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Processes controlling nitrogen release and turnover in Arctic tundra

Kielland, Knut, Ph.D.

University of Alaska Fairbanks, 1990

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

PROCESSES CONTROLLING NITROGEN

RELEASE AND TURNOVER IN

ARCTIC TUNDRA

by

Knut Kielland

RECOMMENDED:

Advisory Committee Chair

Department Head

APPROVED:

Dean, College of Natural Sciences

Dean of the Graduate School

5/1/90

Date

PROCESSES CONTROLLING NITROGEN RELEASE AND TURNOVER IN ARCTIC TUNDRA

A

THESIS

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for the Degree of

DOCTOR OF PHILOSOPHY

by

Knut Kielland, B.S.

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Abstract

This thesis provides data on nitrogen cycling among communities representative of the major vegetation types in arctic Alaska. Through field studies, I examined the pattern of nitrogen dynamics in four tundra ecosystems (dry lichen heath, wet meadow, tussock tundra, and deciduous shrub tundra) of contrasting structure and productivity near Toolik Lake, Alaska. In addition, through field and laboratory experiments, I sought to identify the major controls over nitrogen release and turnover in these nitrogen-limited systems.

These ecosystems, representing extremes of productivity in arctic Alaska, show order-of-magnitude differences in biomass and net primary productivity, and likewise, exhibit order-of-magnitude differences in net nitrogen mineralization and nitrogen turnover. Decomposition, soil respiration, net nitrogen mineralization, and the turnover of soil inorganic nitrogen were all highly correlated with net primary production. These results show that nutrient availability, in particular nitrogen availability, is a major control over tundra ecosystem function.

Soil pools of organic nitrogen are large, whereas the pools of inorganic nitrogen are small, and the net

rate of nitrogen mineralization *in situ* is low. Thus, nitrogen mineralization represents a major control point in the nitrogen cycle.

Net nitrogen mineralization is relatively insensitive to changes in soil temperature, but highly responsive to changes in available soil carbon and nitrogen. Thus, the effect of organic matter quality on microbial activity is a more important control of nitrogen release than is the direct effect of temperature.

Free amino acids constitute a larger proportion of extractable soil nitrogen than do ammonium and nitrate. Tundra species have the capacity to absorb some amino acids directly at rates comparable to ammonium absorption. These experimental results contrast with the widely held assumption that mineral nitrogen is the only form of nitrogen available to plants. I conclude that we must examine the behavior of both inorganic and organic soil nitrogen in order to adequately understand nitrogen cycling in tundra soils and the functioning of arctic ecosystems.

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I dedicate this thesis to my parents who first took me out in the woods and taught me about its ways.

INTRODUCTION

The structure and function of arctic ecosystems has attracted a great deal of attention from biologists interested in adaptation to environmental extremes. In the 1970s, the coastal tundra at Barrow, Alaska, was the subject of intensive ecological research under the auspices of the International Biological Program (Brown et al. 1980). The extensive research on element cycling at Barrow and other circumpolar tundra sites provided much insight into the functioning of arctic ecosystems. An important conclusion from these studies was that nutrient availability, in particular nitrogen availability, represents an important control over net primary production in these systems (Bliss et al. 1981).

Tundra ecosystems represent a wide range of plant community types and productivity, from the cushion-lichen communities in the polar deserts (Bliss 1975) to the productive deciduous shrub communities in the low Arctic (Ostbye 1975). Even in the Alaskan Arctic net primary production may differ ten-fold among major tundra communities (Shaver and Chapin, personal communication). However, no studies have investigated the range of variation in basic soil parameters over the extremes of productivity in Alaskan tundra communities. More

specifically, there has been no direct comparison of nitrogen dynamics among vegetation types in the Alaskan Arctic. The intent of this thesis is to: 1) provide new and more detailed data on soil carbon and nitrogen chemistry from different vegetation types in an attempt to increase our knowledge concerning the nature of, and variation in, basic soil properties among tundra communities, and 2) through field and laboratory experiments attempt to identify the major controls over nitrogen release and turnover in tundra communities of differing species and growth form composition. In the process I advance a new hypothesis regarding the soil-plant relationships of tundra species and the dynamics of nitrogen cycling in arctic ecosystems.

Arctic tundra ecosystems share many structural similarities with boreal and temperate ecosystems. For example, tundra communities may be dominated by graminoids (analogous to temperate grasslands), deciduous shrubs (analogous to deciduous temperate forests), evergreen shrubs (analogous to coniferous ecosystems), or a mix of growth forms. From a functional standpoint, however, tundra ecosystems exhibit many unique characteristics as a consequence of the low annual solar irradiance in this environment. Although low temperature and low light intensity limit photosynthesis and other physiological

processes directly, the temperature conditions in tundra environments are most strongly exerted indirectly by the short length of the season suitable for biological activity. Thus, the low annual productivity and slow rates of energy flow and nutrient cycling in arctic environments are to a great extent a function of the short growing season (Chapin 1983).

A salient characteristic of arctic ecosystems is the presence of permafrost. Permafrost prevents drainage and thus nutrient loss by leaching from the system, but it also contributes to high soil moisture and reduced redox potentials of these soils. Under these conditions microbial activity is decreased, resulting in lowered decomposition rates and accumulation of soil organic matter. Equally important to nitrogen dynamics is the fact that permafrost restricts the volume of soil as an active compartment in nitrogen cycling.

The existence of permafrost above the parent material essentially prevents weathering, and reduces this avenue of nitrogen input to a minimum. Thus, nitrogen in precipitation and nitrogen fixation provide the major inputs to the system. Nitrogen fixation appears to be strongly temperature-dependent even in tundra soils (Alexander and Schell 1973), and the annual nitrogen input in coastal tundra (75% as nitrogen fixation) is 10-100

times lower than precipitation inputs alone in temperate forests (Barsdate and Alexander 1975).

In spite of the low rate of external nitrogen input, tundra systems have more accumulated nitrogen than do temperate ecosystems. This finding suggests that there are strong environmental limitations imposed on the rate of denitrification. Indeed, experimental studies show that denitrification is very low in tundra ecosystems, on the order of 40% of nitrogen fixation (calculated from Alexander et al. 1973). Considering that the annual nitrogen input is generally less than 5% of the quantity cycling through the vegetation (Chapin et al. 1980), internal recycling of nitrogen (relative to external input and loss) takes on a much greater importance in tundra compared with temperate ecosystems. Consequently, processes such as decomposition and net nitrogen mineralization that control rates of internal recycling of nitrogen become particularly important in arctic systems. The present study examines the rates and controls of these processes of internal recycling in relation to ecosystem attributes that are unique to tundra ecosystems.

Chapter one of this thesis documents the spatial and temporal variability of soil pools of carbon and nitrogen among four tundra communities of contrasting structure and function. This chapter provides the first information on

detailed soil carbon and nitrogen fractions from several tundra communities that span the range of productivity in arctic Alaska. With this data set I demonstrate the large variability found in these soil parameters among tundra communities, and discuss how this variability is reflected in different community structure and growth-form composition. Chapter two focuses on the controls over decomposition processes, in terms of soil respiration, cellulose decomposition and net nitrogen mineralization, and shows how these processes are related to soil physico-chemical properties and net primary production. In chapter three I present turnover rates for various soil nitrogen compartments using data presented in chapters one and two, and relate these integrative measures of nitrogen supply to net primary productivity. In the fourth chapter I provide data on the distribution and abundance of free amino acids in arctic tundra soils and relate these soil parameters to nitrogen turnover in tundra ecosystems. Chapter five reports on free amino acid absorption by tundra plants and discusses patterns of uptake capacity among growth forms and absorption of different amino acids by a range of major tundra species. In the light of these experimental data I discuss the ecological implications of amino acid absorption in terms of plant nitrogen nutrition and nitrogen cycling in arctic ecosystems.

CHAPTER ONE: SOIL CARBON AND NITROGEN FRACTIONS.

Introduction

The tundra of arctic Alaska is far from uniform in its many components. Topographic heterogeneity and fluctuations in local environmental conditions produce large variations in plant species associations and soil characteristics across the landscape. In addition, arctic ecosystems may be dominated by a variety of growth forms (e.g. graminoids, deciduous shrubs, evergreen shrubs) which impart great structural differences among communities. This diversity of growth form composition is further reflected in diverse patterns of growth, nutrient requirements and storage (Shaver and Chapin 1980). The coupling of these biological processes to the physical heterogeneity and geological history of tundra regions results in an ecological complex that varies greatly in several important soil parameters.

One of the observations made during the IBP Tundra Biome study was that the variation in net primary production was greater within a given tundra area than across all the tundra biome sites. Moreover, net primary production was poorly correlated with most climatic variables (Wielgolaski 1975), suggesting that soil

conditions are the major determinants over net primary production in tundra.

In this chapter I provide data on soil carbon and nitrogen fractions from four contrasting tundra ecosystems. The analysis is restricted to the organic soil horizons in which living biomass and biological activity are concentrated (Gersper et al. 1980). The main objective of this work was to document the range of variation in soil parameters from structurally different, but geographically proximate ecosystems. In particular, I wanted to examine the extent to which variation in soil chemical charateristics could be explained by differences in growth-form composition among tundra ecosystems. From these data I seek to identify the salient features of carbon and nitrogen chemistry of the arctic tundra of northern Alaska.

Methods

Research sites

The research was carried out in four contrasting tundra ecosystems (dry lichen heath, wet sedge meadow, tussock tundra, and deciduous shrub tundra) in the northern foothills of the Brooks Range, Alaska (Fig. 1-1). Three ecosystems were located near Toolik Lake (68°38'N,

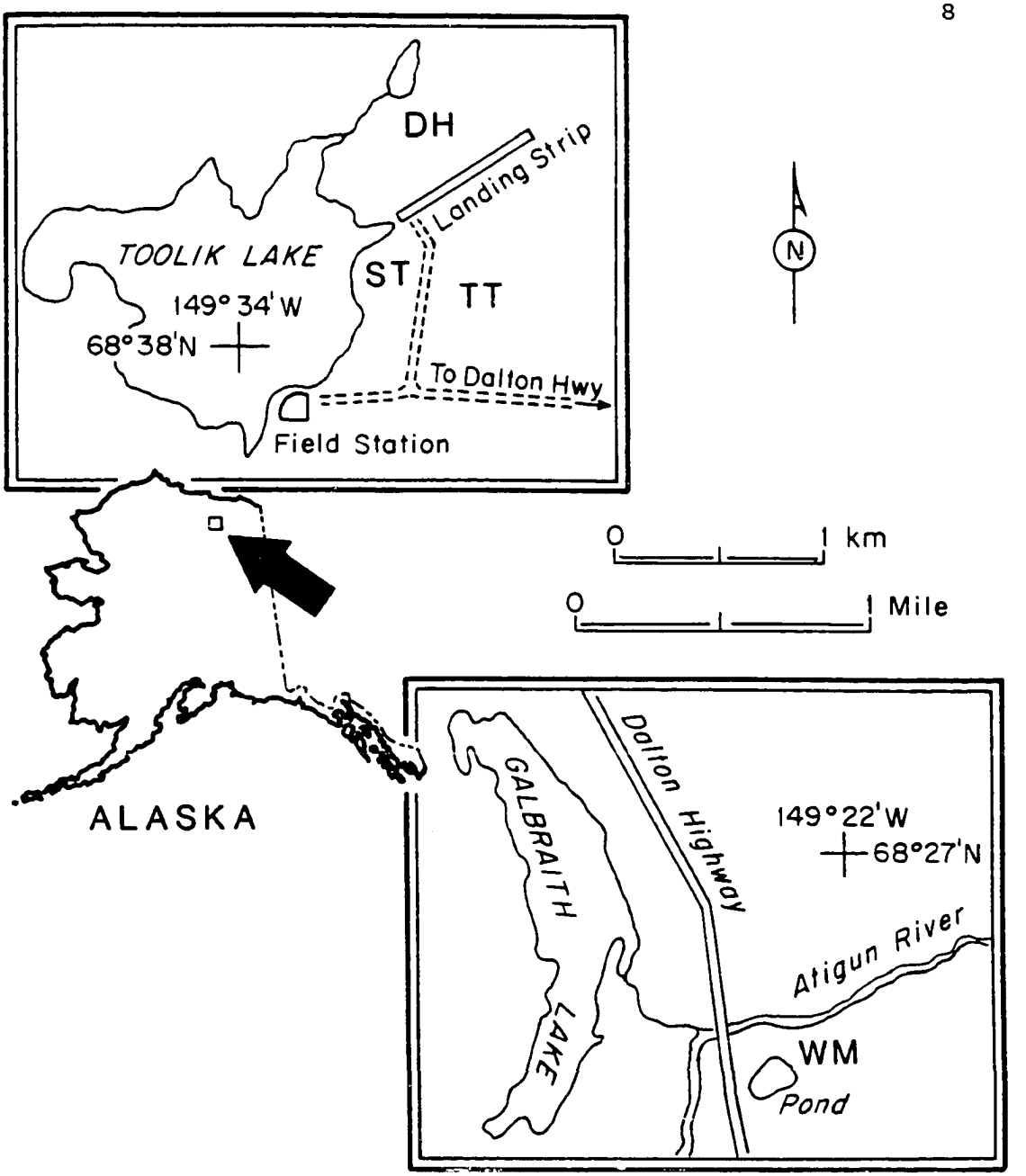

Fig. 1-1. Map over the study area showing the location of the study sites. Community designations are: DH= dry lichen heath, WM= wet meadow, TT= tussock tundra, and ST= shrub tundra.

149°34'W, elevation 760 m), and the fourth approximately 18 km south of Toolik Lake, on a former floodplain of the Atigun River (68°27'N, 149°22'W, 850 m elevation).

Climatic data collected from Barrow, Alaska, by the National Oceanic and Atmospheric Administration over the last 30 years show winter (October-April) temperatures to average between -28 to -18°C and summer (May-September) temperatures to average -7 to 4°C (Local Climatological Data, Monthly Summary, NOAA, 1988). There are no long term (30+ years) climate data from the North Slope except from the coast. Climatological data from Toolik Lake collected in 1986 and 1987 (Murray et al. 1989) show air temperatures to range between 0-20°C during the active growing season (June-August) with a seasonal average of about 12°C. Annual precipitation during this period averaged about 130 mm.

Soils within the study areas are Histosols (wet meadow), Inceptisols (tussock tundra), and Mollisols (lichen heath and shrub tundra).

Three of the four communities are characterized by the dominance of one of the major vascular growth forms of arctic Alaska. The first site, the dry lichen heath, was dominated by the evergreen shrubs Ledum palustre and Loiseleuria procumbens. The soil in this community is predominantly Pergelic Cryoborolls (Rieger et al. 1979)

characterized by a thin organic horizon and a sandy mineral horizon underlain by gravel. The second community, shrub tundra, was also dominated by a single growth form. This community is typically found on the gravel bars along rivers throughout the Brooks Range and the North Slope of Alaska (Robus 1981) and is composed primarily of deciduous shrubs such as Salix pulchra and S. glauca. Despite its importance as feeding habitat for several large herbivores, especially moose and caribou (LeResche et al. 1974, Kuropat and Bryant 1980), this ecosystem has received little attention as to its functional characteristics. This soil is classified as Pergelic Cryaquolls and, like the heath soil, is also underlain by a rocky subsoil.

The third vegetation type, a wet sedge meadow ecosystem located near Atigun River, is dominated by the sedges Carex aquatilis and Eriophorum angustifolium, and is similar in structure to the tundra of the arctic coastal plain of Alaska. This ecosystem type has been intensively studied near Barrow, Alaska (Brown et al. 1980). Soil frost phenomena (e.g., ice wedge polygons), that are common at the coastal plain, were absent at Atigun River. The soil is mostly Pergelic Cryofibrists characterized by a thick peaty organic horizon over a silty mineral soil.

The fourth ecosystem, tussock tundra, has vegetation typical of the northern and part of the southern foothills of the Brooks Range (Walker et al. 1989). In this system, graminoids, evergreen shrubs, and deciduous shrubs occur in approximately equal proportions (Chapin and Shaver 1985). The soil is classified as Histic Pergelic Cryaquept (Rieger et al. 1979). Soil frost activity is common, accounting for disruptions in the organic soil. These four ecosystems represent the major vegetation types of arctic Alaska (Murray 1978, Webber 1978) and span the range of net primary productivity and species composition of this geographic region. The growth form of the dominant species and selected soil characteristics of these ecosystems are presented in Table 1-1.

Sampling procedures

Ten replicate soil samples were randomly collected with a 6.5 cm diameter soil corer from the organic (O2) horizon of each of the four communities. Because of the spongy nature of these soils, thickness of the organic horizons was measured after cutting trenches in the soil with a serrated knife to avoid compaction. Similarly, samples for bulk density were obtained by cutting rectangular blocks of soil of the entire organic horizon.

Table 1-1. Dominant species and selected soil characteristics of four tundra communities near Toolik Lake, Alaska. Community designations are DH = dry lichen health, WM = wet meadow, TT = tussock tundra, and ST = deciduous shrub tundra.

Community	Major Growth Form	Major species	Mean depth of organic soil (cm)	Maximum depth of thaw (cm)
DH	Lichens and evergreen shrubs	Cetraria cuculata C. islandica Loiseleuria procumbens Ledum palaustre	3	20*
WM	Graminoids	Carex aquatilis Eriophorum angustifolium	12	50
TT	Mixed growth forms	Eriophorum vaginatum Salix pulchra Betula nana Ledum palustre Vaccinium vitis-idea	19	40
ST	Deciduous shrub	Salix pulchra Betula nana	10	30*

* Soil probe impeded by rocks beyond this depth.

Extractable nitrogen

The extractable (exchangeable) nitrogen fractions examined in this study were nitrate, ammonium and soluble organic nitrogen. Sampling methods were identical to those for total nitrogen, and the sample sizes were eight for each fraction. These fractions were sampled three times over the growing season: immediately following thaw in early June, in mid-July, and in late August just prior to freeze-up in 1985.

Laboratory methods

To determine bulk densities, samples of known volume were oven-dried at 67° for at least 48 h, weighed and the value expressed as g dry soil cm^{-3}. Horizon thickness, bulk density, soil organic matter and total nitrogen concentration were used to calculate pools of total carbon and nitrogen in the organic soil horizon of each community. Soil pH was determined on a saturation paste using a PHM64 Research pH meter. Cation exchange capacity (CEC) was estimated from the relationship between soil organic matter content and CEC in coastal tundra (Gersper et al. 1980).

Organic matter content was determined by mass loss, following combustion of oven-dried samples at 400°C. Organic carbon was estimated by assuming carbon was 48% of

the volatile material (Vitousek et al. 1982). Carbohydrate fractions (cellulose, lignin, and neutral detergent fiber) were determined by the Van Soest Method (Goering and Van Soest 1975) at the Agricultural Research Station in Palmer, Alaska. Nitrogen was determined on 100 mg oven-dried samples (67°C) by a MacroKjeldahl method (Bremner and Mulvaney 1982) and assayed colorimetrically with salicylic acid (Technicon Industrial Method no. 334-77W).

Extractable nitrogen

Concentrations of extractable ammonium and extractable nitrate were determined by extracting samples of 10 g wet mass with 75 ml 2M KCl under slow shaking action for one hour (Bremner and Mulvaney 1982). The extracts were suction-filtered and analyzed colorimetrically on a dual channel Technicon II Autoanalyzer System. Ammonium was measured by a modification of the phenol-hypochlorite method (Whitledge et al. 1981). Nitrate determinations were made after reducing nitrate to nitrite by passing the extract through a column packed with copperized cadmium. Total nitrite was then determined by the Griess reaction and Technicon Industrial Method no. 100-70W. Soluble organic nitrogen was determined by digesting the KCl extracts with

concentrated sulphuric acid using a modified MacroKjeldahl method (Bremner and Mulvaney 1982) and calculated by subtracting the extractable ammonium concentration from the total ammonium concentration after digestion.

Statistical analysis

Data analyses were performed using SAS statistical package (SAS Institute 1985) on an IBM personal computer. Deviations from normality were tested using the Shapiro-Wilk's statistic. The GLM procedure of SAS was used to perform one-factor and two-factor analyses of variance (Zar 1974). When the GLM procedure showed statistical significance, the Student-Newman-Keul or Scheffe's tests (Neter and Wasserman 1974) were used to separate differences among categories.

Within the research design of the present study, samples from each community types were collected from an area no larger than 1 ha. Although the samples were randomly located within the study area and replicated, only one site per community type was studied. The lack of multiple study sites per community constitutes pseudoreplication (Hurlbert 1984), which limits the conclusions to the study sites which I sampled. I have carried out significance tests on the experimental data,

but I recognize that there are differing views regarding the validity of such tests when study sites are not replicated.

Results

Carbon and total nitrogen

Organic matter concentrations in the four communities studied ranged nearly two-fold across ecosystems from 56.6% in the dry heath to 98.9% in tussock tundra (Fig. 1-2a). The differences in organic carbon pools among ecosystems are magnified when expressed on g m^{-2} basis by horizon (Fig. 1-2b), primarily due to the differences in organic horizon depth (Table 1-1). The dry matter composition of the organic soil horizon is presented in Fig. 1-3. Hemicellulose and neutral detergent solubles (largely soluble carbohydrates, organic acids and other cell contents) made up the largest proportions of the organic constituents of the soil organic matter. The highest concentration was found in the graminoid-dominated wet sedge meadow (60%) and the lowest in shrub tundra (35%), dominated by willows (Salix spp) and dwarf birch (Betula spp). Soil organic matter content correlated positively with cellulose content (r^2=0.70, $p<0.05$, n=10). Among ecosystems, cellulose makes up 10-25% of the soil

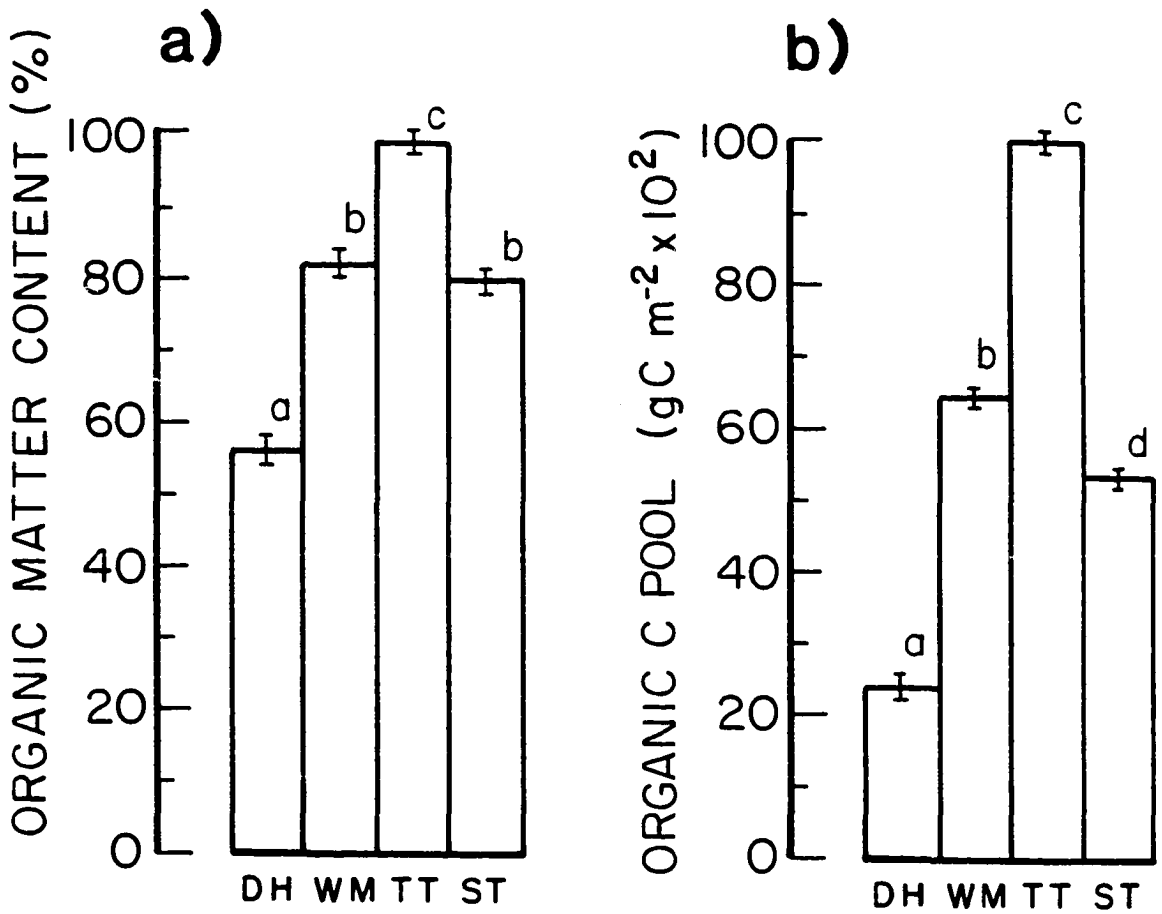

Fig. 1-2. Organic matter content (a) and organic carbon pool (b) in the organic soil horizon of four tundra ecosystems near Toolik Lake, Alaska (mean ± S.E., n=10). Values denoted with the same letter are not significantly ($p<0.05$) different. Community designations as in Fig. 1-1.

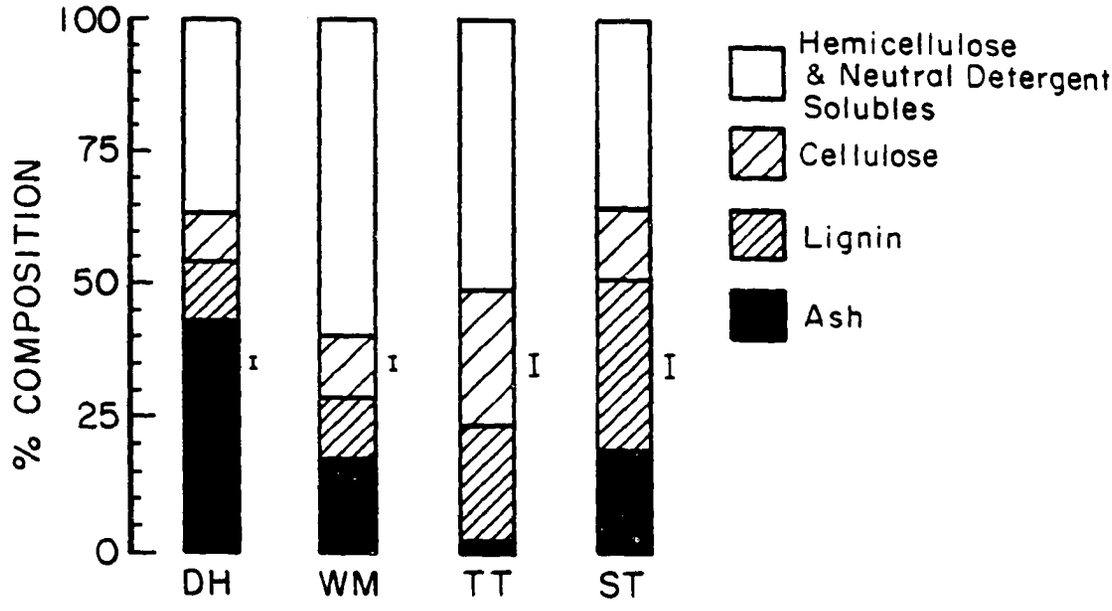

Fig. 1-3. Dry matter composition of organic soil expressed as percent of total organic matter. Largest standard errors indicated. Community designation as in Fig. 1-1.

organic matter. Lignin is another important component of the soil organic matter, which in the communities near Toolik Lake ranged between 11-32%. The lignin profile closely paralleled that of cellulose in all but the shrub community. Not surprisingly, the latter ecosystem had significantly higher lignin concentration than any other community, probably as a function of the dominant growth form (deciduous shrubs). These shrubs confer a high lignin input to the soil because of both high stem biomass and rapid woody stem turnover (Shaver 1986). Cellulose and lignin showed roughly the same pattern of significant differences among communities: the shrub community was different from tussock tundra, and these two communities were both different from the dry heath and wet sedge meadow. The latter two communities did not differ significantly from one another in any of these parameters.

Kjeldahl nitrogen ranged from 0.63% in tussock tundra to 1.30% in deciduous shrub tundra (Fig. 1-4a). As with organic matter content, the differences among ecosystems in total soil nitrogen are magnified when expressed as g m^{-2} (1-4b), due both to differences in horizon depth and in soil bulk density. The lowest total soil nitrogen pool was found in the heath community (90 g m^{-2}) and the highest in wet sedge tundra (245 g m^{-2}).

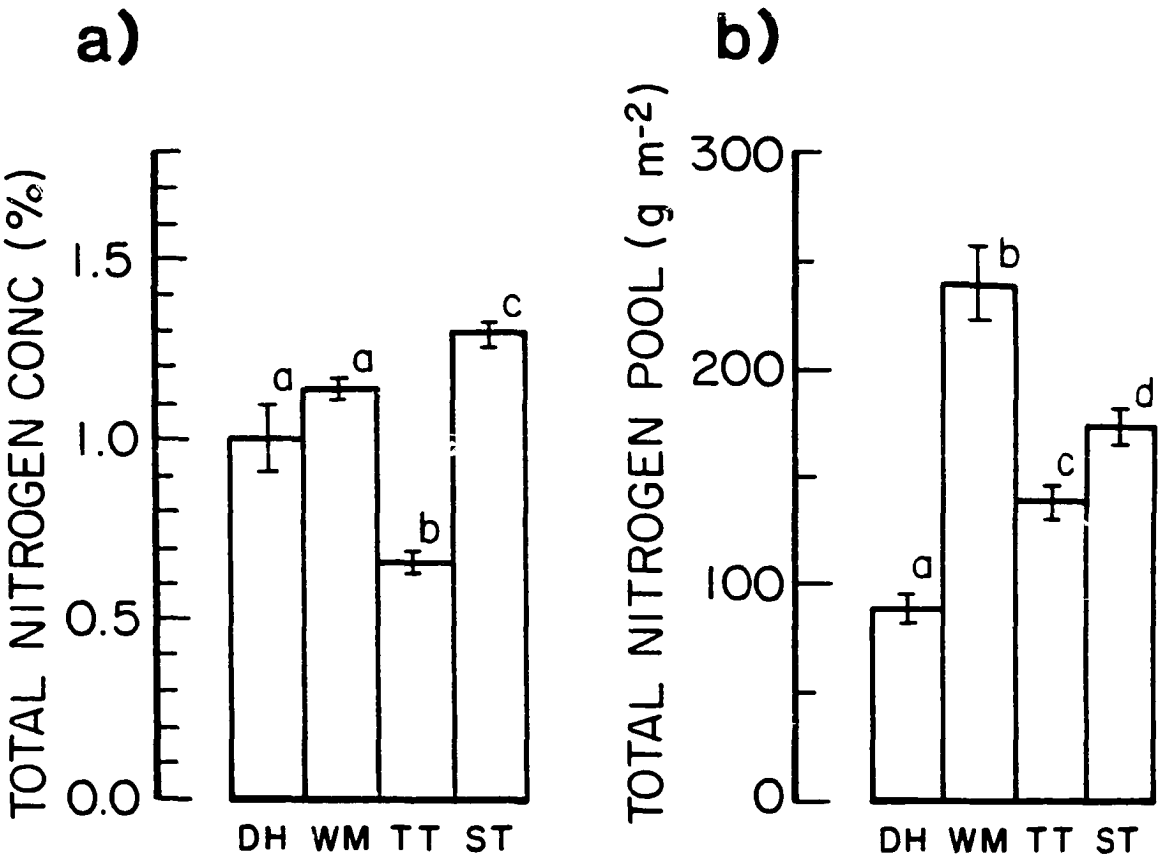

Fig. 1-4. Total (Kjeldahl) nitrogen concentration (a) and total nitrogen pool (b) in the organic soil horizon (mean ± S.E., n=10). Community designation and significance as in Fig. 1-2.

Extractable nitrogen

The concentrations of extractable nitrate, ammonium, and soluble organic nitrogen together constituted less than 1% of total soil nitrogen. That is, in these four ecosystems over 99% of the total soil nitrogen is tied up in the soil organic matter. Of the extractable nitrogen fractions, nitrate concentrations were by far the lowest in each ecosystem (Fig. 1-5a). There was a relatively high concentration of nitrate in shrub tundra in June (2.43 ug g^{-1}), but this concentration was still nearly an order of magnitude less than the ammonium concentration determined at this date (22.65 ug g^{-1}). The highest seasonal mean concentration of nitrate was found in shrub tundra (1.06 ug g^{-1}), and the lowest in the dry lichen heath (0.37 ug g^{-1}). Soil nitrate concentrations differed significantly ($p<0.05$) among all sampling dates in each ecosystem. The highest values were found in early June. Concentrations then dropped precipitously in July, and rose again in August to approximately 30% of June levels (Fig 1-5a). These large seasonal fluctuations attest to the labile nature of this form of nitrogen.

As was the case for nitrate, the shrub community exhibited the highest concentration of ammonium (13.95 ug g^{-1}), and dry lichen heath showed the lowest concentration (1.42 ug g^{-1}) (Fig 1-5b). The shrub community showed the

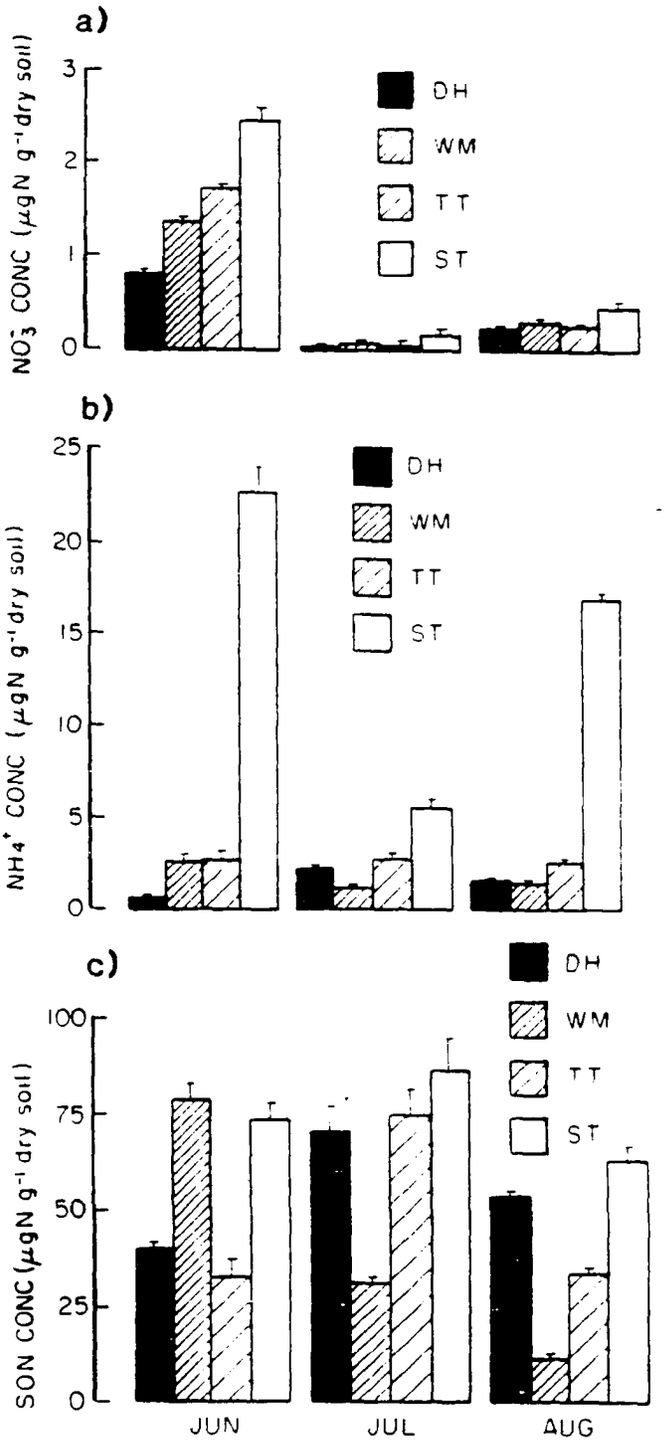

Fig. 1-5. Seasonal concentrations of (a) nitrate, (b) ammonium, and (c) soluble organic nitrogen (mean ± S.E., n=8).

same pattern of seasonal change in ammonium concentration as as it did for nitrate. The dry lichen heath, on the other hand, showed the opposite seasonal trend. In this community, ammonium concentration was lowest in June and highest in July. In both shrub tundra and dry lichen heath the ammonium concentrations differed significantly ($p<0.05$) from one another at all sampling dates, albeit to a lesser extent than they did for nitrate. In contrast, neither the wet sedge meadow nor tussock tundra showed any significant seasonal fluctuations in ammonium concentrations.

Soluble organic nitrogen represented the largest pool of exchangeable nitrogen in any community at any time during the growing season (Fig. 1-5c), making up approximately 90% of the total extractable nitrogen. Again, shrub tundra had the highest seasonal mean concentration (74 ug g^{-1}), whereas the lowest concentration was found in the wet meadow (40 ug g^{-1}). The seasonal pattern of soluble organic nitrogen showed an intermediate level of variation relative to nitrate and ammonium. Except for high June values in the wet meadow, the concentrations of soluble organic nitrogen rose from early spring to mid-season, followed by a decline in the fall to approximately the initial spring concentrations. These patterns of seasonal fluctuations are very similar

to those reported for inorganic nitrogen in the soil solution at Point Barrow, Alaska (Flint and Gersper 1974).

Within a given community, the pattern of significant differences in concentration among nitrate, ammonium, and soluble organic nitrogen differed across the season. Moreover, these seasonal patterns differed among communities as well. For instance, in tussock tundra ammonium and nitrate concentrations were not significantly different from one another in June, although they were both significantly lower than the concentration of soluble organic nitrogen. When sampled in August, all fractions differed significantly from one another. In contrast, these fractions were all significantly different in the shrub community at both of the above sampling dates. A two-factor analysis of variance showed a highly significant ($p<0.001$) date*fraction interaction (Table 1-2), supporting the inferences drawn from the one-factor ANOVAs.

The seasonal mean concentrations of nitrate, ammonium, and soluble organic nitrogen are shown in Fig. 1-6. These averages give a general picture of the relative nutrient concentration among communities. Both nitrate and ammonium show the same pattern of differences among the communities: shrub tundra>tussock tundra>wet sedge meadow>dry lichen heath. The concentration of

Table 1-2. Results from two-factor analysis of variance on soil nitrogen concentration by date and fraction (nitrate, ammonium, and soluble organic nitrogen). Significant F values denoted by symbls: n.s., $p>0.05$; **, $p<0.01$.

Source	DH	WM	TT	ST
Date	11.46^{**}	64.07^{**}	13.84^{**}	$2.37^{n.s.}$
Fraction	365.00^{**}	304.10^{**}	209.85^{**}	413.28^{**}
D*F	11.02^{**}	66.40^{**}	15.17^{**}	8.32^{**}

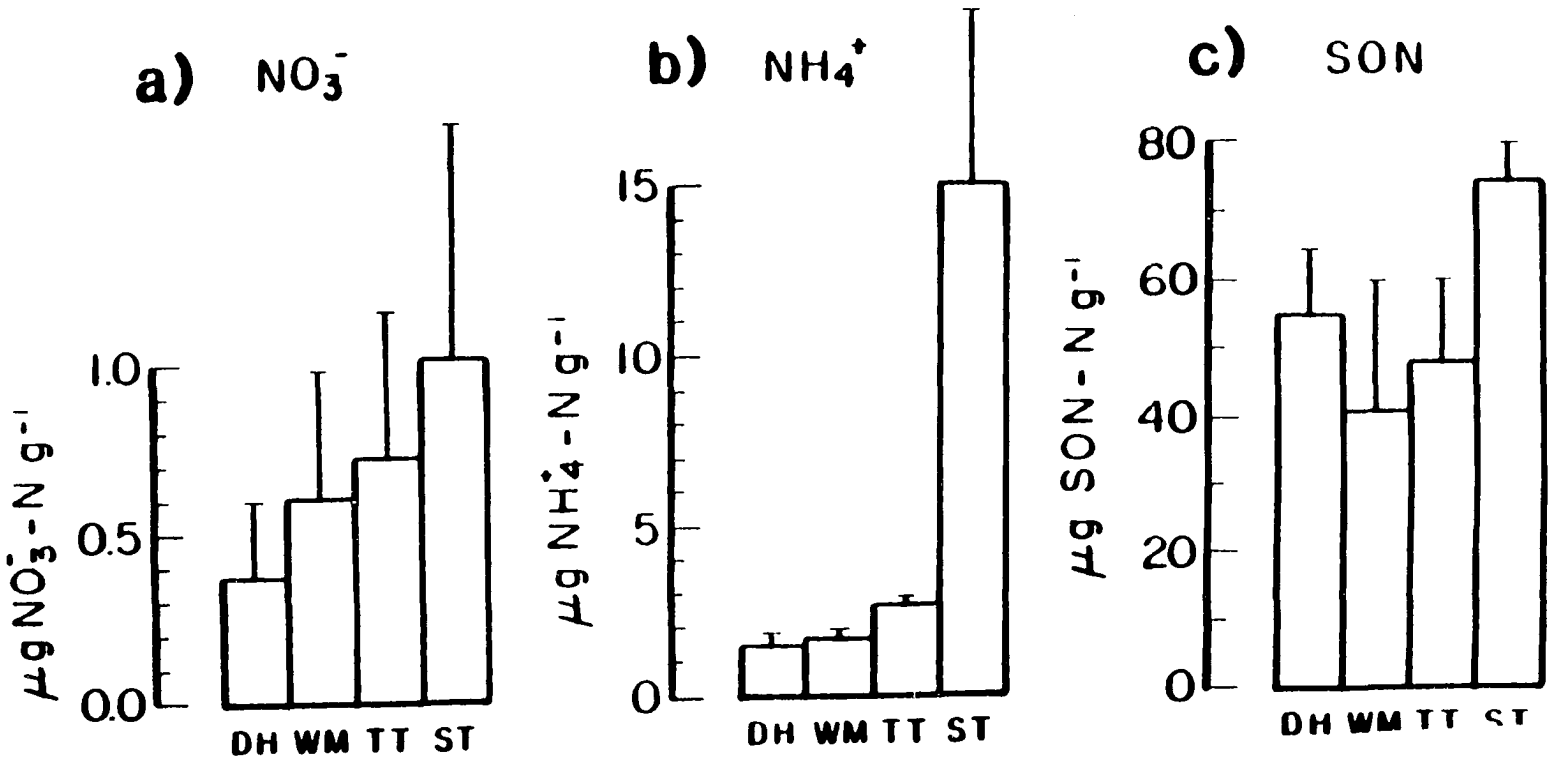

Fig. 1-6. Seasonal mean concentrations of (a) nitrate, (b) ammonium, and (c) soluble organic nitrogen based on three sampling dates (mean ± S.E., n=3).

soluble organic nitrogen, on the other hand, was greatest in the shrub-dominated ecosystem and lowest in the wet sedge meadow where no woody species occured.

Discussion

The high organic matter content of arctic tundra soils is due to a combination of factors (low soil temperature, high soil moisture, short active season, etc.) that reduce the rate and extent of decomposition to a greater degree than net primary production. This characteristic feature of arctic tundra confers important structural and physico-chemical properties upon the soils such as stability of soil aggregates, water-holding capacity, cation exchange, and energy supply to microorganisms (Bohn et al. 1982). For instance, high organic matter content is correlated with reduced bulk density (Fig. 1-7) and increased water-holding capacity. In the coastal tundra at Barrow, Alaska, soil moisture and bulk density can account for 66% of the variation in soil thaw depth (Gersper et al. 1980). Thus, at the ecosystem level, organic matter content is a major element defining the soil energy budget. The close correlation (r^2=0.94) between organic carbon concentration and cation exchange capacity (Gersper et al. 1980) implies that the organic

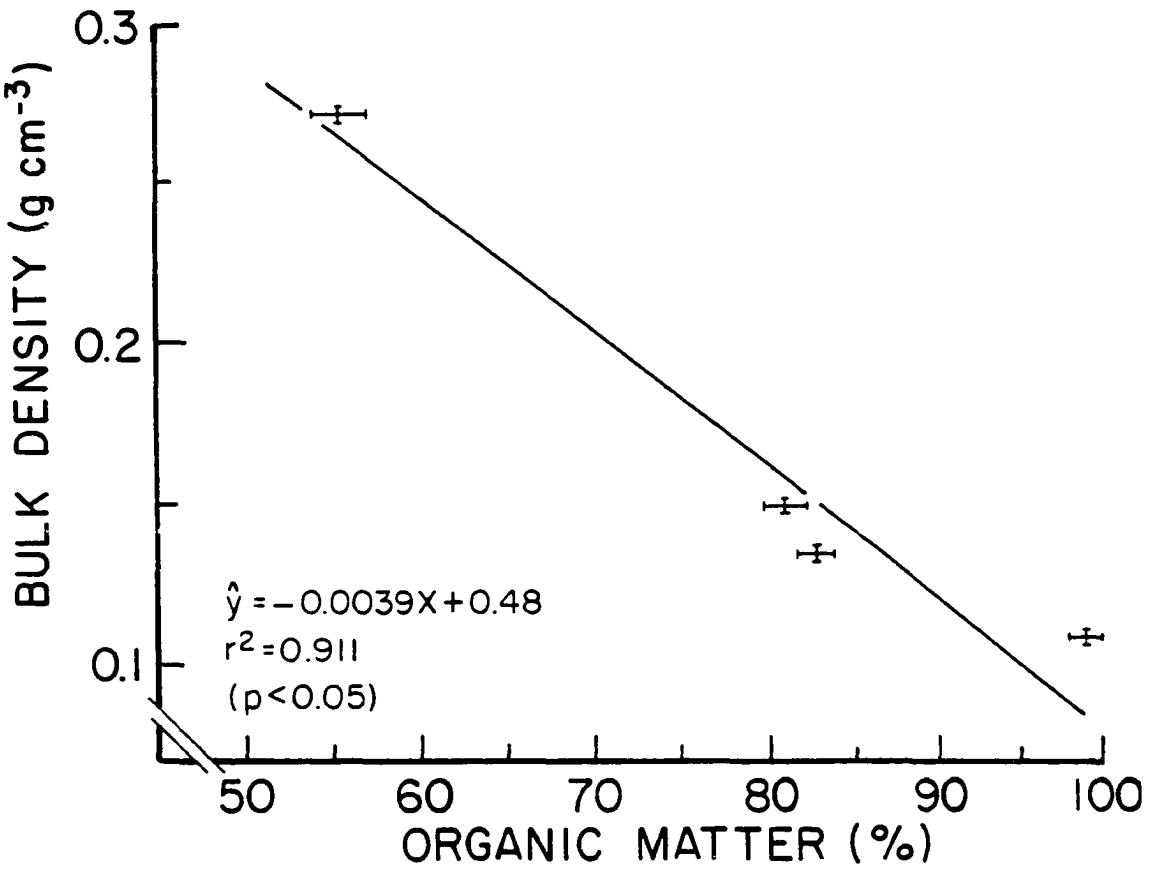

Fig. 1-7. Relationship between percent organic matter and bulk density of the organic soil horizon in four tundra communities near Toolik Lake, Alaska.

soil horizon represents an important reservoir of exchangeable cations such as ammonium, potassium, calcium, and magnesium. The estimated CEC of the soils near Toolik Lake investigated in this study ranged from 74-118 meq 100 g^{-1} (Table 1-3), which is far above that of most mineral soils (Brady 1974).

Soil organic matter composition is an important control over (and result of) decomposition and nutrient release in many ecosystems (e.g., Aber and Melillo 1982), but up until now there has been no detailed published data on soil carbon fractions from arctic tundra. The differences in organic matter composition are primarily due to differences in the rates of input of the various carbon fractions. For instance, the graminoid-dominated wet meadow exhibited low lignin concentrations but high levels of neutral detergent solubles (NDF) plus hemicellulose (Fig. 1-3). In contrast, in the shrub tundra, where deciduous shrubs made up more than 90% of the total biomass, lignin concentrations were correspondingly high and NDF levels low (Fig. 1-3).

The factors accounting for the accumulation of dead organic matter in arctic tundra ecosystems are also responsible for the high total nitrogen content found in these soils. Although tundra plants have relatively high tissue nitrogen concentrations (Chapin 1980, Chapin 1982),

Table 1-3. Selected soil physical and chemical properties of diverse circumpolar tundra ecosystems.

Ecosystem	Latitude	Location	Horizon	Organic carbon (%)	Kjeldahl N (%)
Lichen heath	68°	Toolik Lake	O2	27.2	1.0
Wet sedge tundra	68°	Toolik Lake	O2	39.6	1.1
Tussock tundra	68°	Toolik Lake	O2	47.5	0.6
Deciduous shrub tundra	68°	Toolik Lake	O2	38.8	1.3
Wet sedge tundra	71°	Barrow	O2	20.0	1.0
Sedge madow	75°	Devon island	Of2	42.2	2.7
Peaty bog	73°	Taimyr USSR	A_T	50.9	0.6
Lichen heath	60°	Hardanger-vidda, Norway	A_O	17.3	0.7
Wet meadow	60°	Finse, Norway	A_O	44.4	2.1
Peat bog	68°	Stordalen, Sweden	O2	45.8	1.2

Table 1-3 continued.

pH	CEC (meq 100 g^{-1})	Bulk density (g cm^{-3})	Soil field moisture (% vol)	Ref.
4.7	74	0.27	60	1
6.3	100	0.13	90	1
3.7	118	0.14	85	1
5.9	99	0.15	75	1
5.4	59	0.51	69	2
6.2	125	0.20	70	3
5.8	59	n.d.	n.d.	4
4.0	49	0.6	20	5
5.3	102	0.14	90	5
4.1	n.d.	0.69	85	6

Ref.

1) This study
2) Gersper et al. 1980
3) Babb and Whitfield 1982
4) Vassiljevskaya 1972
5) Wielgolaski 1975
6) Rosswall 1975

most of the nitrogen returned to the soil is incorporated into recalcitrant fractions (e.g. humic and fulvic acids). The low rates of decomposition (Flanagan and Veum 1974) and denitrification (Alexander et al. 1973) in tundra systems result in very slow turnover and consequently accumulation of soil nitrogen.

Extractable nitrogen

Despite large spatial and temporal variations, it is clear that in the tundra soils of northern Alaska both bound (structural) and extractable nitrogen are dominated by organic forms. Ammonium is the dominant form of inorganic nitrogen. Nitrate is uniformly low in these ecosystems, because the soils are relatively acidic and nitrifying microorganisms tend to be inhibited below pH 5 (Brock 1980). Moreover, ammonification appears to be less temperature-sensitive than nitrification (Haynes and Goh 1978), further contributing to the difference in concentration between ammonium and nitrate.

The magnitude of the seasonal fluctuations of each fraction is related to both biological and chemical processes. The biological processes include transformation and incorporation into other soil nitrogen compartments. The chemical processes include primarily exchange reactions on the soil organic matter. Since it

is negatively charged, nitrate is not held by the cation exchange complex but exists largely dissolved in the soil pore water. Ammonium on the other hand is positively charged at most pHs of tundra soils (pK_a=9.4), and thus a large fraction is held as adsorbed cations. The ions on the exchange surfaces represent a reservoir that may buffer fluctuations of ammonium ions in the soil solution. Hence the seasonal fluctuations of this form of nitrogen are less pronounced. The soluble organic nitrogen fraction consists of several chemical species, some of which may participate in cation exchange reactions (e.g. some of the free amino acids), but as a whole this heterogeneous fraction shows greater seasonal variation than does ammonium.

I conclude that in the four northern Alaskan ecosystems I examined, the composition of selected carbon and nitrogen fractions of the soil organic matter is associated with the growth form composition of the vegetation. High organic matter content dominates the soil profile of the principal rooting horizon, with which other soil properties (e.g. bulk density and cation exchange capacity) are closely correlated. This characteristic holds for several circumpolar ecosystems (Table 1-3). In this comparison, the ecosystems near Toolik Lake take on largely intermediate values. It is

noteworthy in this context that the latter ecosystems nevertheless show an impressive variation in many soil parameters. Thus total organic carbon and total nitrogen both vary approximately 2-fold among sites. With repect to the organic carbon fractions, cellulose varies over 2-fold and lignin 3-fold. As regards extractable nitrogen, nitrate varies by nearly a factor of three, ammonium by a factor of about ten, and soluble organic nitrogen varies by a factor of nearly two across the ecosystems I examined. I suggest that generalizations regarding the structure and function of arctic tundra ecosystems should be made with the diversity of both growth form composition and fundamental soil properties borne in mind.

CHAPTER TWO: CONTROLS OVER DECOMPOSITION AND NITROGEN RELEASE.

Introduction

Suboptimal supply of nitrogen for plant growth is a common feature of ecosystems over a wide range of climatic conditions (Chabot and Mooney 1985). Despite this characteristic, the pool sizes, fluxes, and turnover of nitrogen vary greatly among natural ecosystems (Clark and Rosswall 1981). This is true even within the arctic biome, and every study to date of arctic ecosystems has concluded that nutrients, in particular nitrogen supply, limits net primary production (Chapin and Van Cleve 1978, Chapin 1987). It is not clear, however, what factors control nitrogen supply to plants. Arctic ecosystems show an impressive variation in many important plant community characteristics (e.g., species composition, growth habit, phenology etc.) and soil parameters (e.g., total carbon and nitrogen, exchangeable nitrogen pools, cation exchange capacity, pH, moisture content and temperature), suggesting that the controls over nitrogen supply may differ among communities as well. The present study focused on identifying the salient physico-chemical controls over nitrogen dynamics in four contrasting plant

communities in arctic Alaska, and on determining the relationship between plant productivity and nitrogen availability.

Nitrogen availability is best defined by the concentration of nitrogen at the root surface. However, because it is very difficult to measure this concentration under field conditions, nitrogen availability is generally defined in terms of soil nitrogen pools, the rate at which nitrogen is released from decomposing organic matter, or by the amount of nitrogen taken up by plants annually (Vitousek and Matson 1985, Nadelhoffer et al. 1985). Nitrogen release from dead organic matter, mineralization, is affected by several factors such as soil moisture, temperature, and the quantity and composition of the decomposing substrate. Since low temperature is such a conspicuous feature of the arctic environment, the role of temperature in controlling ecosystem functions in this biome has received considerable attention. Several ecosystem processes are apparently controlled by temperature, e.g., soil respiration (Flanagan and Veum 1974), nitrogen fixation (Kallio et al. 1972), and plant nutrient uptake (Chapin and Bloom 1976). Thus, one aspect of the present research addressed the importance of temperature in controlling nitrogen release in the prevailing cold soils of northern

Alaska. In addition, the relative effect of carbon and nitrogen limitation of microorganisms on nitrogen mineralization was evaluated through soil amendment experiments. This study was focused around three main questions: 1) How sensitive are decomposition and net nitrogen release in arctic tundra to temperatures within the normal range? 2) Is nitrogen release in different arctic tundra communities equally controlled by the same set of factors (e.g., temperature, pH, organic matter quality), or are some factors more important in some communities than others? 3) What are the common characteristics of nitrogen release in Alaskan arctic tundra?

To date research on nitrogen cycling in arctic tundra has largely focused on decomposition studies and plant growth measurements from which rates of nitrogen cycling were calculated. Few studies of arctic tundra have measured net nitrogen mineralization directly. In the present study I measured nitrogen and carbon mineralization in the field and in the laboratory under a variety of conditions. Coupling the dynamics of carbon and nitrogen allowed me to draw inferences about the rates and controls over decomposition in general and nitrogen release in particular.

Methods

Research sites

This research was carried out in four contrasting ecosystems near Toolik Lake, Alaska (68°38'N, 149°34'W, elevation 760 m). The four vegetation types: dry lichen heath, wet sedge meadow, tussock tundra, and deciduous shrub tundra are described in Chapter 1. Biomass and aboveground net primary production of each ecosystem were measured by G. R. Shaver and F. S. Chapin (unpublished) and are shown in Table 2-1.

Carbon dynamics

Decomposition potentials were measured in the four communities using litter bag and soil respiration experiments. The litter bag experiment was designed to measure rates of cellulose decomposition. Discs of No. 1 Whatman filter paper were cut into 1 x 5 cm strips and enclosed in polyester mesh bags (Rosswall 1974). Each bag measured approximately 15 x 15 cm, had a mesh size of 2 mm, and contained about 320 mg of material. The bags were buried in the soil at a 30° angle in the O2 horizon (5-15 cm depth). Twenty bags were placed in each community at

Table 2-1. Biomass of vascular plants and aboveground net primary production in each community. Data collected by Shaver and Chapin (personal communication). Community designations are: DH= dry lichen heath, WM= wet meadow, TT= tussock tundra, ST= deciduous shrub tundra.

	DH	WM	TT	ST
Biomass (g m^{-2})	108	90	337	920
Aboveground vascular net primary production (g m^{-2} yr^{-1})	32	51	144	303

the beginning of the growing season (early June). From each community 10 bags were retrieved at the end of the first growing season (three months incubation), and the remaining bags following the second growing season (15 months incubation). The fractional mass loss, F, (Fox and Van Cleve 1983), of each bag was calculated as initial dry mass minus final dry mass, divided by initial dry mass.

Measurements of soil respiration were made using Gilson respirometry according to standard methods (Umbreit et al. 1964). Ten soil samples per community of approximately 2 g wet mass each were placed in standard 15 ml reaction flasks. The flasks were stoppered, sealed with vaseline, and allowed to equilibrate for 1 h after they had been attached to the respirometer (Van Cleve et al. 1978). Moisture content was determined for each individual sample. Respiration rate of the soil from each community was measured at field moisture content at the ambient soil temperature of that community (1-7°C, determined at the time of sampling) and at 10°C and was expressed on a dry mass basis as ug CO_2 g^{-1} h^{-1}. Manometer readings were taken every 30 min, and the respiration rate was calculated from a mean of six readings per sample. The temperature sensitivity of soil respiration was evaluated by calculating the Q_{10} for soil

respiration between 10° and the ambient temperature, using the equation $Q_{10}=(R_2/R_1)^{10/(T_1-T_2)}$, where R_2 and R_1 are the observed respiration rates at temperatures T_2 and T_1 respectively (Schmidt-Nielsen 1975).

Nitrogen dynamics

Field experiments

Measurements of net nitrogen mineralization in all the field experiments were carried out using the *in situ* buried bag technique (Eno 1960, Westerman and Crothers 1980, Vitousek and Matson 1985). Soil samples were collected with a 6.5 cm diameter soil corer at random points along established transects in each community. Soil from the O2 horizon was enclosed in a 0.8 mil (0.02 mm) polyethylene bag (Presto Products, Inc., Appleton, WI), and incubated in this horizon for four weeks. Subsamples from each core were taken prior to incubation to determine moisture contents and initial KCl-extractable nitrogen (ammonium and nitrate) concentrations. Net mineralization rate was calculated as the increase in extractable ammonium-nitrogen plus nitrate-nitrogen during incubation. Nitrification was calculated from the increase in extractable nitrate-nitrogen during the incubation. The average seasonal mineralization rate was calculated from monthly incubations in June, July, and

August (Nadelhoffer et al. 1984) and expressed as ug N g^{-1} dry soil $week^{-1}$.

Temperature sensitivity experiment

To determine how ambient soil temperature affects nitrogen mineralization under field conditions, soil samples from each community were incubated reciprocally in all four communities, including the community of origin. The samples (n=20 per community) were incubated for three weeks to assure proper temperature equilibration. A bi-hourly temperature profile of the soil in each community, measured with a Campbell 21 data logger between June 26 and July 5 1983, is shown in Fig. 2-1. The relative magnitude of temperature differences among sites remained the same throughout the season (based on measurements coinciding with other soils work), but no systematic measurements of soil temperatures were made after July 15.

^{15}N immobilization experiment

To estimate microbial nitrogen uptake (immobilization), ^{15}N labelled ammonium chloride (99% enrichment) was added to buried bag samples (n=5) in each community. The cores were broken up manually to facilitate uniform mixing of the label. The label itself was added in 5 ml of distilled water (1-5 ug g^{-1}), and

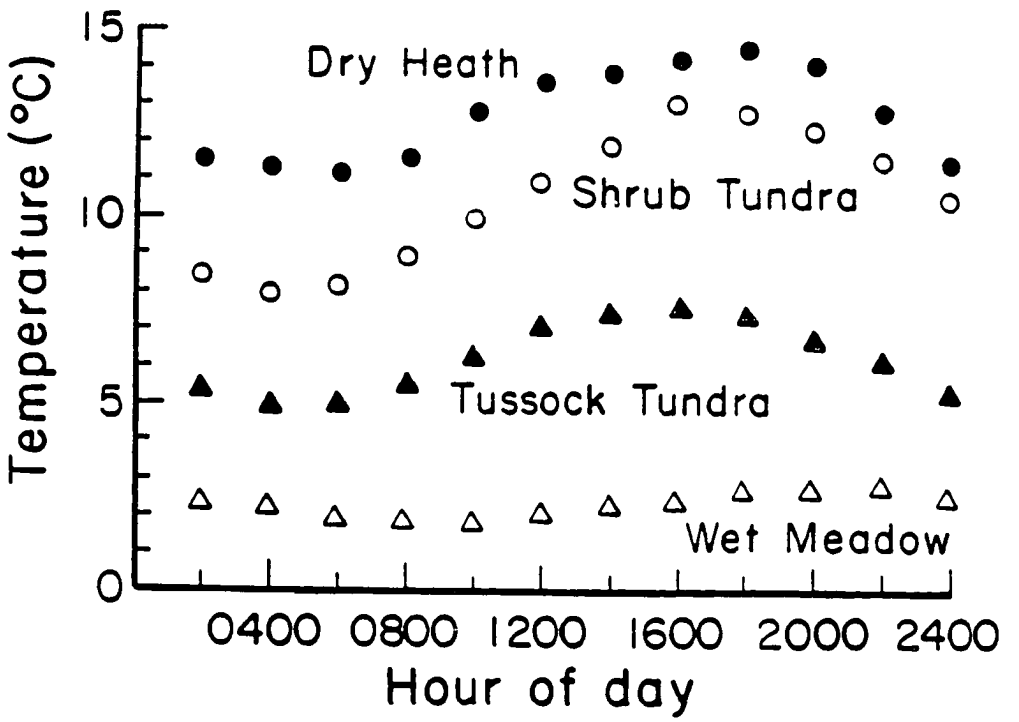

Fig. 2-1. Bi-hourly soil temperature profiles at -10 cm for each community measured between 26 June and 5 July 1983.

the samples incubated for four weeks in the manner described above. This amount of label was approximately 5-20% of the extractable ammonium pool. Immobilization of ^{15}N was calculated from recovery of ^{15}N at the end of the incubation period using standard isotope dilution techniques (Van Cleve and White 1980).

Laboratory experiments

Nitrogen mineralization rate was measured under controlled conditions in the laboratory to (1) determine the temperature sensitivity of net nitrogen mineralization over the temperature range observed in the field; (2) evaluate the relative limitation of energy versus nitrogen of the soil microorganisms through soil amendments of carbon and nitrogen; and (3) determine the effects of disturbance (freeze-thaw cycles) on net nitrogen release. In each of these experiments approximately 20 g wet mass of soil was put in clear plastic cups which were covered with a sheet of polyethylene (made from the bags used in the field experiments) to prevent moisture loss. The cups (n=8 per community) were placed in environmental chambers and incubated at constant temperature and moisture for two weeks. The experimental temperatures were 4°, 8°, 12°, and 16°C. Carbon versus nitrogen limitation of soil microbial activity was evaluated at 12°C. Amendments

consisted of 50 mg corn starch (carbon) or 50 ug ammonium sulphate (nitrogen). These amendments both represented less than 1% increase in the total soil C and N pools. The disturbance experiment involved freezing the samples at -18°C for several days, letting them thaw out at room temperature over night, and then putting them back in the freezer again. This cycle was repeated at regular intervals four times over two weeks. Initial nitrogen concentrations were determined from subsamples and analyzed colorimetrically on an autoanalyzer as described above.

Statistical analysis

Due to greatly heterogenous variances, differences between means were tested using nonparametric one-factor analysis of variance (Kruskal-Wallis test). When this test procedure showed statistical significance, nonparametric multiple range testing was performed to separate the means (Zar 1974).

Results

Soil temperature

Soil temperatures in the two warmest communities (Dry Heath and Shrub Tundra) tended to oscillate more over the

course of a day (Fig. 2-1) than in the colder communities (Tussock Tundra and Wet Meadow), primarly because of lower soil moisture (Chapter 1) in the warmer communities. Further, due to high soil moisture (90%) and delayed thawing of the soil, maximum soil temperatures in the Wet Meadow occured later in the growing season than in the other communities. For example, on June 1 1983, the thaw depth in Dry Heath, Shrub Tundra and Tussock Tundra were 7, 4 and 4 cm respectively, whereas less than 1 cm had thawed in the Wet Meadow (Kielland personal obs_rvation).

Carbon dynamics

Final mass loss of cellulose strips incubated for two growing seasons differed six-fold among communities (Fig. 2-2). The rate of mass loss was relatively constant over the two years. There was no direct correlation between mass loss and soil temperature. The warmest and driest community (Dry Heath) showed the least decomposition (10%), whereas the coldest and wettest community (Wet Meadow) exhibited the second-least mass loss (17%). The greatest mass loss (52%) occurred in the deciduous shrub community. Thus, cellulose decomposition (Fig. 2-2) was better correlated (r^2=0.99) with plant productivity than with either soil temperature or moisture.

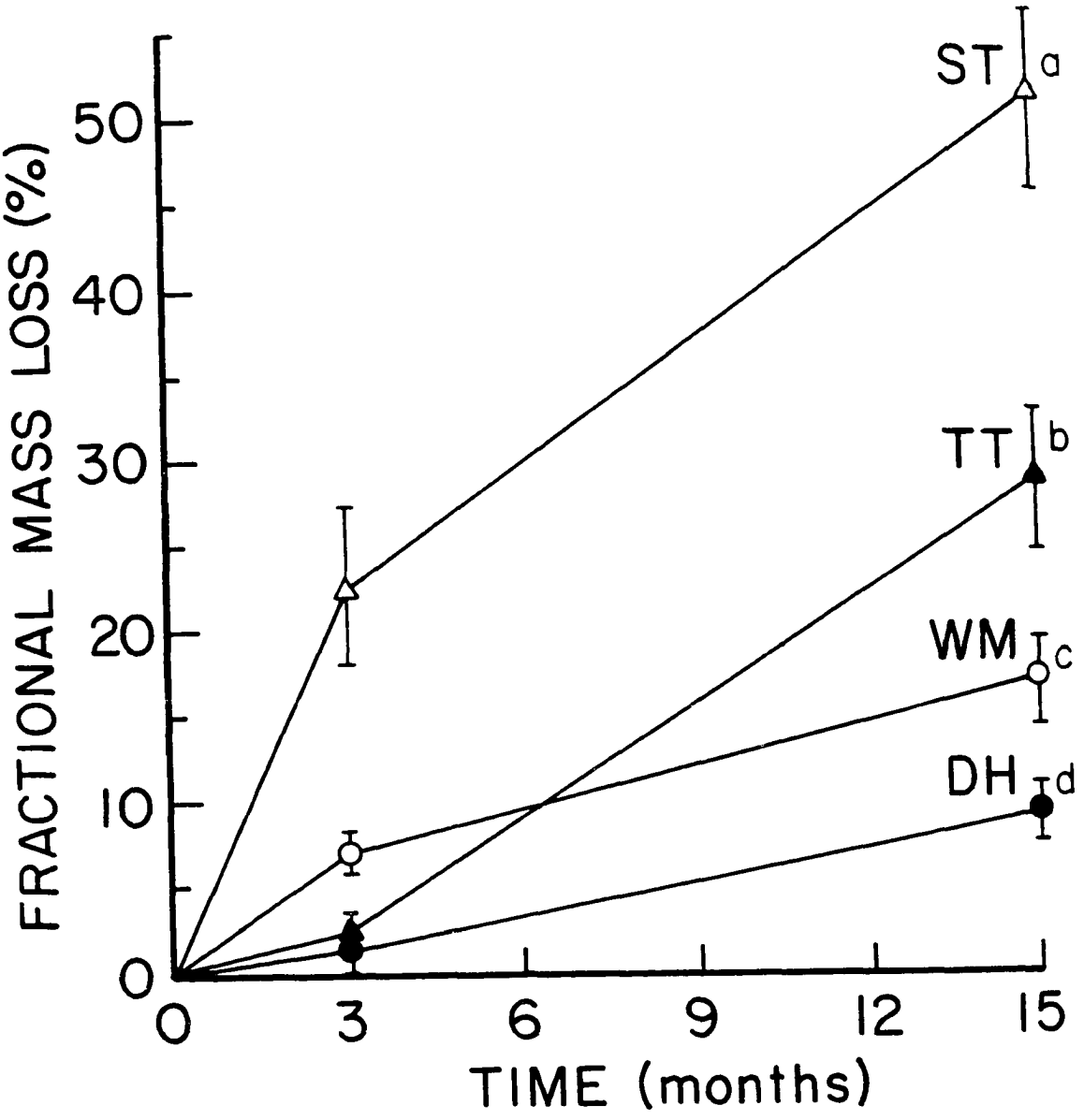

Fig. 2-2. Time course of cellulose decomposition over two growing seasons in four tundra communities near Toolik Lake, Alaska (mean ± S.E., n=10). Values designated with the same letter are not significantly different ($p>0.05$).

The pattern of soil respiration measured at 10° (Fig. 2-3a) paralleled that of cellulose decomposition (Fig. 2-2), being highest in the most productive community (Shrub Tundra) and lowest in the least productive community (Dry Heath). Moreover, respiration rates also differed six-fold among the communities. Soil respiration measurements conducted at 10° and ambient temperatures (1-3°) allowed estimation of apparent Q_{10}. The apparent Q_{10} values calculated for this temperature range were all relatively low, ranging from 1.0-2.0 (Table 2-2). This range of Q_{10} brackets values found in some taiga studies (Flanagan and Van Cleve 1977, Gordon et al. 1987), suggesting that most soil microbes in both taiga and tundra are relatively insensitive to fluctuations in temperature within their normal range.

Nitrogen dynamics

As observed with carbon mineralization (cellulose decomposition and soil respiration), net nitrogen mineralization was highest in the most productive community and lowest in the least productive community. However, the range in average nitrogen mineralization among communities (20X) was much greater (Fig. 2-4a) than the range in either measure of carbon mineralization. The Tussock Tundra and Shrub Tundra showed roughly opposite

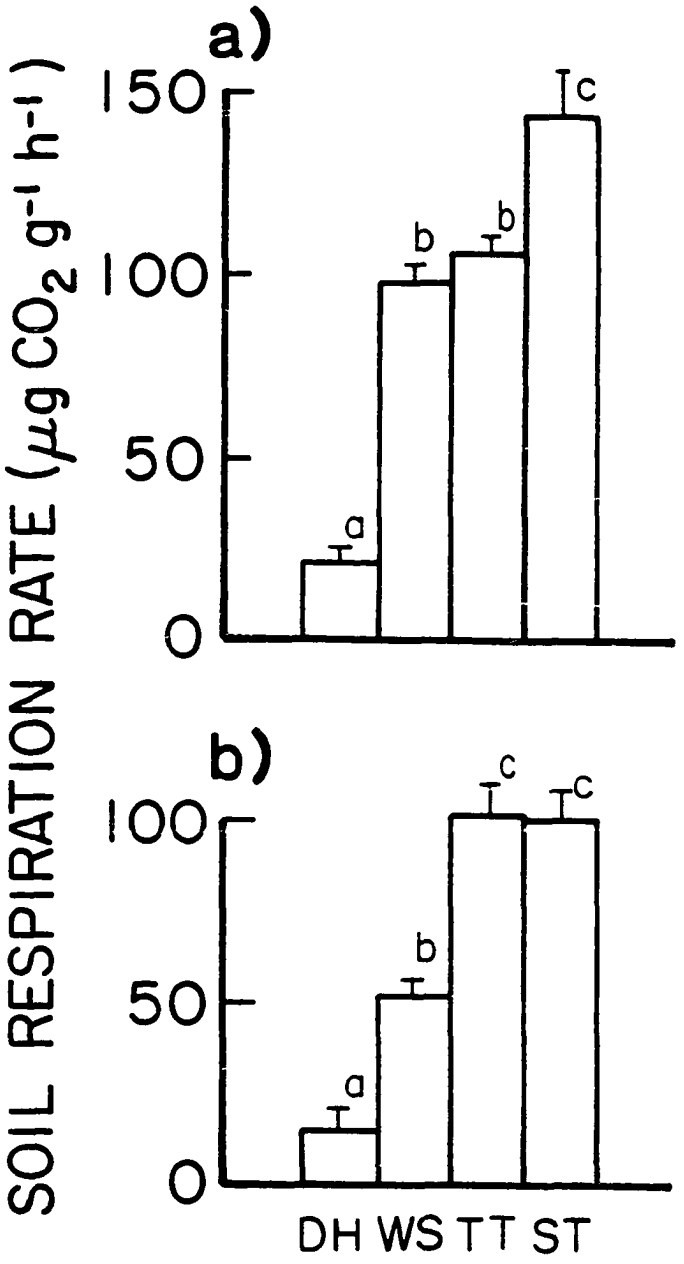

Fig. 2-3. Rates of soil respiration at (a) 10° and (b) ambient temperature (mean ± S.E., n=10). Significance as in Fig. 2-2.

Table 2-2. Temperature sensitivity of soil respiration (Q_{10}) in the organic horizon, and ranges of seasonal soil temperature in each vegetaion type. The temperature range for the dry heath community was not broad enough to justify Q_{10} calculation (*).

Community	Seasonal temperature range	Q_{10}	Temperature interval for Q_{10}
DH	1-20	*	7-10
WM	1-6	2.0	1-10
TT	1-14	1.0	3-10
ST	1-14	1.6	2-10

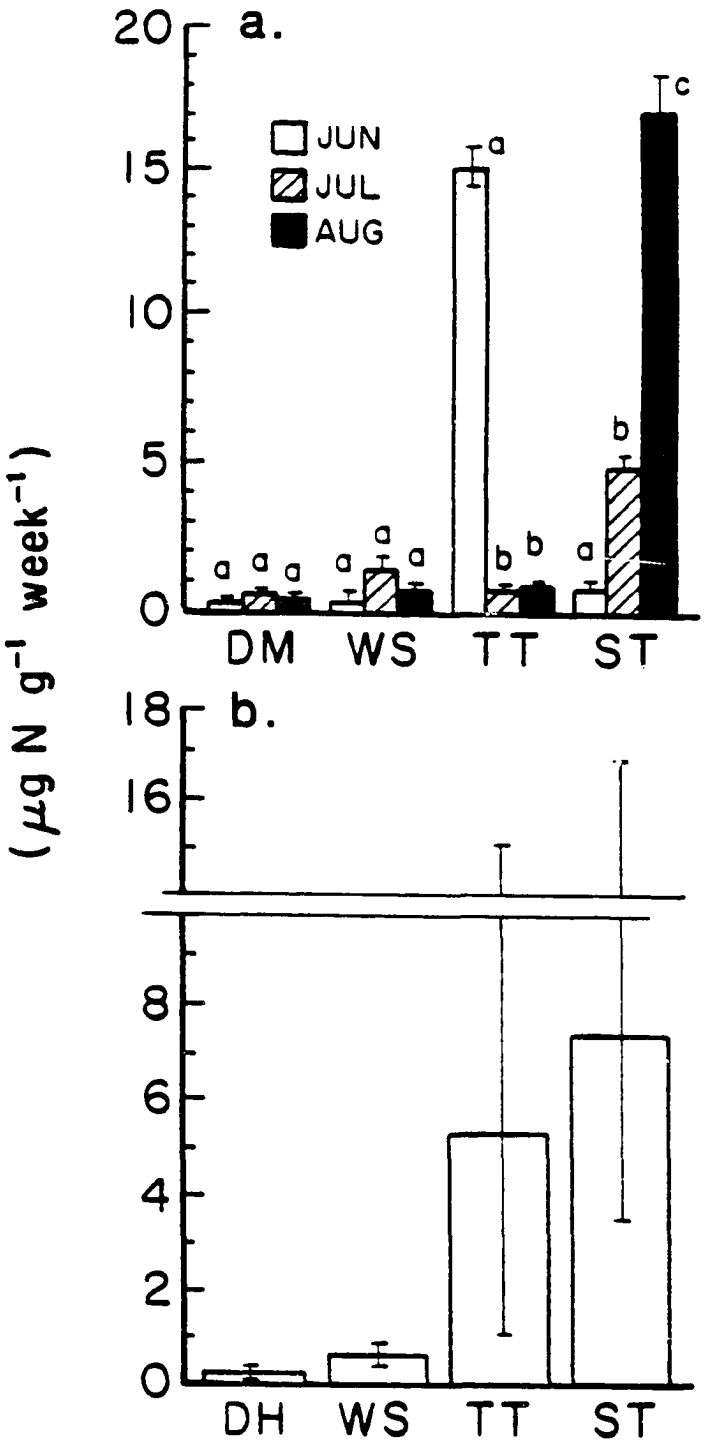

Fig. 2-4. Net nitrogen mineralization in the field by (a) month (mean ± S. E., n=8) and (b) average and range across the season (n=3) in each community. Community designations and significance as in chapter 1.

seasonal trends in rates of net nitrogen mineralization with highest rates in the spring and autumn respectively (Fig. 2-4b). In contrast, both the Wet Meadow and Dry Heath exhibited very low rates across the entire season.

The soil reciprocal transplant experiment conducted in the field failed to show strong temperature sensitivity of net nitrogen mineralization (Fig. 2-5a). In this experiment tussock tundra showed nearly constant mineralization rate across the temperature range. By contrast, the shrub community was characterized by large fluctuations, but the variation in nitrogen mineralization was not closely correlated with between-site variation in temperature. The wet meadow soil immobilized nitrogen in all communities except those incubated in the dry heath community. The soil from the dry heath site showed highest net nitrogen release during incubation in the warmest soil (same as that of origin). However, like in the other soils, nitrogen mineralization was not correlated with temperature. Nitrification showed approximately the same variation across communities as did mineralization (Fig. 2-5b). High rates of nitrification were measured in shrub tundra soil, but soil from the other communities showed negligible rates of net nitrate production. The same lack of consistent temperature response of nitrogen mineralization in the field was found

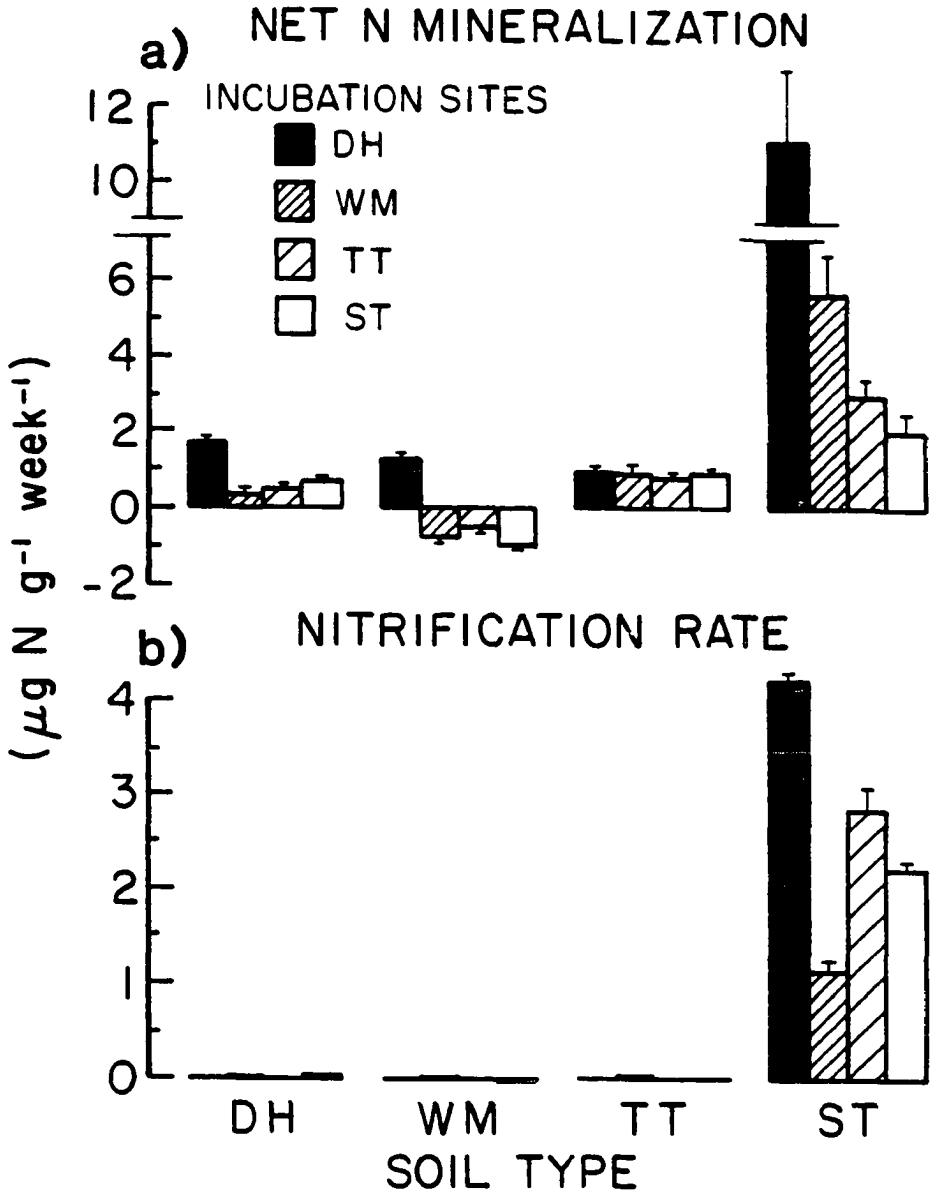

Fig. 2-5. Temperature response to (a) net nitrogen mineralization and (b) nitrification in the field (mean ± S.E. n=20).

under laboratory conditions (Fig. 2-6a). In shrub tundra, mineralization increased greatly from 4 to 8°C, but none of the communities showed a steady increase in mineralization with increased temperature. It therefore appeared that net nitrogen mineralization rate was not a simple function of soil temperature over the temperature range observed in the field. As in the field experiments, the patterns of nitrification under laboratory conditions closely resembled those of mineralization (Fig. 2-6b).

The recovery of added ^{15}N in the field (^{15}N immobilization experiment) differed significantly among communities. The highest recovery was found in the Shrub Tundra, and the lowest in the Dry Heath (Table 2-3). The significant negative correlation between immobilization potential (defined as the inverse of the ^{15}N recovered) and average seasonal net nitrogen mineralization (Fig. 2-7) suggests that differential rates of microbial nitrogen uptake can partially explain differential rates of net nitrogen release among communities.

Contrary to the modest effects of temperature on nitrogen mineralization, the various soil amendments had profound effects on this process. In all communities, energy enrichment (starch addition) resulted in net nitrogen immobilization (Fig. 2-8a). The extent of immobilization was greatest in the most fertile and

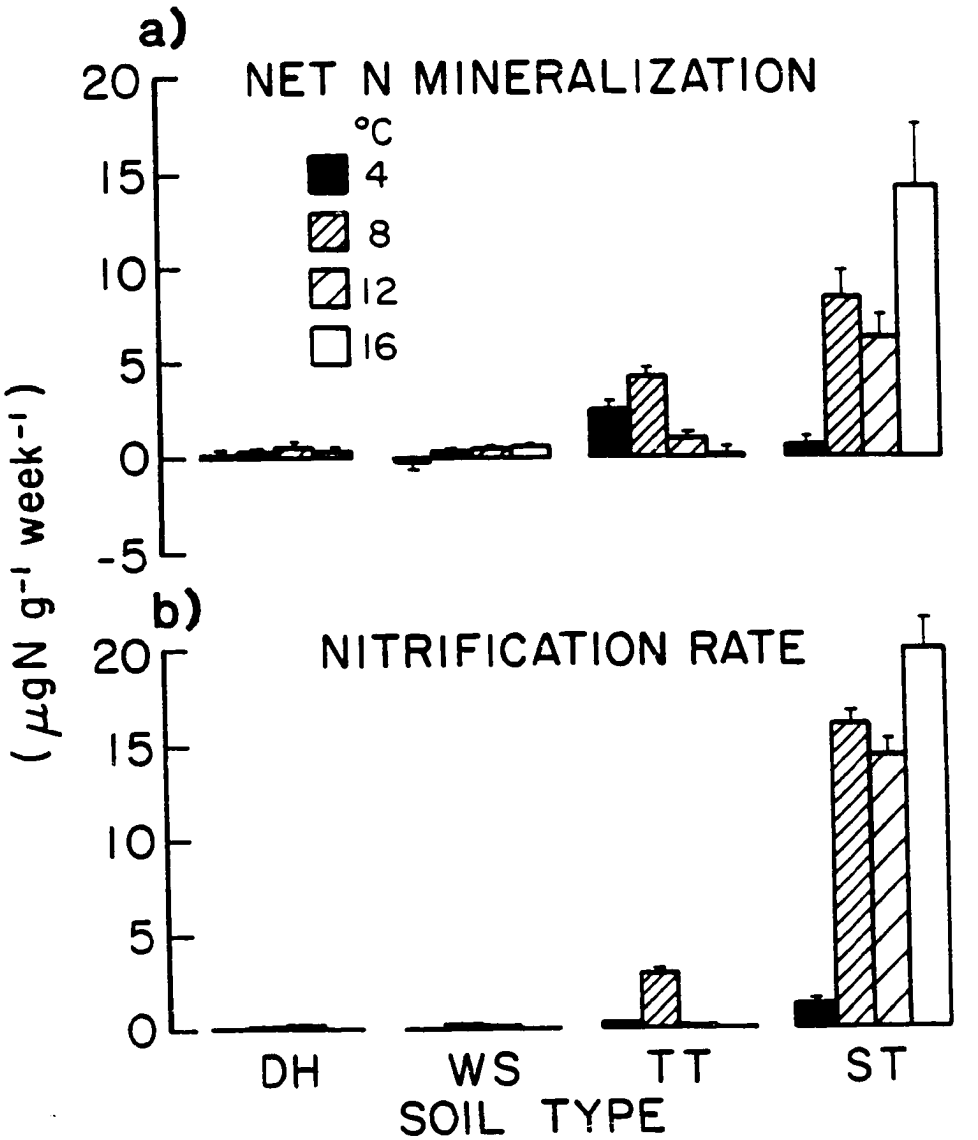

Fig. 2-6. Temperature response to (a) net nitrogen mineralization and (b) nitrification under laboratory conditions (mean ± S.E., n=8).

Table 2-3. Recovery of ^{15}N label added to soil as KCl-extractable nitrogen after 30 d incubation in the field (mean ± S.E., n=5).

	DH	WM	TT	ST
^{15}N abundance (%)	0.501 (0.006)	0.471 (0.009)	0.799 (0.046)	0.473 (0.002)
^{15}N recovered (ug ug $^{14}N^{-1}$ g^{-1})	0.17	0.18	1.20	3.21

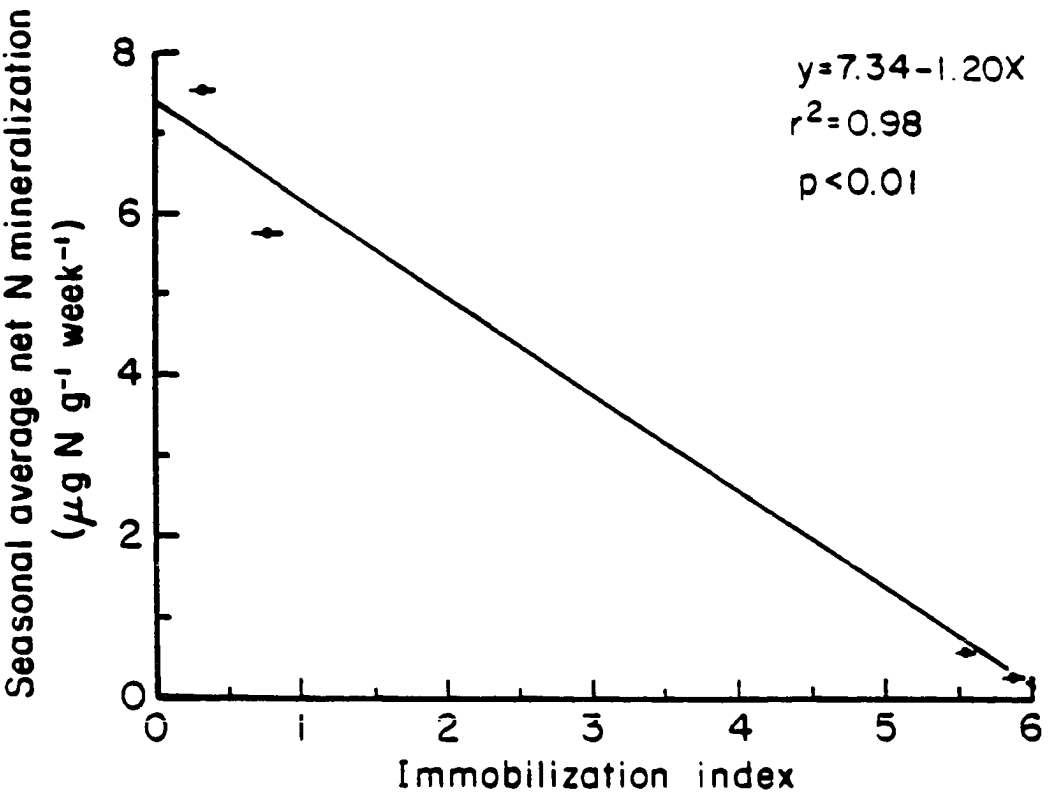

Fig. 2-7. Correlation between ^{15}N immobilization potential (immobilization index) and seasonal average net nitrogen mineralization. The immobilization index is defined as the inverse of ^{15}N recovered.

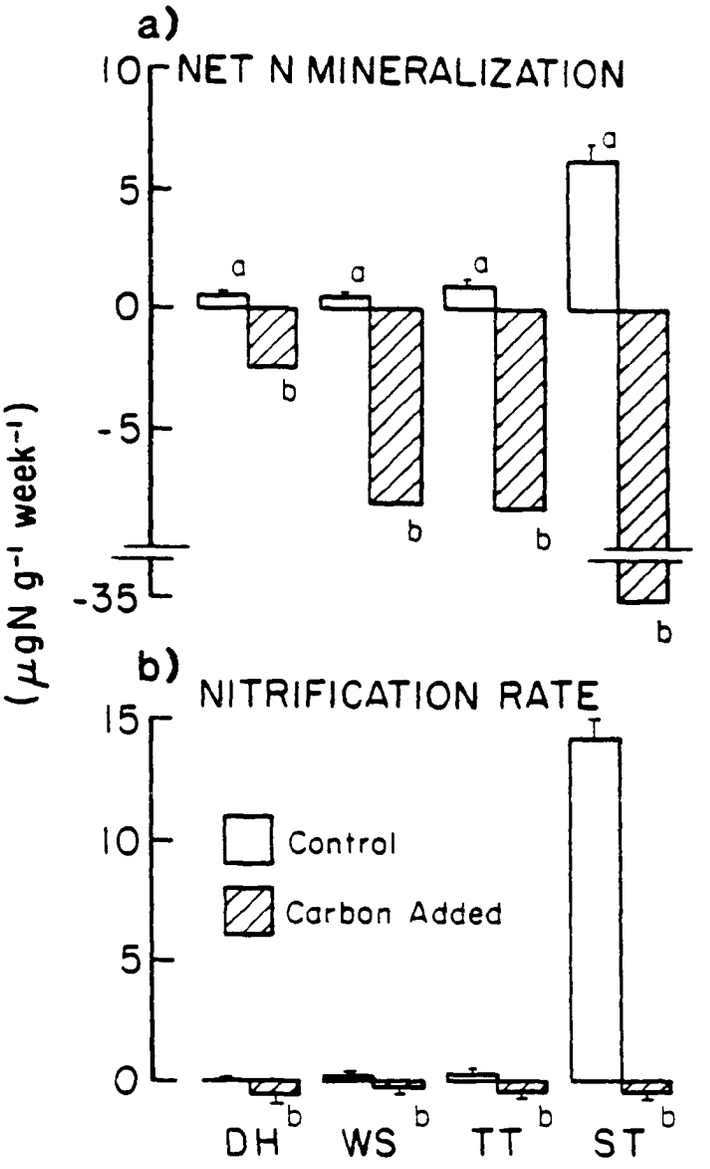

Fig. 2-8. Effect of carbon addition on (a) net nitrogen mineralization and (b) nitrification (mean ± S.E., n=8).

productive community (Shrub Tundra), with largest nitrogen pools and highest rate of net nitrogen mineralization and the highest concentration of soil lignin (32%; see Ch. 1). The lowest immobilization was found in the least fertile community (Dry Heath). The lignin concentration in this soil is also the lowest (11%; see Ch. 1) of the communities studied. Whereas energy supplementation resulted in nitrogen being sequestered by soil microbes, nitrogen additions tended to stimulate net nitrogen release (Fig. 2-9a). This effect was greatest in the two least fertile communities (Dry Heath and Wet Meadow). In the most nitrogen-rich communities (Tussock Tundra and Shrub Tundra) nitrogen addition had no significant effect on net nitrogen mineralization. In the shrub community, this treatment even tended to depress net nitrogen release. These results suggest that nitrogen release may be strongly influenced by the nitrogen:energy balance of microorganisms.

Nitrate production showed the same directional response to carbon (Fig. 2-8b) and nitrogen (Fig. 2-9b) as had net mineralization, probably because of the biochemical linkage between these microbial processes. Thus, ammonium addition increased nitrate production significantly above control levels except in the shrub community (Fig. 2-9b). Carbon addition, on the other

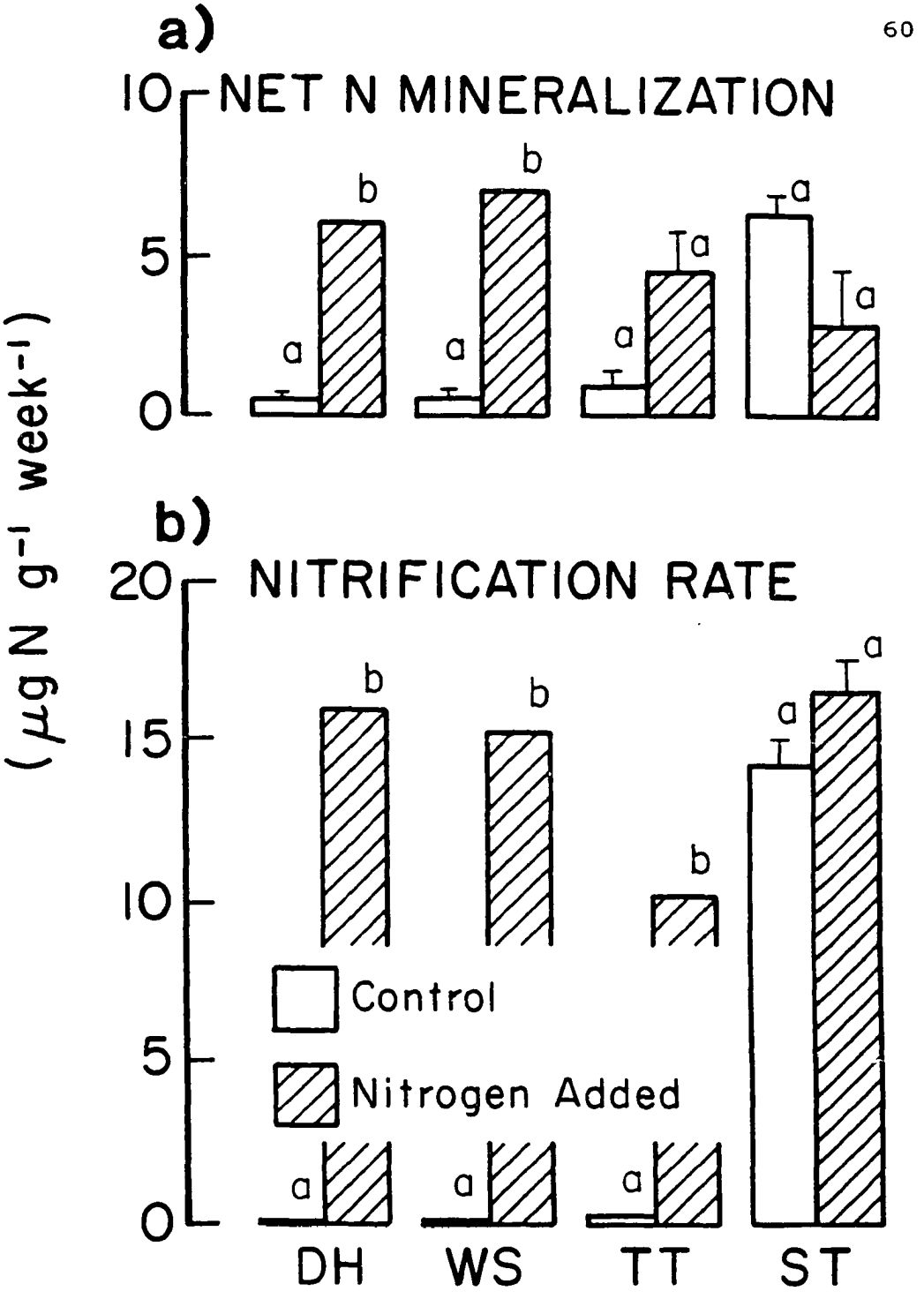

Fig. 2-9. Effect of nitrogen addition on (a) net nitrogen mineralization and (b) nitrification (mean ± S.E., n=8).

hand, resulted in only slight immobilization of nitrate (Fig. 2-8b). This could be due to microbial preference for ammonium over nitrate (Jones and Richards 1977), as well as the simple result of lack of substrate for nitrifiers as other microbes immobilized ammonium. The significant positive relationship between soil lignin and net nitrogen (N-14) immobilization following starch addition (Fig. 2-10), indicates that soil lignin concentration is inversely related to microbial energy availability.

Although soil temperature during the growing season (biologically active period of the year) may not exert primary control over net nitrogen mineralization, the fluctuations in temperature can profoundly affect this process. Subjecting the soils to repeated freeze-thaw cycles tended to increase net nitrogen release in all communities (Fig. 2-11a), but the increase was statistically significant in only the wet meadow and tussock tundra. The effect was greatest in the tussock community, which has the greatest mineralization rates in the spring following soil thaw. The warmest community, however, (Dry Heath) showed no significant response to this treatment. Repeated freezing and thawing of the soil may result in lysing of microorganisms and thus release of readily mineralizable substrates (Sparling et al. 1985).

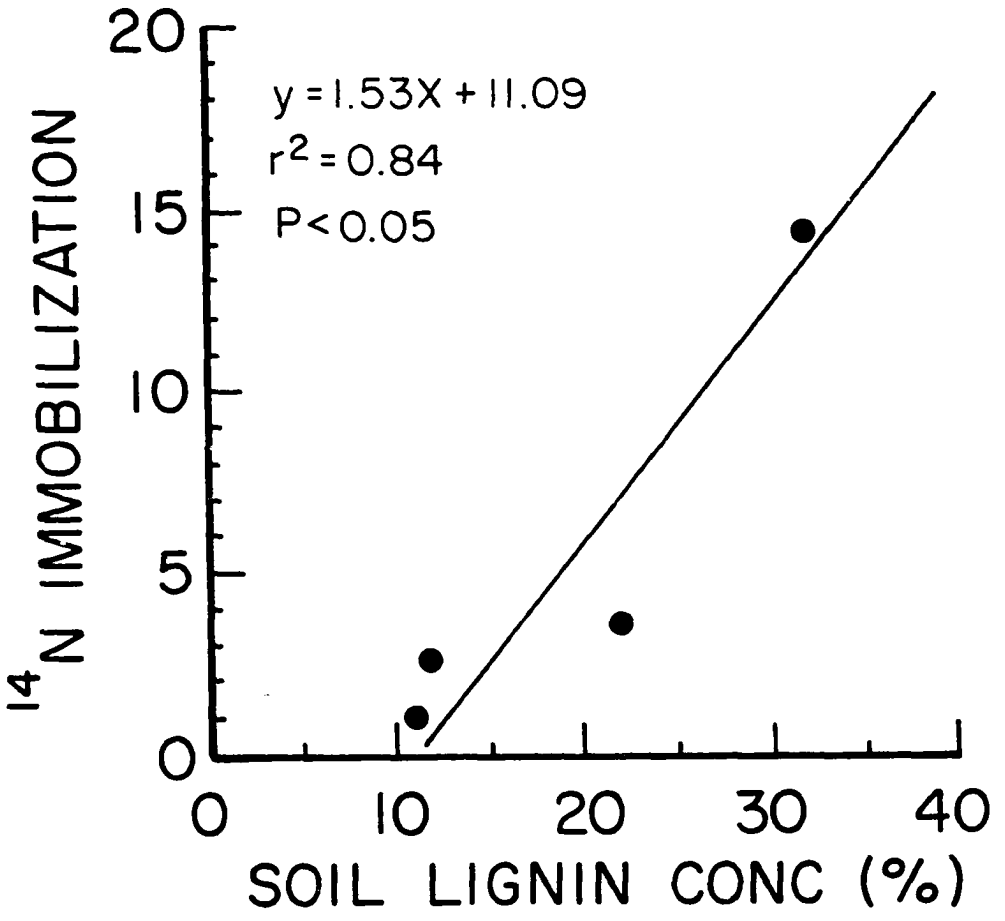

Fig. 2-10. Correlation between soil lignin and ^{14}N immobilization following starch additions to the soils.

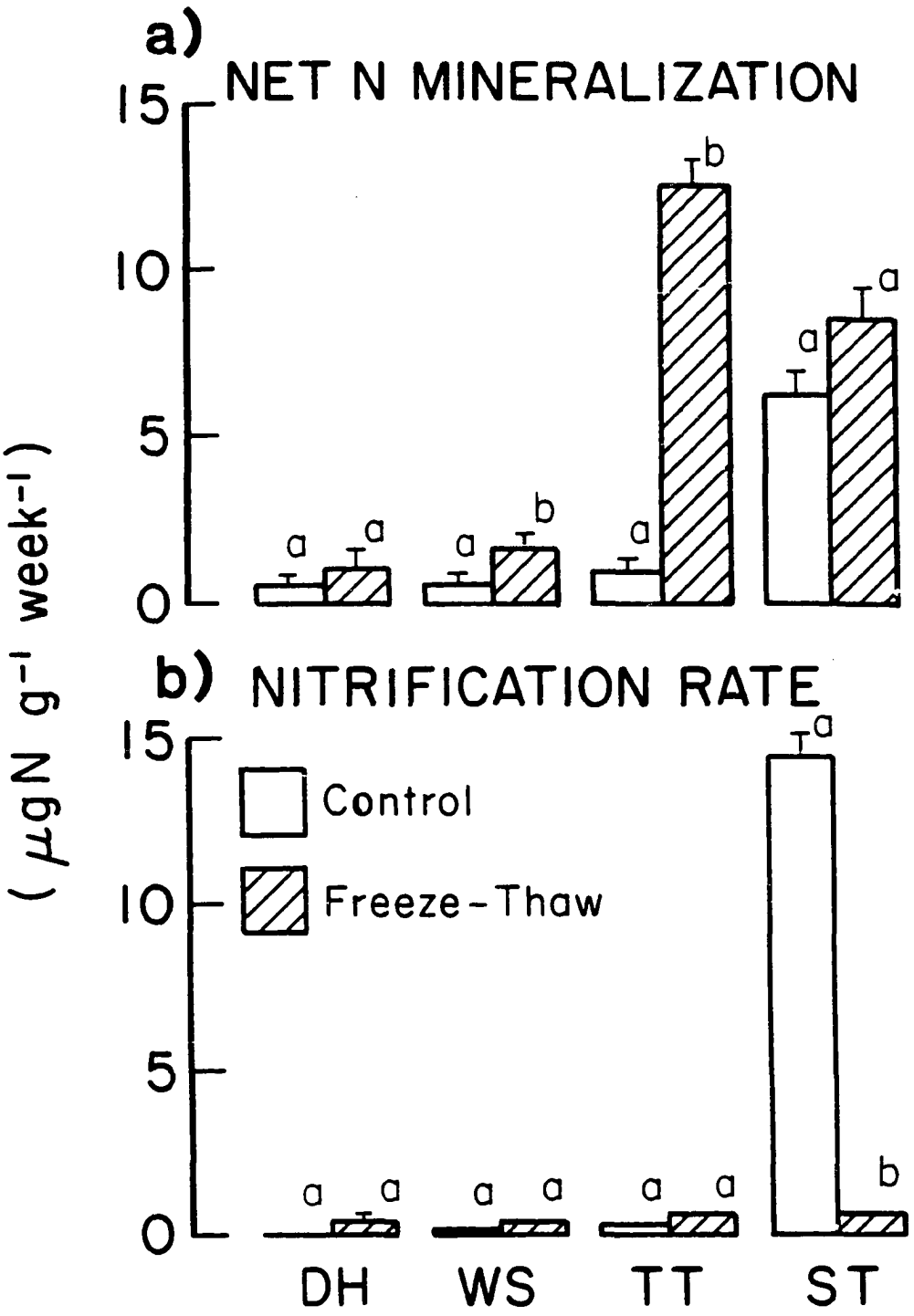

Fig. 2-11. Effect of repeated freezing and thawing on (a) net nitrogen mineralization and (b) nitrification (mean, ± S.E., n=8).

Thus, the observed differences in net nitrogen mineralization in response to freezing and thawing may be largely a function of differences in soil microbial biomass, independent of microbial respiration per individual organism. Recent data suggest that, indeed, shrub and tussock tundra have higher microbial biomasses than do dry heath communities (E. Vance pers. comm.). Freeze-thaw cycles did not appear to have any stimulatory effect on nitrification in any community, even depressing it greatly in the shrub community (Fig. 2-11b).

The strong correlations between community net primary productivity and indices of soil biological activity: cellulose decomposition, soil respiration and net nitrogen mineralization (Table 2-4), suggest that microbial activity and net primary production are closely linked in these arctic plant communities.

Discussion

The close relationships between net primary productivity and the various measures of microbial activity (cellulose decomposition, soil respiration, and net nitrogen mineralization) underscores the importance of microbial activity in nutrient release and turnover and in regulating ecosystem processes in arctic tundra.

Table 2-4. Correlation matrix for selected ecosystem processes of the four tundra communities studied near Toolik Lake, Alaska. Significance levels for r are shown by symbols: n.s., $p>0.05$; *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$. F= fractional mass loss (cellulose decomposition), R= soil respiration at 10°C, Nmin(1)= net nitrogen mineralization per gram dry soil, Nmin(2)= net nitrogen mineralization per gram soil organic matter, NPP= net primary production of aboveground vascular biomass.

	F	R	Nmin(1)	Nmin(2)
R	0.88^{*}			
Nmin(1)	0.93^{*}	0.65^{ns}		
Nmin(2)	0.97^{**}	0.81^{ns}	0.99^{***}	
NPP	0.99^{***}	0.89^{*}	0.94^{**}	0.97^{**}

Cellulose decomposition has been reported to correlate reasonably well with litter turnover among vegetation types (Fox and Van Cleve 1983). Thus, it is a practical index for comparisons of decomposition among communities. In the present study the decomposition rates of cellulose strips were within the range reported from other such studies in both tundra (Rosswall 1974) and taiga (Flanagan and Van Cleve 1983). Mass loss over two growing seasons ranged from 10-52%, indicating that the turnover time for this relatively labile carbon fraction is on the order of 4-20 years in arctic Alaska. This is in marked contrast to tropical ecosystems where the total carbon input from litter may turn over in the course of a few months (Swift et al. 1979).

The large variation among communities in rates of soil respiration is likely a function of differences in microbial populations which reflect different physico-chemical properties of the soils (see Ch. 1). Different microbial functional groups may have different temperature optima for respiration (Widden 1977, Widden and Parkinson 1978). Moreover, the nature of the carbon substrate affects both the respiration rate and the temperature optimum even within a given taxon (Flanagan and Scarborough 1974). In addition, the great variability of

soil organic matter among the communities suggests significant differences in microinvertebrate populations (MacLean 1974), which may be important in the initial stages of litter processing (Swift et al. 1979). The rates of CO_2 evolution and net primary productivity in tundra communities are approximately 5-20% of those of productive taiga communities (Gordon et al. 1987). This relationship between soil respiration and primary productivity also holds for arctic tundra versus sub-arctic peatlands (Moore 1986). Thus, soil respiration appears to be closely linked to net primary productivity across the boreal forest as well as within tundra. Because soil temperatures in arctic tundra rarely exceed 10°C in the rooting horizon during the growing season (MacLean and Ayres 1985), it seemed most relevant to examine the temperature response of soil respiration between 1-10°. The Q_{10} for soil respiration in these arctic soils averaged 1.5 (CV=33%), which is about the same as in Alaskan taiga soils. Cowling and MacLean (1981) found higher temperature responses in a black spruce forest, whereas Gordon et al. (1987) reported slightly lower values for interior Alaskan white spruce ecosystem.

The apparent insensitivity of net nitrogen mineralization to temperature between 4-16° under both field and laboratory conditions is consistent with earlier

findings from arctic tundra (Marion and Miller 1982, Marion and Black 1987). Low temperature sensitivity of nitrogen mineralization has also been demonstrated in certain taiga soils (Klingensmith 1988), although temperature appears to be a strong determinant over productivity and element cycling among taiga forest types (Van Cleve et al. 1983). The experimental design of the temperature sensitivity experiments did not allow differentiation between physiological plasticity of a particular class of microorganisms versus a shift in microbial functional group to explain a change in respiration or nitrogen mineralization with increased temperature. The absence of such a response, however, indicates low physiological plasticity of the soil microbes, or that they are highly plastic in a compensatory fashion. These data indicate that during the biologically active portion of the year temperature is not a direct primary control over net nitrogen mineralization in these Alaskan tundra soils.

Redox conditions have been shown to have significant effects on microbial activity in agricultural soils (Tate 1979, DeLaune et al. 1981). The potential interaction among soil aeration and temperature was not addressed in this study, but may have confounded the interpretation of the reciprocal transplant experiment in the field

(regarding the relationship between temperature and net nitrogen mineralization.) However, the insignificant effect of soil moisture on net nitrogen mineralization in tundra (Marion and Miller 1982) suggest that soil redox potential is not an important control over nitrogen release in these systems.

The negative correlation I found between net nitrogen mineralization and ^{15}N immobilization is similar to relationships demonstrated in a range of tropical soils (Vitousek and Matson 1988), suggesting that microbial nitrogen uptake may be an important factor regulating net nitrogen release in a wide variety of ecosystems. Microbial nitrogen immobilization itself appears to be strongly influenced by the relative availability of carbon versus nitrogen. This inference is supported by the differential responses of nitrogen mineralization to carbon and nitrogen additions among communities. Thus in a soil high in available nitrogen (i. e. large concentrations of extractable nitrogen and high mineralization rates) and high in lignin (reduced energy supply) such as the Shrub Tundra, microorganisms tend to be limited by carbon, rather than nitrogen. Large additions of carbon alter the relative resource supply, and nitrogen is sequestered by the microbes, resulting in negative mineralization values (immobilization). On the

other hand, in soils such as the Dry Heath community with lower concentrations of both nitrogen and lignin, microbes tend to be more limited by nitrogen than carbon. Therefore starch additions have much less effect on net nitrogen release. The significant nitrogen immobilization following starch addition in all the soils studied here, however, indicates that microbial energy availability in Alaskan tundra soils is very important to the process of net nitrogen release irrespective of community.

The enhanced rate of nitrogen mineralization resulting from freezing and thawing suggests that a significant proportion of the annual nitrogen production may be released in pulses rather than at a steady rate. For instance, in tussock tundra, where freezing and thawing appears to have the greatest effect, this treatment yielded a nitrogen mineralization rate that was approximately twice the average rate calculated over the season in this vegetation type. Clearly, short-term fluctuations in environmental conditions may have profound effects on nitrogen dynamics in these ecosystems. Consequently, measurements of nitrogen mineralization in the laboratory under constant temperature and moisture conditions (as was also done in this study and others) may not adequately predict the dynamics of nitrogen release in the field. Moreover, since inferences about the controls

over nitrogen release may differ depending on the predominant mode (steady rate versus pulse-release) by which nitrogen becomes available to plants, these sorts of data should be interpreted with caution.

I contend that there are multiple controls over decomposition and net nitrogen mineralization in the arctic tundra of northern Alaska. The controls consist of both physical (e.g., freeze-thaw) and chemical (e.g., lignin concentration) characteristics of the soil environment. Some of these soil properties (e.g., nitrogen concentration) may take on greater importance in some communities than others. Other soil parameters (e.g., temperature fluctuations) change in importance within a given community during the growing season. Irrespective of this spatial and temporal variation, there are certain common trends among communities with respect to nitrogen dynamics. I conclude that in the Alaskan arctic tundra nitrogen release is:

1) relatively insensitive to variation in soil temperature within the normal range encountered during the biologically active portion of the year.
2) directly related to the activity level of soil microorganisms,
3) greatly affected by the energy and nitrogen status of the soil, and, by inference, of the microorganisms,

4) **closely coupled to net primary productivity.**

CHAPTER THREE: NITROGEN TURNOVER IN RELATION TO PRODUCTIVITY.

Introduction

Nutrient limitation is generally defined in terms of plant growth response to nutrient additions (Ulrich and Hills 1973). However, Chapin et al. 1986 pointed out that, in natural ecosytems, plant species from nutrient poor soils have intrinsically lower potential growth rates and respond less to fertilization than do species that occur in more nutrient rich soils. Hence, the growth response of wild species to nutrient addition, particularly by those from infertile soil, may not be the most sensitive measure of nutrient limitation in natural ecosystems.

Estimates of nutrient turnover time or rate provide meaningful parameters for comparisons of nutrient cycling among ecosystems and among compartments within a given ecosystem. Inferences about nutrient limitation among ecosystems are often made from comparisons of nutrient turnover, fluxes, and pool sizes (Radwan and Shumway 1983, Van Cleve et al. 1983). However, few studies have tried to link explicitly patterns of nutrient turnover to indices of nutrient limitation. In this chapter I analyze the response of arctic tundra species to nitrogen addition

in the field in terms of both growth and nitrogen accumulation. Furthermore, in light of the hypothesis proposed by Chapin et al. 1986, I use soil nitrogen turnover as an integrative measure of the potential supply of nitrogen to plants to determine whether there is a consistent relationship between nitrogen supply and the responsiveness to nitrogen additions among species from communities of differing nitrogen availability and net primary productivity.

Methods

Research sites

The research was conducted in four tundra communities of contrasting structure and nitrogen availability in the northern foothills of the Brooks Range near Toolik Lake, Alaska (68°38'N, 149°34'W, elevation 760 m). Three of the communities were dominated by different single growth forms. The Dry Heath community was dominated by prostrate evergreen shrubs such as Ledum palustre, Loiseleuria procumbens, and Diapensia lapponica. The Wet Meadow was dominated by the sedges Eriophorum angustifolium and Carex aquatilis. In the third community, Shrub Tundra, deciduous shrubs such as Betula nana and Salix pulchra predominated. The last community type, Tussock Tundra,

had an equal representation of the above growth forms. Total biomass and net above-ground productivity varied 5X and 10X, respectively, among communities (Shaver and Chapin, personal communication). Details on community composition, productivity, soils, and nitrogen dynamics are given by Shaver and Chapin (1985b), and in Chapters 1 and 2.

Fertilization experiment

In each community four 5 x 5 m plots, separated by 2-m buffer strips, were established. Fertilizer was applied in an N*P factorial with a single plot per treatment. Nitrogen was applied as ammonium nitrate in commercial fertilizer at the same rate (25 g m^{-2} N) as in other studies of Alaskan tundra (Tamm 1954, Shaver and Chapin 1980). The application level of phosphorus (as triple superphosphate) was 10 g m^{-2} P (i.e. 40% of the application rate in the above cited studies). The application was made once in June 1982, and the vegetation was randomly sampled along transects in each plot two growing seasons following fertilizer application. Four replicate samples of 20 shoots from each major species within each plot were collected, and biomass and nitrogen concentrations (Kedrowski 1983) were determined on current shoots for each vascular species.

Soil nitrogen turnover

Turnover of soil nitrogen is closely tied to soil carbon dynamics (Melillo et al. 1982). There are currently data available suggesting that the arctic tundra of northern Alaska is not in steady-state with respect to carbon balance (Poole and Miller 1982), but it is uncertain whether tundra ecosystems are undergoing net gains or losses (Billings et al. 1982). For the purposes of this paper, I have therefore assumed that the compartments and processes constituting the nitrogen cycle in tundra systems are close to steady-state.

Calculations

Estimation of turnover time for the various soil nitrogen compartments (dissolved inorganic nitrogen, soluble organic nitrogen, and structural nitrogen) were calculated conventionally as the pool size (Chapter 1) divided by the annual rate of net nitrogen mineralization (net nitrogen mineralization, ug N g^{-1} $week^{-1}$ times 12 weeks per year, expressed on a m^{-2} basis, Chapter 2), using seasonal average rates for both pools and rates (cf. Marrs et al. 1988).

Statistical analysis

The data were analyzed with Systat statistical package. Differences between treatment means and the responsiveness to nitrogen addition (ratio of nitrogen accumulation in fertilized to that in control plants) were analysed using nonparametric analysis of variance (Kruskal-Wallis test). When this test showed statistical significance, nonparametric multiple comparisons testing (Conover 1980) was employed to identify differences among species.

Although the samples were collected from only one plot per treatment, the study area within each community was uniform with repect to vegetation and topography, so I presume that the large differences among plots reflect true treatment effects rather than plot-to-plot variability.

Results

Growth

All species except Ledum palustre from Tussock Tundra, exhibited significantly enhanced growth (expressed as mass in current year's shoot) following nitrogen addition, generally on the order of 20-50% (Fig. 3-1). The

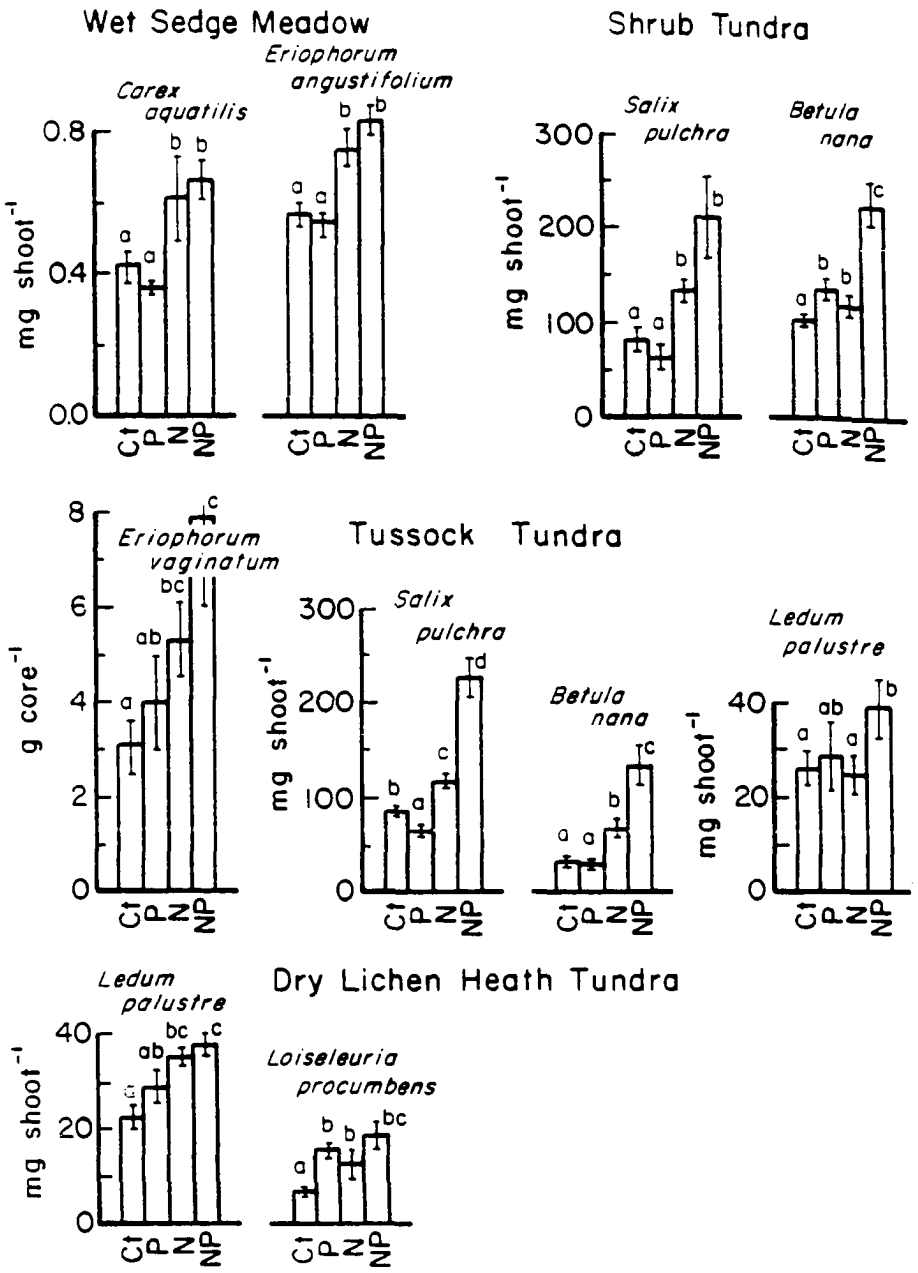

Fig. 3-1. Response of current year's shoot mass to nitrogen and phosphorus fertilization alone and in combination in major species of different growth forms from four tundra ecosystems. Mean ± S.E., n=4 replicates of 20 shoots. Values identified with the same letter are not significantly different ($p>0.05$).

growth response tended to be greatest in the rapidly growing deciduous shrubs, but species such as Eriophorum vaginatum (a sedge) and Loiseleuria procumbens (an evergreen shrub) also showed substantial (70%) increase in apical shoot growth under the nitrogen treatment. In contrast to nitrogen, only two species (Betula nana in Shrub Tundra and Loiseleuria procumbens in the Dry Heath) showed a significant positive response to phosphorus addition. All species exhibited significantly increased shoot mass under the N*P treatment. Because nitrogen was the major growth-limiting nutrient in each community, the remainder of the results will focus on nitrogen.

Nitrogen accumulation

The growth response of the sedges from the Wet Meadow (Carex aquatilis and Eriophorum angustifolium) was proportional to nitrogen uptake, i.e., tissue nitrogen concentration did not increase significantly with nitrogen fertilization (Fig. 3-2). All the other species showed increases in nitrogen accumulation relative to growth under the fertilizer treatment, i.e., exhibiting luxury consumption (Epstein 1972, Chapin 1980). In all species the nitrogen pool of current shoots increased significantly with nitrogen addition (Fig. 3-3). Thus, nitrogen uptake increased in response to increased soil

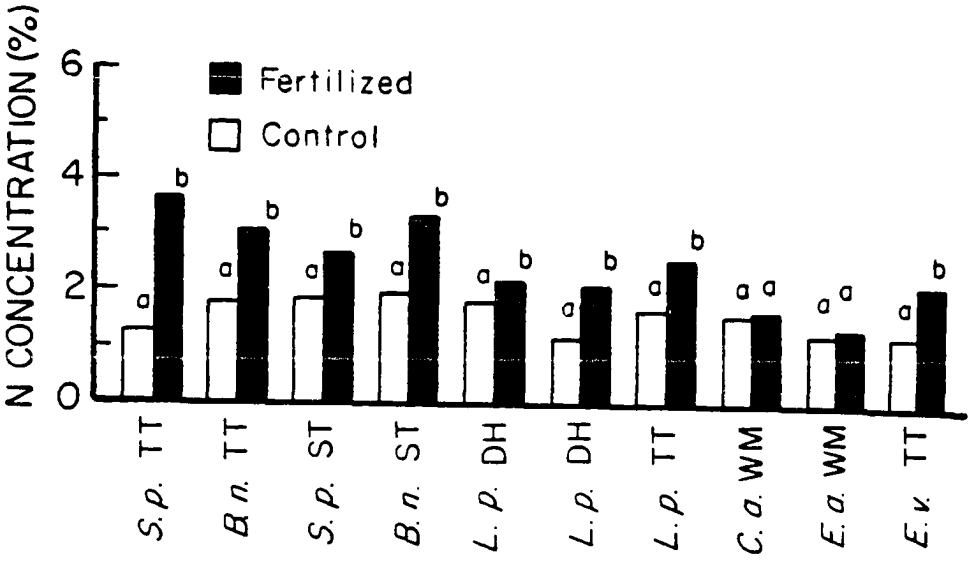

Fig. 3-2. Response of nitrogen concentration in current year's shoots to nitrogen fertilization in major species of different growth forms from four tundra ecosystems. Mean ± S.E., n=4 replicates of 20 shoots. S.p.=Salix pulchra, B.n.=Betula nana, L.p.=Ledum palustre, C.a.=Carex aquatilis, E.a.=Eriophorum angustifolium, E.v.=E. vaginatum. DH=Dry Heath, WM=Wet Meadow, TT=Tussock Tundra, ST=Shrub Tundra. Significance as in Table 1.

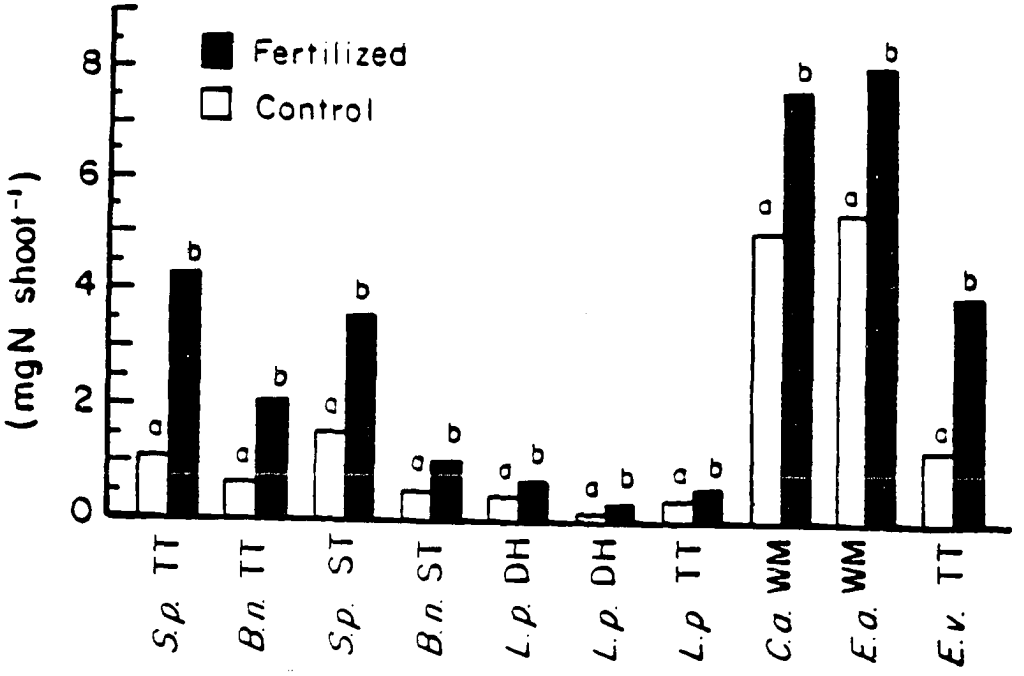

Fig. 3-3. Effect of nitrogen fertilization on pools of nitrogen in current year's shoots in major species of different growth form from four tundra ecosystems. Mean ± S.E., n=4 replicates of 20 shoots. Species and community designations, and significance as in Table 1.

nitrogen supply. I conclude that nitrogen availability limits nitrogen acquisition and net primary productivity of these tundra species.

Turnover of soil nitrogen

In all communities, the soil pools of dissolved inorganic nitrogen turned over most rapidly (Table 3-1), on the average 89-fold faster than the soluble organic pool. The bound (structural) organic nitrogen was by far the least labile soil nitrogen fraction with an annual turnover rate of 0.04-1.3% (Table 3-1), contrasted with dissolved inorganic nitrogen of 900-14000%, depending on community. Turnover time for bound (structural) organic nitrogen was on the order of 80-2500 years, and for soluble organic nitrogen of 0.7-14 years. In contrast, the pool of dissolved inorganic nitrogen turns over approximately once every few days (even less than a day in the case of Shrub Tundra).

There were important differences among communities in the turnover of the various soil nitrogen compartments. For instance, in the Dry Heath community, which has relatively low soil organic matter content (56%, Chapter 1), the dissolved inorganic pool turned over 175 times faster than the soluble organic pool, which again turned over 130 times faster than the bound organic nitrogen. In

Table 3-1. Nitrogen flux (rate of net nitrogen mineralization, g N m^{-2} yr^{-1}), pool sizes, and turnover rate (% of pool per year) of various soil nitrogen compartments in four tundra communities near Toolik Lake, Alaska. All values are rounded off for the purposes of presentation in table format and this procedure accounts for any appearent discrepancies in pools and turnover rates.

	DH	WM	TT	ST
Flux				
(g N m^{-2} yr^{-1})	0.034	0.14	1.76	1.08
Pool				
(g N m^{-2})				
Bound organic N	90	245	140	180
Soluble organic N	0.50	0.72	1.35	0.89
Dissolved inorganic N	0.004	0.01	0.03	0.008
Turnover rate				
(% of pool yr^{-1})				
Bound organic N	0.04	0.06	1.3	0.6
Soluble organic N	7	20	143	122
Dissolved inorganic N	910	1428	5882	14285

the other three communities, all of which have high soil organic matter content (80-98%, Chapter 1), the inorganic nitrogen pools turned over 41 to 117 times faster than the soluble organic nitrogen. In addition, the turnover of soluble organic nitrogen was much more rapid (110-333X) than the bound organic pool in these communities. Above-ground vascular productivity across all communities significantly correlated with the turnover of dissolved inorganic nitrogen ($r=0.99$, $p<0.01$), but not with soluble organic nitrogen ($r=0.78$, $p>0.05$), or bound organic nitrogen ($r=0.50$, $p>0.05$) (Table 3-2).

Discussion

The fertilizer experiment showed clearly that nitrogen limited shoot growth at each of the four study sites. The growth responses observed following nitrogen fertilization are probably a conservative measure of the degree of nitrogen limitation. Tundra species also respond to enhanced nutrient availability through increased number of shoots (Chapin and Shaver 1985b), and, in some shrub species, by increased secondary growth (Shaver 1986). Thus, the growth response to altered nutrient availability can be more complex than simple changes in shoot biomass would indicate.

Table 3-2. Matrix of correlation coefficients (r values) for turnover among selected compartments of soil nitrogen, and responsiveness to fertilization (ratio of nitrogen pool in fertilized and control plants, F/C), and net primary production (NPP). Significance levels for r are shown by symbols: *, $p<0.01$.

	Soluble organic N turnover	Bound organic N turnover	F/C	NPP
Dissolved inorganic N	0.76	0.49	0.16	0.99*
Soluble organic N		0.65	0.55	0.78
Bound organic N			0.47	0.50
F/C				0.17

There were no clear differences among growth forms in the response to nitrogen addition either in terms of apical growth or nitrogen accumulation in the field. The deciduous shrubs tended to accumulate more nitrogen than did the evergreen shrubs or the graminoids (Fig. 3-4), but these growth-form differences were generally not statistically significant. Moreover, I found no evidence for higher responsiveness to nitrogen addition in communities with more rapid flux of nitrogen (Fig. 3-5). On the other hand, the results agree with the hypothesis put forth by Chapin et al. (1986) concerning the response to changes in nutrient availability of individual species from nutrient-rich and nutrient-poor soil. Whereas different species growing under dissimilar soil nutrient conditions tend to have adapted to the prevailing nutrient availability, individuals of the same species occurring on low nutrient soil are likely to be more nutrient limited than are individuals growing in higher nutrient soil. Consequently plants from low-nutrient soil tend to respond more strongly to nutrient addition than plants of the same species on richer sites. Thus, Ledum palustre from the Dry Heath tended to show a greater response than did Ledum palustre from the more nitrogen rich Tussock Tundra (Fig. 3-4). Likewise, Betula and Salix from Tussock Tundra tended to show greater response than did representatives

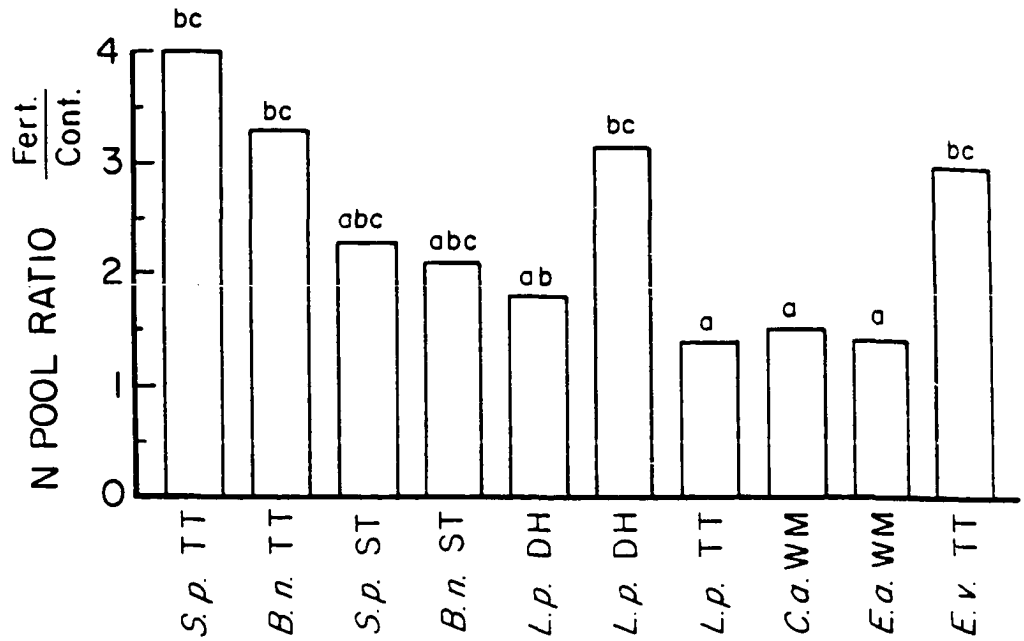

Fig. 3-4. Responsiveness to nitrogen fertilization expressed as the mean ratio of the nitrogen pool in current year's shoots in fertilized and control plants of major species of different growth forms from four tundra ecosystems. Species and community designation, and significance as in Table 1.

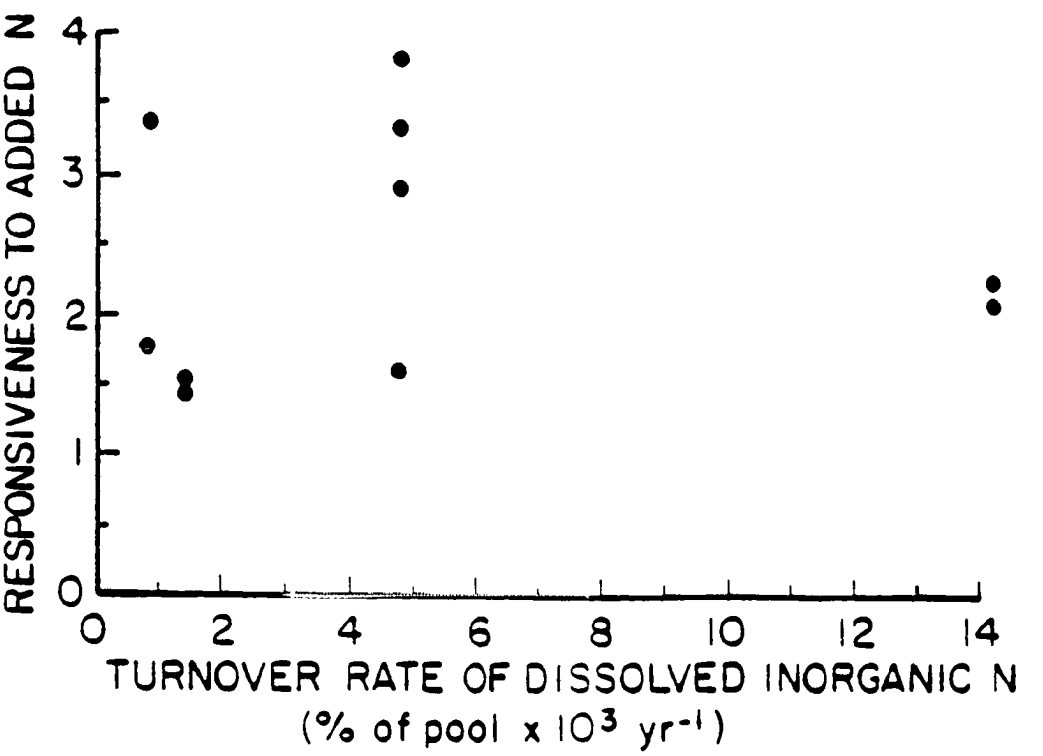

Fig. 3-5. Relationship between the responsivness to fertilization (ratio of nitrogen pool in fertilized and control plants) of several major tundra species and rate of nitrogen supply expressed as the turnover rate of dissolved inorganic nitrogen.

of these species from the yet more nitrogen-rich Shrub Tundra.

Despite the rapid turnover of soluble organic nitrogen in these communities, the high correlation between inorganic nitrogen turnover and plant productivity (Table 3-2) suggests that the supply of ammonium (and to a lesser extent nitrate) is the most important control over NPP. This finding is in agreement with previous data from these communities showing an equally strong correlation between annual productivity and net nitrogen mineralization (Chapter 2).

Whereas the disparity in turnover among soil nitrogen compartments within a community was due to dissimilar pool sizes, differences in turnover among communities were due to up to 50-fold differences in annual nitrogen flux (Table 3-1).

The values reported here for turnover of dissolved inorganic and soil organic nitrogen bracket those reported by Chapin et al. (1980) for the the coastal tundra at Barrow, Alaska. An important finding made in the present study near Toolik Lake is that the turnover of soil nitrogen shows order-of-magnitude variation among communities of different structure and productivity. The turnover rate of bound organic nitrogen varied 32-fold across communities, soluble organic nitrogen varied 20-

fold, and dissolved organic nitrogen varied 15-fold, demonstrating that local variation in edaphic characteristics have great effects on nitrogen dynamics in tundra ecosystems. Moreover, this magnitude of variation across tundra communities is as great as between tundra and tropical ecosystems (cf. Marrs et al. 1988), again suggesting that latitudinal variation in climatic variables are of less importance than such variables as microclimate, aspect, slope, and topography in explaining the nature of nitrogen dynamics in arctic tundra.

I conclude that the availability of nitrogen alone and in combination with phosphorus can strongly limit plant growth in a range of tundra vegetation types and that the turnover of inorganic soil nitrogen is a useful predictor of net primary productivity in these tundra communities.

CHAPTER FOUR: DISTRIBUTION AND ABUNDANCE OF FREE AMINO ACIDS IN ALASKAN TUNDRA SOILS.

Introduction

There is presently a wealth of information on total (Kjeldahl) soil nitrogen concentrations from a variety of ecosystems (Rosswall and Clark 1981). This soil parameter has been related to many ecosystem properties, such as the rate of nitrogen mineralization (Fyles and McGill 1986), total mineralizable nitrogen (Stanford and Smith 1972, Whitehead 1981), and net primary productivity (Pastor et al. 1984, Nadelhoffer et al. 1985). However, in view of the heterogeneous nature and largely unknown chemical composition of "total soil nitrogen," it is not clear what functional relationships underlie the correlations between total soil nitrogen and various ecosystem processes.

Irrespective of geographic locality, the bulk of soil nitrogen in both natural and agroecosystems exists in organic form, as amino acids, amino sugars, and hydrolyzable unknown fractions (Stevenson 1982). In arctic ecosystems the proteinaceous nitrogen fraction makes up approximately one third of total soil nitrogen (Sowden et al. 1977). The portion of amino acids bound in protein not associated with the humus is biochemically very active, and thus may be important in nitrogen

transforming processes in the soil. Nitrogen mineralization (ammonification) is the process by which organic nitrogen is enzymatically converted into NH_4^+. The high proportion of organic nitrogen made up of proteinaceous compounds (Stevenson 1982) suggests that free amino acids are both qualitatively (Ladd and Jackson 1982) and quantitively important sources of NH_4^+. Despite the central role that free amino acids thus may represent in nitrogen cycling, there is a scarcity of data on soil amino acids from any ecosystem where nitrogen cycling studies have been carried out.

In this chapter I present qualitative and quantitative data on soil free amino acids from four major tundra vegetation types in northern Alaska. My main objective is to demonstrate the quantative importance of amino acids as a component of the bio-available soil nitrogen in some tundra systems. In addition, I discuss the relationship between free amino acids and nitrogen turnover in arctic tundra.

Methods

Research sites

The research was conducted near Toolik Lake, Alaska (68°38'N, 149°34'W, elevation 760 m), in four communities

of contrasting structure and function. The characteristics of these communities are described in Chapter 1 and in Chapin and Shaver (1985).

Field sampling

Soils from the O2 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) were kept cool (3-7°) until extracted (within 24 h of collection). The samples were not frozen prior to extraction since this may inflate the concentration of free amino acids (Ivarson and Sowden 1966).

Extraction procedures

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 an extractant to give a better estimate of the concentration of amino acids in the soil under natural conditions. Extractants such as water combined with CCl_4 tend to extract several-fold more amino acids than water alone,

probably as a consequence of cellular degradation during extraction (Ivarson and Sowden 1968). 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. Concentrations of each amino acid were measured using high performance liquid chromatography (HPLC), following a modified precolumn fluorescence derivatization procedure using a o-pthaldialdehyde/2-mercaptoethanol reagent (Lindroth and Mopper 1979, Jones et al. 1981). Amino acid concentration in roots (g N m^{-2}) was calculated done by multiplying root biomass (g m^{-2}; Shaver and Chapin unpublished data) with average seasonal concentration of amino acids in roots (Chapin et al. 1986).

HPLC procedures

Apparatus. The samples were injected and eluted with a solvent gradient produced by a Spectra Physics solvent delivery system fitted with a Hamilton PRP-1 column (4.6 mm x 250 mm, packing diameter 10 um). 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.

Mobile phases. The eluting solvents were glass-distilled methanol and a filtered phosphate buffer made up using glass-distilled water (0.025 mol L^{-1}, pH 4.5). For the phosphate buffer the pH was set by mixing 1.73 g Na_2HPO_4 and 1.77 g NaH_2PO_4 in 1 L of water. The solvents were thoroughly degassed with helium prior to and during each run.

Reagent. The o-pthaldialdehyde (OPA) solution was made up of 50 mg o-pthaldialdehyde, 100 mg sodium lauryl sulphate ($Na_2[CH_3(CH_2)_{11}]SO_4$), and 50 uL 2-mercaptoethanol, dissolved in 5 mL of distilled methanol. The reagent solution was made up fresh every 3-4 days.

Borate buffer. The saturated boric acid solution (0.4 mol L^{-1}) had a pH of approximately 9.5.

Buffered reaction solution. Five hundred microliters of the borate buffer was mixed with 1.5 mL water, 50 uL sample, and 50 uL of â-aminoadipic acid (an internal standard, usually about 5 umol L^{-1}).

Derivatization procedure. The reaction solution containing the sample was reacted with 50 uL of the OPA reagent at room temperature. Then 1 mL was injected after 2 min. The flow rate was set at 1 mL min^{-1}, and all the samples had eluted in approximately 45 min.

The elution programs for the set-up gradient, sample run and shut-down gradient are shown in Appendix 1. After

every run the column was thoroughly flushed with methanol.

Statistical analysis

The data were analyzed using Systat statistical package on a personal computer. Unequal sample sizes and heterogenous variances dictated the use of nonparametric one-factor analysis of variance (Kruskal-Wallis test). When this test procedure showed significant differences, nonparametric multiple comparisons testing were performed to separate the individual means (Conover 1980).

Results

Total free amino acid (TFAA) concentrations varied over five-fold among communities (Table 4-1). The highest seasonal mean concentration was found in tussock tundra (8.29 ug N g^{-1}), and the lowest in the anoxic wet meadow soil (1.57 ug N g^{-1}). In each community, the concentration of available (water-extractable) amino acid-nitrogen was 4-10 fold higher than that of ammonium, the predominant form of inorganic nitrogen in these soils (Table 4-1). Tussock tundra showed the greatest seasonal variation (n=3 sampling dates) in free amino acid concentration (CV=89%) and the wet meadow the least

Table 4-1. Mean seasonal concentrations (across three sample dates) of water-extractable total free amino acids (TFAA) and ammonium in the organic soil horizon of each community. Values are in ug N g^{-1} dry soil, coefficients of variation in parenthesis.

	DH	WM	TT	ST
TFAA	2.19 (82%)	1.57 (29%)	8.29 (89%)	2.88 (80%)
Ammonium	0.34 (59%)	0.38 (44%)	0.84 (4%)	0.64 (58%)

(CV=29%). The pattern of seasonal variations in TFAA concentrations also differed among communities. In tussock and shrub tundra the concentrations decreased from June to July and then rose again in the fall. 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 (Fig. 4-1). This pattern of seasonal fluctuations roughly parallel the pattern expected for seasonal nitrogen release (mineralization of material following freeze-thaw cycles in the spring, Chapter 2, and leaching of leaf litter and initial decomposition of newly produced litter in the autumn), suggesting that the free amino acid pool is tied to inorganic nitrogen release.

There was a large variety of free amino acids found in these tundra soils (Fig. 4-2). The most important 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. These amino acids occured in every sample. Variable amounts of alanine, lysine, ornithine, methionine, valine, and phenylalanine were also found. In some samples the concentrations of these amino acids were as high as those of any of the other amino acids, but they were not found as consistently in all samples from a given

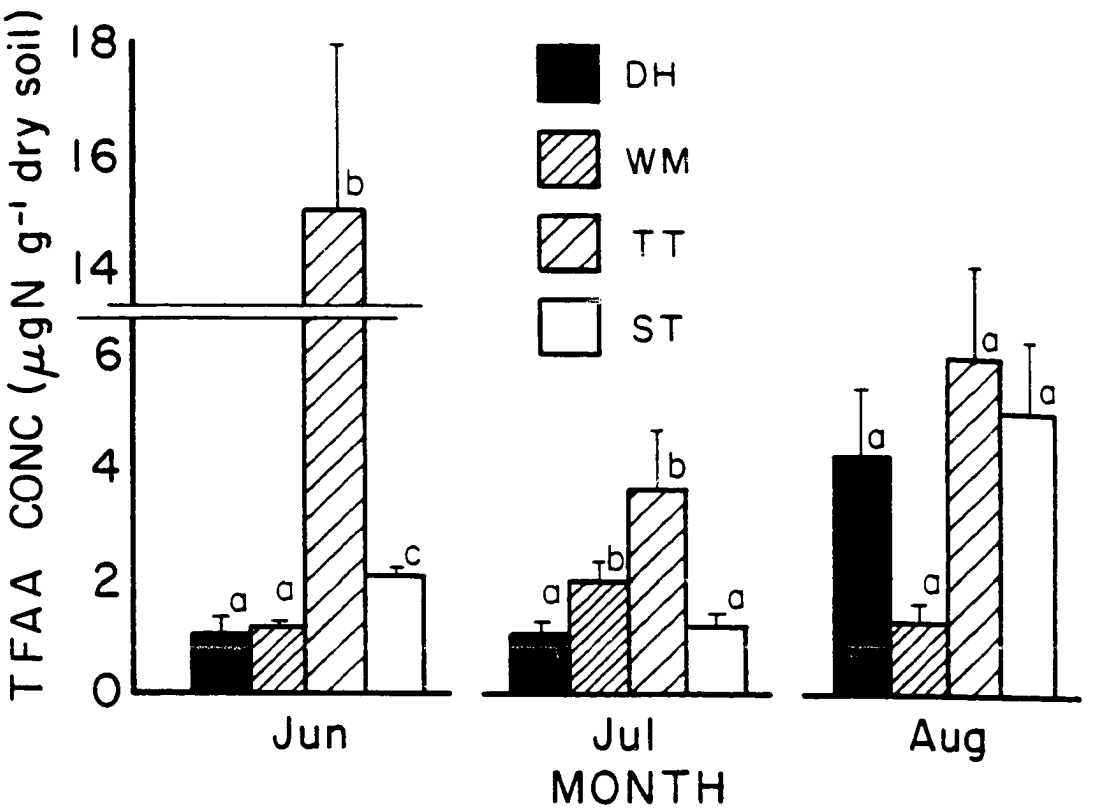

Fig. 4-1. Seasonal changes in concentration (ug g^{-1} dry soil) of total free amino acids in each community (mean + S.E., n=8).

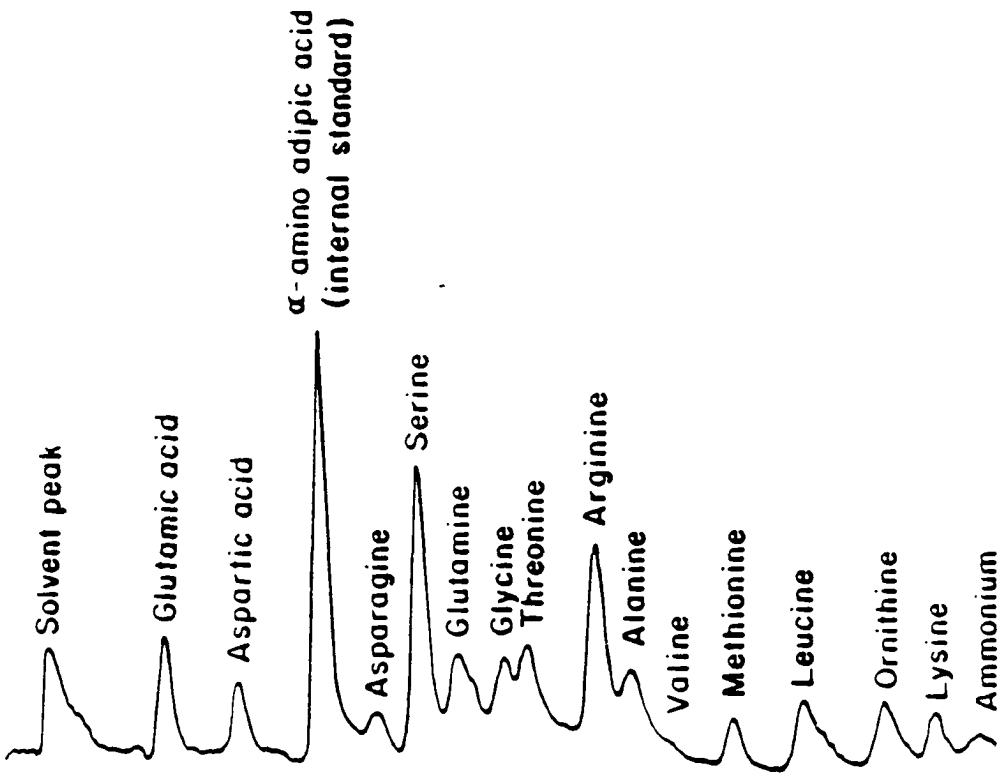

Fig. 4-2. HPLC chromatogram showing a typical elution profile of individual free amino acids.

community.

Of the 15 amino acids identified in these soils (Table 4-2), glycine, aspartic acid, and glutamic acid figure prominently in the assimilation and metabolism of nitrogen in plants, and for this reason the seasonal dynamics of these amino acids will be discussed in detail.

In tussock tundra and the dry lichen heath the average seasonal concentrations of soil glycine, aspartic acid, and glutamic acid ranked inversely to their molecular weight, i.e., the concentration of glycine>aspartic acid>glutamic acid. In the shrub community, on the other hand, aspartate was higher than glycine, and in the wet meadow glutamate had slightly higher concentration than aspartate (Table 4-3). The seasonal average concentration ranged up to 5-fold across communities for a single amino acid (glutamic acid), and nearly 4-fold among amino acids within a single community (DH). The concentrations in the soil of glycine, aspartate, and glutamate were all higher in the fall than in the spring within any given community (Fig. 4-3). In the dry heath community these amino acids dropped slightly in concentration from June to July and then rose above spring levels in the fall. In the other communities, the same amino acids increased steadily in concentration over the season. The seasonal increase in absolute

Table 4-2. Free amino acids identified in the organic horizon of tundra soils from four ecosystems near Toolik Lake, Alaska. Concentrations are in ug amino-N 100 g^{-1} dry soil.

Amino acid	Typical concentration range
Acidic	
Aspartic acid	15 - 60
Asparagine	1 - 8
Glutamic acid	10 - 40
Glutamine	1 - 12
Basic	
Arginine	15 - 50
Lysine	1 - 10
Neutral	
Glycine	20 - 60
Alanine	1 - 5
Leucine	5 - 15
Phenylalanine	1 - 3
Serine	30 -100
Threonine	10 - 30
Ornithine	5 - 15
Methionine	1 - 10
Valine	1 - 3

Table 4-3. Average seasonal concentration (ug N 100 g^{-1} dry soil) of glycine, aspartic acid, and glutamic acid in each community. Coefficients of variation in parenthesis.

	DH	WM	TT	ST
Glycine	31.6 (87%)	20.3 (69%)	65.7 (18%)	22.1 (68%)
Aspartic acid	22.7 (126%)	14.9 (50%)	62.2 (23%)	31.1 (107%)
Glutamic acid	8.5 (83%)	18.7 (53%)	40.8 (57%)	19.1 (101%)

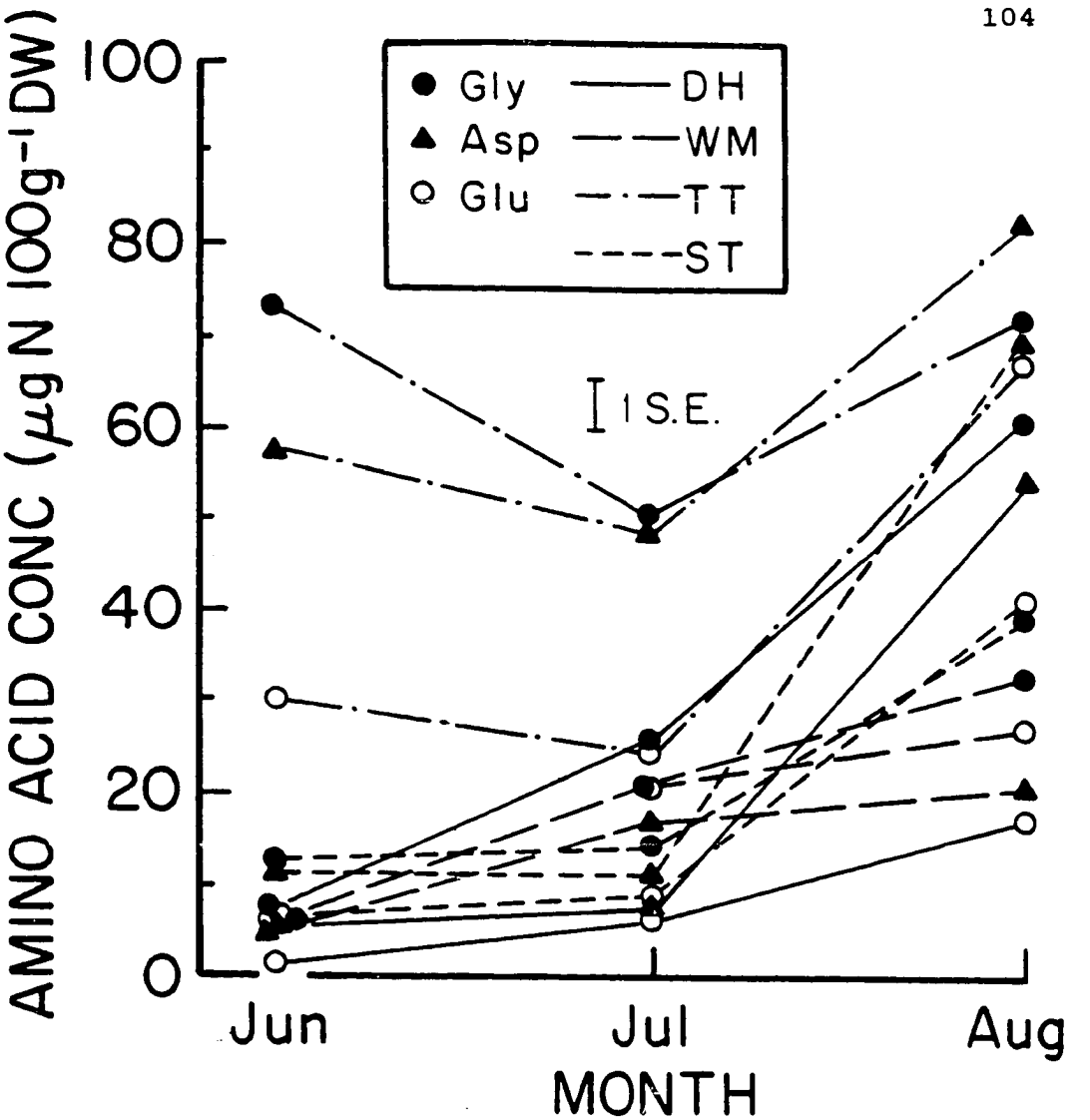

Fig. 4-3. Seasonal concentrations (ug 100 g^{-1} dry soil) of glycine, aspartic acid, and glutamic acid in each community. Typical standard errors indicated.

concentrations was roughly matched by a parallel proportional increase relative to other amino acids (Fig. 4-4). However, there were some notable site differences among amino acids. In the dry heath (Fig. 4-4a) glutamate was rarer than expected (under the presumption of equal concentration of all amino acids) on all sampling dates, whereas glycine increased greatly during mid-season and was about twice as high in the fall as expected under the null hypothesis of equal concentration of all amino acids. Likewise, aspartate was higher than expected in the fall, but fell within expected values earlier in the season. In contrast, these three amino acids all increased in concentration over the season in the wet meadow (Fig. 4-4b), and were 2 to 3-fold more important than expected at the August sampling date. In tussock tundra (Fig. 4-4c), the concentration of glutamate was half and twice of the expected value in June and August respectively but showed no statistical difference in July. Likewise, glycine and aspartate had lower concentrations than expected in the spring, but increased to 2-fold over expected when sampled in July. The same proportional values were found in August. In contrast to the other communities, only the shrub community had a proportionally greater concentration of aspartate than expected during August. Glutamate contributed significantly less in June and glycine

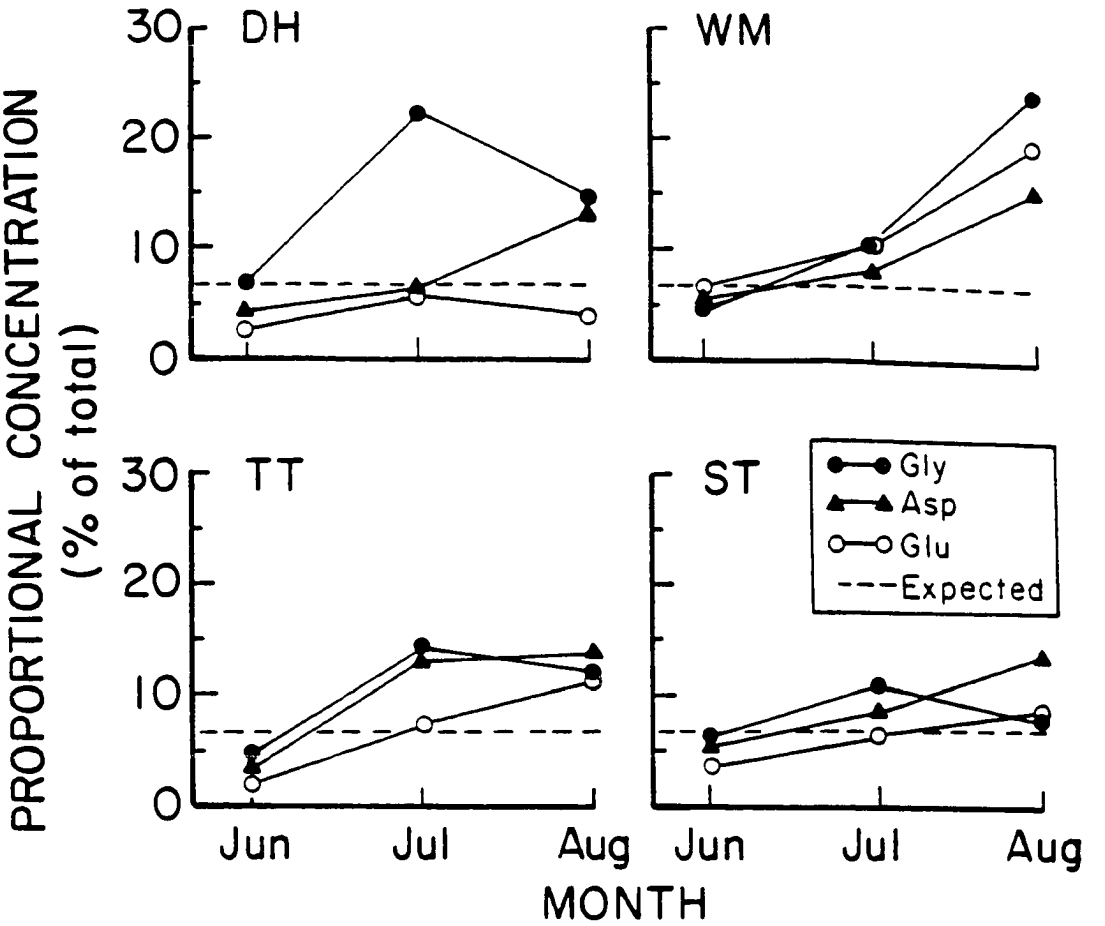

Fig. 4-4. Seasonal changes in proportional contribution (% of total) of glycine, aspartic acid, and glutamic acid to the total free amino acid pool in each community. The dashed line represents the expected proportion under the null hypothesis of equal concentrations of all amino acids.

significantly more in July, but otherwise these amino acids were no different from expected at any sampling date (Fig. 4-4d). Thus, the relative distribution and absolute abundance of free amino acids differed in both space (among communities) and time (over the season).

Discussion

Since free amino acids represent such a ready energy and nitrogen source for microorganisms, it is perhaps surprising that they can be found in detectable concentrations in soil systems. Moreover, the concentration of free amino acids in plant tissues and xylem sap is several-fold greater than in the soil (Sauter 1981, Chapter 5). This raises the question whether free amino acids extracted from soil are derived from root exudates (due to severing of the roots and other forms of trauma) during soil sampling and not from the soil itself (soil solution, colloids etc). If this were true, the concentration of free amino acids should be proportional to the root density and root free amino acid concentration per unit of area. I found, however, that soil free amino acid concentration was not correlated with root free amino acid concentration (calculated from Chapin et al. 1986) across communities (Fig. 4-5). I conclude therefore that

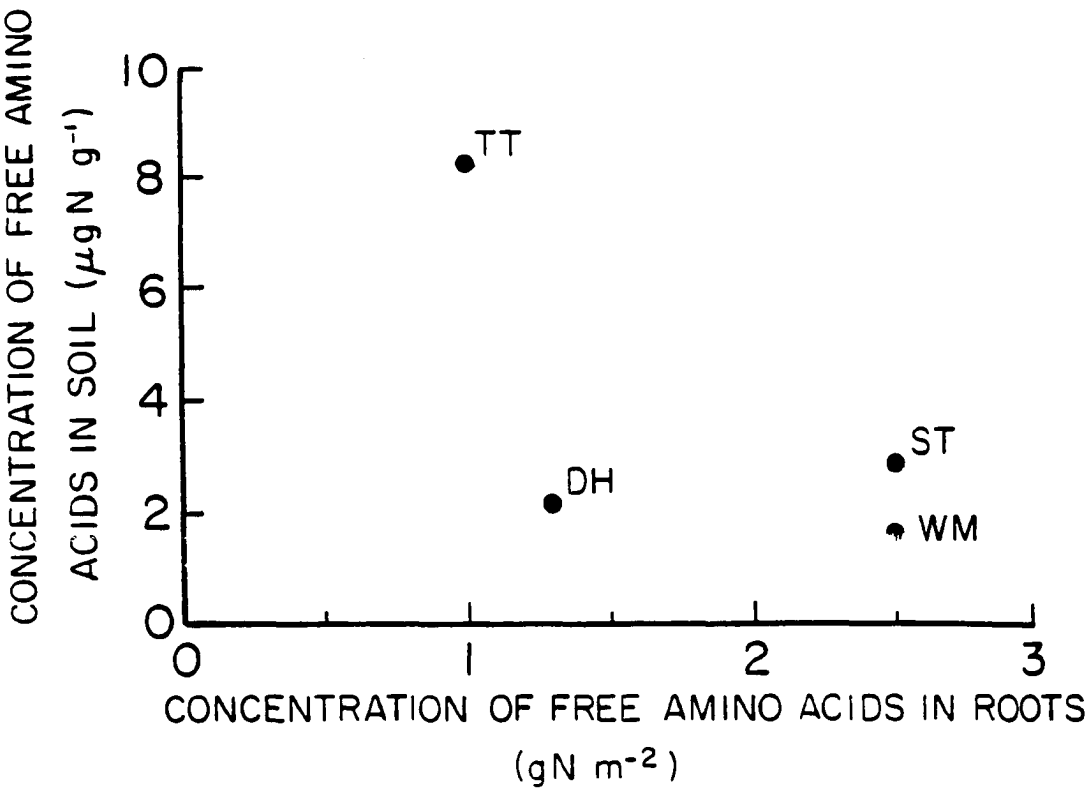

Fig. 4-5. Relationship between free amino acids in roots and that in the soil across vegetation types. DH= dry heath, WM= wet meadow, TT= tussock tundra, ST= shrub tundra.

even though free amino acid extraction from soil most likely includes amino acids released from roots during the sampling process, the concentration or the composition of the estimated pool of soil free amino acids are not artifacts of amino acid levels in plant roots. The high organic matter content and the large concentrations of (uncharacterized) soluble organic nitrogen found in these arctic soils (Chapter 1) makes high concentrations of soil amino acids quite probable. Geochemical studies of marine sediments have shown that the concentration of free amino acids in interstitial pore water can be over 200 umol L^{-1} (Henrichs et al. 1984). In sediment porewaters the turnover time of the free amino acid pool can be quite short, on the order of a few hours to several days (Jörgensen and Söndergaard 1984, Henrichs and Doyle 1986).

The average concentration of free amino acid-nitrogen in the present study (~3.7 ug g^{-1}) is only 0.1% of the averaged fraction of amino acids as constituents of proteins (~3300 ug g^{-1}, Sowden et al. 1977). Thus, both free amino acids as well as ammonium are in low concentrations relative to the soil reservoirs from which they are derived. The present study is the first to report on free amino acids from arctic tundra soils, so no immediate comparison is available with other arctic systems. However, the range in seasonal mean

concentrations from these communities (1-8 ug g^{-1}) compares reasonably with values given by Ivarson and Sowden (1969) for Canadian agricultural soils (2.16 ug g^{-1}), also using water extracts. Read and Bajwa (1985) reported 2.36 ug g^{-1} in the A_O horizon of Calluna heath soils, and the concentration was approximately 10 ug g^{-1} in a study of south temperate alpine soils (calculated from Labroue and Carle 1977). The high concentrations of free amino acids 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).

The high amino acid concentrations immediately following soil thaw may in part be ascribed to the release of soluble cell contents of lysed microorganisms (Sparling 1985). The concentration was particularly high in June in tussock tundra, during which period net nitrogen mineralization was at its highest (Chapter 2). The increase in total free amino acid concentration in the autumn can be explained by 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). The high concentrations of glycine, aspartic acid, and glutamic acid during this

period is most likely due to their inherent large proportions in humic acids and in the protein of primary producers (Mopper 1982).

Glycine, aspartic acid, and glutamic acid contributed 20-34% to the total free amino acid pool. This brackets the value (30%) found in some alpine soils (calculated from Labroue and Carle 1977), and that reported from heath soils (22% calculated from Read and Bajwa 1985). Thus, glycine, aspartic acid, and glutamic acid appear to be important constituents of the soil amino acid pool in a variety of community types. In particular, the high concentrations of aspartate and glutamate in the soil is probably a reflection of the high concentration of their amides in the xylem sap of many plant species (Pate 1962, Sauter 1981) and large pools of glutamate in microorganisms (Brown and Stanley 1972).

Reports on protease activity in tundra soils measured under laboratory conditions (Chapin et al. 1988) suggest that the potential rate of free amino acid production from peptide hydrolysis is far more rapid than the rate of ammonification. It seems likely that the high concentrations of free amino acids in tundra soils and their inferred rapid rate of generation makes this organic nitrogen form a prime substrate for nitrogen mineralization. From a plant perspective, free amino

acids may represent a direct source of nitrogen. Direct absorption of amino acids by plants has been demonstrated in several studies (e.g., Miettinen 1959, Soldal and Nissen 1978, Bledsoe and Sangvanit 1984), and has recently been demonstrated in several tundra species (see Chapter 5). Thus, in arctic tundra soils, free amino acids participate in both nitrogen release and uptake. The active role that amino acids play in processes of nitrogen turnover underscores the importance of this nitrogen fraction to the dynamics of nitrogen cycling in Alaskan arctic ecosystems.

CHAPTER FIVE: AMINO ACID ABSORPTION BY TUNDRA PLANTS: IMPLICATIONS FOR PLANT NITROGEN NUTRITION AND NITROGEN CYCLING.

Introduction

Since nitrogen is generally the most limiting element to plant growth in tundra ecosystems (Russsell 1940, McKendrick et al. 1978, Shaver and Chapin 1980), its abundance and behavior in soil has attracted a great deal of attention. Most studies of plant-nitrogen relationships and nitrogen cycling in both arctic and other ecosystems have focused on the dynamics of inorganic forms of nitrogen (Clark and Rosswall 1981), because mineral nitrogen was presumed to be the exclusive form of nitrogen absorbed by plants. Earlier studies of nutrient absorption have demonstrated that many plant species are capable of taking up organic forms of nitrogen, such as amino acids (Miettinen 1959). However, these reports sought to elucidate the mechanisms of nutrient absorption (e.g., Newton 1974, Watson and Fowden 1974, Borstlap 1977, Soldal and Nissen 1978) rather than to determine the ecological implications thereof. More recent studies of amino acid absorption have further focused on the characteristics of the carrier systems and other mechanistic aspects of the uptake process (Blackman and

McDaniel 1980, McDaniel et al. 1982, Wyse and Komor 1984, Datko and Mudd 1985, Schneegurt and McDaniel 1986).

Uptake of organic nitrogen is well documented in marine systems (Eppley 1971, McCarthy 1972a, Eppley et al. 1977, Kristiansen 1983). Contrary to the work on terrestrial plants, the aquatic studies have emphasized the role of organic nitrogen as an integral component of the nitrogen budget of marine primary producers. Their findings suggest that organic nitrogen may contribute up to 30% of the annual N requirement of these organisms (McCarthy 1972a). The ecological ramifications of direct use of organic nitrogen by terrestrial plants have only recently been adressed. Studies on ericaceous shrubs and their mycorrhizal endophytes have shown that these species have the capacity to directly absorb organic nitrogen compounds such as amino acids and polypeptides (Stribley and Read 1980, Read and Bajwa 1985). Amino acid absorption has also been documented in ectomycorrhizal Douglas-fir (Bledsoe and Sangvanit 1984). These studies concluded that mycorrhizae enhanced the capacity of the plant to absorb amino acids as well as aiding absorption of inorganic nutrients.

Since mycorrhizal associations are prevalent among all major growth-forms of vascular tundra species (Miller 1982), and since arctic tundra soils have high

concentrations of free amino acids (Chapter 4), it appears plausible that organic nitrogen could play a role in the nitrogen economy of arctic plants. In this respect, there are several questions of ecological interest to be answered: To what extent are arctic species capable of absorbing amino acids relative to ammonium? Do species with different degrees of mycorrhizal infection have differential access to the soil amino acid pool? If some species can absorb amino acids in addition to ammonium and nitrate at a higher rate than other species, what bearing does this have on interspecific competition for nitrogen? If the quantity and form of soil nitrogen utilized by plants differ among species in a given community, what is then the most relevant definition of "plant-available" soil nitrogen?

In this chapter I attempt to answer these questions in the light of data on soil amino acid concentrations and measurements of amino acid absorption kinetics for a range of arctic tundra species. From these experiments I advance the hypothesis that soil amino acids represent an important source of nitrogen to tundra plants, and discuss the ecological ramifications that this soil-plant relationship has to our understanding of nitrogen cycling processes in arctic ecosystems.

Methods

Research sites

The research was conducted in the northern foothills of the Brooks Range, Alaska. Three communities (Dry 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 Atigun River (68°22'N, 149°22'W, 850 m elevation). These four communities are representative of the major vegetation types in the Alaskan Arctic (Murray 1978, Webber 1978). The plant communities and soils of these sites have been described more completely in Chapter 1, and by Chapin and Shaver (1985b) and Gartner et al. (1986).

Soil amino acids

Soils from the O2 horizon in each of the four communities were sampled (n=8) for amino acids three times over the growing season: immediately after soil thaw in early June, in mid-July, and late August just prior to freeze-up, as described in Chapter 4. The soil samples were kept cool (3-7°C) until extracted (within 24 hs of collection). Samples were not frozen prior to extraction because this may increase the concentration of free amino acids (Ivarson and Sowden 1966). Samples of 10 g fresh

weight were extracted with 75 ml distilled water for five min in acid-washed polyethylene bottles under slow shaking action. Following extraction the sample was passed through a glass fiber filter and the filtrate frozen at -18°C until further analysis. Concentrations of each amino acid were measured using high performance liquid chromatography, following a precolumn derivatization procedure using the o-pthaldialdehyde/2-mercaptoethanol reagent (Lindroth and Mopper 1979, Jones et al. 1981). Detailed procedure for field sampling and amino acid analyses are presented in Chapter 4.

Amino acid uptake

Uptake experiments were carried out between July 2-12 in 1985. Roots of seven tundra species representing three major growth-forms (graminoids, deciduous shrubs, and evergreen shrubs) were collected in the field from the same horizon as the soil samples. Roots of each species were carefully removed from the soil and rinsed in 0.5 mmol L^{-1} $CaCl_2$. Only unsuberized, healthy-looking fine roots (<0.5 mm) were used; damaged or scenescent roots were discarded. The roots were enclosed in cheese cloth bags and allowed to equilibrate for 30 min at 14°C, the temperature of the experimental solution (Epstein et al. 1963), which is the approximate maximum July soil

temperature at 5-10 cm depth. After temperature equilibration, roots were placed for 10 min in 1 L of a well aerated, well-mixed solution containing the ^{14}C-labeled substrate (methylamine or amino acids). Following absorption, roots were rinsed for 2 min in a 1 L solution containing 1 mmol L^{-1} KCl to exchange off any label that might be left in the free space (Epstein et al. 1963, Chapin and Bloom 1976), dried at 67°C and weighed. The holding solution (where roots were inspected and held prior to the experiment), experimental solution (which contained the radioisotope), and the rinse solution, all contained 0.5 mmol L^{-1} $CaCl_2$ to maintain cell membrane integrity (Epstein 1961). Four concentrations of amino acids and methylamine (10, 50, 100, 500 umol L^{-1}) were used to describe the kinetics of uptake. These concentrations bracket the total amino acid concentrations found in the soils (15-250 umol L^{-1}). Three amino acids (glycine, aspartic acid, and glutamic acid) were chosen for the uptake experiments to allow for comparisons among substrates. These amino acids have low molecular weights, are important in plant nitrogen metabolism, and occur in high concentrations in many organic soils (e.g., Labroue and Carles 1977, Read and Bajwa 1985, Thurman 1985, Chapter 4). Methylamine was used as an ammonium analog (Hackette et al. 1970, Richie 1987) to evaluate absorption

of amino acids relative to ammonium, using the same analytical techniques.

The kinetic parameters (V_{max} and apparent K_m) were calculated from linear transformations of the uptake curves (Wood et al. 1981). Uptake rates in the field were estimated by calculating the absorption rate at mean seasonal concentration of the individual amino acids or ammonium using the equation $v=V_{max}S/(K_m+S)$, where v is uptake rate (umol g^{-1} h^{-1}) and S is the seasonal mean concentration (umol L^{-1}) of amino acids or ammonium in each community. This equation is equivalent to the Michaelis-Menten equation developed to describe enzyme kinetics, and has been adopted in numerous studies of nutrient absorption kinetics both in aquatic and terrestrial systems (MacIsaac and Dugdale 1969, Chapin and Bloom 1976, Whalen and Alexander 1984).

There are several ways of calculating the kinetic parameters V_{max} and apparent K_m. The double reciprocal plot (Lineweaver-Burke plot) has been the most commonly used in the past (Lehninger 1981). However, since it employs reciprocals, 1/v versus 1/S, it is greatly affected by even small errors in the measurement of v and S. Presently this method is not recommended (Wood et al. 1981). Of the two other commonly used plots, Eadie-Hofstee and Hanes-Wolf, the latter is considered superior

(Wood et al. 1981) and was employed in this study.

Radioisotope analysis

^{14}C is a weak ß-particle emitter (E_{max} = 0.156MeV, Health Physics and Radiological Handbook 1984) which does not readily penetrate intact tissue. Hence, roots were combusted in a Harvey Biological Materials Oxidizer (Harvey Instrument Corp., New Jersey). The $^{14}CO_2$ was collected in a scintillation cocktail (1:1:3, methanol:phenethylamine:toluene with 98% diphenyloxazol and 2% p-bis-(o-methylstyryl) benzene 4 g L^{-1}). The samples were then analyzed by liquid scintillation on a Beckman LS 7500 liquid scintillation counter.

Xylem sap of the deciduous shrubs Betula nana and Salix pulchra from the Dry Heath, Tussock Tundra, and Shrub tundra (n=3-6) was collected with a pressure bomb, and free amino acid concentration was determined with the same analytical techniques as for the soil samples (Chapter 4).

Statistical analysis

Data analysis was performed using SYSTAT statisical package (SYSTAT, Inc., 1987). Differences among means were tested using nonparametric one-factor analysis of

variance (Kruskal- Wallis test). Nonparametric multiple range testing (Conover 1980) was used to separate individual means.

Results

In all communities the concentrations of ammonium tended to be similar to or greater than any of the individual amino acids used in the uptake experiments (Fig. 5-1). Similarily, maximum uptake capacity (V_{max}) for methylamine (ammonium) was generally greater than that of any of the amino acids tested (Fig. 5-2, 5-3, 5-4, 5-5). However, irrespective of community affiliation, all species showed high affinity (low apparent K_m) for amino acids compared to methylamine. The half-saturation constant (K_m) for methylamine uptake were generally well above 200 umol L^{-1} (Table 5-1), whereas the K_m for amino acid absorption were mostly below 200 umol L^{-1} (Table 5-2).

The differences in rates of methylamine versus amino acid uptake were greatest at the highest (500 umol L^{-1}) solution concentration. At this concentration methylamine uptake ranged from approximately 4-30 umol g^{-1} h^{-1} among all species. In comparison glycine and aspartic acid

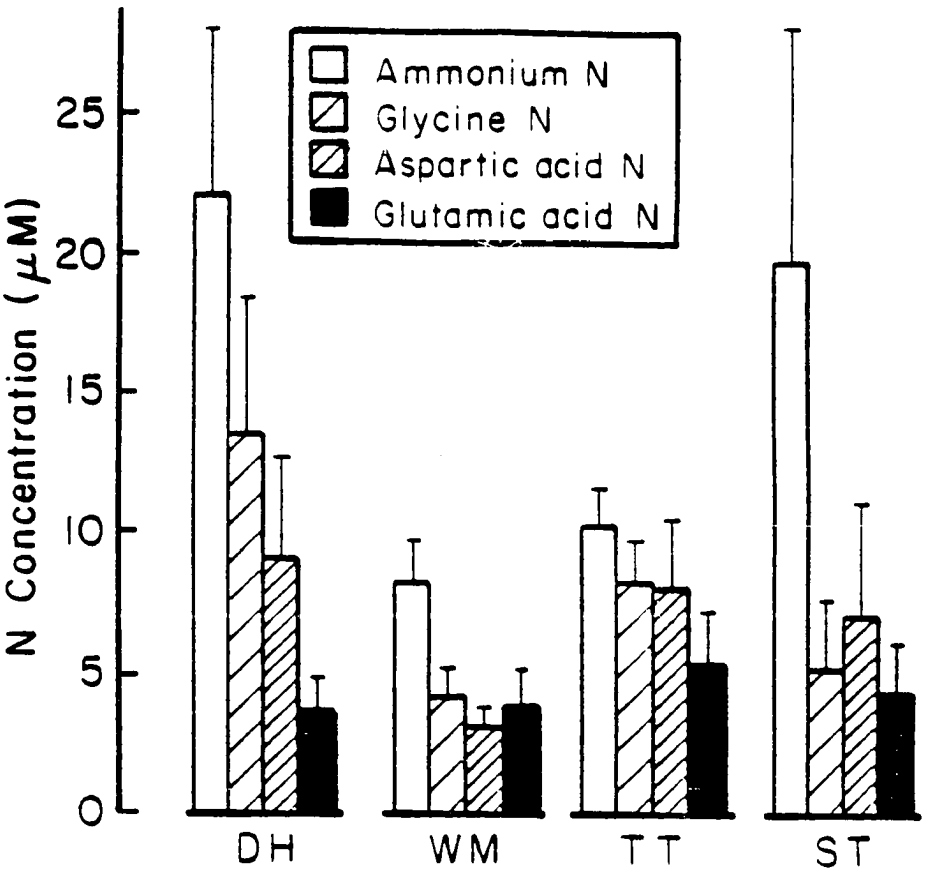

Fig. 5-1. Average seasonal concentration of water-extractable soil ammonium, glycine, aspartic acid, and glutamic acid in four Alaskan tundra communities (mean ± S.E., n=3).

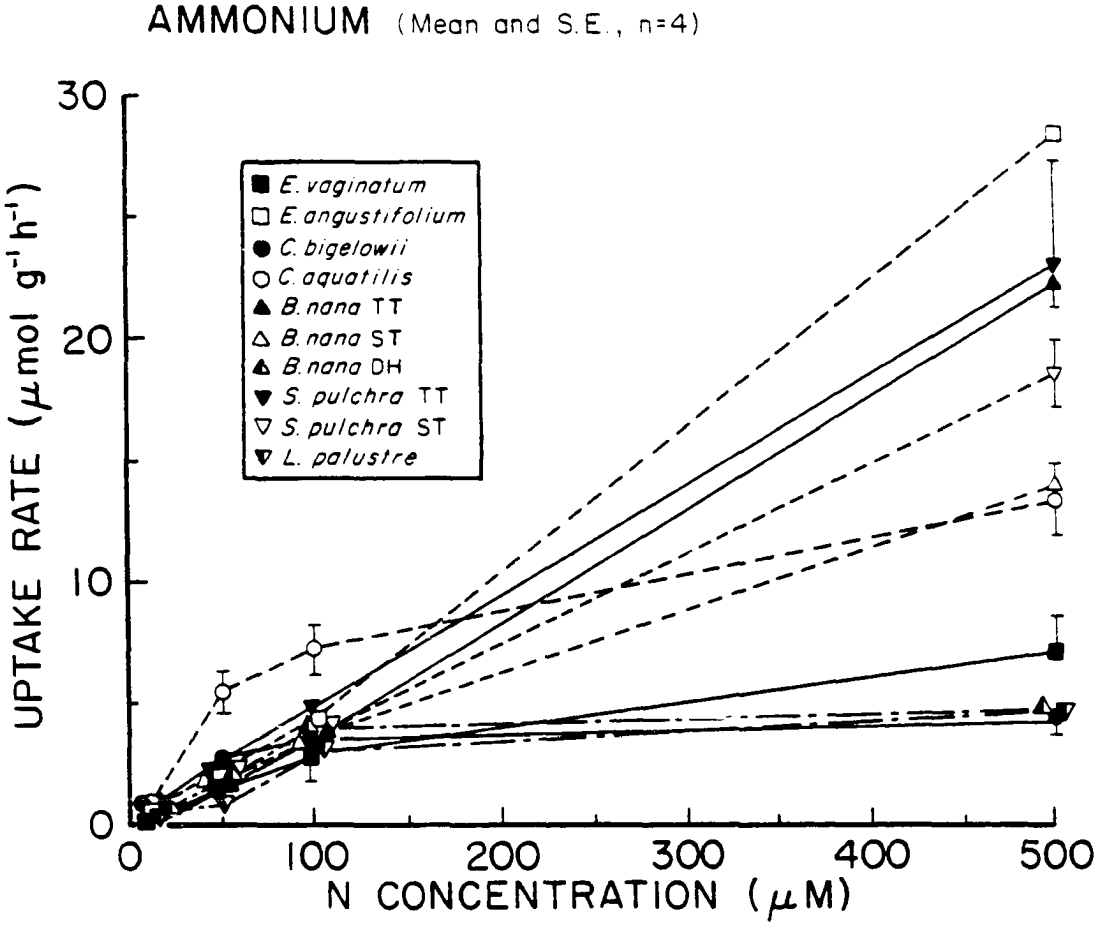

Fig. 5-2. Rate of methylamine absorption by major tundra species of different growth forms (mean ± S.E., n=4).

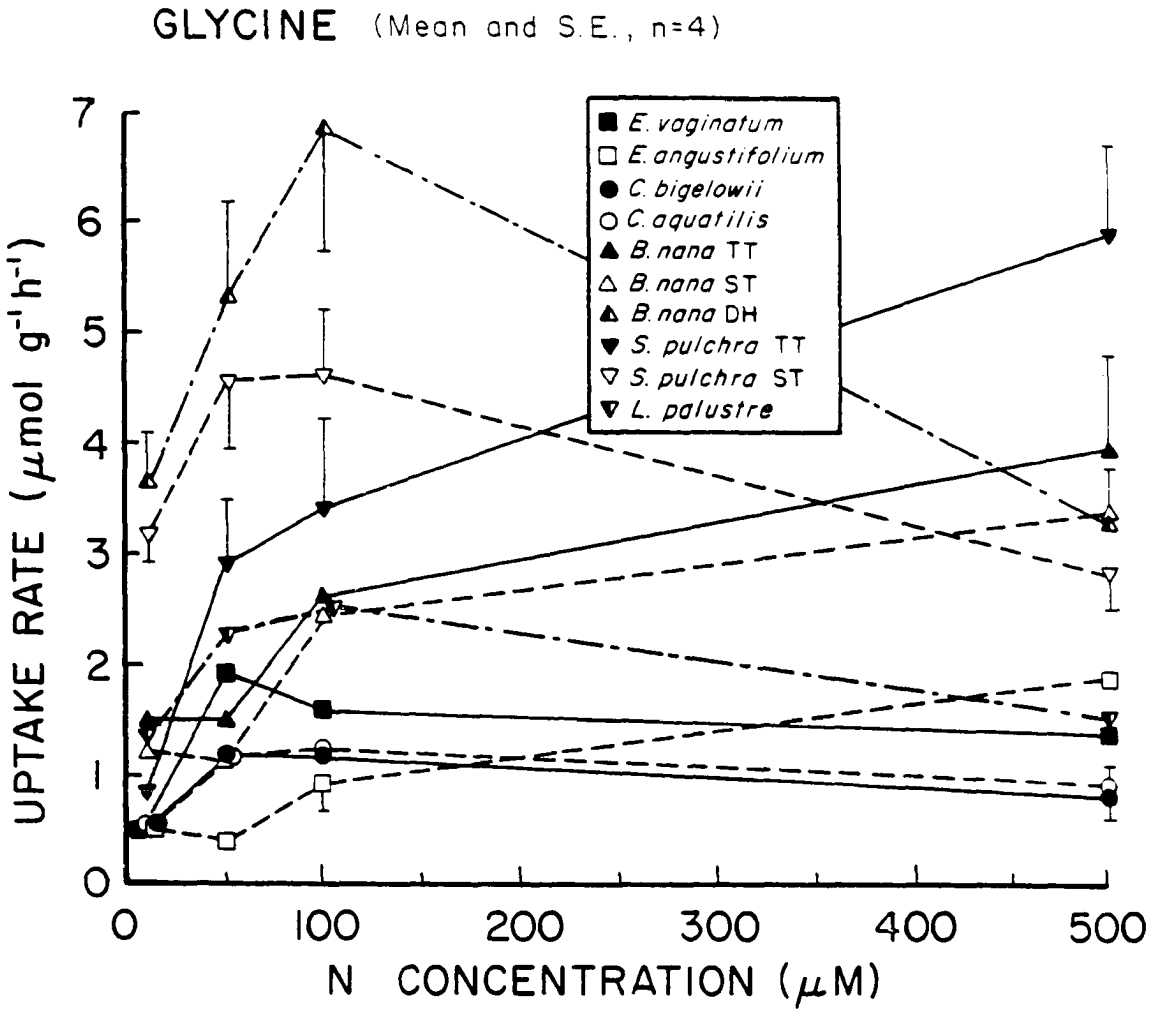

Fig. 5-3. Rate of glycine absorption by major tundra species of different growth forms (mean ± S.E., n=4).

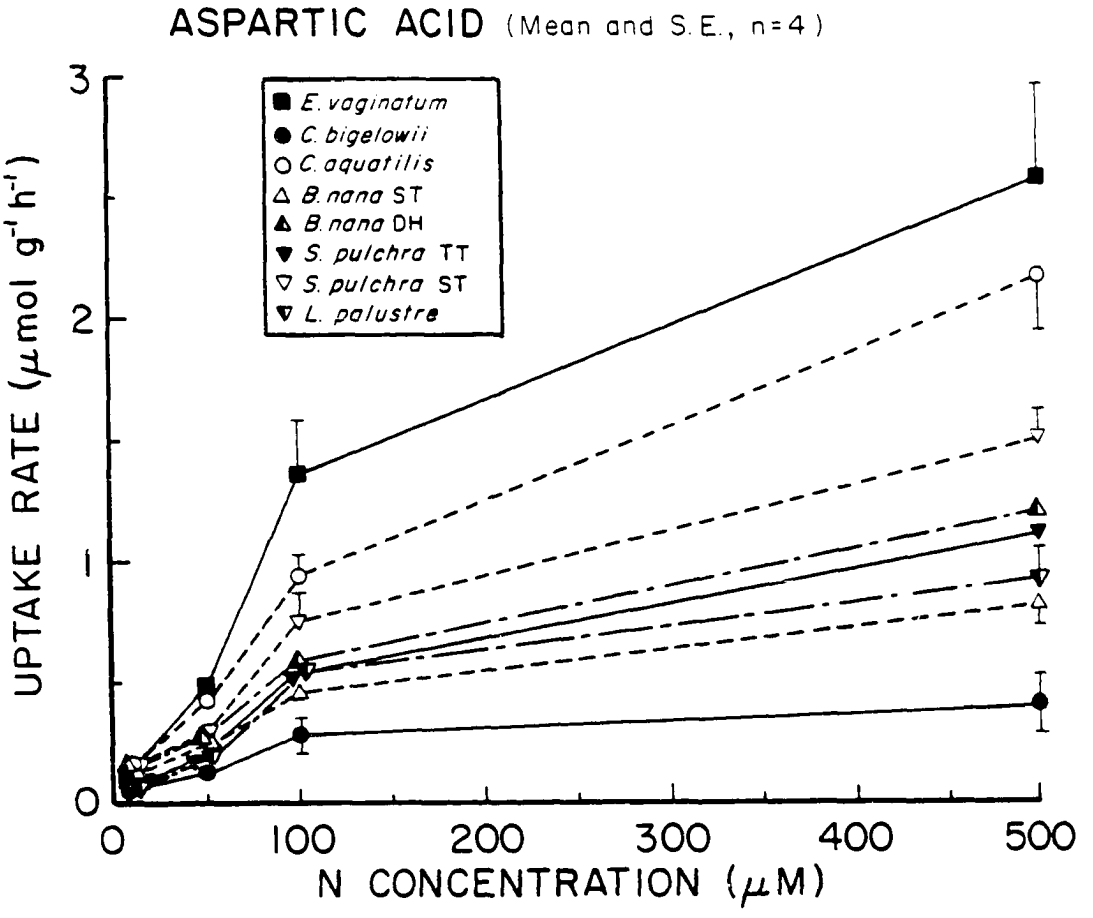

Fig. 5-4. Rate of aspartic acid absorption by major tundra species of different growth forms (mean ± S.E., n=4).

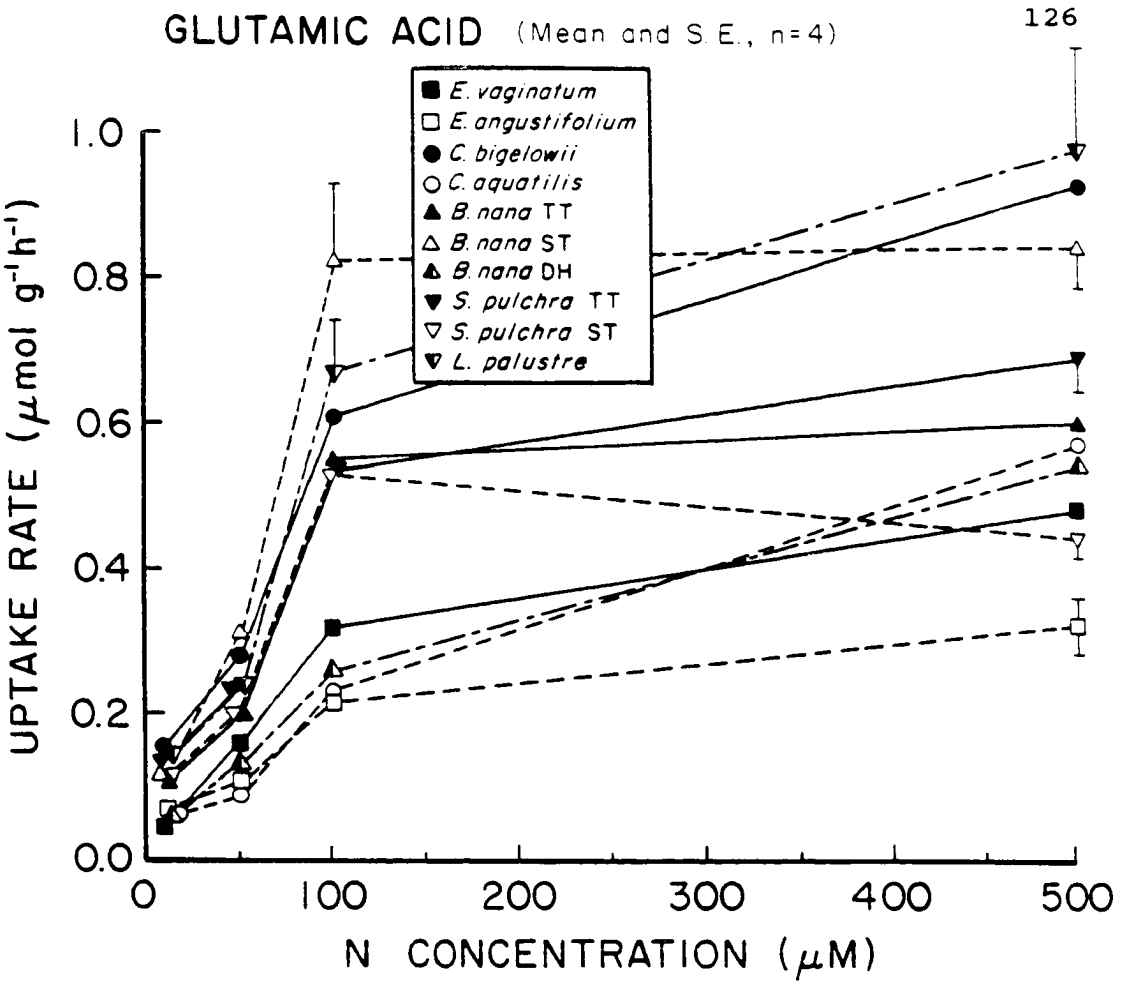

Fig. 5-5. Rate of glutamic acid absorption by major tundra species of different growth forms (mean ± S.E., n=4).

Table 5-1. Kinetic parameters for methylamine (ammonium) uptake by excised roots of major plant species from four arctic tundra communities. Kinetic constants were calculated from four replicates measurements at each of four solution concentrations. DH= dry heath, WM= wet meadow, TT= tussock tundra, ST= shrub tundra.

Community	Species	K_m (umol L^{-1})	V_{max} (umol g^{-1} h^{-1})
DH	Betula nana	67	5.6
WM	Carex aquatilis	153	17.8
	Eriophorum angustifolium	935	17.8
TT	Betula nana	3821	142.8
	Carex bigelowii	78	5.4
	Eriophorum vaginatum	242	13.7
	Ledum palustre	256	7.6
	Salix pulchra	1197	75.9
ST	Betula nana	663	31.7
	Salix pulchra	6717	272.8

Table 5-2. Kinetic parameters for amino acid uptake by excised roots of major plant species from four arctic tundra communities. Kinetic constants were calculated from four replicate measurements at each of four solution concentrations. Amino acid designations are: Gly=glycine, Asp=aspartic acid, Glu=glutamic acid. Community designations as in Table 1.

Community	Species	Amino acid	K_m (umol L^{-1})	V_{max} (umol $g^{-1}h^{-1}$)
DH	Betula nana	Gly	13	6.8
		Asp	152	1.5
		Glu	176	0.7
WM	Carex aquatilis	Gly	9	1.3
		Asp	258	3.2
		Glu	296	0.9
	Eriophorum angustifolium	Gly	143	2.4
		Asp	n.d.	n.d.
		Glu	86	0.4
TT	Betula nana	Gly	64	4.5
		Asp	n.d.	n.d.
		Glu	70	0.7

Table 5-2. Continued.

	Carex bigelowii	Gly	7	1.2
		Asp	81	0.5
		Glu	100	1.1
	Eriophorum vaginatum	Gly	12	2.0
		Asp	293	4.1
		Glu	118	0.6
	Ledum palustre	Gly	9	2.6
		Asp	202	1.3
		Glu	123	1.2
	Salix pulchra	Gly	87	7.0
		Asp	377	1.9
		Glu	30	0.6
ST	*Betula nana*	Gly	96	3.9
		Asp	107	0.9
		Glu	69	0.9
	Salix pulchra	Gly	19	4.6
		Asp	192	2.0
		Glu	32	0.5

uptake at this concentration ranged up to 4-6 umol g^{-1} h^{-1}, whereas glutamic acid absorption was less than 1 umol g^{-1} h^{-1} for all species. At the lower, more ecologically common concentrations, these differences among forms of nitrogen were less pronounced. This was especially true for glycine uptake which was as high as, and in some instances higher than, methylamine uptake at natural substrate concentrations. Under these conditions the rate of aspartic acid and glutamic acid absorption accounted for a maximum of 32% of the rate of methylamine uptake (Table 5-3). These results show that the relative facility of tundra species to absorb amino acids compared with methylamine (ammonium) is greatest at substrate concentrations that reflect natural conditions. The relative rates of methylamine uptake versus that of glycine, aspartic acid, and glutamic acid suggest that under field conditions, amino acids and ammonium may be equally important as a source of nitrogen for many tundra species.

Among the amino acids, glycine (Fig. 5-3) was absorbed at a higher rate than aspartic acid (Fig. 5-4), which in turn was taken up more rapidly than glutamic acid (Fig. 5-5). Thus, for the three amino acids absorption was negatively correlated with molecular weight of the amino acid (Fig. 5-6). Uptake rates differed roughly

Table 5-3. Estimated rates of uptake of ammonium and amino acids in the field, calculated from seasonal mean concentrations of (water-extractable) ammonium or amino acids substituted into the kinetic equation $v=(S * V_{max})/(K_m + S)$, where v= uptake rate (umol g^{-1} h^{-1}), and S refers to the seasonal average concentration (umol L^{-1}) of soil ammonium or amino acids. Column 5 (% of total) denotes the contribution of ammonium and the three amino acids relative to their combined uptake assuming no inhibition among substrates.

Community	Species	Substrate	v	% of total
DH	Betula nana	NH_4	1.41	27.8
		Gly	3.56	70.1
		Asp	0.09	1.8
		Glu	0.02	0.3
WM	Carex aquatilis	NH_4	0.91	67.4
		Gly	0.39	28.9
		Asp	0.04	2.9
		Glu	0.01	0.8
	Eriophorum angustifolium	NH_4	0.73	89.5
		Gly	0.07	8.5
		Asp	n.d.	n.d.
		Glu	0.02	2.0

Table 5-3 continued.

TT	Betula nana	NH_4	0.38	40.9
		Gly	0.50	53.8
		Asp	n.d.	n.d.
		Glu	0.05	5.3
	Carex bigelowii	NH_4	0.63	45.2
		Gly	0.66	47.4
		Asp	0.04	3.2
		Glu	0.03	1.8
	Eriophorum vaginatum	NH_4	0.56	37.1
		Gly	0.81	53.7
		Asp	0.11	7.4
		Glu	0.03	1.8
	Ledum palustre	NH_4	0.29	17.7
		Gly	1.25	76.2
		Asp	0.05	3.1
		Glu	0.05	3.0
	Salix pulchra	NH_4	0.65	46.8
		Gly	0.61	43.9
		Asp	0.04	2.9
		Glu	0.09	6.4

Table 5-3. Continued.

ST	Betula nana	NH_4	0.93	69.9
		Gly	0.28	21.1
		Asp	0.06	4.5
		Glu	0.06	4.5
	Salix pulchra	NH_4	0.81	33.3
		Gly	1.49	61.2
		Asp	0.08	3.1
		Glu	0.06	2.4

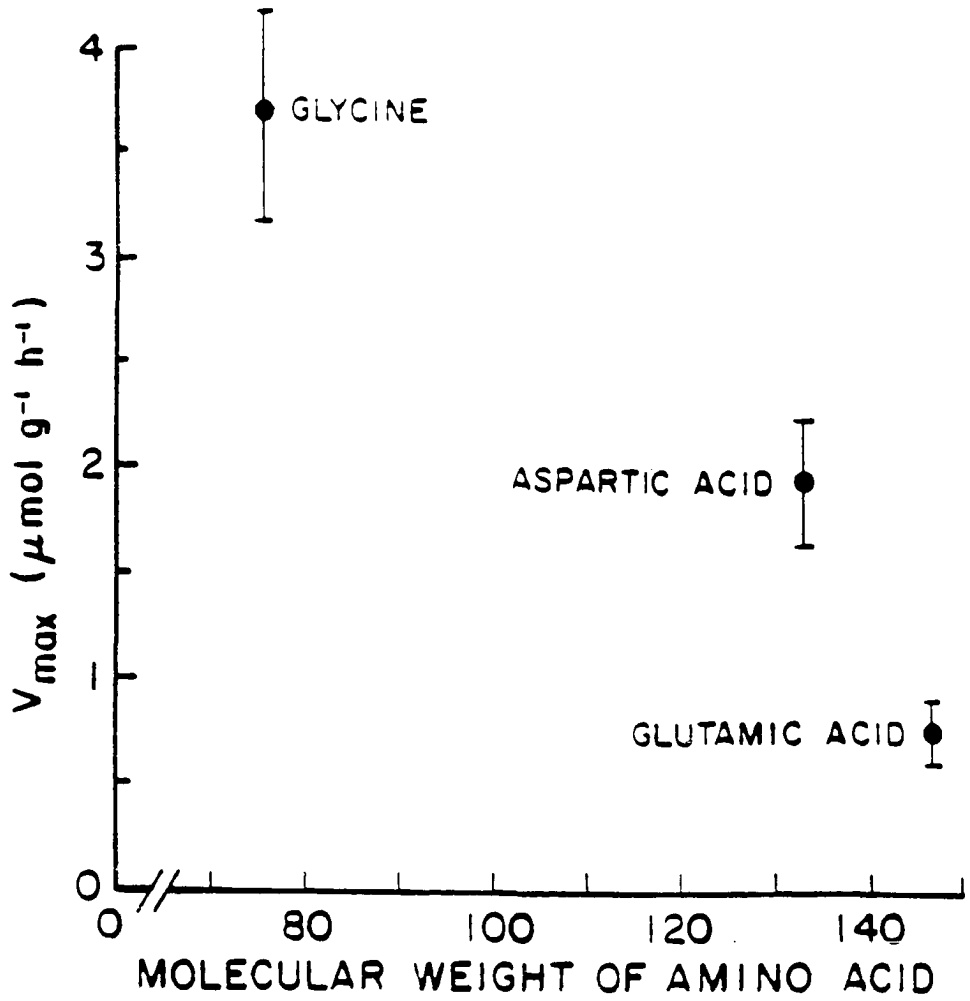

Fig. 5-6. Relationship between molecular weight of individual amino acids and V_{max} among all species used in the uptake experiments. (r^2=0.94, n=10, $p<0.05$).

2-fold between glycine and aspartic acid, and 5-fold between glycine and glutamic acid.

The kinetics of uptake also differed among amino acids. Not only did maximum uptake rate vary depending on substrate (Table 5-2), but the general uptake response as a function of solution concentration differed as well. Most species showed overall high absorption capacity (high V_{max}) and high affinity (low apparent K_m) for glycine. In comparison, aspartate uptake kinetics showed both lower absorption capacity and lower affinity. Glutamate uptake was characterized by the lowest uptake capacity and intermediate affinity, with saturation occuring slightly above 100umol L^{-1} (Fig. 5-5).

Differences in amino acid uptake potential among growth forms depended on the specific amino acid used in the comparison (Fig. 5-7). For example, the deciduous shrubs had the greatest uptake capacity for glycine, whereas the graminoids showed the least capacity. The evergreen shrub showed intermediate capacity. For the higher molecular weight amino acid, aspartic acid, again the deciduous shrubs were generally greater than the evergreen shrub. The graminoids were quite variable, having both the species with the highest and the lowest absorption capacity. Absorption of glutamic acid, the heaviest amino acid, showed no difference among growth

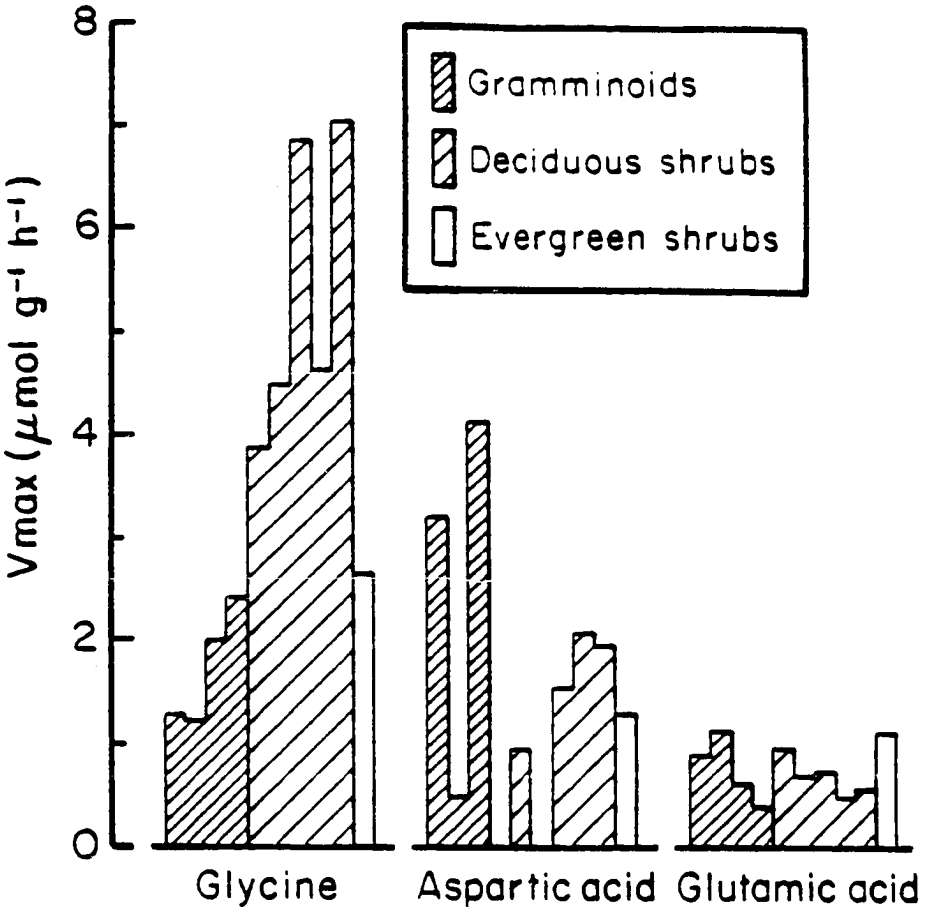

Fig. 5-7. Pattern of V_{max} among growth forms for uptake of glycine, aspartic acid, and glutamic acid.

forms. However, within the graminoids, the finely rooted Carex species had higher uptake capacity than the sparsely branched and thick rooted Eriophorum species. Also, the highly mycorrhizal shrub Betula nana had higher uptake capacity than the less mycorrhizal Salix species, suggesting that variation in root morphology among species within a growth form can account for differences in amino acid absorption.

For those species that occurred in more than one community, uptake capacity for a given amino acid tended to be highest in those populations exposed to the highest soil concentration of that amino acid (Fig. 5-8). For example, in the case of Salix and Betula, both extractable concentrations of soil glycine and and V_{max} of glycine uptake increased from Shrub Tundra to Tussock Tundra to Dry Heath. Similarly, Betula showed highest absorption capacity for aspartic acid in the Dry Heath, where soil concentration of this amino acid was relatively high. By contrast, there was no clear relationship between V_{max} of uptake in graminoids and soil glycine concentration, or aspartic acid absorption capacity in Carex and Salix along soil gradients of aspartic acid concentration. Absorption capacity for glutamic acid showed the strongest trends of increased Vmax with increased soil amino acid concentration. With the exception of Betula from the

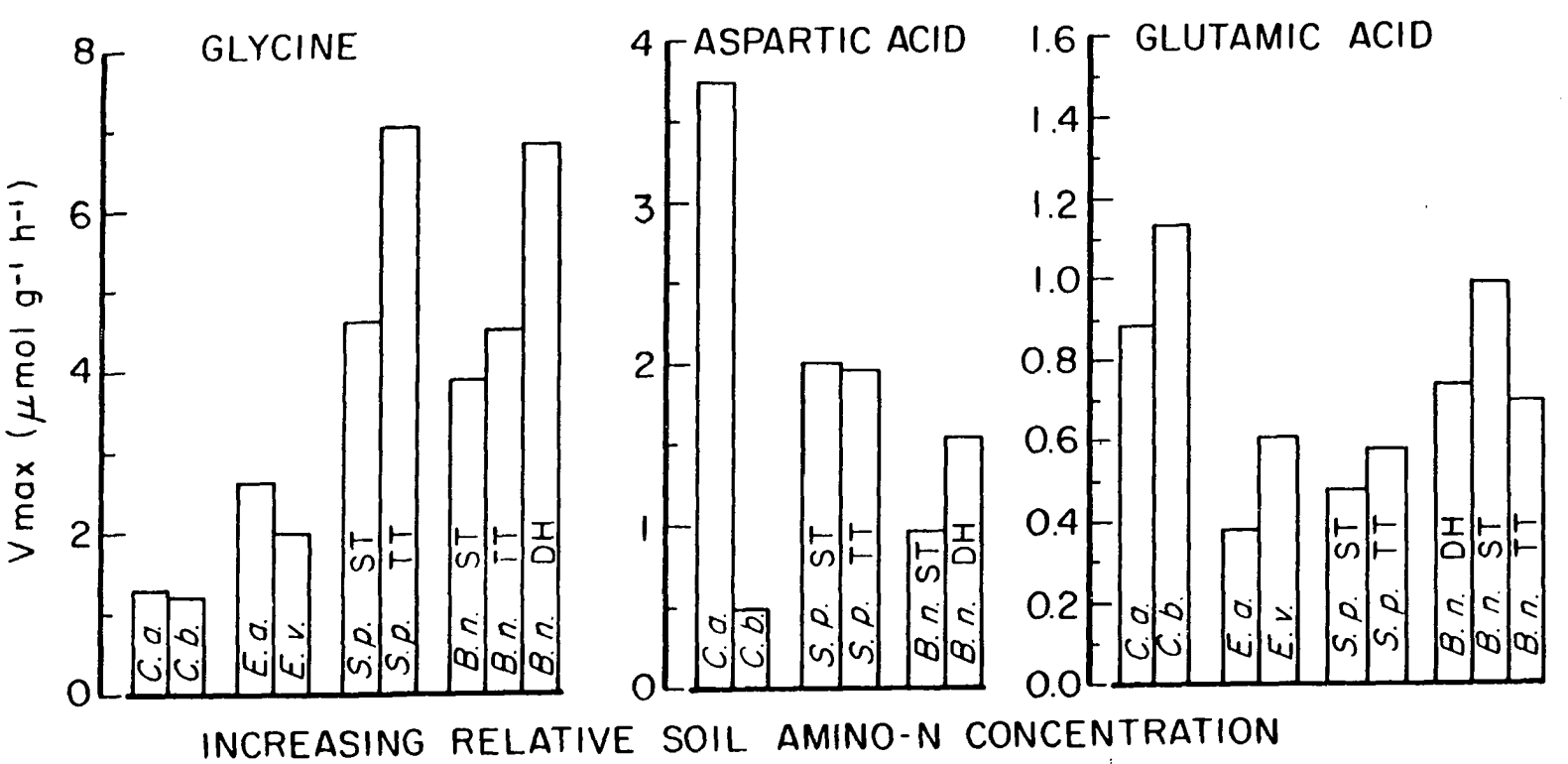

Fig. 5-8. Pattern of V_{max} among populations of species and genera occurring in more than one community for uptake of glycine, aspartic acid, and glutamic acid.

tussock community, all comparisons showed increased V_{max} under higher ambient soil glutamic acid concentration. Despite these trends, the variation in the data renders it unclear to what extent absorption capacity is controlled by soil amino acid concentration.

It is clear, however, that both mycorrhizal and nonmycorrhizal (or weakly infected) species have the capacity to absorb certain free amino acids. The ratio of amino acid to methylamine absorption at ecological nitrogen concentrations (~5-10 umol L^{-1}) was significantly ($p<0.05$) greater in mycorrhizal than nonmycorrhizal species. The difference in absorption was not significant under saturating conditions. Hence, mycorrhizal fungi are important in the absorption of free amino acids by tundra plants primarily under natural (limiting) conditions or in communities with low nitrogen availability.

A few measurements of amino acid concentrations in xylem sap from Salix and Betula in Dry Heath, Tussock Tundra, and Shrub Tundra made in June (Table 5-4) and show very similar concentrations to those reported for Salix smithiana by Sauter (1981). The values for the tundra shrubs should be interpreted with caution, however, since they represent one time measurements, and have few (3-6) replicates per site. Detectable concentrations of asparagine were only recored in two (out of nine) samples

Table 5-4. Concentrations of selected free amino acids in xylem sap from *Salix pulchra* (n=3) and *Betula nana* (n=6) in arctic tundra. The samples were collected in late June and the values expressed in umol L^{-1} (mean ± S.E.).

Amino acid	*Salix pulchra*	*Betula nana*
Glycine	407 ± 86	594 ± 411
Alanine	552 ± 135	282 ± 142
Aspartic acid	1524 ± 560	586 ± 306
Glutamic acid	1867 ± 240	456 ± 216
Glutamine	1039 ± 292	808 ± 629

and were omitted from this data set. Glutamate, aspartate, and glutamine exhibited the highest concentrations in Salix. In Betula glutamine was by far the highest. Glycine had high concentrations in both species, possibly due to its high concentration in the soil (Chapter 4).

Discussion

Although the rates of amino acid absorption were generally lower than those of ammonium absorption, especially at high solution concentrations, it is evident that all the tundra species examined have the capacity to absorb this form of organic nitrogen. Similar findings have been made for ericaceous heath species (Stribley and Read 1980, Read and Bajwa 1985) as well as for conifers (Bledsoe and sangvanit 1984). These observations support the hypothesis advanced here that organic forms of nitrogen such as free amino acids may represent an important source of nitrogen to plant species growing in organic soils.

The half saturation constants (K_m) for amino acid absorption were within the range (100-300 umol L^{-1}) determined in other studies (Wyse and Komor 1984). Many

neutral amino acids however, tend to have K_m's less than 100 umol L^{-1} (Borstlap 1977), as was the case for glycine in the present study.

There are little data available on the use of methylamine as a ammonium analog in higher plants. It appears to work reasonably well in algae and fungi (Hackette et al. 1970, Ritchie 1987), although K_m for methylamine absorption is often several times higher than ammonium (Kleiner 1981). Studies of steady-state ammonium uptake by the arctic sedge Eriophorum vaginatum (F. S. Chapin, III pers. comm.) show very similar rates of absorption compared to those of methylamine reported here for the same species. Recently, other studies of ammonium uptake by Eriophorum vaginatum using $^{15}NH_4^+$ (50-250 umol L^{-1} range) reported higher V_{max} than in my study, but the rates of uptake (at the same measurement temperature) at common concentrations (50 and 100 umol l^{-1}) were as high for methylamine as for ammonium (Marion and Kummerow personal communication). At similar solution concentrations methylamine absorption by tundra plants is as high as ^{15}N-ammonium uptake by Alaskan taiga species (Chapin et al. 1986), despite the higher soil ammonium concentration and higher productivity of the latter ecosystems (Van Cleve et al. 1983). These data are summarized in Table 5-5. Thus, in this study, methylamine

Table 5-5. Comparisons of ammonium versus methylamine uptake at similar temperatures in taiga and tundra species.

	Range of uptake rates @ 500 umol L^{-1} (umol $g^{-1}h^{-1}$)	Uptake rates by *Eriophorum vaginatum* @ 50 and 100 umol L^{-1} (umol $g^{-1}h^{-1}$)	
		50	100
Ammonium	2-30 (taiga species)[1]	4.3[2]	7.7[2]
Methylamine	4-30 (tundra species)[3]	4.4[3]	8.5[3]

[1]Chapin, F.S., K. Van Cleve and P.R. Tryon. 1986. Oecologia 69:238-242.

[2]Marion, G.M. and J. Kummerow. Holarctic Ecology. *In press*.

[3]This study.

appeared to be a reasonable analog for ammonium.

The measurements of rates of absorption and uptake capacity in a laboratory situation cannot be extended ipso facto to field condition because these experiments only define the physiological potential for nutrient absorption. The flux of ions to the root surface is a major controlling factor of nutrient supply (Nye 1977). Ion movement is a function of the diffusion coefficient of the particular ion, its concentration in the soil solution, and the buffer capacity of the soil. Thus, in addition to kinetic characteristics, ion mobility is a major determinant over the ultimate nutrient acquisition of the plant. Table 5-6 depicts some of the physical and chemical properties of the substrates used in the uptake experiments. Ammonium and to a lesser extent glycine exist as cations under the pH conditions of most tundra soils. Aspartate and glutamate exist primarily as zwitterions. However, the protonated amino group of these (and other) amino acids will not fully dissociate until above pH 9. Thus, even though they are neutrally charged, both aspartate and glutamate are likely to participate in cation exchange reactions. It therefore appears that the neutral and acidic amino acids, roughly 85% of the total amino acids (Chapter 4), diffuse neither radically faster nor much slower than does ammonium in the soil. By

Table 5-6. Selected physical and chemical properties of ammonium, glycine, aspartic acid, and glutamic acid.

		pK[2]			
	MW[1]	$-COO^-$	$-NH_4^+$	other	pI[3]
Ammonium	18	-	9.4	-	-
Glycine	75	2.3	9.6	-	6.0
Aspartic acid	133	2.0	9.9	3.8	2.9
Glutamic acid	147	2.1	9.8	4.3	3.2

[1]Molecular weight

[2]Dissociation constant

[3]Isoelectric point

contrast, the basic amino acids (e.g., arginine and lysine) would tend to be bound more tightly to the cation exchange complex, and thus show reduced mobility relative to ammonium. Thus, for the majority of free amino acids in tundra soils, appparent rates of diffusion to the root surface will not greatly alter my estimates of their relative importance based on kinetic studies.

The differences in uptake capacities among amino acids may be attributed to a combination of plant responses to the availability of individual amino acids in the soil, and reduced facility of transfer of higher molecular weight substrates across the plasmalemma. Uptake rates, as indicated by dry weight yield, were negatively correlated with the molecular weight of the substrate (alanine chains, 1-6 units in length) in several ectomycorrhizae associated with the genus Pinus (Abuzinadah and Read 1986), in an analogous fashion to the absorption rates I observed for three amino acids in tundra plants. However, I would hesitate to carry this analogy too far since glycine (a neutral amino acid) and aspartate and glutamate (two acidic amino acids) are very different chemically, and the differences I observed in absorption among these amino acids may be more a function of chemical characteristics than molecular weight.

Differences in uptake capacity among the amino acids

may reflect substrate-specific carriers in the plasmalemma. These carriers, or carrier systems, may be specific to individual amino acids or to classes of amino acids. For instance, Wyse and Komor (1984) recognized three distinct amino acid carrier systems in sugar cane suspension cells. Uptake system I is specific for neutral amino acids (alanine, glycine, serine etc.), aromatic amino acids (eg. phenylalanine and tyrosine), the amides of glutamate and aspartate (glutamine and asparagine), as well as histidine. Uptake system II transports the basic amino acids arginine and lysine. The third system is specific for the acidic amino acids, glutamic acid and aspartic acid.

The existence of such discrete uptake systems would explain why the absorption characteristics of glutamic and aspartic acid were much more similar to one another than either were to glycine. Moreover, a study of uptake of a wide range of organic compounds in Lemna found as many as eight discrete carrier systems, among which were one for neutral amino acids and one for basic amino acids (Datko and Mudd 1985). However, McDaniel et al. (1982), working with Nicotiana tabacum, concluded that arginine (a basic amino acid), aspartic acid (an acidic amino acid) and phenylalanine (an aromatic amino acid) were all transported by a single carrier system. This finding

conflicts with those of the other studies cited above. Thus, it is unclear to what extent or in what form substrate specificity of amino acid absorption exists. Moreover, it is most parsimonious to assume that such a fundamental physiological process as ion absorption operates by the same mechanics across plant species, and that differences in nutrient transport rates among species are not explained by species-specific carrier systems. Nutrient uptake both within and among species is very sensitive to the nutrient status of the plant (Chapin 1988), and the observation that Betula exhibited higher rates of amino acid absorption than did Salix, which has higher tissue concentrations of protein and amino acids (Chapin and Shaver 1988), is in agreement with this finding.

Differences among growth forms in amino acid uptake capacity can better be explained by root characteristics (root diameter, mycorrhizal infection) than by other physiological parameters (e.g., photosynthetic rate, relative growth rate). In particular, it is important to note that mycorrhizal fungi are primarily associated with the deciduous shrubs, presumably accounting for the high amino acid absorption capacity in this growth form. The deciduous and evergreen shrubs tended to have higher uptake rates of amino acids than the graminoid species,

both in terms of absolute rates and relative to ammonium, despite slower growth and lower photosynthetic rates, (Shaver and Chapin pers. comm.).

Many of the fungal hyphae of mycorrhizae associated with deciduous shrubs were undoubtedly severed and removed when the roots were collected. The (inadvertent) omission of these fine hyphae in the absorption experiments suggests that amino acids are even more important for the nitrogen nutrition of mycorrhizal tundra species than I have indicated.

There were no great differences in individual amino acid concentrations among the four communities (Fig. 5-1), nor were there great differences in uptake capacities across gradients of soil amino acid concentrations (Fig. 5-7). Eight of the 13 comparisons showed increased absorption capacity under increased soil amino acid concentration, and the magnitudes of the increased absorption capacities with increased soil concentration were greater than when the trend went in the opposite direction. However, these proportions are not significantly different. Thus, consistent increase in absorption capacity under increased soil ion concentration, that has been documented in these communities for phosphate (Kielland and Chapin 1985), was not observed in the present experiments. Irrespective of

these patterns however, it is clear that many tundra species are capable of absorbing glycine, aspartic and glutamic acid. Considering the concentrations of these amino acids in the soil, and their mobility relative to ammonium, I propose that amino acids play an important role in the nitrogen economy of tundra species.

Several issues of ecological interest arise from the use of amino acids, as well as ammonium, by tundra species. From a soil-process point of view, amino acids represent an important nitrogen mineralization substrate (Ladd and Jackson 1982). Hence, quantifying and characterizing the soluble organic nitrogen pool could help explain differences in mineralization rates between communities and ecosystems. Moreover, soluble organic nitrogen may be a useful index of potentially mineralizable nitrogen (Nakas and Klein 1981).

In addition, amino acid absorption provides a mechanism by which plants can short-circuit the process of nitrogen mineralization, which hitherto has been considered the bottleneck in the nitrogen cycle in arctic ecosystems (Chapin et al. 1980b). Plant-available nitrogen is generally approximated as extractable inorganic nitrogen (ammonium and nitrate) (Vitousek and Matson 1985, Nadelhoffer et al. 1985), and thus nitrogen mineralization precedes plant uptake (Fig. 5-9a). Direct

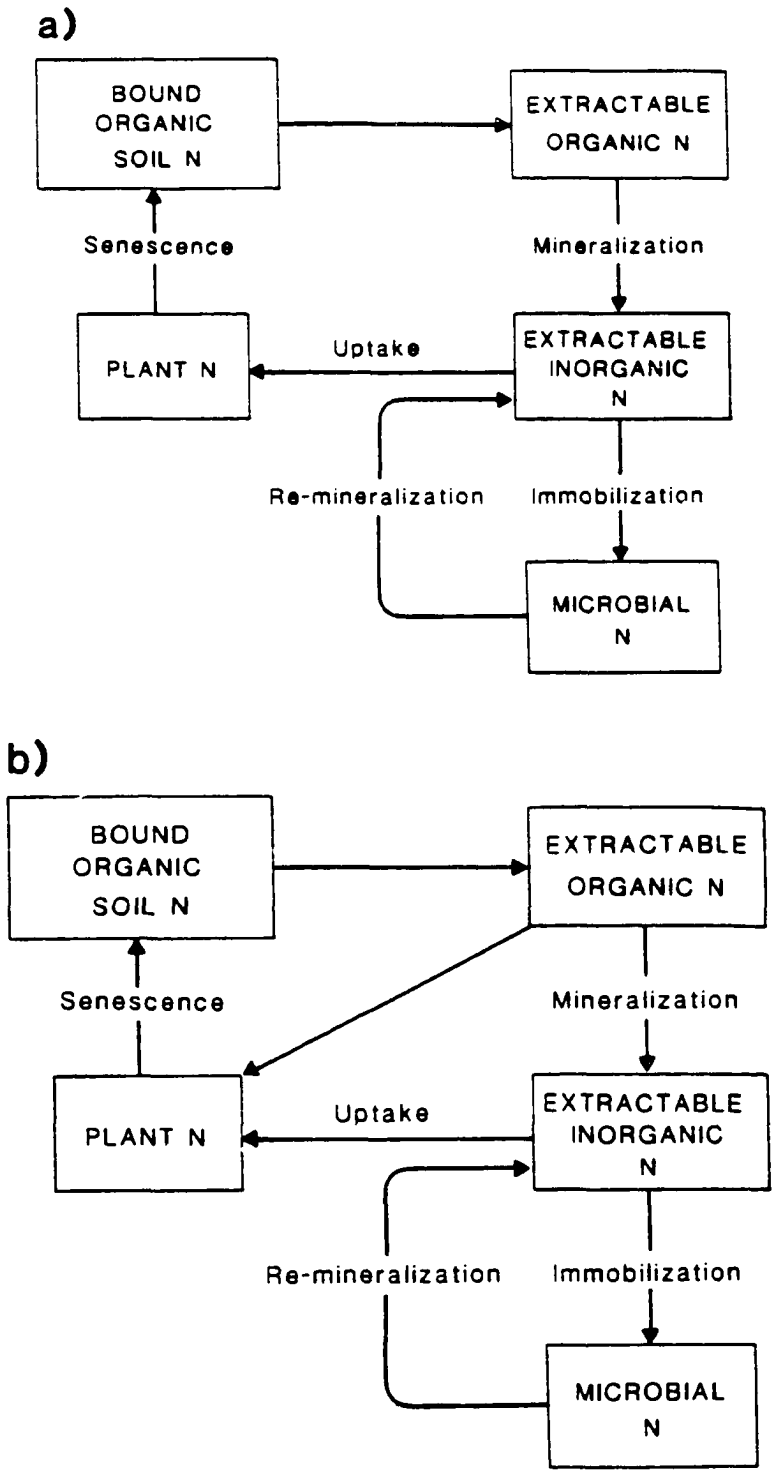

Fig. 5-9. Generalized diagram of the nitrogen cycle under the absence (a) or presence (b) of free amino acid uptake by plants.

uptake by plants of organic nitrogen , such as amino acids, circumvents the mineralization step and may accelerate nitrogen cycling (Fig. 5-9b). Moreover, soil protease activity releases amino acids at a higher rate than mineralization processes generate ammonium (Chapter 2, calculated from Chapin et al. 1988). In arctic ecosystems where a large proportion of the flora may absorb amino acids as well as inorganic forms of nitrogen, ammonium and nitrate pools and net nitrogen mineralization rates are hence insufficient measures of nitrogen availability and supply.

To the extent that plants have differential access to the soil organic nitrogen pool due to their root morphology, mycorrhizal associations etc., a new dimension is added to the issue of plant competition for soil nitrogen which may well have a bearing on plant species distributions along soil physical and chemical gradients (Tilman 1982). Thus, shrub species which have a high capacity to utilize amino acids have a potentially higher rate of supply of nitrogen than graminoid species which rely primarily on ammonium. This discrepancy may be augmented through the timing of amino acid versus ammonium release, as well as through the spatial location of these processes in the soil relative to the distribution of fine root biomass. For instance, in tundra graminoids such as

Eriophorum vaginatum root growth tracks the receding permafrost over the course of the growing season with the result that much of the new, unsuberized roots extract nutrients in colder and deeper soil horizons than do roots of deciduous shrubs (Cnapin et al. 1988). Since much of the annual input of free amino acids may come from leaching of senescing leaves in the autumn and initial litter decomposition in the spring (Nykvist 1963), shrub species may have an advantage in accessing the newly released free amino acids.

Differential access to the soil amino acid pool among plant species also cautions us to keep the anatomy and physiology of the plant in perspective when we set out to define plant available soil nitrogen. Insofar as species are unequal in their capacities to exploit the organic soil nitrogen, "soil nitrogen availability" can no longer be considered strictly a soil parameter. That is to say, given certain soil solution pool sizes of nitrate, ammonium, and amino acids, the availability of soil nitrogen will differ between mycorrhizal and non-mycorrhizal species insofar as the former have greater access to the organic nitrogen, i.e. they have a larger effective soil pool from which they can absorb this nutrient.

I conclude that tundra species are quite capable of

absorbing amino acids. The rates of uptake differ among individual amino acids, but under ecological substrate concentrations these uptake rates are nearly as high as those for ammonium. Consequently, amino acid absorption appears to be ecologically important to tundra species. Mycorrhizal species have higher absorption rates of amino acids than nonmycorrhizal (or weakly mycorrhizal) species under natural amino acid concentrations. There were only slight, and generally non-significant differences in individual amino acid concentrations among communities. This was reflected in small differences in absorption capacity among populations of species across communities. As a collorary to these results, the plant-soil nitrogen relationships explored in this study show that in arctic tundra

1. Quantifying the pools of Kjeldahl nitrogen, ammonium, and nitrate are insufficient to define instantaneous pool sizes of plant-available soil nitrogen.
2. Net mineralization rates underestimate the release of nitrogen to plants.
3. In communities where a large proportion of the flora are tapping the amino acid-nitrogen pool, net nitrogen mineralization rate is an underestimate of total nitrogen uptake by the vegetation.
4. The concept of soil nitrogen "availability" should

incorporate plant physiological characteristics as well as soil chemical parameters.

Summary

The flux of nitrogen through an ecosystem entails several pathways and mechanisms of transfer. The present study carried out near Toolik Lake, Alaska, focused on the recycling of nitrogen within the soil-plant system. In particular I concentrated on the processes controlling decomposition and nitrogen release from soil organic matter, and the subsequent absorption of nitrogen in both inorganic and organic forms by tundra plant species.

The tundra communities studied near Toolik Lake showed a surprising diversity in a number of soil properties and vegetation characteristics. Whereas these soils all tended to be relatively acidic, wet, cold, and high in organic matter, they showed several chemical differences that have important bearings on microbial activity and nutrient dynamics. In terms of organic matter composition, soil lignin concentration, which is inversely related to microbial energy supply, varied 3-fold among vegetation types (Chapter 1). Kjeldahl nitrogen and soluble organic nitrogen both varied 2-fold, and extractable ammonium varied 10-fold across the communities examined (Chapter 1).

The dynamics of carbon and nitrogen also varied substantially among communities (Chapter 2). For

instance, the annual rate of cellulose decomposition varied over 5-fold, from slightly less than 5% in the Dry Heath to approximately 25% in Shrub Tundra. Community-wide differences in the average seasonal rate of net nitrogen mineralization were even more pronounced. Here the difference between the highest rate (in Shrub Tundra) and the lowest rate (in Dry Heath) was more than 20-fold.

Measurements of nitrification in the field and under laboratory conditions showed very low rates of net nitrate production. However, nitrification rates could be greatly increased experimentally by adding ammonium to the soils (Chapter 2). Thus, nitrifying bacteria do exist in these soils, but their level of activity is low possibly due to the low rates of ammonification.

Net nitrogen mineralization was relatively insensitive to changes in soil temperature within the normal range (4-16°C) during the growing season (Chapter 2). This finding suggests that, contrary to popular assumption, the direct effect of temperature is not a primary control over net nitrogen release in arctic tundra.

On the other hand, microbial energy and nitrogen availability strongly affect net nitrogen mineralization (Chapter 2). Soils amended with starch (energy) strongly immobilized nitrogen, but the effect was greatest in Shrub

and Tussock Tundra that have high concentrations of soil lignin, i.e., where soil microorganisms are likely to be most carbon limited. Analogously, nitrogen addition stimulated net nitrogen release most in the Dry Heath and Wet Meadow communities that have the lowest pools of extactable nitrogen and the slowest rates of nitrogen mineralization. From these experiments I conclude that organic matter quality is an important control over nitrogen dynamics in arctic Alaska.

Turnover of the principal nitrogen fractions shows order-of-magnitude differences among communities, but is generally on the order of centuries for Kjeldahl nitrogen, decades for soluble organic nitrogen, and days for dissolved inorganic nitrogen (Chapter 3).

Organic nitrogen, not only as structural components of soil organic matter, but in extractable, labile fractions, dominates the composition of the soil nitrogen pool. A sizeable proportion of the extractable organic nitrogen is in the form of free amino acids (Chapter 4). Aspartic acid, arginine, glutamic acid, glycine, and serine make up the largest portion of this nitrogen pool. Uptake experiments demonstrated that many tundra plant species have the capacity to absorb this form of nitrogen directly (Chapter 5). These kinetic experiments showed that at natural (low) solution concentrations, some tundra

species have the capacity to absorb amino acids at rates equal to ammonium. Based on my own data on amino acid uptake kinetics and soil amino acid concentrations, as well as calculations made from the literature with respect to annual nitrogen flux and plant nitrogen requirement, I propose that amino acids represent a very important source of nitrogen to tundra species.

I conclude that nitrogen cycling in the tundra ecosystems in northern Alaska exhibits several unique features. Over 99% of the total soil nitrogen is structurally associated with the soil organic matter, so even though the system contains large stores of nitrogen, only a small fraction exist in plant-available form. The small pools of inorganic nitrogen and the slow rates of inorganic nitrogen production account for nitrogen limitation of most tundra species. Soil respiration, cellulose decomposition, net nitrogen mineralization, and the turnover of inorganic nitrogen were all significantly correlated with net primary productivity, suggesting that the rate of nitrogen supply is a major control over productivity in these tundra ecosystems.

The low rates of nitrogen input by biological fixation and in precipitation, coupled to the low rates of nitrogen loss from the system by denitrification and leaching, imply that the cycling of nitrogen within the

soil-plant system is very tight. This is further accentuated by the circumvention of net nitrogen mineralization by tundra plants through uptake of free amino acids. The above features of nitrogen dynamics reflect unique patterns of nitrogen cycling in arctic tundra ecosystems.

Appendix A. Elution programs for HPLC amino acid analysis using the pre-column derivatization procedure with o-pthaldialdehyde.

A - Phosphate buffer
B - Distilled methanol
C - Glass distilled water

Set-up gradient

Time (min)	A%	B%	C%
0	0	100	0
15	80	20	0
300	80	20	0

Sample runs

0	80	20	0
45*	20	80	0
50	20	80	0
60	80	20	0
70	80	20	0

Shut down gradient

0	20	80	0
15	0	0	100
30	0	100	0
300	0	100	0

* variable (40-50 min)

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