Climate change effects on species interactions in an alpine plant community

KARI KLANDERUD

Department of Ecology and Natural Resource Management, The Agricultural University of Norway, PO Box 5003, N0-1432 Ås, Norway

Summary

1 I examined the role of species interactions on the population dynamics of the herb *Thalictrum alpinum* and the sedge *Carex vaginata* by removing the dwarf shrub *Dryas octopetala* over four growing seasons at Finse, in the alpine region of south Norway, Furthermore, by increasing temperature (open top chambers) and nutrient availability (nutrient addition), I assessed the effects of climate warming on biotic interactions.

2 *Dryas* removal increased the number of *Thalictrum* and *Carex* leaves, and flowering frequency of *Carex*. Flower stems and leaf stalks of *Thalictrum*, and the leaves of *Carex*, became significantly shorter following *Dryas* removal. Warming and nutrient addition increased vegetative plant growth, whereas warming alone had positive effects on sexual reproductive effort of the target species. My results suggest that there is both competition for nutrients, and a facilitative shelter effect of *Dryas* on its neighbours.

3 Species interactions affected population dynamics of *Thalictrum* and *Carex*. Interactions between the impacts of *Dryas* removal and abiotic factors on leaf production, suggested that interactions between *Dryas* and neighbouring species might be modified if temperature and, in particular, nutrient availability increase under global warming.

4 This study shows that both biotic interactions and abiotic environmental conditions may affect alpine plant population dynamics. Furthermore, it shows that climate change may modify species interactions.

5 Species interaction effects should be included in climate change experiments and in future models predicting plant community changes under global warming.

Key-words: biotic and abiotic factors, competition, dominant species, *Dryas octopetala*, facilitation, nutrient availability, plant functional types, population dynamics, removal experiment, warming

Introduction

Both biotic factors, such as species properties and species interactions, and abiotic factors, such as climate and soil characteristics, affect ecosystem structure and processes (Huston & McBride 2002). However, the relative importance of the biotic and abiotic factors for community dynamics in habitats of contrasting environmental severity and productivity is far from clear (Callaway & Walker 1997). Competition appears to play an important role in structuring plant communities of high productivity (e.g. Grime 1979), but there is still a debate about the role of biotic interactions when productivity is low, such as in alpine and arctic plant communities of high abiotic stress. Competition may be strong here because resources are scarce (e.g. Chapin & Shaver 1985; Tilman 1988), or facilitation may be stronger, with neighbouring vegetation improving the survival potential for individual plants (e.g. Callaghan & Emanuelson 1985; Bertness & Callaway 1994). Alternatively, species interactions may have less impact on community composition in areas of high abiotic stress because plant growth here is primarily limited by the environmental conditions (e.g. Savile 1960; Billings & Mooney 1968; Grime 1977).

Global warming may modify abiotic conditions that influence individual plant performance, with alpine and arctic ecosystems predicted to be particularly affected (e.g. Callaghan & Jonasson 1995; Guisan *et al*. 1995; Körner 1995, 1999). Climate change may alter soil moisture and increase nutrient availability and, in

Correspondence: Kari Klanderud (fax + 4764948502; e-mail kari.klanderud@ina.nlh.no).

combination with the direct warming effect, these factors may impact the growth, reproduction and resource allocation of the plants. However, functional groups (Arft *et al*. 1999; Dormann & Woodin 2002; Brooker & van der Wal 2003) or individual plant species (see Henry & Molau 1997) may differ in their responses to environmental changes. Furthermore, changes in the performance of one species or a functional group may change any current relationship between positive and negative plant–plant interactions, i.e. changes in competition or facilitation hierarchies between co-occurring species or growth forms.

The role of species interactions in structuring tundra plant communities differs between sites (see Hobbie *et al*. 1999). Moreover, effects of climate change on plant–plant interactions are rarely studied (but see Shevtsova *et al*. 1997; Hobbie *et al*. 1999), and species interactions are mostly ignored in models predicting how plant communities or ecosystems respond to climate change (Mooney 1991; Pacala & Hurtt 1993). Bertness & Callaway (1994) predicted a shift from facilitative to competitive effects of neighbouring plant species along gradients of decreasing abiotic severity and, in a study of 11 alpine sites, Callaway *et al*. (2002) found that species interactions shifted from positive to negative when summer temperatures increased along latitudinal and altitudinal gradients. They predicted that such shifts may speed changes in community composition and diversity compared with more physiologically based climate change models, and concluded that there is a need for more experiments on climate change effects on individual plant–plant interactions. There is also a lack of knowledge about how plant interactions affect resource allocation to reproduction vs. vegetative growth. Studies show contrasting results, which may indicate that both competition and facilitation may contribute to higher reproductive effort, though with varying responses between species (Kikvidze *et al*. 2001).

The aim of this study is to assess the relative impacts of biotic and abiotic factors on the growth and reproduction of two plant species in a *Dryas* heath community in alpine south Norway, and to gain an understanding of how interspecific interactions may be modified by abiotic conditions predicted to change under global warming. Hobbie *et al*. (1999) manipulated air temperature and the presence of seven dominant species in Alaskan tussock tundra, and found that the environmental conditions were more important for plant growth and biomass production than the impacts of species interactions. Moreover, as they found no interactions between warming and species removal, they concluded that global warming might not alter species interactions in tundra. In northern Finland, on the other hand, Shevtsova *et al*. (1997) found a number of interactions between environmental conditions (temperature and water) and species removal on the growth of sub-arctic dwarf shrubs, suggesting that community composition may modify the effects of climate change here. The contrasting results between the Alaskan

tundra and the European sub-arctic site suggest that there is a need for more research on species interactions and their responses to climate change. Moreover, none of these studies assessed the impact of increased nutrient availability resulting from climate warming (but see Bret-Harte *et al*. 2004), although this is predicted to provide the largest effects on tundra plant community composition (e.g. Chapin *et al*. 1995; Shaver & Jonasson 1999; Dormann & Woodin 2002).

Dryas heaths are plant diversity 'hot spots' in the Scandinavian mountains, dominated by the long-lived 'wintergreen' dwarf shrub *Dryas octopetala* L. (*Dryas* hereafter). *Dryas* grows in dense clones that may have positive or negative impacts on community diversity (Klanderud & Totland, in press). The relatively simple vegetation structure, with few and compressed vegetation layers, as well as predictions of large climatic impacts on species composition in alpine areas, make this an ideal arena to test questions related to species interactions and climate change. I used experimental removal of *Dryas*, warming (open top chambers, OTCs) and nutrient addition, to examine the role of these factors on the population dynamics of *Thalictrum alpinum* L. and *Carex vaginata* Tausch. Furthermore, I assessed if species interactions might be modified under climate warming. *Thalictrum* and *Carex* are abundant in the alpine *Dryas* heaths, and they belong to different functional groups (herbs and sedges, respectively) that may contrast in their responses to other species and to the abiotic environment (e.g. Wilson & Whittaker 1995; Dormann & Woodin 2002; Brooker & van der Wal 2003). Three predictions were addressed. (i) The two target species will differ in their responses to *Dryas* removal and to changes in the abiotic environment. (ii) Higher productivity at our site will lead to plant–plant interactions playing a greater role in plant community dynamics than reported in the Alaskan tundra (Hobbie *et al*. 1999; Bret-Harte *et al*. 2004). (iii) Species interactions will be modified by increased temperatures and nutrient availability.

Methods

STUDY SYSTEM

The experiment started in early July 2000 and lasted until the end of the growing season (late August) in 2003. The study site was situated on a south-west exposed slope of a *Dryas octopetala* L. heath at *c*. 1500 m elevation on Sandalsnuten, Finse, northern part of Hardangervidda (60° N, 7° E) in alpine south-west Norway. The snow normally disappears in late May/early June. Mean summer (June, July, August) temperature at 1222 m elevation at Finse is 6.3 °C (Aune 1993), and mean summer precipitation is 89 mm (Førland 1993).

The dwarf shrub *Dryas octopetala* is widely distributed in alpine and arctic areas. At Sandalsnuten, dense *Dryas* mats cover *c*. 35% of the ground of the *Dryas* heath community (Klanderud & Totland, in press). Other

abundant species here are the herbs *Thalictrum alpinum* L., *Potentilla crantzii* Crantz., *Bistorta vivipara* L. and *Cerastium alpinum* L., the dwarf-shrub *Salix reticulata* L., the grasses *Festuca vivipara* L. and *Poa alpina* L., and the sedges *Carex vaginata* Tausch., *C. atrofusca* Schkuhr, *C. rupestris* All. and *Luzula* spp. (nomenclature follows Lid & Lid 1994), in addition to a number of bryophytes and a few lichens.

Vegetative regeneration is common for alpine plants. *Thalictrum alpinum* and *Carex vaginata* grow clonally by producing new ramets from below-ground rhizomes, and seedlings of these species are rarely found at Sandalsnuten. Therefore I studied the responses of mature individuals rather than seedling responses.

EXPERIMENTAL DESIGN

To assess the possible effects of removal of *Dryas*, warming and increased nutrient availability on the population dynamics of *Thalictrum alpinum* and *Carex vaginata*, and whether environmental conditions affected any species interactions, I randomly selected 20 plots within a relatively homogenous area of the *Dryas* heath. I placed OTCs upon 10 of these plots and left the 10 others as controls. The OTC/control plots are the main-plots in a split-plot design with 10 replicates (see, e.g. Underwood 2001). In each of the 20 main-plots, I selected eight *Thalictrum* and eight *Carex* ramets growing inside *Dryas* mats, and inserted half a slow-dissolving NPK-fertilizer stick into the soil *c.* 1 cm upslope of half of the individuals of each species immediately after snowmelt and again in late July (*c.* 0.2 g N, 0.04 g P and 0.17 g K per ramet/growing season). Ramets receiving fertilizer were selected so that the added nutrients could not move to unfertilized ramets, i.e. they were grouped, or situated down-slope from other ramets. Thereafter, I clipped the above-ground parts of neighbouring *Dryas*, and carefully removed below-ground parts that could be pulled up with minimal soil disturbance, from a diameter of *c.* 10 cm around half of the fertilized ramets and around half of the ramets not receiving any fertilizer. I removed re-growth twice during each of the four growing seasons. This provided a split-plot design with temperature treatment as a fixed factor conducted on main-plot level, 20 plots as a random factor nested within the main-plot factor (temperature), and nutrient addition and removal treatments as fixed factors conducted on subplot level. Thus, for each of the 10 replicates, two ramets of each of the two target species in each temperature treatment (inside and outside OTCs) received nutrient addition, two experienced *Dryas* removal, two nutrient addition and *Dryas* removal, and two were untreated controls. The responses of the two individuals receiving similar treatments were averaged prior to statistical analysis.

Removal experiments may be problematic for several reasons. Removal of above-ground biomass may leave dead roots to decompose and increase soil nutrient levels (Putwain & Harper 1970; Berendse 1983).

However, these resources have most likely been obtained by competition in the past, and their release may benefit those plants that have been denied these resources earlier (Aarssen & Epp 1990). Vegetation removal may also disturb the soil, resulting in a nutrient flush. However, the primary removal in this study was of above-ground *Dryas* shoots, and there were probably only minor effects on below-ground processes and soil disturbance.

The OTCs are hexagonally shaped polycarbonate chambers with an inside diameter of *c.* 1 m, and with qualities as described in Marion *et al*. (1997). OTCs are commonly used to raise the temperature in climate change experiments (e.g. Marion *et al*. 1997; Hollister & Webber 2000). The chambers did not affect the duration of snow cover (personal observation) and were therefore left in place throughout the experiment. The site was fenced to inhibit sheep grazing.

ABIOTIC MEASUREMENTS

Air (*c.* 5 cm above ground) and ground surface temperatures were measured with a Grant Squirrel data logger during 10 days of late July/early August 2000, and soil (*c.* 5 cm below ground) temperatures were measured with Tinytag 12 Plus G data loggers (Intab Interface-Teknik AB, Stenkullen, Sweden) from early June to late August 2002, inside and outside the OTCs, in plots where *Dryas* had been removed, and in undisturbed plots. Leaf surface temperature of *Dryas* inside and outside the OTCs was measured using an infrared thermometer (FLUKE 65, Fluke Corporation, Everett, USA). Soil moisture was measured at the end of the final growing season by inserting a 6 cm long sensor (Theta Probe, Delta-T Devices Ltd, Cambridge, England) into the soil immediately beneath each target ramet (averaging three measurements per ramet).

GROWTH MEASUREMENTS

I measured growth and reproductive variables of *Thalictrum alpinum* and *Carex vaginata* in late August after the first (2000), second (2001), third (2002) and fourth (2003, reproductive variables only) growing seasons. To assess differences in within-season growth rates, I also measured the growth variables in late May (before any growth had started), late June, and again in late July during the second and the third growing season. However, to limit possible legacy effects of the removal treatment, only the 2002 and 2003 measurements are used in the analyses, with the 2000 measurements as covariables.

Sexually reproductive *Carex* ramets normally die the year after flowering, with new tillers growing out from the old ramet (*Carex vaginata*, K. Klanderud, personal observation; *C. bigelowii*, see Brooker *et al*. 2001). To simplify interpretation of growth and sexual reproduction independently of flowering year, I obtained target ramets at similar developmental stages by selecting flowering *Carex* individuals at the start of the experiment.

To obtain an estimate of vegetative growth of *Thalictrum* and *Carex*, I counted the number of green leaves on each target ramet and the total number of leaves on new tillers growing out from the target ramet. The data from the target ramet and daughter tillers are pooled in the statistical analyses. As number of leaves is not reported per tiller, possible changes may be due either to increased tillering or increased size of the tillers. Furthermore, I measured the length and the width of the largest and the smallest leaf and the length of their leaf stalk (*Thalictrum*), and the length of the longest leaf (*Carex*), using a digital caliper. I calculated an approximate leaf area of *Thalictrum* leaves by multiplying the width by the length and then calculated the average area of the smallest and the biggest leaf. Leaf number, average leaf area of the largest and the smallest leaf, and the length of their leaf stalks, are parameters commonly used for herbs, whereas leaf number and the length of the longest leaf are commonly used for sedges to obtain non-destructive measures of vegetative growth (Molau & Edlund 1996; Arft *et al.* 1999). To estimate mortality I recorded dead target ramets. Measuring mortality on clonal plants is, however, not easily applied because individuals usually persist, and only parts of the plants die. The data for *Carex* are not analysed because mortality here coincides with sexual reproduction.

SEXUAL REPRODUCTION MEASUREMENTS

To estimate the sexual reproductive effort of *Thalictrum* and *Carex*, I measured the height of flower stems and collected mature infructescences at the end of each season and recorded the number of flowers and number and weight of dried seeds. There were not enough flowering *Carex* individuals to test for seed production and seed weight. Arctic and alpine plants normally do not produce flowers each year (Sonesson & Callaghan 1991) and the same ramet did not reproduce more than once during the experiment for either of the two species. To increase the sample size, I therefore pooled all flowering individuals from 2002 to 2003 to estimate flowering frequency for both species, as well as height of flower stem and number of flowers and seeds for *Thalictrum*. There were too few mature seeds to conduct statistical tests on seed weight.

STATISTICAL ANALYSES

Data on the number of leaves, leaf area (*Thalictrum*) and leaf length (*Carex*) were log transformed to fulfil the ANCOVA assumptions of normality and equal variances. All graphs are shown with untransformed data. To determine if warming, nutrient addition and removal of *Dryas* had any impact on the vegetative growth of *Thalictrum* and *Carex*, and whether possible species interactions were affected by the environmental factors, I used general linear models (GLM, SYSTAT 10) with the temperature treatment (main-plot factor), nutrient addition, removal of *Dryas*, and their inter-

actions (subplot factors) as fixed factors, and plot nested within temperature as a random factor in a split-plot ANCOVA. I used the first year (2000) measurements as covariables in the analyses to increase the model's ability to detect treatment effects. The effect of temperature was tested over the plot error (main-plot term), whereas all other effects were tested over the model error (subplot term) (see, for example, Underwood 2001). Analyses were conducted separately for the two species. To examine if the removal of *Dryas* or the environmental factors had any impact on the combination of growth phenology and absolute size differences of *Carex* and *Thalictrum* during the third (2002) growing season after experimental onset, I used repeated-measures ANOVA with the same factors as above, and with ramet identity during three measurements throughout the season (time) as the repeated measures factor. A significant interaction between time and treatment may then indicate that treatments differ in the pattern of growth during the season.

Because of low sample sizes for reproductive parameters, I used the Mann–Whitney *U*-test to assess significant differences in height of flower stem, number of flowers per ramet and number of seeds per flower within each treatment separately (temperature vs. control, nutrient addition vs. natural, removal vs. undisturbed). I used Pearsons chi-square test to assess significant differences in flowering frequency for *Thalictrum* and *Carex* and mortality for *Thalictrum*, between the same treatments as above. The small sample sizes for sexual reproduction may result in conservative results.

Results

ABIOTIC FACTORS

The OTCs increased mean *Dryas* leaf temperature and air temperature by 1.5 °C, and ground temperature by 2.5 °C (Table 1). When soil temperature was measured, the OTCs increased values in undisturbed vegetation by 1.5 °C, while *Dryas* removal caused a decrease of 0.5 °C inside the OTCs, and an increase of 0.5 °C outside (Table 1).

VEGETATIVE GROWTH

Removal of *Dryas octopetala* increased the number of leaves of *Thalictrum alpinum* by 79.2% and of *Carex vaginata* by 56.4% across all treatments (Table 2, Figs 1a and 2a). The *Thalictrum* leaves became 35.1% smaller and the *Carex* leaves became 14.1% shorter after *Dryas* removal, although this was only statistically significant for *Carex* (Table 2, Figs 1b and 2b). The length of *Thalictrum* leaf stalks decreased by 49.3% after *Dryas* removal, although a close to significant three-way interaction indicated that temperature, nutrient addition and removal treatment all affected each other (Table 2, Fig. 1c). Significant measures from 2000 suggested treatment effects on *Thalictrum* leaf stalks after the first growing season.

Table 1 Mean temperature of *Dryas* leaf surface, air (*c.* 5 cm above ground), ground surface and soil (*c.* 5 cm below ground) where vegetation was experimentally removed or intact, and soil moisture, outside (control) and inside OTCs at alpine Finse. Standard errors, minimum and maximum measures are given

	Control		OTC	
	Mean ± SE	Minimum–Maximum	Mean ± SE	Minimum–Maximum
Dryas leaf surface (°C)	12.1 ± 0.1	9.7–14	13.6 ± 0.2	12.1–16.2
Air (°C)	7.8 ± 0.2	−2.2–28.1	9.3 ± 0.2	−2.5–36.9
Ground (°C)	10.4 ± 0.4	−2.1–45.1	12.9 ± 0.5	−2.5–55
Soil, *Dryas* removal (°C)	9.2 ± 0.1	2.1–18.2	9.6 ± 0.1	2.7–18.6
Soil, no removal (°C)	8.7 ± 0.1	2.3–17.0	10.2 ± 0.1	2.8–22.3
Soil moisture (%)	28.2 ± 0.6	17.9–44.2	27.9 ± 0.8	11.8–42.5

Table 2 $F_{d.f.}$ and *P* values (significant at < 0.05 in bold, < 0.1 in bold italics) of treatments performed in alpine *Dryas octopetala* heaths; T = temperature (OTC vs. control, main-plot fixed factor), N = nutrient addition (increased vs. ambient, subplot fixed factor), R = removal of *Dryas* (yes vs. no, subplot fixed factor), their interactions, plot nested in T (random factor), and measurements from 2000 included as covariables in split-plot ANCOVAs on number of leaves of *Thalictrum alpinum* and *Carex vaginata*, average leaf area and length of leaf stalk of the biggest and the smallest leaf of *Thalictrum*, and length of the longest leaf of *Carex*. *n* = 10 for each treatment

Sources of Variation	Number of leaves		Leaf area/length		Leaf stalk	
	$F_{d.f.}$	*P*	$F_{d.f.}$	*P*	$F_{d.f.}$	*P*
Thalictrum alpinum						
T	$0.33_{1,18}$	0.572	$0.16_{1,18}$	0.695	$1.14_{1,18}$	0.300
N	**$4.91_{1,46}$**	**0.032**	$1.41_{1,46}$	0.242	**$5.35_{1,46}$**	**0.025**
R	**$22.13_{1,46}$**	**< 0.001**	$2.08_{1,46}$	0.156	**$15.51_{1,46}$**	**< 0.001**
T × N	**$9.90_{1,46}$**	**0.003**	$2.23_{1,46}$	0.142	$0.49_{1,46}$	0.486
T × R	$0.59_{1,46}$	0.447	$0.48_{1,46}$	0.494	$1.57_{1,46}$	0.217
N × R	$1.84_{1,46}$	0.181	$0.00_{1,46}$	0.982	$0.57_{1,46}$	0.454
T × N × R	$0.11_{1,46}$	0.744	$1.64_{1,46}$	0.206	***$3.38_{1,46}$***	***0.073***
Plot (T)	***$1.78_{1,46}$***	***0.059***	$0.97_{1,46}$	0.511	$1.12_{1,46}$	0.368
2000 measure	$1.39_{1,46}$	0.244	***$2.96_{1,46}$***	***0.092***	**$5.17_{1,46}$**	**0.028**
Carex vaginata						
T	$1.50_{1,18}$	0.237	$0.37_{1,18}$	0.552		
N	**$6.59_{1,38}$**	**0.014**	$1.93_{1,38}$	0.173		
R	**$4.74_{1,38}$**	**0.036**	**$4.75_{1,38}$**	**0.036**		
T × N	***$2.98_{1,38}$***	***0.092***	$1.48_{1,38}$	0.231		
T × R	$0.25_{1,38}$	0.619	$0.19_{1,38}$	0.667		
N × R	$2.12_{1,38}$	0.153	$0.36_{1,38}$	0.552		
T × N × R	$0.02_{1,38}$	0.896	$0.04_{1,38}$	0.850		
Plot (T)	$1.23_{1,38}$	0.288	$1.22_{1,38}$	0.295		
2000 measure	$0.11_{1,38}$	0.74	$1.79_{1,38}$	0.189		

Nutrient addition increased the number of *Thalictrum* leaves by 32.3% and the number of *Carex* leaves by 59.1%, with interactions (only marginally significant for *Carex*) between temperature and nutrient addition suggesting that the number of leaves increased on ramets receiving both warming and nutrients, whereas there were no significant effects of either of these treatments separately (Table 2, Figs 1a and 2a). Warming and nutrient addition increased *Thalictrum* leaf area by 21.4% and 18.6%, respectively, and *Carex* leaf lengths by 8.7% and 10.8%, although these responses were not statistically significant (Table 2, Figs 1b and 2b).

GROWTH PHENOLOGY

The increased number of *Thalictrum* leaves after *Dryas* removal (Table 2, Fig. 1a) was primarily caused by pro-

duction of more leaves early in the season (May, June), and again later in the growing season (August). This was particularly pronounced when nutrients were added in combination with *Dryas* removal, suggesting that removal of a competitor increased the benefit of the additional nutrient availability for *Thalictrum* (significant time × nutrients × removal, Fig. 3a). A significant interaction (time × temperature × nutrients, Fig. 3b) on *Thalictrum* leaf area indicated that leaves on fertilized plants, which in mid-June were bigger than leaves in all other treatments, decreased significantly in mean size from mid-July outside the OTCs, but remained bigger than all other leaves throughout August inside OTCs. *Thalictrum* leaf stalks, which also were longest on fertilized leaves, declined by the end of the growing season in most treatments except where *Dryas* was removed inside the OTCs, where they continued to
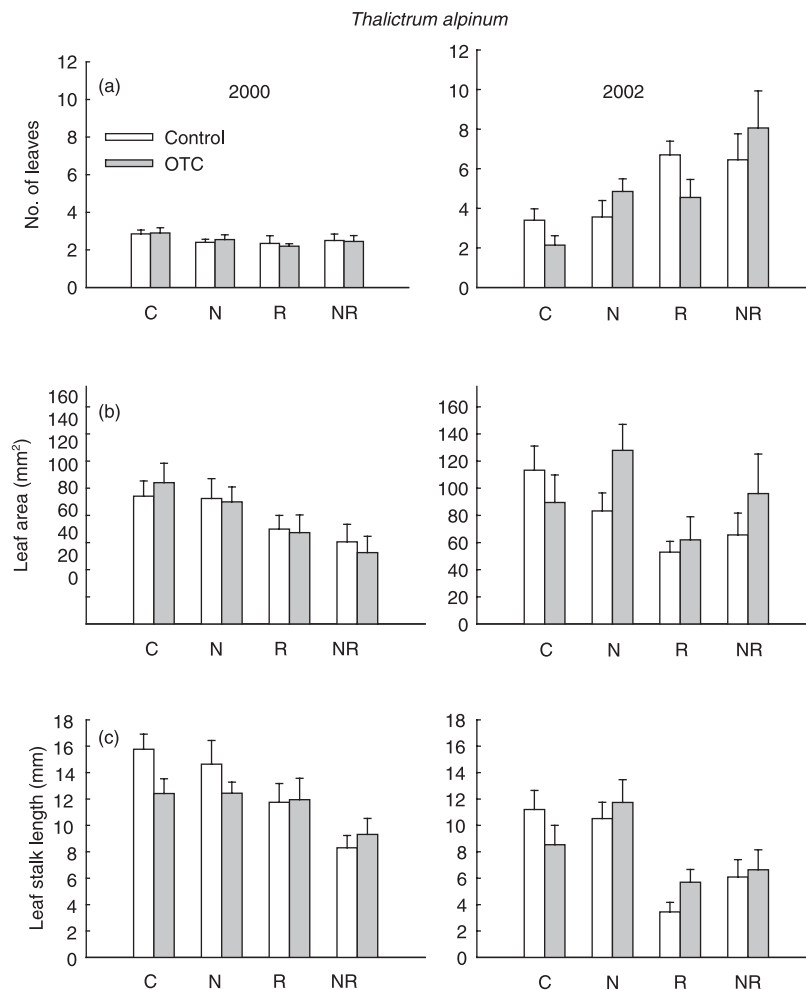
Fig. 1 Means and standard errors of (a) the number of leaves, (b) leaf area, and (c) length of leaf stalks of *Thalictrum alpinum* measured at the start of the experiment in 2000 (ANCOVA pre-treatment values) and by the end of the 2002 growing season in a *Dryas octopetala* heath outside (controls) and inside OTCs, on ramets receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatments (C), at Finse, alpine south Norway. $n = 10$ for each treatment.

grow throughout the season (significant time × removal, and time × temperature × nutrients, Fig. 3c).

For *Carex*, the combination of *Dryas* removal and nutrient addition clearly increased the number of leaves, primarily because of late season growth (July, August) when leaf production in the other treatments had terminated (significant time × removal × nutrients, Fig. 4a). No other seasonal growth pattern differed significantly between treatments on the vegetative growth of *Carex*.

SEXUAL REPRODUCTION AND MORTALITY

For the *Thalictrum* ramets, 2.5%, 5.0%, 37.5% and 3.8% reproduced sexually in 2000, 2001, 2002 and 2003, respectively. *Dryas* removal or nutrient addition had no effect on flowering frequency of *Thalictrum* (Pearsons $\chi^2 < 0.001$, $P > 0.10$ in both cases). Warming on the other hand, decreased flowering frequency by 32.5% (Pearsons $\chi^2 = 8.90$, $P = 0.003$) but increased the height of the flower stems of *Thalictrum* by 36.2%

(Mann–Whitney $U = 89$, $P = 0.061$, Fig. 5a). There were no effects of any of the treatments on number of flowers per ramet (Mann–Whitney $U < 71$, $P > 0.311$ in all cases, Fig. 5b), whereas nutrient addition marginally decreased the number of seeds per flower by 25.5% (Mann–Whitney $U = 86$, $P = 0.093$, Fig. 5c).

For *Carex*, 95%, 2.5%, 2.5% and 5.0% of the target ramets reproduced sexually in 2000, 2001, 2002 and 2003, respectively. *Dryas* removal and warming increased flowering frequency by 13.6% (Pearsons $\chi^2 = 5.97$, $P = 0.015$) and 11.3% (Pearsons $\chi^2 = 3.82$, $P = 0.051$), respectively. Nutrient addition had no effect on flowering frequency of *Carex* (Pearsons $\chi^2 = 2.22$, $P = 0.136$). None of the treatments had any effects on the height of flower stem of *Carex* (Mann–Whitney < 80, $P > 0.100$ in all cases).

Thalictrum mortality decreased by 2.5%, 12.5% and 7.5% due to *Dryas* removal, warming and nutrient addition, respectively, although none of these responses were statistically significant (Pearsons $\chi^2 < 0.001$, $P > 0.98$ in all cases).
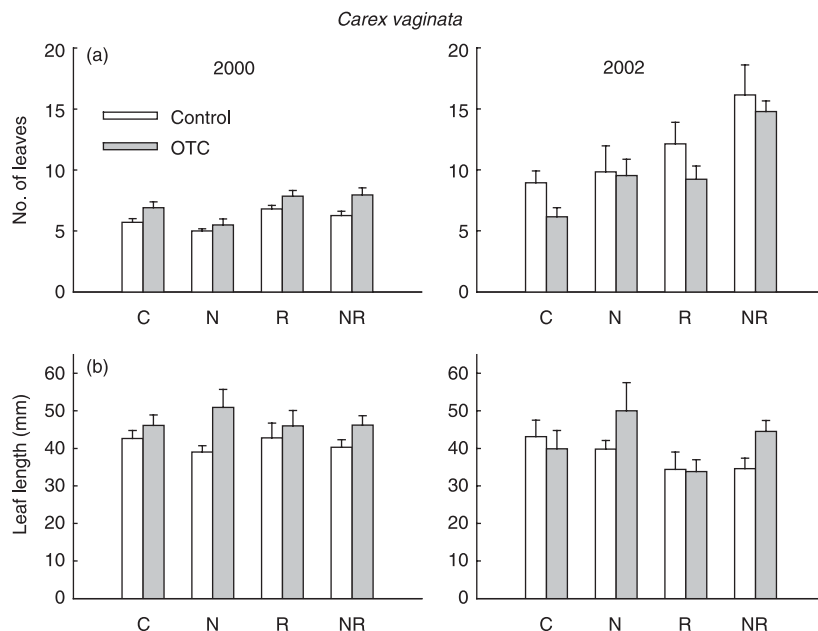
Carex vaginata

Fig. 2 Means and standard errors of (a) the number of leaves and (b) leaf length of *Carex vaginata* measured in a *Dryas octopetala* heath by the end of the 2000 and 2002 growing season outside (controls) and inside OTCs, on ramets receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatment (C), at Finse, alpine south Norway. $n = 10$ for each treatment.
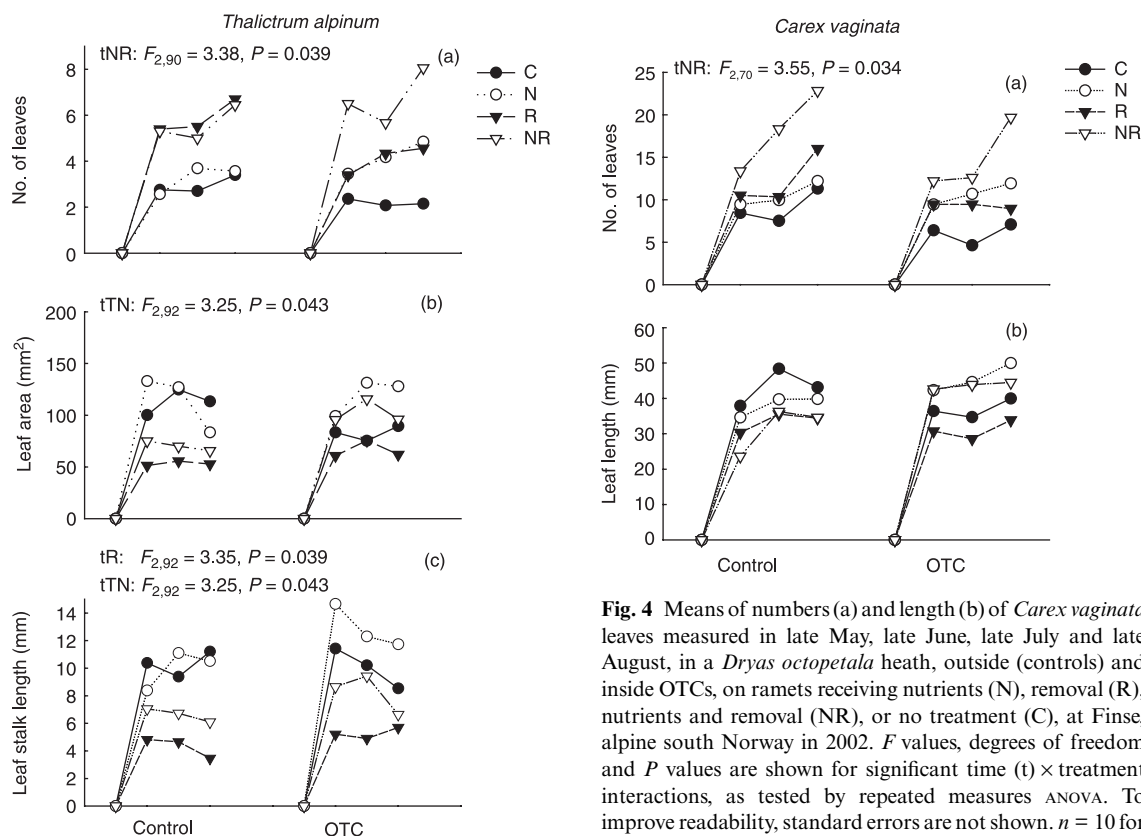

Fig. 3 Means of the number of leaves (a), leaf area (b) and leaf stalk length (c) of *Thalictrum alpinum* measured in a *Dryas octopetala* heath in late May, late June, late July and late August, outside (controls) and inside OTCs, on ramets receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatments (C), at Finse, alpine south Norway in 2002. *F* values, degrees of freedom and *P* values are shown for significant time (t) × treatment interactions, as tested by repeated measures ANOVA. To improve readability, standard errors are not shown. $n = 10$ for each treatment.

Fig. 4 Means of numbers (a) and length (b) of *Carex vaginata* leaves measured in late May, late June, late July and late August, in a *Dryas octopetala* heath, outside (controls) and inside OTCs, on ramets receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatment (C), at Finse, alpine south Norway in 2002. *F* values, degrees of freedom and *P* values are shown for significant time (t) × treatment interactions, as tested by repeated measures ANOVA. To improve readability, standard errors are not shown. $n = 10$ for each treatment.

Discussion

BIOTIC EFFECTS

Species interactions clearly affected plant growth, and thus could potentially influence population dynamics, of *Thalictrum alpinum* and *Carex vaginata* at alpine
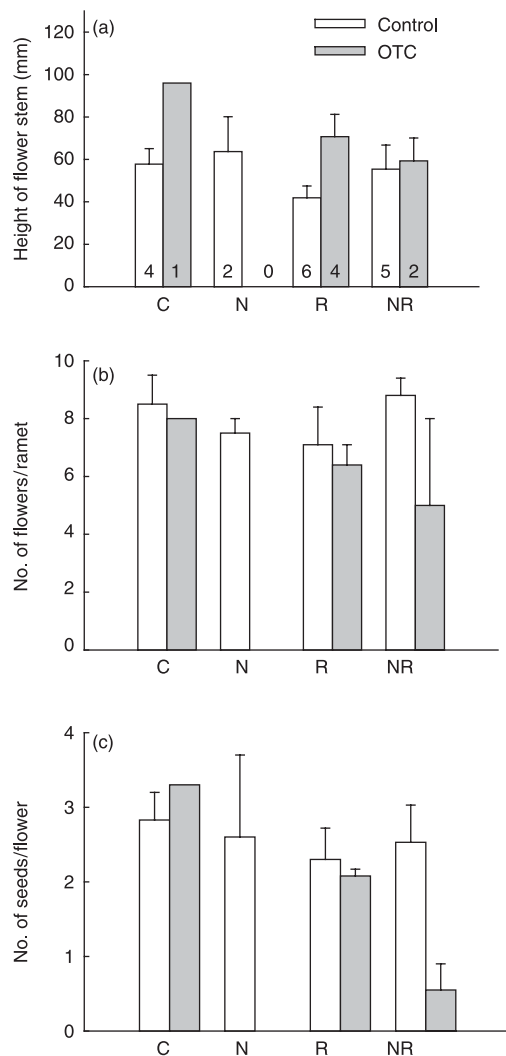
Fig. 5 Means and standard errors of (a) the height of flower stems, (b) number of flowers per ramet, and (c) number of seeds per flower of *Thalictrum alpinum* measured in a *Dryas octopetala* heath by the end of the 2002 and 2003 growing season outside (controls) and inside OTCs, on ramets receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatment (C), at Finse, alpine south Norway. Numbers in the columns are sample sizes for each treatment.

Finse, which is in contrast to Hobbie *et al.* (1999), who found no effects of removal treatments on the remaining species in Arctic tundra, and thus no evidence for species interactions.

Removal of *Dryas* increased the number of leaves of *Thalictrum alpinum* and *Carex vaginata*, and flowering frequency of *Carex* (Table 3). On the other hand, leaf stalks of *Thalictrum* and leaves of *Carex* became significantly shorter, suggesting a shift in internal resource allocation in both species after *Dryas* removal. The increased number of leaves (*Thalictrum* and *Carex*) and flowering frequency (*Carex*) after removal of *Dryas*, suggest competitive rather than facilitative impacts of *Dryas* at Finse. This is in line with Klanderud & Totland (in press), who found that *Dryas* decreased plant community diversity at Finse, and it is in line with other removal experiments detecting negative plant–plant

interactions in alpine and subarctic sites (Aarssen & Epp 1990; Shevtsova *et al.* 1995). The same neighbour may, however, have multiple effects (Aarssen & Epp 1990), and the reduced length of *Thalictrum* leaf stalks and *Carex* leaves after *Dryas* removal may be caused by a loss of facilitative shelter against low temperature and strong winds. Bret-Harte *et al.* (2004) found possible facilitation of *Ledum palustre* on one forb in the Alaskan tundra. Moreover, Shevtsova *et al.* (1995) found decreased shoot length in some species after neighbour removal in sub-arctic Finland, which they suggested could be due to either a loss of facilitative protection or a release from negative shading effects. Shading may be considerable at high latitudes with low angle of sunlight and low annual solar input (Shevtsova *et al.* 1995), and the plants may produce larger leaves (e.g. Dormann & Woodin 2002; Totland & Esaete 2002), or longer shoots, to compensate for shading or to position flowers, seeds or photosynthetically active tissue above neighbouring plants (Grime 1979). When associated vegetation is removed, the influx of solar radiation increases, and the plants no longer need to compensate, or escape from shading, and this may result in shorter leaves and leaf stalks. However, the positive warming effects on various growth and reproductive parameters at Finse suggest that loss of facilitation effects may explain these responses, at least in part.

Dryas had similar effects on the vegetative growth of *Thalictrum* and *Carex*, although leaf production for *Thalictrum* increased proportionally more than for *Carex* after *Dryas* removal, suggesting a stronger role of competition from *Dryas* on *Thalictrum*. For sexual reproduction on the other hand, no *Dryas* effects were detected for *Thalictrum*, whereas competition from *Dryas* reduced the sexual reproductive effort of *Carex*.

ABIOTIC EFFECTS

Warming had positive effects on sexual reproductive parameters of the two target species, such as the height of flower stems of *Thalictrum alpinum* and flowering frequency of *Carex vaginata* (Table 3). Nutrients, on the other hand, increased the vegetative growth of both *Thalictrum* and *Carex*, although in most cases only in combination with warming. This shows that both warming and nutrient availability limited vegetative growth of these species at Finse (Table 3). Increased nutrient availability had no effect on the sexual reproduction of the target species, except a close to significant negative effect on the number of seeds of *Thalictrum*. These results are in line with other climate change experiments, showing that nutrients limit plant growth in alpine and arctic environments, with only minor effects of temperature alone, but often with synergistic effects of warming and nutrients (e.g. Chapin & Shaver 1985; Robinson *et al.* 1998; K. Klanderud & Ø. Totland, unpublished data). Warming, on the other hand, has been shown to increase the reproductive effort of several alpine and arctic species (Arft *et al.* 1999). These

Table 3 Summary responses of treatments with significant effects ($P < 0.05$, $P > 0.05$ in parentheses) on growth and reproductive parameters of *Thalictrum alpinum* and *Carex vaginata* growing in alpine *Dryas octopetala* heaths, as tested by different methods (see text). + = positive response; – = negative response; empty cells indicate no response ($P \geq 0.1$), and dots (.) indicate that no tests are done. Treatment abbreviations as in Table 2

Species and parameters	Treatments and responses						
	+ T	+ N	+ R	+ T + N	+ N + R	+ T + R	+ T + N + R
Thalictrum alpinum							
No. of leaves			+	+			
Leaf area							
Length of leaf stalk		+	–				(–)
Height of flower stem	(+)			.	.	.	.
No. of flowers				.	.	.	.
No. of seeds		(–)		.	.	.	.
Flowering frequency	–			.	.	.	.
Mortality				.	.	.	.
Carex vaginata							
No. of leaves		+	+	(+)			
Leaf length			–				
Height of flower stem				.	.	.	.
Flowering frequency	+		+	.	.	.	.

results are also in line with the meta-analysis of Dormann & Woodin (2002), although they found that nutrients also limit reproduction of arctic plants.

Vegetative growth increased more after nutrient addition in *Carex* than in *Thalictrum*, which is also in line with a number of experiments showing that graminoids respond more to increased nutrient availability than other functional groups (e.g. Jonasson 1992; Dormann & Woodin 2002; Bret-Harte *et al*. 2004; K. Klanderud & Ø. Totland, unpublished data).

SPECIES INTERACTIONS

Increased nutrient availability caused by climate change may modify the interactions between *Dryas* and other species at Finse. Nutrients appeared to be a limiting factor for plant growth at Finse, and the increase in late season leaf production of *Thalictrum* and *Carex* after *Dryas* removal combined with nutrient addition, suggests that these species benefit more from the increased nutrient availability when *Dryas* was removed. This is in line with Bret-Harte *et al*. (2004) who found increased graminoid biomass after removal treatment combined with fertilization, probably in response to increased nutrient availability when neighbours were removed. My results indicate that *Dryas* is a stronger competitor for nutrients than *Thalictrum* and *Carex*, which again may suggest that the role of competition from *Dryas* may be greater if nutrient availability increases under global warming.

Furthermore, warming reduced *Thalictrum* flowering frequency, while nutrient addition slightly decreased the number of seeds of *Thalictrum*, which may suggest that the possible negative effects of growing inside a *Dryas* mat may be greater when resources increase, most likely because of increased competition from *Dryas*. This is in line with findings of a greater role of com-

petition under higher productivity (e.g. Bertness & Shumway 1993; Callaway 1998; Choler *et al*. 2001; Klanderud & Totland, in press), and it corresponds with Callaway *et al*. (2002), who found shifts from positive to negative species interactions of alpine plants when temperatures increased along latitudinal and altitudinal gradients.

The predicted response to increased nutrient availability varies among functional groups (e.g. Dormann & Woodin 2002). Grasses have been shown to respond strongly to nutrient addition, and increased nutrient availability caused by climate change may influence competition hierarchies, and thus species composition of plant communities. This is in line with Grime (1977) and others, who have found altered competition hierarchies in several ecosystems after changes in nutrient conditions (Austin & Austin 1986; DiTomasso & Aarssen 1989; Gurevitch & Unnasch 1989), whereas species interactions have not changed after short-term warming treatments alone (Hobbie *et al*. 1999). Overall, *Dryas* appeared to protect other species from low temperatures at Finse, but at the same time, there may be interspecific competition for nutrients. Thus, global warming may result in a shift towards increased competition, because increased nutrient availability may change competition hierarchies, resulting in more competition for light and space.

IMPLICATIONS FOR CLIMATE CHANGE MODELS

Previous climate change experiments have primarily focused on abiotic effects on plant growth, and most climate change models tend to ignore species interactions (Mooney 1991; Pacala & Hurtt 1993; Davies *et al*. 1998). This study clearly shows that both biotic and abiotic conditions affect alpine plant growth and possible population dynamics. Furthermore, climate

change may alter species interactions, e.g. the role of competition from *Dryas* or other species may become greater in a future with more resources. Thus, species interactions should be considered in climate change experiments and in models predicting future plant community responses to global warming.

References

Aarssen, L.W. & Epp, G.A. (1990) Neighbour manipulations in natural vegetation: a review. *Journal of Vegetation Science*, **1**, 13–30.

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M. *et al.* (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491–511.

Aune, B. (1993) *Temperaturnormaler: Normalperiode 1961–90.* Det Norske Meteorologiske Institutt, Oslo.

Austin, M.P. & Austin, B.O. (1986) Behaviour of experimental plant communities along a nutrient gradient. *Journal of Ecology*, **68**, 891–918.

Berendse, F. (1983) Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. *Journal of Ecology*, **71**, 379–390.

Bertness, M.D. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.

Bertness, M.D. & Shumway, S.W. (1993) Competiton and facilitation in marsh plants. *American Nauralist*, **142**, 718–724.

Billings, W.D. & Mooney, H.A. (1968) The ecology of arctic and alpine plants. *Biology Review*, **43**, 481–529.

Bret-Harte, M.S., García, E.A., Sacré, V.M., Whorley, J.R., Wagner, J.L., Lippert, S.C. *et al.* (2004) Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. *Journal of Ecology*, **92**, 635–647.

Brooker, R., Carlsson, B.Å. & Callaghan, T.V. (2001) *Carex bigelowii* Torrey ex Schweinitz (*C. rigida* Good., non Schrank; *C. hyperborean* Drejer). Biological Flora of the British Isles. *Journal of Ecology*, **89**, 1072–1095.

Brooker, R. & van der Wal, R. (2003) Can soil temperature direct the composition of high arctic plant communities? *Journal of Vegetation Science*, **14**, 535–542.

Callaghan, T.V. & Emanuelson, U. (1985) Population structure and process of tundra plants and vegetation. *The Population Structure of Tundra Vegetation* (ed. J. White), pp. 399–439. Junk, Dordrecht.

Callaghan, T.V. & Jonasson, S. (1995) Implications for changes in arctic plant biodiversity from environmental manipulation experiments. *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences, Ecological Studies*, Vol. 113 (eds F.S. Chapin & C. Körner), pp. 151–166. Springer Verlag, Berlin.

Callaway, R.M. (1998) Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos*, **82**, 561–573.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortle, C.J., Michalet, R. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.

Chapin, F.S. & Shaver, G.R. (1985) Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, **66**, 564–576.

Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.

Choler, P., Michalet, R. & Callaway, R.M. (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology*, **82**, 3295–3308.

Davies, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Woods, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.

DiTomasso, A. & Aarssen, L.W. (1989) Resource manipulations in natural vegetation: a review. *Vegetatio*, **84**, 9–29.

Dormann, C.F. & Woodin, S.J. (2002) Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology*, **16**, 4–17.

Førland, E.J. (1993) *Precipitation Normals, Normal Period 1961–90.* The Norwegian Meteorological Institute, Oslo.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes.* John Wiley, Chichester.

Guisan, A., Theurillat, J.P. & Spichiger, R. (1995) Effects of climate change on alpine plant diversity and distribution: the modelling and monitoring perspectives. *Potential Ecological Impacts of Climate Change in the Alps and Fennoscandian Mountains* (eds A. Guisan, J.I. Holten, R. Spichiger & L. Tessier), pp. 129–135. Conservatoire et Jardin botaniques, Genève.

Gurevitch, J. & Unnasch, R.S. (1989) Experimental removal of a dominant species at two levels of soil fertility. *Canadian Journal of Botany*, **67**, 3470–3477.

Henry, G.H.R. & Molau, U. (1997) Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology*, **3** (Suppl. 1), 1–9.

Hobbie, S.E., Shevtsova, A. & Chapin, F.S. III (1999) Plant responses to species removal and experimental warming in Alaskan tussock tundra. *Oikos*, **84**, 417–434.

Hollister, R.D. & Webber, P.J. (2000) Biotic validation of small open-top chambers in a tundra ecosystem. *Global Change Biology*, **6**, 835–842.

Huston, M.A. & McBride, A.C. (2002) Evaluating the relative strengths of biotic versus abiotic controls on ecosystem processes. *Biodiversity and Ecosystem Functioning* (eds M. Loreau, S. Naeem & P. Inchausti), pp. 47–60. Oxford University Press, New York.

Jonasson, S. (1992) Plant responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos*, **63**, 420–429.

Kikvidze, Z., Khetsuriani, L., Kikodze, D. & Callaway, R.M. (2001) Facilitation and interference in subalpine meadows of the central Caucasus. *Journal of Vegetation Science*, **12**, 833–838.

Klanderud, K. & Totland, Ø. (in press) Habitat dependent nurse-effects of the dwarf-shrub *Dryas octopetala* on alpine and arctic plant community structure. *Ecoscience*, **11**, in press.

Körner, C. (1995) Impact of atmospheric changes on alpine vegetation: the ecophysiological perspective. *Potential Ecological Impacts of Climate Change in the Alps and*

Fennoscandian Mountains (eds A. Guisan, J.I. Holten, R. Spichiger & L. Tessier), pp. 13–120. Conservatoire et Jardin botaniques, Genève.

Körner, C. (1999) *Alpine Plant Life*. Springer, Germany.

Lid, J. & Lid, D.T. (1994) *Norsk Flora*, 6th edn. Det Norske Samlaget, Oslo.

Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H. *et al.* (1997) Open–top designs for manipulating field temperature in high latitude ecosystems. *Global Change Biology*, **3**, 20–32.

Molau, U. & Edlund, S. (1996) Plant response variables. *The ITEX Manual* (eds U. Molau & P. Mølgaard), pp. 20–29. Danish Polar Center, Copenhagen.

Mooney, H.A. (1991) Biological responses to climate change: an agenda for research. *Ecological Applications*, **1**, 112–117.

Pacala, S.W. & Hurtt, G.C. (1993) Terrestrial vegetation and climate change: integrating models and experiments. *Biotic Interactions and Global Change* (eds P.M. Kareiva, J.G. Kingsolver & R.B. Huey), pp. 57–74. Sinauer, Sunderland, Massachusetts.

Putwain, P.D. & Harper, J.L. (1970) Studies in the dynamics of plant populations. III. The influence of assosiated species on populations of *Rumex acetosa* L. & *R. acetosella* L. in grassland. *Journal of Ecology*, **58**, 251–264.

Robinson, C.H., Wookly, P.A., Lee, J.A., Callaghan, T.V. & Press, M.C. (1998) Plant community responses to stimulated environmental change at a high arctic polar semi-desert. *Ecology*, **79**, 856–866.

Savile, D.B.O. (1960) Limitations of the competitive exclusive principle. *Science*, **132**, 1761.

Shaver, G.R. & Jonasson, S. (1999) Response of Arctic ecosystems to climate change: results of long-term field experiments. I. Sweden and Alaska. *Polar Research*, **18**, 245–252.

Shevtsova, A., Haukioja, E. & Ojala, A. (1997) Growth response of subarctic dwarf shrubs, *Empetrum nigrum* and *Vaccinium vitis-idaea*, to manipulated environmental conditions and species removal. *Oikos*, **78**, 440–458.

Shevtsova, A., Ojala, A., Neuvonen, S., Vieno, M. & Haukioja, E. (1995) Growth and reproduction of dwarf shrubs in a subarctic plant community: annual variation and above-ground interactions with neighbours. *Journal of Ecology*, **83**, 263–275.

Sonesson, M. & Callaghan, T.V. (1991) Strategies of survival in plants of the Fennoscandian tundra. *Arctic*, **44**, 95–105.

Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton.

Totland, Ø. & Esaete, J. (2002) Effects of willow canopies on plant species performance in a low-alpine community. *Plant Ecology*, **161**, 157–166.

Underwood, A.J. (2001) *Experiments in Ecology. Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, Cambridge.

Wilson, J.B. & Whittaker, R.J. (1995) Assembly rules demonstrated in a saltmarsh community. *Journal of Ecology*, **83**, 801–807.