

Facilitation and competition in the high Arctic: the importance of the experimental approach

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Abstract

In the last decade, plant ecologists have focussed more on the occurrence of positive plant–plant interactions than ever before. Especially in severe environments, such as the Arctic, species removal experiments tend to find facilitative rather than competitive effects, casting doubt on the importance of competition under extreme growing conditions. Two approaches to measure plant–plant interactions presented here reveal that competition affects plant growth even in the high Arctic. *Luzula confusa* and *Salix polaris* show a reduced growth in mixed stands compared with pure. This competition effect is not detected in a removal experiment, which inevitably also alters site microclimate. Indeed, in the latter experiment, facilitative effects of *Luzula* on *Salix* were found. Evidently, both facilitation and competition are acting and important. Causes and implications are discussed using a conceptual model derived from that of Brooker and Callaghan (1998). © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

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1. Introduction

Perennial plants living in severe environments have adapted to unpredictable resource availability, disturbances and physical limitations of growth. They are, by definition, stress-tolerant (sensu Grime, 1979) and commonly show features of resource storage to buffer environmental fluctuations (Chapin et al., 1990). For example, succulent desert plants grow self-sustained on water and nutrients acquired during periods of plenty, with greatly reduced root growth during the intervening ‘dormant’ period (Larcher, 1995). Thus periods of plant competition are seemingly restricted in such environments. Examples like this gave rise to the idea that (interspecific) competition is less intense in ecosystems with low productivity (Grime, 1979). Indeed in these systems beneficial effects of neighbours were postulated and detected (Callaway and Pugnaire, 1999; e.g. nurse plants: Callaway, 1992; Barnes and Archer, 1999; associational refuge: Hay, 1986; Mulder and Ruess, 1998; physical

amelioration: Bertness and Shumway, 1993; Bertness and Hacker, 1994).

Tilman (1988), Oksanen (1990) and more recently Körner (1999) argued that the few resources available are under strong demand and plants adapted to these harsh environments can exploit them efficiently—leading to (nutrient) competition even in the Arctic tundra. Moreover, modelling approaches have indicated that while the intensity of interspecific competition (compared with performance in monospecific stands, Weldon and Slauson, 1986) might be lower in harsh environments, its importance (proportional input relative to other factors) might still be very high indeed (Chesson and Huntly, 1997): plants are living closer to the brink of existence, and even slight decreases in resource availability may thus have very strong effects.

Over the last decade studies investigating positive interactions among plants have increased dramatically (Fig. 1), leaving little doubt of their generality and importance (Holmgren et al., 1997; Kareiva and Bertness, 1997; Bertness, 1998), and rather questioning the assumed importance of competition. Competition experiments in the Arctic have generally found negative effects of neighbour removal

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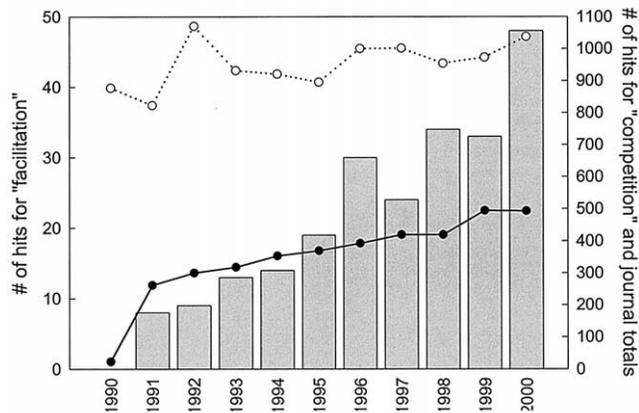


Fig. 1. Web of science search hits on the terms: [(‘positive interactions’ or facilitation) and plant], shown as bars, [(‘negative interactions’ or competition) and plant] in filled points and total publications of *American Naturalist*, *Ecology*, *Journal of Ecology*, *Oecologia* and *Oikos*, shown as open points, from 1990 to 2000.

(Jonasson, 1992; Shevtsova et al., 1995; Shevtsova et al., 1997; Hobbie et al., 1999), indicating the greater importance of facilitation compared to competition (Carlsson and Callaghan, 1991; Callaway and Walker, 1997; Holmgren et al., 1997; Brooker and Callaghan, 1998). For example the removal of *Betula nana* led to a decreased abundance of *Vaccinium myrtillus* (Jonasson, 1992), and similarly the growth of *Empetrum nigrum* was impeded after the removal of *V. myrtillus* (Shevtsova et al., 1995). Interactions between removal and water and warming treatments (Shevtsova et al., 1997) indicated that in this case the mechanism of facilitation was by alteration of the microclimate.

One reason why some neighbour removal experiments in the Arctic have failed to detect competition might be that they also inevitably manipulate facilitation, and examine only the net outcome of interactions, not isolating either competition or facilitation. Removal of neighbours will lead to a higher exposure to the physical stress of the environment (e.g. lower temperature, soil drying, Brooker and Callaghan, 1998). To investigate whether this might mask the existence of competitive interactions, we compared two approaches to the study of plant–plant interactions: first, the removal of the competitor and second, a comparison of plant performance in pure and mixed stands. Plants growing with neighbours experience amelioration of the environment, but the performance also depends on neighbour identity: as interspecific competition is generally stronger than intraspecific, performance in pure stands should be higher than in mixed stands. As our findings indicate, different approaches should be employed simultaneously to gain a fuller understanding of plant–plant interactions.

2. Methods

The study was carried out in Semmeldalen (77.90°N 15.20°E), a valley approximately 20 km south of Longyear-

byen, Svalbard, in a *Salix polaris*-heath (Rønning, 1996). The dominant plant types in terms of cover are bryophytes (mostly > 60%; in our sites dominated by the liverwort *Ptilidium ciliare* and mosses *Polytrichum* spp. and *Drepanocladus uncinatus*), while *Luzula confusa* (ca. 10%) and *S. polaris* (ca. 20%) are the main vascular plants. Lichens and bare soil (peat) cover is usually less than 10%. The *S. polaris*-heath occupies slightly elevated ground and the soil dries out rapidly over the course of the growing season. Nutrient availability is low and there is also evidence for water limitation (van de Graaf, 1999; van der Wal and Dormann, in prep.). Summer air temperatures average between 5 and 10 °C, with soil temperatures approximately 2 °C at 5 cm in depth (unpublished data). The vegetation is grazed heavily by reindeer.

2.1. Neighbour removal experiment

This experiment was set up in August 1998 as a species removal experiment, nested within a factorial \pm nitrogen by \pm phosphorus fertilisation experiment (four treatment combinations, five replicates, resulting in 20 independent removal subplots per species). Within each fertilised plot (1.5 \times 1.5 m) one subplot of 50 \times 50 cm was cleared of *L. confusa*, one was cleared of *S. polaris* and a third one left as control (the 25 cm buffer zone around each subplot received the same treatment). For *Luzula*, leaves and shoot-bases were removed (resulting in no regrowth), whilst for *Salix* a less complete removal of stems was repeated twice per year. Subplots were trenched to a depth of approximately 20 cm at the beginning of the experiment. Data presented are averaged over the fertilisation treatments as there were no significant treatment effects other than the effect of phosphorus on *Salix*, and in this case only the phosphorus-free plots are used for analysis.

2.2. Comparison of growth in pure and mixed stands

Plots were established in June 1999 at the onset of the growing season. They ($N = 15$; 60 cm diameter) comprised a dense stand of *Luzula*, a dense stand of *Salix* and a mixtures of both. This allowed for sampling of shoots of either species in ‘pure’ neighbourhoods, i.e. where it was surrounded by conspecifics, and in ‘mixed’ neighbourhoods, where both species were present. For both *Luzula* and *Salix* the ‘mixed’ situation was selected in such a way that the other species was much more abundant than the target species (density of target species was less than half of that of pure stands). As in the other experiment, plots were trenched to a depth of approximately 20 cm at the beginning of the experiment.

2.3. Harvest and statistical analysis

On 1–5 August 2000, after two seasons, five shoots of each species were randomly sampled above-ground from

each subplot. These five shoots were sorted into live and dead leaves (*Luzula*) or leaves and stem (*Salix*), dried at approximately 45 °C and weighed. Stems of the five *Salix* per subplot were frozen and transported back to the lab. Their growth over the last 3 years was analysed retrospectively, using the stem length increments, which were transformed into biomass growth (for details see Dormann and Skarpe, 2002).

For both experiments, subsamples within subplots were averaged. Data were \log_{10} -transformed to successfully meet assumptions of ANOVA and analysed with the Generalised Linear Model procedure of SAS (SAS Institute Inc., 1989). Block effects for the removal experiment and for *Luzula* in the stand comparison were not significant ($p > 0.8$), and therefore, dropped from the model.

3. Results

The removal of *Luzula* led to a 30% decrease in *Salix* shoot weight ($F_{1,18} = 6.60$, $p < 0.05$; Fig. 2), indicating facilitation. On the other hand, *Salix* performed slightly better in pure stands than in mixed ($F_{1,28} = 3.75$, $p = 0.0731$; block: $F_{14,29} = 2.10$, $p = 0.0881$), suggesting interspecific competition. There was no significant effect of the fertilisation treatments or their interaction with removal.

For *Luzula*, the results are very different: *Salix* removal had no effect on shoot biomass ($F_{1,37} = 0.05$, $p = 0.8238$), while plants performed significantly better in pure than in mixed stands ($F_{1,28} = 10.24$, $p < 0.01$), which indicates a dominance of competitive interactions over facilitative effects of neighbours (Fig. 2).

4. Discussion

Our results demonstrate clearly the effect of experimental approach on the detection of competition in a severe environment. Simplistic interpretation of the removal experiment would lead to the following conclusions: (1) *Salix* has no impact on *Luzula* and (2) *Luzula* has a facilitative impact on *Salix* (due to the negative response of *Salix* and the lack of response of *Luzula*). A possible mechanism for the facilitative relationship being the prevention of water stress or increased tissue temperatures in *Salix* as a result of the presence of its *Luzula* neighbours. However, the second experiment, comparing mixed and pure stands, provides evidence that this simplistic initial conclusion is erroneous; both species perform better in pure rather than mixed stands, indicating that interspecific competition is of some importance.

The growth of Arctic plants is generally nutrient limited (Shaver and Chapin, 1980; Shaver and Chapin, 1986; Chapin et al., 1986; Henry et al., 1986; Parsons et al., 1994). Thus, it is likely that in addition to facilitative interactions *Salix* and *Luzula* are also competing for soil resources,

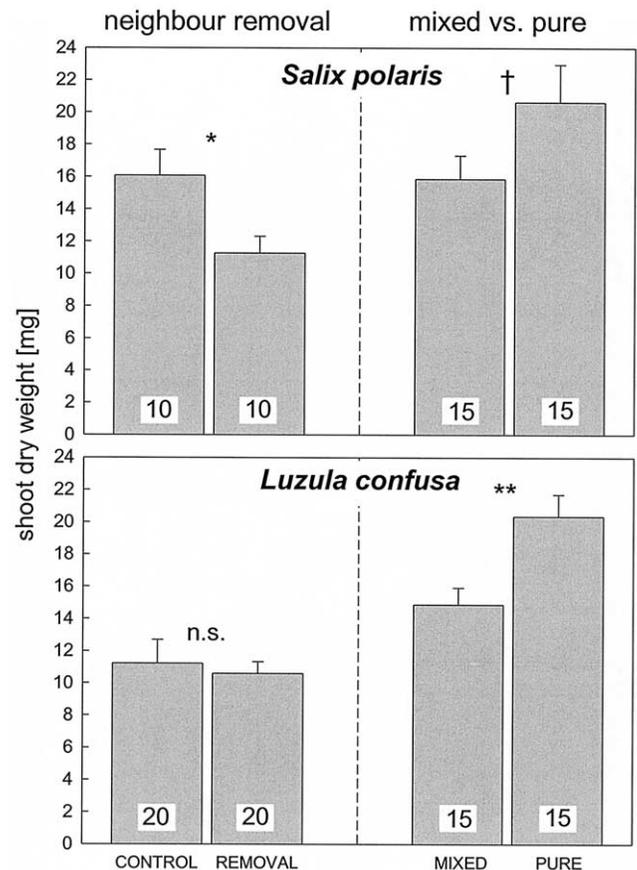


Fig. 2. Shoot biomass of *S. polaris* (upper panel) and *L. confusa* (lower panel) in untreated controls and after two seasons without interspecific competition (left half) and growing unmanipulated in mixed and pure stands (right half). Error bars depict standard errors. †, * and ** refer to $p < 0.1$, 0.05 and 0.01, respectively. Numbers indicate level of replication.

probably nitrogen and/or phosphorus (Shaver and Chapin, 1986; Baddeley et al., 1994), although the factorial fertilisation experiment, of which the removal experiment is a subset, found no consistent increases in biomass with nitrogen or phosphorus addition (*Salix* showed a marginally significant response to phosphorus). In recent years, water limitation has drawn more ecological attention in the Arctic (see review by Hodkinson et al., 1999). A watering experiment at the same site could find no significant effect of adding water every other day for one season, on either *Salix* or *Luzula*, although the latter had a tendency to grow better when watered (Van der Graaf, 1999). We could thus not identify the limiting resource with any certainty.

However, it is clear from the combination of these two experimental approaches that both negative and positive plant interactions are occurring at the same time. One recent synthesis (Brooker and Callaghan, 1998) provides a hypothetical framework that links the importance of both facilitation and competition, and the type of interaction observed in neighbour removal experiments, to the harshness of the physical environment, leaving aside biotic harshness (Bertness, 1998). Fig. 3 is a modified representation of this concept. Its main assumptions are that the importance of

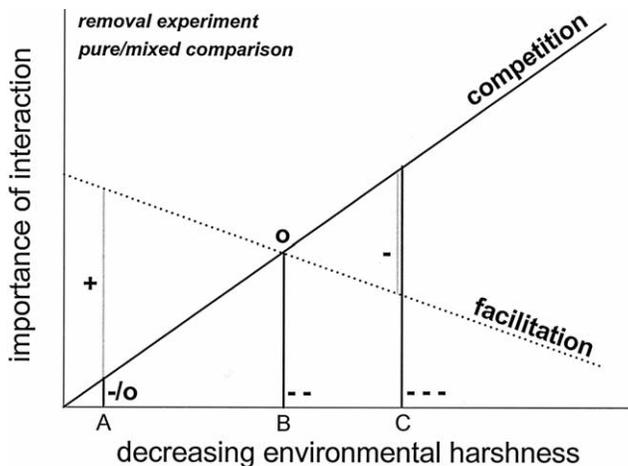


Fig. 3. Intensity of facilitation and competition along a gradient of decreasing environmental harshness adopted from Brooker and Callaghan (1998). The observed net outcome of the two types of interactions is illustrated for three points: in (A) facilitation outweighs competition, leading to a negative effect of neighbour removal (grey vertical lines and symbols, indicating positive (+), neutral (o) or negative (-) net effects). In (B) both interactions cancel each other out and in (C) competition is dominant over facilitation, leading to positive effects of neighbour removal. Comparing the performance in mixed and pure stands (black vertical lines and symbols) leads to different conclusions, however. As facilitation is acting in both stands, only competition effects are detected. Assuming that interspecific competition is stronger than intraspecific, plant performance should be lower in mixed stands over the entire gradient, with the difference to pure stands increasing with decreasing environmental harshness.

facilitation increases along a gradient of increasing environmental harshness, while the importance of competition decreases. Thus the net outcome of plant–plant interactions (observable by simple neighbour removal experiments) changes along the gradient. In a low productivity environment (point A), facilitation is more important than competition, the net interaction is facilitative, and neighbour removal would have negative effects on the performance of the target plant. With decreasing severity, competition and facilitation may be equal (point B) leading to no observable outcome of neighbour removal, and even further on (point C) competition dominates, leading to a positive response of the target plant in response to neighbour removal.

With respect to Fig. 3, the impact of *Luzula* on *Salix* represents the situation at A, with removal having a net negative effect, but competition (which would not be detectable through neighbour removal but can be observed by the mixed vs. pure comparison) still being evident. The impact of *Salix* on *Luzula*, on the other hand, may represent the situation at B, with removal of competitors having no effect as facilitation and competition cancel each other out, while interspecific competition is still occurring (Fig. 2). What these results demonstrate is the potential complexity of examining multispecies interactions. The initial framework (Fig. 3) was constructed to examine the simple response of mono-specific stands. In this study, we must now consider both inter- and intraspecific competitive and facilitative effects, which may vary independently along the

severity gradient and differ between species because of factors such as plant growth form.

For example, the tussock growth form exhibited by *Luzula* may lead to a high recycling of nutrients from litter, as most of the roots are found within the tussock ('cannibalistic nutrition': Callaghan, 1988). *Salix*, on the other hand, has a high belowground biomass, which not only accesses nutrients from deeper in the soil than *Luzula*, but presumably also serves as nutrient storage (Chapin et al., 1980). These differences in growth form may cause differences in the relative interspecific competitive effect of the species.

Similarly both of our target species are clonal. Clonality may have evolved in harsh environments to enhance intra-specific facilitation (Callaghan and Emanuelsson, 1985). It is difficult to distinguish within a species between selections due to direct, physiological support and more indirect, environment mediated facilitation through the increased density of con-specifics (and therefore, environmental amelioration with the minimum degree of competition) in the vicinity of the parent plant. However, our results suggest that there are differences in the facilitative ability of the different growth forms. *Luzula* has a significant facilitative effect on *Salix* whilst the reverse is not true. As *Luzula* is a taller species, amelioration of the physical environment (wind stress, evaporation Brooker and Callaghan, 1998) is a possible candidate of the facilitative mechanism. Temperatures in the *Luzula*-tussock were 0.9 °C higher than among *Salix* plants (7.6 compared to 6.7 °C, measured in 60 tussocks; CFD, unpublished data). Protection of *Salix* from reindeer grazing by the dead leaves of *Luzula* is also a plausible mechanism (Van der Wal et al., 2000).

In conclusion, as both competition and facilitation are possibly acting, both will structure the community. Disregarding facilitative interactions in the experimental design can lead to misconceptions about forces shaping communities in harsh environments. Thinning experiments would make the removal of a co-occurring species comparable to that of the target species and thus allow testing the assumption of equality of facilitation by different species (asymmetry of facilitation) and the greater intensity of inter-compared to intraspecific competition.

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