CONSTRAINTS OF NUTRIENT AVAILABILITY ON PRIMARY PRODUCTION IN TWO ALPINE TUNDRA COMMUNITIES[1]

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Abstract. A nutrient amendment experiment was conducted for two growing seasons in two alpine tundra communities to test the hypotheses that: (1) primary production is limited by nutrient availability, and (2) physiological and developmental constraints act to limit the responses of plants from a nutrient-poor community more than plants from a more nutrient-rich community to increases in nutrient availability. Experimental treatments consisted of N, P, and N+P amendments applied to plots in two physiognomically similar communities, dry and wet meadows. Extractable N and P from soils in nonfertilized control plots indicated that the wet meadow had higher N and P availability. Photosynthetic, nutrient uptake, and growth responses of the dominants in the two communities showed little difference in the relative capacity of these plants to respond to the nutrient additions. Aboveground production responses of the communities to the treatments indicated N availability was limiting to production in the dry meadow community while N and P availability colimited production in the wet meadow community. There was a greater production response to the N and N+P amendments in the dry meadow relative to the wet meadow, despite equivalent functional responses of the dominant species of both communities. The greater production response in the dry meadow was in part related to changes in community structure, with an increase in the proportion of graminoid and forb biomass, and a decrease in the proportion of community biomass made up by the dominant sedge *Kobresia myosuroides*. Species richness increased significantly in response to the N+P treatment in the dry meadow. Graminoid biomass increased significantly in the wet meadow N and N+P plots, while forb biomass decreased significantly, suggesting a competitive interaction for light. Thus, the difference in community response to nutrient amendments was not the result of functional changes at the leaf level of the dominant species, but rather was related to changes in community structure in the dry meadow, and to a shift from a nutrient to a light limitation of production in the wet meadow.

Key words: alpine tundra; community response to nutrient amendments; nitrogen; nutrient limitation; phosphorus; photosynthesis; primary production.

INTRODUCTION

Determination of the factors which control primary production is critical to understanding ecosystem function. Primary production is of central importance in the transfer of radiant energy to chemical energy available to heterotrophs, the inputs of detritus to soil organic pools, and the fluxes of CO_2, water, and soil nutrients. In the absence of a water limitation, soil nutrient availability is often implicated as the principal factor determining variation in primary production of terrestrial ecosystems (Schlesinger 1991). Nitrogen availability in particular is often cited as the most common nutrient limiting plant growth (Epstein 1972, Chapin 1980), because of its central role in the photosynthetic apparatus (Field and Mooney 1986, Evans

1989), and its mobility in the soil system (Vitousek and Howarth 1991).

Relatively little attention has been given to the constraints of nutrient availability on primary production in alpine tundra (Körner 1989). A substantial effort has been made to understand the nature of nutrient limitations in arctic tundra (McKendrick et al. 1978, Shaver and Chapin 1980, 1986). Alpine tundra differs substantially from arctic tundra in patterns of soil moisture, light regimes, atmospheric CO_2 partial pressures, and wind (Billings 1988). Studies of alpine tundra production have focused more attention on the potential importance of soil water availability and subsequent effects on plant water relations, particularly for the central and southern Rocky Mountains (Johnson and Caldwell 1975, Ehleringer and Miller 1975, Caldwell et al. 1978, Oberbauer and Billings 1981, Greenland et al. 1984, Isard 1986). The relatively cold, dry nature of alpine tundra soils suggests that low mineralization rates of

soil organic matter constrains the supply of soil nutrients, which in turn may limit tundra production (Bliss 1971, Billings 1974, Holzmann and Haselwandter 1988). Seasonal patterns of NO_3^- losses from vegetated and unvegetated alpine catchments in conjunction with N deposition records (Reddy and Caine 1990, Sievering et al. 1992) indicate that there is strong biotic control over N losses from alpine tundra, implying this nutrient could limit alpine primary production. Success of the establishment and growth of seedlings of alpine plants has also been linked with N availability (Chambers et al. 1990). Alternatively, Körner (1989) has suggested that nutrient availability is less important in controlling primary production of alpine tundra than inherent developmental growth constraints which limit the ability of plants to respond to nutrient supply. Plants from high elevations tend to have higher foliar N concentrations than their lowland congeners, indicating an apparent developmental limitation to growth in alpine plants (Körner 1989).

Evidence for nutrient constraints of primary production is derived principally from nutrient amendment experiments. There are several limitations to this approach (Chapin et al. 1986). Plants native to ecosystems with low nutrient supply, such as arctic and alpine tundras, often show a limited response to increases in soil nutrients as a consequence of adaptations which promote conservative use, loss, and uptake of nutrients (Chapin 1980, 1991). Assessing community-level nutrient limitations of primary production is hindered by variation in physiological characteristics and requirements of plants. Species which comprise a community may show individualistic responses to environmental perturbations, indicating no single factor limits community primary production (Chapin and Shaver 1985). There may also be variation in the type and degree of nutrient limitation among the communities making up an ecosystem. Nutrient additions also may not increase soil fertility, but may instead result in increased microbial immobilization (Vitousek and Matson 1985). Although these problems constrain the usefulness of nutrient amendment experiments, such experiments are still the most effective for investigating nutrient limitations of primary production, provided caution is used in interpreting the results. Nutrient addition experiments have been used with success in studies of arctic tundra (McKendrick et al. 1978, Ulrich and Gersper 1978, Shaver and Chapin 1980, Chapin and Shaver 1985, Kummerow et al. 1987), taiga (van Cleve et al. 1983), shortgrass steppe (Dodd and Lauenroth 1979), montane meadows (Hunt et al. 1988), deserts (Fisher et al. 1988), and others.

The primary goals of our research were to determine whether alpine tundra production is constrained by nutrient availability and whether variation in the response to nutrient amendments exists between communities differing in apparent nutrient availability. The response to nutrient amendment treatments (N, P,

$N+P$) was compared between two physiognomically similar communities, wet and dry meadows dominated by sedge species, to determine whether the production responses to these treatments varied according to differences in existing nutrient supply. We proposed that the wet meadow would have higher nutrient availability due to higher net mineralization rates and closer proximity to snowfields, which are a large potential source of N (Bowman 1992). Inherent developmental and physiological constraints may be relatively more important in determining the responses of plants from the dry meadow community to nutrient addition, consistent with the slow growth strategy proposed by Chapin (1980) for plants of low nutrient environments. Additionally, we address whether the production response results from stimulation of growth of the dominant species or species which are relatively rare in the community. Tilman (1984, 1987) and Körner (1989) have suggested changes in species composition may be a more important long-term response to nutrient addition than increases in biomass production of dominant species.

MATERIALS AND METHODS

Study site

The research was conducted on Niwot Ridge, an 8-km east–west-oriented ridge extending from the Continental Divide, in the Front Range of the Colorado Rocky Mountains. This site is a UNESCO Biosphere Reserve, administered in part by the University of Colorado's Mountain Research Station. The site is characteristic of alpine tundra of the central and southern Rocky Mountains, and has been used as an alpine tundra research site for the International Biological Programme and Long-Term Ecological Research (LTER) program. The climate is characterized by low air temperatures (mean annual average −3°C), a springtime precipitation maximum, and high westerly wind velocities (Greenland 1989). Although the mean annual precipitation is relatively high (900 mm), the majority falls as snow, which is redistributed by winds during the winter, resulting in uneven precipitation inputs across the alpine landscape. The growing season is relatively short, from 1 to 3 mo, depending on slope position and the amount of snowpack (May and Webber 1982).

Experimental design

Experimental plots were established in May 1990 in two physiognomically similar alpine tundra communities (sensu May and Webber 1982, Billings 1988) at 3510 m, dry meadow dominated by *Kobresia myosuroides* (Villars) Fiori & Paoli, and wet meadow dominated by *Carex scopulorum* Holm (nomenclature follows Weber 1976). The communities are located within 50 m of each other on a south-facing slope of <5°. These communities exhibit similar phenologies, ini-

tiating growth in early to mid-June, and senescing by mid-August. The wet and dry meadows are dominated by graminoids, principally species in the Cyperaceae, with forbs as the next major growth form. The plots were subjectively chosen based on homogeneity of species composition. To minimize potential interference from nutrient leaching and trampling the plots were established 1–5 m apart. Treatments were assigned to the plots such that control plots were not within 5 m downslope from fertilized plots, and treatments were not adjacent to one another.

Four experimental treatments were used: N, P, N + P, and control. The N (NPK 40-0-0, using urea-N) and P (NPK 0-40-0, using P_2O_5-P) fertilizers were applied as Osmocote pellets (Sierra Chemical Company, Milpitas, California), which are designed to slowly release the fertilizer during precipitation events. Each treatment was applied individually to 5 replicate 2 × 2 m plots in each community, for a total of 20 plots in each community. Five hundred grams of pellets were applied to the N and P plots, and 1000 g (500 g of each nutrient) were applied to the N + P plots in mid-June of 1990 and early July of 1991. The total inputs of the nutrients were calculated by subtracting the mass of sample pellets collected and dried in October from the mass of dried unused pellets. The average N and P inputs were 25 g·m^{-2}·yr^{-1} in both communities.

Soil nutrient extracts

Soil nutrient availability was estimated using field soil extracts to evaluate the fertilization effect of the nutrient amendment treatments. Three soil cores from the rooting zone (0–25 cm) were collected from each plot. The samples were composited, mixed, and a subsample was collected for dry mass determination. Samples for N analyses were collected in mid-July of 1991, and extracted with saturated KCl within 1–2 h of collection. Phosphorus samples were collected in early August 1991, and extracted with a modified Bray's solution. The soil samples were analyzed for NO_3^--N, NH_4^+-N, and PO_4^3-P using a flow-injection colorimetric autoanalyzer (Lachat Instruments, Mequon, Wisconsin). NO_3^- was analyzed using a sulfanalamide colorimetric reaction, following reduction to NO_2^- with a cadmium column. NH_4^+ was analyzed colorimetrically using a phenolate reaction, enhanced by nitroprusside. PO_4^3 was analyzed using an ammonium molybdate and antimony potassium tartrate reaction under acidic conditions.

Plant measurements

Species richness was measured as the number of species in each plot. In 1990 the plots were censused in late June. Plots were censused several times in 1991 from mid- to late July.

Photosynthesis measurements were made on single leaves after full leaf elongation had occurred (mid- to late July) in 1990 and 1991. Precipitation during this period was above average, minimizing any potential water limitation of photosynthesis. Measurements were made during the late morning (1000–1200 mountain daylight savings time), under full sunlight (photosynthetic photon flux densities of 1800–2200 μmol· m^{-2}·s^{-1}) with air temperature from 15 to 20°C. Photosynthetic rates were measured as net CO_2 assimilation using a LI-COR LI-6200 gas exchange system. Measurements were made on a fully expanded leaf from 2 or 3 plants per plot of *Kobresia myosuroides* (1990 and 1991) and *Bistorta bistortoides* (1990 and 1991) in the dry meadow, and *Carex scopulorum* (1990 and 1991), *B. bistortoides* (1990 and 1991), and *Caltha leptosepala* DC (1991) in the wet meadow. These species combined made up 40–80% of the total cover in the communities at the start of the experiment.

Foliar N and P were measured for the same species used in the photosynthesis measurements. Leaves were collected at the time of the photosynthesis measurements, dried in an oven at 60°C, ground in a Tecator mill or with a mortar and pestle, digested, and analyzed for total N (1990 and 1991) and P (1991) using a Lachat flow-injection colorimetric analyzer. The 1990 samples were digested in a sulfuric acid/copper sulfate catalyst mixture for 3 h at 360°C. The 1991 samples were digested and decolorized in a sulfuric acid/salicylic acid/ hydrogen peroxide mixture. The results of N analyses using the two different digestion techniques were not significantly different. Dried, ground, and homogenized *Plantago lanceolata* L. leaves of known N and P (analyzed at Duke University and Colorado State University) were used as standards. Total N was analyzed using a salicylate and hypochlorite reaction in the presence of an alkaline buffer, with the color intensified by sodium nitroprusside. Total P was analyzed as PO_4^3 as above (see *Soil nutrient extracts*).

Biomass production of the dominant species was estimated in 1990 by collecting tillers of *Kobresia myosuroides* in the dry meadow and *Carex scopulorum* in the wet meadow. Five representative cores per plot were selected. From these cores 15 *Kobresia* or 5 *Carex* tillers were separated, washed, dried at 60°C for 48 h, and weighed.

Aboveground primary production in 1991 was estimated by clipping aboveground live biomass at peak season (dates from May and Webber 1982) in 4 0.04-m^2 subplots in each of the plots. The dry meadow was clipped in late July, and the wet meadow in early August. The dry meadow samples were sorted as *Kobresia*, other graminoids, and forbs, and the wet meadow samples were sorted as graminoids and forbs. The samples were weighed after oven drying at 60°C. The proportion of community biomass made up by the different growth forms was calculated as the ratio of the biomass component to the total biomass.

Belowground standing crop was measured by extracting all live belowground biomass at peak season. Three cores (3.8 cm diameter and 30 cm depth, below
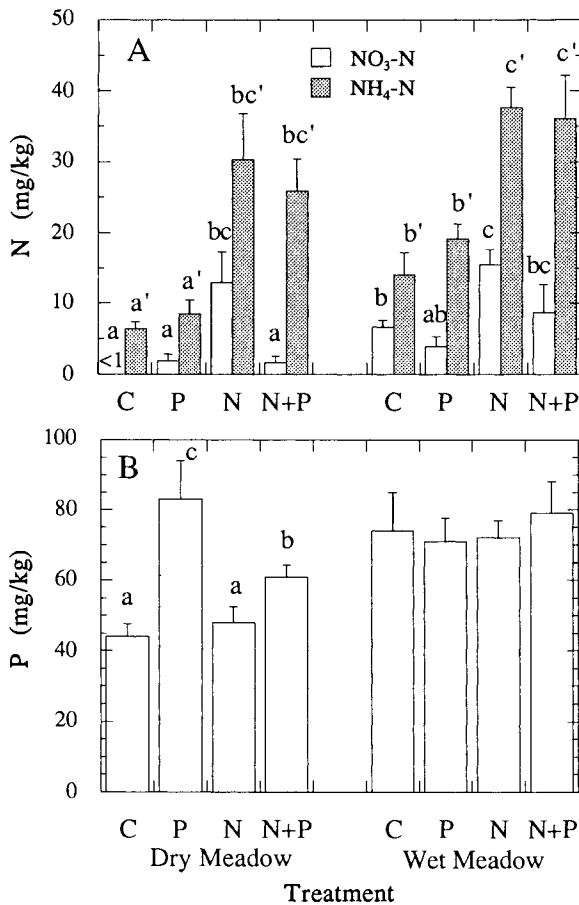
FIG. 1. Extractable N (A) and P (B) from soils of two alpine tundra communities, dry and wet meadow, under four treatments: control (C) and P, N, and N+P amendments. Bars show means and 1 SE of five plots in each treatment. Letters indicate homogeneous means determined using a Tukey's multiple comparisons test. Separate ANOVA tests were run for NH_4-N (indicated with prime symbols) and NO_3-N.

maximum depth of rooting, Webber and May 1977) were collected from each plot in late July of 1991. The cores were gently washed and live roots and stems were sorted from the soil and detritus. The values for peak season belowground standing crop were used with the clip harvest data to calculate belowground : aboveground biomass ratios for each plot.

Statistical analyses

The results of the experiment were analyzed using one-way (most photosynthesis and foliar N and P measurements) and two-way model I analyses of variance. The biomass data (total aboveground and belowground, components, and belowground : aboveground ratios) and some of the foliar chemistry data required log transformations, and the proportion of biomass components making up community biomass were arcsine transformed, to normalize their distributions. Nutrient treatments and community type were treated as class variables. Tukey's multiple-range test was used when a significant ANOVA result occurred to determine significant differences among means.

RESULTS

Soil N and P extracts

Extractable NH_4^+-N varied significantly among the treatments ($P < .001$, $F = 22.7$, df $= 3, 36$) and between communities ($P < .01$, $F = 15.2$, df $= 1, 9$), and was highest in soils from the N and N+P treatments and in the wet meadow community (Fig. 1A). NO_3^--N showed a similar pattern ($P < .01$ for community effect, $F = 24.0$, df $= 1, 9$; $P < .001$ for treatment effect, $F = 15.1$, df $= 3, 36$), but was not significantly higher in the N+P treatment. The lower extractable NO_3^--N in the N+P plots was probably due to greater plant uptake as a result of greater biomass. There were no significant community × treatment interactions, indicating similar inputs and uptake of N in both communities. The N amendment treatments resulted in approximately

TABLE 1. Photosynthesis rates for the dominant graminoid and forb species of dry and wet meadow tundra communities in the Colorado Rocky Mountains, USA, in 1990 and 1991, under four treatments: control (C) and P, N, and N+P amendments. Values are means ± 1 SE for 15 plants in five replicate plots. Superscript letters indicate statistically homo-

	Photosynthesis rates* $(\mu mol \cdot m^{-2} \cdot s^{-1})$ or $(\mu mol \cdot g^{-1} \cdot s^{-1})$			
	1990			
	C	P	N	N+P
Dry meadow species				
Kobresia myosuroides	1.05 ± 0.08[a]	1.10 ± 0.05[a]	1.36 ± 0.06[b]	1.22 ± 0.08[ab]
Bistorta bisotortoides	13.8 ± 0.7	14.0 ± 0.7	13.9 ± 0.6	14.9 ± 0.8
Wet meadow species				
Carex scopulorum	11.4 ± 0.5[a]	11.4 ± 0.6[a]	13.2 ± 0.6[b]	13.0 ± 0.5[b]
Bistorta bistortoides	17.0 ± 0.5[a]	17.2 ± 0.7[a]	18.4 ± 0.8[b]	18.6 ± 0.7[b]
Caltha leptosepala	...	...	...	...

* Note that photosynthesis rates for *Kobresia* are expressed on a dry mass basis, while other species are on a leaf area basis.

five times higher extractable N (NH_4^+-N + NO_3^--N) in the dry meadow, and three times higher extractable N in the wet meadow relative to control plots.

Extractable soil PO_4^{3-}-P was significantly higher in the wet meadow community ($P < .01$, $F = 8.5$, df = 1, 9), and showed a significant treatment effect only in the P and N+P plots in the dry meadow ($P < .05$, $F = 3.0$, df = 3, 36 for treatment effect; $P < .05$, $F = 3.4$, df = 3, 36 for treatment × community interaction; Fig. 1B). Extractable P was approximately double in the dry meadow P plots compared with the control plots.

Photosynthesis measurements

Photosynthetic rates measured during 1990, the first year of the nutrient amendment treatment, varied significantly for Kobresia ($P < .01$, $F = 4.3$, df = 3, 48) and Carex ($P < .05$, $F = 2.8$, df = 3, 56), the dominant graminoids in the communities, and for Bistorta ($P < .05$, $F = 3.2$, df = 3, 56) in the wet meadow (Table 1). Photosynthetic rates of the wet meadow species were significantly higher in the N and N+P plots, while Kobresia photosynthetic rates were significantly higher for the N treatment only. Photosynthetic rates measured in 1991 showed a different pattern (Table 1). There was significant variation among the treatments for Kobresia, Bistorta, and Caltha. Photosynthetic rates in Kobresia were higher only in the N+P plots ($P < .001$, $F = 14.6$, df = 3, 48). Dry meadow Bistorta 1991 photosynthetic rates were higher in the N plots, but significantly lower in the N+P plots, while no significant differences were found for wet meadow Bistorta plants ($P < .05$, $F = 3.1$, df = 3, 56 for treatment effect). The wet meadow Bistorta plants had significantly higher photosynthesis rates than the dry meadow Bistorta ($P < .001$, $F = 13.7$, df = 1, 196 for community effect). Caltha leptosepala in the wet meadow had significantly higher photosynthesis rates in the P and N+P treatments relative to rates of the control plants ($P < .05$, $F = 3.5$, df = 3, 56).

Foliar N and P

There were significant differences in foliar N concentration among the treatments for all species except Kobresia in 1990 ($P < .05$, $F = 3.1$, df = 3, 56 for Bistorta, $P < .05$, $F = 4.2$, df = 3, 56 for Carex, Table 2). Higher N concentrations were measured in the N and N+P plots. Significant treatment responses were measured in all species except Caltha in 1991 ($P < .001$, $F = 13.1$, df = 3, 196 for Bistorta; $P < .001$, $F = 6.9$, df = 3, 56 for Carex; and $P < .001$, $F = 29.8$, df = 3, 48 for Kobresia). The magnitude of the treatment response tended to increase in 1991 relative to 1990, particularly for Bistorta. There was a significant community effect for Bistorta ($P < .001$, $F = 30.1$, df = 1, 116), with higher leaf N concentration in the wet meadow plants relative to the dry meadow plants. In general the wet meadow plants had higher foliar N, with averages between 3.0 and 4.0% in the controls, while the dry meadow control plants ranged from 2.3 to 3.2%.

Foliar P concentration was measured in 1991 only. For all species except Caltha there was a significant response to treatment ($P < .001$, $F = 20.8$, df = 3, 48 for Kobresia; $P < .001$, $F = 37.7$, df = 3, 56 for Carex; $P < .001$, $F = 43.9$, df = 3, 116 for Bistorta). Bistorta in both the wet and dry meadow and Carex had significantly higher foliar P concentrations in the P and N+P treatments (Table 3). There was a significant response only in the P plots for Kobresia. The response to the P amendment was most pronounced in Bistorta dry meadow plants, which had six-fold higher P concentrations than the control plants. These plants also showed some necrosis, which may be associated with these high P concentrations. Photosynthesis rates, however, were not affected. There was not a significant community effect in the Bistorta plants. Although Caltha did not show a significant response to treatment, foliar P concentrations in control plants were significantly higher than all the other species in control plots ($P < .001$, $F = 131$, df = 3, 56 for species effect).

Production measurements

Biomass production on a per tiller basis of the dominant graminoids in 1990 was higher in the N and N+P treatments ($P < .05$, $F = 3.2$, df = 3, 96 for Kobresia), but was statistically significant only at $P < .07$ for Carex ($F = 2.6$, df = 3, 96) (Fig. 2). Tiller biomass of both species from the N+P plots was $\approx$22–24% greater than biomass of control tillers. Aboveground biomass production in 1991 was significantly related to treatment ($P < .001$, $F = 24.0$, df = 3, 36) and community ($P < .001$, $F = 88.3$, df = 1, 9). Production in the dry meadow community responded significantly to the N and N+P treatments, while the wet meadow community responded significantly to the N+P treatment alone (Fig. 3, Table 4). The greatest response to the nutrient amendments was in the dry meadow, with a

geneous means within the year of measurement determined from Tukey's multiple comparison test when significant ($P < .05$) ANOVA results were determined.

Photosynthesis rates* (μmol·m^{-2}·s^{-1}) or (μmol·g^{-1}·s^{-1})			
1991			
C	P	N	N+P
Dry meadow species			
0.91 ± 0.05[a]	1.06 ± 0.04[a]	0.92 ± 0.06[a]	1.30 ± 0.05[b]
13.2 ± 0.8[b]	13.2 ± 1.1[b]	15.5 ± 1.3[c]	10.6 ± 1.0[a]
Wet meadow species			
11.4 ± 0.6	11.7 ± 0.7	11.9 ± 0.4	12.6 ± 0.5
17.3 ± 1.5	16.7 ± 1.0	16.4 ± 1.0	16.5 ± 0.7
10.9 ± 0.7[a]	12.6 ± 0.5[b]	12.0 ± 0.5[ab]	12.9 ± 0.8[b]

TABLE 2. Foliar N concentrations in the dominant graminoid and forb species of dry and wet meadow tundra communities, in the first (1990) and second (1991) seasons of a nutrient amendment experiment with four treatments: control (C) and P, N, and N+P amendments. Values are means ± 1 SE for 15 plants in five replicate plots. Superscript letters indicate

	N concentration (% dry mass)			
	1990			
	C	P	N	N+P
Dry meadow species				
Kobresia myosuroides	2.35 ± 0.08	2.32 ± 0.08	2.56 ± 0.07	2.41 ± 0.11
Bistorta bisotortoides	3.11 ± 0.08[a]	3.36 ± 0.13[a]	3.76 ± 0.09[b]	3.69 ± 0.10[ab]
Wet meadow species				
Carex scopulorum	3.12 ± 0.06[a]	3.34 ± 0.09[ab]	3.49 ± 0.06[b]	3.41 ± 0.05[b]
Bistorta bistortoides	3.85 ± 0.20[a]	3.81 ± 0.09[a]	4.15 ± 0.12[b]	4.18 ± 0.40[ab]
Caltha leptosepala	...	...	...	...

63% increase in production in the N treatment, and a 178% increase in production in the N+P treatment relative to controls (Fig. 3, Table 4). The response to N amendment in the dry meadow was the result of an increase in *Kobresia* ($P < .01$, $F = 4.8$, df = 3, 76) and other graminoid biomass ($P < .01$, $F = 12.6$, df = 3, 76). All components of biomass (*Kobresia*, other graminoids, and forbs) increased significantly in the N+P treatment ($P < .001$, $F = 17.4$, df = 3, 76), although the greatest change was in the non-*Kobresia* graminoids, which comprised 8% of the biomass in the control treatment and 18% of the biomass in the N+P treatment ($P < .05$, $F = 3.5$, df = 3, 76) (Fig. 4A, Table 4). Graminoid biomass in the wet meadow plots was significantly higher in the N+P treatment ($P < .001$, $F = 31.4$, df = 3, 76). The graminoids made up a significantly larger proportion of biomass in the N+P plots in the wet meadow ($P < .05$, $F = 3.5$, df = 3, 76), while the converse was true for the forbs ($P < .05$, $F = 3.5$, df = 3, 76) (Fig. 4B, Table 4).

The belowground standing crop was significantly related to community ($P < .001$, $F = 27.1$, df = 1, 56) but not to treatment (Fig. 5). There was almost twice as much belowground biomass in the wet meadow community as the dry meadow community. The be-

lowground : aboveground biomass ratio was significantly related to treatment ($P < .01$, $F = 6.1$, df = 3, 36), but not to community. There were significantly lower belowground : aboveground biomass ratios in the N and N+P plots in both communities (Fig. 6). This was the result of greater aboveground production in the N and N+P plots, since there were no differences in belowground standing crop among the treatments.

Species richness

Species richness did not differ among the treatments in either community in 1990 (Fig. 7). In 1991 species richness was significantly higher in the N+P plots of the dry meadow ($P < .01$, $F = 7.4$, df = 3, 36), but did not differ among the treatments in the wet meadow. There was an average of 5 more species in the dry meadow N+P plots than the other treatments. These were primarily species more characteristic of moister and/or disturbed communities (May and Webber 1982), and included *Deschampsia caespitosa*, *Festuca brachyphylla*, *Androsace chamaejasme*, and *Achillea lanulosa*. The differences in species richness between 1990 and 1991 can be ascribed to differences in the times of the plot surveys. The 1990 censuses were done significantly earlier, and not repeated later during the grow-

TABLE 3. Foliar P concentrations in the dominant graminoid and forb species of dry and wet meadow tundra communities measured in 1991, the second growing season of a nutrient amendment experiment with four treatments: control (C) and P, N, and N+P amendments. Values are means ± 1 SE for 15 plants in five replicate plots. Superscript letters indicate statistically homogeneous means determined from Tukey's multiple comparison test when significant ($P < .05$) ANOVA results were determined.

	P concentration (% dry mass)			
	C	P	N	N+P
Dry meadow species				
Kobresia myosuroides	0.217 ± 0.003[a]	0.406 ± 0.046[b]	0.195 ± 0.002[a]	0.242 ± 0.007[a]
Bistorta bisotortoides	0.219 ± 0.006[a]	1.193 ± 0.167[c]	0.201 ± 0.008[a]	0.455 ± 0.034[b]
Wet meadow species				
Carex scopulorum	0.135 ± 0.003[a]	0.292 ± 0.032[b]	0.144 ± 0.002[a]	0.338 ± 0.0008[b]
Bistorta bistortoides	0.250 ± 0.011[a]	0.690 ± 0.183[b]	0.271 ± 0.010[a]	0.749 ± 0.144[b]
Caltha leptosepala	0.356 ± 0.005	0.393 ± 0.019	0.362 ± 0.013	0.384 ± 0.009

statistically homogeneous means within the year of measurement determined from Tukey's multiple comparison test when significant ($P < .05$) ANOVA results were determined.

	N concentration (% dry mass)		
	1991		
C	P	N	N+P
Dry meadow species			
2.71 ± 0.05^a	2.59 ± 0.04^a	3.56 ± 0.05^c	3.20 ± 0.14^b
3.31 ± 0.14^a	3.72 ± 0.17^a	4.13 ± 0.09^b	4.34 ± 0.13^b
Wet meadow species			
3.02 ± 0.06^a	3.08 ± 0.10^a	3.46 ± 0.08^b	3.41 ± 0.08^b
4.21 ± 0.11^a	3.88 ± 0.17^a	4.80 ± 0.07^b	4.69 ± 0.12^b
3.60 ± 0.06	3.42 ± 0.19	3.66 ± 0.14	3.89 ± 0.10

ing season; thus some species with late phenologies were probably missed.

DISCUSSION

Nutrient limitation of primary production in alpine tundra

A nutrient limitation of primary production in alpine tundra of Niwot Ridge was indicated based on aboveground biomass production and photosynthesis responses to nutrient amendments. There were signifi-
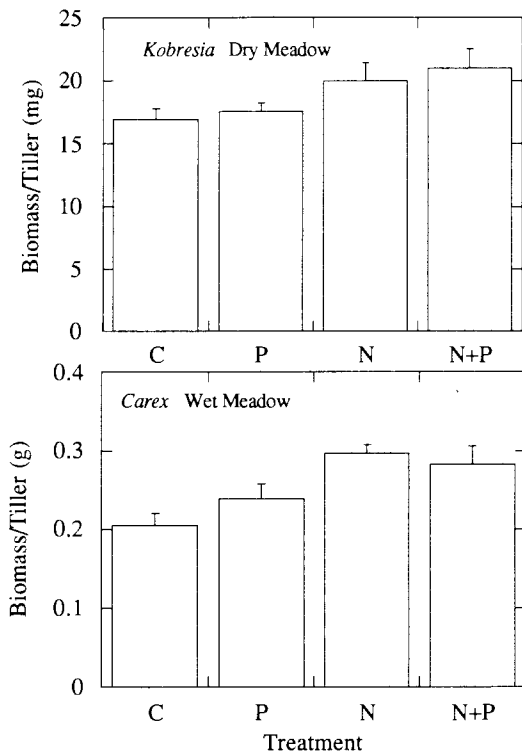

FIG. 2. Aboveground biomass production on a per tiller basis of the dominant sedges in the wet and dry meadow tundra communities in four treatments: control (C), and N, P, and N+P amendments ($n = 5$, means and 1 SE).
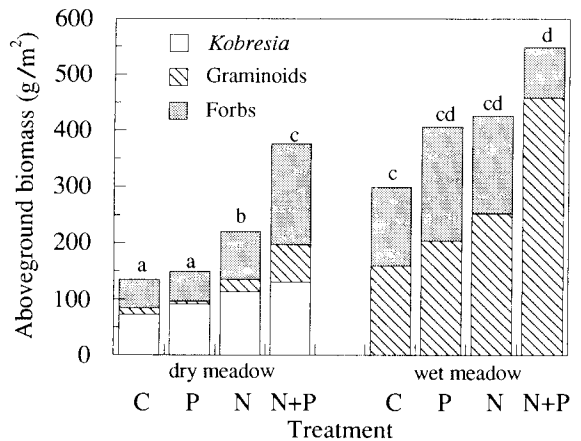

FIG. 3. Aboveground biomass production for two alpine tundra communities, dry and wet meadows, in four treatments: control (C), and P, N and N+P amendments. Component growth forms are also shown. Letters above bars indicate homogeneous means, as determined by a Tukey's multiple range test ($P < .05$, log-transformed data). *Kobresia* biomass was significantly higher in the N and N+P treatment, graminoid biomass was significantly higher in the N and N+P treatment in both communities, and forb biomass was significantly lower in the wet meadow N+P treatment ($n = 5$).

cant responses to N and N+P amendments, indicating N is the principal nutrient which constrains tundra production in the dry meadow communities, and N and P colimit production in the wet meadow community. This pattern of response is very similar to arctic tundra (McKendrick et al. 1978, Shaver and Chapin 1980, 1986), and in part confirms our hypothesis that N limits primary production of alpine tundra, which is based on evidence from seasonal changes in N losses from alpine catchments (Sievering et al. 1992) and soil conditions favoring low mineralization rates of soil organic matter. Extractable soil N in control plots was relatively low, similar to values in other N limited systems (e.g., shortgrass steppe [Schimel and Parton 1986], arctic tundra [Marion and Miller 1982]).

There were substantial differences in the responses of the dry and wet meadow communities to nutrient amendments. The greater response in biomass production was in the dry meadow community. The production response to fertilization of the dry meadow was 20% greater in the N treatment and 94% greater in the N+P treatment relative to the wet meadow. While the dry meadow showed an N limitation of production, the wet meadow community appears to be near the point of an N–P colimitation. The wet meadow community production response to the N and P amendments were equivalent, although not statistically different from the control, and a significant production response occurred in response to the N+P treatment. Additionally the photosynthetic response of the forb *Caltha leptosepala* indicates that some species of the wet meadow are more P than N limited, since pho-
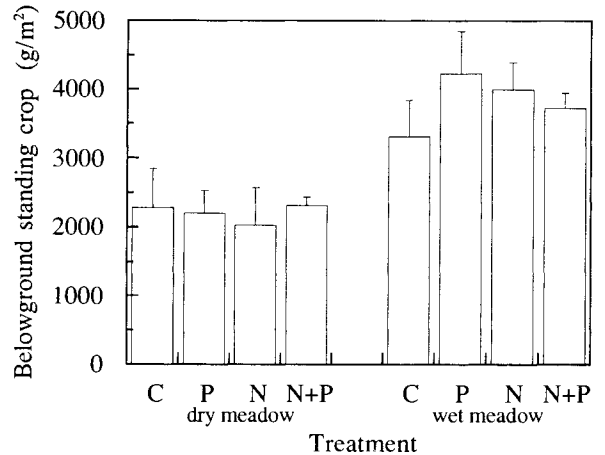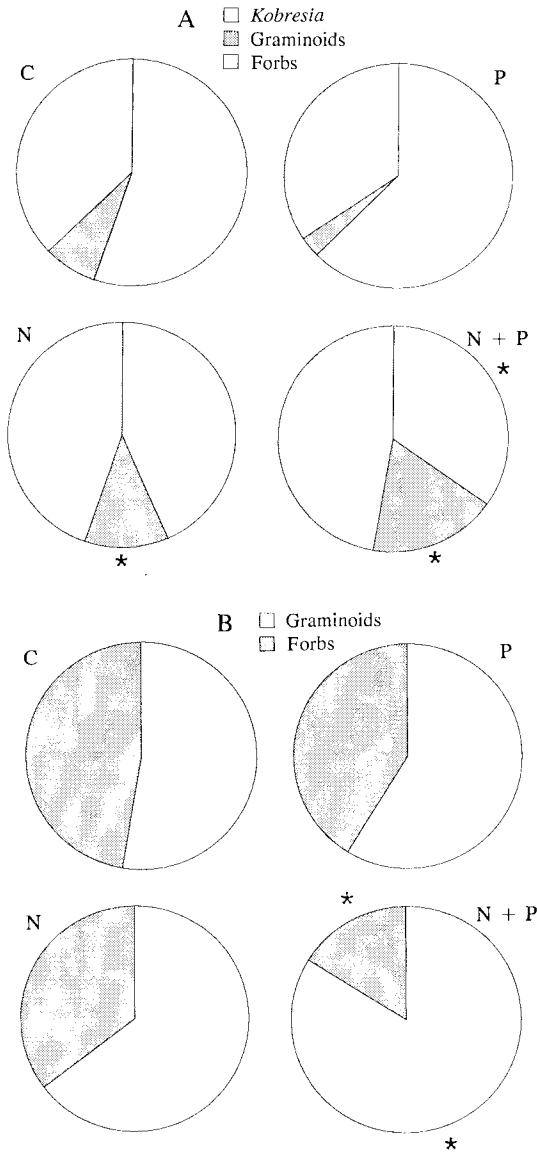
FIG. 5. Belowground standing crop for two alpine tundra communities, dry and wet meadows, under four treatments: control (C) and P, N, and N+P amendments, measured at peak season (late July) in the second growing season of the experiment. Bars show means of five plots in each treatment, and error bars show + 1 SE. The wet meadow had significantly higher belowground standing crop than the dry meadow ($P < .001$, ANOVA, log-transformed data), while there was no significant treatment effect.

tosynthesis rates were higher in the P and N+P plots. The wet meadow community may therefore be near the point of N saturation, i.e., the point at which the N supply in the soil is not exhausted during the growing season.

There were differences in the relative growth responses to the nutrient amendments among the plant

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FIG. 4. Proportion of community biomass made up by *Kobresia*, forbs, and non-*Kobresia* graminoids, for a dry meadow (A) and a wet meadow (B) alpine community in Colorado, USA. Asterisks denote proportions significantly different from control values (at $P < .05$, determined using a Tukey's multiple range test on arcsine-transformed data).

TABLE 4. Total biomass, biomass of the growth form components, and the proportion of total biomass made up by the growth forms from two alpine tundra communities, dry and wet meadows, after 2 yr of treatment with P, N, or N+P fertilizer pellets, or a control (C) treatment. Data are means ± 1 SE from five replicate treatment plots within each community. Superscript letters indicate statistically homogeneous means determined by a Tukey's multiple range test when a significant ($P < .05$) ANOVA result occurred (log-transformed biomass data, arcsine square-root transformation for the proportion data).

|	Dry biomass (g/m²)				% total dry biomass			
	C	P	N	N+P	C	P	N	N+P
			Dry meadow					
Kobresia	74 ± 6[a]	91 ± 6[ab]	113 ± 10[bc]	131 ± 12[c]	55 ± 5[b]	61 ± 5[b]	52 ± 6[b]	35 ± 2[a]
Other graminoids	11 ± 2[a]	5 ± 2[a]	23 ± 5[a]	66 ± 12[b]	8 ± 2[a]	3 ± 8[a]	10 ± 4[a]	18 ± 5[b]
Forbs	51 ± 9[a]	53 ± 6[a]	84 ± 12[a]	179 ± 26[b]	37 ± 4	34 ± 5	37 ± 3	47 ± 4
Total	136 ± 8[a]	149 ± 11[a]	221 ± 11[b]	376 ± 19[c]				
			Wet meadow					
Graminoids	160 ± 9[a]	204 ± 16[ab]	253 ± 29[b]	460 ± 20[c]	53 ± 2[a]	59 ± 10[ab]	65 ± 11[ab]	84 ± 4[b]
Forbs	139 ± 10	203 ± 97	174 ± 87	89 ± 26	47 ± 2[b]	41 ± 10[b]	35 ± 11[b]	16 ± 4[a]
Total	299 ± 12[a]	407 ± 94[ab]	427 ± 62[ab]	549 ± 19[b]				
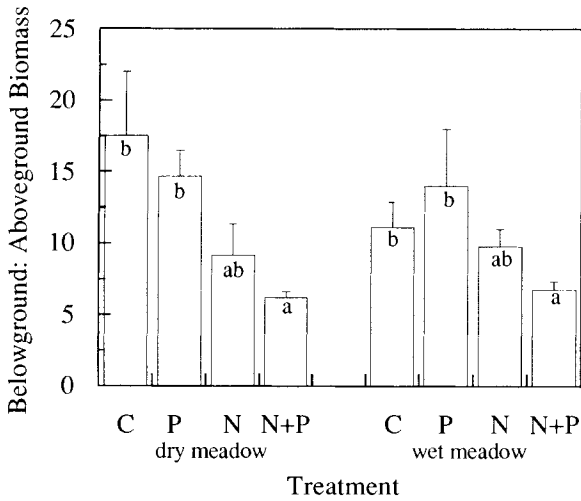
FIG. 6. Belowground : aboveground biomass ratios measured at peak growing season in two alpine tundra communities, dry and wet meadows, under three nutrient amendment treatments and a control (C). Bars and letters are as in Fig. 1. Differences are the result of greater allocation to aboveground biomass in the N and N+P treatments.

growth forms. Graminoid (including *Kobresia*) biomass increased in response to the N amendments in both communities. Forbs on the other hand increased in biomass only in the dry meadow N+P treatment, and decreased in biomass in the wet meadow N+P treatment. This decrease of forb biomass in the wet meadow N+P treatment appears indicative of a competitive interaction between forbs and graminoids. There was a significant negative correlation between graminoid and forb biomass in the wet meadow N+P treatment ($P < .01$, $r = -0.52$, $n = 20$, correlation analysis, data from subplots of wet meadow N+P treatments). Since this interaction occurs in the presence of an excess of soil resources (assuming extractable N and P estimate available), we suggest that competition for light becomes important as biomass of the graminoids increases such that significant shading occurs. The magnitude of the response to nutrient amendments in the wet meadow may therefore be constrained by a light limitation beyond a certain threshold of community biomass. Shifts from nutrient to light limitations of production occur in the tallgrass prairie at a similar biomass threshold during the growing season and with time following fire (Knapp and Seastedt 1986, Schimel et al. 1991, Seastedt et al. 1991).

We hypothesized that the greater production response to nutrient amendments would be in the wet meadow community, based on the arguments presented by Chapin (1980, 1991) and Körner (1989) that the physiological and developmental capacity to respond to soil resources is more constrained in plants from low resource environments. Nutrient availability, as indicated by extractable soil N and P (Fig. 1) and

net N mineralization rates (M. Fisk, *unpublished data*), was higher in the wet meadow community relative to the dry meadow community. However, nutrient supply did not exert the same degree of constraint on primary production in the wet meadow as it did in the dry meadow, nor did the wet meadow plants exhibit greater functional responses to increased nutrient supply than dry meadow plants. This community-level difference in response to increased nutrient availability appears related to a transition from a nutrient to a light limitation of production in the wet meadow under the N+P treatment, limiting the magnitude of the biomass response to increased nutrient supply, and a change in community structure in the dry meadow community, increasing the production response above the potential of the existing community (discussed in *Changes in community structure and composition*).

Functional responses to nutrient amendments

All of the species measured in this experiment responded functionally to the nutrient amendments. However, these responses did not indicate that there were differences in the capacity to respond to increased nutrient availability between the communities, nor that there were differences in the constraints on production imposed by nutrient availability for these species.

All species except *Caltha* showed increases in foliar N in response to N and N+P treatments, indicating alpine species are capable of sequestering N in response to increases in soil N supply. There was no indication that the responsiveness to N amendments in *Bistorta* was any greater in the wet meadow population relative to the dry meadow population (no significant community × treatment interaction in the ANOVA), although the wet meadow population had higher foliar
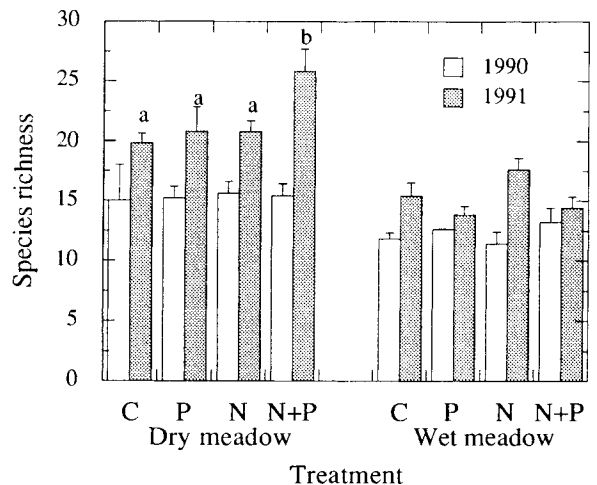

FIG. 7. Species richness for two alpine tundra communities, dry and wet meadows, in the first (1990) and second (1991) seasons of a nutrient amendment experiment with four treatments, control (C) and P, N, and N+P amendments. Bars and letters are as in Fig. 1.

N at all treatment levels. The response to soil N availability in this species is likely buffered by the large corm and shoot primordia that act as storage organs for N and carbohydrates (Mooney and Billings 1960, Jaeger and Monson 1992). The greater response in 1991 relative to 1990 in *Bistorta* probably reflects the buffering effect of these storage organs, since nutrient inputs in both years were similar. Aboveground N storage may occur only after the belowground storage pool increases (Chapin et al. 1990). There was also a notable increase in foliar N of *Kobresia* in 1991 relative to 1990 in the N and N+P treatments. Less is known about the potential storage role of roots in this species, but carbohydrate and nutrient storage has been shown to be important in arctic graminoids (Shaver and Billings 1976, Shaver and Chapin 1980).

Foliar P was higher in the P and N+P treatments in all species except *Kobresia,* which had higher foliar P in the P treatment, and *Caltha,* which didn't respond to any of the treatments. Greater stimulation of growth in the N+P treatment could have resulted in more dilution of the P in *Kobresia,* consistent with the pattern observed for foliar N. Foliar uptake of N and P in excess of that needed for growth (= luxury consumption) is relatively common in plants native to low nutrient soils (Chapin et al. 1982, Bloom 1985). This response was most pronounced in *Bistorta,* especially the dry meadow populations, which had greater than a five-fold increase in foliar P in the P treatment. Despite equivalent P availability in the soils of the two communities under the P treatment, as indicated by extractable soil P, dry meadow plants showed a greater response to the P treatment than wet meadow plants. Abiotic factors affecting P uptake include availability of soil P and temperature, while biotic factors include root : shoot ratios and mycorrhizal infection (Chapin 1981, Clarkson 1985). The differential response of P uptake between the wet and dry meadow *Bistorta* plants may be due to differences in allocation to fine roots between the populations under different nutrient regimes, which has been noted in a growth chamber experiment (T. A. Theodose and W. D. Bowman, *unpublished data*), or differences in mycorrhizal infection between the populations. *Bistorta* plants on Niwot Ridge are infected with ectomycorrhizae (D. Luoma, *personal communication*), which should facilitate uptake of P from the soil. The cooler, wetter environment of the wet meadow soils is less conducive to mycorrhizal infection than soils of the dry meadow (Bowen 1987), and may slow the kinetics of P uptake by the roots and mycorrhizae. Mycorrhizal infections have not been found in *Caltha* (S. Schmidt, *personal communication*), and may explain the lack of a change in foliar P and N in response to the nutrient amendments.

A potential drawback to nutrient storage aboveground is the increased likelihood of herbivory. Herbivores are sensitive to differences in foliar nutrient concentrations, particularly N (Mattson 1980, Mattson and Scriber 1987). This may be especially true for phytophagous insects of the alpine tundra, which have a relatively short growing season in which to feed. There was a significant increase in the densities of grasshoppers in the N and N+P plots of the dry meadow in 1991. In a separate study these grasshoppers also showed a significant feeding preference for *Kobresia* from the N plots which had higher N concentrations relative to the control plots (Coxwell 1992).

All species showed increases in photosynthetic rates at the leaf level in response to some of the nutrient treatments in one or both years. Leaf N concentration is often correlated with photosynthetic capacity, since the majority is allocated to photosynthetic enzymes, particularly ribulose 1,5 bisphosphate carboxylase/oxygenase (Field and Mooney 1986, Evans 1989). Although photosynthetic rates increased in $\approx 50\%$ of the cases in the N and N+P treatments, these increases did not always coincide with increases in foliar N. For example, photosynthesis rates in *Kobresia* increased in the N treatment in 1990 without a significant increase in foliar N concentration, and was not higher in 1991 despite a significant increase in foliar N concentration. The dry meadow *Bistorta* in the N+P treatment had significantly lower photosynthesis rates in 1991 despite higher foliar N concentrations. Photosynthetic rates in *Caltha* were more sensitive to P amendments. The reasons for these discrepancies in the relationship between foliar N concentration and photosynthetic rates may be related to several factors. Foliar N may be allocated differently to the photosynthetic apparatus under different conditions not necessarily related to soil nutrient status. N can be stored in compounds which are not related to photosynthetic capacity. Allocation of N to defense compounds may be a substantial fraction of leaf N in plants of low nutrient environments (Coley et al. 1985). Chapin (1991) has proposed that regulation of growth and photosynthesis in stressful environments, including those of infertile soils, may be the result of hormonal feedbacks independent of foliar nutrient status. Such a response has been documented in barley and tomato (Chapin et al. 1988), but we know of no studies investigating this for plants of low nutrient soils.

Changes in community structure and composition

Nutrient amendments had significant effects on the proportion of biomass made up by the different growth forms in both the dry and wet meadows. In both communities graminoid growth was favored more than forbs by the N and N+P amendment treatments. In the dry meadow the proportion of community biomass made up by both forbs and non-*Kobresia* graminoids increased, while the proportion of biomass made up by the dominant graminoid *Kobresia* decreased. There was also a significant increase in the number of species in the N+P plots of the dry meadow community, with species characteristic of both more nutrient-rich and

disturbed soils invading within 2 yr of the start of the experiment. Thus, our hypothesis of community response to nutrient amendments is supported for the dry meadow, with the dominant *Kobresia* contributing less to the increase in biomass relative to more rare species. This pattern was not apparent in the more nutrient-rich wet meadow community. There was a significant decrease in the composition of community biomass made up by forbs, possibly related to competition for light. Suppression of forbs by increases in biomass of grasses has also been related to increases in available nutrients in annual grasslands (Huenneke et al. 1990). An opposite response was observed in tallgrass prairie, where forbs outcompeted the dominant C_4 grasses in fertilized, unburned prairie (Seastedt et al. 1991). Thus, the response observed here may be more characteristic for C_3 graminoids.

Changes in the wet meadow community structure were small. There was no change in species richness in response to nutrient additions. The dominant graminoid *Carex scopulorum* showed no significant change in cover in response to the nutrient treatments (T. A. Theodose and W. D. Bowman, *unpublished data*). In general, higher species diversity is expected during the transition from nutrient-poor to nutrient-rich soils, with an eventual decrease in species richness and a shift in dominance to species more able to utilize nutrients for growth (Tilman 1982, Begon et al. 1990).

Conclusions

From our results we would expect that increases in soil nutrient availability, particularly N, would have an impact on primary production in alpine tundra of Niwot Ridge. The greatest response to an increase in N availability would be expected in the nutrient-poor communities, where changes both in production and community structure would occur. Smaller changes would be expected in the more nutrient-rich communities, which are co-limited by N and P and are closer to a light limitation of production. This hypothesis contrasts to hypothesized community responses based on the relative capacity of individual dominant species to respond to variation in soil nutrient supply (Chapin 1980, 1991). Thus, the production responses of communities in alpine tundra cannot be predicted based on responses of individual plants in the existing communities. Community characteristics, such as changes in structure and composition and shifts in the environmental limitations of production due to biotic interactions, modify the community response to increased nutrient supply.

The largest reservoir of nutrients in alpine tundra is in soil organic matter, yet controls over mineralization are poorly understood. Soil temperature and moisture are likely determinants of mineralization rates (Meentemeyer 1978), although litter quality may also play an important role (Melillo et al. 1982). N mineralization rates have been studied in the European Alps

(Rehder 1976, Gokceoglu and Rehder 1977, Rehder and Schafer 1978), but little is known of the mechanisms controlling them.

Atmospheric deposition is a potentially large source of N for support of plant growth on Niwot Ridge. Bulk deposition accounts for the vast majority of intersystem N inputs (Bowman 1992, Sievering et al. 1992), much of which is anthropogenically derived (Lewis and Grant 1980, Lewis et al. 1984, Parrish et al. 1986). Approximately one half of the inputs from bulk deposition occur in the winter, with much of this N associated with snow. Strong prevailing westerly winds redistribute the snow and the associated N reservoir. This results in uneven inputs of N during snowmelt, with communities in close association with snowfields (including wet meadows) receiving the majority of this N, which may approach as much as 30% of the N derived from mineralization (Bowman 1992). While this N input may be increasing production and altering community structure, a potential exists for N saturation of alpine tundra on Niwot Ridge, as biomass is relatively low compared with deposition rates. N saturation would potentially have deleterious effects on plants (Aber et al. 1989), increasing sensitivity to water stress, frost, and herbivory, and may result in important changes in stream chemistry and acidity.

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