

## ORIGINAL PAPER

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## Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: implications for differential community response to environmental change

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**Abstract** Physiological and growth measurements were made on forbs and graminoids following additions of water and N+water in a graminoid-dominated dry meadow and a forb-dominated moist meadow, to determine if the community-level response was related to differential responses between the growth forms. Graminoids had higher photosynthetic rates and lower transpiration rates and foliar N concentrations than forbs, and consequently maintained higher photosynthetic N- and water-use efficiencies. Photosynthetic rates, stomatal conductance, and transpiration rates increased significantly only in response to N fertilization and only in moist meadow species. The increase in photosynthetic rates was unrelated to variation in foliar N concentration, but instead correlated with variation in stomatal conductance. Growth based N-use efficiency was higher in moist meadow graminoids than in moist meadow forbs, but did not differ between the growth forms in the dry meadow. The moist meadow community had higher biomass and N standing crops, but the relative increase in these factors in response to N fertilization was greater in the dry meadow. Graminoids had a greater relative increase in biomass and N accumulation than forbs following N fertilization, but moist meadow graminoids exhibited a greater response than dry meadow graminoids. The difference in the growth response between the dry meadow and moist meadow graminoids to N fertilization was correlated with more conservative leaf gas exchange responses in dry meadow species, presumably related to a higher frequency of soil water deficits in this community. Community-level response to the resource additions was therefore mediated by the plant growth form response, corresponding with differences between the growth forms in physiological factors related to resource acquisition and use.

**Key words** Alpine tundra · Nitrogen · Physiological response to resource additions · Plant growth form · Primary production

### Introduction

Plant growth forms are the result of the evolution of plant morphological and physiological characters responding to environmental and life-history constraints (Schimper 1903; Raunkiaer 1934; Cain 1950; Cody 1991). The predominance of one growth form in a community is often used as an integrated measure of environmental conditions. For example, in arctic tundra, dominance by evergreen species indicates sites of low nutrient availability, whereas deciduous species tend to dominate communities of higher fertility (Webber 1978; Miller 1982). Additionally the capacity of plants to respond to increases in resource supply is partially associated with plant growth form (Shaver and Chapin 1980, 1986, 1991; Aerts et al. 1991; Bowman et al. 1993). Directional changes in resource availability can lead to changes in the growth form composition of a community, with associated changes in ecosystem properties such as primary production and nutrient cycling (Tamm 1991). Differential responses of growth forms to high levels of N deposition from anthropogenic sources resulted in a shift from evergreen-shrub-dominated communities to graminoid-dominated communities in the Netherlands (Roelofs et al. 1987). Thus, the degree to which production at the community level responds to environmental variation may be associated with the growth form composition of the community.

Differences among plant growth forms in the rate of growth response following changes in resource supply may be the result of differences in physiological responses, including resource allocation and photosynthetic response, developmental constraints in producing new tissues, longevity of photosynthetic tissues, and/or differences in the resources limiting growth (Poorter 1989; Lambers and Poorter 1992). Few studies have simulta-

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neously addressed the growth response to resource manipulations at the community level and the physiological response of growth forms that make up the communities (Bigger and Oechel 1982; Schimel et al. 1991; Tilman and Wedin 1991).

Variation in snow accumulation and slope exposure across alpine landscapes results in the formation of distinct plant communities in relatively close proximity to one another (Billings 1988; Walker et al. 1993). The variation in growth-form composition among these communities provides a useful system for investigating potential differences in the physiological and growth responses of plant growth forms to resource additions and the subsequent impact on variation in whole-community production.

Previous experimental and descriptive research has indicated that nutrient and water availability are most important in limiting production of alpine tundra in the southern Rocky Mountains (Greenland et al. 1984; Isard 1986; Bowman et al. 1993; Walker et al. 1994). Soil moisture availability has a direct influence on plant water relations (Ehleringer and Miller 1975; Oberbauer and Billings 1981) and subsequently on photosynthesis and growth of alpine plants (Johnson and Caldwell 1975; Peterson and Billings 1982; Enquist and Ebersole 1994), and on N mineralization rates in alpine soils (Fisk and Schmidt, in press).

We examined species, growth form, and community responses to N and water additions in alpine tundra. We also wished to gain information on potential biotic responses to increased N supply. Atmospheric N deposition from anthropogenic sources has increased six-fold in the past few decades, and may have significant biological impacts on alpine ecosystems in the Colorado Rocky Mountains (Sievering et al. 1992; Williams et al. 1993). The physiological responses of the growth forms were evaluated by measuring leaf gas exchange, foliar N concentration, and N resorption efficiency for representative species for each growth form. Furthermore, we measured resource-use efficiencies (index of the capacity of the plant to translate resource uptake into photosynthesis and growth) for the representative species. The responses of these physiological factors were compared with the production and N standing crops of the growth forms within each community, to determine whether the degree of physiological response by the growth forms corresponded with the biomass and N accumulation responses. The subsequent impact of differential growth-form responses to increases in limiting resources on community production and N accumulation was also examined.

## Materials and methods

### Study site and treatments

The study was conducted on Niwot Ridge in the Front Range of the Colorado Rocky Mountains. Mean annual temperature at the site is  $-3^{\circ}\text{C}$ , and annual average precipitation is c. 900 mm (Greenland 1989). Depth of snow cover in the winter is spatially heterogeneous, ranging from 0 to  $>4$  m, and plant community

composition is correlated with winter snow distribution (Walker et al. 1993).

The research was done in two alpine tundra communities differing in their composition of plant growth forms. Dry meadow communities (*sensu* May and Webber 1982) consist primarily of graminoid species (59% of cover, 41% forb cover), whereas in moist meadow communities forbs make up the majority of the cover (67% forb cover, 33% graminoid cover). Replicated blocked treatment plots were established in dry and moist meadows at 3520 m elevation in the Saddle research area in May 1991. Five blocks in the two communities each had three plots, including a control and two treatment plots. Treatments consisted of added N in solution (+N+H<sub>2</sub>O) and added water (+H<sub>2</sub>O). The +N+H<sub>2</sub>O treatment included biweekly additions of 2 g of NH<sub>4</sub>NO<sub>3</sub> dissolved in deionized water (identical volumes to the +H<sub>2</sub>O treatment). The +H<sub>2</sub>O treatment consisted of biweekly additions of 5 l of deionized water to the plots, approximately doubling the average growing season precipitation input. The treatments were applied using backpack sprayers during the growing season (first week of June to early August). Total seasonal inputs of water and N from the treatments were 85 mm water m<sup>-2</sup> and 15.8 g N m<sup>-2</sup>. The treatments were applied for two growing seasons. All measurements were made during the second year of the experiment, to allow for potential release from plant developmental constraints on the growth response to changes in resource supply that may occur only after two or more growing seasons (Körner 1989; Bowman and Conant 1994).

To assess differences in N supply between the communities we measured net N mineralization from 24 July to 6 September 1992 (2nd year of the experiment) using PVC incubation tubes (DiStephano and Gholz 1986). Ion exchange resin bags were placed in the bottom of each tube to catch leachate. Incubation tubes placed in the +N+H<sub>2</sub>O plots were capped with stoppers during application of the N fertilizer. An equivalent amount of deionized water was added to the incubation tubes in the +N+H<sub>2</sub>O and +water treatments to match the rest of the plot treatment. Inorganic nitrogen (NO<sub>3</sub><sup>-</sup>+NH<sub>4</sub><sup>+</sup>) concentrations were determined before and after the incubation period by extracting the soils with 2 M KCl. The extractant was analyzed using a flow injection colorimetric analyzer (Lachat Instruments) as described in Bowman et al. (1993). Net N mineralization was calculated as the difference in inorganic N between the end and the start of the incubation.

### Plant measurements

Leaf gas exchange measurements (photosynthesis, transpiration, and stomatal conductance) were made after full leaf elongation had occurred (mid- to late-July) on three or four species from each community that made up the majority of plant cover. In the dry meadow this included the dominant graminoid *Kobresia myosuroides* (Villars) Fiori & Paoli, the subdominant grass *Calamagrostis purpurascens* R. Brown, and the sub-dominant forbs *Acomastylis rossii* (= *Geum rossii*) (R. Brown) Greene and *Bistorta vivipara* (L.) S. Gray. These species make up 72% of the graminoid cover and 42% of the forb cover in the dry meadow. In the moist meadow gas exchange measurements were made on the dominant forb *A. rossii*, the dominant graminoid *Deschampsia caespitosa* (L.) P. Beauvois, and the sub-dominant forb *B. bistortoides* (Pursh) Small. These species make up 55% of the graminoid cover and 34% of the forb cover in the moist meadow. All species are perennials. Measurements were made on two to four leaves per plant, two to three plants per plot, using a Li-Cor LI-6200 gas exchange system (Lincoln Neb.). Measurements were made during the late morning (1000–1200 hours, mountain daylight saving time), under full sunlight (photosynthetic photon flux densities of 1800–2200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and air temperatures of 15–20°C.

Leaves used in the photosynthesis measurements were collected for N analysis. Total Kjeldahl N was determined as described in Bowman et al. (1993). Leaves of species whose morphology were less conducive to leaf gas exchange measurements were also collected for foliar N analysis, including the forb *Artemisia scopulorum* Gray (moist meadow) and the sedge *Carex rupestris* Allioni (dry meadow).

Photosynthetic water-use efficiencies (PWUE, photosynthesis rate/transpiration rate) and nitrogen-use efficiencies (PNUE, photosynthesis rate/foliar N concentration) were calculated from the leaf gas exchange and foliar N measurements.

Senescent leaves were collected from four to five plants of each of the study species in each treatment plot in late September. The leaves were oven-dried, and then ground with a mortar and pestle. A subsample was analyzed for N concentration, to estimate the amount of external N required to support new growth [growth-based nitrogen-use efficiency (NUE), Gerloff (1976)] and to measure the efficiency of N resorption following senescence. Another subsample was analyzed for carbon isotope composition ( $\delta^{13}\text{C}$ , Ehleringer and Rundel 1989) to estimate growth-based water-use efficiency (WUE, Farquhar et al. 1989). Following combustion of the samples in an elemental analyzer (Carlo Erba NA1500) the liberated  $\text{CO}_2$  was trapped, purified, and analyzed for carbon isotope composition using a ratio mass spectrometer (SIRA series II, VG Isogas) at the Duke University Phytotron Stable Isotope Facility.

Aboveground biomass accumulation (~primary production) was measured for the two dominant plant growth-forms (graminoids and forbs) and *Kobresia*. Differences in plant age, initial plant size, and cover made accurate measurement of single species growth responses to the treatments impractical, with the exception of *Kobresia*, which has a large enough cover (40%, May and Webber 1982) to allow the assumption of uniform cover within each of the dry meadow plots prior to the start of the experiment. All live aboveground vascular plant biomass in the moist and dry meadow communities are derived from the current growing season, and peak season aboveground biomass is a good approximation of primary production (May and Webber 1982). All aboveground vascular biomass was harvested from three 0.04-m<sup>2</sup> representative subplots in each of the plots in late July, at the period of peak biomass accumulation (May and Webber 1982). The biomass was oven dried at 70°C to constant weight (48 h), and then weighed.

Belowground biomass was estimated using root cores. Two 3.8 cm diameter, 30 cm deep cores were collected from each plot in early August. All live roots and stems were collected from each core, gently washed in deionized water, oven-dried, and weighed.

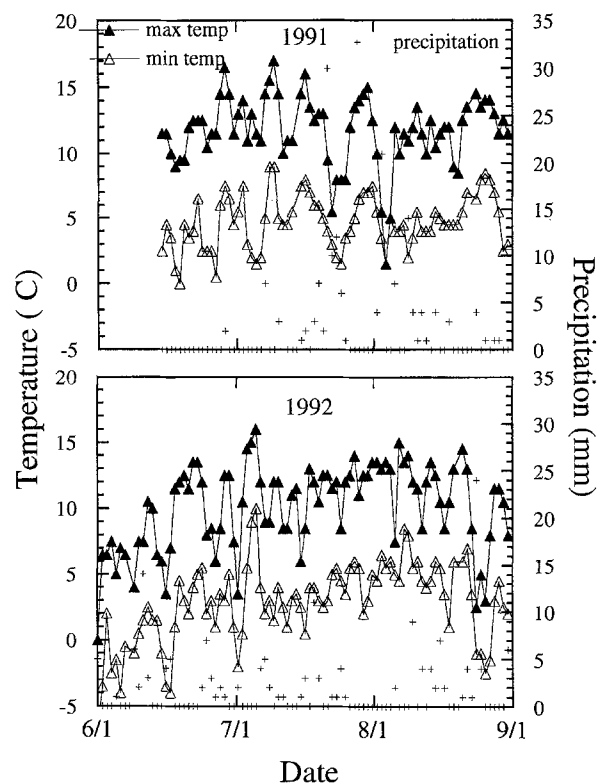
#### Statistical analysis

The leaf gas exchange, foliar N, N resorption efficiency, WUE, and NUE data were analyzed statistically using three-way analyses of variance (ANOVAs) with community, growth form, and treatment as categorical variables (Wilkinson 1990). The community  $\times$  treatment interaction term was excluded from the model, since the physiological measurements did not adequately represent physiological response of the entire community. The community  $\times$  treatment  $\times$  growth form interaction term was also excluded, since it did not relate to the questions addressed by the research. The same variables were also analyzed by two-way ANOVAs using species and treatment as categorical variables. The biomass and N standing crop data were analyzed using two-way ANOVAs, both with treatment and block, and community and treatment as categorical variables. Transformations were necessary for the biomass (log), N accumulation (log), growth-based NUE (arcsin), and N mineralization rate (arcsin) data to meet the assumptions of the ANOVA tests.

## Results

### Site climate

Maximum and minimum air temperatures and precipitation were near average for the Niwot Ridge Saddle research site during the summers of 1991 and 1992 (Fig. 1, data from Mountain Research Station Climate Program). Maximum air temperatures rarely exceeded 15°C, and there was only one period (~10 days) of continuous low or no precipitation in mid-June 1991. Summer precipita-



**Fig. 1** Course of growing season minimum (*open triangles*) and maximum (*closed triangles*) temperatures and precipitation during 1991 and 1992 at the Saddle research site, Niwot Ridge, Colorado

**Table 1** Net N mineralization rates and *F* ratios and significance levels from analysis of variance for moist and dry meadow tundra communities subjected to +N+H<sub>2</sub>O and +water treatments. Rates are means and  $\pm$ SE (*n*=5)

	Net N mineralization rate ( $\mu\text{g N g}^{-1}$ dry weight soil 45 days <sup>-1</sup> )		
	Control	+N+H <sub>2</sub> O	+Water
Dry meadow	-21.0 $\pm$ 22.5	43.0 $\pm$ 6.2	-2.1 $\pm$ 2.7
Moist meadow	-17.1 $\pm$ 5.6	55.2 $\pm$ 19.5	13.9 $\pm$ 4.9

Variable	Source	<i>F</i> ratio
N mineralization	community	1.049
	treatment	14.44***
	community $\times$ treatment	0.117

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

tion in 1991 and 1992 was slightly less (80–90%) than the average in the Saddle (12-year record).

### N mineralization

N supply rates to plants, as indexed by net N mineralization measurements, did not differ between the communities (Table 1). High microbial immobilization was indicated by the negative net N mineralization rates in the control plots of both communities, suggesting N supply limits mi-

Variable	Dry meadow	
	Source	F ratio
<i>Biomass</i>		
Total	treatment	23.33***
	block	1.42
Graminoid	treatment	24.37***
	block	3.22
Forb	treatment	8.25**
	block	0.82
<i>Kobresia</i>	treatment	6.43*
	block	1.90
<i>N accumulation</i>		
Total	treatment	46.27***
	block	1.421
Graminoid	treatment	12.24**
	block	0.41
Forb	treatment	6.79*
	block	0.76
<i>Kobresia</i>	treatment	18.13**
	block	1.69
Variable	Moist Meadow	
	Source	F ratio
<i>Biomass</i>		
Total	treatment	16.28**
	block	17.08***
Graminoid	treatment	5.83*
	block	8.95**
Forb	treatment	3.79
	block	8.52**
<i>N accumulation</i>		
Total	treatment	26.74***
	block	16.32***
Graminoid	treatment	11.82**
	block	7.08*
Forb	treatment	6.13*
	block	7.86**
Variable	Combined	
	Source	F ratio
<i>Biomass</i>		
Total	community	7.38*
	treatment	10.69***
	community×treatment	0.87
Graminoid	community	59.68***
	treatment	6.50**
	community×treatment	0.44
Forb	community	44.18***
	treatment	6.98**
	community×treatment	2.80
<i>N accumulation</i>		
Total	community	8.31**
	treatment	20.24***
	community*treatment	0.766
Graminoid	community	15.01**
	treatment	22.48***
	community×treatment	1.94
Forb	community	30.21***
	treatment	6.10**
	community×treatment	0.14

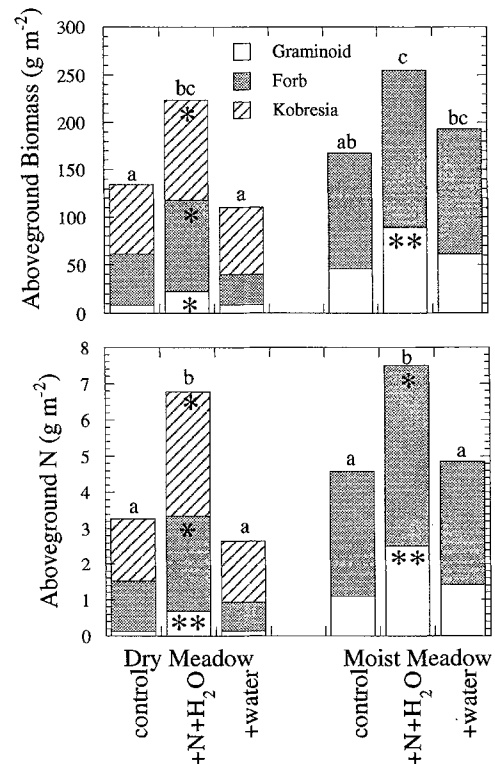
\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ 

**Table 2** F ratios and significance levels from analyses of variance for aboveground biomass and N accumulation of moist and dry meadow tundra communities subjected to +N+H<sub>2</sub>O and +water treatments. Biomass was log transformed to meet the assumptions of the analysis of variance.

crobial growth at least during the latter half of the growing season. Measurements in other dry and moist meadow communities and during other years on Niwot Ridge has also indicated similar N mineralization rates in these two communities (M.C. Fisk, unpublished work). Fertilization with N resulted in positive N mineralization rates in both communities, presumably resulting from inputs of higher quality litter from the previous growing season, which would lower the N limitation of microbial growth.

### Biomass and N accumulation

Aboveground community biomass was higher in the moist meadow than the dry meadow (Table 2, Fig. 2). Graminoids (with *Kobresia* included) made up the greater proportion of biomass in the dry meadow, while forbs were the larger component of biomass in the moist meadow. Both communities showed increases in above-



**Fig. 2** Biomass and N standing crops for dry and moist meadow alpine tundra communities under control, N fertilized (+N+H<sub>2</sub>O), and watered (+water) treatments. Letters indicate heterogeneous means for total biomass and N standing crop (Tukey-Kramer HSD multiple range test), and asterisks denote significant differences from the control values within the biomass components (\* $P < 0.05$ , \*\* $P < 0.01$ , ANOVA)

**Table 3** *F* ratios and significance levels from analyses of variance for leaf gas exchange of alpine plant growth forms (3-way ANOVA) and species (2-way ANOVA) from moist and dry meadow tundra communities subjected to +N+H<sub>2</sub>O and +water treatments

Variable	Source	<i>F</i> ratio	Source	<i>F</i> ratio
Photosynthesis	species	13.77***	community	0.55
	treatment	6.46**	growth form	8.40**
	species×treatment	0.43	treatment	4.33*
Stomatal conductance	species	treatment	community×growth form	0.001
			growth form×treatment	0.93
			community	12.17***
			growth form	5.35*
			treatment	2.30
Transpiration	species	treatment	community×growth form	9.01**
			growth form×treatment	0.27
			community	10.86***
			growth form	4.68*
			treatment	0.37
PWUE	species	treatment	community×growth form	0.37
			growth form×treatment	0.32
			community	10.01***
			growth form	0.764
			treatment	0.721
PNUE	species	treatment	community×growth form	1.10
			growth form×treatment	0.25
			community	23.37***
			growth form	3.009
			treatment	1.350
PNUE	species	treatment	community×growth form	2.56
			growth form×treatment	0.44
			community	0.47
			growth form	23.59***
			treatment	2.56

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$  (PWUE photosynthetic water-use efficiency, PNUE photosynthetic nitrogen use efficiency)

ground biomass in response to the +N+H<sub>2</sub>O treatment, while addition of water alone had no effect on biomass. The response to the +N+H<sub>2</sub>O treatment in the moist meadow community was mediated by an increase in graminoid biomass, since there was no significant increase in forb biomass. Biomass of both growth form components and *Kobresia* increased significantly in the dry meadow in response to the +N+H<sub>2</sub>O treatment. There was no significant microsite (block) effect on biomass accumulation in the dry meadow, whereas microsite effect explained as much variation in biomass accumulation as the treatment effect did in the moist meadow (Table 2).

There were no differences between the communities, nor did treatment or microsite have an influence on belowground biomass. The mean and SE for the belowground biomass in the dry and moist meadow communities were  $790 \pm 185$  and  $799 \pm 79$ , respectively.

Aboveground N accumulation followed similar trends as aboveground biomass, with greater N accumulation in the moist meadow, and a significant N treatment effect (Table 2, Fig. 2). The N accumulation response to the +N+H<sub>2</sub>O treatment was greater than the biomass response in the dry meadow, as a result of an increase in tissue N concentrations. While the greater response was in the graminoid component in both communities, there was also a significant increase in N accumulation in the forbs.

#### Leaf gas exchange

Photosynthetic and transpiration rates and stomatal conductance were significantly related to species, growth

form, and treatment (Tables 3, 4, Fig. 3). Graminoids had higher photosynthesis rates than forbs, but lower stomatal conductances and transpiration rates. The effect of growth form on stomatal conductance was significant only in the moist meadow (community × growth form interaction, Table 3). The +N+H<sub>2</sub>O treatment resulted in higher photosynthesis and transpiration rates and stomatal conductances, but this result was community related, since only moist meadow species responded to the treatment.

PNUE and PWUE were both species- and growth-form-specific (Tables 3, 4, Fig. 3). Graminoids had higher photosynthetic-resource use efficiencies than forbs. There were no treatment effects on PNUE or PWUE, despite significant leaf gas exchange responses to the +N+H<sub>2</sub>O treatment, indicating the variables making up these resource-use efficiencies changed in concert with the treatment.

#### Foliar N, NUE, and N resorption efficiency

Species and growth forms differed significantly in foliar N concentrations (Tables 5, 6, Fig. 4). Forbs had higher N concentrations than graminoids. The +N+H<sub>2</sub>O treatment resulted in higher foliar N concentrations, but only in dry meadow species.

Growth-based NUE was also species and growth form specific (Tables 5, 6, Fig. 4). The growth form effect varied according to community, as moist meadow graminoids had higher NUE than moist meadow forbs, but there was equivalent NUE in dry meadow graminoids and forbs. NUE decreased in the +N+H<sub>2</sub>O treatment, but not significantly in all species.

**Table 4** Photosynthesis and transpiration rates, stomatal conductance, and photosynthetic water- and nitrogen-use efficiencies for alpine tundra species from two communities, moist and dry meadows, in control, +N+H<sub>2</sub>O, and +water plots. Values are means ±SE

Treatment:	Control	+N+H <sub>2</sub> O	+Water
Photosynthesis rate (μmol m <sup>-2</sup> s <sup>-1</sup> )			
Dry meadow species:			
<i>Acomastylis rossii</i>	13.0 ± 1.4	15.9 ± 2.1	15.5 ± 1.9
<i>Bistorta vivipara</i>	20.4 ± 1.6	21.4 ± 1.0	20.4 ± 1.3
<i>Calamagrostis purpurascans</i>	22.4 ± 2.0	25.9 ± 3.1	26.4 ± 1.9
<i>Kobresia myosuroides</i>	16.9 ± 1.2	17.2 ± 1.6	17.3 ± 1.5
Moist meadow species:			
<i>Acomastylis rossii</i>	14.1 ± 1.1	19.9 ± 0.8*	14.7 ± 1.1
<i>Bistorta bistortoides</i>	21.2 ± 0.6	22.2 ± 0.5	20.2 ± 0.9
<i>Deschampsia caespitosa</i>	18.1 ± 2.4	25.2 ± 1.3*	20.4 ± 1.4
Stomatal conductance (mmol m <sup>-2</sup> s <sup>-1</sup> )			
Dry meadow species:			
<i>Acomastylis rossii</i>	677 ± 131	825 ± 158	821 ± 132
<i>Bistorta vivipara</i>	935 ± 73	1020 ± 32	1089 ± 162
<i>Calamagrostis purpurascans</i>	1128 ± 184	1183 ± 215	1176 ± 151
<i>Kobresia myosuroides</i>	714 ± 64	704 ± 58	824 ± 66
Moist meadow species:			
<i>Acomastylis rossii</i>	591 ± 59	777 ± 59*	741 ± 122
<i>Bistorta bistortoides</i>	968 ± 84	1133 ± 99*	990 ± 62
<i>Deschampsia caespitosa</i>	408 ± 75	640 ± 47*	611 ± 112
Transpiration rate (mmol m <sup>-2</sup> s <sup>-1</sup> )			
Dry meadow species:			
<i>Acomastylis rossii</i>	14.4 ± 2.4	15.7 ± 2.8	15.2 ± 1.5
<i>Bistorta vivipara</i>	14.9 ± 1.0	17.2 ± 1.2	18.1 ± 2.2
<i>Calamagrostis purpurascans</i>	15.1 ± 1.4	17.9 ± 2.4	17.7 ± 2.1
<i>Kobresia myosuroides</i>	10.2 ± 1.2	10.6 ± 1.2	10.3 ± 0.8
Moist meadow species:			
<i>Acomastylis rossii</i>	10.2 ± 1.0	12.8 ± 1.8	12.0 ± 1.6
<i>Bistorta bistortoides</i>	17.4 ± 0.4	20.3 ± 0.9*	18.0 ± 0.9
<i>Deschampsia caespitosa</i>	10.4 ± 2.2	15.5 ± 0.7*	15.4 ± 2.9
PWUE (μmol CO <sub>2</sub> mmol <sup>-1</sup> H <sub>2</sub> O)			
Dry meadow species:			
<i>Acomastylis rossii</i>	0.93 ± 0.09	1.03 ± 0.04	1.02 ± 0.06
<i>Bistorta vivipara</i>	1.38 ± 0.10	1.26 ± 0.09	1.15 ± 0.13
<i>Calamagrostis purpurascans</i>	1.49 ± 0.09	1.54 ± 0.26	1.63 ± 0.29
<i>Kobresia myosuroides</i>	1.67 ± 0.08	1.63 ± 0.06	1.69 ± 0.10
Moist meadow species:			
<i>Acomastylis rossii</i>	1.42 ± 0.13	1.65 ± 0.24	1.28 ± 0.10
<i>Bistorta bistortoides</i>	1.22 ± 0.03	1.10 ± 0.05	1.13 ± 0.01
<i>Deschampsia caespitosa</i>	1.83 ± 0.14	1.62 ± 0.07	1.43 ± 0.19
PNUE (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> % <sup>-1</sup> N)			
Dry meadow species:			
<i>Acomastylis rossii</i>	6.29 ± 1.42	8.11 ± 1.94	7.99 ± 0.82
<i>Bistorta vivipara</i>	5.35 ± 0.39	4.71 ± 0.23	5.88 ± 0.38
<i>Calamagrostis purpurascans</i>	12.68 ± 1.6	11.41 ± 1.41	15.29 ± 1.10
<i>Kobresia myosuroides</i>	7.23 ± 1.09	5.34 ± 0.43	7.26 ± 0.93
Moist meadow species:			
<i>Acomastylis rossii</i>	5.44 ± 0.65	7.42 ± 0.37	6.48 ± 0.48
<i>Bistorta bistortoides</i>	6.51 ± 0.69	5.62 ± 0.30	6.77 ± 0.39
<i>Deschampsia caespitosa</i>	7.46 ± 0.58	9.35 ± 0.90	9.13 ± 1.26

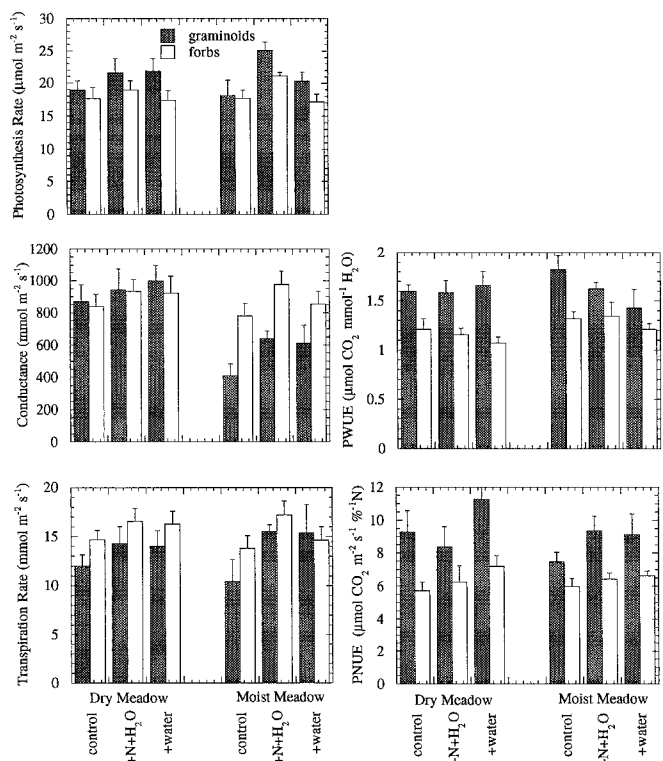
Significant differences from control means within a species population are designated by \* ( $P < 0.05$ ) determined using Tukey-Kramer HSD multiple range test following one-way ANOVA for each species (only if treatment effect was significant in two-way ANOVA)

N resorption efficiency differed among the species, but not according to growth form or community (Tables 5, 6). There was no treatment effect on N resorption efficiencies.

## WUE

Integrated WUE (estimated using  $\delta^{13}\text{C}$ ) varied significantly among the species, with the highest WUE (highest

$\delta^{13}\text{C}$ ) in *Calamagrostis*, and the lowest WUE in *Artemisia* (Tables 5, 6). There was no difference in WUE between the growth forms, but the dry meadow community had higher WUE than the moist meadow community. Generally there was little variation among the species in  $\delta^{13}\text{C}$  within a given treatment, but a significant increase in  $\delta^{13}\text{C}$  (increase in WUE) resulted from the +N+H<sub>2</sub>O treatment in two moist meadow species, *Deschampsia* and *Bistorta*.



**Fig. 3** Leaf gas exchange rates and photosynthetic water- (PWUE) and N-use (PNUE) efficiencies for graminoids and forbs in two alpine tundra communities on Niwot Ridge, Colorado, under control, N fertilized (+N+H<sub>2</sub>O), and watered (+water) conditions. Bars are means and error bars are +1 SE. Means and SEs for species used to estimate growth form responses are listed in Table 4

## Discussion

### Physiological and growth responses

The community-level responses to N fertilization reflected the differential capacities of the growth forms to increase biomass and N standing crops. Graminoid biomass and N standing crop increased 73% and 121% relative to controls, while forb biomass and N standing crop increased 49% and 58%. The graminoid-dominated dry meadow had greater responses to N fertilization (67% increase in biomass and 107% increase in N standing crop relative to controls) than the forb-dominated moist meadow (53% and 64% increases in biomass and N standing crop, respectively). Growth form composition therefore appears to be an important determinant of the capacity of these alpine communities to respond to environmental change.

Several physiological factors may have underlain the differential responses of the growth forms to N fertilization. Graminoids had higher photosynthetic rates than forbs on a per unit leaf area basis, and thus greater potential supply of carbohydrates for growth. Graminoids also had higher photosynthetic N- and water-use efficiencies than forbs, and thus acquired more carbon per investment of growth limiting resources. Differences in the capacities of growth forms to respond to environmental perturbations have been demonstrated, but the potential physiological mechanisms underlying the responses have received less attention (Chapin and Shaver 1989; Aerts 1990).

While there was a correlation between the relative biomass responses of the growth forms and their physiological responses, it is likely that other factors, including differences in the ability to produce new meristems during the current growing season (Bowman and Conant 1994), cell size (Körner and Menendez-Riedl 1989), and plasticity of biomass allocation (Chapin 1980; Poorter

**Table 5** *F* ratios and significance levels from analyses of variance components for foliar N concentration, nitrogen-use efficiency (NUE), and N resorption for alpine species and growth forms from moist and dry meadow tundra communities subjected to +N+H<sub>2</sub>O and +water treatments. The foliar N data were arcsin square root transformed and the NUE data were log transformed to meet the assumptions of the analysis

Variable	Source	<i>F</i> ratio	Source	<i>F</i> ratio
Foliar N	species	37.50***	community	1.59
	treatment	33.40***	growth form	26.03***
	species×treatment	2.35**	treatment	14.66***
			community×growth form	1.03
			growth form×treatment	1.24
NUE	species	36.73***	community	8.51**
	treatment	31.35***	growth form	13.78***
	species×treatment	2.39**	treatment	28.30***
			community×growth form	4.38*
			growth form×treatment	2.55
N resorption efficiency	species	2.25*	community	0.04
	treatment	1.89	growth form	1.48
	species×treatment	1.34	treatment	1.93
			community×growth form	4.40*
			growth form×treatment	3.11*
δ <sup>13</sup> C	species	120.4***	community	35.12***
	treatment	9.164***	growth form	2.20
	species×treatment	0.658	treatment	1.50
			community×growth form	0.07
			growth form×treatment	0.002

\* *P*<0.05, \*\* *P*<0.01, \*\*\* *P*<0.001

**Table 6** Foliar N concentrations, NUE, N resorption efficiency, and  $\delta^{13}\text{C}$  [wateruse efficiency (WUE)] for alpine tundra species from two communities, moist and dry meadows, in control, +N, and +water plots. Values are means + SE

Treatment:	Control	+N+H <sub>2</sub> O	+Water
<b>Foliar N (%)</b>			
Dry meadow species:			
<i>Acomastylis rossii</i>	2.21 ± 0.28	2.10 ± 0.22	1.97 ± 0.19
<i>Bistorta vivipara</i>	3.83 ± 0.21	4.56 ± 0.15*	3.49 ± 0.25
<i>Calamagrostis purpurascans</i>	1.82 ± 0.06	2.28 ± 0.08	1.74 ± 0.11
<i>Carex rupestris</i>	1.49 ± 0.06	2.96 ± 0.18*	1.64 ± 0.11
<i>Kobresia myosuroides</i>	2.42 ± 0.18	3.23 ± 0.17*	2.43 ± 0.21
Moist meadow species:			
<i>Acomastylis rossii</i>	2.67 ± 0.18	2.68 ± 0.03	2.18 ± 0.10
<i>Artemisia scopulorum</i>	3.07 ± 0.08	3.59 ± 0.13	2.92 ± 0.16
<i>Bistorta bistortoides</i>	3.38 ± 0.29	3.98 ± 0.16	3.02 ± 0.07
<i>Deschampsia caespitosa</i>	2.40 ± 0.34	2.78 ± 0.25	2.31 ± 0.24
<b>NUE (g biomass g<sup>-1</sup> senescent foliar N)</b>			
Dry meadow species:			
<i>Acomastylis rossii</i>	1303 ± 160	1056 ± 146	1363 ± 95
<i>Bistorta vivipara</i>	1048 ± 23	569 ± 23*	800 ± 86*
<i>Calamagrostis purpurascans</i>	1338 ± 132	820 ± 97*	1225 ± 134
<i>Carex rupestris</i>	1297 ± 73	925 ± 78*	1646 ± 99*
<i>Kobresia myosuroides</i>	959 ± 54	750 ± 61*	1039 ± 136
Moist meadow species:			
<i>Acomastylis rossii</i>	904 ± 75	706 ± 27	967 ± 46
<i>Artemisia scopulorum</i>	901 ± 40	737 ± 74	889 ± 131
<i>Bistorta bistortoides</i>	749 ± 47	590 ± 20*	764 ± 44
<i>Deschampsia caespitosa</i>	1013 ± 86	842 ± 48*	1350 ± 116*
<b>N resorption efficiency</b>			
Dry meadow species:			
<i>Acomastylis rossii</i>	59.3 ± 3.6	47.0 ± 5.9	56.9 ± 3.4
<i>Bistorta vivipara</i>	74.7 ± 1.7	60.6 ± 2.7	62.7 ± 5.5
<i>Calamagrostis purpurascans</i>	57.5 ± 4.2	43.5 ± 6.2	50.9 ± 4.0
<i>Carex rupestris</i>	47.3 ± 2.3	62.5 ± 1.9	61.8 ± 3.4
<i>Kobresia myosuroides</i>	55.6 ± 3.6	56.8 ± 5.2	54.1 ± 10.3
Moist meadow species:			
<i>Acomastylis rossii</i>	56.8 ± 4.4	45.3 ± 1.7	52.9 ± 3.5
<i>Artemisia scopulorum</i>	64.0 ± 1.6	62.1 ± 4.2	58.0 ± 7.8
<i>Bistorta bistortoides</i>	58.6 ± 4.2	56.9 ± 2.4	55.9 ± 2.9
<i>Deschampsia caespitosa</i>	54.6 ± 6.9	54.6 ± 4.6	66.8 ± 5.5
<b><math>\delta^{13}\text{C}</math> (‰)</b>			
Dry meadow species:			
<i>Acomastylis rossii</i>	-26.7 ± 0.4	-26.2 ± 0.2	-26.4 ± 0.2
<i>Bistorta vivipara</i>	-25.6 ± 0.1	-25.4 ± 0.1	-25.7 ± 0.1
<i>Calamagrostis purpurascans</i>	-24.7 ± 0.1	-24.5 ± 0.1	-24.7 ± 0.1
<i>Carex rupestris</i>	-26.8 ± 0.1	-26.5 ± 0.2	-26.9 ± 0.3
<i>Kobresia myosuroides</i>	-26.2 ± 0.2	-26.0 ± 0.1	-26.2 ± 0.1
Moist meadow species:			
<i>Acomastylis rossii</i>	-26.4 ± 0.1	-26.3 ± 0.1	-26.3 ± 0.1
<i>Artemisia scopulorum</i>	-28.2 ± 0.2	-28.3 ± 0.2	-28.2 ± 0.2
<i>Bistorta bistortoides</i>	-26.6 ± 0.1	-26.1 ± 0.1*	-26.6 ± 0.2
<i>Deschampsia caespitosa</i>	-26.9 ± 0.1	-26.4 ± 0.03*	-26.8 ± 0.1

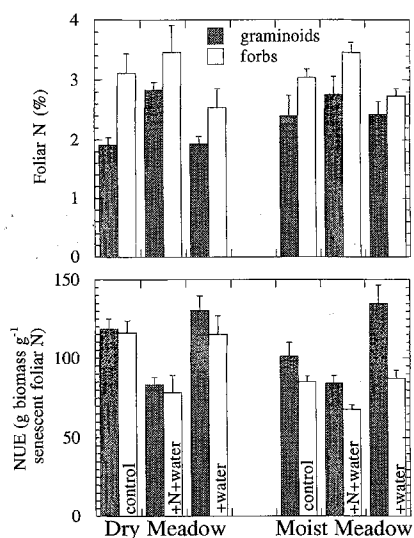
Significant differences from control means within a species population are designated by \* ( $P < 0.05$ ) as determined using Tukey-Kramer HSD multiple range test following one-way ANOVA for each species (only if treatment effect was significant in two-way ANOVA)

1989) also influenced the relative capacity of the growth forms to respond to increases in the supply of N. Additionally forb growth may also be less limited by N than by P, as indicated by biomass measured in years 2 and 4 in a different ongoing long-term fertilization experiment on Niwot Ridge (Bowman et al. 1993; W.D. Bowman, unpublished data). Arctic species show individualistic resource limitations (Chapin and Shaver 1985), potentially promoting greater species coexistence.

The association between the biomass and physiological responses of the growth forms was influenced by the

community in which the plants grew. This was demonstrated by the growth form × community interaction terms in the ANOVAs (Tables 3, 5) that indicated there were community-specific responses of the growth forms in stomatal conductance, NUE, and N resorption to N fertilization. Generally there was a greater physiological response to the treatments in the moist meadow than the dry meadow, particularly for leaf gas exchange parameters. The dominant graminoids in the two communities show this pattern clearly. *Deschampsia*, the dominant of the moist meadow, had significant increases in photosyn-





**Fig. 4** Foliar N concentrations and N-use efficiencies for graminoids and forbs in two alpine tundra communities on Niwot Ridge, Colorado. Bars are means and error bars are +1 SE. Means and SEs for species used to estimate growth form responses are listed in Table 6

thesis, conductance, transpiration, and WUE in response to N fertilization, while *Kobresia* showed no response in these parameters. In a different field study, N uptake per unit of root biomass was greater for *Deschampsia* than co-occurring *Kobresia* (Theodose et al., unpublished work). The biomass and N accumulation responses of the moist meadow graminoids to N fertilization were greater than the responses of the dry meadow graminoids and *Kobresia*, consistent with the greater physiological response of *Deschampsia* relative to the dry meadow graminoids. The lesser response of the dry meadow graminoids relative to the moist meadow graminoids may result from more conservative patterns of leaf gas exchange and biomass allocation (root: shoot ratio, T.A. Theodose and W.D. Bowman, unpublished work), reflecting the more frequent occurrence of soil water deficits in the dry meadow (Greenland et al. 1984; Taylor and Seastedt 1994).

The results of this experiment have implications for the response of alpine tundra to environmental change. Watershed losses of  $\text{NO}_3^-$ -N during the growing season in the valleys adjacent to Niwot Ridge have increased during the past decade in conjunction with an increase in N deposition rates (Lewis and Grant 1980; Parrish et al. 1986; Sievering et al. 1992; Williams et al. 1993), despite indications that the Colorado alpine tundra is N limited. Continued increases in N deposition may result in an increase in the relative proportion of graminoid biomass in Colorado alpine tundra, a pattern that has been documented in a separate fertilization experiment (Bowman et al. 1993; W.D. Bowman, unpublished work). Such changes may have important biotic feedbacks on N uptake and cycling (Hobbie 1992). Alpine graminoids have a greater capacity to sequester N, and produce litter with lower N concentrations (lower C:N ratios) than forbs (NUE in this

study, Bowman 1994). The relative capacity of alpine terrestrial communities to retain additional N, preventing leakage into aquatic systems, would increase under such a scenario, as a result of increased long-term accumulation of N in plant biomass, and decreased turnover rates of soil organic N through the production of lower quality litter. Thus, a change from a forb- to a graminoid-dominated community following an increase in N inputs may have a negative feedback on soil N supply, similar to that found in graminoid-dominated seres of old field successions (Wedin and Tilman 1990).

The addition of water alone produced no effect on leaf gas exchange rates or biomass accumulation in either community. This indicates that in years of near average precipitation water does not directly limit primary production in alpine tundra of the southern Rocky Mountains. Low water availability will limit production in years of low summer precipitation (Ehleringer and Miller 1975; Caldwell et al. 1978; Greenland et al. 1984; Isard 1986; Enquist and Ebersole 1994; Walker et al. 1994). Since most plants are relatively long-lived (up to 70 years) and summer droughts are a relatively stochastic event, alpine tundra can be considered to be both N- and water-limited, depending on the prevailing climatic conditions.

#### Physiological interactions

Photosynthetic rates increased following N fertilization in moist meadow species without a concomitant increase in foliar N, while the converse was true for dry meadow species, i.e., foliar N increased without an increase in photosynthetic rates. Foliar N is often correlated with photosynthetic capacity (Field and Mooney 1986) and increases in both photosynthesis rates and foliar N have been measured following fertilization (e.g., Field et al. 1983; Lajtha and Whitford 1989). The increase in photosynthesis rates following N fertilization in this study was correlated with an increase in stomatal conductance associated with N fertilization ( $r = 0.59$ ,  $P < 0.001$ , Pearson correlation for all leaf gas exchange measurements), while there was no correlation between foliar N concentration and photosynthesis rates ( $r = 0.15$ ,  $P = 0.20$ ). Bowman and Conant (1994) reported the same pattern in the photosynthesis-stomatal conductance-foliar N response in alpine willows. Chapin (1991) and Radin et al. (1982) suggested the link between soil N status and plant stomatal conductance is mediated by hormonal signals between roots and leaves. This link would provide a mechanism for plants to exploit pulses of soil resource inputs that may result from freezing/thawing and drying/wetting cycles in the alpine.

#### Conclusions

Plant growth form composition was an important determinant of the response of these alpine communities to

increases in N supply. Graminoids had a greater capacity to increase biomass in response to N fertilization, and therefore the graminoid dominated community had a greater relative response than the forb dominated community. The greater relative response of graminoids was correlated with greater resource acquisition and investment in photosynthesis than in forbs, although other important factors not examined may also have played a role. There was also evidence of a species-specific response to resource additions, as dry meadow graminoids exhibited more conservative responses in leaf gas exchange and growth relative to moist meadow graminoids. The photosynthetic response to N fertilization was related more to changes in stomatal conductance than to changes in foliar N, indicating a direct link between soil N status and leaf gas exchange. These differential responses of plant growth forms to environmental changes are likely to mediate the response of alpine tundra to increases in N deposition.

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