# Neighbour identity modifies effects of elevated temperature on plant performance in the High Arctic

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### Abstract

**Competition among plants in extreme environments such as the High Arctic has often been described as unimportant, or even nonexistent; environmental factors are thought to overrule any negative plant–plant interactions. However, few studies have actually addressed this question experimentally in the Arctic, and those that did found only little evidence for competition. Such species interactions will presumably become more important in the future, as Global Climate Change takes effect on terrestrial ecosystems. We investigated plant–plant interactions in the High Arctic, following the growth of _Luzula confusa_ and _Salix polaris_ in pure and mixed stands, and under elevated-temperature treatment over 2 years. To understand the mechanisms of competition, a parallel experiment was undertaken in phytotrons, manipulating competition, temperature and nutrient availability. Our findings indicate that competition is acting in the natural vegetation, and that climatic warming will alter the balance of interactions in favour of the dwarf shrub _S. polaris_. The phytotron experiment suggested that the mechanism is a higher responsiveness of _Salix_ to nutrient availability, which increased under warming in the field. While _Luzula_ showed a positive response to higher temperature in the lab, its performance in mixed stands in the field was actually reduced by warming, indicating a competitive repression of growth by _Salix_. The growth of _Salix_ was also reduced by the presence of _Luzula_, but it was still able to profit from warming. Our findings suggest that climatic warming will result in greater shrub dominance of High Arctic tundra, but we also conjecture that grazing could reverse the situation to a graminoid-dominated tundra. These two divergent scenarios would have different implications for ecosystem feedbacks to climatic change.**

_Keywords:_ competition, _Luzula confusa_, nutrient availability, _Salix polaris_, warming

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## 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

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change (for a review see Dormann & Woodin, 2002). Long-term field experiments on the effects of elevated summer temperature (Chapin _et al._, 1995) and the indirect consequences of warming (e.g. higher soil mineralization rates and thus increased nutrient availability, Nadelhoffer _et al._, 1991) have demonstrated major changes in plant species composition (Chapin & Körner, 1995; Chapin _et al._, 1995; Press _et al._, 1998; Shaver _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, 2002), 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 Dormann & Brooker, 2002). 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.

The importance of neighbour identity for species responses to environmental change has received very little attention. 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 (Dormann & Brooker, 2002).

This study investigates specifically the question of whether and how warming acts differentially in single and mixed species stands on the growth of the target species. 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 with pure stands, is taken to indicate the occurrence of interspecific 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

*Target species.* Luzula confusa (Hartm.) Lindeb. (Northern Woodrush, syn.: *L. arcuata* subsp. *confusa*), Juncaceae, on Svalbard is a widespread and common species of dry sites, particularly in the inner fjord areas. It grows in loose tufts, where most biomass is previous year's standing dead leaves. It spreads by clonal growth as well as by seeds (Rønning, 1996).

*Salix polaris* Wahlenb. (Polar Willow), Salicaceae, is another common and widespread species on Svalbard. It is a small, prostrate deciduous shrub, with creeping stems in the moss and substrate layer. Due to extensive clonal growth, its roots, rhizomes and stems form a web in the upper soil, from where branches extend above ground. Leaves are virtually only found on current year's growth and at peak biomass above ground contributes the majority to *Salix*'s standing above ground biomass.

### Field experiment

*Experimental set-up.* The study was carried out in Semmeldalen (77.90°N 15.20°E), a valley ca. 20 km south of Longyearbyen, Svalbard. Fifteen pairs of similar plots (60 cm diameter), each of which comprised a dense stand of *Luzula* and a dense stand of *S. polaris*, were selected in a representative patch of *S. polaris*-heath (Rønning, 1996). *Salix* and *Luzula* were the dominating vascular plants in the plots (with $31 \pm 3.5\%$ and $25 \pm 2.6\%$ cover, respectively), with a high cover of bryophytes and crust lichens ($35 \pm 3.3\%$ and $9 \pm 1.8\%$). Both species, however, also occurred in stands of the other species (referred to as 'mixed' as opposed to 'pure' position). Measurements of soil water content, soil depth, soil layering, nutrient availability and species composition made during the experiment indicated that the spatial distribution of these two stand types is apparently random and not caused by microsite differences (data not shown). The experiment consisted of warmed plots and controls, randomly assigned to the paired plots. The whole area of ca. $100 \text{ m} \times 20 \text{ m}$ 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 10 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 integators fitted with a photosynthetically active radiation (PAR) quantum sensor, $\Delta$T, Cambridge, UK) was reduced by $11 \pm 3\%$. This is very little, compared with the ca. 50% (1100 vs. 500 $\mu$mol m$^{-2}$ s$^{-1}$) difference between sunny and overcast sky, and slightly less than the reductions induced by greenhouses of other designs (Chapin et al., 1995; 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 belowground senescence, increasing mineralization 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, UK). Values obtained were transformed into soil water content using a previously established relationship (Rob Rose, CEH Wallingford, UK, 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 551652U and 551642S respectively (VWR International, Poole, UK) were cut into pieces (1 cm × 6 cm) with a plastic thread run through the membrane for easier recovery in the field, and membranes were stored until use in 2 M NaCl in 0.1 M HCl. In the field (23.6.1999 and 21.7.2000, respectively), a pair of membranes was inserted into a ca. 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 2 h. Samples were then analysed with a FIA-Star autoanalyser (Foss Tecator, Hoganas, Sweden) for $NH_4^+$- and $NO_3^-$-nitrogen. For the analysis of $NO_3^-$-nitrogen it was necessary to neutralize 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 the two species were marked in both pure and mixed positions. 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 ca. 45 °C and weighed. These data allowed transformation of the length measurements taken within the experiment into aboveground biomass. In the second treatment year, too few of the tags from 1999 were rediscovered to enable repeat length measurements. Thus on 1–3.7.2000, the experiment was terminated by destructive aboveground biomass harvest of five plants of each species from both pure and mixed positions within each plot. Luzula was sorted into dead and live leaves, Salix into live leaves and stem, and the material (except Salix stems) was dried and weighed. Salix stems were frozen and transported back to the laboratory where the part of the stem grown during the last 2 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 or shoots protruding through the bryophyte cover in that square was counted. Plant cover for *Luzula*, *Salix*, other vascular plants, bryophytes 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 m² for this vegetation type.

*Statistical analysis.* For the growth analysis (1999) and the final harvest (2000), replicate plants were averaged for each position (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$_{10}$ 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. Arcsin-square-root-transformed soil moisture data were analysed as a repeated measurements ANOVA. Untransformed N data were analysed by ANOVA for each year separately.

### Phytotron experiment

*Experimental set-up.* *S. polaris* and *L. confusa* were collected near the site of the field experiment (2–3.9.1999) as cuttings of approximately 12 cm length and whole plantlets, respectively. By collecting all specimen of each species from close to each other, we tried to minimize the variability between samples (possibly all ramets of the same genet). They were 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 conditions, after which they were transplanted into plastic pots (∅ 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 realized by transplanting four individuals into each pot, two of each species in alternating positions, while the competition-free pots contained four plants of the same species (substitutive design, Gibson *et al.*, 1999). This planting density is about half that occurring naturally in the field. During the 4-week initial phase of the experiment, all pots were kept at 12 °C and received weekly addition of 1/100th Hoagland solution (Hendry & Grime, 1993) to enhance establishment of

the transplants. On 2–4.12.1999 dead plants (24%) were replaced by spare plants that had been grown in additional pots under the same conditions, 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 (1/10th Hoagland solution (high nutrients) and 1/100th Hoagland solution (low nutrients)). Throughout the experiment, pots were watered three times a week by adding 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 × nutrient treatment combination (3 species mixtures × 2 nutrient levels) were placed in two phytotrons (Sanyo, Bensenville, IL, 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. Plants were provided with 24 h of daylight. Relative humidity was maintained at 67 ± 2% (SD) and photosynthetic active radiation at the level of the leaves was 370 µmol photon m$^{-2}$ s$^{-1}$. Data loggers (RS logger #13467, RS supplies, Corby, UK; with internal sensor, wrapped in tin foil to eliminate direct warming by the lights, recording at half-hourly intervals; resolution ± 0.5 °C) placed at the level of the pots indicated that the temperatures achieved were 7.5 ± 2.19 °C (SD) for the cold and 13.5 ± 1.7 °C for the warm treatments. Thus, the realized 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 over the course of 3 days after watering from ca. 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 with the fluctuations within the temperature treatments (soil moisture of pots before/after watering: warm = 21.5 ± 0.3%/5.8 ± 0.7% soil dry weight; cold = 19.2 ± 0.1%/3.3 ± 0.4%).

The phytotron experiment was harvested after 3 months (1–5.3.2000). The soil was carefully transferred into a set of sieves (1 and 0.5 mm mesh size) and 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 h 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 fertilization 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).

## Results

### Field experiment

*Impact of treatments on the environment.* The air temperature in the greenhouses was on average 2.3 °C warmer than in controls (11.8 vs. 9.5 °C; $F_{1,3288} = 103.2$, $P < 0.0001$), and paralleled that of controls over the entire period (Fig. 1). Warmed plots did not show amplified differences during mid-day temperature peaks, an undesirable effect strongly criticized (Kennedy, 1995; Marion *et al.*, 1997).

Experimental warming did not influence soil water content consistently ($F = 1.00$, $P = 0.334$), but only on some of the sampling dates (Fig. 2; temp × time interaction: $F_{4,112} = 2.94$, $P < 0.05$). There was also no consistent difference in soil water content between stands of *Luzula* and *Salix* ($P > 0.1$), but dramatic
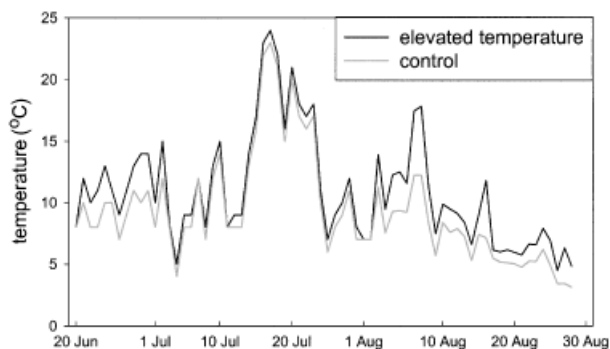
changes between sampling dates (Fig. 2; $F_{4,112} = 16.80$, $P < 0.0001$).

In 1999, ion exchange membranes were in the soil for 3 months, while in 2000 they were employed for 2 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). $NO_3^-$-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 $NH_4^+$ than those in *Salix*
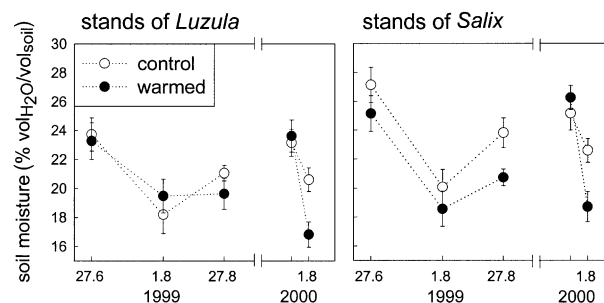
**Fig. 2** Field experiment: soil moisture in the pure stands of *Luzula* (left) and *Salix* (right) and temperature conditions of the experiment ($n = 15$). Filled symbols represent elevated temperature treatment, open symbols controls.
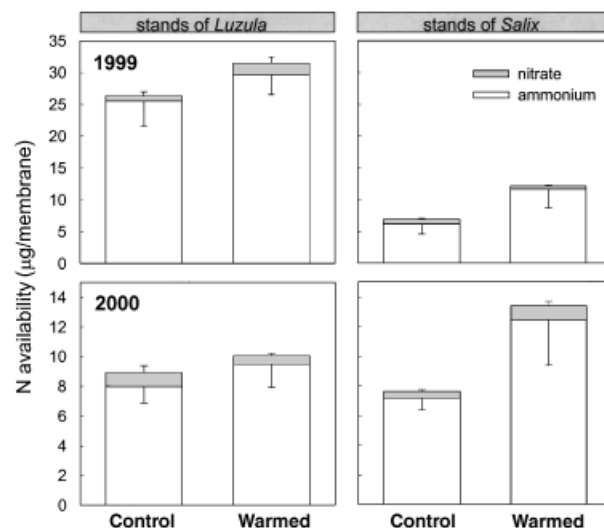
**Fig. 1** Field experiment: temperature during the experimental period of 1999 in the greenhouses (black line) compared with ambient (grey line). Lines are smoothed from 24 h averages based on hourly readings ($n = 3$).

**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 $-1$ SE for ammonium (white) and $+1$ SE for nitrate (grey).

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 $NH_4^+$ 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 $NH_4^+$ (Fig. 3), but nitrogen availability in the soil was too 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, although not significant, were 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 *L. confusa* was only marginally less in mixed than in pure position ($P = 0.104$), 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 position, and there was a tendency for this to be more pronounced in warmed plots (interaction term $P = 0.062$; Fig. 4b, Table 1).

Aboveground biomass of *S. polaris* at ambient temperature was strongly reduced in the presence of *L. 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
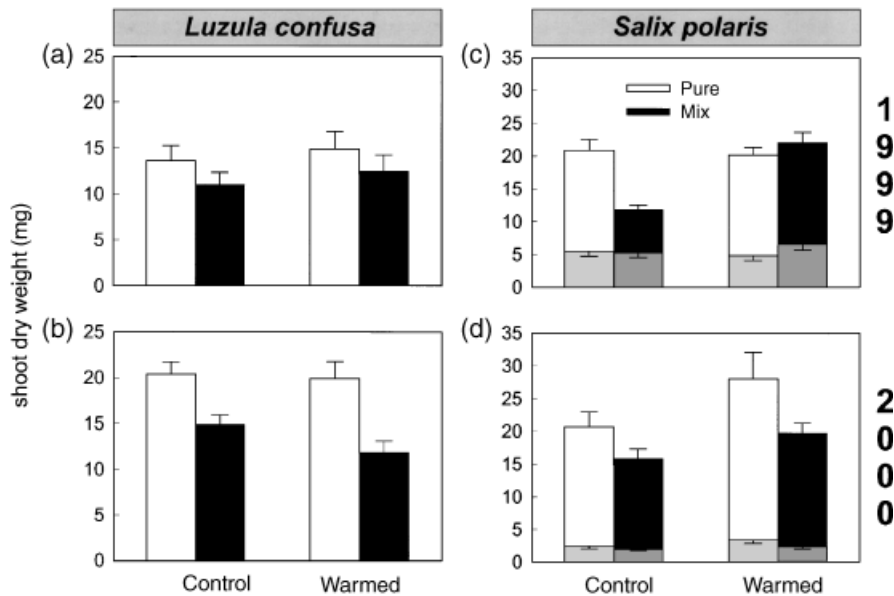


**Fig. 4** Field experiment: aboveground biomass per shoot of *Luzula confusa* (a, b) and *Salix polaris* (c, d) in pure (white) and mixed positions (black), after one (a, c) and two (b, d) season of elevated temperature, compared with controls ($n = 15$). Error bars represent 1 SE. Grey areas for *Salix* refer to biomass contributed by stems.

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

| Source | *L. confusa* | | | *S. polaris* | | |
|---|---|---|---|---|---|---|
| | ndf/ddf | F | P | ndf/ddf | F | P |
| *1999* | | | | | | |
| Initial biomass | 1/28 | 93.89 | 0.0001 | 1/27 | 66.47 | 0.0001 |
| Temperature | 1/14 | 2.64 | 0.1265 | 1/14 | 54.19 | 0.0001 |
| Position type | 1/28 | 2.83 | 0.1037 | 1/27 | 30.89 | 0.0001 |
| Interaction | – | – | – | 1/27 | 21.01 | 0.0001 |
| *2000* | | | | | | |
| Temperature | 1/14 | 4.39 | 0.0547 | 1/14 | 5.99 | 0.0282 |
| Position type | 1/28 | 56.17 | 0.0001 | 1/29 | 9.99 | 0.0037 |
| Interaction | 1/28 | 3.78 | 0.0619 | – | – | – |

–, indicates factors not included in the statistical model.

mixed positions, this time irrespective of temperature (Fig. 4d, Table 1). There was also a positive response to warming which tended to be greater in pure positions (ca. $+40\%$) than in mixed (ca. $+25\%$), although this difference was not significant.

*Relative contributions to vascular biomass.* Warming did not affect the numbers of plant shoots per $100\,cm^2$ (*Luzula*: control $42 \pm 4.7$, warmed $42 \pm 2.6$; *Salix*: control $48 \pm 4.9$, warmed $50 \pm 4.0$). Total aboveground 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 $421 \pm 52$ to $482 \pm 58\,g\,m^{-2}$. The percentage contribution of *Luzula* decreased from $36 \pm 6\%$ to $28 \pm 3\%$, while that of *Salix* increased accordingly from $64 \pm 6\%$ to $72 \pm 3\%$, a shift in *Luzula* : *Salix* ratio from 1 : 1.8 to 1 : 2.6.

## 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 fertilization (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). Fertilization, on the other hand, had no significant effect on any variable measured in *Luzula*, while it significantly increased the weight of stems and roots in *Salix*.

Interspecific 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 positions, while leaves at high temperature
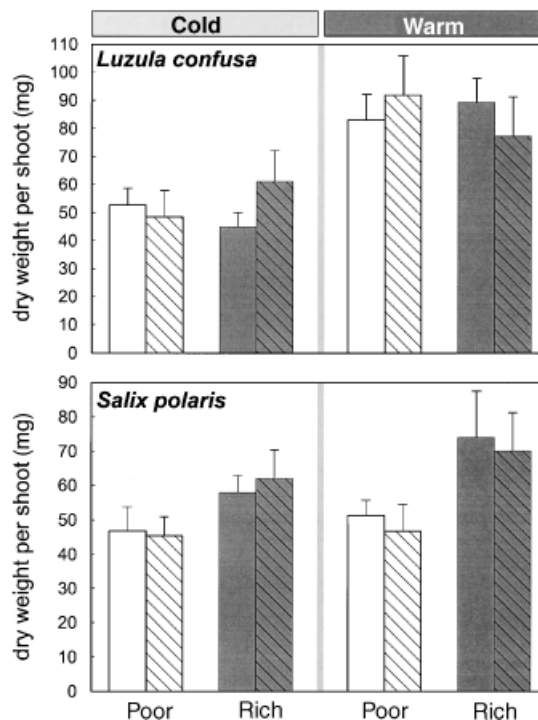


Fig. 5 Phytotron experiment: total dry weight of *Luzula* and *Salix* plants under cold and warm conditions. 'Poor' and 'rich' under the graph refer to nutrient availability. Hatched bars represent data from plants growing under competition. Error bars depict 1 SE.

Table 2 Phytotron experiment: average dry weight of the different plant parts according to treatment $\pm 1\,SE$ for *Luzula confusa* and *Salix polaris*

| Temperature | Cold | | | | Warm | | | |
|---|---|---|---|---|---|---|---|---|
| Nutrient | Poor | | Rich | | Poor | | Rich | |
| Competition | Pure | Mixed | Pure | Mixed | Pure | Mixed | Pure | Mixed |
| *L. confusa* | | | | | | | | |
| 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 | $21.6 \pm 3.04$ | $17.6 \pm 3.83$ | $19.1 \pm 2.04$ | $24 \pm 5.53$ | $38.4 \pm 4.16$ | $46.2 \pm 7.62$ | $42.7 \pm 5.08$ | $33.1 \pm 9.98$ |
| *S. polaris* | | | | | | | | |
| 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 | $36.4 \pm 6.00$ | $36.8 \pm 4.47$ | $46.4 \pm 4.47$ | $41.2 \pm 4.47$ | $33.6 \pm 2.72$ | $32.0 \pm 6.83$ | $39.0 \pm 6.06$ | $53.0 \pm 9.94$ |
| Roots | $6.3 \pm 1.14$ | $5.0 \pm 1.3$ | $8.0 \pm 0.88$ | $11.8 \pm 3.28$ | $13.8 \pm 19.7$ | $10.6 \pm 1.37$ | $25.7 \pm 5.34$ | $12.5 \pm 2.71$ |

Flowers occurred at maximum once per treatment combination, thus no errors are given.

**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)

| | Temperature | | Fertilization | | Others |
| | *Luzula* | *Salix* | *Luzula* | *Salix* | *Salix* |
| --- | --- | --- | --- | --- | --- |
| Total | 39.64*** | 1.19$^{ns}$ | 0.70$^{ns}$ | 10.24** | |
| Leaves | 47.65*** | 0.01$^{ns}$ | 1.64$^{ns}$ | 3.39$^{†}$ | $t \times c$*; $t \times f \times c$* |
| Shoot base | 12.70*** | – | 2.15$^{ns}$ | – | |
| Rhizome/stem | 12.70*** | 0.43$^{ns}$ | 0.01$^{ns}$ | 5.76* | |
| Roots | 42.31*** | 24.49*** | 1.16$^{ns}$ | 9.14** | Competition$^{†}$ |

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 ns indicates nonsignificant effects. $\times$ indicates interactions of $t$ (temperature), $f$ (fertilization) and/or $c$ (competition). – indicates factors not included in the statistical model.

grew better in pure positions (significant competition × fertilization × temperature interaction: Table 3).

## Discussion

### *Do* Salix *and* Luzula *compete in the field?*

Our data show reduced performance of both *S. polaris* and *L. 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 ca. 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, competitive interactions were not observed, most likely due to the planting density being rather low.

A 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 subarctic 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, 1998). 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 competi-

tion) increased aboveground biomass in response to removal of any of four dominant species (Hobbie *et al.*, 1999). In the Scandinavian subarctic *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 subarctic 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 that 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 positions 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 (Dormann & Brooker, 2002).

It should be noted that the site of our investigation is intensively grazed by reindeer, which were excluded from the experiment (all warming chambers exclude grazers, so this is the case for all such warming treatments reported in literature: Kennedy, 1995; Marion *et al.*, 1997). 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.*, 2000). 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, 2002). 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 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, 2002), which makes it difficult to distil generalizations.

The responses of *Luzula* and *Salix* in the field differed from those expected on the basis of the phytotron experiment. Predictions were of an increase in biomass for both species in warmed plots, *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, while 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, in contrast to the phytotron experiment. 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. A trend in the same direction might still have been expected but, if anything, the opposite trend was apparent (in 2000). The lack of positive response cannot be due to competition, as there was no effect of warming on *Luzula* in pure stands either. The conclusion must be that some factor other than temperature is limiting to the shoot growth of *Luzula* in the field.

*S. polaris* clearly gains the most benefit from elevated temperature in the field, probably through the increase in nutrient availability in warmed soil. Even in mixed stands, where both species are suppressed, *Salix* still gains benefit from warming while *Luzula* does not. Thus continued stimulation of the growth of individual *Salix* shoots by increased temperature could cause an eventual decline of *Luzula*, which may be accelerated if branching of *Salix* shoots also increases. This is indeed hinted at by the shifts in the *Luzula* : *Salix* ratios of both individual shoot and total aboveground biomass caused by warming.

### 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 2-year period (C. F. Dormann, 2003 and unpublished data).

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.*, 1995; Wookey *et al.*, 1995; Chapin & Shaver, 1996; Shaver *et al.*, 1998; Jonasson *et al.*, 1999; but see Parsons *et al.*, 1994; Michelson *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), and in the phytotron experiment only *Salix* responded to nutrients. Hence, as already stated, increased growth of *Salix* in the field could be simply a warming-induced fertilization effect, from which *Luzula* does not benefit.

*Salix* and *Luzula* differ in their mycorrhizal status: *Salix* is ectomycorrhizal (Treu *et al.*, 1995), and *Luzula* has no mycorrhizal association (Emmerton *et al.*, 2001). This niche differentiation might be expected to reduce any competition for nitrogen, with *Salix* accessing complex sources unavailable to *Luzula* (e.g. Michelsen *et al.*, 1996b). The ericoid mycorrhizal shrub *V. uliginosum* showed only slight response to change in

inorganic nutrient availability, whereas nonmycorrhizal *Festuca ovina* showed a strong response (Michelsen *et al.*, 1999). In our study, however, *S. polaris* did respond to nutrient addition in the lab and to warming in the field (this study and Baddeley *et al.*, 1994), suggesting that its mycorrhizal symbiont may be of limited importance or efficiency. So it appears that despite having access to complex nitrogen sources, *S. polaris* will preferentially utilize inorganic sources when available, and therefore the potential for nutrient competition exists.

### Community and ecosystem implications

Results of our field experiment corroborate the commonly predicted scenario of a climate-change-induced shift from tundra to taiga due to the better performance of woody species (Emanuel *et al.*, 1985; Starfield & Chapin, 1996; Epstein *et al.*, 2000; Rupp *et al.*, 2000). This is also supported by long-term experimental evidence (Chapin *et al.*, 1995; Shaver & Chapin, 1995; Press *et al.*, 1998) and detailed studies on woody species' responses to global change (Bret-Harte *et al.*, 2001). These studies are primarily based in the American North-West, in areas which are apparently subject to less grazing by megaherbivores (caribou/reindeer, muskox) than the Eastern Canadian Arctic, Greenland or Svalbard (S. Albon & G. Shaver, personal communication). Small browsers (such as hares or voles), although at times very abundant, usually have very localized impact compared with ungulates (Hobbs, 1996). Effects of both big and small grazers are hence not commonly incorporated in ecosystem models for higher latitudes, and may lead to local differences in predictions.

However, the consequences of the changes in growth and competition that we observed will depend heavily on grazing regime. Intense grazing could prevent *Salix* from outcompeting *Luzula* in a warmer climate, and even reverse the gain from warming into a loss to grazing. If air temperatures increase with only marginal increases in soil temperature (as seen in the experiment of Hobbie *et al.*, 1999), *Luzula* and other species of graminoid growth form may profit strongly. Indeed, data from the phytotron experiment demonstrate that *Luzula* can respond strongly to warming in the absence of other limitations. Thus air warming and grazing, in concert with the notorious water shortage in tundra ecosystems (Hodkinson *et al.*, 1999), may cause woody species like *Salix* not to be able to dominate the vegetation as predicted from climate warming models. This scenario would be a grazing-driven, graminoid-dominated, dry system.

These two different scenarios would obviously greatly affect ecosystem properties such as carbon storage (e.g. Hobbie *et al.*, 1998; Jones *et al.*, 1998; Oberbauer *et al.*, 1998; Neff & Hooper, 2002) and snow and water fluxes in the tundra (Liston *et al.*, 2002). These properties are crucial in ecosystem feedbacks to climatic change (e.g. Hobbie *et al.*, 2000, Vaganov *et al.*, 2000). In particular, woody plants sequester more carbon in stems than graminoids, and their leaf litter is less readily decomposable (Hobbie, 1996). Graminoid-dominated tundra systems have a more rapid nutrient and carbon turnover, not least due to herbivore off-take (Hobbie, 1992, 1995). Both these arguments point towards lower sequestration and carbon retention in a grazing-driven, graminoid-dominated, dry system than in a little-grazed system dominated by shrubs.

In the face of climatic change, elucidation of both of the mechanisms behind, and the trajectory of changes within, the competitive balance of plant communities are urgently needed. Successional changes in vegetation will have strong feedbacks on global climate; thus information that improves global and regional vegetation models will facilitate prediction of future environmental change (Kittel *et al.*, 2000). 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.

### Acknowledgements

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