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Landscape patterns of free amino acids in arctic tundra soils

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Abstract. Concentrations of free amino acids were measured in soils from four major ecosystem types in arctic Alaska. Total free amino acid concentrations were several-fold higher than ammonium (the major form of inorganic nitrogen) in water extracts of soils. The dominant free amino acids in these soils were glycine, aspartic acid, glutamic acid, serine, and arginine. Concentrations of total amino acids ranged 5-fold across communities, being highest in tussock tundra and lowest in wet meadows. Incubation experiments indicate that the turnover of amino acids is rapid, which suggests high rates of gross nitrogen mineralization in these soils. The high concentrations and dynamic nature of soil free amino acids suggest that this nitrogen pool is a significant component of nitrogen cycling in these tundra ecosystems.

Key words: amino acids, arctic ecosystems, nitrogen cycling, nutrient availability, organic nitrogen, tundra soils

Introduction

In both natural and agricultural ecosystems across a wide geographic range, the bulk of soil N exists in organic form, as amino acids, amino sugars, and uncharacterized non-hydrolyzable fractions (Stevenson 1982). In arctic ecosystems the proteinaceous N fraction makes up about one third of total soil N (Sowden et al. 1977). That portion of the protein not associated with the humus is biologically very active and is probably the major substrate for N mineralization (Ladd & Jackson 1982). Despite the observation that nitrogen mineralization is 1) significantly correlated with primary productivity in tundra ecosystems as well as 2) closely tied to substrate quality (Kielland 1990), there have been no studies of arctic ecosystems that have addressed the nature of organic N in these soils. In this paper I document seasonal patterns of soil free amino acids in four major tundra ecosystem types in northern Alaska. These data demonstrate that amino acids constitute a significant proportion of the labile N in these tundra ecosystems and represent an important N pool in these systems.

Methods

Study sites

The research was conducted in the northern foothills of the Brooks Range, Alaska. Three communities (dry lichen heath, tussock tundra, and shrub tundra) were studied at Toolik Lake (68°38′ N, 149°34′ W, 760 m elevation), and one community (wet meadow) was studied near the Atigun River 20 km south of Toolik Lake. These four communities are representative of the major vegetation types in the Alaskan Arctic (Webber 1978). Shrub tundra is the most productive of the four study sites with an aboveground net primary production (NPP) of 300 g m^{-2} yr^{-1} (Shaver & Chapin 1991). It is dominated by the deciduous shrubs *Salix pulchra* Cham., *Salix glauca* L., and *Betula nana* L. (nomenclature follows Hultén 1968). Tussock tundra has an approximately equal mixture of graminoids (*Eriophorum vaginatum* L. and *Carex bigelowii* Torr.), deciduous shrubs (*Salix pulchra* and *Betula nana*), and evergreen shrubs (*Ledum palustre* L. and *Vaccinium vitis-idaea* L.) with an aboveground vascular NPP of 144 g m^{-2} yr^{-1}. Wet meadow tundra is graminoid-dominated (*Eriophorum angustifolium* Honck. and *Carex aquatilis* Wahlenb.) with an annual productivity of 51 g m^{-2}. The dry heath is least productive (NPP = 32 g m^{-2} yr^{-1}) and is dominated by *Loiseleuria procumbens* L., *Ledum palustre*, *Vaccinium vitis-idaea*, and *Betula nana*.

Soil sampling

Soils from the upper 10 cm of the organic horizon of each community were collected with a 6.5 cm diameter soil corer at random points along several 30 m long transects in each community at three times over the growing season: immediately after soil thaw in early June, at the height of the growing season in mid-July, and in late August just prior to freeze-up. The soil samples (n=8 per sampling date in each community) were kept cool (3–7 °C) until extracted (within 24 h of collection). The samples were not frozen prior to extraction since this may inflate soluble soil amino acid concentrations (Ivarson & Sowden 1966). Samples of 10 g wet mass were extracted with 75 ml of distilled deionized water for 5 min in polyethylene bottles under slow shaking action. Water was used as solvent because this gives a better estimate of the concentration of amino acids in the soil under natural conditions than do organic solvents or salt solutions (Ivarson & Sowden 1969). Following extraction, the sample was passed through a glass fiber filter and the filtrate frozen at −18 °C until further analysis. All glassware and other equipment associated with the extractions were acid-washed prior to the extractions.

Concentration of each amino acid was measured using high performance liquid chromatography (HPLC).

Turnover experiments

To investigate the potential rate of turnover of soil amino acids, ^{14}C-labeled glycine, aspartate, and glutamate (New England Nuclear, Boston, MA) were added in trace amounts to separate, sealed Mason jars (three jars per amino acid per sampling time) containing sifted organic soil from the dry heath community, and incubated at 20 °C. This community has the lowest rate of nitrogen mineralization (Kielland 1990) and shares many attributes (low pH, high organic matter content, and dominance of ericaceous shrubs) with other soils where amino acid dynamics have been studied (Read & Bajwa 1985; Read 1991). Each jar contained 10 g wet mass of soil and 27.9 nCi of the individually labeled amino acids. Radioactivity in the soil was measured on water extracts after two and six hours. Respired $^{14}CO_2$ was collected on 3 cm^2 strips of filter paper (Whatman No. 1) that were soaked with 250 μL of 1 N sodium hydroxide and suspended inside each jar. The samples were analyzed on a Beckman LS 7500 liquid scintillation counter.

In an additional experiment designed to measure nitrogen mineralization, 20 g wet mass (moisture content 70%) of heath soil (n = 8 per community) was placed in plastic cups and incubated in the dark aerobically at 12 °C for two weeks. The concentrations of amino acids (by HPLC) and mineral nitrogen (by autoanalyzer) were measured on water extracts of subsamples collected before and after incubating.

HPLC procedures

The samples were injected into the HPLC and eluted with a solvent gradient produced by a Spectra Physics solvent delivery system fitted with a Hamilton PRP-1 column (4.6 mm × 250 mm, packing diameter 10 μm). Fluorescence was measured by an FS 950 Fluoromat detector from Schoeffel Instruments, and the peaks were recorded and integrated on a Spectra Physics 4270 integrator, following a modified pre-column fluorescence derivatization procedure using a *o*-pthaldialdehyde/2-mercapto-ethanol reagent (Lindroth & Mopper 1979; Jones et al. 1981).

Amino acid concentration in roots (g N m^{-2}) was estimated by multiplying root biomass (g m^{-2}; Shaver & Chapin 1991) by average seasonal concentration of amino acids in roots of the graminoid *Eriophorum vaginatum* (Chapin et al. 1986), the only species for which this data is available.

Data were analyzed using Systat statistical package (SYSTAT Inc. 1987). Unequal sample sizes and heterogenous variances dictated the use of non-

Table 1. Mean seasonal concentrations (across three sample dates) of water-extractable total free amino acids and ammonium in the organic soil horizon. Coefficients of variation in parenthesis.

	N concentration (μg N/g dry soil)			
	Dry heath	Wet meadow	Tussock tundra	Shrub tundra
Amino acids	2.19	1.57	8.29	2.88
	(82%)	(29%)	(89%)	(80%)
Ammonium	0.34	0.38	0.84	0.64
	(59%)	(44%)	(4%)	(58%)

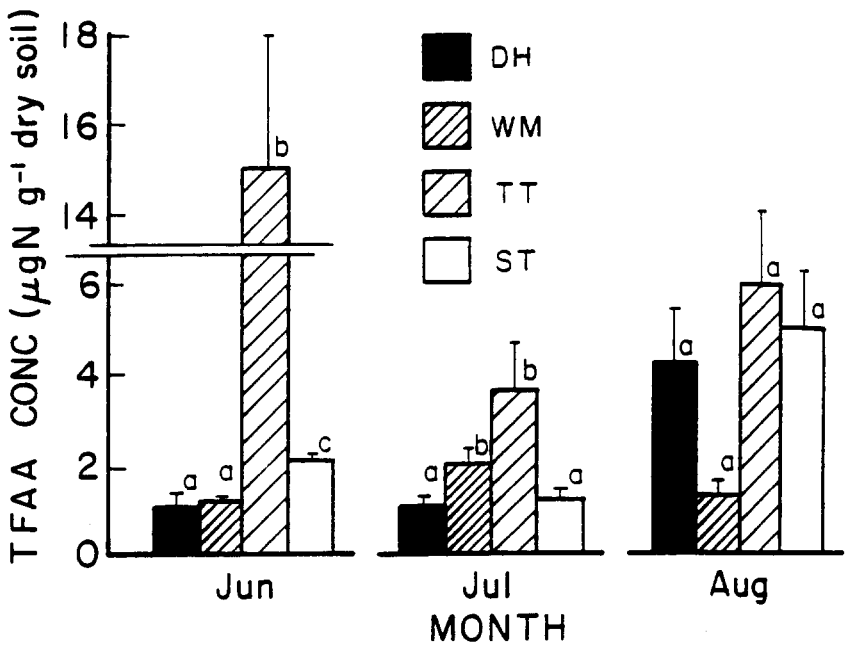

Fig. 1. Seasonal changes in concentration of total free amino acids (TFAA). Letters (a, b, c) indicate significant differences ($P < 0.05$) among communities within a sample date. DH = dry heath, WM = wet meadow, TT = tussock tundra, and ST = shrub tundra. (Mean ± S.E.).

parametric one-factor analysis of variance (Kruskal-Wallis test). When this test procedure showed significant differences, nonparametric multiple comparisons testing was performed to separate the individual means (Conover 1980).

Table 2. Range of monthly mean concentrations of individual free amino acids identified in tundra soils from four ecosystems near Toolik Lake, Alaska.

Amino acid	ng/g dry soil
Acidic	
Aspartic acid	50–830
Asparagine	<10–80
Glutamic acid	20–670
Glutamine	<10–120
Basic	
Arginine	200–1800
Lysine	10–100
Neutral	
Glycine	50–730
Alanine	<10–50
Leucine	50–150
Phenylalanine	<10–30
Serine	30–2860
Threonine	10–900
Ornithine	50–150
Methionine	<10–100
Valine	<10–30

Results

Soil amino acid concentrations

Mean total free amino acid (TFAA) concentrations varied over five-fold among communities (Table 1). Tussock tundra had the highest concentration (8.3 μg N g^{-1}), and the anoxic wet meadow had the lowest concentration (1.6 μg N g^{-1}). In each community, the concentration of water-extractable amino-acid nitrogen was four- to ten-fold higher than that of ammonium, the predominant form of inorganic N in these soils (Kielland 1990). Tussock tundra showed the greatest temporal (monthly) variation (n = 3 sample dates) in TFAA concentration (CV = 89%) and the wet meadow the least (CV = 29%). The temporal pattern of variation (across the season) in TFAA concentrations also differed among communities (Fig. 1). In tussock and shrub tundra the concentrations decreased from June to July and then rose again in the autumn. This pattern of temporal fluctuation roughly paralleled that of nitrogen mineralization in the spring in these communities, and leaching of

Table 3. Average seasonal concentration (ng N/g dry soil) of the five dominant amino acids in in each community. Coefficients of seasonal variation in parenthesis.

	Dry heath	Wet weadow	Tussock tundra	Shrub tundra
Glycine	316 (87%)	203 (69%)	657 (18%)	221 (68%)
Aspartic acid	227 (126%)	149 (50%)	622 (23%)	311 (107%)
Glutamic acid	85 (83%)	187 (53%)	408 (57%)	191 (101%)
Serine	385 (119%)	105 (21%)	1253 (111%)	399 (92%)
Arginine	200 (93%)	93 (14%)	814 (106%)	254 (91%)

leaf litter and initial decomposition of newly produced litter in the autumn. In contrast, the TFAA in the wet meadow soil rose slightly during mid-season. In the dry heath, TFAA concentrations rose in the fall after being stable from early spring to July.

The most abundant amino acids were the neutral amino acids glycine, serine, threonine, and leucine; the acidic amino acids aspartate and glutamate, and their amides (asparagine and glutamine); and the basic amino acid arginine (Table 2). These amino acids occurred in every sample. Variable amounts of alanine, lysine, ornithine, methionine, valine, and phenylalanine were also found. In some samples the concentrations of these variable amino acids were as high as those of any of the other amino acids, but they were not found consistently in all samples from a given community.

Of the 15 amino acids identified in these soils (Table 2), glycine, aspartic acid, glutamic acid, serine, and arginine accounted for over 50% of the TFAA. For this reason the temporal dynamics of these amino acids will be discussed in further detail. Because these amino acids make up the bulk of free amino acids in the soil, their temporal variation (Fig. 2) closely matched the temporal fluctuations in TFAA. However, each community showed a unique distribution of individual amino acids (Fig. 3). For example, the concentrations of serine and arginine remained fairly constant over the season in the wet meadow site (CV = 21% and 14% respectively; Table 3), but showed large variation in tussock tundra (CV > 100%). The average monthly concentration varied up to 12-fold across all communities for a single amino acid (serine), and over 4-fold among the five amino acids within a single community (dry heath).

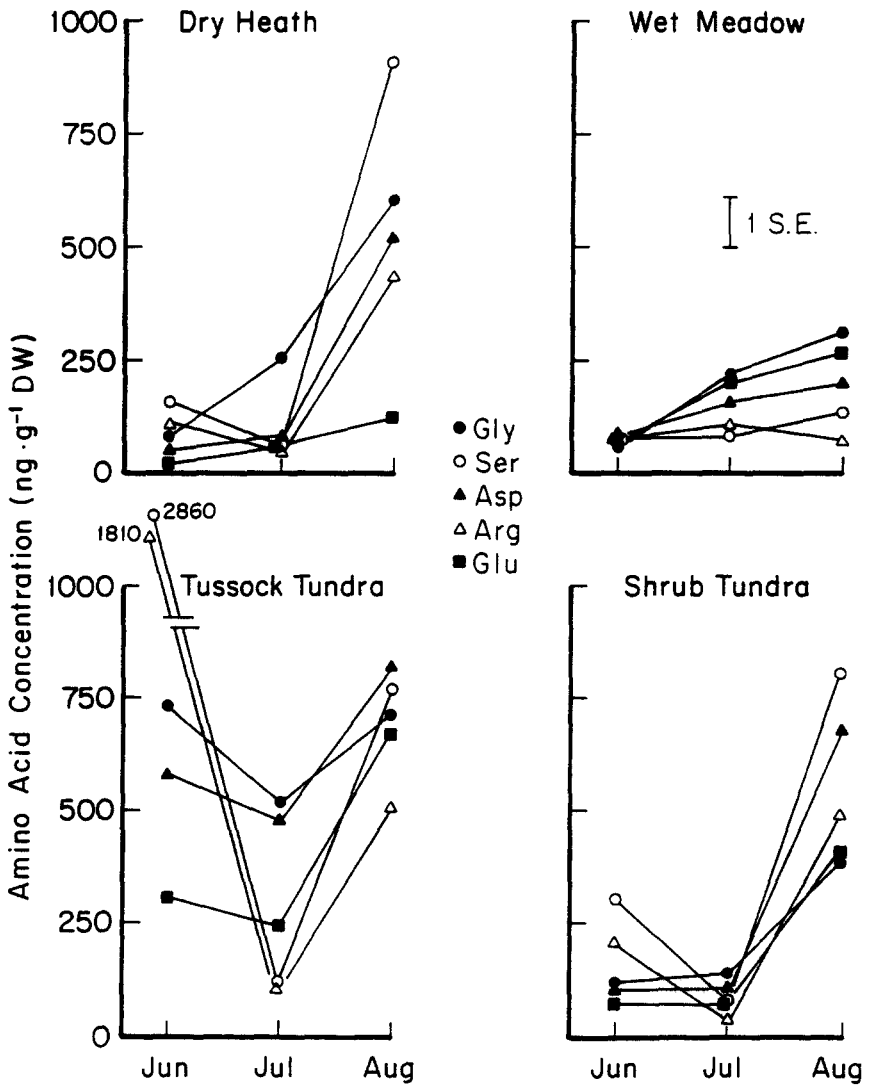

Fig. 2. Seasonal concentrations of glycine (Gly), serine (Ser), aspartic acid (Asp), arginine (Arg), and glutamic acid (Glu) in each community. Maximum standard error is indicated.

Across communities, glycine had the highest concentration in mid-summer and arginine the lowest. Serine tended to be the highest in spring and autumn (Fig. 2). This pattern also reflected the proportional changes in these amino acids over the season, except that the importance of glycine and to a lesser extent aspartate were augmented in mid-season (Fig. 3).

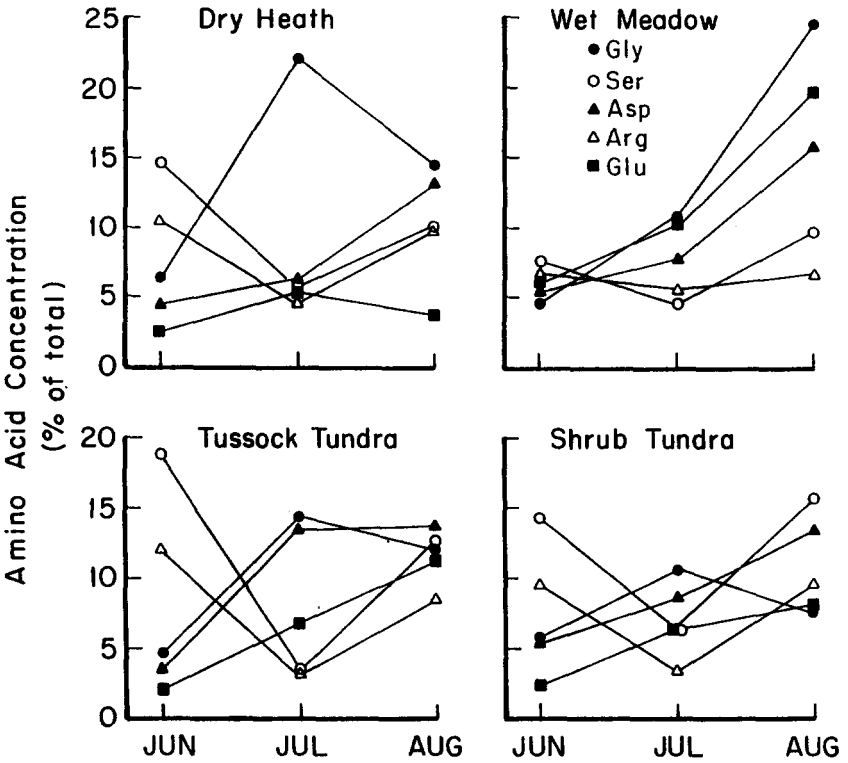

Fig. 3. Seasonal changes in the proportional contribution (% of total) of the major amino acids to the total free amino acids pool in each community.

Table 4. Changes in mineral nitrogen and amino acids (μg N/g) in soil samples incubated aerobically in the laboratory (mean ± S.E.).

	Dry heath	Wet meadow	Tussock tundra	Shrub tundra
Mineral N				
Initial	1.6 (0.2)	1.5 (0.1)	2.8 (0.4)	16.2 (0.3)
Final	2.0 (0.2)	1.9 (0.4)	25.6 (2.6)	17.5 (2.0)
Change	+0.4	+0.4	+22.8	+1.3
Amino acid-N				
Initial	4.2 (0.7)	1.3 (0.2)	9.2 (2.0)	5.2 (0.8)
Final	3.0 (0.1)	6.5 (0.6)	6.4 (0.3)	3.7 (0.3)
Change	−1.2	+5.2	−2.8	−1.5

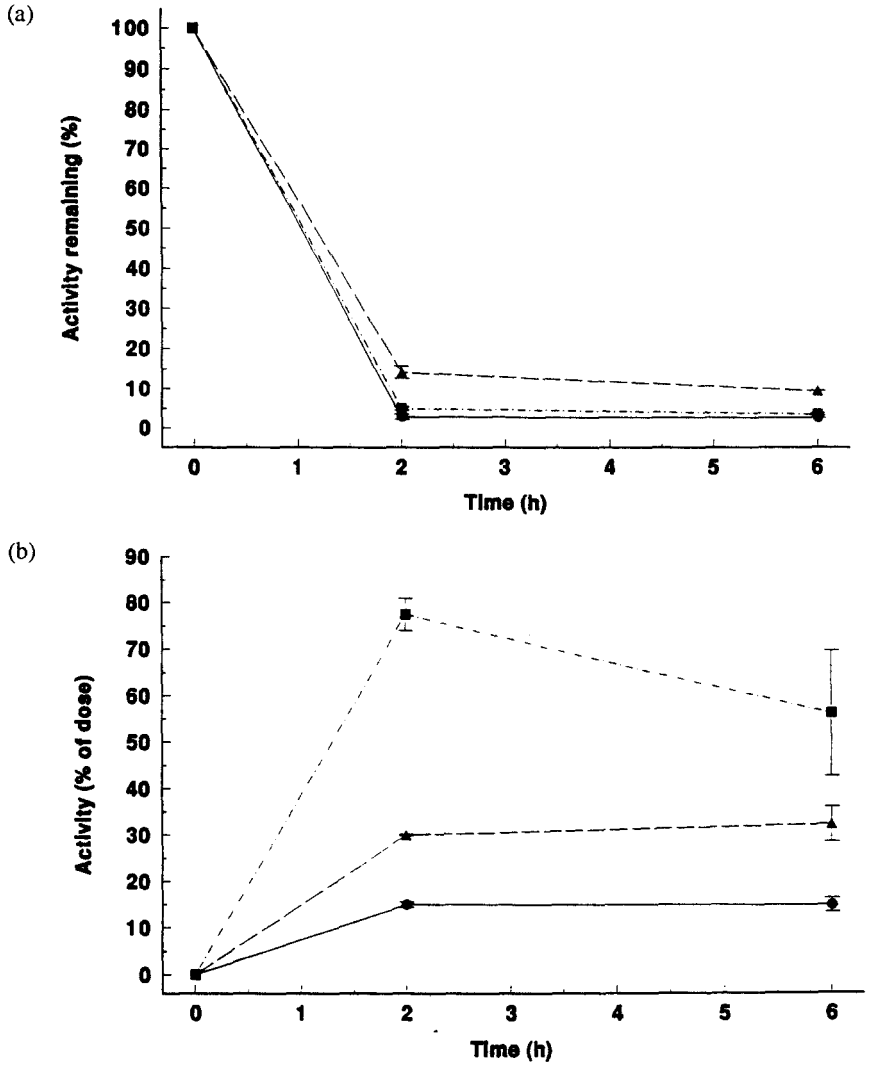

Fig. 4. Activity of ^{14}C-labeled amino acids in (a) soil extracts and (b) as respired CO_2 in dry heath soil. The amino acids are glutamic acid (▲), glycine (●), and aspartic acid (■).

Turnover experiments

The activity of added amino acids in water extracts of the labeled heath soil decreased approximately 80–95% within two hrs (Fig. 4a), showing that free amino acids were rapidly removed from the soil solution. Further change in activity was small. The activity of respired CO_2 (Fig. 4b) increased during the first 2 hrs, then little change ocurred thereafter. Among the three amino acids

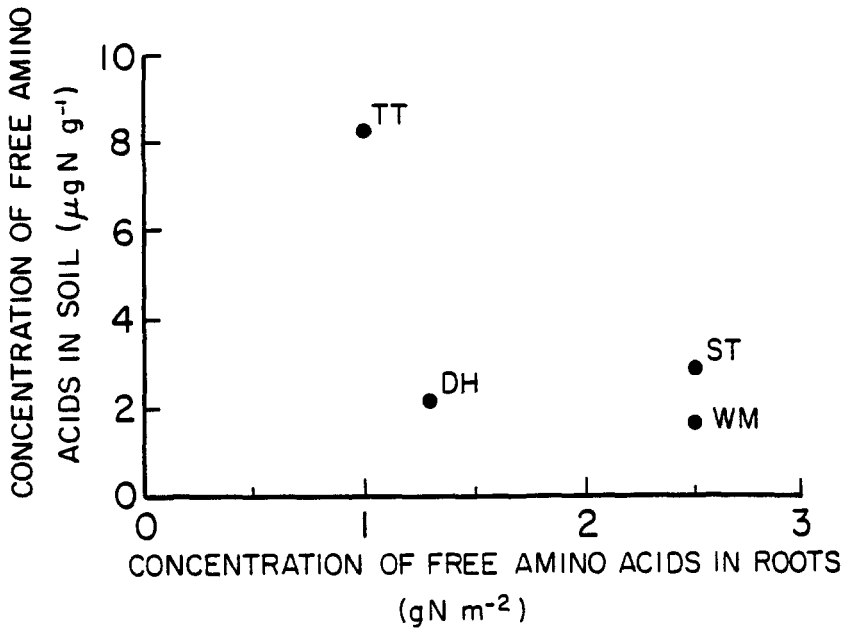

Fig. 5. Relationship between free amino acids in roots and soil across vegetation types. Site designations as in Fig. 1.

examined, aspartic acid exhibited the most rapid potential turnover (nearly 80% of dose respired in 2 hrs), from twice to three times as fast as glutamic acid and glycine, respectively.

In the mineralization experiment all soils showed positive net nitrogen mineralization, but, with the exception of tussock tundra, the rates were very low compared to other measurements employing the same methodology on the same or similar soils (Kielland 1990; Giblin et al. 1991). All sites except the wet meadow showed decreases in free amino acid concentrations concomitant with net mineralization (Table 4). Moreover, mineralization was not proportional to decrease in amino acid concentrations. In only two communities (dry heath and shrub tundra) could the direct decrease in amino acid-nitrogen account for the increase in mineral nitrogen. Thus, it appeared to be no direct relationship between the consumption of amino acids and the net production of mineral nitrogen.

Discussion

The present study is the first report on free amino acids from arctic soils, so it is difficult to know how widely these results can be generalized. However, the

range in seasonal mean concentration among these four tundra communities (1–8 $\mu g\ g^{-1}$) is similar to values measured in Canadian agricultural soils (2.2 $\mu g\ g^{-1}$; Ivarson & Sowden 1969), in a *Calluna* heath in England (2.4 $\mu g\ g^{-1}$; Read & Bajwa 1985), and in temperate alpine soils (10 $\mu g\ g^{-1}$; calculated from Labroue & Carles (1977).

Because free amino acids represent a relatively available energy and nitrogen source for microorganisms, it is perhaps surprising that they are abundant in tundra soils. One possibility is that they are an artifact of severing roots during soil collection. The concentration of free amino acids in plant tissues and xylem sap is several-fold greater than in the soil (Sauter 1981; Kielland 1994). However, soil free amino acid concentration was not positively correlated with the quantity of free amino acids in roots (Fig. 5). I conclude, therefore, that free amino acids are a true soil N pool and not an artifact of severing the roots.

The relatively high concentrations of soil amino acids compared to inorganic nitrogen in these arctic soils (Table 1) are consistent with the high organic matter content and the large concentrations of soluble organic nitrogen in arctic ecosystems (Shaver et al. 1990; Kielland 1990). Marine sediments also can have high concentrations of free amino acids in interstitial pore water ($> 200\ \mu mol\ L^{-1}$; up to 5-fold greater than observed in the present tundra soils), indicating that systems which lack roots and have an active microbial community can be characterized by high concentrations of free amino acids (Henrichs et al. 1984).

The amount of amino acids measured in soil extracts is affected by supply to (through extracellular protease activity) and removal from the soil solution amino acid pool. Removal of amino acids from the soil solution occurs through three mechanisms: physical adsorption, uptake by plants and microbes, and mineralization by exoenzymes. The present experiment did not allow for quantitative comparisons of these processes. However, the differences among radioactivity of the individual amino acids in soil extracts vs respired CO_2 indicate that glutamic acid and glycine were adsorbed and/or immobilized more rapidly than was aspartic acid. The activity of respired CO_2 suggest approximate individual turnover times for aspartate, glutamate, and glycine were minimally on the order of 3, 6, and 15 hrs, respectively. By comparison, ammonium turnover in heath soil in the field is approximately 10 days (Kielland 1990). It should be noted, however, that this difference is partially due to higher temperature in the lab (20 °C) than in the field ($\approx$10 °C).

In the absence of comparable data from other terrestrial studies, it is difficult to evaluate these findings as divergent from, or typical, of organic soils. Available information from marine chemistry demonstrates that in sediment

porewaters the turnover time of the total pool of free amino acids can be quite short, on the order of a few hours to several days (Jörgensen & Söndergaard 1984; Henrichs & Doyle 1986). Individual amino acids may exhibit turnover times of less than one hour (Jörgensen & Söndergaard 1984). Although terrestrial and marine systems are quite different both structurally and functionally, the much higher organic matter content and respiration rate of organic soil compared to most marine sediments suggest that there is a strong potential for rapid turnover of amino acids in terrestrial systems. The mineralization experiment suggests that the amino acid pool in tundra soils may also prove to be a highly dynamic fraction, but indicates that the direct link between fluctuations of organic and mineral nitrogen in the soil can not readily be established without using isotopes to trace these processes.

The high concentrations of free amino acids compared to inorganic N found in the present tundra soils could be partially attributable to low soil pH, under which conditions protease activity is enhanced (Bajwa et al. 1985). Protease activity in tussock-tundra soils measured under laboratory conditions (Chapin et al. 1988) suggests that the potential rate of free amino acid production from peptide hydrolysis is far more rapid than the rate of ammonification under field conditions. These different production rates may consequently explain why amino acids are at higher concentrations than ammonium.

The high amino acid concentrations in spring and autumn may reflect the release of microbial cell contents that are lysed by freeze-thaw cycles (Mack 1963). The concentrations of amino acids were particularly high in tussock tundra in June and may account for the high net N mineralization that occurred at that time (Kielland 1990). The increase in total free amino acid concentration in autumn may also reflect fresh litter input as a consequence of leaf senescence and the subsequent leaching of this material. The bulk of the nitrogen leached from leaf litter is in the form of protein or free amino acids (Nykvist 1963; Chapin et al. 1986). Moreover, amino acid concentrations in precipitation, which are greatest in autumn, can be as high as that of inorganic N (Mopper & Zika 1987).

The high concentrations of free amino acids in tundra soils compared to that of inorganic N, and their inferred rapid rate of generation have important implications for N cycling in tundra. First, free amino acids are a prime substrate for N mineralization and are a direct source of N to plants. Direct absorption of amino acids by plants has been demonstrated in both temperate (e.g., Miettinen 1959; Soldal & Nissen 1978; Bledsoe & Sangvanit 1984) and arctic species (Chapin et al. 1993; Kielland 1994). Thus, both the concentration and behavior of free amino acids indicate that this is a significant soil N pool that mediates plant-microbial interactions. Consequently, understanding

controls over N cycling in ecosystems with organic soils requires that the role of free amino acids should be more thoroughly explored.

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