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TOPOGRAPHIC PATTERNS OF ABOVE- AND BELOWGROUND PRODUCTION AND NITROGEN CYCLING IN ALPINE TUNDRA

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Abstract. Topography controls snowpack accumulation and hence growing-season length, soil water availability, and the distribution of plant communities in the Colorado Front Range alpine. Nutrient cycles in such an environment are likely to be regulated by interactions between topographically determined climate and plant species composition. We investigated variation in plant and soil components of internal N cycling across topographic gradients of dry, moist, and wet alpine tundra meadows at Niwot Ridge, Colorado. We expected that plant production and N cycling would increase from dry to wet alpine tundra meadows, but we hypothesized that variation in N turnover would span a proportionately greater range than productivity, because of feedbacks between plants and soil microbial processes that determine N availability. Plant production of foliage and roots increased over topographic sequences from 280 $g \cdot m^{-2} \cdot yr^{-1}$ in dry meadows to 600 $g \cdot m^{-2} \cdot yr^{-1}$ in wet meadows and was significantly correlated to soil moisture. Contrary to our expectation, plant N uptake for production increased to a lesser degree, from 3.9 g $N \cdot m^{-2} \cdot yr^{-1}$ in dry meadows to 6.8 g $N \cdot m^{-2} \cdot yr^{-1}$ in wet meadows. In all communities, the belowground component accounted for the majority of biomass, production, and N use for production. Allocation belowground also differed among communities, accounting for 70% of total production and 80% of N use for production in dry meadows compared to 55% of production and 65% of N use for production in moist meadows. Variation in microbial processes was highly related to soil moisture, and we found very consistent relationships among microbial respiration, gross N mineralization, and N immobilization among communities. These results indicate that the topographic soil moisture gradient is in fundamental control of the patterns of N turnover among communities and that differences in plant species do not appear to be as important.

Key words: alpine tundra; microbial activity; net primary production; nitrogen cycling; nitrogen transformations; root production; topographic gradient.

INTRODUCTION

Alpine tundra ecosystems in the Colorado Front Range are characterized by small-scale variability in both climate and biota related to topography. Most of the precipitation in the Colorado Front Range alpine region falls as snow (Greenland 1989). The topographically defined snowpack pattern produces a spatial gradient in soil water availability and in the timing of soil dry-down following snowmelt (Taylor and Seastedt 1994). Topographic patterns of snowpack distribution also appear to determine the distribution of plant communities, largely through their effects on growing-season length and soil water availability. Plant species distributions (Webber and Ebert-May 1977, May and Webber 1982, Walker et al. 1993), biomass and aboveground productivity (Billings and Bliss 1959, Scott and Billings 1964, Holway and Ward 1965, May and Webber 1982, Walker et al. 1994), and physiological and production responses to resource manipulations (Bowman et al. 1993, 1995) have been characterized in detail in the different plant communities at Niwot Ridge and in other alpine sites. Absent from our understanding of alpine ecosystem function, however, are corresponding topographic patterns of belowground processes and of internal N cycling. Our objective in this study was to quantify plant biomass, production, and plant and soil N turnover across topographic gradients of dry, moist, and wet alpine tundra meadows.

Variability in both climate and biota lead to multiple factors that potentially affect production and N cycling over the alpine topographic gradient. Patterns of water availability resulting from snowpack distribution are the most obvious. Water availability can limit growth and production in alpine plants (Billings and Bliss 1959, Peterson and Billings 1982, Isard 1986, Enquist and Ebersole 1994) and so probably influences spatial patterns of productivity and N cycling. Furthermore, water availability affects microbial N transformations to varying degrees across alpine topographic gradients (Fisk and Schmidt 1995). Availability of N, limiting to plant growth in some alpine plant communities

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(Bowman et al. 1993), is therefore another factor expected to vary with topography. Finally, the distribution of the plant communities themselves may lead to biotic feedbacks that affect productivity and, through the quality of organic matter substrate available to decomposer organisms, N cycling. The use of nutrients for plant growth and the capacity to increase growth in response to N fertilization differ among alpine plant species and growth forms (Bowman et al. 1993, 1995, Theodose and Bowman 1997*a*, *b*). Topographic variation in allocation of biomass and N to above- vs. belowground production can also result from the different growth constraints of the dominant species (Theodose et al. 1996, Theodose and Bowman 1997*a*), and evidence from other herbaceous ecosystems indicates that this can ultimately influence N turnover and N availability (Aerts 1990, Wedin and Tilman 1990).

Based on previous work in alpine tundra, we expected that production would differ among plant communities distributed across a topographic gradient from dry to wet meadows (Billings and Bliss 1959, Walker et al. 1994). We hypothesized that the cycling of N would vary not only according to topographic patterns of production, but also according to differences in N use among plant species that feed back to affect N availability. Specifically, we expected to find the greatest allocation to root production in dry meadows, and predicted that high microbial immobilization of N would restrict N availability to the greatest extent in this community. In the less N-limited wet meadows (Bowman et al. 1993), we predicted that less conservative N use for production would correspond with greater mineralization processes and higher N availability. To investigate this, we used several replicate alpine topographic sequences in a three-part study of (1) above- and belowground biomass and N pools; (2) above- and belowground plant production, N use for production, and N turnover through biomass; and (3) soil microbial activity and N transformations. The first two components of the study were used to demonstrate the patterns of and relationships among biomass, productivity, and N cycling. The third component further enabled us to investigate whether differences in substrate quality influence the microbial transformations mediating N availability and hence N cycling.

Methods

Study site and sampling design

Plant growth, N uptake, and soil microbial processes were studied in replicate topographic sequences, each including dry, moist, and wet alpine tundra communities. These study sites are on Niwot Ridge, an NSF Long Term Ecological Research site and UNESCO biosphere preserve. Niwot Ridge is located at 3500 m elevation in the Colorado Front Range (40°03′ N, 105°35′ W). Mean annual temperature at Niwot Ridge is −3°C, and the majority of the 900 mm of annual precipitation falls outside the growing season as snow (Greenland 1989).

Dry meadows, dominated by the tussock-forming sedge *Kobresia myosuroides,* occur at the exposed and windblown end of the topographic gradient. Very little snowpack accumulates in these areas, and consequently soils are dry throughout the growing season relative to other plant communities on Niwot Ridge (Taylor and Seastedt 1994, Walker et al. 1994, Fisk and Schmidt 1995). The moist meadow community, characterized by an abundance of the forb *Acomastylis rossii,* occurs at intermediate topographic positions with high snow accumulation (Walker et al. 1993). Soil water content exceeds that of dry meadows, especially in the early parts of the growing season (Taylor and Seastedt 1994, Walker et al. 1994, Fisk and Schmidt 1995). The wet meadow, comprised mostly of the sedge *Carex scopulorum,* occurs in low-lying areas that are the last to melt out in the topographic sequences (mid-June to mid-July). The wet meadows chosen for this study receive snowmelt drainage throughout most of the growing season, and hence the soils remain near saturation (Taylor and Seastedt 1994, Fisk and Schmidt 1995). They differ somewhat from the wet meadows described by Walker et al. (1994), which were dominated by *Caltha leptosepala* and which receive less annual snowpack. Dry and moist meadow soils are primarily Cryumbrepts, while wet meadow soils have been classified as Cryaquepts (Burns 1980).

Sampling was conducted in three replicate topographic sequences located at ~3500 m elevation: the Watershed, Saddle, and north-slope sites of Fisk and Schmidt (1995). Topographic sequences were chosen to be spatially distinct from one another and so that the distribution of each plant community was discontinuous between each sequence. Given these criteria it was necessary that our sites differ in aspect; however, it was not our intent to test the effects of topography beyond the scale at which it affects snow depths. The north-slope toposequence is on the north-facing side of the ridge, the Watershed sequence is south-facing, and the topographic sequence in the Saddle is west-facing. For further characterization of these sites see Fisk and Schmidt (1995).

Each toposequence spanned a snowpack gradient encompassing dry, moist, and wet meadow plant communities. One sample plot (~5 m^2) was established in each plant community on each toposequence, with three replicate plots per community, making a total of nine plots.

Plant biomass and N pools

Aboveground plant biomass was collected on 1 August 1992 and 1993, approximately the time of peak biomass production in the alpine (May and Webber 1982). All vegetation, including mosses and lichens, was clipped at the ground surface. Four replicate 20 × 20 cm squares were harvested within each of the nine

sample plots. Aboveground biomass was sorted in the laboratory into live and dead (litter) fractions and dried to constant mass at 60°C.

Belowground biomass was harvested three times during each of the 1992, 1993, and 1994 snow-free seasons. Early-season collection in dry and moist meadows was on 1 June in 1992 and 1994 and on 15 June in 1993. Wet meadows remained snow-covered until later dates, and collections were made on 15 June 1992 and 30 June 1993. Root biomass was not measured in wet meadows in 1994. A mid-season harvest, coinciding with the peak season aboveground collection, was conducted on 1 August of all three years. The late-season harvests took place on 20 September of all years, following aboveground senescence.

Belowground biomass was estimated from 3.5 cm diameter soil cores collected to 15 cm depth. Previous research has demonstrated that 80–90% of the root biomass is located in the top 10 cm in these plant communities (Webber and Ebert-May 1977). Four cores were collected per plot at each sampling time in 1992 and 1994, and six cores were collected per plot at each sampling time in 1993.

Cores were refrigerated at 2–4°C, and roots were sorted within 6 wk of collection. Cores were washed over a 0.5-mm sieve to remove soil. Roots were sorted into live and dead fractions. Live and dead roots were distinguished by visible criteria, including light color of young roots, presence of a light-colored cortex in brown roots, and resistance to breaking. Live roots were further separated into size classes of <2 mm (fine) and >2 mm (coarse). The coarse-root category also included underground stems and rhizomes. Sorted roots were dried to constant mass at 60°C.

Plant biomass samples were ground and digested for analysis of total N content using a total Kjeldahl nitrogen (TKN) procedure with a cupric sulfate catalyst. Digest NH_4^+ concentration was measured using a Lachat flow injection analyzer (FIA; Lachat, Incorporated, Milwaukee, Wisconsin).

Plant production and N use for production

We used the current year's senescent plant tissue as an estimate of aboveground productivity, and used its N content to estimate plant N use for production. A more standard measure of aboveground production in alpine tundra is to quantify living aboveground biomass at its peak during the growing season (May and Webber 1982). The method that we used was more appropriate for this study, however, because it accounts for resorption of N prior to aboveground senescence and so allows concurrent measurement of biomass production and N use for production. Although leaching losses of N prior to collection cannot be quantified, we made our collections as soon as possible after senescence was complete, during the dry snow-free season before leaching losses would be likely. However, in 1993 wet meadow litter was collected after the first snowfall, and this event probably caused some underestimation of litter mass and N content relative to dry and moist meadows of that year and wet meadows of other years.

The current year's senescent biomass was collected at the same time as the late-season root collection of each year (20 September) by clipping at the ground surface in four 20 $\times$ 20 cm squares in each plot. Senescent biomass of the current year was easily differentiated from previously produced litter, which was gray in color and more fragmented. Senescent biomass was dried to constant mass at 60°C and analyzed for N using the TKN digestion procedure.

Fine root production was estimated using a modified root ingrowth core method (Vogt and Persson 1991). Root ingrowth cores were established on 1 June 1994 by removing four pairs of soil cores (3.5 cm diameter, 15 cm depth) from each plot and filling the resulting holes with a sieved, root-free mixture of dry meadow soil. Root growth into the cores was assessed by recoring (3.2 cm diameter, 15 cm depth) on 1 August and 20 September of 1994. Samples were refrigerated at 2–4°C and processed within 3 wk of collection. Roots were removed from soil cores, washed free of soil, sorted into live and dead fractions, dried, weighed, and analyzed for N content.

Root production is a difficult process to quantify, and each available method requires assumptions that are difficult to verify. Given the objectives of our study, we chose the root ingrowth method as the most appropriate and also most feasible. In the alpine tundra, rocky soils and winter freezing make rhizotron or root window methods impractical. In any ecosystem, sequential coring results can be unreliable because of concurrent growth and death of roots; any differences in root longevity or phenology would call into question comparisons among communities. We assume that errors associated with the root ingrowth method are constant over the topographic gradient, however, and that it thus provides a suitable index of relative patterns of root production in the alpine.

Root proliferation may be enhanced in root ingrowth cores because of the disturbance and the presence of a new root-free environment (Vogt and Persson 1991). Enhanced nutrient availability in disturbed root-free soil is probably one important factor, and we used a single soil type throughout to standardize this effect. Furthermore, any stimulation of root productivity into ingrowth cores would be constrained by soil water availability or by plant growth traits to the same relative degree as would undisturbed root growth in different plant communities. Root production also can be underestimated using the ingrowth method because of the disappearance of roots over the measurement period (Fahey and Hughes 1994). However, root decomposition studies across alpine topographic sequences suggest that this effect would not vary among plant communities (Bryant 1996). We use the N accumulation observed in root ingrowth cores as an estimate of plant

N use for root production; this further assumes that N is not resorbed from senescing roots and that the N accumulated in new roots is an adequate reflection of the relative pattern of N uptake for root production across topographic sequences. The available data support our assumption that N is not resorbed from senescing roots (Nambiar 1987, Aerts et al. 1992); however, we are unable to judge the extent to which N translocation to support new root growth might vary among plant communities.

We used production and N use for production from 1994 and average August 1992 and 1993 biomass and N pools to estimate residence times (N pool/N uptake). These estimates are based on the assumption that N pools are constant from year to year in both living and nonliving plant biomass. While this assumption is tenuous, the relative patterns appear to be consistent from year to year, and so relative comparisons among communities remain valid.

Soil incubations and analyses

Laboratory incubations were used to estimate N mineralization and microbial respiration. Soil for incubations and for measurement of microbial N was collected on 15 June, 10 August, and 20 September 1993. Four 3.5 cm diameter soil cores per plot were collected to 15 cm depth and were refrigerated for ~24 h before processing for incubation. Soil cores were homogenized by hand to minimize structural disturbance, and coarse material greater than 2 mm in diameter was removed. Chloroform-labile microbial N was estimated on subsamples of these soils using a chloroform-fumigation direct-extraction procedure (Brooks et al. 1985). One subsample from each core (~15 g) was shaken for 30 min in 100 mL of a K_2SO_4 solution (0.5 mol/L) at 125 rpm on a rotary shaker and then filtered. A second subsample was fumigated with chloroform for 5 d in a vacuum desiccator, followed by extraction and filtration. Extracts were digested by persulfate oxidation (D'Elia et al. 1977) and analyzed for NO_3^- using a Lachat FIA. The difference in extractable N content of the fumigated and unfumigated soils represented the chloroform-labile N fraction of the soils; a correction factor (K_n) of 0.54 (Brooks et al. 1985) was applied to estimate microbial N.

The four cores from each plot were then pooled for measurement of gross N mineralization and N immobilization using a ^{15}N pool dilution technique. Four subsamples (~25 g dry mass) of composited soil from each plot were placed in Mason jars for incubations, and an additional four subsamples from each plot were placed in 250-mL Erlenmeyer flasks for measurement of initial soil N concentrations. After a 24-h preincubation period at 15°C, 5 μg ^{15}N (99% $(^{15}NH_4^+)_2SO_4$) per gram of soil dry mass was added in 2 mL deionized water to the soil in each flask or jar. This addition of water increased the water content of all subsamples by ~8% above field-moist condition. Initial subsamples in flasks were immediately extracted in 100 mL 2 mol/L KCl. Extracts were analyzed for NH_4^+ and NO_3^- using a Lachat FIA.

After 48 h incubation at 15°C, subsamples in jars were extracted in 100 mL 2 mol/L KCl. Net N mineralization rates were calculated as the difference in NH_4^+ and NO_3^- between the 48-h and initial extracts. Extracts were then diffused in 118-mL sealed specimen cups. Devarda's Alloy was used to reduce NO_3^- to NH_4^+, and powdered MgO was added to transform all NH_4^+ to NH_3. Ammonia was trapped on acidified paper discs, which were analyzed for percentage ^{15}N enrichment using mass spectrometry (Department of Environmental Science, Policy and Management, University of California, Berkeley). Gross N mineralization and immobilization were calculated from percentage ^{15}N enrichment values using the equations of Kirkham and Bartholomew (1954). The diffusion of NH_4^+ and NO_3^- together in this manner leads to a slight overestimation of gross mineralization if nitrification occurs. No net nitrification was observed in wet meadow soils, but net nitrification rates were positive in dry and moist meadow soils. Gross mineralization estimates using both the diffusion of NH_4^+ alone and the diffusion of NH_4^+ and NO_3^- together have been made for a subset of these plots that includes a wide range of nitrification rates. The relationship between nitrification rates and the error associated with the method of diffusion that we used suggests that up to a 10% error may be associated with the estimates of gross mineralization presented in the current study (Fisk 1995).

An NaOH base trap procedure was used to estimate CO_2 evolution (microbial respiration) during the same ^{15}N incubation period. Vials containing 10 mL 0.1 mol/L NaOH were sealed inside Mason jars during the incubation. NaOH was replaced at 24 and 48 h and titrated with 0.1 mol/L HCl in the presence of 2 mol/L $BaCl_2$ to determine how much NaOH had reacted with CO_2.

Total C and N were estimated for soil from all plots to a depth of 15 cm, using C and N concentrations presented by Fisk and Schmidt (1995) and soil bulk density from Fisk (1995).

Statistical analyses

Within-plot averages of all data were used for statistical analyses, resulting in three replicate values (one from each of the three topographic sequences) for each variable in each plant community. We used either two-way or repeated-measures ANOVAs to test effects of communities and sampling time for all variables. For measurements conducted three times within the growing season (root biomass, microbial N, and microbial processes) or measurements conducted in three separate years (senescent biomass) we used repeated-measures ANOVA with sampling time as the within-subjects factor. Other measurements were conducted only twice during the growing season (root ingrowth) or

TABLE 1. Results (F values and significance) of two-way ANOVAs testing effects of plant community and year sampled, for mass and N content of different tundra biomass components.

Source	df	F Biomass	F N
Aboveground living			
Community	2	12.64**	16.16***
Year	1	39.02***	30.09***
Community × Year	2	4.16*	2.40
Error	12		
Aboveground dead			
Community	2	1.64	1.85
Year	1	0.05	0.11
Community × Year	2	2.67	0.78
Error	12		
Belowground dead			
Community	2	16.99***	26.67**
Year	1	0.93	2.14
Community × Year	2	1.44	1.61
Error	12		

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

once per season and in two years (midseason biomass). In these cases, sampling time was treated as another factor in two-way ANOVA. Seasonal relationships between N transformations, microbial N, microbial activity, and soil moisture were tested within each time period using correlation analysis. Significant differences are reported for $P < 0.05$.

RESULTS

Biomass and N pools

Mid-season living aboveground biomass and N increased over topographic sequences from dry (155 g/m^2 and 2.4 g N/m^2, respectively) to moist (262 g/m^2 and 5.1 g N/m^2) and wet meadows (291 g/m^2 and 6.4 g N/m^2) (Table 1; Fig. 1). Mid-season dead aboveground biomass and N exhibited no significant differences among communities or years (Table 1; Fig. 1). Both biomass and N were greater in 1992 than in 1993; however, the same relative pattern, from lowest in dry to highest in wet meadows, was observed in both years, and so we present average values in Fig. 1.

Live fine and coarse root biomass and N also differed

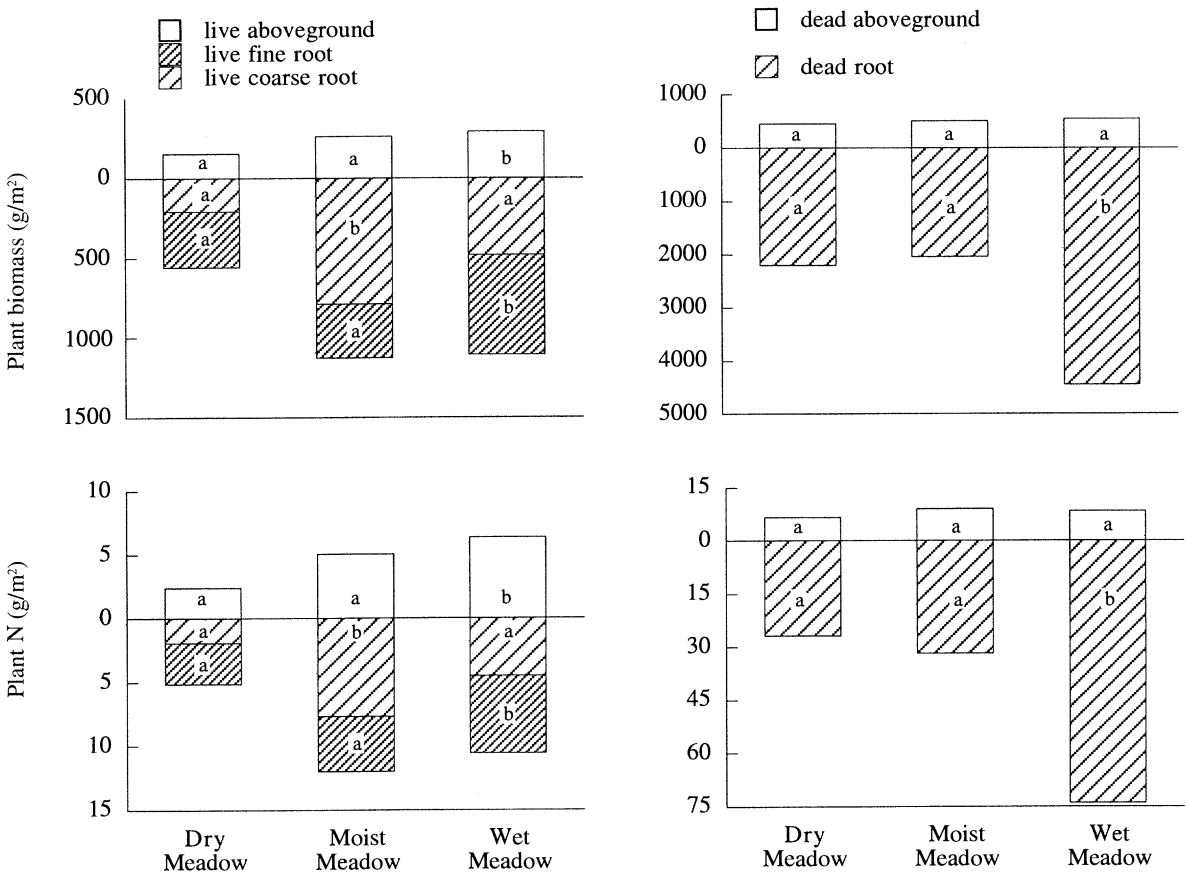

FIG. 1. Average biomass and N pools at mid-season (1 August 1992 and 1993) in living and dead vegetation in alpine tundra topographic sequences. Aboveground pools are depicted above the 0 line; belowground pools below the 0 line. Within each biomass component, different lowercase letters indicate significant differences between communities (Fisher's protected least significant difference [PLSD], $P < 0.05$); see Table 1 for ANOVA results.

TABLE 2. Results (F values and significance) of repeated-measures ANOVAs testing effects of plant community and within-season sampling time for live fine and coarse root biomass and N content. Sampling dates within each year were treated as the within-subjects factor, time.

Source	df	Fine roots		Coarse roots	
		Biomass	N	Biomass	N
Between subjects					
Community	2	35.14***	7.46**	13.77***	8.46**
Year	1	35.51***	11.22**	2.12	0.14
Community × Year	2	0.30	0.08	0.53	0.26
Error	12				
Within subjects					
Time	2	55.74***	42.25***	7.59**	10.24***
Time × Community	4	1.62	0.44	0.65	1.28
Time × Year	2	48.16***	42.32***	3.94*	2.76
Time × Community × Year	4	2.95*	1.70	1.31	2.21
Error	24				
Polynomial tests of linear effects					
1992					
Time	1	169.06***		17.35**	
Time × Community	2	6.68*		0.45	
Error	6				
1993					
Time	1	0.54		0.55	
Time × Community	2	0.45		0.75	
Error	6				

Notes: Because wet meadow roots were not quantified in 1994, only 1992 and 1993 were included in the analysis. Polynomial tests were not conducted on root N content.
* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

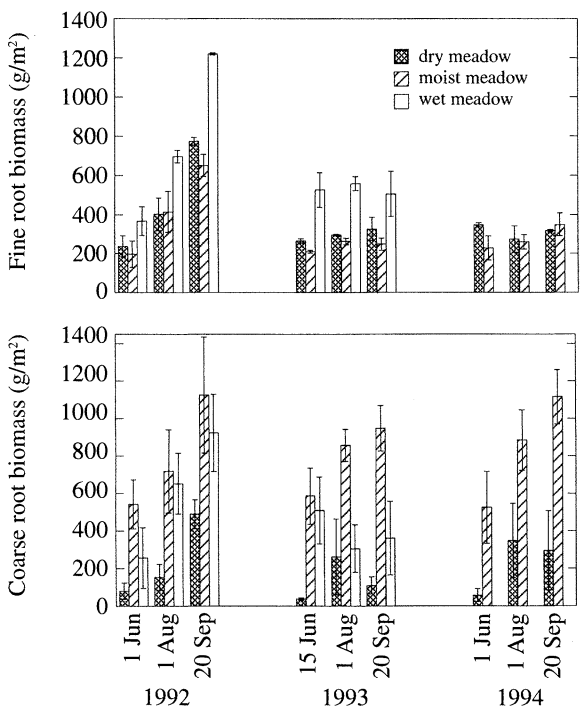

FIG. 2. Seasonal patterns of live fine (top panel) and live coarse (lower panel) root biomass in alpine topographic sequences. Roots were not quantified in wet meadows in 1994. Error bars show standard errors of the mean; $n = 3$. See Table 2 for ANOVA results.

among communities and years (Table 2), and together accounted for ~80% of total live plant biomass and 60–70% of live plant N (Fig. 1). Dead root biomass and N differed among communities (Table 1; Fig. 1), but not between years.

At mid-season, live fine root biomass and N were lowest in dry and moist meadows and greater in wet meadows. Coarse root biomass and N were highest in moist meadows, representing ~70% of total living roots in this community compared to only 40% in dry and wet meadows (Fig. 1). Living root biomass and N quantified earlier and later in the year show that topographic patterns in root biomass and N were consistent throughout the growing season (Table 2; Fig. 2).

Total soil N to a depth of 15 cm did not differ significantly among communities, averaging 660 g/m² in dry meadows, 700 g/m² in moist meadows, and 690 g/m² in wet meadows.

Total plant biomass (living plus dead) at the time of peak aboveground biomass accumulation (1 August) averaged 3360 g/m² in dry meadows, 3930 g/m² in moist meadows, and 6380 g/m² in wet meadows (Fig. 1). Plant N pools likewise increased from dry to wet meadows over the topographic sequences. Total plant N averaged 40 g/m² in dry meadows, 50 g/m² in moist meadows, and 100 g/m² in wet meadows. Dead plant tissue, primarily roots, accounted for three to four times more biomass or N than did live vegetation (Fig. 1).

TABLE 3. Current year's senescent biomass and N content, collected 20 September of each year. Standard errors of the mean are in parentheses; $n = 3$.

Community	Senescent plant biomass (g/m^2)			Senescent plant N (g/m^2)		
	1992	1993	1994	1992	1993	1994
Dry meadow	198[a] (20.5)	137[a] (23.9)	84[a] (14.7)	2.0[a] (0.18)	1.5[a] (0.17)	0.8[a] (0.14)
Moist meadow	189[a] (40.9)	234[a] (58.7)	185[b] (9.9)	1.6[a] (0.16)	2.8[a] (0.98)	1.9[b] (0.21)
Wet meadow	309[a] (82.8)	230[a] (10.4)	249[c] (11.3)	3.0[b] (0.28)	2.3[a] (0.15)	2.2[b] (0.13)

Note: Within each year (columns), values marked with the same superscript letter do not differ significantly (Fisher's protected least significant difference [PLSD], $P < 0.05$).

Together, both live and dead plant matter accounted for 6–12% of total ecosystem N.

Plant production and N use for production

The current year's senescent biomass production and N content were measured in three consecutive years for estimates of aboveground net primary production and N use for production. In 1992 and 1994, senescent biomass production and N content were greatest in wet meadows. In 1993, the greatest production and N were found in moist meadows (Table 3). Temporal variation was most evident in dry meadows, in which senescent biomass in 1992 was more than double that in 1994. Wet meadow senescent biomass was the most consistent among years (Table 3). For all years, differences among plant communities were significant for senescent biomass ($P < 0.05$) but not for N content ($P = 0.09$).

Fine root production estimated in September of 1994 was greater in wet than dry or moist meadows (Table 4). Seasonality of root ingrowth production also differed among communities. Most of the dry and moist meadow production occurred in June and July, whereas a greater proportion of wet meadow production occurred during August and September. Nitrogen accumulation in root ingrowth biomass also was greater in wet than moist or dry meadows late in the season (Table 4).

In 1994 above- and belowground production totaled 280 g/m^2 in dry meadows, 410 g/m^2 in moist meadows, and 600 g/m^2 in wet meadows (Fig. 3). The percentage of production accounted for by roots was higher in dry meadows (70 ± 4%, mean ± 1 SE) than in moist or wet meadows (55 ± 3% and 60 ± 2%, respectively). Total N accumulation for production averaged 3.9 g/m^2 in dry meadows, 5.4 g/m^2 in moist meadows, and 6.8 g/m^2 in wet meadows; roots accounted for 65 ± 2% of N used for production in moist meadows, 70 ± 2% in wet meadows, and 80 ± 3% in dry meadows (Fig. 3).

The ratio of annual biomass production to N uptake (nitrogen use efficiency [NUE], measured in grams of biomass per gram N; Berendse and Aerts 1987) differed among plant communities over the topographic gradient. Wet meadow NUE of 88 ± 2.2 g biomass/g N was greater than that of moist (76 ± 2.5 g) or dry meadows (72 ± 1.2 g).

Nitrogen turnover through plant biomass

Nitrogen residence times in both above- and belowground living biomass varied little among dry, moist, and wet meadows (Fig. 4). Nitrogen use for aboveground production in 1994 was 30–40% of that found in peak season aboveground biomass, for residence times in the aboveground N pool of ~3 yr. Nitrogen accumulation in root production accounted for a much higher percentage of the August fine root biomass (80–90%), resulting in residence times of just over 1 yr (Fig. 4).

Differences in N residence times in dead aboveground and dead root N pools across topographic sequences were more evident than those for living plant biomass (Fig. 4). N residence times in the dead aboveground component of dry meadows were approximately double those in moist or wet meadows, indicating the slowest N turnover through dry meadow litter. For nonliving biomass, belowground N residence times exceeded aboveground N residence times overall. In contrast to the pattern among communities in aboveground biomass, N residence times in dead belowground biomass were greatest in wet meadows.

TABLE 4. Fine root mass and N content in ingrowth cores, established 1 June and collected 1 August and 20 September, 1994. Standard errors of the mean are in parentheses; $n = 3$.

Community	Biomass (g/m^2)		N (g/m^2)	
	1 Aug	20 Sep	1 Aug	20 Sep
Dry meadow	131[a] (11)	198[a] (31)	2.0[a] (0.21)	3.2[a] (0.48)
Moist meadow	125[a] (21)	230[a] (31)	2.5[a] (0.57)	3.5[ab] (0.45)
Wet meadow	150[a] (18)	364[b] (10)	2.2[a] (0.18)	4.7[b] (0.14)

Note: Within each sample date (columns), values marked with the same letter do not differ significantly (Fisher's PLSD, $P < 0.05$).

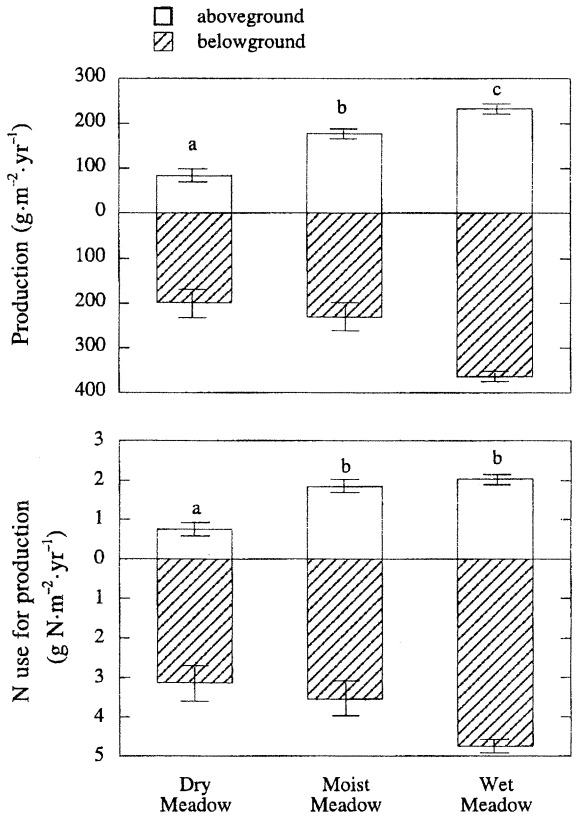

FIG. 3. Above- and belowground production and N use for production over the 1994 growing season in alpine topographic sequences. Aboveground production and N use are depicted above the 0 line; belowground production and N use are below the 0 line. Different lowercase letters indicate significant differences in total production or N use between communities (Fisher's PLSD, $P < 0.05$). Error bars show ± 1 SE; $n = 3$.

Microbial activity and N mineralization

Gross N mineralization, N immobilization, microbial N, and CO_2 evolution (microbial respiration) increased across the topographic gradient from dry to wet meadow soils (Figs. 5 and 6). Immobilization was directly related to and consistently higher than gross N mineralization, resulting in negative net N mineralization. Microbial uptake of N relative to supply was thus uniformly high among communities, and no patterns were evident in net N mineralization. Carbon dioxide evolution, gross mineralization, and N immobilization were correlated to soil water content (Table 5).

For the mid- and late-season incubations, differences in N transformation rates across the topographic gradient were almost entirely dependent on differences in microbial activity (Fig. 7). Gross N mineralization was directly related to CO_2 evolution (Fig. 7; Table 5). The most notable variation in the relationship was due to higher values of gross mineralization relative to respiration in dry and moist meadows in June (Table 5). Assuming that CO_2 evolution is a representative estimate of microbial activity, these data show a constant amount of N mineralized per unit microbial activity in all communities during the mid- and late-season, with a greater quantity of gross N mineralization per unit microbial activity early in the season in moist and dry meadows.

DISCUSSION

Production and decomposition processes in high-elevation alpine tundra are likely to be constrained overall by low temperatures (Holzmann and Haselwandter 1988, Walker et al. 1993), yet distinct patterns of snowpack distribution produce considerable environmental variation over small spatial scales of alpine tundra. Plant species composition also varies with topographic position and the associated snowpack regime (May and

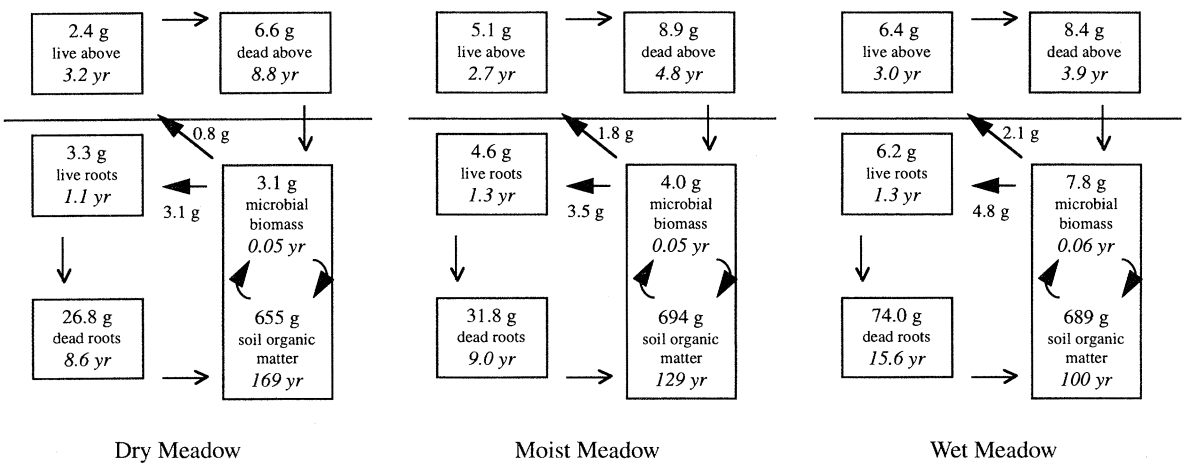

FIG. 4. Nitrogen pools (in boxes), transfers (arrows), and residence times (in italics), in dry, moist, and wet meadow tundra. Nitrogen uptake for production (larger arrows; see Tables 3 and 4) was used for all transfers. Residence times are calculated as N pool per annual uptake.

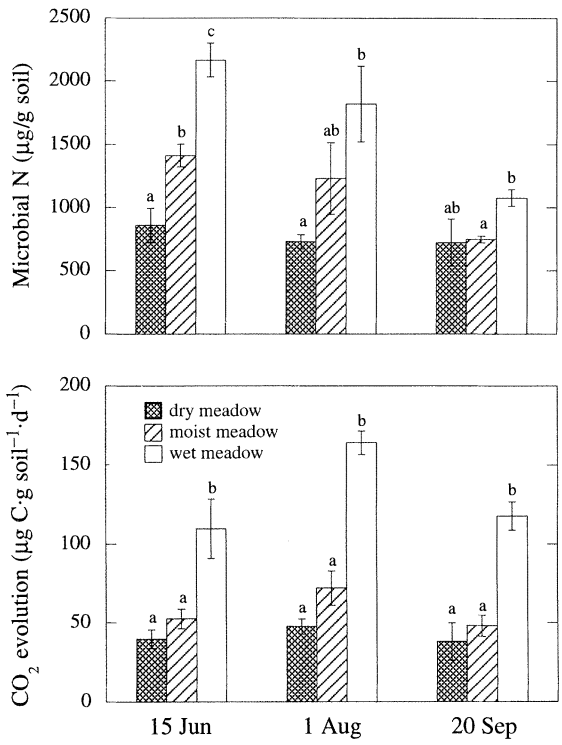

FIG. 5. Microbial N and CO_2 evolution from tundra soils incubated at three times over the snow-free season, 1993. Incubations were conducted for 48 h at 15°C. Different lowercase letters indicate significant differences in means between communities (Fisher's PLSD, $P < 0.05$). Error bars show ± 1 SE; $n = 3$.

Webber 1982, Walker et al. 1993). Our primary objective was to determine whether above- and belowground plant productivity and N cycling patterns coincide with topographic patterns of snowpack distribution, and to what extent differences in plant species composition across the topographic gradient also affect soil processes and hence the pattern of N cycling. Our results indicate that C and N cycling processes vary systematically across topographic gradients of dry, moist, and wet meadow tundra communities. Plant production, plant N uptake, microbial activity, and soil N transformations all increased over the topographic gradient from dry to wet meadows.

These high-elevation ecosystems receive very little growing-season precipitation, and several studies indicate that landscape variation in soil moisture, determined primarily by patterns of snowpack and snowmelt, is an important determinant of patterns of aboveground plant biomass and production in the alpine (Billings and Bliss 1959, Scott and Billings 1964, Holway and Ward 1965, Walker et al. 1993). Our results support this and indicate that soil water availability may be a fundamental topographic control over belowground production as well as internal N cycling.

Plant productivity and N use for production

Although the relationship between snowpack and alpine plant communities is well documented, the exact pattern of aboveground biomass found among plant communities differs among studies. May and Webber (1982) and Walker et al. (1994) found greater aboveground biomass in dry and moist meadows than in wet meadows, whereas Scott and Billings (1964) and Bowman et al. (1993) show greater biomass in wet meadows. Most alpine plant biomass is found belowground (Scott and Billings 1964, Rehder 1976*a*, *b*, Rehder and Schäfer 1978, Webber and Ebert-May 1977), and so we included the belowground component to try to better understand patterns of productivity and N use. The topographic pattern of plant productivity and N uptake

TABLE 5. Correlation coefficients and significance for relationships among soil microbial processes, microbial N, and soil water content, measured in laboratory incubations in 1993; $n = 9$ for each sample date.

	Gross mineralization	Immobilization	Microbial N	Water content
15 June				
CO_2 evolution	0.83	0.88	0.69	0.75
Gross mineralization		0.94	0.73	0.62
Immobilization			0.77	0.87
Microbial N				0.57**
1 August				
CO_2 evolution	0.96***	0.95***	0.78**	0.80**
Gross mineralization		0.99***	0.84**	0.89***
Immobilization			0.84**	0.90***
Microbial N				0.67*
20 September				
CO_2 evolution	0.93***	0.94***	0.86**	0.86**
Gross mineralization		0.98***	0.83**	0.92***
Immobilization			0.83**	0.94***
Microbial N				0.65

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

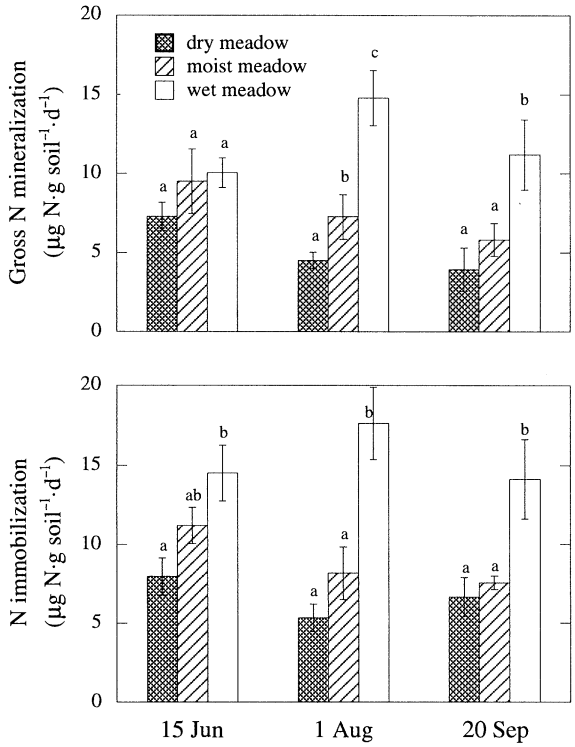

FIG. 6. Gross N mineralization and N immobilization in tundra soils incubated on three occasions over the snow-free season in 1993. Incubations were conducted for 48 h at 15°C. Gross mineralization was calculated using the equations of Kirkham and Bartholomew (1954), and immobilization was calculated by difference from net N mineralization. Different lowercase letters indicate significant differences in means between communities (Fisher's PLSD, $P < 0.05$). Error bars show ± 1 SE; $n = 3$.

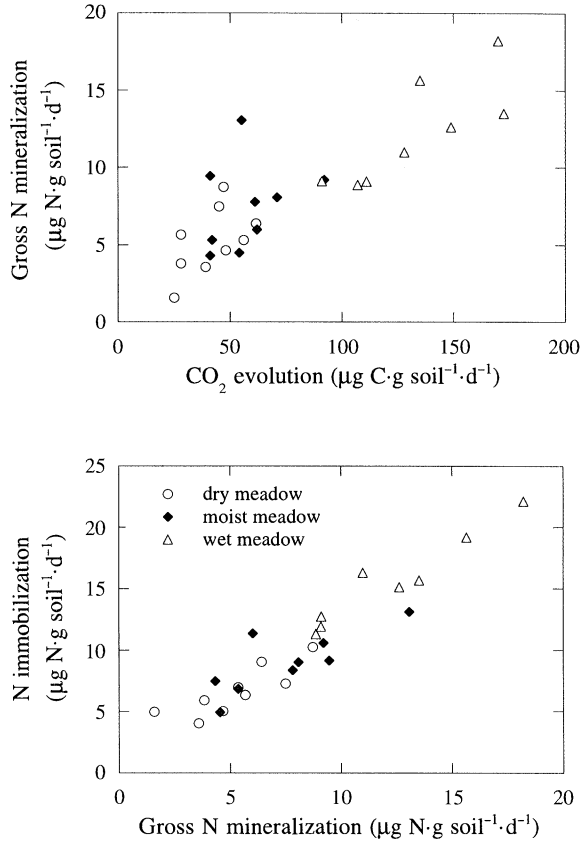

FIG. 7. Relationships between gross mineralization and CO_2 evolution (top panel) and between N immobilization and gross N mineralization (lower panel) over alpine topographic sequences, for three different incubation dates together.

that we observed (highest in wet meadows, intermediate in moist meadows, and lowest in dry meadows) coincides with previously demonstrated spatial patterns of soil moisture (Taylor and Seastedt 1994, Fisk and Schmidt 1995). By including fine roots in our estimates of production, we find a significant relationship with soil moisture measured in these plots in 1992 (from Fisk and Schmidt 1995) and also in 1993 (see *Results*; $R^2 = 0.67$, $P = 0.01$, for each year). Furthermore, much of the production difference between wet meadows and dry and moist meadows is due to late-season root growth. One of the most important factors allowing late-season growth in wet meadows is relatively high water availability from snowmelt, such that these soils do not experience the seasonal dry-down found in dry and moist meadows (Taylor and Seastedt 1994).

Topographic patterns of water availability also are related to productivity in mesic grasslands (Schimel et al. 1991, Benning and Seastedt 1995), yet in contrast to the alpine, patterns of productivity in arctic tundra appear to be less influenced by topographic environmental gradients. Our estimates of annual NPP in the alpine (280–600 g/m^2) are similar to those in arctic tundra of 270 g/m^2 in wet meadows and 590 g/m^2 in tussock meadows (Shaver and Chapin 1991). However, the differences in productivity and nutrient use found among the arctic communities did not follow any systematic trend over the toposequence (Giblin et al. 1991, Shaver et al. 1991). In arctic tundra, microclimatic controls over productivity may be of secondary importance to substrate-quality-mediated differences in nutrient availability (Nadelhoffer et al. 1991). Two factors are probably important in differentiating N cycling patterns between the two tundra systems. Because of the dry alpine growing season, a substantial gradient in soil moisture exists across the alpine topographic sequence, whereas soils are more consistently saturated in the arctic communities (Giblin et al. 1991). The arctic topographic sequence also consists of a more diverse group of plant communities, including graminoid-dominated tussock and sedge tundra, shrub tundra, and heath-dominated communities, compared to the graminoid- and forb-dominated alpine communities included in this study.

Optimal soil moisture, air temperature, and nutrient availability for plant growth coincide with each other

to varying degrees from year to year, due to the short alpine growing season and differences in the timing of snowmelt. The growth of many alpine plants also is constrained by the formation of buds one to several years in advance (Aydelotte and Diggle 1997, Diggle 1997). These multiple factors can lead to high interannual variation in plant growth and production in the alpine (Walker et al. 1994, 1995). High year-to-year variation in aboveground production has been documented over the longer term in alpine tundra (Walker et al. 1994). Our estimates fell within a similar range (80–260 g/m^2) as previous studies on Niwot Ridge (Webber and Ebert-May 1977, 120–300 g/m^2; Walker et al. 1994, 100–240 g/m^2), and also varied among years.

Our data show that root dynamics also vary annually in the alpine. Although the range of interannual variation in belowground production has not previously been documented, the differences in root biomass that we found suggest that annual differences in belowground production probably are larger than those aboveground. The maximum quantity of root biomass and also the seasonal change in biomass differed among years. Both fine and coarse root biomass increased between sampling times in 1992 (Table 2), and we can use these differences in standing crop to estimate root production (McClaugherty et al. 1982). For fine roots, changes in standing crop indicate production of 540 g/m^2 in dry meadows, 450 g/m^2 in moist meadows, and 850 g/m^2 in wet meadows in 1992; however, mean root biomass did not differ among sampling times in 1993 or 1994. This was not the result of high variation among replicate samples at any one time, but rather was the result of consistent root biomass among sampling times (Fig. 2). Changes in standing crop of coarse roots (>2 mm diameter) indicate production of 410 g/m^2 in dry meadows, 535 g/m^2 in moist meadows, and 660 g/m^2 in wet meadows in 1992. Again, differences over time were not significant in the following years. In contrast to fine root biomass, high spatial variation in coarse root biomass is probably responsible for the lack of significant changes over time in 1993 and 1994.

Using changes in standing crop of root biomass can underestimate production because of root death between sampling times; this probably explains the lack of a seasonal change in fine root biomass in 1993 and 1994. The inconsistency in our ability to detect a peak in root biomass suggests that sequential coring, as conducted here, is not a reliable method for estimating root production in the alpine. Nevertheless, these data provide evidence for large interannual differences in root production. Based on annual differences in plant biomass, it is likely that the year in which we estimated belowground production using ingrowth cores was a year of low production. In addition, the root biomass data enable us to make a rough estimate of coarse root productivity, which was not quantified by the root ingrowth method. Data from 1992 suggest that coarse root production can be similar in quantity to that of fine roots, and thus it is an important component of alpine C and N budgets that should be addressed in future research.

Plant allocation to belowground production may vary in response to resource limitation (Bloom et al. 1985), or among plant species that differ in their competitive abilities for resources (McGraw and Chapin 1989, Wedin and Tilman 1990, Theodose et al. 1996, Theodose and Bowman 1997*a*). Allocation in alpine plants may differ according to topography for both reasons (Scott and Billings 1964, Theodose and Bowman 1977*a*). We found the highest belowground allocation in dry meadows, which are the most N limited (Bowman et al. 1993), and in which soil processes may be the most constrained by water availability (Fisk and Schmidt 1995). The growth characteristics of *K. myosuroides,* the dominant dry meadow species, probably are an important determinant of the high allocation belowground (70% of total NPP, 80% of total N) that we observed in dry meadows. Experimental studies by Theodose and Bowman (1997*a*) suggest that *K. myosuroides* is competitively superior to other species under N- and water-limited conditions. Moreover, the relatively high root : shoot ratio of *K. myosuroides* is less responsive than that of other species to increases in resource availability (Theodose 1995, Theodose and Bowman 1997*a*). Not surprisingly, the dominance of *K. myosuroides* declines in the dry meadow community following addition of N (Bowman et al. 1993).

The lowest allocation to root production occurred in moist meadows, and this also could be an indication of differing biology of plant species or growth forms in this community compared to dry and wet meadows. *Acomastylis rossii,* the dominant species in these moist meadows, is a broadleafed forb and would be expected to have lower belowground allocation than the graminoids (Weaver 1954) that are common in dry and wet meadows. Lower belowground allocation in moist meadows could also be affected by resource availability, compared to dry meadows. The dominant graminoid in moist meadows, *Deschampsia caespitosa,* is better able to alter allocation belowground in response to resource availability than *K. myosuroides* in the dry meadow (Theodose 1995, Theodose and Bowman 1997*a*).

Differences in the proportion of allocation to root production resulted in differences in N use for production among communities. Nitrogen use efficiency was lowest in dry meadows because of the 10–15% greater allocation of N belowground compared to other communities, and was highest in wet meadows because of less allocation belowground and also lower root N concentration. This topographic pattern of NUE is the opposite of that found for aboveground plant production alone (Bowman 1994, Bowman et al. 1995), and might be unexpected based on the greater production response to N additions in dry than wet meadows (Bow-

man et al. 1993). Although comparable whole-plant studies have not been made in other alpine or arctic tundra, research in dry heath ecosystems has demonstrated that differences in C and N allocation patterns affect whole-plant NUE (Aerts 1990, Aerts et al. 1992).

Microbial activity and N transformations

Paralleling the topographic pattern in plant production and N uptake, the increase in microbial respiration and N transformations from dry to wet meadows and their highly significant relationships with soil moisture are further evidence of climate control over spatial patterns of N turnover in the alpine. We also predicted that the variation in plant species and growth form composition would interact with the soil moisture gradient to affect N cycling over topographic sequences. However, we did not find any large differences in the microbial processes that mediate N supply, apart from an overall increase in process rates at higher soil moisture.

Plant chemical composition and NUE can have strong feedbacks on N cycling, through their effects on decomposition and plant N availability (Vitousek 1982). The differences that we found in plant NUE, in allocation of N to above- vs. belowground production, and in N turnover times through above- and belowground plant litter all illustrate possible sources of variation in substrate quality that could affect N cycling. Substrate quality feedbacks are mediated by microbial processes, and so we use comparisons of microbial respiration, N mineralization, and N immobilization to infer whether differences in substrate quality affect N availability for plant uptake (Vitousek and Matson 1985, Schimel et al. 1986, Burke et al. 1989, Hart et al. 1994).

The N content of decomposed substrates is one means by which substrate chemistry can affect N mineralization processes. The amount of N mineralized when adjusted for total microbial activity (milligrams N per gram C mineralized) should reflect the overall N content of the substrates being utilized (Schimel 1986, Hart et al. 1994). This assumes that CO_2 evolution, or net C mineralization, is an adequate reflection of the total C mineralization, including that incorporated into microbial biomass. Across all plant communities we found little variation in the relationship between gross mineralization and microbial respiration, suggesting that the N content of mineralized substrates was not widely different in soils of the different communities. Some deviation in the relationship is evident in June (Figs. 5, 6, and 7), when higher gross mineralization relative to CO_2 evolution occurred in dry and moist meadows. The ratio of gross N mineralization to CO_2 evolution (estimated from Fig. 6) varied only between 46 and 60 mg N/g C for all but early-season dry and moist meadow soils, which mineralized 94 mg N/g C. These results, together with the lower NUE found for dry and moist meadow plants, indicate the potential for greater N mineralization in dry and moist meadows than we would expect based on soil moisture patterns alone.

Substrate quality also can affect N availability by determining the proportion of gross mineralization that is immobilized by microorganisms, and thus the relationship between gross and net mineralization (Vitousek and Matson 1985, Burke et al. 1989, Hart et al. 1994). We found a consistent relationship between gross mineralization and immobilization. Microbial demand for N was uniformly high relative to its supply among plant communities, resulting consistently in negative net N mineralization. Thus the effect of substrate quality on microbial sequestration of N is not likely to be an important determinant of differences in N availability across alpine topographic sequences.

The very high short-term immobilization and corresponding negative net mineralization rates that we demonstrate here agree with previous measurements of very low and negative net N mineralization during longer in situ incubations (Fisk and Schmidt 1995). High microbial immobilization rates can cause in situ net N mineralization to underestimate plant available N in some ecosystems (Vitousek and Andariese 1986), and in both the arctic and alpine tundra, in situ estimates of net N mineralization have underestimated plant N uptake (Rehder 1976*a*, Rehder and Schäfer 1978, Giblin et al. 1991). Similarly, we find that annual plant N uptake (3.9–6.8 g $N \cdot m^{-2} \cdot yr^{-1}$) is not adequately accounted for by previous in situ estimates of net N mineralization at Niwot Ridge (1 $g \cdot m^{-2} \cdot yr^{-1}$; Fisk and Schmidt 1995). Furthermore, the clear topographic pattern that we find for gross N mineralization is notably different from net N mineralization measurements on Niwot Ridge from two previous years, in which no consistent differences in net N mineralization rates were detected among communities (Fisk and Schmidt 1995). The in situ net N mineralization method appears inadequate for estimating plant available N in this ecosystem, and also fails to provide even a relative index of N turnover patterns over alpine toposequences.

The discrepancy between net N mineralization and plant N uptake is evidence for efficient plant competition for N in soil, either through roots or mycorrhizae. In addition, several other sources of N may be available to plants in the alpine. The direct uptake of simple forms of organic N by tundra plants has been noted in both arctic and alpine plants (Kielland 1994, Raab et al. 1996) and would allow plants access to N not accounted for in measurements of net N mineralization. Another potential source of N is from atmospheric deposition: ~0.5 g $N \cdot m^{-2} \cdot yr^{-1}$ is deposited on Niwot Ridge (Sievering et al. 1995). This represents 7–12% of annual plant N uptake and, if taken up and sequestered in dead biomass or soil (Fisk and Schmidt 1996), could be increasing the internal cycling of N in this and other high-elevation sites. Nitrogen fixation by *Trifolium* spp. is a final source of N inputs. Bowman et

al. (1996) estimated inputs of 0.3 g/m^2 in dry meadows, 0.7 g/m^2 in moist meadows, and 0.1 g/m^2 in wet meadows, from 1 to 13% of our estimates of annual plant N use for production.

In summary, plant biomass, productivity, and N use for production increased over alpine topographic sequences from dry to wet meadows. Roots were a higher fraction of total production and N use for production in dry meadows than in moist and wet meadows, and this difference led to increases in both NUE and N residence times in nonliving plant biomass from dry to wet meadows. Corresponding to the pattern of plant N cycling, microbial processes also increased from dry to wet meadows. Relationships among microbial activity, gross mineralization, and N immobilization did not vary over topographic sequences, suggesting that substrate quality does not contribute to differences in N availability and cycling among communities. Rather, the close relationships between soil water content, NPP, and microbial processes indicate that topographic environmental variation is the primary factor affecting spatial patterns of plant production and plant and soil components of N turnover in alpine tundra.

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Literature Cited

Aydelotte, A. R., and P. K. Diggle. 1997. Analysis of developmental preformation in the alpine herb, *Caltha leptosepala*. American Journal of Botany, **84**:1646–1657.

Aerts, R. C. 1990. Nitrogen use efficiency in evergreen and deciduous species from heathlands. Oecologia **84**:391–397.

Aerts, R. C., C. Bakker, and H. DeCaluwe. 1992. Root turnover as determinant of the cycling of C, N, and P in a dry heathland ecosystem. Biogeochemistry **15**:175–190.

Benning, T. L., and T. R. Seastedt. 1995. Landscape-level interactions between topedaphic features and nitrogen limitation in tallgrass prairie. Landscape Ecology **10**:337–348.

Berendse, F., and R. Aerts. 1987. Nutrient-use-efficiency: a biologically meaningful definition? Functional Ecology **1**: 293–296.

Billings, W. D., and L. C. Bliss. 1959. An alpine snowbank environment and its effect on vegetation, plant development, and productivity. Ecology **40**:389–397.

Bloom, A. F., F. S. Chapin III, and H. A. Mooney. 1985. Resource limitation in plants—an economic analogy. Annual Review of Ecology and Systematics **16**:363–392.

Bowman, W. D. 1994. Accumulation and use of nitrogen and phosphorus following fertilization in two alpine tundra communities. Oikos **70**:261–270.

Bowman, W. D., T. A. Theodose, and M. C. Fisk. 1995. Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: implications for differential community response to environmental change. Oecologia **101**:217–227.

Bowman, W. D., J. C. Schardt, and S. K. Schmidt. 1996. Symbiotic N_2-fixation in alpine tundra: ecosystem input and variation in fixation rates among communities. Oecologia **108**:345–350.

Bowman, W. D., T. A. Theodose, J. C. Schardt, and R. T. Conant. 1993. Constraints of nutrient availability on primary production in two alpine tundra communities. Ecology **74**:2085–2097.

Brooks, P. C., A. Landman, G. Pruden, and D. S. Jenkinson. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method for measuring microbial biomass nitrogen in soil. Soil Biology and Biochemistry **17**:837–842.

Bryant, D. M. 1996. Litter decomposition in an alpine tundra. Thesis. University of Colorado, Boulder, Colorado, USA.

Burke, I. C., W. A. Reiners, and D. S. Schimel. 1989. Organic matter turnover in a sagebrush steppe landscape. Biogeochemistry **7**:11–31.

Burns, S. F. 1980. Alpine soil distribution and development, Indian Peaks, Colorado Front Range. Dissertation. University of Colorado, Boulder, Colorado, USA.

D'Elia, C. F., P. A. Steudler, and N. Corwin. 1977. Determination of total nitrogen in aqueous samples using persulfate digestion. Limnology and Oceanography **22**:760–764.

Diggle, P. K. 1997. Extreme preformation in alpine *Polygonum viviparum*: an architectural and developmental analysis. American Journal of Botany **84**:154–169.

Enquist, B. J., and J. J. Ebersole. 1994. Effects of added water on photosynthesis of *Bistorta vivipara*: the importance of water relations and leaf nitrogen in two alpine communities, Pikes Peak, Colorado, USA. Arctic and Alpine Research **26**:29–34.

Fahey, T. J., and J. W. Hughes. 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. Journal of Ecology **82**:533–548.

Fisk, M. C. 1995. Nitrogen dynamics in an alpine landscape. Dissertation. University of Colorado, Boulder, Colorado, USA.

Fisk, M. C., and S. K. Schmidt. 1995. Nitrogen mineralization and microbial biomass N dynamics in three alpine tundra communities. Soil Science Society of America Journal **59**:1036–1043.

Fisk, M. C., and S. K. Schmidt. 1996. Microbial responses to excess nitrogen in alpine tundra soils. Soil Biology and Biochemistry **28**:751–755.

Giblin, A. E., K. J. Nadelhoffer, G. R. Shaver, J. A. Laundre, and A. J. McKerrow. 1991. Biogeochemical diversity along a riverside toposequence in arctic Alaska. Ecological Monographs **61**:415–435.

Greenland, D. 1989. The climate of Niwot Ridge, Front Range, Colorado. Arctic and Alpine Research **21**:380–391.

Hart, S. C., G. E. Nason, D. D. Myrold, and D. A. Perry. 1994. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. Ecology **75**:880–891.

Holway, J. G., and R. T. Ward. 1965. Phenology of alpine plants in northern Colorado. Ecology **46**:73–83.

Holzmann, H. P., and K. Haselwandter. 1988. Contribution of nitrogen fixation to nitrogen nutrition in an alpine sedge community (*Caricetum curvulae*). Oecologia **76**:298–302.

Isard, S. A. 1986. Factors influencing soil moisture and plant community distribution on Niwot Ridge, Colorado, USA. Arctic and Alpine Research **18**:83–96.

Kielland, K. 1994. Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. Ecology **75**:2373–2383.

Kirkham, D., and W. V. Bartholomew. 1954. Equations for

following nutrient transformations in soil, utilizing tracer data. Soil Science Society of America Proceedings **18**:33–34.

May, D. E., and P. J. Webber. 1982. Spatial and temporal variation of the vegetation and its productivity on Niwot Ridge, Colorado. Pages 35–62 *in* J. C. Halfpenny, editor. Ecological studies of the Colorado alpine: a Festschrift for John W. Marr. Occasional Paper Number 37. Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado, USA.

McClaugherty, C. A., J. D. Aber, and J. M. Melillo. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology **63**:1482–1490.

McGraw, J. B., and F. S. Chapin III. 1989. Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. Ecology **70**:736–749.

Nadelhoffer, K. J., A. E. Giblin, G. R. Shaver, and J. A. Laundre. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology **72**:242–253.

Nambiar, E. K. S. 1987. Do nutrients retranslocate from roots? Canadian Journal of Forest Research **17**:913–918.

Peterson, K. M., and W. D. Billings. 1982. Growth of alpine plants under controlled drought. Arctic and Alpine Research **14**:189–194.

Raab, T. K., D. A. Lipson, and R. K. Monson. 1996. Nonmycorrhizal uptake of amino acids by roots of the alpine sedge *Kobresia myosuroides*: implications for the alpine nitrogen cycle. Oecologia **108**:488–494.

Rehder, H. 1976*a*. Nutrient turnover in alpine ecosystems. I. Phytomass and nutrient relations in four mat communities in the northern calcareous Alps. Oecologia **22**:411–423.

———. 1976*b*. Nutrient turnover in alpine ecosystems. II. Phytomass and nutrient relations in the *Caricetum firmae*. Oecologia **23**:49–62.

Rehder, H., and A. Schäfer. 1978. Nutrient studies in alpine ecosystems. IV. Communities of the Central Alps and comparative survey. Oecologia **34**:309–327.

Schimel, D. S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochemistry **2**:345–357.

Schimel, D. S., T. G. F. Kittel, A. K. Knapp, T. R. Seastedt, W. J. Parton, and V. B. Brown. 1991. Physiological interactions along resource gradients in a tallgrass prairie. Ecology **72**:672–684.

Scott, D., and W. D. Billings. 1964. Standing crop and productivity of an alpine tundra. Ecological Monographs **34**: 243–270.

Shaver, G. R., and F. S. Chapin III. 1991. Production : biomass relationships and elemental cycling in contrasting arctic vegetation types. Ecological Monographs **61**:1–32.

Shaver, G. R., K. J. Nadelhoffer, and A. E. Giblin. 1991. Biogeochemical diversity and element transport in a heterogeneous landscape, the North slope of Alaska. Pages 105–125 *in* M. G. Turner and R. H. Gardner, editors. Quantitative methods in landscape ecology. Ecological Studies Volume 82. Springer-Verlag, New York, New York, USA.

Sievering, H., D. Rush, and L. Marquez. 1995. Nitric acid, particulate nitrate and ammonium in the continental free troposphere: nitrogen deposition to an alpine tundra ecosystem. Atmospheric Environment **30**:2527–2537.

Taylor, R. V., and T. R. Seastedt. 1994. Short- and long-term patterns of soil moisture in alpine tundra. Arctic and Alpine Research **26**:14–20.

Theodose, T. A. 1995. Interspecific plant competition in alpine tundra. Dissertation. University of Colorado, Boulder, Colorado, USA.

Theodose, T. A., and W. D. Bowman. 1997*a*. The influence of interspecific competition on the distribution of an alpine graminoid: evidence for the importance of plant competition in an extreme environment. Oikos **79**:101–114.

Theodose, T. A., and W. D. Bowman. 1997*b*. Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. Ecology **78**:1861–1872.

Theodose, T. A., C. H. Jaeger III, W. D. Bowman, and J. C. Schardt. 1996. Uptake and allocation of ^{15}N in alpine plants: implications for the importance of competitive ability in predicting community structure in a stressful environment. Oikos **75**:59–66.

Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist **119**:553–572.

Vitousek, P. M., and S. W. Andariese. 1986. Microbial transformations of labelled nitrogen in a clear-cut pine plantation. Oecologia **68**:601–605.

Vitousek, P. M., and P. A. Matson. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. Ecology **66**:1360–1376.

Vogt, K. A., and H. Persson. 1991. Measuring growth and development of roots. Pages 477–501 *in* J. P. Lassoie and T. M. Hinkley, editors. Techniques and approaches in forest tree ecophysiology. CRC, Boca Raton, Florida, USA.

Walker, D. A., J. C. Halfpenny, M. D. Walker, and C. A. Wessman. 1993. Long-term studies of snow-vegetation interactions. BioScience **43**:287–301.

Walker, M. D., R. C. Ingersoll, and P. J. Webber. 1995. Effects of interannual climate variation on phenology and growth of two alpine forbs. Ecology **76**:1067–1083.

Walker, M. D., P. J. Webber, E. A. Arnold, and D. Ebert-May. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. Ecology **75**:393–408.

Weaver, J. E. 1954. North American prairie. Lakeside, Chicago, Illinois, USA.

Webber, P. J., and D. Ebert-May. 1977. The magnitude and distribution of belowground plant structures in the alpine tundra of Niwot Ridge, Colorado. Arctic and Alpine Research **9**:157–174.

Wedin, D. A., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia **84**: 433–441.