

## CHAPTER 4

# FACILITATION AND COMPETITION IN THE HIGH ARCTIC: THE IMPORTANCE OF EXPERIMENTAL APPROACH<sup>1</sup>

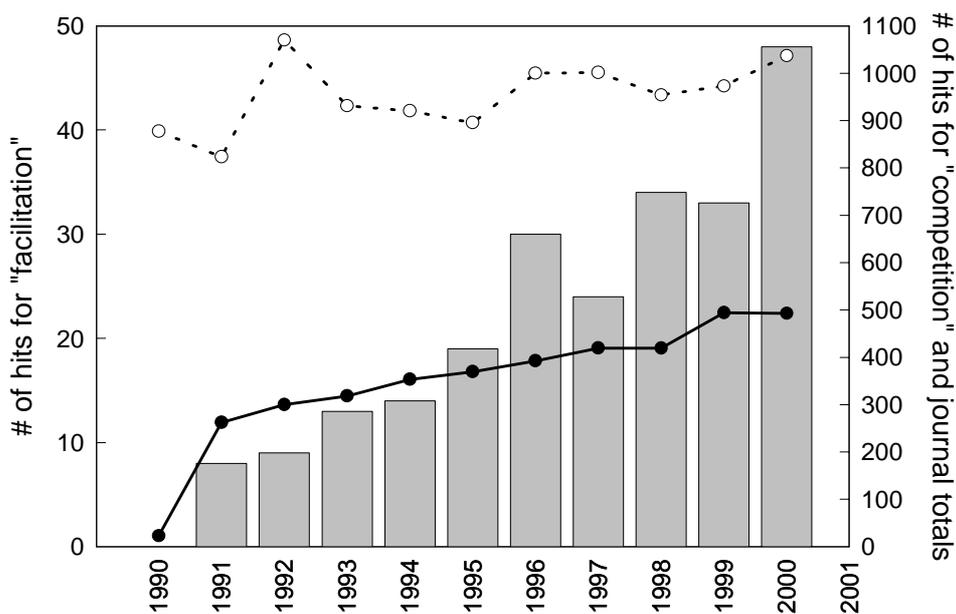
*Abstract* In the last decade, plant ecologists have focussed more on the occurrence of positive plant-plant interactions than ever before. Especially in severe environments, such as the Arctic, species removal experiments tended to find facilitative rather than competitive effects, casting doubt on 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. The comparison of *Luzula confusa* and *Salix polaris* in pure and mixed stands indicates a pronounced reduction in growth in mixed stands. This could not be detected in a removal experiment, which inevitably also altered site microclimate. Causes and implications are discussed using a conceptual model derived from that of Brooker & Callaghan (1998).

## 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

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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.

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 (e.g. nurse plants: Callaway 1992; Barnes & Archer 1999; associational refuge: Hay 1986; Mulder & Ruess 1998; physical amelioration: Bertness & Shumway 1993; Bertness & Hacker 1994).

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 & Bertness 1997; Bertness 1998), and rather questioning the assumed importance of *competition*. 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 competition (compared to performance in monospecific stands, Weldon & Slauson 1986) might be lower in harsh environments, its *importance* (relative to other factors) might still be very high

indeed (Chesson & Huntly 1997): plants are living closer to the brink of existence, and even slight decreases in resource availability may thus have very strong effects.

Competition experiments in the Arctic have generally found negative effects of neighbour removal (Jonasson 1992; Shevtsova *et al.* 1995; 1997; Hobbie *et al.* 1999), indicating the importance of facilitation compared with competition (Carlsson & Callaghan 1991; Callaway & Walker 1997; Holmgren *et al.* 1997; Brooker & 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 *Vaccinium myrtillus* (Shevtsova *et al.* 1995). Interactions between removal and water and warming treatments (Shevtsova *et al.* 1997) indicated that 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 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 & Callaghan 1998). To investigate whether this masks effects of competitive interactions, we compared two approaches to the study of competition: firstly, the removal of the competitor and secondly, 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 (i.e. intra- vs. interspecific competition). As our findings indicate, different approaches should be employed simultaneously to gain a fuller understanding of plant-plant interactions.

## METHODS

The study was carried out in Semmeldalen (77.90 °N 15.20 °E), a valley c. 20 km south of Longyearbyen, Svalbard, in a *Salix polaris*-heath (Rønning 1996). The dominant plant type 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* (c. 10%) and *Salix polaris* (c. 20%) are the main vascular plants. Lichens and bare soil (peat) cover is usually less than 10%. The *Salix 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 der Graaf 1999). Summer air temperatures average between

5 and 10 °C, with soil temperatures c. 2 °C at 5 cm depth (unpublished data). The vegetation is grazed heavily by reindeer.

### 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 fertiliser treatment one subplot of 50 cm  $\times$  50 cm was cleared of *Luzula confusa*, one was cleared of *Salix polaris* and a third one left as control. For *Luzula*, leaves and shootbases were removed (resulting in no re-growth), whilst for *Salix* a less complete removal of stems was repeated twice per year. 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.

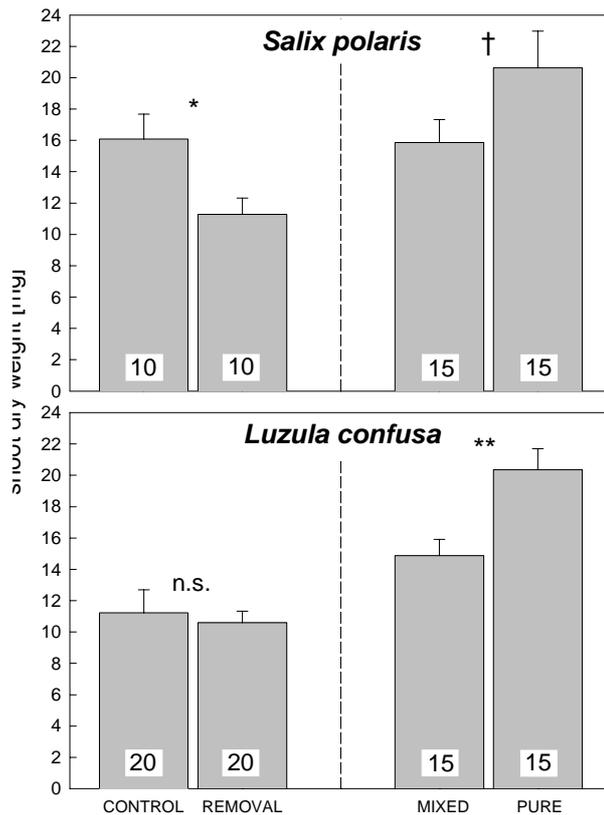
### 2. Comparison of growth in pure and mixed stands

Plots were established in June 1999 at the onset of the growing season. They (N = 15; 60 cm diameter) each comprised a dense stand of *Luzula*, a dense stand of *Salix* and a mixture of both.

#### 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 c. 45 °C and weighed. Stems of the five *Salix* per subplot were frozen and transported back to the lab. Their growth over the last three years was analysed retrospectively, using the stem length increments, which were transformed into biomass growth (CHAPTER 6).

For both experiments, subsamples within subplots were averaged. The model structure accounted for the nesting of competition plots within fertilisation treatments (experiment 1 only) and for blocking. Data were  $\log_{10}$ -transformed to successfully meet assumptions of ANOVA and analysed with the MIXED procedure of SAS (SAS Institute Inc. 1989).



**Figure 2** Shoot biomass of *Salix polaris* (upper panel) and *Luzula 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.

## RESULTS

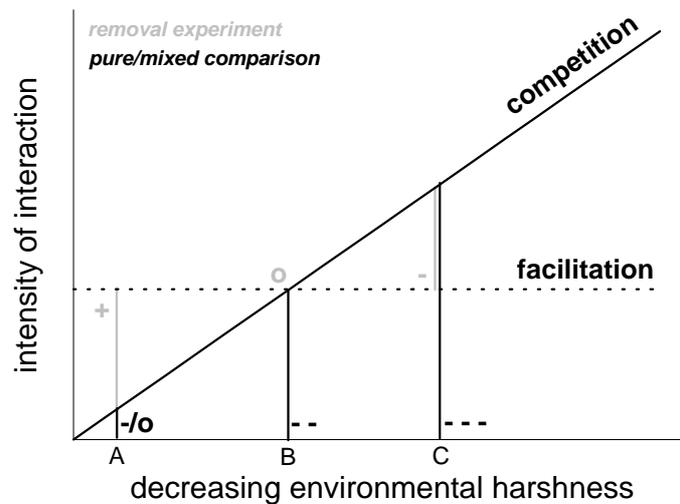
The removal of *Luzula* led to a 30% decrease in *Salix* shoot weight ( $F_{1, 18} = 6.41$ ,  $P < 0.05$ ; Fig. 2), indicating facilitation. On the other hand, *Salix* performed slightly better in pure stands than in mixed ( $F_{1, 28} = 3.75$ ,  $P = 0.0731$ ; block:  $F_{14, 29} = 2.10$ ,  $P = 0.0881$ ) suggesting interspecific competition.

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 competitive interactions without facilitative effects of neighbours (Fig. 2).

## DISCUSSION

Our results demonstrate clearly the effect of experimental approach on the detection of competition in a severe environment. The classical removal experiment (Aarssen & Epp 1990) would lead to the conclusion that there is no competition among the plant species investigated (due to the negative response of *Salix polaris* and the lack of response of *Luzula confusa*). Hence, a facilitative relationship rather than one of competition would be concluded. However, both species perform better under intra- than interspecific competition, indicating that competition is of some importance.

One recent synthesis (Brooker & Callaghan 1998) provides a framework for explaining the occurrence of both facilitation and competition, focussing especially on harshness of the physical environment, leaving aside biotic harshness (Bertness 1998).



**Figure 3** Intensity of facilitation and competition along a gradient of decreasing environmental harshness adapted from Brooker & Callaghan (1998) to represent the intensity rather than the importance of interactions. The observed net outcome of the two types of interactions is illustrated for three points: in A, facilitation overweighs 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.

Figure 3 is a modified representation of this concept. Its main assumptions are: the intensity of facilitation is constant along a gradient of environmental harshness, while the intensity of competition increases. Thus the *net* outcome of plant-plant interactions 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. At decreased severity, competition and facilitation are equal (point B), and even further on (point C) competition dominates, leading to positive performance of the target plant in response to neighbour removal.

With respect to figure 3, *Salix* represents the situation at A, with removal having a negative effect, but competition still being evident. *Luzula*, on the other hand, represents the situation at B, with removal of competitors having no effect as facilitation and competition cancel each other out, while interspecific competition is very ap-

parent in the comparison of stands (Fig. 2). This means that two plant species within the same community might experience their environment differently, in this case possibly because of a better environmental adaptation of *Luzula*.

Two assumptions of the concept have to be regarded with caution: firstly, competition intensity might not increase as the environment becomes more benign, but stay constant or even decrease (Goldberg *et al.* 1999). And secondly, depending on the mechanism, facilitation intensity may also not be constant along the environmental gradient. However, a constant intensity of facilitation seems a reasonable null model (Brooker & Callaghan 1998), and also the increase in competitive intensity along a productivity gradient with standing crop below 350 g m<sup>-2</sup> seems plausible (Belcher *et al.* 1995; Bonser & Reader 1995; Dormann *et al.* 2000).

There is, however, an alternative explanation to the pattern depicted in figure 2. A stronger intra- than interspecific facilitation would also lead to an increased performance of *Salix* in pure stands compared to controls, as there are more *Salix*-plants facilitating each other. Still the performance would be reduced with the removal of *Luzula*, as this species still provided *some* facilitation. For *Luzula*, this mechanism would be the same: asymmetric facilitation, with a high facilitative value of *Luzula* and a low one for *Salix*. The concept of intra- versus interspecific competition is much more a commonplace than the same idea for facilitation, but the latter might be equally valid.

The mechanism of facilitation in our study is unknown. Amelioration of the physical environment (e.g. reduced wind stress) as described for most facilitation studies (see Brooker & Callaghan 1998) is a possibility, but protection of *Salix* from reindeer grazing by the dead leaves of *Luzula* is also plausible (Van der Wal *et al.* 2000c).

The growth of Arctic plants is generally nutrient limited (Shaver & Chapin 1980; 1986; Chapin *et al.* 1986c; Henry *et al.* 1986; Parsons *et al.* 1994). Thus, it is likely that in addition to facilitation, *Salix* and *Luzula* are also competing for soil resources, probably nitrogen and/or phosphorus (Shaver & Chapin 1986; Baddeley *et al.* 1994). However, 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). We could thus not identify with any certainty the limiting resource.

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.

## **ACKNOWLEDGEMENTS**

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