r^2 = 0.39$, $P = 0.054$). However, we acknowledge that some of the amino acid label could have been mineralized during the experiment, and that due to the very low tracer levels used in the study, we could not derive similar relationships for the willow stands and thus demonstrate that all the amino acids were taken up intact. The results for black spruce, however, mirror our previous observations of amino acid uptake based on molar ratios of $^{13}\text{C}:^{15}\text{N}$ of tracer in taiga forests along the Tanana River floodplain (McFarland et al. 2002). Our finding that neither soil exhibited significant increase in recovery of ^{15}N label originating from amino acids in the soil ^{15}N -DIN pool during the

uptake experiment (Fig. 4), suggest that the mineralization during this period was relatively minor. This observation along with a concomitant, albeit moderate, increase in root ^{13}C (Fig. 4), suggest that the increase in root $\delta^{15}\text{N}$ represents uptake of largely intact amino acids in both stands, which is consistent with other studies of coniferous (Näsholm et al. 1998; Öhlund and Näsholm 2001) and deciduous (Persson et al. 2003) species in boreal ecosystems. We ascribe the higher ^{15}N enrichment of plant roots from the willow stands than the black spruce forest primarily to differences of inter-specific nutrient absorption capacity, which in part may be due to species differences of the mycorrhizae associated with *Salix* and *Picea* (Wallenda and Read 1999). Moreover, differences in our field observations were probably further augmented by the higher soil temperatures in willow stands (12°C) than in the spruce forests (3°C).

Discussion

Plant uptake of N in the form of amino acids has recently been recognized as a widespread ecological phenomenon that includes both agricultural species and species from natural ecosystems across broad latitudinal gradients (Kielland 2001; Lipson and Näsholm 2001). The capacity for absorbing amino acids appears to be a widespread characteristic of boreal plants (Persson and Näsholm 2001a). In the taiga of interior Alaska, experimental evidence suggests that in situ uptake of organic N occurs across forests that differ widely in N cycling characteristics. These include

Fig. 2 Relative uptake of soil free amino acids versus ammonium (expressed as ratio) in willow (grey bar) and black spruce (black bar) stands along the Tanana River, interior Alaska. Horizontal stippled line represent the 1:1 uptake ratio between amino acids and ammonium. Mean \pm SE, $n = 6-9$

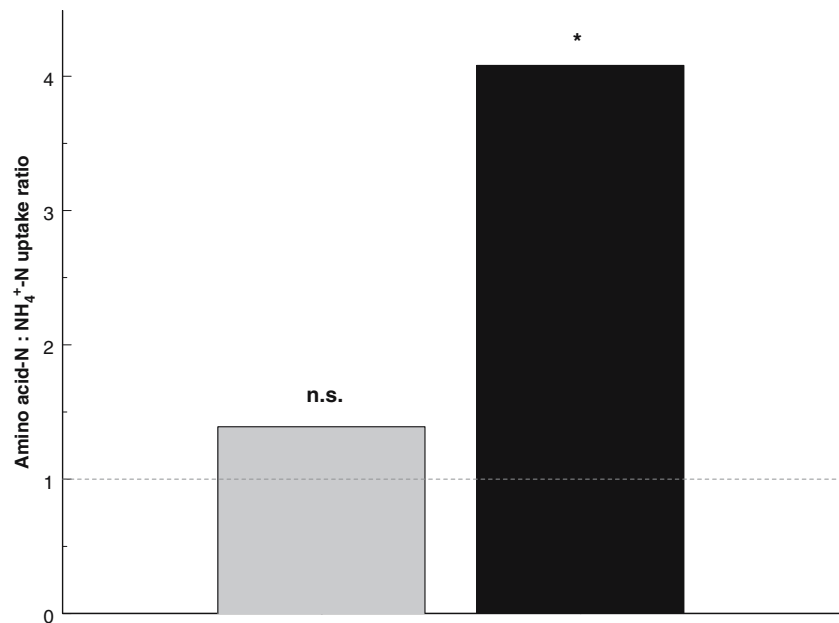
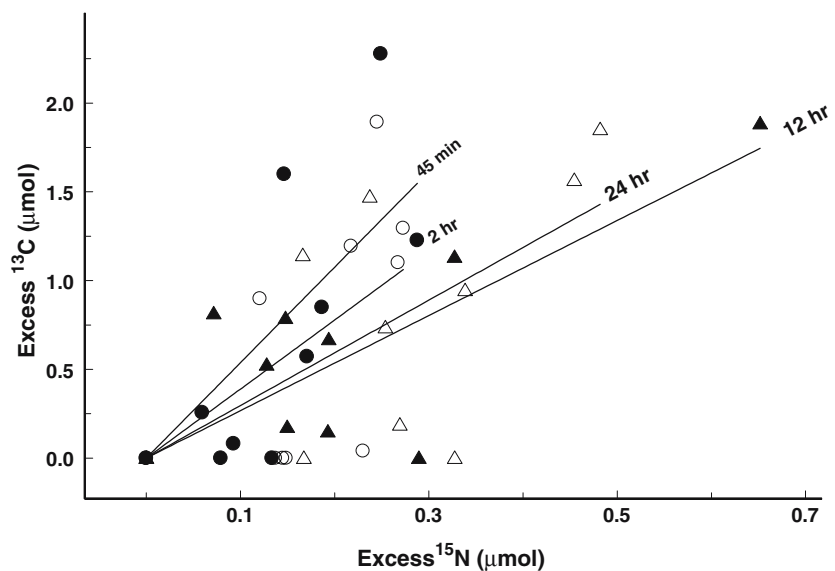


Fig. 3 Molar ratios of excess ^{13}C and excess ^{15}N in roots of black spruce from the amino acid treatment. Sampling periods are denoted above each regression line. Slopes (s) and r^2 values for each regression is as follows: open circles (\circ) 45 min ($s = 6.0$, $r^2 = 0.56$); filled circles (\bullet), 2 h ($s = 5.3$, $r^2 = 0.40$); open triangle (\triangle), 12 h ($s = 2.4$, $r^2 = 0.54$); filled triangle (\blacktriangle), 24 h ($s = 3.1$, $r^2 = 0.39$)

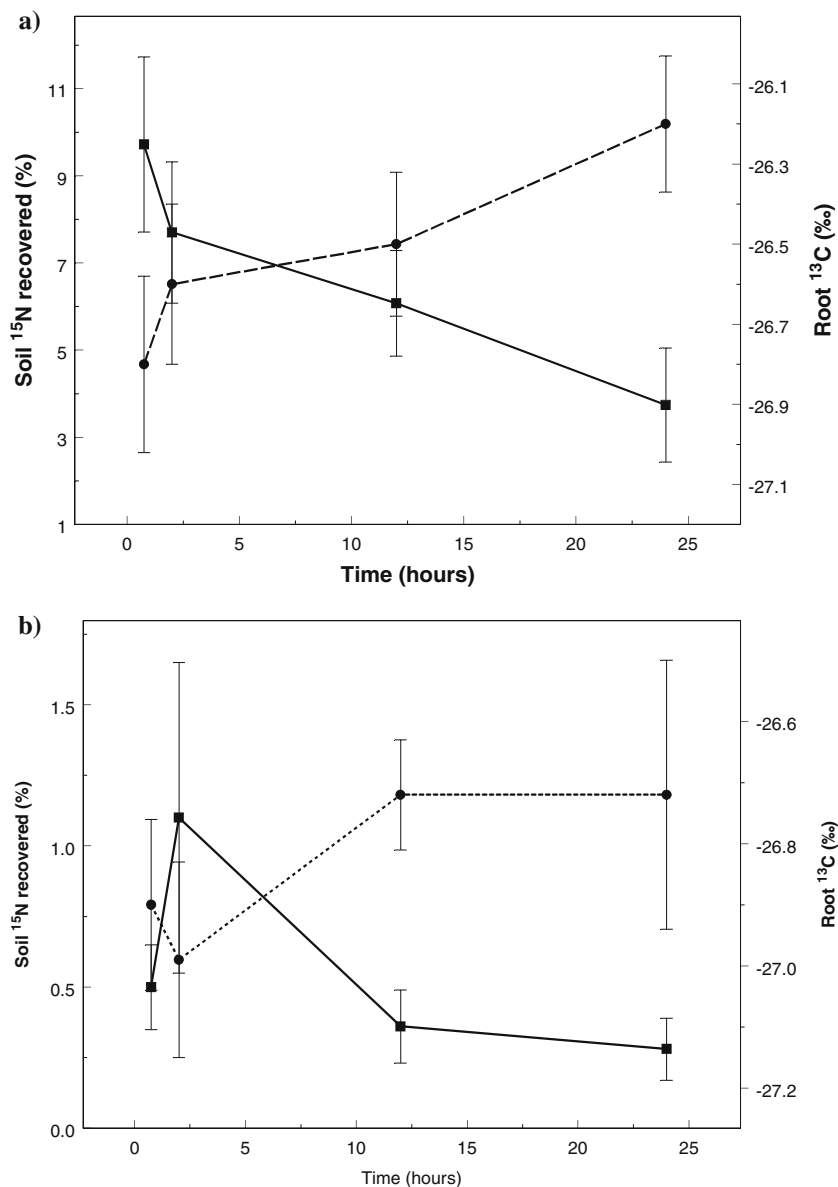


early successional willow communities which have low rates of N mineralization (Klingensmith and Van Cleve 1993), but also low soil organic matter content and relatively small fluxes of DON; mid-successional balsam poplar forests (McFarland et al. 2002) with high rates of N mineralization and moderate pools of amino acid N; and late-successional black spruce forests, where the flux of

DON dominate the N cycle (Jones and Kielland 2002; Kielland et al. in press b).

The relationship between apparent N uptake and soil N characteristics is still not clear, as are the appropriate metrics for evaluating this relationship (Jones et al. 2005). Moreover, though flux of amino acid N in a variety of ecosystems have been shown to exceed apparent plant

Fig. 4 Recovery of ^{15}N -amino acids in the dissolved inorganic nitrogen of soils (solid line—■), and enrichment of root- ^{13}C (stippled line—●) from (a) willow and (b) black spruce stands along the Tanana River. Mean \pm SE, $n = 6\text{--}9$



requirement, we recognize that high rates of proteolytic activity (amino acid production) does not necessarily equate to high amino acid availability due to competition with soil microbes, sorption processes in the soil, and rapid turnover of the amino acid pool (Lipson and Monson 1998; Jones and Hodge 1999; Lipson et al. 1999; Raab et al. 1999; Jones and Kielland 2002). However, based on both relative production rates and instantaneous pools sizes, there is reasonable evidence to support the contention that the

supply of organic N is often as great as inorganic N in many natural ecosystems (Read and Bajwa 1985; Kielland 1995; Nordin et al. 2001). We have shown that uptake of ammonium and amino acids were near unity for early successional willow communities, where the soil concentrations of ammonium and amino acids are very similar. By contrast, late successional black spruce forests absorbed amino acids to a much greater extent than ammonium. The increased uptake of amino acids relative to ammonium, however, is roughly

proportional to the increase in soil amino acid availability. Thus, we reject our hypothesis that the dominance by DON in N cycling of black spruce forests has conferred an apparent physiological “preference” for amino acid uptake in these ecosystems. Rather, uptake of different N forms appears more related to the size of the specific N pool (“availability”), than by changes in plant physiology. Similar inferences have been made from field experiments in arctic tundra (Nordin et al. 2004). Our findings are relevant in the context of increased fire frequency of boreal forests (Chapin et al. 2003), as well as intensified forestry and increased N deposition. These disturbances entail changes in the soil N economy of late-successional conifer forests from more DON dominated (Jones and Kielland 2002) to more DIN dominated, both with respect to N mineralization and nitrification (Gordon and Van Cleve 1982; Wan et al. 2001; Boerner and Brinkman 2005). In light of the inherent differences in physiological absorption capacity for ammonium and nitrate of late successional conifer species (Chapin et al. 1986; Kronzucker et al. 1997; Hags et al. 2003) and the importance of free amino acids to the N economy of other mid-to-late successional species (Öhlund and Näsholm 2001; McFarland et al. 2002), the consequence of shifts in soil N cycling characteristics have potential significant effects on forest regeneration and productivity, including that of black spruce which currently is the dominant forest type in interior Alaska (Yarie and Billings 2002).

We acknowledge that we could not ascertain uptake of intact amino acids in the willow stands due to our inability to accurately measure molar ratios of $^{13}\text{C}:^{15}\text{N}$ in willow roots. We suggest this failure was in part due to the extremely conservative levels of tracer that we applied in our experiments; approximately 10-fold less than has been applied in arctic tundra systems (e.g. Schimel and Chapin 1996) and less than half of some previous applications in boreal forests (Näsholm et al. 1998).

We recognize that to calculate the magnitude of isotopic dilution used to estimate N uptake it is important to identify the appropriate N pool (Nordin et al. 2004). For an experiment involving several amino acids the appropriate N pool may

be the total soil free amino acid pool. However, in single-amino acid experiments the appropriate N pool would be the concentration of that particular amino acid. Alternatively, the total free amino acid concentration could be used if a correction factor can be applied for the uptake of the amino acid in question relative to other amino acids. Such data may be difficult to come by, but information pertinent to such an approach is available for selected amino acids, plant species, and ecosystems (Kielland 1994; Lipson et al. 1999; Persson and Näsholm 2001a). Techniques for detecting the intact label in roots, such as GC-MS (Persson and Näsholm 2001b), allows for direct measurement of the label, but require an experimental design that let the investigator track metabolic conversions and translocation of the label over time (Persson et al. 2003).

Our observations are consistent with other studies of resource-based niche partitioning regarding N uptake. For example, species dominance in Alaskan tussock tundra is associated with acquisition of N forms that are most abundant in the soil, whereas less dominant species absorb higher proportions of less available forms of N (McKane et al. 2002). Analogous modifications of N uptake in relation to differential availability of different N forms have been found along fertility/productivity gradients in boreal forests (Nordin et al. 2001) and grasslands (Weigelt et al. 2005). Similarly, studies of N uptake from a wide variety of plant functional types in arctic and alpine tundra, suggest that intra-specific uptake capacity can be proportional to N availability for many, but not for all species (Raab et al. 1999, Kielland 2001).

Conclusions

We have shown that soil N in the form of ammonium or amino acids is rapidly taken up in taiga forests. Soil amino acids are clearly taken up as intact molecules by black spruce, and the rate of uptake of either N form appears to be in proportion their relative concentration in the soil. The observation from taiga forests in interior Alaska, that the forest types with highest growth rates and highest rates of soil N mineralization

(balsam poplar) still take up amino acids at equivalent rates to that of ammonium in situ (McFarland et al. 2002), indicate that amino acids are an important component of the N cycle and the N economy of these forests. Though the mechanisms of N supply and the controls thereof are likely to differ among early successional forests (e.g. mineralization; DIN) and late successional forests (e.g. proteolysis; DON), our study shows that patterns of relative uptake of amino acid and ammonium varies across succession on concert with the apparent availability of inorganic and organic forms of N. This ecological relationship with respect to soil N dynamics and plant physiological function lead us to suggest that the uptake of soil amino acids is a pervasive characteristic of taiga forest ecosystems. These findings are relevant to our understanding of how taiga ecosystems may respond to increases in temperature, fire frequency, N deposition, and other potential consequences of global change.

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