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**Institutions:** Umeå University

**Published on:** 01 Nov 2004 - Arctic, Antarctic, and Alpine Research (Institute of Arctic and Alpine Research (INSTAAR), University of Colorado)

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Author: Olofsson, Johan

Source: Arctic, Antarctic, and Alpine Research, 36(4) : 464-467

Published By: Institute of Arctic and Alpine Research (INSTAAR),  
University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(2004\)036\[0464:PANPII\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2004)036[0464:PANPII]2.0.CO;2)

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# Positive and Negative Plant-Plant Interactions in Two Contrasting Arctic-Alpine Plant Communities

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## Abstract

Positive interactions in alpine plant communities have been reported to increase in importance with increasing altitude and exposure. Positive and negative interactions between plants might occur simultaneously, so the net plant-plant interaction is determined by the balance between positive and negative effects. I investigated the relative effect of facilitation and resource competition by surrounding dwarf shrubs on *Carex bigelowii* in two contrasting arctic-alpine tundra heathlands. *Carex bigelowii* was positively associated with dwarf shrubs on an exposed mountain ridge but negatively associated with dwarf shrubs on a protected heath. A removal experiment indicated that positive associations at the exposed site are the result of facilitation of *C. bigelowii* by the dwarf shrub canopy. Our understanding of arctic and alpine plant communities can be enhanced by regarding plant interactions as combinations of positive and negative components.

## Introduction

Negative interactions, especially competition between plants, are important for community organization and plant coexistence in most ecosystems (Connell, 1983; Schoener, 1983). Belowground competition between plants has been found in most ecosystems, where it has been studied (Wilson, 1988; Casper and Jackson, 1997; Coomes and Grubb, 2000). Although most experimental studies assessing competition as a function of habitat productivity have recorded a decrease in the magnitude of belowground competition with increased soil resource levels (Grime, 1979; Twolan-Strutt and Keddy, 1996) indifferent or even increased belowground competition at higher resource availability have been recorded (Goldberg and Barton, 1992). However, in many environments, positive interactions between plants are also important for community processes (Hay, 1986; Bertness and Callaway 1994; Callaway, 1995; Jones et al., 1997). Positive plant-plant interactions typically occur where the presence of one species ameliorates the abiotic environment for another (Bertness and Shumway, 1993; Bertness and Hacker, 1994; Berkowitz et al., 1995; Brooker and Callaghan, 1998).

In arctic and alpine environments at lower altitudes, plant communities seem to be dominated by negative interactions (Shevtsova et al., 1995, 1997; Sammul et al., 2000; Choler et al., 2001; Callaway et al., 2002; Olofsson et al., 2002). However, at higher altitudes the importance of such negative plant-plant interactions seems to decrease (Sammul et al., 2000; Olofsson et al., 2002) and positive interactions may become more important (Choler et al., 2001; Callaway et al., 2002). However, spatial proximity of plants has been observed in numerous studies during the last 50 yr and this has been interpreted as an indication of positive interactions between plants (Choler et al., 2001, and references therein). Even though experimental studies have shown that positive associations sometimes indicate positive interactions (Choler et al., 2001), positive associations are sometimes simply a feature of different plants preferring the same microclimate (Moen et al., 1993; Olofsson et al., 1999).

The net interaction between plants is a balance between negative and positive components (Callaway, 1994; Callaway and Walker, 1997; Holmgren et al., 1997; Brooker and Callaghan, 1998; Levene 2000). The shift from negative to positive interactions at higher altitudes could, thus, be due to either an increase in the positive

component (facilitation) or a decrease in the negative component (competition). It is often difficult to distinguish the intensity of facilitation and competition in field experiments. However, in systems where facilitation occurs mainly aboveground and competition mainly belowground, the intensity of competition and facilitation should be investigated separately by manipulating canopy cover and root distribution (Dormann and Brooker, 2002). A suitable system to study these complex interactions is the interaction between the sedge *Carex bigelowii* and surrounding dwarf shrubs in arctic heathlands. As tundra heathlands are often nitrogen limited (Bowman et al., 1993; Atkin, 1996; Grellmann, 2001), belowground competition is likely to occur. Moreover, Carlsson and Callaghan (1991) showed that *C. bigelowii* benefits from wind protection and grows better in close proximity to the two dwarf-shrubs *Empetrum nigrum* and *Cassiope tetragona*.

Increased knowledge of the role of competition and facilitation in arctic and alpine ecosystems can give a better and more realistic insight into why positive and negative interactions shifts along altitudinal gradients. Thus, I studied the spatial associations between *C. bigelowii* and surrounding dwarf shrubs on an exposed mountain ridge and on a more protected heath in arctic-alpine tundra in northern Norway. To investigate whether the observed spatial association is the result of interactions between plants or of microsite quality, I manipulated dwarf shrub canopy and root distribution around target plants at the two sites during one growing season.

## Study Area

The research was conducted in the Joatkajavri area of northern Norway (69°46'N; 23°58'E). This area is in the orohemiarctic zone (Ahti et al., 1968; Oksanen and Virtanen, 1995), and the vegetation is a mixture of forest and tundra. Two contrasting study sites were examined. One site was located on an exposed mountain ridge, about 620 m above sea level. The vegetation is sparse and plants are only a few centimeters high. Plants grow in aggregated patches with areas of bare ground in between. The soil organic horizon is thin and varies between 0 and 2 cm. As the site is on the top of a ridge, it is exposed to winds from all directions. Thus, snow is often blown away during the winter and frost heaving disturbance of the soil is common. Moreover, as the site is on top of the ridge, the soil often dries out in the absence of precipitation. The other site was located on a more protected dwarf-

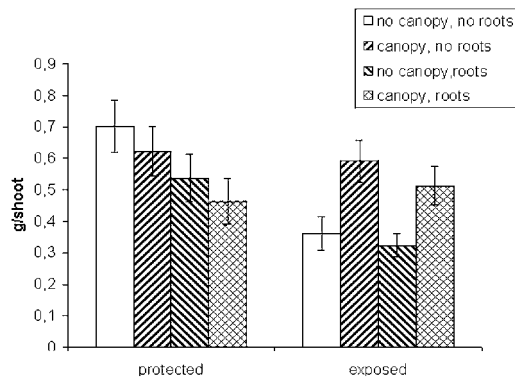


FIGURE 1. Final biomass of *Carex bigelowii* shoots (mean  $\pm$  SE) in four experimental treatments, where canopy cover and roots of surrounding dwarf shrubs in a sheltered and an exposed area were manipulated.

shrub heath, about 450 m a.s.l., on a gentle south-facing slope, lower down on the same mountain as the exposed site. The vegetation cover is almost continuous in the protected site, with only a few patches of bare ground and the height of the dominating dwarf shrubs is 10 to 20 cm. The soil organic horizon is about 10 cm. It experience higher temperatures than the exposed site. The snow cover during winter is deeper here and plants receive groundwater and meltwater during the entire summer. The area is a migration area for reindeer in late autumn and early spring, but no reindeer are present in the summer.

## Methods

Presence/absence data for all vascular plant species were collected for four plots (0.75 m  $\times$  0.75 m) /site in late July. Presence/absence data were also recorded in the 900 2.5 cm  $\times$  2.5 cm quadrats making up each of the larger plots. The cover of each species was calculated as the percentage of the cells occupied.

At the end of June, soon after the snow had melted in this area, canopy removal and root exclusion experiments were set up at the two study sites. One hundred small *C. bigelowii* plants, as evenly sized as possible and without visible connections to other shoots, were chosen. Almost all suitable plants in the chosen size class at the sites were used and the interaction between target plants should thus reflect the interactions that occur in the area. Plots of 0.2 m  $\times$  0.2 m were marked out with one of the *C. bigelowii* plants in the middle. These plots were randomly allocated to one of the four different treatments, yielding 25 replicates. The following four treatment combinations were applied: canopy excluded and roots excluded; canopy excluded and roots present; canopy present and roots excluded; and canopy present and roots present.

Plots were trenched, severing roots along the plot boundary, and 20-cm-deep PVC sheets were inserted along the edges of all plots where exclusion of surrounding plant roots was required. Because root exclusion using this technique can be confounded by the effects of decaying roots and soil disturbance (Callaway, 1994), I also trenched the plots that included root competition. In this case, no PVC sheet was inserted, so roots were able to grow back into the plots. The 20-cm-deep PVC sheets reached into the mineral soil and no roots were found beneath this depth. It was not necessary to cut any clonal connections between our target plants and the surrounding *Carex* plants. Canopy exclusion was achieved by bending away the aboveground parts of surrounding dwarf shrubs. As the plots were quite small, most of the dwarf shrub shoots were rooted outside the treatment plots. Therefore, without damaging the plants, they could easily be bent out of the way and bound to surrounding plants with a nylon string. However, a few

TABLE 1

Results of within effects from a split-plot analysis of variance for shoot weight of *Carex bigelowii*. Figures in bold are considered as significant

Source	d.f.	SS	F	p
Exposed				
Root	1	520	0.7	0.407
Canopy	1	9937	<b>13.3</b>	<b>&lt;0.001</b>
Canopy $\times$ Roots	1	91	0.1	0.729
Error	86	64483		
Protected				
Roots	1	633	0.5	0.482
Canopy	1	5380	<b>4.2</b>	<b>0.043</b>
Canopy $\times$ Roots	1	12	0.0	0.923
Error	75	95203		

shoots that were rooted inside the plots had to be cut. Since only ca. 10 shoots in total had to be cut in the 100 canopy exclusion plots, it is unlikely that they had any effect on the outcome of this study. In the middle of August, at the end of the growing season, the *C. bigelowii* shoots were harvested and dried at 60°C for 48 h. Shoot biomass and seed biomass were assessed separately.

The spatial relationship between dwarf shrubs and *C. bigelowii* was examined by pooling all data from the four 0.75 m  $\times$  0.75 m plots at each site. Presence/absence of different plant species for each of the 3600 subplots were used to produce two by two contingency tables. The presence of associations between dwarf shrubs and *C. bigelowii* were examined using a chi-square test. The influences of roots and canopy on shoot biomass and total seed biomass were tested with separate two-way ANOVA's for each site to avoid pseudoreplication. The data fulfil the assumptions of normality and homoscedasticity.

## Results

The cover of dwarf shrubs in the protected site was 94.0%. The most abundant dwarf shrubs were *Empetrum nigrum* (86.0%), *Betula nana* (44.9%), and *Vaccinium vitis-idaea* (24.8%); the cover of *C. bigelowii* was 3.8%. At the exposed site, the cover of dwarf shrubs was 83.0%. The same three dwarf shrub species were most abundant at this site: *E. nigrum* (58.1%), *B. nana* (34.9%) and *V. vitis-idaea* (38.2%). The cover of *C. bigelowii* at the exposed site was 6.1%. *Carex bigelowii* was positively associated with dwarf shrubs at the exposed site ( $\chi^2 = 9.604$ , d.f. = 1,  $P = 0.002$ ; Fig. 1) and negatively associated with dwarf shrubs at the protected site ( $\chi^2 = 7.283$ , d.f. = 1,  $P = 0.007$ ; Fig. 1). The survival of *C. bigelowii* shoots was not significantly influenced by the root and canopy manipulations at either the protected site (d.f. = 3,  $\chi^2 = 2.87$ ,  $P = 0.411$ ) or the exposed site (d.f. = 3,  $\chi^2 = 0.755$ ,  $P = 0.860$ ).

A significant positive effect of canopy was found in the exposed site, but not in the protected site (Table 1). A significant negative effect of belowground competition was found in the protected site, but not in the exposed site (Table 1).

The frequency of flowering of *C. bigelowii* shoots was not significantly influenced by the root and canopy manipulations. The seed production per flowering shoot followed the same trend as the total shoot weight, but the differences were not statistically significant (Fig. 2).

## Discussion

The net effect of surrounding plants was positive at the exposed high-altitude site and negative at the protected low altitude site. Thus, the change from a positive spatial association between dwarf shrubs and *C. bigelowii* at the exposed site to a negative spatial association at

the protected site is probably the result of a switch from positive to negative net interactions between plants. The seed mass followed the same trend as the shoot weight, but the effects were not significant. The two study sites differ both in altitude and level of exposure. In a study in the western Alps, Choler et al. (2001) demonstrated that both increased exposure and altitude increase the prevalence of positive plant-plant interactions. I cannot separate the effects of altitude and exposure in this study, since the difference between the study sites is the result of a combination of these two factors.

The facilitative effect of dwarf shrub canopy on the growth of *C. bigelowii* may be the result of increased shelter, as suggested by Carlsson and Callaghan (1991). In their study, they showed that artificial shelters enhanced the growth of *C. bigelowii*. The positive effect of shelter could be due either to direct protection against wind (Carlsson and Callaghan, 1991) or to the relatively dense stands of dwarf shrubs creating a warmer and moister microclimate (Warren Wilson, 1959; Carlsson and Callaghan, 1991). Dwarf shrubs can facilitate neighboring plants through accumulating snow (Hadley and Smith, 1987; Callaghan et al., 1989) or litter (Svoboda, 1977; Muller, 1953). However, as this manipulation was done only during one growing season, neither of these mechanisms is likely to explain the facilitation observed here.

Excluding root competition had a positive impact upon the growth of *C. bigelowii* plants. Previous studies on belowground competition along gradients of resource availability or stress have produced varying results. Wilson (1993) recorded that root competition increased with altitude. In old fields, root competition has been shown to increase with decreasing soil fertility and productivity (Wilson and Tilman 1991, 1995). In contrast, root competition intensity did not vary along gradients of soil depth in alvar meadows (Belcher et al., 1995) or between wetlands with different levels of productivity (Twolan-Strutt and Keddy, 1996). I cannot state whether the competition intensity is similar or different between my two sites as the results from the analysis are partly contradictory. However, the significant main effect shows that belowground competition is important in both sites. Still, the effect of belowground competition recorded here is small compared to the facilitating effect of plant canopy. The method used to measure belowground interactions probably underestimates the competition intensity, since roots from neighboring plants had to re-grow before they could start competing with the target plants. However, since all surrounding dwarf-shrub species are highly dependent upon mycorrhiza for their nutrient uptake (Read and Haselwandter, 1981; Bajwa and Read, 1985; Emmerton et al., 2001), the plants might have reconnected with mycorrhizal hyphae almost immediately after the roots were cut. At the time of harvesting, I could observe that roots had indeed re-grown in the belowground competition treatment but the root densities were much lower than before the start of the experiment.

The net interaction between plants in this dwarf shrub heath is indeed a balance between positive and negative components. The shift from positive net interactions at the exposed high-altitude site to negative net interactions at the protected low altitude site is, however, mainly caused by a switch in the aboveground interactions, since the belowground competition were of less importance and at least did not change substantially. Brooker and Callaghan (1998) proposed that the intensity of positive interactions should increase and the intensity of negative interactions should decrease along gradients of increasing stress and disturbance. This study shows that the net interaction can switch from positive to negative even if the competition intensity for soil resources remains constant. Changes in negative and positive interactions appear to be less closely linked than Brooker and Callaghan (1998) proposed.

My results support the conclusion of Choler et al. (2001) that positive associations between plants can be indicative of positive interactions, and not preference for the same microclimate. As an

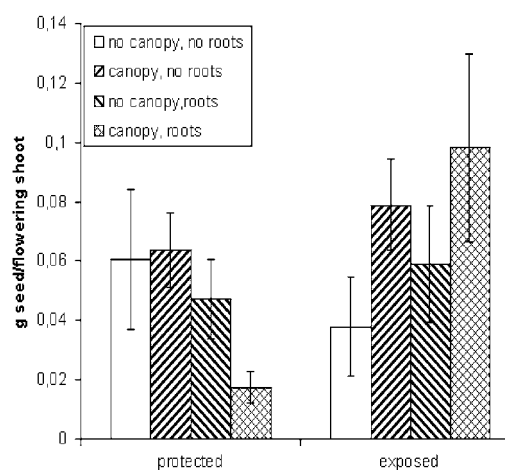


FIGURE 2. Final seed production (biomass) of *Carex bigelowii* (mean  $\pm$  SE) in four experimental treatments, where canopy cover and roots of surrounding dwarf shrubs in a sheltered and an exposed area were manipulated. No significant differences were found.

aggregated spatial pattern is common in arctic and alpine plant communities (see Choler et al., 2001 and references therein), positive interactions between plants may be common as well. Choler et al. (2001) also revealed that responses to neighbors are highly species specific. In their study, species were shown to experience facilitation from neighbors in the higher part of their altitudinal range, and competition in the lower part of their altitudinal range. Since this study examined a target plant that is well adapted for harsh environments and for growth at altitudes far higher than the highest of the study sites, it is possible that an even stronger positive effect would have been found with a target plant that normally grows at lower altitudes. The results of Callaway et al. (2002) indicate that interactions between plants are weaker in arctic than in alpine sites. In the three arctic locations, Brooks Range, Kluane Range, and Abisko, significant differences between high and low sites were only found in Brooks Range. Significant positive effects were, however, recorded in the high-altitude site in all these locations but no significant competitive effects were found. When comparing my results with this study, one has to be aware of the fact that they did not cut roots, so root competition could still be important in the neighbor removal treatment.

My results show that the positive association between plants in the exposed site were indeed caused by positive interactions between the plants as the presences of dwarf shrub canopy facilitate the growth of *Carex bigelowii*. However, competition was still important and both competition and facilitation have to be considered to get a realistic view of interactions in arctic plant communities.

## Acknowledgments

I wish to thank Lauri Oksanen and Joachim Strengbom for their helpful comments on previous versions of this manuscript. This study was supported by grants from the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning.

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Ms submitted June 2003