

The Influence of Interspecific Competition on the Distribution of an Alpine Graminoid:
Evidence for the Importance of Plant Competition in an Extreme Environment

Author(s): Theresa A. Theodose and William D. Bowman

Source: *Oikos*, May, 1997, Vol. 79, No. 1 (May, 1997), pp. 101-114

Published by: Wiley on behalf of Nordic Society Oikos

Stable URL: <http://www.jstor.com/stable/3546095>

REFERENCES

Linked references are available on JSTOR for this article:

http://www.jstor.com/stable/3546095?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



and Wiley are collaborating with JSTOR to digitize, preserve and extend access to
Oikos

JSTOR

The influence of interspecific competition on the distribution of an alpine graminoid: evidence for the importance of plant competition in an extreme environment

Theresa A. Theodose and William D. Bowman

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

The importance of interspecific competition to plant distribution in an unproductive environment was investigated for two alpine tundra graminoids that differed in community of origin, *Kobresia myosuroides* from a resource poor dry meadow and *Deschampsia caespitosa* from a more resource rich moist meadow. It was hypothesized that *Deschampsia* is absent from the resource poor dry meadow due to competitive displacement by *Kobresia*, rather than low resource availability. A removal experiment was performed in the dry meadow, where *Deschampsia* growth, physiology, and mortality in response to both vegetation removal and N additions were examined. Water availability was monitored throughout the experiment. The effect of removal on *Deschampsia* was more pronounced than that of N addition. Removal resulted in a significant decrease in *Deschampsia* mortality, and significant increases in *Deschampsia* shoot and root biomass, tillering, biomass per tiller, root:shoot ratio, root N concentrations, water-use-efficiency and flowering. Soil moisture differences between intact and removal plots suggest that *Kobresia* is able to competitively displace *Deschampsia* from the dry meadow by reducing water levels below which *Deschampsia* can grow and reproduce. A second experiment, conducted in removal plots only, examined the mortality, growth, and physiology of *Deschampsia* and *Kobresia* in response to variations in neighbor and N availability. *Kobresia* exhibited no adverse response to competition with *Deschampsia*, even under high N conditions. These results demonstrate that a species of a resource poor community is capable of competitively displacing a species from a more resource rich community. Since this experiment was conducted in alpine tundra, these results illustrate that competition can be an important force structuring plant community composition in an extreme environment.

T. A. Theodose and W. D. Bowman, Dept of Environmental, Population, and Organismal Biology, Univ. of Colorado, Boulder, CO 80309-0334, USA (present address of TAT: Dept of Biological Sciences, Univ. of Southern Maine, 96 Falmouth St., Portland, ME 04103-4899, USA).

The role of interspecific competition in influencing plant community composition in unproductive environments is often debated (Grime 1979, Thompson 1987, Tilman 1988, Grace 1991). The theoretical basis for the debate lies with the models put forth by Grime (1977, 1979) and Tilman (1988). Grime's theory of life histories assumes that intensity and importance of competi-

tion is low in unproductive environments relative to productive environments. In contrast, Tilman's resource ratio based theory assumes that the intensity and importance of competition does not vary with habitat productivity (Grace 1991). Empirical evidence has further confounded this debate, with some studies supporting Tilman's views (Fowler 1990, Wilson and Shay

Accepted 2 September 1996

Copyright © OIKOS 1997

ISSN 0030-1299

Printed in Ireland – all rights reserved

1990, Wilson and Tilman 1991, 1993, Wilson 1993) and others supporting Grime's views (Del Moral 1983, Gurevitch 1986, Wilson and Keddy 1986, Reader and Best 1989, Campbell and Grime 1992). Experiments that specifically address competition intensity and its relation to habitat productivity have been especially problematic, since intensity can be expressed in both absolute and relative terms (Grace 1995). However, there may be no relationship between the intensity of competition and the importance of competition in structuring plant communities (Welden and Slausen 1986). Ultimately, competition, regardless of its intensity, must be shown to affect the distribution and abundance of species if we are to believe that it is a determinant of community composition in unproductive environments.

An alternative way of addressing the role of competition in unproductive environments is to demonstrate its importance to plant distribution patterns within an unproductive environment. Removal experiments have often been utilized to show how competition can influence plant distribution across communities, but several problems have been associated with the methods (Goldberg and Barton 1992, Gurevitch et al. 1992, McLellan et al. 1995). The soil disturbance and root death caused by vegetation removal can alter soil microbial processes, possibly resulting in increases in nitrogen (N) availability leading to what appears to be competitive release (Wilson and Tilman 1991, Reader et al. 1994; but see Seastedt 1988). In addition, most removal experiments have failed to demonstrate that a target species from outside a site is more negatively affected by competition than a species occurring at that site (Goldberg and Barton 1992; but see Gurevitch 1986 and McGraw and Chapin 1989). Lastly, most removal experiments simply examine the outcome of competition, while ignoring the mechanisms of the interaction (Caldwell 1987). In many cases, the resource being competed for is not even known (Tilman 1987).

When these problems are addressed, removal experiments can be used to illustrate the importance of competition to plant distribution and community composition. When conducted on infertile sites, removal experiments help determine the importance of competition in unproductive habitats. This approach has been used with success in arctic tundra and wet heathland, where native species from infertile sites were found to outcompete species from more fertile sites (McGraw and Chapin 1989, Aerts et al. 1990, Berendse et al. 1992). However, these studies failed to establish concretely the resources for which plants were competing.

We used a removal experiment to examine the importance and mechanisms of competition in an extreme environment, alpine tundra. We specifically examined the effects of competition on the distribution and physiology of the graminoid *Deschampsia caespitosa*. *Deschampsia* is a codominant of alpine moist meadow

communities, but is rarely found in adjacent *Kobresia myosuroides* dominated dry meadow communities (May and Webber 1982). Moist meadow communities have greater productivity, are less nutrient limited, and are more resource rich, in terms of water availability and extractable N, than are dry meadow communities (May and Webber 1982, Walker et al. 1994, Bowman et al. 1995). Previous studies have established that relative to one another, *Deschampsia* has a suite of traits characteristic of a competitive species from a resource rich habitat, while *Kobresia* has a suite of traits characteristic of a stress tolerator from a resource poor habitat (Theodose 1995, 1996).

In order to decipher both the outcome and the mechanisms of competition between *Kobresia* and *Deschampsia*, two field experiments were conducted simultaneously. The first was a removal experiment that compared mortality, growth, and physiology of *Deschampsia* transplanted into the dry meadow plots with vegetation removed with that of *Deschampsia* transplanted into plots with vegetation intact. It was hypothesized that removal of dry meadow vegetation (70% *Kobresia*) would allow for *Deschampsia* establishment. Because N is limiting to primary production in both dry and moist meadow communities (Bowman et al. 1993, 1995) and water can be limiting in certain years (Walker et al. 1994), N levels were manipulated and water levels monitored in order to ascertain if plants were competing for one of these resources. Due to differences in extractable N between the two communities, a more pronounced production response to N in the moist meadow, and increases in abundance of grass species to N fertilization in the dry meadow (Bowman et al. 1993, 1995, Theodose and Bowman in press), a second hypothesis was that low levels of N rather than competitive displacement prevent establishment of *Deschampsia* in the dry meadow community.

The second experiment sought to demonstrate further the mechanisms of interaction between *Deschampsia* and *Kobresia* under both high and low N availability. This neighbor experiment was conducted only in removal plots and examined mortality, growth, and physiology of *Deschampsia* and *Kobresia* targets in response to neighbor treatment (lone, intraspecific, and interspecific) and N regime (high and low). It was hypothesized that under fertilized conditions *Deschampsia* would outcompete *Kobresia*, whereas under unfertilized conditions *Kobresia* would outcompete *Deschampsia*.

In order to address the problems of removal experiments, the following modifications were made. Removal was accomplished by clipping vegetation at ground level rather than applying herbicide. It was believed that this method would minimize rate of root death and thus microbial N-immobilization relative to herbicide treatment, while still removing plant competition for belowground resources (McLellan et al. 1995). In order to assess any effects of clipping on plant

available N, extractable ammonium and nitrate were measured and compared between removal plots and intact plots. In order to compare competitive release of *Deschampsia* following vegetation removal with that of a dry meadow species, we statistically compared the effects of dry meadow vegetation removal on *Kobresia* as well as on *Deschampsia*. However, we did not conduct a parallel experiment with *Kobresia* in the moist meadow, since it has been established that *Kobresia* does not grow in that community due to high levels of winter snow accumulation (Bell and Bliss 1979).

Materials and methods

Field site and study organisms

All field work was conducted on Niwot Ridge, located in the Front Range of the Rocky Mountains in Colorado. Mean annual temperature is -3°C and average yearly precipitation is 900 mm (Greenland 1989). During the study period, mean monthly summer precipitation was lower than average, with 1992 precipitation 90%, 1993 precipitation 63%, and 1994 precipitation 59% of average. The site is located at an elevation of approximately 3510 m and typifies alpine tundra in the Colorado Front Range. Niwot Ridge is administered by the Univ. of Colorado Mountain Research Station and is the site of an NSF sponsored Long-Term-Ecological-Research program.

The experiment was conducted in a dry meadow community located on a gentle south facing slope. Like dry meadows elsewhere on Niwot Ridge (May and Webber 1982), this community was dominated by the sedge *Kobresia myosuroides* (70% relative cover). *Deschampsia*, which codominates alpine moist meadows (40% cover), is rarely found in dry meadow communities even though the two community types are often adjacent (May and Webber 1982, Theodose and Bowman 1995). Primary production in both communities is low relative to other graminoid dominated systems, but is higher in the moist meadow than in the dry meadow (Bowman et al. 1993, 1995).

Experimental design

In June of 1992, sixteen experimental plots were established at the dry meadow site. The plots were arranged in four blocks with four treatment plots in each block. Location of the blocks was based on homogeneity of community type and the blocks were located approximately 50 m apart from each other. Two 90×135 cm plots in each block were designated removal plots, and two 90×75 cm plots in each block were designated intact plots (see below). In each block one of the removal plots and one of the intact plots received a N

fertilization treatment. On 4 June, 1992 fertilizer was applied as osmocote pellets (urea) at a rate of approximately $25 \text{ g N m}^{-2} \text{ yr}^{-1}$. The fertilization treatment was repeated in June of 1993. Previous use of the fertilizer resulted in significantly higher extractable inorganic N without a change in soil pH (Bowman et al. 1993, Fisk and Schmidt 1995).

From 2–3 June, 1992, all vegetation was cut at ground level prior to transplanting. Vegetation regrowth was cut at ground level every two weeks throughout the summers of 1992–1994. *Deschampsia* and *Kobresia* tiller plugs, 2 cm in diameter, were used for transplants. *Deschampsia* plugs were collected from a nearby moist meadow on the same south facing slope, and *Kobresia* plugs were collected from the dry meadow in which plots were located. Transplanting was conducted between 24 June and 24 July, 1994. Two grids were used for transplanting tiller plugs: a 90×135 cm grid for removal plots and a 90×75 cm grid for intact plots. The removal plot grid had 40 points, spaced 15 cm apart and the distance from points to plot edge was also 15 cm. The intact plot grid had 20 points, each spaced 15 cm apart and a distance from points to plot edge of 15 cm (after Fowler 1990). At each grid point within a plot, a pair of plants or a single plant was transplanted. Within each removal plot, the following combinations were planted: 10 lone *Deschampsia*, 10 lone *Kobresia*, 5 intraspecific pairs of *Deschampsia*, 5 intraspecific pairs of *Kobresia*, and 10 interspecific pairs of *Deschampsia* and *Kobresia*. Within each intact plot, 10 lone *Deschampsia* and 10 lone *Kobresia* were planted. This resulted in a total sample size per treatment of 40, with a sample size of 10 for each block. Positions of all plants and plant pairs were randomized in each plot. In order to standardize targets, plant heights were trimmed to 5 cm above ground and number of tillers was counted. *Deschampsia* tiller number varied from 14 to 16 tillers, and *Kobresia* tiller number varied from 24 to 28 tillers, corresponding to similarities in tiller plug diameter between the two species. To maximize transplant success, plots were watered twice weekly with melt water from a nearby snowfield throughout the summer of 1992. On 27 August, at the end of the first growing season, mortality was recorded. This initial mortality was attributed to transplant shock. All succeeding mortality was attributed to treatment effects.

Soil measurements

Throughout the growing season of 1993, soil moisture availability was monitored using Time Domain Reflectometry, using the procedure described by Taylor and Seastedt (1994). Differences in soil N availability between fertilized and unfertilized plots, and between intact and removal plots, were estimated using soil

extracts. On 15 July, 1994 three soil cores of 3 cm width and 25 cm depth were collected from each plot. The three samples from each plot were sieved through a 9-mm mesh and extracted with 2N KCl within two h of collection. The soil samples were analyzed for both $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ using a flow-injection colorimetric autoanalyzer (Lachat Instruments, Mequon, WI). NO_3^- was analyzed using a sulfanilamide colorimetric reaction, following reduction to NO_2^- with a cadmium column. NH_4^+ was analyzed using a phenolate colorimetric reaction.

Plant measurements

Plants were harvested from 21–27 July, 1994. Care was taken to extract as much of the root system as possible for each plant. In removal plots, it was noted that root overlap between individuals within a plant pair occurred, while root overlap between pairs was not apparent. Plants were washed and number of tillers and inflorescences were counted. Plants were then separated into roots and shoots (including inflorescences) and placed in a 50°C drying oven. After two weeks, roots and shoots of all plants were weighed in order to obtain biomass.

Shoot and root N concentrations were determined on 3 randomly selected plants of each neighbor treatment in each plot. Roots and shoots were ground separately using either a Tecator mill or a mortar and pestle. Plant material was then digested in a sulfuric acid/copper sulfate catalyst mixture and analyzed for total Kjeldahl N using a Lachat flow-injection colorimetric analyzer.

In order to determine growth-based water-use-efficiencies (WUE), a subsample of dried material was analyzed for carbon isotope composition ($\delta^{13}\text{C}$) (Ehleringer and Rundel 1989, Farquhar et al. 1989). The samples were combusted in an elemental analyzer, the liberated CO_2 was then analyzed for carbon isotope composition using a ratio mass spectrometer at the Univ. of California, Berkeley.

Statistical analysis

The effects of fertilization and vegetation removal on soil parameters ($\text{NO}_3^+\text{-N}$, $\text{NH}_4^+\text{-N}$, and moisture) and percent mortality were determined using two-way ANOVAs with plot as the experimental unit ($n = 4$). The main effects of the ANOVAs were removal and N (soil parameters and removal experiment) and neighbor and N (neighbor experiment).

Prior to analyses of plant responses, three-way ANOVAs were used to determine any significant effect of block on variation of dependent variables. The three main factors used in each analysis were block, vegeta-

tion removal, and N treatment. No significant block effects of block by treatment interactions were detected, and therefore all blocks were pooled for further analyses. Thus for all plant responses, plant was the experimental unit giving the analyses potential sample sizes of 40.

Two-way ANOVAs were subsequently used for the removal experiment and the neighbor experiment. Each species was analyzed separately. For the removal experiment, two-way ANOVAs using vegetation removal and N treatment as main effects were utilized. This set of analyses examined responses of dependent variables of lone individuals in intact and removal plots. For the neighbor experiment, two-way ANOVAs using neighbor treatment (lone, conspecific, heterospecific) and N availability were used. This experiment analyzed plant responses in removal plots only. Dependent variables for both experiments included shoot biomass, tiller number, biomass per tiller, number of inflorescences, root biomass, root:shoot ratio, tissue N concentration, and WUE. Some variables were transformed to meet the assumptions of ANOVA.

In order to compare competitive release following vegetation removal between *Deschampsia* and *Kobresia*, two-way ANOVAs utilizing species (*Kobresia* and *Deschampsia*) and removal (intact and removed) were utilized. Only parameters that varied significantly with removal for both species were utilized as dependent variables. The significance of the interaction term in each ANOVA was used to compare competitive release between the two species.

Results

Soil parameters

During the third growing season N fertilization had a significant effect on both extractable soil ammonium ($F = 33.74$; $P \leq 0.0001$) and nitrate ($F = 217.0$; $P \leq 0.0001$). Both forms of N were higher in fertilized plots than in unfertilized plots (Fig. 1). Removal of vegetation led to a decrease in extractable ammonium levels ($F = 4.922$; $P \leq 0.05$), but did not significantly affect nitrate levels. A significant fertilization \times removal interaction ($F = 4.592$; $P \leq 0.05$) revealed that this effect of removal was only important in fertilized plots. These differences in extractable ammonium levels between fertilized intact plots and fertilized removal plots indicate a probable increase in microbial immobilization of N due to dying roots acting as a carbon source. Since soil ammonium levels were greater in plots where competition was present than in plots where competition was absent, there was no danger that increases in plant performance due to N availability would mimic those due to competitive release.

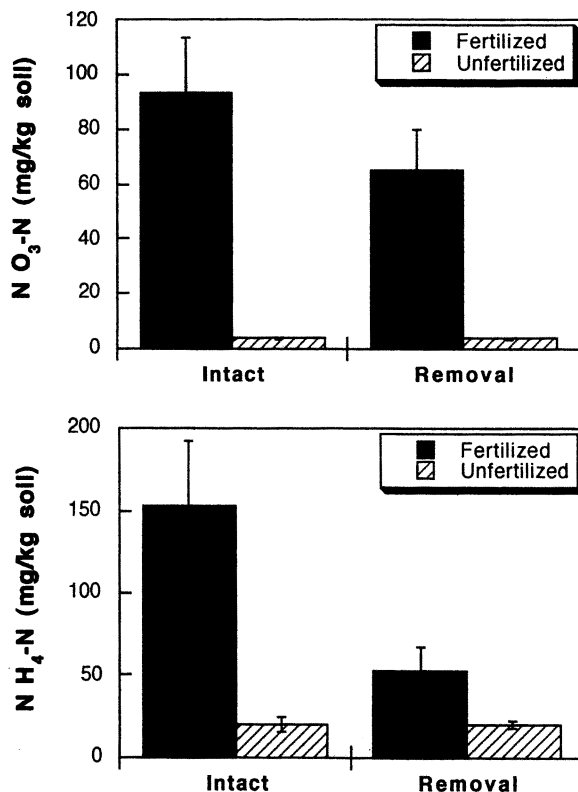


Fig. 1. Extractable nitrate and ammonium from soils of plots in the dry meadow community. Treatments include vegetation removal (intact or removal) and fertilization (fertilized with N or unfertilized). The effect fertilization was significant for both nitrate ($P < 0.0001$) and ammonium ($P < 0.0001$). The effect of removal was significant only for ammonium ($P < 0.05$).

Moisture availability was significantly affected by removal ($F = 97.22$; $P \leq 0.0001$), but was not affected by fertilization. Removing vegetation led to an increase in moisture availability at all times during the growing season (Fig. 2).

Removal experiment: *Deschampsia*

Deschampsia mortality was significantly lower in removal plots than in intact plots (Fig. 3, Table 1). N addition had no significant effect on mortality in intact plots, but in removal plots it led to a decrease in *Deschampsia* mortality, so that all successfully transplanted *Deschampsia* survived (Fig. 3, Table 1).

When pooled across removal and intact plots, shoot biomass of lone *Deschampsia* plants was significantly greater in fertilized plots than in unfertilized plots (Fig. 4, Table 1). However, a significant interaction term revealed that shoot biomass in unfertilized removal plots was actually higher than that of fertilized intact plots (Table 1). Thus, the effect of vegetation removal on shoot biomass was greater than that of fertilization.

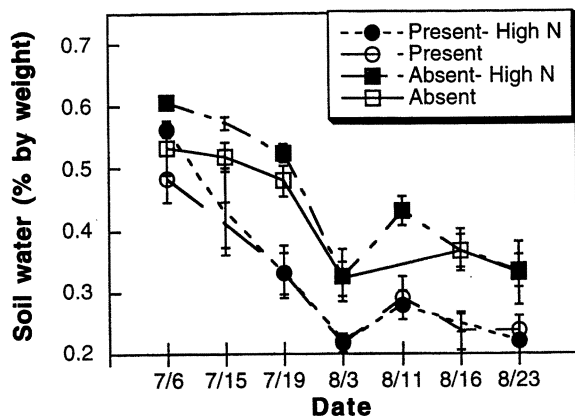


Fig. 2. Dry meadow soil moisture availability during the growing season of 1993, as determined by time-domain-reflectometry (TDR). Treatments include plots with vegetation intact or removed, fertilized with N or unfertilized. Moisture availability was significantly affected by vegetation removal ($P < 0.0001$) but not by fertilization.

In both fertilized and unfertilized plots, removal led to large increases in shoot biomass (Fig. 4, Table 1). This was more pronounced in fertilized plots, where shoot biomass was almost four times greater with vegetation removal than without it. The increases in shoot biomass with fertilization and removal were due primarily to

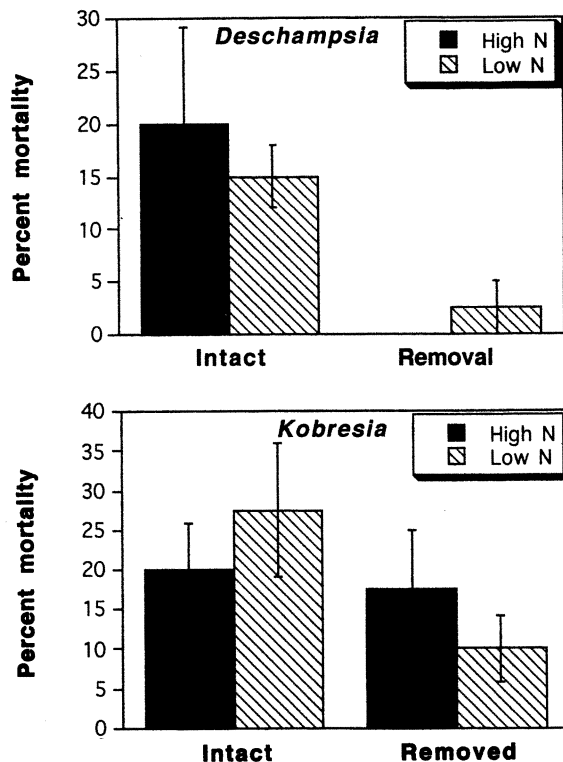


Fig. 3. *Deschampsia* and *Kobresia* mortality in response to dry meadow vegetation removal (intact and removal plots) and N level (high = fertilized; low = unfertilized).

Table 1. Removal experiment: significance of *Deschampsia* responses to fertilization and vegetation removal. Results are from ANOVAs of *Deschampsia* growth and physiology parameters. Main effects in the ANOVAs were nitrogen level (high and low) and vegetation removal (intact and removal). See text for details. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant at $P < 0.05$ level.

Dependent variable	Source	F
Shoot biomass	Nitrogen	9.806**
	Vegetation removal	31.53***
	Nitrogen \times Removal	1.376*
Tiller number	Nitrogen	17.991***
	Vegetation removal	84.670***
	Nitrogen \times Removal	18.363**
Shoot biomass per tiller	Nitrogen	2.853 ns
	Vegetation removal	0.732 ns
	Nitrogen \times Removal	0.078 ns
Inflorescences	Nitrogen	7.838**
	Vegetation removal	10.77**
	Nitrogen \times Removal	5.130*
Root biomass	Nitrogen	5.536*
	Vegetation removal	38.21***
	Nitrogen \times Removal	1.376 ns
Root:shoot ratio	Nitrogen	0.049 ns
	Vegetation removal	10.81**
	Nitrogen \times Removal	0.479 ns
Shoot percent N	Nitrogen	290.0***
	Vegetation removal	0.785 ns
	Nitrogen \times Removal	9.999**
Root percent N	Nitrogen	146.0***
	Vegetation removal	12.94***
	Nitrogen \times Removal	0.081 ns
WUE	Nitrogen	3.799 ns
	Vegetation removal	4.885*
	Nitrogen \times Removal	0.006 ns

increases in tillering, as the pattern of variation of this parameter was similar to that of shoot biomass (Fig. 4, Table 1). In contrast, biomass per tiller did not vary significantly with either fertilization or removal (Fig. 4, Table 1), suggesting that this parameter did not contribute to the increase in shoot biomass observed.

Deschampsia flowering varied significantly with both fertilization and removal (Fig. 4, Table 1). Number of inflorescences produced was greater in fertilized plots than in unfertilized plots. However, this effect of fertilization was much more pronounced in removal plots than in intact plots, as indicated by a significant fertilizer \times removal interaction (Table 1). In unfertilized plots, removal of vegetation led to only modest (but significant) increases in flowering (Table 1). No inflorescences were formed in any *Deschampsia* plants growing in intact unfertilized plots (Fig. 4), which represented the natural conditions of the dry meadow.

Deschampsia root biomass increased both with fertilization and with removal of vegetation (Fig. 5, Table

1). However, the effect of removal was much greater than that of fertilization, with plants in removal plots having over four times the root biomass of plants growing in intact plots (Fig. 5). Since shoot biomass also increased in fertilized plots, root:shoot ratio did not vary significantly with fertilization (Fig. 5, Table 1). However, root:shoot ratios were almost twice as large in plots with vegetation removed than in those with vegetation intact (Fig. 5).

Deschampsia tissue N concentrations were affected significantly by fertilization, with both shoot and root N concentrations higher in plants from fertilized plots than in those from unfertilized plots (Fig. 6, Table 1). However, a significant fertilization \times removal interaction revealed that this effect was only significant for plants growing in removal plots (Table 1). Shoot N was unaffected by removal, but root N was higher in removal plots than in intact plots (Fig. 6, Table 1).

Deschampsia WUE was significantly affected by removal of dry meadow vegetation (Table 1, Fig. 7). Plants had higher WUE (less negative $\delta^{13}\text{C}$ values) when growing in removal plots than when growing in intact plots. Fertilization had no significant effect on *Deschampsia* WUE.

Removal experiment: *Kobresia*

Although *Kobresia* mortality was high, it did not vary significantly with N treatment or vegetation removal (Fig. 3). Fertilization did not significantly influence any *Kobresia* growth parameter except for root:shoot ratios, which were higher in fertilized plots than in unfertilized plots (Tables 2, 3).

Kobresia shoot biomass was greater in removal plots than in intact plots (Tables 2, 3), due primarily to increases in tillering. Shoot biomass per tiller was not significantly affected by vegetation removal (Tables 2, 3). *Kobresia* produced more root biomass in removal plots than in intact plots (Tables 2, 3). However, the shoot response to removal was greater than the root response, and the resulting root:shoot ratios were greater in intact plots than in removal plots (Tables 2, 3). This removal effect on root:shoot ratio was stronger in fertilized plots, as indicated by a significant fertilization \times removal interaction (Tables 2, 3). Flowering, as measured by number of inflorescences, was unaffected by vegetation removal (Tables 2, 3).

Kobresia tissue N concentrations were significantly affected by fertilization (Tables 2, 3). Both shoot and root percent N increased in fertilized plots relative to unfertilized plots. However, this effect was greater in intact than in removal plots, as indicated by a significant fertilization \times removal interaction (Table 2). Tissue N concentrations were not significantly affected by vegetation removal (Tables 2, 3).

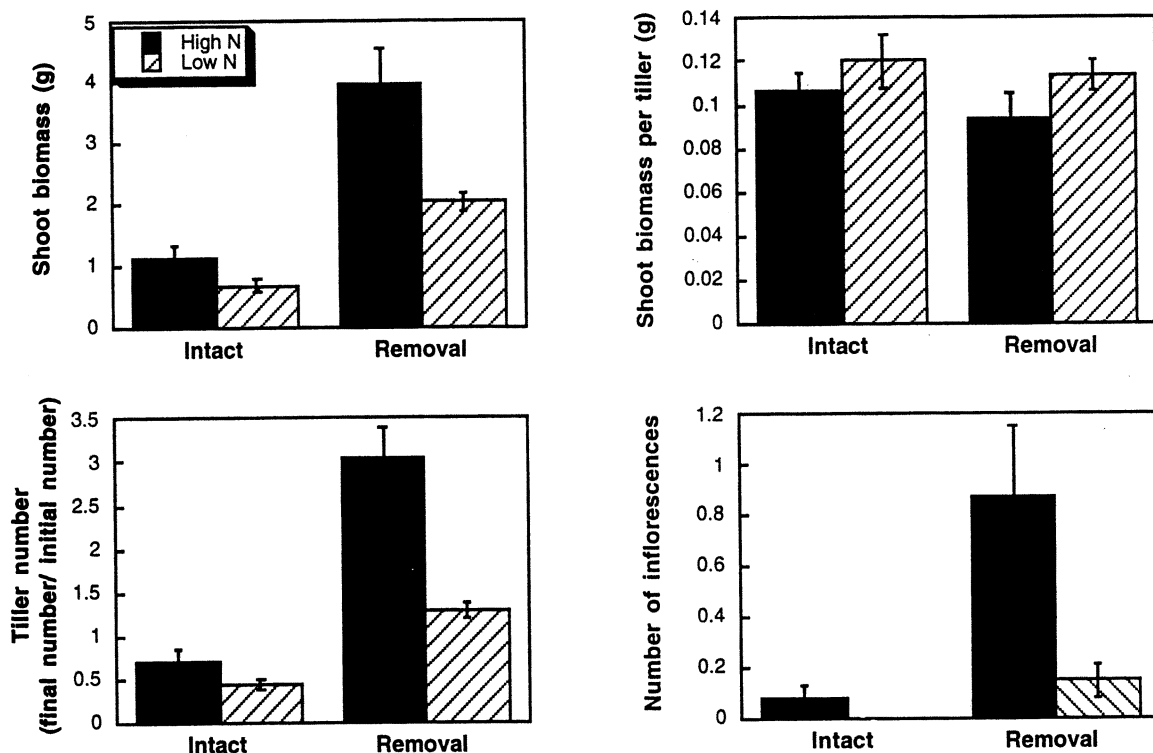


Fig. 4. *Deschampsia* shoot parameters (biomass, tillering, biomass per tiller, and number of inflorescences) in response to dry meadow vegetation removal (intact and removal plots) and N level (high = fertilized; low = unfertilized).

Comparison of *Deschampsia* and *Kobresia* responses to vegetation removal

Although mortality was similar for the two species in intact plots, *Kobresia* mortality was higher than *Deschampsia* mortality in removal plots (Figs 5–7). For surviving plants, all growth parameters that varied significantly with removal within a species were compared between species. Significant species \times removal interactions revealed that the effect of removal was greater on *Deschampsia* than on *Kobresia*. Thus shoot biomass ($F = 10.57$, $P \leq 0.01$), root biomass ($F = 12.91$, $P \leq 0.001$), total biomass ($F = 12.07$, $P \leq 0.001$) and tillering ($F = 6.867$, $P \leq 0.01$) were all enhanced by vegetation removal to a greater extent in *Deschampsia* than in *Kobresia*.

Neighbor experiment: *Deschampsia*

In removal plots *Deschampsia* mortality increased significantly with fertilization ($F = 6.959$; $P \leq 0.05$), but was unaffected by neighbor treatment (Fig. 7). *Deschampsia* shoot parameters were significantly affected by fertilization as well (Tables 4, 5). Shoot biomass was almost two times greater in fertilized plants than in unfertilized plants (Tables 4, 5). This increase in biomass was due primarily to an increase in number of tillers, which was almost two times greater

with fertilization than without (Tables 4, 5). However, biomass per tiller was lower in fertilized plants than in unfertilized plants (Tables 4, 5). Flowering was also enhanced with fertilization, with fertilized plants producing almost three times as many inflorescences as unfertilized plants (Tables 4, 5).

Neighbor affected shoot growth as well, with *Deschampsia* accumulating more shoot biomass in the presence of either *Kobresia* or another *Deschampsia* than when growing alone (Tables 4, 5). Again, the increase was due primarily to an increase in tillering, as biomass per tiller did not vary significantly with neighbor treatment (Tables 4, 5). However, a significant fertilization \times neighbor interaction revealed that these increases in biomass and tillering with neighbor only occurred in fertilized plots (Table 4). In unfertilized plots there was no significant neighbor effect on either shoot parameter.

Flowering was not affected by neighbor as a main effect, but a significant fertilization \times neighbor interaction indicated that the flowering response to neighbor treatment depended on fertilization (Tables 4, 5). In fertilized plots, flowering was greater in the presence of *Kobresia* (Table 5). However, in unfertilized plots, the presence of *Deschampsia* was associated with increased flowering (Table 5).

Deschampsia root biomass and root:shoot ratios were not affected by neighbor (Tables 4, 5). Fertilization

significantly increased the amount of root biomass accumulated, but had no effect on root:shoot ratio (Tables 4, 5).

Shoot N concentrations were almost twice as high in plants growing in fertilized plots than in unfertilized plots (Table 5). Root N concentrations were also greater in fertilized plots (Tables 4, 5). The effect of neighbor on shoot N concentration was dependent on fertilizer treatment, as indicated by a significant fertilization \times neighbor interaction (Table 4). In fertilized plots, *Deschampsia* growing with *Kobresia* had higher shoot N concentrations than when growing either intraspecifically or alone (Table 5). The effect of neighbor on root N concentrations did not differ among treatments (Tables 4, 5). *Deschampsia* WUE in removal plots did not differ significantly with either fertilization or neighbor treatment (Tables 4, 5).

Neighbor experiment: *Kobresia*

In removal plots, neighbor treatment had no effect on *Kobresia* mortality (Fig. 8). However, *Kobresia* mortality was over two times greater in fertilized plots than in unfertilized plots (Fig. 8). Surviving *Kobresia* plants

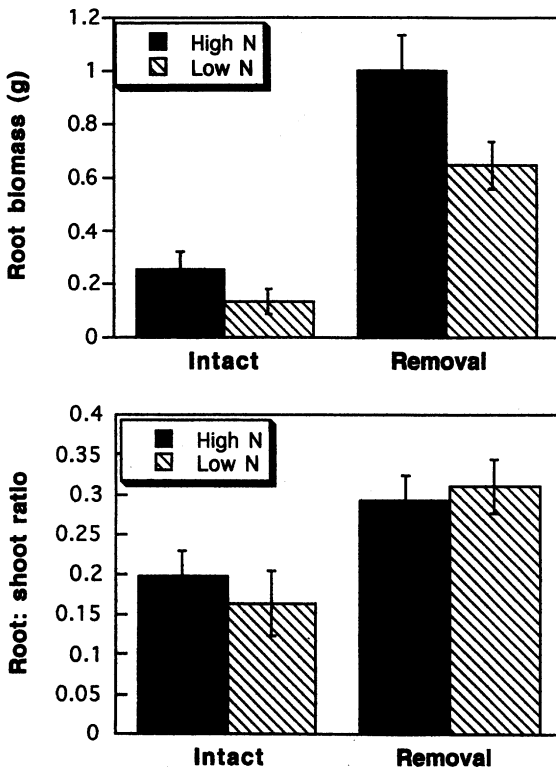


Fig. 5. *Deschampsia* root biomass and root:shoot ratio in response to dry meadow vegetation removal (intact and removal plots) and N level (high = fertilized; low = unfertilized).

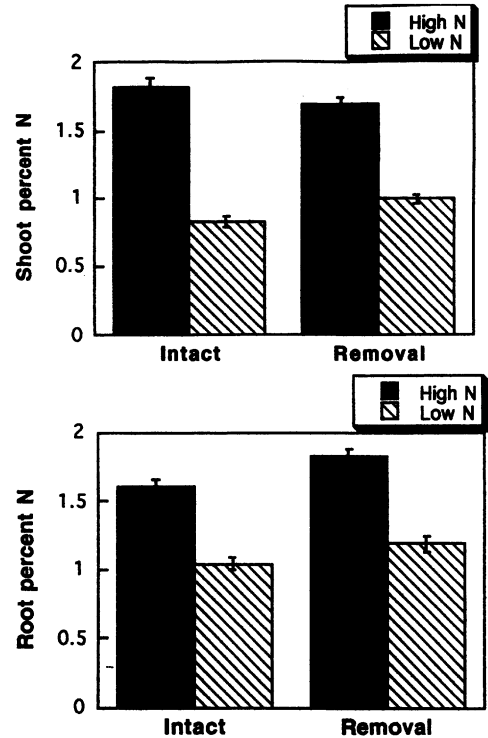


Fig. 6. *Deschampsia* tissue N concentrations (shoot and root) in response to dry meadow vegetation removal (intact and removal plots) and N level (high = fertilized; low = unfertilized).

were generally unaffected by neighbor or fertilization (Tables 6, 7). Neighbor treatment had no effect on any *Kobresia* growth parameter (shoot biomass, root biomass, biomass per tiller, root:shoot ratio, and flowering), except that *Kobresia* plants growing alone produced more tillers than those growing with a neighbor. However, increased tillering did not lead to a significant increase in shoot biomass. Likewise, fertilization had no effect on shoot biomass, number of new tillers, shoot biomass per tiller, and flowering (Tables 6, 7). Root biomass and root:shoot ratio were unaffected by fertilization (Tables 6, 7).

Fertilization in removal plots did lead to increases in *Kobresia* tissue N concentrations (Tables 6, 7). Both shoot and root concentrations were significantly higher in *Kobresia* plants growing in fertilized plots than in those growing in unfertilized plots. Neighbor treatment had no significant effect on tissue N concentrations (Tables 6, 7).

Kobresia's WUE in removal plots was significantly influenced by N fertilization (Tables 6, 7). Plants growing in fertilized plots had higher WUE (less negative $\delta^{13}\text{C}$ values) than those growing in unfertilized plots.

Discussion

Removal experiment

Under natural conditions, the moist meadow *Deschampsia* is rarely found in the *Kobresia* dominated dry meadow community. However, *Deschampsia* transplanted into dry meadow plots with vegetation removed survived, grew, and flowered to a greater extent than *Deschampsia* transplanted into plots with vegetation intact. This competitive release with vegetation removal was significantly more pronounced for *Deschampsia* transplants than for *Kobresia* transplants, indicating that interspecific competition is in part responsible for the absence of *Deschampsia* in the dry meadow community. These results demonstrate that a slow growing species in a resource poor community is capable of competitively displacing a fast growing species from a more resource rich community. Since this experiment was conducted in alpine tundra, these results also illustrate that competition can be an important force structuring plant community composition in an extreme environment.

Although production in alpine dry meadows is N limited (Bowman et al. 1993), low N availability had a much weaker inhibitory effect on *Deschampsia* success than the presence of *Kobresia*. Only with *Kobresia* removal was *Deschampsia* able to take advantage of

Table 2. Removal experiment: significance of *Kobresia* responses to fertilization and vegetation removal. Results are from ANOVAs of *Kobresia* growth and physiology parameters. Main effects in the ANOVAs were nitrogen level (high and low) and vegetation removal (intact and removal). See text for details. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant at $P < 0.05$ level.

Dependent variable	Source	F
Shoot biomass	Nitrogen	0.007 ns
	Vegetation removal	9.087**
	Nitrogen \times Removal	0.016 ns
Tiller number	Nitrogen	0.014 ns
	Vegetation removal	13.04***
	Nitrogen \times Removal	0.073 ns
Shoot biomass per tiller	Nitrogen	0.596 ns
	Vegetation removal	3.474 ns
	Nitrogen \times Removal	0.176 ns
Inflorescences	Nitrogen	0.120 ns
	Vegetation removal	0.488 ns
	Nitrogen \times Removal	0.120 ns
Root biomass	Nitrogen	0.023*
	Vegetation removal	3.979 ns
	Nitrogen \times Removal	0.274 ns
Root:shoot ratio	Nitrogen	4.250*
	Vegetation removal	11.75**
	Nitrogen \times Removal	4.213*
Shoot percent N	Nitrogen	37.88***
	Vegetation removal	2.200 ns
	Nitrogen \times Removal	11.71**
Root percent N	Nitrogen	35.29***
	Vegetation removal	1.458 ns
	Nitrogen \times Removal	2.750 ns

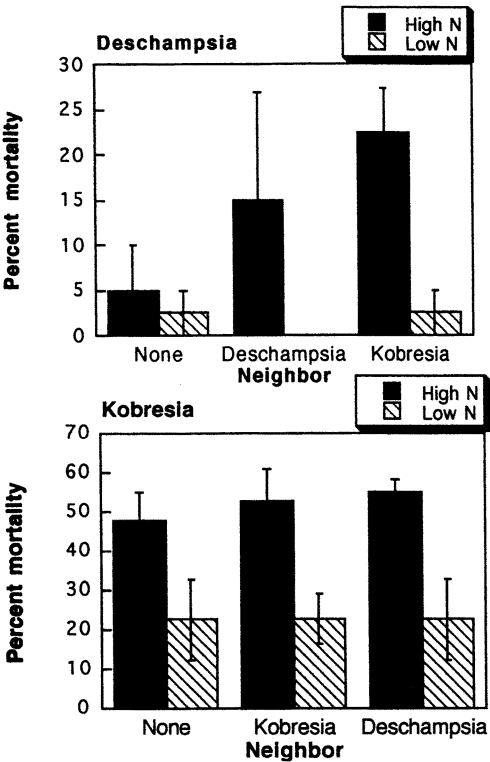


Fig. 7. *Deschampsia* and *Kobresia* mortality in removal plots in response to neighbor treatment (none, conspecific, and heterospecific) and N level (high = fertilized; low = unfertilized).

increased soil N availability, with increases in biomass and flowering. This result is further supported by the extractable soil N results. Although N availability was higher in fertilized intact plots than in fertilized removal plots, the increases in *Deschampsia* growth parameters with fertilization were much more pronounced in removal plots.

The soil moisture results strongly suggest that competition for water leads to competitive displacement of *Deschampsia* from the dry meadow community. Significant differences in water availability between intact and removal plots imply that *Kobresia* reduces water availability below which *Deschampsia* can establish. It has been suggested by Kiener (1967) that competition for water with *Kobresia* prevents establishment of plant species in alpine dry meadow communities.

Kobresia may be capable of reducing soil water availability due to its tussock forming growth habit. *Kobresia* leaf sheaths form dense tussocks that continue to accumulate in thickness (up to 5 cm thick) over the lifetime of the plant. It is probable that these tussocks, alive and dead, form a boundary to water reaching soil layers below. Several authors have indeed suggested

that *Kobresia* tussocks control the microclimate of dry meadows (Osburn 1958, Bell and Bliss 1979).

Kobresia's root morphology in relation to that of *Deschampsia* may also contribute to its ability to reduce water levels. Results from a growth chamber experiment suggest that *Kobresia* has a more shallow root system and thinner roots than *Deschampsia* (Theodose 1995). Although competitive ability for water is often imparted by longer roots (Caldwell and Richards 1986, Caldwell 1987), the difference in water sources between the moist and dry meadow may explain how a shallow root system can be competitive in this community. Dry meadow moisture comes primarily from summer thunderstorms, whereas moist meadow moisture is derived mainly from snowmelt, at least during the first half of the growing season (May and Webber 1982, Isard 1986, Walker et al. 1994). It is probable that snowmelt water reaches deeper soil levels than does rain from thunderstorms. In the dry meadow, *Kobresia*'s shallow root system may be capable of sequestering

Table 3. Removal experiment: *Kobresia* growth parameters and tissue N concentrations in response to N amendment and vegetation removal in the dry meadow community. Results are presented as means \pm SE. See Table 1 for results from ANOVAs.

Dependent variable	Nitrogen level	Vegetation removal	Mean \pm S.E.
Shoot biomass (g)	High	Intact	0.093 \pm 0.041
		Removed	0.262 \pm 0.044
	Low	Intact	0.091 \pm 0.034
		Removed	0.274 \pm 0.034
Tiller number final/initial)	High	Intact	0.19 \pm 0.07
		Removed	0.68 \pm 0.12
	Low	Intact	0.16 \pm 0.05
		Removed	0.74 \pm 0.09
Shoot biomass per tiller (g)	High	Intact	0.026 \pm 0.005
		Removed	0.020 \pm 0.001
	Low	Intact	0.023 \pm 0.003
		Removed	0.019 \pm 0.001
Inflorescences (number per plant)	High	Intact	0 \pm 0
		Removed	0.04 \pm 0.04
	Low	Intact	0.00 \pm 0.00
		Removed	0.13 \pm 0.10
Root biomass (g)	High	Intact	0.075 \pm 0.017
		Removed	0.118 \pm 0.022
	Low	Intact	0.054 \pm 0.018
		Removed	0.129 \pm 0.018
Root:shoot ratio	High	Intact	1.020 \pm 0.212
		Removed	0.497 \pm 0.073
	Low	Intact	0.627 \pm 0.103
		Removed	0.496 \pm 0.031
Shoot percent N	High	Intact	3.07 \pm 0.19
		Removed	2.30 \pm 0.08
	Low	Intact	1.57 \pm 0.11
		Removed	1.88 \pm 0.10
Root percent N	High	Intact	1.42 \pm 0.22
		Removed	1.18 \pm 0.06
	Low	Intact	0.77 \pm 0.03
		Removed	0.81 \pm 0.03

Table 4. Neighbor experiment: significance of *Deschampsia* responses to fertilization and neighbor in removal plots only. Main effects in the ANOVAs were nitrogen level (high and low) and neighbor (none, *Deschampsia*, and *Kobresia*). * P < 0.05, ** P < 0.01, *** P < 0.00.

Dependent variable	Source	F
Shoot biomass	Nitrogen	59.84***
	Neighbor	5.228***
	Nitrogen \times Neighbor	3.728*
Tiller number	Nitrogen	107.2***
	Neighbor	7.171***
	Nitrogen \times Neighbor	5.642***
Shoot biomass per tiller	Nitrogen	11.73***
	Neighbor	0.509 ns
	Nitrogen \times Neighbor	0.218 ns
Inflorescences	Nitrogen	30.35***
	Neighbor	1.318 ns
	Nitrogen \times Neighbor	3.315*
Shoot biomass	Nitrogen	32.09***
	Neighbor	1.635 ns
	Nitrogen \times Neighbor	2.545 ns
Root:shoot ratio	Nitrogen	0.804 ns
	Neighbor	1.916 ns
	Nitrogen \times Neighbor	0.030 ns
Shoot percent N	Nitrogen	370.0***
	Neighbor	1.170 ns
	Nitrogen \times Neighbor	3.550*
Root percent N	Nitrogen	212.0***
	Neighbor	0.494 ns
	Nitrogen \times Neighbor	1.465 ns
WUE	Nitrogen	0.733 ns
	Neighbor	1.858 ns
	Nitrogen \times Neighbor	2.390 ns

moisture from summer rain events before it reaches deeper soil layers.

Previous work indicates that *Kobresia* is more capable of tolerating low water conditions than is *Deschampsia*. *Kobresia* can maintain high photosynthesis rates under low soil moisture availability (Johnson and Caldwell 1975). Leaf water potentials as low as -2.4 MPa appear to have little effect in reducing *Kobresia* net CO_2 assimilation (Johnson et al. 1974). In contrast, photosynthesis rates are significantly decreased by water stress in *Deschampsia* (Johnson and Caldwell 1975). Thus *Kobresia*'s ability to tolerate drought may contribute to its ability to outcompete the less tolerant *Deschampsia* in dry areas. This combination of resource reduction and tolerance has been described by Tilman as the primary mode of plant competition (Tilman 1988).

Deschampsia's morphological and physiological responses to the presence of *Kobresia* further allude to the mechanisms of competition between the two species. *Deschampsia* responded to the *Kobresia* induced reduction in water availability by allocating a higher proportion of biomass to shoots than roots. This decrease in root:shoot ratio in response to water reduction is un-

usual, since root:shoot ratios usually increase with a reduction in soil resources (Chapin 1980) and may have contributed to *Deschampsia* mortality.

Table 5. Neighbor experiment: *Deschampsia* growth and physiological parameters in response to N amendment and neighbor in removal plots. Results are presented as means \pm SE. See Table 1 for results from ANOVAs.

Dependent variable	Nitrogen level	Neighbor treatment	Mean \pm S.E.
Shoot biomass (g)	High	^a None	3.96 \pm 0.58
	Low	None	2.04 \pm 0.14
	High	^b <i>Deschampsia</i>	5.21 \pm 0.76
	Low	<i>Deschampsia</i>	2.57 \pm 0.17
	High	^c <i>Kobresia</i>	6.71 \pm 0.82
	Low	<i>Kobresia</i>	2.28 \pm 0.17
Tiller number	High	^a None	2.3 \pm 0.4
	Low	None	1.3 \pm 0.4
	High	^b <i>Deschampsia</i>	3.9 \pm 0.5
	Low	<i>Deschampsia</i>	1.4 \pm 0.01
	High	^c <i>Kobresia</i>	5.3 \pm 0.6
	Low	<i>Kobresia</i>	1.4 \pm 0.1
Shoot biomass per tiller (g)	High	None	0.09 \pm 0.01
	Low	None	0.11 \pm 0.01
	High	<i>Deschampsia</i>	0.09 \pm 0.01
	Low	<i>Deschampsia</i>	0.13 \pm 0.01
	High	<i>Kobresia</i>	0.09 \pm 0.01
	Low	<i>Kobresia</i>	0.11 \pm 0.01
Inflorescences	High	None	0.87 \pm 0.22
	Low	None	0.15 \pm 0.07
	High	<i>Deschampsia</i>	0.84 \pm 0.21
	Low	<i>Deschampsia</i>	0.45 \pm 0.12
	High	<i>Kobresia</i>	1.40 \pm 0.35
	Low	<i>Kobresia</i>	0.13 \pm 0.07
Root biomass (g)	High	None	0.01 \pm 0.133
	Low	None	0.64 \pm 0.087
	High	<i>Deschampsia</i>	1.11 \pm 0.165
	Low	<i>Deschampsia</i>	0.67 \pm 0.083
	High	<i>Kobresia</i>	1.47 \pm 0.159
	Low	<i>Kobresia</i>	0.60 \pm 0.097
Root:shoot ratio	High	None	0.29 \pm 0.041
	Low	None	0.31 \pm 0.034
	High	<i>Deschampsia</i>	0.24 \pm 0.022
	Low	<i>Deschampsia</i>	0.27 \pm 0.032
	High	<i>Kobresia</i>	0.23 \pm 0.015
	Low	<i>Kobresia</i>	0.25 \pm 0.026
Shoot percent N	High	None	1.69 \pm 0.06
	Low	None	0.99 \pm 0.04
	High	<i>Deschampsia</i>	1.76 \pm 0.07
	Low	<i>Deschampsia</i>	0.99 \pm 0.04
	High	<i>Kobresia</i>	1.93 \pm 0.05
	Low	<i>Kobresia</i>	0.95 \pm 0.05
Root percent N	High	None	1.83 \pm 0.05
	Low	None	1.19 \pm 0.06
	High	<i>Deschampsia</i>	1.98 \pm 0.07
	Low	<i>Deschampsia</i>	1.16 \pm 0.06
	High	<i>Kobresia</i>	1.83 \pm 0.07
	Low	<i>Kobresia</i>	1.19 \pm 0.05
WUE ($\delta^{13}\text{C}$)	High	None	-23.1 \pm 0.3
	Low	None	-23.7 \pm 0.3
	High	<i>Deschampsia</i>	-24.7 \pm 0.4
	Low	<i>Deschampsia</i>	-23.6 \pm 0.7
	High	<i>Kobresia</i>	-23.9 \pm 0.2
	Low	<i>Kobresia</i>	-23.5 \pm 0.2

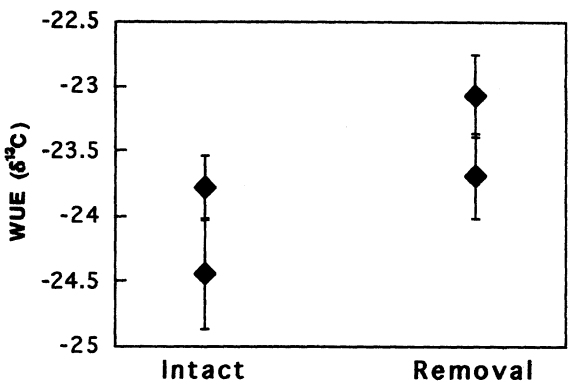


Fig. 8. *Deschampsia* integrated water-use efficiency in response to vegetation removal (intact and removal plots) and N level (high and low). Water-use-efficiency is estimated as $\delta^{13}\text{C}$. Less negative values indicate greater water-use-efficiency. In both vegetation treatments, the more efficient plants were those under the high N treatment.

Deschampsia's WUE was also compromised in intact plots relative to removal plots, as indicated by a more negative $\delta^{13}\text{C}$ value when growing in competition with *Kobresia*. A similar water use efficiency response to root competition has been demonstrated in tussock

Table 6. Neighbor experiment: significance of *Kobresia* responses to fertilization and neighbor in removal plots only. Main effects in the ANOVAs were nitrogen level (high and low) and neighbor (none, *Kobresia*, and *Deschampsia*). * $P < 0.01$, *** $P < 0.001$.

Dependent variable	Source	F
Shoot biomass	Nitrogen	2.042 ns
	Neighbor	1.063 ns
	Nitrogen \times Neighbor	1.094 ns
Tiller number	Nitrogen	0.270 ns
	Neighbor	4.327*
	Nitrogen \times Neighbor	0.490 ns
Shoot biomass per tiller	Nitrogen	1.424 ns
	Neighbor	1.478 ns
	Nitrogen \times Neighbor	0.811 ns
Inflorescences	Nitrogen	0.984 ns
	Neighbor	0.019 ns
	Nitrogen \times Neighbor	1.763 ns
Shoot biomass	Nitrogen	0.447 ns
	Neighbor	0.177 ns
	Nitrogen \times Neighbor	0.854 ns
Root:shoot ratio	Nitrogen	0.007 ns
	Neighbor	0.664 ns
	Nitrogen \times Neighbor	0.111 ns
Shoot percent N	Nitrogen	56.34***
	Neighbor	1.892 ns
	Nitrogen \times Neighbor	1.517 ns
Shoot biomass	Nitrogen	150.0***
	Neighbor	2.604 ns
	Nitrogen \times Neighbor	2.412 ns
WUE	Nitrogen	4.220*
	Neighbor	0.980 ns
	Nitrogen \times Neighbor	1.092 ns

Table 7. Neighbor experiment: *Kobresia* growth and physiological parameters in response to N amendment and neighbor in removal plots. Results are presented as means \pm SE. See Table 1 for results from ANOVAs.

Dependent variable	Nitrogen level	Neighbor treatment	Mean \pm S.E.
Shoot biomass (g)	High	None	0.262 \pm 0.044
	Low	None	0.274 \pm 0.034
	High	<i>Kobresia</i>	0.254 \pm 0.051
	Low	<i>Kobresia</i>	0.206 \pm 0.032
	High	<i>Deschampsia</i>	0.243 \pm 0.059
	Low	<i>Deschampsia</i>	0.161 \pm 0.024
Tiller number (final/initial)	High	^a None	0.68 \pm 0.12
	Low	None	0.74 \pm 0.09
		^b <i>Kobresia</i>	0.53 \pm 0.08
	Low	<i>Kobresia</i>	0.47 \pm 0.09
	High	^b <i>Deschampsia</i>	0.53 \pm 0.09
	Low	<i>Deschampsia</i>	0.41 \pm 0.06
Shoot biomass per tiller (g)	High	None	0.02 \pm 0.001
	Low	None	0.02 \pm 0.001
		<i>Kobresia</i>	0.02 \pm 0.002
	Low	<i>Kobresia</i>	0.02 \pm 0.001
	High	<i>Deschampsia</i>	0.02 \pm 0.003
	Low	<i>Deschampsia</i>	0.02 \pm 0.001
Inflorescences (number per plant)	High	None	0.04 \pm 0.04
	Low	None	0.13 \pm 0.10
		<i>Kobresia</i>	0.12 \pm 0.08
	Low	<i>Kobresia</i>	0.03 \pm 0.03
	High	<i>Deschampsia</i>	0.18 \pm 0.13
	Low	<i>Deschampsia</i>	0 \pm 0
Root biomass (g)	High	None	0.118 \pm 0.022
	Low	None	0.129 \pm 0.018
		<i>Kobresia</i>	0.115 \pm 0.023
	Low	<i>Kobresia</i>	0.111 \pm 0.016
	High	<i>Deschampsia</i>	0.135 \pm 0.029
	Low	<i>Deschampsia</i>	0.094 \pm 0.01
Root:shoot ratio	High	None	0.497 \pm 0.073
	Low	None	0.496 \pm 0.031
		<i>Kobresia</i>	0.588 \pm 0.170
	Low	<i>Kobresia</i>	0.553 \pm 0.058
	High	<i>Deschampsia</i>	0.571 \pm 0.070
	Low	<i>Deschampsia</i>	0.628 \pm 0.127
Shoot percent N	High	None	2.30 \pm 0.08
	Low	None	0.188 \pm 0.10
		<i>Kobresia</i>	2.28 \pm 0.10
	Low	<i>Kobresia</i>	1.80 \pm 0.06
	High	<i>Deschampsia</i>	2.56 \pm 0.10
	Low	<i>Deschampsia</i>	1.85 \pm 0.08
Root percent N	High	None	1.18 \pm 0.06
	Low	None	0.81 \pm 0.03
		<i>Kobresia</i>	1.35 \pm 0.08
	Low	<i>Kobresia</i>	0.81 \pm 0.03
	High	<i>Deschampsia</i>	1.37 \pm 0.05
	Low	<i>Deschampsia</i>	0.82 \pm 0.04
WUE ($\delta^{13}\text{C}$)	High	None	-23.6 \pm 0.5
	Low	None	-23.8 \pm 0.3
		<i>Kobresia</i>	-23.7 \pm 0.2
	Low	<i>Kobresia</i>	-24.0 \pm 0.4
	High	<i>Deschampsia</i>	-23.6 \pm 0.2
	Low	<i>Deschampsia</i>	-24.9 \pm 0.4

grasses in the Great Basin desert (Williams et al. 1991). *Deschampsia* may respond to competition with increases in growth rate, as suggested by the increase in biomass exhibited in response to neighbors in the neigh-

bor experiment. A high growth rate often translates into low WUE, since stomata regulate both fluxes of CO₂ and water vapor (Cohen 1970). An increased growth rate in response to competition would be favorable when water levels are high, but could be detrimental to *Deschampsia* when water is limiting.

In order for a plant population to establish and persist in an area, it must be capable of reproduction. *Deschampsia*'s reduced ability to flower in intact plots implies that even if individuals established in the dry meadow, the population would not survive. This reduction in flowering was most pronounced in unfertilized intact plots (the natural condition of the dry meadow), where no *Deschampsia* plants flowered. A similar reduction of reproduction from competition was reported in arctic tundra graminoids (McGraw and Chapin 1989).

Neighbor experiment

Gopher disturbance, although rare in dry meadow communities, can temporarily increase soil resource availability, especially water availability. *Deschampsia* is sometimes able to move into dry meadows via these disturbances (Chambers et al. 1984, B. Willard pers. comm.). The increase in water availability with vegetation removal allowed us to examine how competition between *Deschampsia* and *Kobresia* might result under elevated resource conditions, similar to those created by disturbance. In removal plots *Deschampsia* was not inhibited by a *Kobresia* neighbor. Many studies have illustrated that competition under high resource conditions favors competitive species from resource rich habitats over more stress tolerant species from resource poor habitats (Berendse and Elberse 1990, Aerts et al. 1991, Campbell and Grime 1992). However, in contrast to these studies, the stress tolerant *Kobresia* demonstrated no adverse response to competition with *Deschampsia* under elevated water or N availability. Neither shoot biomass, biomass per tiller, root biomass, root:shoot ratio, or number of inflorescences were significantly reduced while in the presence of *Deschampsia*, even under high N conditions. A growth chamber experiment examining interactions between the two species produced similar results (Theodose 1995). Thus a low resource microhabitat created by the presence of *Deschampsia* may simply mimic the conditions of the dry meadow, conditions to which *Kobresia* is well adapted. However, fertilization often leads to a shift from belowground competition to aboveground competition (Tilman 1988). Under resource rich conditions *Kobresia* may ultimately respond to a light limitation induced by *Deschampsia*. After five yr of elevated N and P availability, competition with dry meadow grass species has led to a decrease in *Kobresia* absolute abundance, possibly due competitive displacement (Theodose and Bowman unpubl.). Previous studies

have demonstrated that *Kobresia* is extremely susceptible to shading (Osburn 1958, Bell and Bliss 1979).

Conclusions

This study illustrates that interspecific competition can influence plant distribution patterns in an unproductive environment. A mechanistic approach was used to demonstrate that a species of a resource poor site is capable of displacing a species from a more resource rich site. Soil moisture results suggest *Kobresia*'s ability to reduce water levels, coupled, with *Deschampsia*'s inability to tolerate those conditions, may determine the competitive outcome between the two species in the dry meadow. Thus *Kobresia*'s ability to lower soil moisture and to tolerate low water conditions contributed to its competitive superiority, suggesting that stress tolerance may be an important component of competitive ability in resource poor sites.

Acknowledgements – The authors would like to acknowledge Brian Thomas, David Barker, David Bryant and David Evans who assisted in field and laboratory work. Advice on experimental design and presentation were provided by Pamela Diggle, Tim Seastedt, Russell Monson, and Nel Caine. This work was funded by the Colorado Mountain Club, the John Marr foundation, the Univ. of Colorado Dean's Small Grant Awards and the Dept of Biology, and NSF's Long Term Ecological Research Program. Logistical support was provided by the Univ. of Colorado's Mountain Research Station.

References

- Aerts, R., Berendse, F., DeCaluwe, H. and Schmitz, M. 1990. Competition in heathlands along an experimental gradient of nutrient availability. – *Oikos* 57: 310–318.
- , Boot, R. G. A., van der Aart, P. J. M. 1991. The relation between above- and belowground biomass allocation patterns and competitive ability. – *Oecologia* 87: 551–559.
- Bell, K. L. and Bliss, L. C. 1979. Autecology of *Kobresia bellardii*: why winter snow accumulation limits local distribution. – *Ecol. Monogr.* 49: 377–402.
- Berendse, F. and Elberse, W. Th. 1990. Competition and nutrient availability in heathland and grassland ecosystems. – In: Grace, J. B. and Tilman, D. (eds), *Perspectives on plant competition*. Academic Press, San Diego, CA, pp. 93–116.
- , Elberse, W. Te. and Geerts, R. H. M. E. 1992. Competition and nitrogen loss from plants in grassland ecosystems. – *Ecology* 73: 46–53.
- Bowman, W. D., Theodose, T. A., Schardt, J. C. and Conant, R. T. 1993. Constraints of nutrient availability on primary production in two alpine communities. – *Ecology* 74: 2085–2097.
- , Theodose, T. A. and Fisk, M. 1995. Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: implications for differential community response to environmental change. – *Oecologia* 101: 217–227.
- Caldwell, M. M. 1987. Competition between root systems in natural communities. – In: Gregory, R. J., Lake, J. V. and Rose, D. A. (eds), *Root development and function*. Cambridge Univ. Press, Cambridge, pp. 167–185.
- and Richards, J. H. 1986. Competing root systems: morphology and modes of absorption. – In: Givnish, T. J. (ed.), *On the economy of plant form and function*. Cambridge Univ. Press, Cambridge, pp. 251–273.
- Campbell, B. D. and Grime, J. P. 1992. An experimental test of plant strategy theory. – *Ecology* 73: 15–29.
- Chambers, J. C., Brown, R. W. and Johnson, R. S. 1984. Examination of plant successional stages in disturbed alpine ecosystems: a method of selecting revegetation species. – In: Colbert, T. (ed.), *High altitude revegetation workshop No 7.*, Colorado Water Resources Research Inst. Fort Collins, CO, pp. 215–224.
- Chapin, F. S., III 1980. The mineral nutrition of wild plants. – *Annu. Rev. Ecol. Syst.* 11: 233–260.
- Cohen, D. 1970. The expected efficiency of water utilization in plants under different competition and selection regimes. – *Israel J. Bot.* 19: 50–54.
- Del Moral, R. 1983. Competition as a control mechanism in subalpine meadows. – *Am. J. Bot.* 70: 232–245.
- Ehleringer, J. R. and Rundel, P. W. 1989. Stable isotopes: history, units, and instrumentation. – In: Ehleringer, J. R. and Nagy, K. A. (eds), *Stable isotopes in ecology*. Springer, Berlin, pp. 1–16.
- Farquhar, G. D., Hubick, K. T., Conhdon, A. G. and Richards, R. G. 1989. Carbon isotope fractionation and plant water-use efficiency. – In: Ehleringer, J. R. and Nagy, K. A. (eds), *Stable isotopes in ecology*. Springer, Berlin, pp. 21–40.
- Fisk, M. C. and Schmidt, S. K. 1995. Nitrogen mineralization and microbial biomass nitrogen dynamics in three alpine tundra communities. – *Soil Sci. Soc. Am. J.* 59: 1036–1043.
- Fowler, N. L. 1990. The effects of competition and environmental heterogeneity on three coexisting grasses. – *J. Ecol.* 78: 389–402.
- Goldberg, D. E. and Barton, A. M. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. – *Am. Nat.* 139: 771–801.
- Grace, J. B. 1991. A clarification of the debate between Grime and Tilman. – *Funct. Ecol.* 5: 583–587.
- 1995. On the measurement of plant competition intensity. – *Ecology* 76: 305–308.
- Greenland, D. 1989. The climate of Niwot Ridge, Front Range, Colorado, USA. – *Arct. Alp. Res.* 21: 380–391.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – *Am. Nat.* 111: 1169–1219.
- 1979. *Plant strategies and vegetation processes*. – Wiley, London.
- Gurevitch, J. 1986. Competition and the local distribution of the grass *Stipa neomexicana*. – *Ecology* 67: 46–57.
- , Morrow, L. L., Wallace, A. and Walsh, J. S. 1992. A meta-analysis of competition in field experiments. – *Am. Nat.* 140: 539–572.
- Isard, S. A. 1986. Factors influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, USA. – *Arct. Alp. Res.* 21: 71–82.
- Johnson, D. A. and Caldwell, M. M. 1975. Gas exchange of four arctic and alpine tundra plant species in relation to atmospheric and soil moisture stress. – *Oecologia* 21: 93–108.
- , Caldwell, M. M. and Tieszen, L. I. 1974. Photosynthesis in relation to leaf water potential in three alpine plant species. – In: Bliss, L. C. and Wielgolaski, F. E. (eds), *Primary production and production processes, Tundra Biome*, Dublin, Ireland, April, 1973. Univ. of Alberta, Edmonton, pp. 205–210.
- Kiener, W. 1967. Sociological studies of the alpine vegetation on Longs Peak. – Univ. of Nebraska studies, New Series 34. Lincoln, NE.
- May, D. E. and Webber, P. J. 1982. Spatial and temporal variation of vegetation and its productivity on Niwot Ridge, Colorado. – In: Halfpenny, J. (ed.), *Ecological studies in the Colorado alpine, a festschrift for John W. Marr*. Inst. of Arctic and Alpine Research, Univ. of Colorado, Boulder, CO, pp. 35–62.

- McGraw, J. B. and Chapin, F. S., III 1989. Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. – *Ecology* 70: 736–749.
- McLellan, A. J., Fitter, A. H. and Law, R. 1995. On decaying roots, mycorrhizal colonization and the design of removal experiments. – *J. Ecol.* 83: 225–230.
- Osburn, W. S. 1958. Ecology of winter snow-free areas of the alpine tundra of Niwot Ridge, Boulder County, Colorado. – Dissertation. Univ. of Colorado, Boulder, CO.
- Reader, R. J. and Best, B. J. 1989. Variation in competition along an environmental gradient: *Hieracium floribundum* in an abandoned pasture. – *J. Ecol.* 77: 673–684.
- , Wilson, S. D., Belcher, J. W., Wisheu, I., Keddy, P. A., Tilman, D., Morris, E. C., Grace, J. B., McGraw J. B., Olff, H., Turkington, P., Klein, E., Leung, Y., Shipley B., van Hulst, R., Johansson, M. E., Nilsson, C., Gurevitch, J., Grigulls, K. and Beisner, B. E. 1994. Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. – *Ecology* 75: 1753–1760.
- Seastedt, T. R. 1988. Mass, nitrogen and phosphorus dynamics in foliage and root detritus of tallgrass prairie. – *Ecology* 69: 59–65.
- Taylor, R. V. and Seastedt, T. R. 1994. Short- and long-term patterns of soil moisture in alpine tundra. – *Arct. Alp. Res.* 26: 29–34.
- Theodose, T. A. 1995. Interspecific plant competition in alpine tundra. – Ph.D. Diss., Univ. of Colorado. Boulder, CO.
- and Bowman, W. D. Responses of plant abundance and species diversity to nutrient availability in two alpine tundra plant communities. – *Ecology* (in press).
- , Jaeger, C. H., III, Bowman, W. D. and Schardt, J. C. 1996. Uptake and allocation of ^{15}N in alpine plants: implications for the importance of competitive ability in predictability community structure in a stressful environment. – *Oikos* 75: 59–66.
- Thompson, K. 1987. The resource ratio hypothesis and the meaning of competition. – *Funct. Ecol.* 1: 297–315.
- Tilman, D. 1987. The importance of the mechanisms of interspecific competition. – *Am. Nat.* 129: 769–774.
- 1988. Plant strategies and the dynamics and structure of plant communities. – Princeton Univ. Press, Princeton, NJ.
- Walker, M. D., Webber, P. J., Arnold, E. H. and May, D. E. 1994. Effects of interannual climate variation on above-ground phytomass in alpine vegetation. – *Ecology* 75: 393–408.
- Welden, C. W. and Slausen, W. L. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. – *Q. Rev. Biol.* 61: 23–43.
- Williams, K., Richards, J. H. and Caldwell, M. M. 1991. Effect of competition on stable carbon isotope ratios of two tussock grass species. – *Oecologia* 88: 148–151.
- Wilson, S. D. 1993. Competition and resource availability in heath and grassland in the Snowy Mountains of Australia. – *J. Ecol.* 81: 445–451.
- and Keddy, P. A. 1986. Measuring diffuse competition along an environmental gradient: results for a shoreline community. – *Am. Nat.* 127: 862–869.
- and Shay, J. M. 1990. Competition, fire and nutrients in a mixed-grass prairie. – *Ecology* 71: 1959–1967.
- and Tilman, D. 1991. Components of plant competition along an experimental gradient of nitrogen availability. – *Ecology* 72: 1050–1065.
- and Tilman, D. 1993. Plant competition and resource availability in response to disturbance and fertilization. – *Ecology* 74: 599–611.