

# CHAPTER 5

## COMPETITION IN A CHANGING ENVIRONMENT: A CASE STUDY FROM THE HIGH ARCTIC<sup>1</sup>

*Abstract* Competition among plants in extreme environments such as the High Arctic has often been described as unimportant, or non-existent. Environmental factors have been suggested to overrule any negative plant-plant interactions. Few studies have actually addressed this issue in the Arctic experimentally, and those that did found little evidence for competition. Species interactions will presumably become more important in the future, as Global Climate Change takes effect on arctic terrestrial ecosystems.

We investigated plant-plant interactions in the High Arctic, following the growth of the wood rush *Luzula confusa* and the dwarf willow *Salix polaris* under conditions of intra- and inter-specific competition, and under elevated temperature treatment, over two growing seasons. Our findings indicate that competition is acting in the natural vegetation, and that warming will alter the balance of interactions in favour of *Salix polaris*, probably due to increased nitrogen availability in warmed plots. To aid understanding of the mechanisms of competition, a controlled environment growth experiment was conducted, manipulating competition, temperature and nutrient availability. The mechanism of competition is unclear, but *Salix* is more responsive to nutrient availability than *Luzula*. Also, while *Luzula* showed a positive response to higher temperature in the laboratory, its performance was actually reduced by interspecific competition in the warmed plots in the field. The consequences of altered

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competitive balance, and the role of herbivores in influencing plant competition, are discussed in the light of our findings.

## INTRODUCTION

Polar regions will be most affected by anthropogenic climate changes (IPCC 1990; Serreze *et al.* 2000). In particular, atmospheric warming due to increasing greenhouse gas emissions is predicted to be most pronounced in the Arctic and Antarctic (IPCC 1998). Arctic terrestrial ecosystems, particularly the vegetation, have been frequently found to respond strongly to experimental perturbations simulating environmental change (for review see Dormann & Woodin 2001; CHAPTER 2). Long-term field experiments on the effects of elevated summer temperature (Chapin *et al.* 1995b) and the indirect consequences of warming (e.g. higher soil mineralisation rates and thus increased nutrient availability, Nadelhoffer *et al.* 1991) have demonstrated major changes in plant species composition (Chapin *et al.* 1995b; Chapin & Körner 1995; Shaver *et al.* 1996; Press *et al.* 1998).

What are the causes of changes in plant species abundance and performance? To date the majority of studies point to individualistic responses of species to environmental perturbations (Chapin & Shaver 1985; Press *et al.* 1998; Dormann & Woodin 2001), rather than competitive displacement, although change in competitive balance is in general one of the best investigated processes underlying changes in vegetation composition (Glenn-Lewin & van der Maarel 1992). In fact, the occurrence of competition among neighbours at high latitudes has been disputed on the basis of theoretical arguments (Grime 1979) and empirical findings: the few competition experiments in the Arctic have rarely found positive effects of neighbour removal, but often negative ones (Jonasson 1992; Shevtsova *et al.* 1997; Hobbie *et al.* 1999), indicating the importance of facilitation over competition (Carlsson & Callaghan 1991; Callaway & Walker 1997; Holmgren *et al.* 1997; Brooker & Callaghan 1998; but see CHAPTER 4). On the other hand Tilman (1988), Oksanen (1990) and, more recently, Körner (1999) reject the idea of competition-free environments. They argue that in harsh environments the few resources available are under strong demand and plants adapted to these environments can exploit them efficiently, leading to (nutrient) competition even in the Arctic tundra. Modelling approaches have indicated that while the *intensity* of competition (*sensu* Weldon & Slauson 1986) might be lower in harsh environments, its *importance* might still be high (Chesson & Huntly 1997). For plants

living close to the brink of survival, any, albeit slight, decrease in resource availability through competition may have strong effects. Moreover, as changes in the Arctic climate result in more favourable conditions for plant growth (longer seasons, higher temperatures, increased nutrient availability), the intensity of competition might be expected to increase.

Competition experiments in the High Arctic are difficult to perform, as the neighbour removal approach favoured in temperate systems (Aarssen & Epp 1990) has potentially serious shortcomings. Brooker & Callaghan (1998) argued that neighbours can facilitate the growth of the target plant, by ameliorating the harshness of the environment (e.g. reduction in wind stress). The removal of neighbours would thereby not only reduce competitive interactions, but also eliminate positive plant interactions. A resulting net-negative effect of neighbour removal does not necessarily indicate the absence of competition in a closed canopy, but the overriding effects of facilitation (CHAPTER 4). This study investigates specifically three main questions: 1. Is competition occurring between two dominant species of High Arctic tundra vegetation? 2. How does warming affect the intensity of interaction between the two species? and 3. What resources do the species compete for? Given the problems of studying competition in an extreme environment, this investigation follows the natural growth of plants in pure and mixed stands in the field, thus overcoming the limitations of a removal experiment. A lower performance of a species in mixed stands compared to pure stands is taken to indicate the occurrence of inter-specific competition. To aid interpretation of the mechanisms of effect of warming, comparison is made between a field temperature manipulation experiment and a controlled environment study in which both temperature and nutrient supply are manipulated.

## METHODS

### 1. Field experiment

#### Experimental set-up

The study was carried out in Semmeldalen (77.90 °N 15.20 °E), a valley c. 20 km south of Longyearbyen, Svalbard. 15 pairs of plots (60 cm diameter) each of which comprised a dense stand of *Luzula*, a dense stand of *Salix* and a mixture of both were carefully selected in a representative patch of *Salix polaris*-heath (Rønning 1996),

within an overall area of c. 100 by 20 m. The experiment consisted of warmed plots and controls, randomly assigned to the paired plots. The whole site was enclosed by an electric fence to prevent disturbance by reindeer.

The 15 treatment plots were subjected to warming over most of the 1999 growing season, from 16.6.1999, i.e. about ten days after snowmelt, to 29.8.1999, and over the whole snow-free period in 2000 until harvest (13.6.2000 - 3.8.2000). Greenhouses of a modified “cloche” type (Strathdee & Bale 1993) were used to raise air temperature. They consisted of an open cylinder ( $\varnothing$  57 cm, height 45 cm) made of a sheet of transparent plastic, with a thin, optically neutral polyester gauze as a roof. While the gauze allowed gas exchange with the surrounding air, and rain to reach the plots, it did retain warm air in the greenhouse by preventing convection to the surrounding atmosphere (Strathdee & Bale 1993). This design avoids the problems of closed constructions as discussed by Kennedy (1995). Air temperature at vegetation level was measured with three RS temperature loggers per treatment at hourly intervals.

The relatively tall structure of the greenhouses prevented the gauze from shading the plot, as the sun was never high enough. Light intensity in the greenhouses (measured using microvolt integrators fitted with a PAR quantum sensor,  $\Delta T$ , Cambridge, U.K.) was reduced by  $11 \pm 3\%$ . This is very little, compared to the c. 50% ( $1100$  vs.  $500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) difference between sun and overcast sky, and slightly less than the reductions induced by greenhouses of other designs (Chapin *et al.* 1995b; Michelsen *et al.* 1996a).

The soil around all plots was trenched to about 20 cm depth with a knife to let the greenhouse rim into the soil to prevent entry of cold air, as well as to sever connections of plants within the plot to plants outside. As the soil closed immediately, no noticeable gap remained. All measurements were performed inside the circle, allowing a 10 cm buffer strip around the perimeter. It could be argued that trenching might cause an increase in below-ground senescence, increasing mineralisation rate and thus plant performance. However, soil nitrogen concentrations and growth rates measured in trenched control plots were very similar to those measured in untrenched plots nearby (data not shown).

Soil water content was measured four times during the 1999 season and twice in 2000, using a soil conductivity insertion probe (SCIP, CEH Wallingford, U.K.). To avoid disturbing the plots more than necessary, measurements were only taken in the

pure stands. Values obtained were transformed into soil water content using a previously established relationship (Rob Rose, CEH Wallingford, U.K., unpublished data).

Ion exchange membranes were used to assess treatment impacts on nutrient availability, following the method of Weih (1998). Cation and anion exchange membranes (BDH, U.K., #55164 and #55165, respectively) were cut into pieces (1 × 6 cm), with a plastic thread run through the membrane for easier recovery in the field, and membranes were stored until use in 2M NaCl in 0.1M HCl. In the field (23.6.1999 and 21.7.2000, respectively), a pair of membranes was inserted into a c. 5 cm deep slit in the soil cut with a knife at an angle of 45° to the surface. The slit was closed again, and membranes stayed in place until recovery (28.8.1999 and 1.8.2000, respectively). To assess differences between species stands, pairs of membranes were placed in stands of both *Salix* and *Luzula*. At recovery, the membranes were separately transferred into small tubes filled with distilled water. The tubes were stored cool until further processing in the lab. There, ions were extracted from individual membranes with 20 ml 2 M NaCl in 0.1 M HCl by shaking for two hours. Samples were then analysed with a FIA-Star autoanalyser (FIA, Norway) for NH<sub>4</sub><sup>+</sup>- and NO<sub>3</sub><sup>-</sup>-nitrogen. For the analysis of NO<sub>3</sub><sup>-</sup>-nitrogen it was necessary to neutralise the HCl of the sample by adding equivalent amounts of NaOH to the carrier solution. Without an extensive test series under field conditions it is not possible to translate the N-concentrations on the membrane into actual nitrogen availability to the plants, but this still provides a valid integrative measure of the relative availability of nitrogen in the different stands and treatments (Weih 1998).

### Growth measurements

Within each greenhouse and control plot three randomly chosen individuals of each species were marked in both pure and mixed stands. In the first treatment year the responses of *Luzula* and *Salix* plants were assessed by measurement of the length of each leaf and branch, respectively, of marked individuals at the beginning (16.6.1999) and at the end (29.8.1999) of the growing season. Plants sampled from the plots at the beginning and end of the experiment were measured (leaf and branch length), dried for 7 days at c. 45 °C and weighed. These data allowed transformation of the length measurements taken within the experiment into above-ground biomass. In the second treatment year, too few of the tags from 1999 were re-discovered to enable repeat

length measurements. Thus on 1-3 August 2000 the experiment was terminated by destructive above-ground biomass harvest of five plants of each species from both pure and mixed stands within each plot. *Luzula* was sorted into dead and live leaves, *Salix* into live leaves and stem, and material (except *Salix* stems) was dried for 7 days at c. 45°C and weighed. *Salix* stems were frozen and transported back to the laboratory where the part of the stem grown during the last two years was severed with a razor blade, dried and weighed. Additionally, a patch of pure stand of each species (10 cm × 10 cm) was harvested destructively to enable extrapolation from individual shoots to the whole stand. The number of ramets/shoots in that square was counted. Plant cover for *Luzula*, *Salix*, other vascular plants, mosses and lichens was estimated by eye for each plot. Cover estimates and biomass data from the 10 cm × 10 cm samples were used to calculate the average biomass of *Luzula* and *Salix* per m<sup>2</sup> for this vegetation type.

### Statistical analysis

For the growth analysis (1999) and the final harvest (2000), replicate plants were averaged for each stand type (pure, mixed) within each plot. Years were analysed separately because different measurement methods were used, hence any between year difference would be confounded with growth assessment method. The model structure accounted for the nesting of stand types within warming treatments and for blocking. Data were log<sub>10</sub>-transformed to successfully meet assumptions of ANOVA and analysed employing the MIXED procedure of SAS (SAS Institute Inc. 1989). Initial biomass was used as a covariate. Error bars depict standard error of the mean for untransformed data.

## 2. Phytotron experiment

### Experimental set-up

*Salix polaris* and *Luzula confusa* were collected at the site of the field experiment (2-3 September 1999) as cuttings and whole plants, respectively, and kept wrapped in wet tissue paper in plastic bags in a refrigerator unit during transport back to the laboratory. There, all plants were kept in a freezer at -7°C for 8 weeks to simulate winter situations, after which they were transplanted into plastic pots (Ø 7.5 cm, height 7.5 cm) filled with a 90:10 v/v mixture of sand and peat, placed on individual

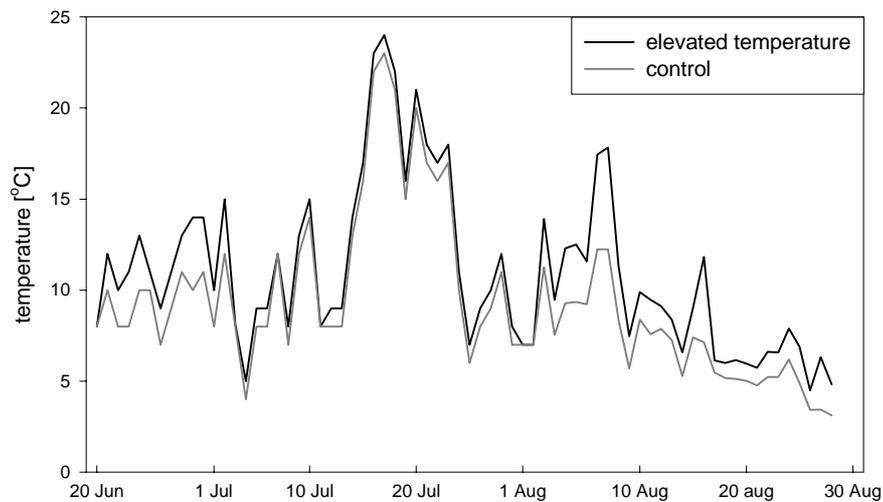
saucers. The competition treatment was realised by transplanting four individuals into each pot, two of each species, while the competition-free pots contained four plants of the same species (substitutive design, Gibson *et al.* 1999). During the four week initial phase of the experiment, all pots were kept at 12°C and received weekly addition of 1/100<sup>th</sup> Hoagland solution (Hendry & Grime 1993) to enhance establishment of the transplants. On 2-4 December 1999 dead plants (24%) were replaced and the experimental treatments were started.

The three competition treatments (*Luzula* monoculture, *Salix* monoculture and *Luzula/Salix* mixture) were maintained at two temperatures (7.5 and 13.5°C) and two levels of nutrient availability (1/10<sup>th</sup> Hoagland solution (high nutrients) and 1/100<sup>th</sup> Hoagland solution (low nutrients)). Throughout the experiment pots were watered three times a week by addition of distilled water to the saucers. Nutrient treatments were applied once a week with the distilled water (65 ml per pot).

Ten replicates of each competition x nutrient treatment combination (3 species mixtures × 2 nutrient levels) were placed in two phytotrons (Sanyo, USA), one at each temperature. Pots were arranged in a block design and, to reduce within- and between-chamber effects, pots were shuffled within each chamber weekly, and plants and temperature regimes were swapped between chambers every other week. Relative humidity was maintained at  $67 \pm 2$  % (S.D.) and photosynthetic active radiation at the level of the leaves was  $370 \mu\text{molphoton}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Data loggers (RS logger #13467, Radio Supply, UK; with internal sensor, wrapped in tin foil to eliminate direct warming by the lights, recording at half-hourly intervals; resolution  $\pm 0.5^\circ\text{C}$ ) placed at the level of the pots indicated that the temperatures achieved were  $7.5 \pm 2.19^\circ\text{C}$  (S.D.) for the cold and  $13.5 \pm 1.7^\circ\text{C}$  for the warm treatments. Thus, the realised temperature difference between treatments was 6°C.

Soil moisture in the pots was measured gravimetrically on an additional set of pots without plants. It decreased between watering events from c. 21 to 13% soil dry weight, which was due to the high evaporation of water caused by the high-light environment. The differences in soil moisture between temperature treatments, however, were marginal compared to the fluctuations within the temperature treatments (soil moisture of pots before/after watering: warm =  $21.5 \pm 0.3\%$  /  $5.8 \pm 0.7\%$  soil dry weight; cold =  $19.2 \pm 0.1\%$  /  $3.3 \pm 0.4\%$ ).

The phytotron experiment was harvested after three months (1-5.3.2000). The soil was carefully transferred into a set of sieves (1 mm and 0.5 mm mesh size) and

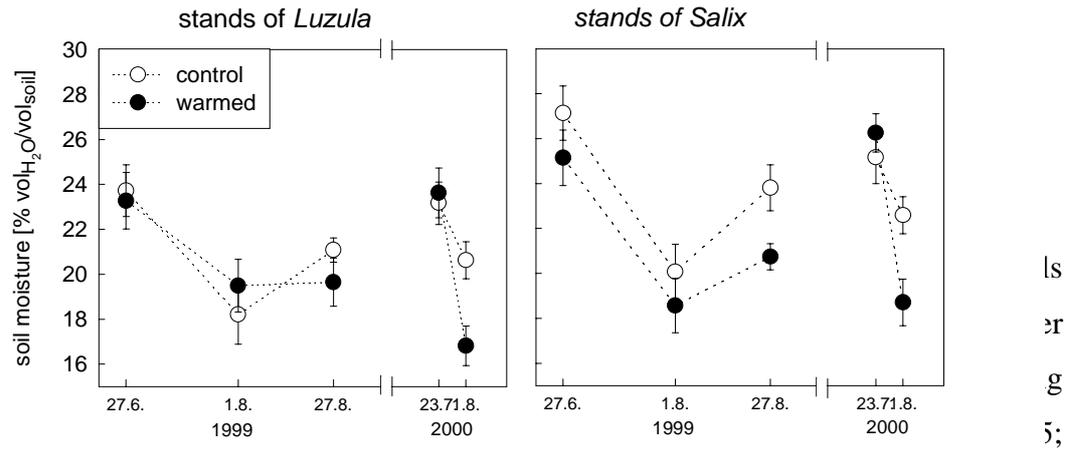


**Fig. 1** Field experiment: Temperature during the experimental period of 1999 in the greenhouses (black line) compared to ambient (grey line). Lines are smoothed from 24 hour averages based on hourly readings ( $N = 3$ ).

rinsed until roots disentangled. *Luzula* plants were divided into roots, rhizome, shoot bases, and live leaves, while dead leaves were discarded. *Salix* plants were divided into roots, stem and leaves only, keeping the occasional inflorescences separate as well. All plant parts were washed, bagged, dried at 70 °C for 48 hours, and weighed to the nearest 0.01 mg.

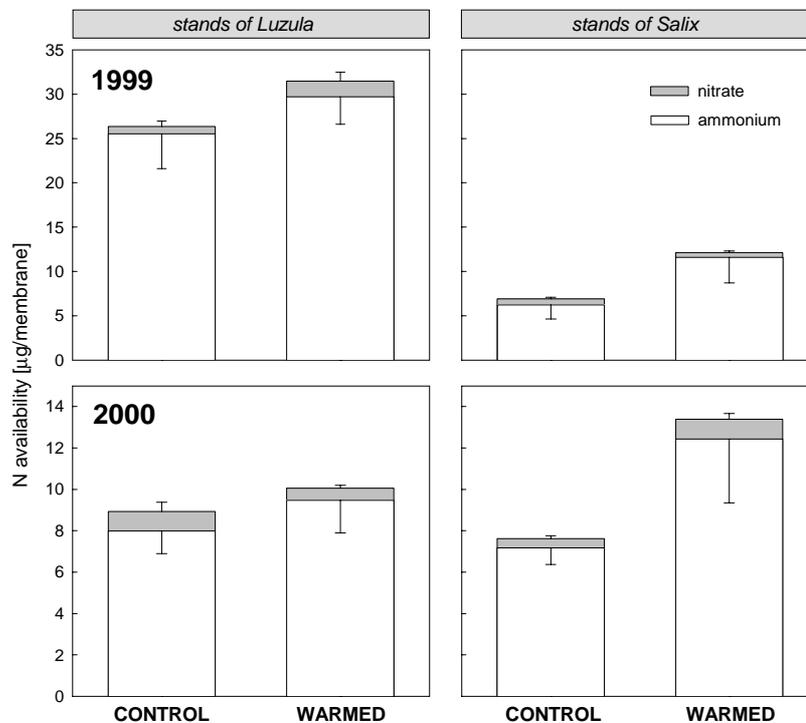
### Statistical analysis

Logistic regression showed that plant mortality was not significantly ( $P > 0.05$ ) related to any of the experimental factors, and we thus assumed no distortion of plant biomass data by mortality. For the statistical analysis, data for average dry weight of a species per pot were  $\log_{10}$ -transformed to meet assumptions of General Linear Models (homoscedasticity and normal distribution of residuals). The models contained a block factor as random effect, temperature, competition and fertilisation as fixed effects, and the interactions between the fixed effects. The full model was tested and then stepwise simplified with a threshold level of  $P < 0.1$  (Crawley 1993).

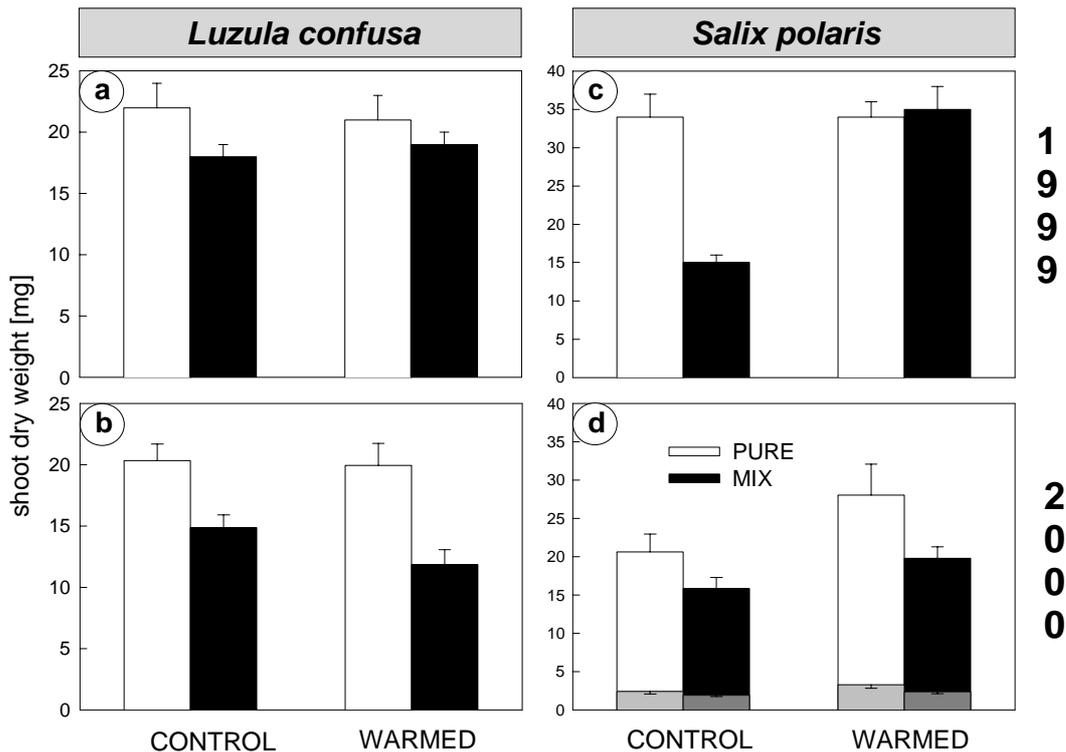


**Fig. 2** Field experiment: Soil moisture in the pure stands of *Luzula* (left) and *Salix* (right) and temperature conditions of the experiment (N = 15). Filled symbols represent elevated temperature treatment, open symbols controls.

water content between stands of *Luzula* and *Salix* ( $P > 0.1$ ), but dramatic changes between sampling dates (Fig. 2;  $F_{4, 112} = 16.80$ ,  $P < 0.0001$ ).



**Fig. 3** Field experiment: Cumulative nitrogen availability in the pure stands of *Luzula* (left) and *Salix* (right) and temperature conditions (N = 15). Error bars are  $-1SE$  for ammonium (white) and  $+1SE$  for nitrate (grey).



**Fig. 4** Field experiment: Current years above-ground growth per shoot of *Luzula confusa* (a, b) and *Salix polaris* (c, d) in pure (white) and mixed stands (black), after one (a, c) and two (b, d) season of elevated temperature, compared to controls (N = 15). Shading indicates biomass of stems. Error bars represent +1 SE.

In 1999, ion exchange membranes were in the soil for three months, while in 2000 they were employed for three weeks during the warmest period of the summer only. Accordingly total nitrogen absorbed on the membranes differed by a factor of three between the years in *Luzula* stands (Fig. 3).  $\text{NO}_3^-$ -nitrogen comprised less than 1% of the total N, and did not differ between stands (or treatments) in either year ( $P > 0.35$  in all cases). Effects of stand and treatment on absorbed nitrogen were consistent in both years, as there were no significant interactions of year with either factor ( $P > 0.2$ ).

Nitrogen availability differed greatly between stands and treatments. At ambient temperature in 1999, ion exchange membranes in *Luzula* stands contained more than four times the amount of  $\text{NH}_4^+$  than those in *Salix* stands (Fig. 3;  $F_{1,32} = 48.57$   $P < 0.0001$ ). In 2000 there was no such discrepancy ( $F_{1,32} = 0.05$ ,  $P = 0.819$ ), suggesting that the greater amounts of  $\text{NH}_4^+$  in the *Luzula* stands are available earlier and/or later in the season, when membranes were not in place in 2000. Warming increased the availability of  $\text{NH}_4^+$  (Fig. 3), but nitrogen availability in the soil was too

**Table 1** Field experiment: Statistical analysis of effects of temperature (ambient vs. elevated) and stand type (pure vs. mixed) on biomass of *Luzula confusa* and *Salix polaris*.

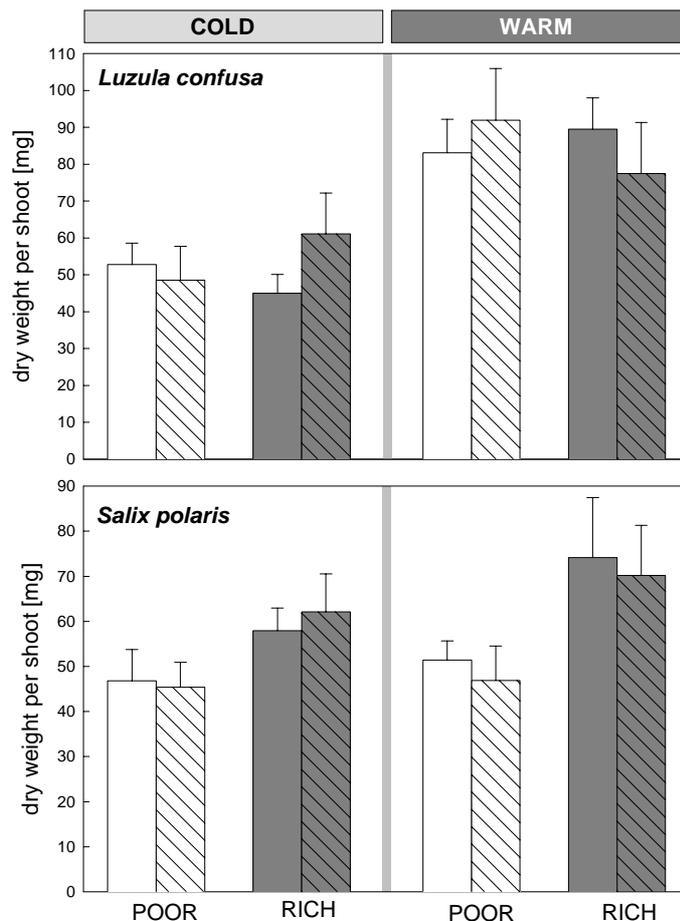
	source	<i>Luzula confusa</i>			<i>Salix polaris</i>		
		ddf/ndf	F	P	ddf/ndf	F	P
1	initial length	1/28	93.89	0.0001	1/27	66.47	0.0001
9	temperature	1/14	2.64	0.1265	1/14	54.19	0.0001
9	stand type	1/28	2.83	0.1037	1/27	30.89	0.0001
	interaction	--	--	--	1/27	21.01	0.0001
2	temperature	1/14	4.39	0.0547	1/14	5.99	0.0282
0	stand type	1/28	56.17	0.0001	1/29	9.99	0.0037
0	interaction	1/28	3.78	0.0619	--	--	--

heterogeneous to yield a significant difference between treatments ( $F_{1, 14} = 2.09$  and  $2.42$ ,  $P = 0.167$  and  $0.142$  for 1999 and 2000, respectively). Relative effects of warming on nitrogen availability to plants were, however, much more pronounced in the *Salix* stands (+ 86% and + 34% for 1999 and 2000, respectively) than in those of *Luzula* (+ 16% and + 19%; Fig. 3).

### Treatment effects on plant growth

In 1999, shoot growth of *Luzula confusa* was only marginally less in mixed than in pure stands, and showed no detectable response to elevated temperature (Fig. 4a, Table 1). In contrast, the next year *Luzula* shoot biomass was significantly reduced in mixed stands, and there was a tendency for this to be more pronounced in warmed plots (Fig. 4b, Table 1).

Above-ground biomass of *Salix polaris* at ambient temperature was strongly reduced in the presence of *Luzula confusa* in 1999. However, under elevated temperature, this difference completely disappeared, suggesting a release from competition (Fig 4c, Table 1). The following year *Salix* biomass was again lower in mixed stands, this time irrespective of temperature (Fig. 4d, Table 1). There was also a positive response to warming which tended to be greater in pure stands (+ c. 40%) than in mixed (+ c. 25%) . Overall, temperature effects were slightly stronger than competition effects (Table 1).



**Fig. 5** Phytotron experiment: Total dry weight of *Luzula* and *Salix* plants under cold and warm conditions. “Poor” and “rich” under the graph refer to nutrient availability. Hatched bars represent data from plants growing under competition. Error bars depict +1 standard error of the mean.

### Relative contributions to vascular biomass

Warming did not affect the numbers of plant shoots per 100 cm<sup>2</sup> (*Luzula*: control 42 ± 4.7, warmed 42 ± 2.6; *Salix*: control 48 ± 4.9, warmed 50 ± 4.0). Total above-ground biomass of vascular plants (i.e. essentially *Luzula* and *Salix*, as other species were only represented at very low biomass) increased due to warming from 421 ± 52 g m<sup>-2</sup> to 482 ± 58 g m<sup>-2</sup>. The percentage contribution of *Luzula* decreased from 36 ± 6% to 28 ± 3%, while that of *Salix* increased accordingly from 64 ± 6% to 72 ± 3%.

**Table 3** Phytotron experiment: Statistical results (F-values) for effect of treatments on total biomass and biomass allocation to plant parts for *Luzula* and *Salix* (Table 2). Flowering occurred too rarely to allow analysis. N = 74 and 80 for *Luzula* and *Salix*, respectively. †, \*, \*\* and \*\*\* refer to  $P < 0.1$ ,  $< 0.05$ ,  $< 0.01$  and  $< 0.001$ , respectively, while <sup>ns</sup> indicates non significant effects. × indicates interactions of t (temperature), f (fertilisation) and/or c (competition). -- indicates factors not included in the statistical model.

	temperature		fertilisation		others
	<i>Luzula</i>	<i>Salix</i>	<i>Luzula</i>	<i>Salix</i>	<i>Salix</i>
total	39.64***	1.19 <sup>ns</sup>	0.70 <sup>ns</sup>	10.24**	
leaves	47.65***	0.01 <sup>ns</sup>	1.64 <sup>ns</sup>	3.39 †	t×c*; t×f×c*
shoot base	12.70***	--	2.15 <sup>ns</sup>	--	
rhizome/stem	12.70***	0.43 <sup>ns</sup>	0.01 <sup>ns</sup>	5.76 *	
roots	42.31***	24.49***	1.16 <sup>ns</sup>	9.14**	competition†

### Phytotron experiment

The two species differed strikingly in their response to experimental treatments: total biomass of *Luzula* was affected only by temperature, while that of *Salix* responded only to fertilisation (Fig. 5, Table 2). Temperature significantly increased the growth of leaves, shoot bases, rhizomes and roots of *Luzula*, but only enhanced root growth of *Salix* (Tables 2 and 3). Fertilisation, on the other hand, had no significant effect on any parameter measured in *Luzula*, while it significantly increased the weight of stems and roots in *Salix*.

Competition had very little effect on either species, the only main effect being a marginally significant reduction in *Salix* root biomass (Table 3). *Salix* leaves showed complex treatment responses. There were no effects of warming or competition in low nutrient conditions. However with high nutrient supply, leaves at low temperature grew better in mixed stands, while leaves at high temperature grew better in pure stands (significant competition × fertilisation × temperature interaction: Table 3).

**Table 2** Phytotron experiment: Average dry weight of the different plant parts according to treatment  $\pm$  1 SE for *Luzula confusa* and *Salix polaris*. Flowers occurred at maximum once per treatment combination, thus no errors are given.

temperature	COLD				WARM			
	POOR		RICH		POOR		RICH	
	pure	mixed	pure	mixed	pure	mixed	pure	mixed
<i>Luzula confusa</i>								
flowers	0	0	0.85	0	0	0	1.5	0
leaves	7.8 $\pm$ 1.11	6.5 $\pm$ 1.13	7.2 $\pm$ 0.66	9.1 $\pm$ 1.41	13.7 $\pm$ 1.97	15.1 $\pm$ 2.64	16.3 $\pm$ 1.61	10.0 $\pm$ 2.01
shoot bases	1.4 $\pm$ 0.14	1.8 $\pm$ 0.28	1.6 $\pm$ 0.19	1.9 $\pm$ 0.36	2.07 $\pm$ 0.23	1.9 $\pm$ 0.26	2.2 $\pm$ 0.17	3.3 $\pm$ 0.46
rhizome	21.9 $\pm$ 2.76	22.6 $\pm$ 4.44	16.3 $\pm$ 2.76	26.1 $\pm$ 5.08	28.9 $\pm$ 3.46	28.6 $\pm$ 4.42	26.8 $\pm$ 2.74	35.9 $\pm$ 4.71
roots	21.6 $\pm$ 3.04	17.6 $\pm$ 3.83	19.1 $\pm$ 2.04	24 $\pm$ 5.53	38.4 $\pm$ 4.16	46.2 $\pm$ 7.62	42.7 $\pm$ 5.08	33.1 $\pm$ 9.98
<i>Salix polaris</i>								
flowers	0.3	0.13	0	1.5	0	0.52	1.1	0.94
leaves	3.9 $\pm$ 0.54	3.9 $\pm$ 0.58	3.6 $\pm$ 0.36	7.6 $\pm$ 2.2	4.0 $\pm$ 0.64	3.8 $\pm$ 0.91	8.3 $\pm$ 1.77	3.8 $\pm$ 0.87
stem	36.4 $\pm$ 6.00	36.8 $\pm$ 4.47	46.4 $\pm$ 4.47	41.2 $\pm$ 5.87	33.6 $\pm$ 2.72	32.0 $\pm$ 6.83	39.0 $\pm$ 6.06	53.0 $\pm$ 9.94
roots	6.3 $\pm$ 1.14	5.0 $\pm$ 1.3	8.0 $\pm$ 0.88	11.8 $\pm$ 3.28	13.8 $\pm$ 1.97	10.6 $\pm$ 1.37	25.7 $\pm$ 5.34	12.5 $\pm$ 2.71

## DISCUSSION

### **Does competition occur between dominant species of High Arctic tundra?**

Our data show reduced performance of both *Salix polaris* and *Luzula confusa* in the presence of the other species. Competition between the two species is thus clearly detectable, and is of relatively high intensity, reducing shoot biomass of both *Salix* and *Luzula* by c. 25% (at ambient temperature, averaged across years). This demonstrates that the harsh environment does not preclude the occurrence of interspecific competition, as also suggested by Oksanen (1990) and Theodose & Bowman (1997). In the phytotron experiment such competitive interactions were not observed, most likely due to the planting density being rather low.

Few other arctic field experiments have shown evidence for competition, but they are exceptions. Reducing competition by clipping neighbours increased bulb and root mass of *Triglochin palustris* (Mulder & Ruess 1998), hinting at competitive suppression of growth in this sub-arctic salt marsh. Also, in a transplantation experiment of boreal trees into tundra habitats two species (*Betula papyrifera* and *Picea glauca*) had significantly greater growth in the reduced competition treatment (Hobbie & Chapin 1998a). However, the majority of arctic studies that employ the classical neighbour removal approach (Aarssen & Epp 1990) have failed to detect competition consistently. Jonasson (1992) found no significant increase in any species following the removal of the dominant species in three vegetation types, suggesting that "... competition from them was not a major limiting factor to the growth of co-occurring species" (p. 420). Similarly, in the Alaskan Arctic, no vascular species (except *Ledum palustre*, which is particularly sensitive to light competition) increased aboveground biomass in response to removal of any of four dominant species (Hobbie *et al.* 1999). In the Scandinavian Sub-Arctic *Empetrum nigrum* did respond positively to removal of *Vaccinium vitis-idaea*, but *Vaccinium* suffered from the removal of *Empetrum* (Shevtsova *et al.* 1997). It was suggested that *Vaccinium* dominated the competition for light, but *Empetrum* created a moister and warmer microclimate, favouring *Vaccinium*. The communities in these three studies were more species-rich than our *Luzula-Salix* heath, which may cause competition to be diffuse, rather than species specific (Hobbie *et al.* 1999). However, in a sub-arctic

dune system of comparable structural simplicity to our heath, removal of the nitrogen-fixing Fabaceae *Lathyrus japonicus* resulted in no change in the biomass of the grass *Elymus mollis*, and vice versa (Houle 1998).

Following the argument of Brooker & Callaghan (1998) this apparent lack of positive responses to species removal may be due to the balance between facilitation and competition which occurs in extreme environments. Removal of neighbours also removes physical shelter, which is regarded as being very important in the Arctic (Carlsson & Callaghan 1991). However, our comparison of growth of species in pure and mixed stands supports the notion of Theodose & Bowman (1997) that "... competition can be an important force structuring plant communities in an extreme environment." (p. 109). As long as a certain level of protection is provided by neighbours, whether they be conspecifics or other species, competition for resources also operates. Decreased protection (as in a removal experiment) may reduce the performance of a plant such that it is unable to respond positively to resources made available by the removal of its neighbour. Further experiments on competition in the Arctic should take this into account, and develop approaches that allow comparison of different neighbour densities without alteration of the level of physical protection.

It should be noted that the site of our investigation is intensively grazed by reindeer, which were excluded from the experiment. It is unclear, how far grazing would alter the observed competitive (and facilitative) interactions between *Luzula* and *Salix*. Work by Mulder & Ruess (1998) in a low-arctic salt marsh indicates that the subdominant species might profit from the grazing of its neighbours, but, if the herbivore is positively selecting it, competitive effects would be enhanced (see also Huisman *et al.* 1999). Both *Luzula* and *Salix* are extensively grazed over winter and early spring, after which the use of *Luzula* rapidly drops over the course of the growing season, but *Salix* remains an important food item throughout the summer (Van der Wal *et al.* 2000c). Thus, the losses due to grazing are likely to be far greater for *Salix*, and it has been shown to suffer 40% reduction in leaf biomass in response grazing in the previous year (Skarpe & Van der Wal 2001). In contrast, simulated winter grazing of *Luzula* did not influence its performance during the growing season (R. van der Wal, unpublished data). Thus grazing might be expected to shift the competitive balance observed in this study observed in favour of *Luzula*.

## How does warming affect the interaction between the two species?

Elevated temperature in the field had a dual effect on the microsite conditions, increasing both air temperature and soil nitrogen availability. In the phytotron experiment the plants demonstrated strong, species specific responses to both these factors, with *Luzula* profiting from higher temperatures, and *Salix* from increased nutrient availability. The individualistic nature of plant species' responses to environmental manipulations is a recurrent theme in global change ecology (Chapin & Shaver 1985; Press *et al.* 1998; Dormann & Woodin 2001), which makes it difficult to distil generalisations.

The responses of *Luzula* and *Salix* in the field differed from those expected on the basis of the results of the phytotron experiment. Predictions were of an increase in biomass for both species, *Luzula* profiting from warming, and *Salix* from the accompanying higher nutrient availability. However, only *Salix* significantly increased in biomass. A similar discrepancy was observed by McGraw & Chapin (1989), when, in the laboratory, two *Eriophorum* species responded similarly to nutrient enrichment, whilst in the field the species adapted to the respective site outcompeted the other. It is difficult to explain the complete lack of response of *Luzula* to warming in the field. The temperature difference between treatments in the field was less than half of that in the phytotrons, and thus possibly not sufficient to produce analogous effects. However, a trend in the same direction might have been expected, while in fact the opposite was observed. Another possibility is that *Salix* suppresses the response of *Luzula* to warming. There is some evidence that the reduced growth of *Luzula* in mixed stands, seen in the second year of the experiment, is greater at elevated temperature. This possibly results from the warming-induced stimulation of *Salix* in the mixed stands the previous year. However, competition cannot explain the lack of response of *Luzula* in pure stands to warming, and the conclusion must be that some factor other than temperature is limiting to the shoot growth of *Luzula* in the field.

*Salix polaris* clearly gains the most benefit from elevated temperature in the field, probably through the increase in nutrient availability in warmed soil. *Salix* is also apparently able to suppress the growth of its competitor. Thus continued stimulation of the growth of individual *Salix* shoots by increased temperature would cause an eventual decline of *Luzula*, which may be accelerated if branching of *Salix* shoots also increases. Grazing could prevent *Salix* from outcompeting *Luzula* in warmer climate, and be responsible for persistent co-dominance of the two species in this high-Arctic system.

However, the take-over of arctic vegetation by shrubs and eventually trees fits the predictions derived from climate warming models (Emanuel *et al.* 1985; Starfield & Chapin 1996; Epstein *et al.* 2000) as well as long-term experimental evidence (Chapin *et al.* 1995b; Shaver & Chapin 1995; Press *et al.* 1998).

### **What resources are *Salix* and *Luzula* competing for?**

We cannot provide a clear answer to this question. Light competition is unlikely, because the density of vegetation is very low, and the occurrence of shading is presumably scant. In dense stands of *Luzula* the removal of dead *Luzula* leaves increased light availability at ground level from  $64 \pm 2\%$  of incident PAR to  $85 \pm 1\%$ , a 25% relative increase (data not shown). However, a light availability of 64% is still very high and in a field shading experiment a light availability of only 47% did not significantly affect growth of either species over a two year period (CHAPTER 8).

It has been frequently shown that Arctic plants are nutrient rather than temperature limited (Chapin & Shaver 1985; Shaver *et al.* 1986; Wookey *et al.* 1994; Chapin *et al.* 1995b; Wookey *et al.* 1995; Chapin & Shaver 1996; Shaver *et al.* 1998; Jonasson *et al.* 1999; but see Parsons *et al.* 1994; Michelsen *et al.* 1996a; Graglia *et al.* 1997). It is thus likely that competition among plants would be for soil nutrients, most likely nitrogen and/or phosphorus. In this study nitrogen availability was increased considerably by elevated temperature (Fig. 3). In the phytotron experiment only *Salix* responded to nutrients. The increased growth of *Salix* in the field could be simply a warming-induced fertilisation effect, from which *Luzula* does not benefit. This would explain the better performance of *Salix* than *Luzula* in response to warming.

As nutrient availability is higher in stands of *Luzula*, why then is *Salix* biomass in control plots lower there? Possibly *Luzula* preempts nutrients from *Salix* (mixed controls in Fig. 4d), but is unable to transform this into growth, due to other limitations. Alternatively, one could speculate that *Salix* is more flexible in its response, while *Luzula* follows a conservative growth pattern. In the longer term *Salix* would thus be favoured, as it could make use of nutrient flushes within that season, thereby outgrowing *Luzula* (see data on biomass in pure stands).

In the face of climatic change, confirmation both of the mechanisms behind, and the trajectory of changes within, the competitive balance of plant communities are urgently needed. Controlled environment growth experiments may not provide reliable predictors of plant interactions in the field. Further field research of plant competition in

harsh environments should embrace different approaches to avoid the pitfalls of a facilitation-competition trade-off situation, as negative interactions are important even in one of the most extreme environments, and may dictate vegetation response to climate change.

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