Herbivore and neighbour effects on tundra plants depend on species identity, nutrient availability and local environmental conditions

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Summary

1. I performed a factorial transplant experiment to test the roles of plant–plant interactions, herbivory by mammal grazers and resource availability for plant performance in two contrasting habitat types in a mountain tundra environment.

2. Three perennial dicot herbs, *Solidago virgaurea*, *Erigeron uniflorus* and *Saussurea alpina*, were used as target plants to study the effects of neighbour removal and grazer exclusion, and nutrient enrichment and liming on plant growth, survival and reproductive success. These treatments were replicated in two contrasting habitat types, infertile acidic and fertile non-acidic tundra heaths.

3. The effects of plant–plant interactions on *Saussurea* varied from facilitation in infertile acidic habitats to competition in fertile non-acidic habitats and in nutrient-enriched conditions, while the overall performance of *Saussurea* was strongly negatively influenced by the presence of grazers, the effects being greater when plants were fertilized and in fertile non-acidic heaths. *Erigeron* performed better under nutrient-enriched conditions than in unfertilized plots, when neighbours had been removed. *Solidago* was negatively affected by grazing and this impact was greater in nutrient-enriched plots and in non-acidic heaths than in acidic heaths and for unfertilized controls. There were no interactions between neighbour removal and herbivory in any of the three species, indicating that these processes operated independently.

4. Grazer-preferred tall plants are strongly limited by consumption by mammal herbivores in nutrient-enriched conditions and in inherently fertile habitats. By contrast, arctic–alpine specialists and species of low stature experience increased competition with neighbouring vegetation in fertile habitats and in enriched nutrient conditions.

5. *Synthesis*. Overall, the results suggest that the strength and directions of plant–plant and plant–herbivore interactions depend on plant species identity and are modified by soil edaphic factors to govern vegetation processes in tundra plant communities. These findings have important implications for understanding the forces structuring vegetation in barren tundra ecosystems under a changing environment.

Key-words: competition, facilitation, grazing, landscape heterogeneity, local environmental conditions, plant community, productivity, reindeer, soil fertility, soil pH

Introduction

There is an increasing body of theoretical and empirical evidence that competition, facilitation and herbivory interact with abiotic environmental gradients (e.g. gradients of productivity and nutrient availability) to govern the dynamics of plant populations, communities and ecosystem functioning (Grace & Tilman 1990; Bertness & Callaway 1994). At present,

there are divergent views upon their roles in relatively unproductive ecosystems such as arctic and alpine environments. According to one view, the importance of competition is negligible in habitats with low productivity where severe abiotic conditions primarily limit plant growth and occurrence, whereas the importance of competition increases with increasing productivity (Grime 1973, 1979). A more recent view considers that positive interactions between plants (i.e. facilitation) contribute to individual plant performance, species distributions and community composition, especially

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in abiotically harsh environments (e.g. Bertness & Callaway 1994; Brooker & Callaghan 1998; Kikvidze *et al.* 2005; Brooker *et al.* 2007). Other theories maintain that competitive interactions have an important role even in low-productivity environments. The resource competition model developed by Tilman (1982, 1988) predicts that competition is equally important in habitats of both low and high productivity but that competition for light prevails in habitats of high productivity. In low-productivity environments, plants compete intensely for nutrients and species with the lowest nutrient requirements are competitively superior.

Plant–neighbourhood interactions along productivity gradients are likely to interconnect with other biotic forces shaping plant performance, of which one of the most apparent is herbivory (Harper 1977; Louda *et al.* 1990; Mulder 1999). Several theories of plant–herbivore interactions along productivity gradients predict a change in plant species composition coupled with shifts in grazing pressure when moving from low to high productivity (e.g. Oksanen *et al.* 1981; Leibold 1996). According to Oksanen *et al.* (1981), plant biomass in ecosystems of relatively low or intermediate productivity is limited to a constant level by herbivores, and hence interspecific competition among plants is reduced. In such grazer-controlled systems, increased plant production due to nutrient enrichment should lead to an increase in consumption by herbivores while plant biomass should remain constant.

The net outcome of plant–neighbourhood interactions may vary from positive to negative depending on the relative strength of habitat amelioration and resource competition. Some studies have reported net neutral or negative responses to neighbours, thus demonstrating the importance of competition for plant performance in abiotically severe habitats (Olofsson *et al.* 1999; Klanderud & Totland 2005; Sammul *et al.* 2006). In other studies net responses to neighbours have been demonstrated to vary along environmental gradients (Choler *et al.* 2001; Callaway *et al.* 2002; Olofsson 2004), while in others net positive responses have been observed irrespective of the extent of environmental severity (Freestone 2006). Evidence for amelioration and competition by neighbouring species in severe habitats is contradictory, possibly because most studies have neglected to consider the impact of herbivores on plant–neighbourhood interactions. Therefore, further studies are needed to elucidate the circumstances in which facilitation and competition occur and how these are related to grazing and other habitat properties that affect plant distributions and abundance.

Herbivores may indirectly alter the competitive environment experienced by a plant by reducing the amount of the biomass of neighbouring vegetation. This can lead to increased plant growth if neighbours compete for shared resources (e.g. Mulder & Ruess 1998; Van der Wal *et al.* 2000). In tundra ecosystems, where productivity is considered to be strongly constrained by limited nutrient availability (Shaver & Chapin 1980), pronounced herbivore impacts on plants could be anticipated (Louda *et al.* 1990). Thus far, only a few studies have provided experimental evidence of herbivore-controlled plant performance that is contingent upon soil nutrient availability (Grellman 2002; Gough *et al.* 2007), while how these factors are related to plant–plant interactions in tundra ecosystems has not been investigated.

Plant–plant and plant–herbivore interactions are likely to be influenced by local environmental conditions (e.g. soil pH, fertility; Hobbie *et al.* 2005; Gough 2006; Gough *et al.* 2007). In arctic and alpine environments, striking differences in plant community composition prevail between acidic and non-acidic habitats (Gough *et al.* 2000; Virtanen *et al.* 2003, 2006), possibly because the low availability of nutrients in acidic heaths leads to diminished plant growth and survival (Peet *et al.* 2003; Nordin *et al.* 2004). Given these habitat-specific differences, it is reasonable to expect that plant–plant and plant–herbivore interactions would diverge among these habitat types. However, to my knowledge there are no well-replicated studies directly testing how plant–neighbourhood interactions and the impact of herbivores on plants are related to these environmental conditions.

I conducted a factorial transplant experiment in the alpine tundra of northern Europe to examine the relative and interactive importance of biotic and abiotic factors for plant performance in a heterogeneous tundra landscape varying in habitat fertility and soil pH. I used three perennial dicot herbs, *Solidago virgaurea* L., *Saussurea alpina* (L.) DC. and *Erigeron uniflorus* L., as target plants to study the joint effects of environmental amendments (fertilization and liming) and biotic interactions (herbivore exclusion and neighbour removal) on the growth, survival and flowering of the plants. Treatments were replicated in two community types, nutrient-poor acidic heaths and fertile non-acidic heaths, which also differed in community composition and species richness.

I addressed the following specific questions. (i) Do the strength and direction of plant–plant and plant–herbivore interactions depend on nutrient availability and local environmental conditions? (ii) Do herbivore and neighbour effects interact along soil fertility gradients to determine plant performance? (iii) What is the direct role of the abiotic environment for plant performance in a heterogeneous tundra landscape?

Methods

STUDY AREA AND SPECIES

This study was conducted on Mt Saana in Kilpisjärvi (69°03′ N, 20°50′ E), north-western Finland. The treeline of mountain birch (*Betula pubescens* ssp. *czerepanowii*) lies at an altitude of 600–700 m a.s.l. The mean annual temperature in the area is –2.6 °C and the mean annual precipitation is 420 mm (Järvinen 1987). The bedrock in the area consists partly of dolomitic rocks, resulting in non-acid and relatively fertile soils characterized by herb and grass-rich *Dryas* heaths, and partly of siliceous rocks, resulting in acid barren soils where dwarf shrub-dominated *Empetrum* heaths prevail. The main herbivores in the study area are semi-domesticated reindeer (*Rangifer tarandus* L.), which pass through the area in June–July, microtine rodents such as grey-sided voles (*Clethrionomus rufocanus* Sund.) and mountain hares (*Lepus timidus* L.), which are encountered occasionally.

All three transplant species are perennial herbs of the family Asteraceae and occur frequently in the study area. *Erigeron uniflorus* (hereafter *Erigeron*) is a circumboreal arctic–alpine herb with a low stature (5–15 cm), a basal leaf rosette and only one relatively large flower head per flowering stalk. It grows preferentially in non-acidic meadow and snowbed communities. *Solidago virgaurea* (hereafter *Solidago*) is a medium-sized herb (10–50 cm) with many small flower heads per flowering stalk and a wide distribution throughout Europe. *Solidago* grows in a variety of habitats ranging from siliceous tundra heaths to lowland forests and rich fens. It is a preferred foodplant for reindeer (Bråthen & Oksanen 2001; personal observation). *Saussurea alpina* (hereafter *Saussurea*) is a medium-sized herb (10–60 cm) with a wide leaf rosette and many flower heads per flowering stalk. *Saussurea* is distributed throughout the alpine and arctic areas of Europe and north-west Asia. It grows most abundantly in fertile and base-rich habitats such as calcareous tundra meadows and heaths, and also in rich fens.

EXPERIMENTAL SITES AND DESIGN

Five non-acidic and five acidic sites distributed on the south-west and north-east slopes of Mt Saana at altitudes ranging from 720 to 800 m a.s.l. were chosen in autumn 2004. Different types of sites were interspersed among each other within a distance of 5 km and represented as similar topographical and moisture conditions as possible. Acidic sites were dominated by the dwarf shrub *Empetrum nigrum* (60–65% cover), other prostrate dwarf shrubs (*Vaccinium vitis-idaea*, *Vaccinium uliginosum* and *Betula nana*, 25–30%) and graminoids (e.g. *Carex bigelowii*, *Calamagrostis lapponica* and *Festuca ovina*, 5–10%); some forbs (e.g. *Bistorta vivipara* and *Pedicularis lapponica*, < 5%) occurred sparsely. The characteristic species of non-acidic sites were: *Dryas octopetala* (30–35%), shrubs preferring non-acidic habitats (e.g. *Cassiope tetragona*, *Salix reticulata*, *Rhododendron lapponicum*, 5–10%), graminoids (e.g. *Carex rupestris*, *Carex vaginata*, 20–25%) and arctic–alpine forbs (e.g. *Saxifraga oppositifolia*, *Silene acaulis* and *Thalictrum alpinum*, 15–20%). Most of the species of siliceous heaths were also encountered abundantly. Nomenclature follows Hämet-Ahti *et al.* (1998). Before the experiment, the average soil pH was 5.28 (4.1–6.3) at acidic sites and 6.44 (5.7–6.9) at non-acidic sites, and the mean number of vascular plants per 1 m^2 was 11 (6–18) at acidic sites and 17 (11–26) at non-acidic sites.

At each of the 10 sites, eight plots 50 × 25 cm in size were established, resulting in 80 plots in total. Each plot was further split into two 25 × 25 cm subplots, and one of these was randomly assigned to the neighbour removal treatment. The transplants of the target plants were later planted into these subplots, either with or without neighbouring vegetation. The main plots (consisting of two subplots) were randomly assigned to three treatments in a factorial design: (i) herbivore exclusion, (ii) fertilization, (iii) liming or control. This design resulted in one replicate of each treatment combination per site. In total, there were 160 subplots in the experiment.

To obtain plants to be transplanted into the field experimental sites, seeds were collected from the study area in autumn 2004, cold-stratified for 5 months and set to germinate. Plantlets were transferred to small pots (5 × 5 cm in diameter and 7 cm deep) and grown in a glasshouse for 3.5 months. Two seedlings of *Solidago* and *Erigeron* were planted per pot whereas only one seedling of *Saussurea* was planted per pot. The seedlings of all three species were transplanted in the experimental plots at Mt Saana at the beginning of June in 2005. One pot of each species was assigned into each 25 × 25 cm subplot with neighbouring vegetation either present or not. Pots were removed around the soil cores and these were planted into the subplots at approximately equal distances from each other and from the corners of the subplots. The plots were fertilized, limed and watered (500 mL water from nearby brooks) for the first time just after the planting.

FIELD MANIPULATIONS

The neighbour removal treatment was accomplished by removing all above-ground plant biomass from an area of 25 × 25 cm. To avoid disturbance of the soil, roots were left intact. The first biomass removal was done in August 2004 to allow the subsequent pulse of nutrients from the decaying roots to occur before planting of the transplants in spring 2005. Regrowth was removed twice during the following growing seasons. However, especially at acidic sites, regrowth was negligible, indicating a strong decline in the vitality of the roots. Trenching the edges of the experimental plots was not done as it would have severely disturbed the soil and affected the functioning of soil communities.

For the grazer exclusion treatment, 80- to 100-cm-high exclosures were established on half of the experimental plots in late autumn 2004. The exclosures were circular, *c*. 1.5 m in diameter, made of galvanized net (mesh size 1.2 × 1.2 cm) and dug into the soil to a depth of 10 cm. The exclosures prevented all mammal herbivores, including voles, from grazing in the fenced plots. Commercial fast-dissolving NPK fertilizer (16-9-22) was applied to the fertilization treatment plots twice per growing season (in mid-June and at the end of July in 2005 and 2006, a total of 9.6 g N m^{-2}, 5.4 g P m^{-2}, 13.2 g K m^{-2} per year). To manipulate soil pH, dolomite lime (CaMg(CO$_3$)$_2$) was applied to the liming treatment plots, with 150 g m^{-2} twice per growing season in 2005, at the same time that fertilizer was applied, a total of 300 g m^{-2} year^{-1}. As the first application of lime did not alter soil pH sufficiently, the dose was doubled in 2006 to a total of 600 g m^{-2} year^{-1}. Immediately following fertilization and lime application, all experimental blocks were watered with 500 mL of water from nearby brooks. Both fertilizer and lime applications were also extended to a 10- to 15-cm-wide zone around each experimental plot.

The transplanted target plants were harvested in mid-August 2006 at the end of the growing season. The numbers of flower heads and surviving individuals were recorded. Following these measurements, the above-ground biomass of the plants was cut to ground level, brought to the laboratory, dried at 60 °C for 3 days and weighed. The below-ground plant parts were not harvested because of the difficulty of obtaining all the root material and separating the target plant roots from those of neighbours.

SOIL ANALYSIS

To evaluate the treatment effects on soil nutrient availability and pH, composite soil samples consisting of three soil cores (3 cm diameter) were collected from the humus layer from a 10- to 15-cm-wide buffer zone around each experimental plot. As neighbour removal treatment had not been applied to this buffer zone, its effect on soil properties could not be evaluated. Samples were collected in mid-August 2006, just after the transplant harvesting. In the laboratory, all plant material was removed from the samples, which were homogenized and frozen until analysis. Soil pH was measured in 3 : 5 (v/v) soil/water suspensions (Denver Instrument Model 220). A subsample of *c*. 3 g fresh soil was extracted with 50 mL of 0.5 M K$_2$SO$_4$, and the NH$_4$-N concentration in the extracts was determined by flow injection analysis (FIA 5012, Perstorp).
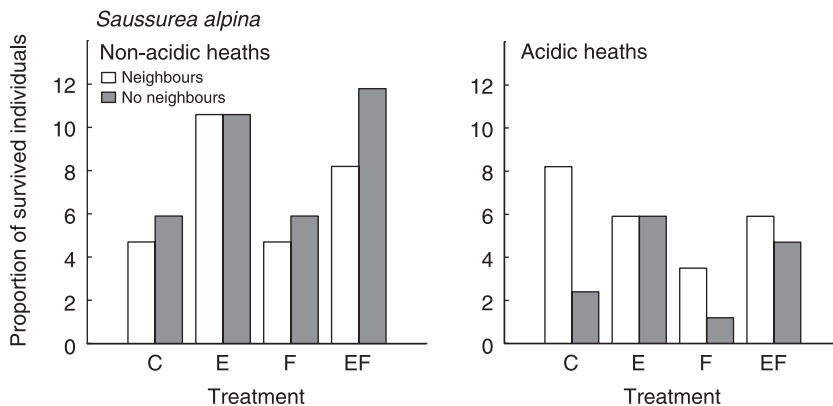
Saussurea alpina

Fig. 1. Proportion of survived individuals of *Saussurea alpina* per total number of survived individuals in different treatments with and without neighbours and in non-acidic and acidic habitats. C, control; E, exclosure; F, fertilizer. Liming had no effect on the transplant survival, and the data on limed plants were pooled among other treatments for the figures.

STATISTICAL ANALYSES

The effects of treatments and habitat type on soil NH_4^+ concentrations, soil pH and biomass data for the transplants of *Solidago*, *Saussurea* and *Erigeron* were analysed using linear mixed-effects models (LME; Pinheiro & Bates 2000; Crawley 2002). For soil-extractable NH_4^+ concentrations and soil pH, I used hierarchical mixed effects models where plot-level treatments (fertilization, liming and herbivore exclusion) and habitat type were treated as fixed factors and plot identity was nested within sites (random factors). For the biomass data, I used hierarchical models in which neighbour removal, fertilization, liming, herbivore exclusion and habitat type were treated as fixed factors, and neighbour removal treatment (subplots) was nested within plots (either fertilized, limed or fenced) that were nested within sites. Analyses were conducted separately for all the three species. The heteroscedasticity of variances were checked using model diagnostic plots, and all biomass data were square-root transformed prior to statistical analyses to improve the homogeneity of variances. These data fullfilled the homogeneity assumptions of variances.

The proportion of surviving transplants per treatment combination was analysed using generalized linear models with a binomial error distribution and a logit link function (McCullagh & Nelder 1989; Crawley 2002). As all explanatory variables were categorical, the data were pooled across sites for these analyses (Crawley 2002), and no hierarchical random formulas were included in the models. The treatment effects on the number of flowering transplants were analysed using traditional chi-square tests as there were relatively few flowering transplant individuals in the entire data and these were aggregated into only a few treatments. This prevented the use of more sophisticated analyses. For flowering data, only the main treatment effects and their first-order interactions were analysed while other analyses were restricted to three-way interactions. All the analyses were carried out using R statistical environment (R Development Core Team 2005).

Results

PLANT SURVIVAL IN RESPONSE TO HABITAT AND TREATMENTS

During the two study years, the overall survival of *Saussurea* was the lowest of all three transplant species. Of 160 *Saussurea* individuals, 75 (47%) died during the two years while 67 of the

320 *Solidago* individuals (21%) and 90 of the 320 *Erigeron* individuals (28%) died. Habitat was the only factor that significantly affected the proportion of surviving individuals of *Solidago* and *Erigeron* ($\chi_1^2 = 35.9$, $P < 0.0001$, and $\chi_1^2 = 17.7$, $P < 0.0001$, respectively); 81% of dead *Solidago* individuals and 85% of dead *Erigeron* individuals were found in acidic heaths. The survival of *Saussurea* was also significantly lower in acidic sites ($\chi_1^2 = 47.3$, $P = 0.001$, Fig. 1); however, the probability of survival also depended on experimental treatments. In acidic heaths, *Saussurea* had the lowest survival when neighbours had been removed, while in non-acidic heaths, neighbour removal led to increased survival (significant habitat × neighbour removal interaction, $\chi_1^2 = 20.9$, $P = 0.025$, Fig. 1). Exclusion of herbivores had a positive main effect on *Saussurea* survival ($\chi_1^2 = 32.7$, $P < 0.001$) and this effect was greater in non-acidic than in acidic heaths (significant habitat × exclosure interaction, $\chi_1^2 = 26.5$, $P = 0.034$, Fig. 1).

PLANT GROWTH RESPONSES TO NEIGHBOUR REMOVAL

Growth of one of the studied species, *Solidago*, was totally independent of the presence or absence of neighbours (Table 1, Fig. 2a). The responses of the other two species to neighbour removal were dependent on habitat type and/or fertilizer addition. With both *Erigeron* and *Saussurea*, there was a significant interactive effect of neighbour removal and fertilization on plant growth (Table 1). Removal of neighbouring vegetation led to increased growth in fertilized plots and neutral or slightly reduced growth in unfertilized plots, indicating a shift from no impact on growth at lower fertility to competition at higher nutrient availability (Fig. 2b,c). In the growth of *Saussurea*, opposing responses to neighbour removal also occurred depending on habitat type (significant habitat × neighbour removal interaction, Table 1). In acidic habitats removal of neighbouring biomass caused slightly reduced growth, suggesting a neutral or slightly facilitative effect of neighbours, while in non-acidic habitats neighbour removal led to substantial biomass increment, suggesting a significant role of competition (Fig. 2c).

Table 1. Results of linear mixed effects models (LME), where biomasses (g) of each three plant species (*Solidago virgaurea*, *Erigeron uniflorus*, *Saussurea alpina*) were used as response variables in separate analyses, and habitat quality, exclosure, fertilizer, liming, neighbour removal and their interactions were used as explanatory variables. In the models, neighbour removal treatment was nested within blocks (either fertilized, limed or fenced), which were nested within habitats. Biomass data were square-root transformed before the analysis. All main effects but only significant interactions are reported. Significant *P*-values (< 0.05) are given in bold, and marginally significant *P*-values (< 0.06) are in bold italics

| | Biomass (g) | | | | | |
| | *Solidago virgaurea* | | *Erigeron uniflorus* | | *Saussurea alpina* | |
Source of variation	F_{df}	*P*	F_{df}	*P*	F_{df}	*P*
Habitat	$22.631_{1,8}$	**0.0014**	$12.878_{1,8}$	**0.0071**	$11.067_{1,8}$	**0.0104**
Exclosure	$28.123_{1,57}$	**<0.0001**	$1.191_{1,57}$	0.2797	$31.519_{1,57}$	**<0.0001**
Fertilizer	$121.664_{1,57}$	**<0.0001**	$36.716_{1,57}$	**<0.0001**	$15.554_{1,57}$	**0.0002**
Liming	$0.183_{1,57}$	0.6707	$0.105_{1,57}$	0.7470	$0.393_{1,57}$	0.5334
Neighbour removal	$0.003_{1,69}$	0.9583	$2.631_{1,69}$	0.1094	$0.187_{1,69}$	0.6669
Habitat × Exclosure	$7.585_{1,57}$	**0.0079**	$0.352_{1,57}$	0.5553	$10.672_{1,57}$	**0.0018**
Habitat × Fertilizer	$4.804_{1,57}$	**0.0325**	$6.100_{1,57}$	**0.0165**	$8.593_{1,57}$	**0.0048**
Habitat × Neighbour removal	$0.866_{1,69}$	0.3552	$0.062_{1,69}$	0.8048	$5.765_{1,69}$	**0.0191**
Exclosure × Fertilizer	$25.069_{1,57}$	**<0.0001**	$0.989_{1,57}$	0.3241	$7.651_{1,57}$	**0.0076**
Fertilizer × Neighbour removal	$0.392_{1,69}$	0.5332	$8.283_{1,69}$	**0.0053**	$4.211_{1,69}$	**0.0440**
Habitat × Exclosure × Fertilizer	$3.801_{1,57}$	***0.0562***	$0.389_{1,57}$	0.5351	$0.919_{1,57}$	0.3417
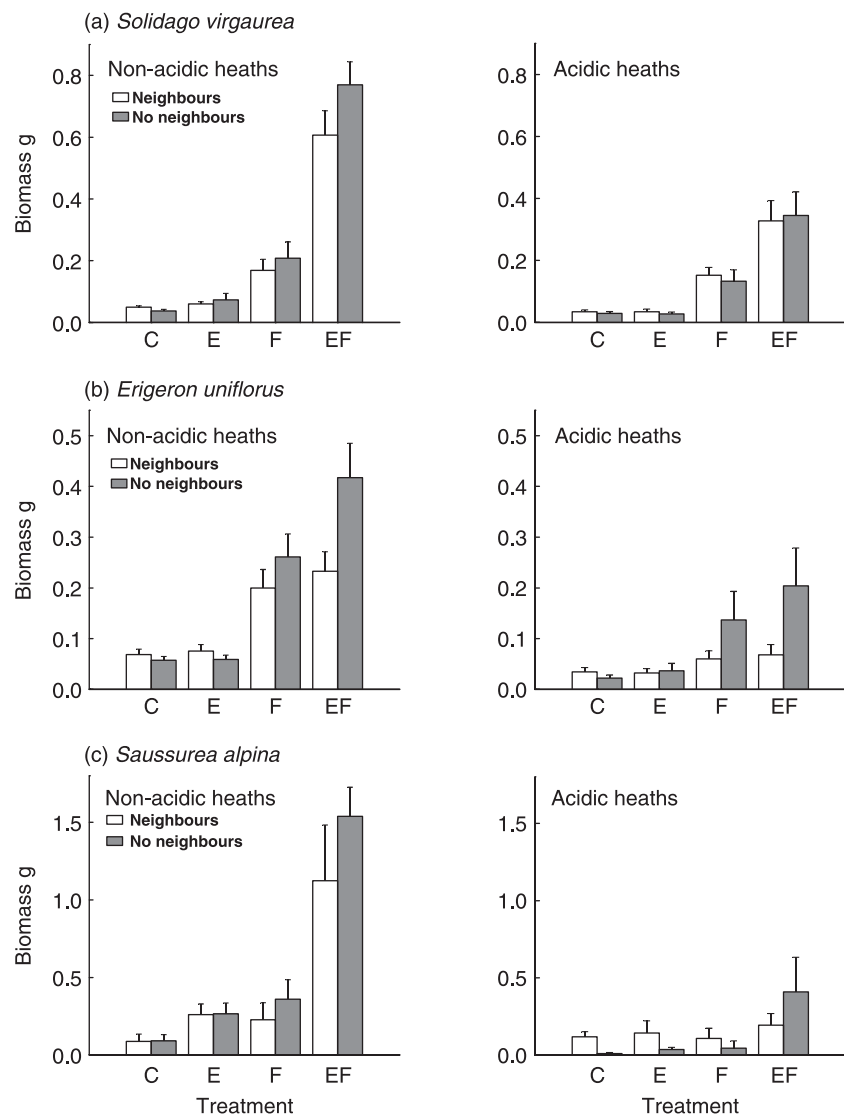
Fig. 2. Means and standard errors for aboveground biomass (g) of *Solidago virgaurea* (a), *Erigeron uniflorus* (b) and *Saussurea alpina* (c) with and without neighbours in different treatments and in non-acidic and acidic habitats. C, control; E, exclosure; F, fertilizer. Liming had no effect on the growth of transplants, and the data on limed plants were pooled among other treatments for the figures.

PLANT GROWTH RESPONSES TO HERBIVORY

The presence of herbivores had a negative effect on the growth of the two taller species, *Solidago* and *Saussurea*, as indicated by the significant main effect of herbivore exclusion (Table 1). For both species, the impact of herbivores differed between non-acidic and acidic heaths (significant herbivore exclusion × habitat interaction), and was contingent on fertilizer addition (significant herbivore exclusion × fertilizer addition interaction, Table 1). Grazers reduced plant above-ground biomass more in fertile non-acidic heaths than in infertile acidic heaths, as plant growth was much higher in fenced plots of non-acidic heaths than in those of acidic heaths (Fig. 2a,c). Similarly, the negative influence of grazers on plant biomass was greater in fertilized plots. Biomass production was greatest in fertilized plots in the absence of herbivores; however, the benefit for plants from added fertilizer was much less when plants were not protected from herbivores (Fig. 2a,c). These results indicate that much of the greater plant production in non-acidic heaths and in fertilized plots is consumed by herbivores. In *Solidago*, the herbivore exclusion × fertilizer addition interaction tended to be stronger in non-acidic than in acidic heaths, as indicated by a marginally significant three-way interaction between habitat, exclusion of herbivores and fertilizer addition (Table 1). In contrast, the smallest of the transplant species, *Erigeron*, was totally independent of herbivore presence, and there were no interactions with other treatments (Table 1, Fig. 2b).

PLANT GROWTH RESPONSES TO HABITAT AND ENVIRONMENTAL AMENDMENTS

Non-acidic heaths provided a more favourable growing environment for all three species, as indicated by the significant main effect of the habitat on plant growth (Table 1, Fig. 2a–c). Also, fertilizer addition significantly positively affected biomass production of all transplant species (Table 1, Fig. 2a–c). In all cases, fertilizing interacted significantly with the habitat, leading to a much greater increase in plant biomass in non-acidic than in acidic heaths. There was no effect of liming, either as a single factor or in interaction with other factors (Table 1). For the figures, data on limed plots were therefore pooled among other treatments.

REPRODUCTIVE SUCCESS IN RESPONSE TO HABITAT AND TREATMENTS

Only a fraction of transplants flowered or had their flowering stalks intact when the transplants were harvested. Of 253 surviving *Solidago* individuals, 46 (18%) plants had flowers. Similarly, 36 of 85 surviving *Saussurea* individuals (42%) and 82 of 231 surviving *Erigeron* individuals (35%) flowered at the end of the experiment. Habitat type significantly affected the flowering probability of *Solidago* ($\chi^2_1 = 5.6$, $P = 0.0182$), *Erigeron* ($\chi^2_1 = 21.5$, $P < 0.0001$) and *Saussurea* ($\chi^2_1 = 13.4$, $P = 0.0002$). Most flowering individuals of all three transplant species were found in non-acidic habitats (Fig. 3a–c). Mammal herbivores heavily influenced flowering of *Solidago*

and *Saussurea* ($\chi^2_1 = 25.1$, $P < 0.0001$ and $\chi^2_1 = 7.1$, $P = 0.0077$, respectively, Fig. 3a,c) with most of the flowering individuals found within exclosures. In unprotected plots, flowering stems had been eaten by reindeer. In contrast, flowering of *Erigeron* was totally unaffected by herbivore presence ($\chi^2_1 = 0.4$, $P = 0.5076$, Fig. 3b).

Nutrient availability significantly affected the flowering probability of *Solidago*: most of the sexually reproducing individuals were found in fertilized plots ($\chi^2_1 = 34.8$, $P < 0.0001$, Fig. 3a). Although the majority of sexually reproducing *Solidago* transplants were found in fertilized exclosures, there was no interaction between these factors. *Erigeron* significantly responded to the interaction between fertilizer addition and biomass removal ($\chi^2_1 = 4.3$, $P = 0.0389$). In fertilized plots, neighbour removal led to increased flowering frequency whereas in non-fertilized plots, neighbour removal led to slightly decreased flowering frequency (Fig. 3b). There were no further significant treatment effects on the flowering frequency of any transplant species.

HABITAT AND TREATMENT EFFECTS ON SOIL NUTRIENT AVAILABILITY AND PH

Soil nitrogen availability measured as extractable NH_4^+ concentration [mg kg^{-1} organic matter (OM)] was significantly higher in non-acidic than in acidic heaths ($F_{1,8} = 11.5$, $P = 0.0095$, Fig. 4). It was also significantly increased by fertilizer treatment ($F_{1,57} = 4.9$, $P = 0.0309$). However, fertilizer addition significantly interacted with exclosure ($F_{1,57} = 4.6$, $P = 0.0363$) in such a way that fertilizer increased soil NH_4^+ concentration only within exclosures, while there was no difference in soil NH_4^+ concentrations between fertilized and unfertilized plots outside the exclosures (Fig. 4). Soil pH was significantly higher in non-acidic than in acidic heaths (6.7 ± 0.04 and 5.7 ± 0.08, mean across all treatments ± SE, respectively, $F_{1,8} = 34.5$, $P = 0.0004$) and was significantly increased by liming ($F_{1,57} = 21.3$, $P < 0.0001$, 6.3 ± 0.08 and 6.1 ± 0.11, mean across habitats and other treatments in limed and unlimed plots, respectively). However, despite liming, soil pH remained clearly lower at acidic than at non-acidic sites (5.9 ± 0.07 and 6.8 ± 0.04, mean ± SE, respectively).

Discussion

DIRECT EFFECTS OF NUTRIENT AVAILABILITY AND ENVIRONMENT ON PLANT PERFORMANCE

Soil edaphic factors generally had a profound influence upon the performance of the three study species, emphasizing the importance of the abiotic environment for plant performance in alpine tundra. Acidic heaths were much less favourable sites for the growth, survival and sexual reproduction of transplants. This finding corresponds to the observed lower nutrient availability in acidic sites and may partly explain the general scarcity of forbs in these shrub-dominated, species-poor heaths (Gough *et al*. 2000; Peet *et al*. 2003; Nordin *et al*. 2004).
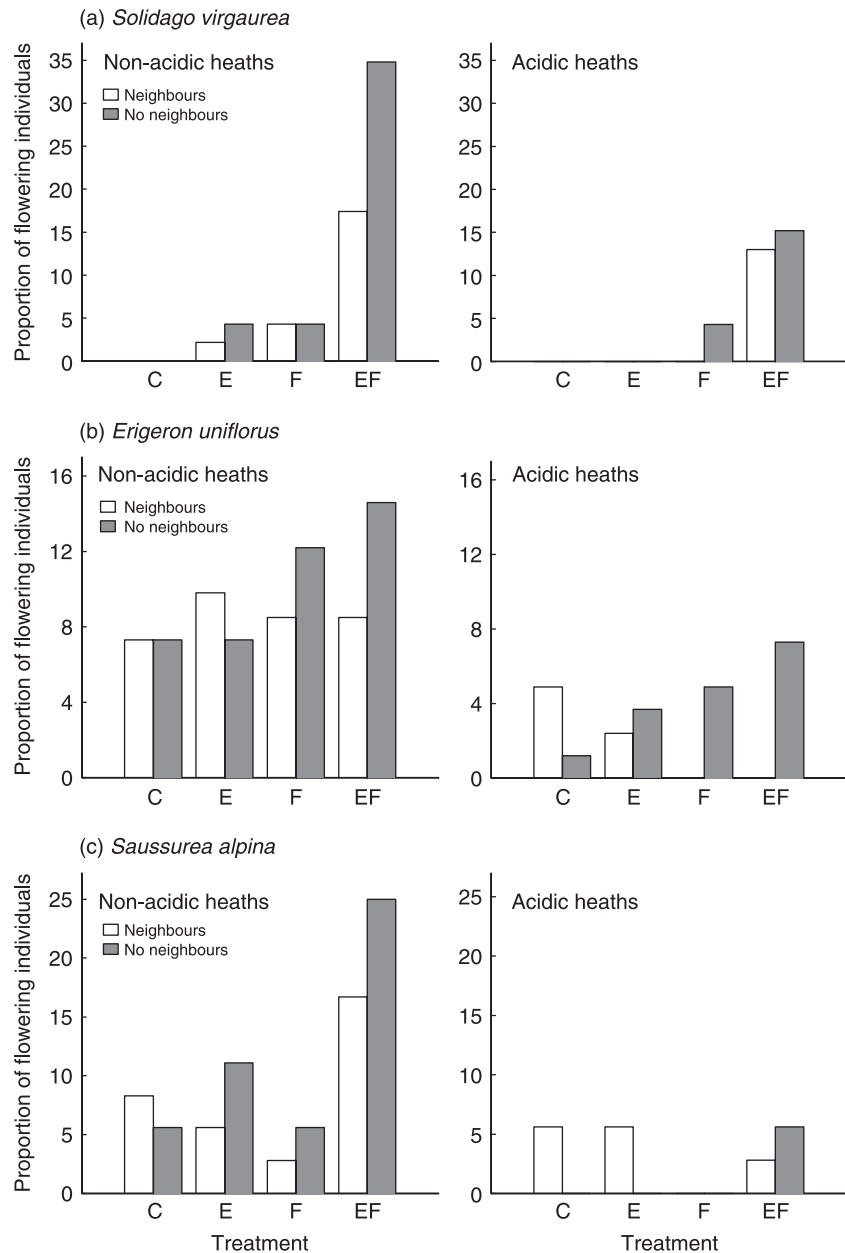
Fig. 3. Proportion of flowering individuals of *Solidago virgaurea* (a), *Erigeron uniflorus* (b) and *Saussurea alpina* (c) per total number of flowering individuals in different treatments with and without neighbours and in non-acidic and acidic habitats. C, control; E, exclosure; F, fertilizer. Liming had no effect on the flowering of transplants, and the data on limed plants were pooled among other treatments for the figures.

All the studied species also responded to nutrient addition, indicating nutrient-limited growth under natural conditions (see e.g. Shaver & Chapin 1980; Klanderud & Totland 2005; Gough *et al*. 2007). However, nutrient enrichment led to a greater growth increase in non-acidic than in acidic heaths, which was unexpected considering that acidic heaths are more nutrient-limited and therefore a proportionally greater response to nutrient addition could have been expected. This result suggests that, besides soil nitrogen availability, acidic and non-acidic habitats may also differ in soil functioning and physiological properties with disadvantageous composition of soil microbial communities, slow nutrient cycling, scarcity of mycorrhizal symbionts and abundance of allelopathic substances in shrub-dominated acidic heaths (Bååth & Anderson 2003; Männistö *et al*. 2007; A. Eskelinen, S. Stark & M. Männistö, unpublished data), which could all potentially affect plant

nutrient uptake and subsequent growth. In addition, soil pH, clearly lower at acidic sites despite liming, may further reduce nutrient supply rates to plants (Kinzel 1983). This environmental severity in terms of adverse soil conditions may constrain plants in acidic heaths from responding to short-term nutrient pulses.

EFFECTS OF NUTRIENT AVAILABILITY AND ENVIRONMENTAL CONDITIONS ON PLANT–PLANT INTERACTIONS

The surrounding vegetation negatively affected the growth of *Saussurea* and *Erigeron* under nutrient-enriched conditions, whereas the effect of neighbours was neutral or slightly positive when no nutrients were added. Neither competition nor facilitation was detected for *Solidago*, suggesting that
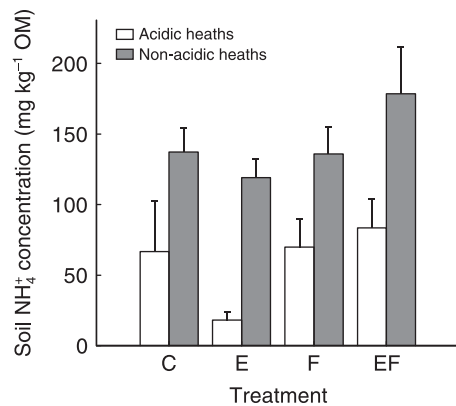
Fig. 4. Soil nitrogen availability measured as extractable NH_4^+ concentration (mg kg^{-1} OM, mean ± SE) in different treatments and in non-acidic and acidic habitats. C, control; E, exclosure; F, fertilizer. Liming had no effect on NH_4^+ concentrations in the soil, and the data on limed plots were pooled among other treatments for the figures.

the importance of neighbourhood interactions depends on the target species and associated plant traits. Nevertheless, the increase in the importance of competition with productivity for *Saussurea* and *Erigeron* provides support for the hypothesis of Grime (1973, 1979) that overall competition is more important at higher productivity. Small arctic–alpine species such as *Erigeron*, whose growth and flowering were most clearly positively affected by the removal of neighbours, are probably most easily suppressed by increased biomass of neighbouring vegetation (i.e. light competition) in response to nutrient enrichment. Furthermore, *Erigeron* and *Saussurea*, which are both arctic-alpine forbs adapted to a relatively narrow range of habitat conditions (i.e. relatively nutrient-rich habitats with low or intermediate biomass), may have especially profound responses to increased productivity. The reduced growth and sexual reproduction of *Erigeron* and *Saussurea* imply that competition for light may constrain 'specialist' arctic–alpine forbs if nutrient supply rates are increased in tundra ecosystems (see also Klanderud & Totland 2005). Tall 'generalist' species such as *Solidago*, with distributions covering a wide range of habitat productivity levels and a large geographical range, may be less influenced by neighbours.

In addition, growth and survival of *Saussurea* were negatively influenced by the presence of neighbouring vegetation in the fertile non-acidic heaths to which *Saussurea* is almost exclusively confined. In contrast, *Saussurea* survival was impaired by neighbour removal in the nutrient-poor acidic habitats where it rarely occurs. This result supports the hypothesis that net positive responses to neighbouring vegetation would be more likely in abiotically severe habitats near the distributional limits of a species, whereas net negative responses to neighbours would prevail in more benign habitats (e.g. Choler *et al.* 2001; Kikvidze *et al.* 2005). *Saussurea*, which was the only facilitated species, also seemed to respond most strongly to nutrient addition (see Fig. 2c), emphasizing that

Saussurea was the species most limited by low nutrient concentrations in controls but exhibited highest growth rate in nutrient-amended conditions. It appears that in nutrient-poor acidic heaths, nutrient concentrations are depleted below the tolerance of species with high nutrient demands (e.g. *Saussurea*) and such species are most likely to experience a net positive outcome of neighbourhood interactions (see Liancourt *et al.* 2005).

Despite the facilitative effects of neighbours on *Saussurea* survival in acidic heaths, the scarcity of forbs in these habitats indicates that positive plant–neighbourhood interactions may not have a selective impact on the occurrence of forbs at these sites. It is conceivable that the benefits of habitat amelioration by dense shrub cover (e.g. water retention and shelter against wind) are offset by extreme soil conditions (as discussed earlier) (Brooker *et al.* 2007), which maintain species-poor habitats where only a small group of ericaceous dwarf shrubs [i.e. the good nutrient competitors of Tilman (1988) or the stress tolerators of Grime (1979)] are able to thrive.

EFFECTS OF NUTRIENT AVAILABILITY AND ENVIRONMENTAL CONDITIONS ON PLANT–HERBIVORE INTERACTIONS

The growth and flowering of *Saussurea* and *Solidago*, and *Saussurea* survival, were highly affected by the presence of mammal herbivores. In contrast, *Erigeron* was totally independent of the presence of grazers, suggesting that the responses of these three species to herbivores are also species-specific. The characteristic low stature and hairy appearance of *Erigeron* are traits of alpine plants traditionally considered to be selected to cope with a severe abiotic environment (Körner 2003). However, these traits are also likely to be favoured because they affect grazer preference via both palatability (McNaughton 1978; Miller *et al.* 2007) and small stature in relation to neighbouring vegetation (e.g. Oksanen 1990; Mulder & Ruess 1998; Fowler 2002; Brooker *et al.* 2006). By contrast, *Solidago* and *Saussurea* are relatively tall species; their flowering stalks reach higher than the neighbouring vegetation. *Solidago* is also preferred forage for reindeer (Bråthen & Oksanen 2001) and is commonly favoured by the experimental exclusion of grazers (Virtanen 1998; Olofsson *et al.* 2002). These species-specific responses to grazers emphasize that, in the long term, intensive grazing and selective consumption of tall herbs may potentially act as a selective force leading to the evolution of low-statured herbaceous plants with structures that reduce their vulnerability to grazer attacks (Oksanen 1990).

The magnitude of herbivore effects on *Solidago* and *Saussurea* were stronger in nutrient-enriched conditions and in non-acidic heaths. The interactive effect of herbivore exclusion and nutrient enrichment on the growth of *Solidago* tended to be more pronounced in non-acidic than in acidic heaths. Moreover, plant responses to grazer exclusion and fertilization coincided with soil nitrogen concentration in experimental plots, which was virtually the same in fertilized and unfertilized plots outside the exclosures but clearly

increased by nutrient addition inside exclosures. These results together imply that the majority of the increased plant growth in response to nutrient enrichment is actually consumed by mammal herbivores. Similar results were recently reported from the Alaskan arctic tundra by Gough *et al.* (2007), who found that herbivores had a greater impact on the performance of graminoids and a deciduous shrub under amended nutrient conditions (see also Bonser & Reader 1995; Grellmann 2002). The results from this study and from the above cited studies provide evidence to support the predictions of Oksanen *et al.* (1981) and Oksanen (1990) that increased plant productivity leads to increased consumption by herbivores in relatively unproductive environments.

Empirical studies from more productive savanna ecosystems show how grazing ungulates selectively consume plant biomass in more nutrient-rich and productive sites (McNaughton *et al.* 1989; Milchunas & Lauenroth 1993; Augustine *et al.* 2003). Consistent with these savanna studies, my finding that the impact of herbivores on the performance of *Solidago* and *Saussurea* was greater in non-acidic than in acidic heaths is most probably caused by the greater productivity coupled with higher nutritional value of transplants in non-acidic habitats. In heterogeneous tundra landscapes, grazing by mammal herbivores appears to be concentrated in nutrient-rich habitats, which attract grazers and, consequently, are grazed to a greater extent.

The potentially strong role of grazers controlling plant performance was also seen in the reduction of flowering individuals of *Solidago* and *Saussurea* outside the fertilized exclosures. This finding concurs with the long-term observational data from the same study area suggesting that herbaceous plants suffer from intensive grazing pressure, potentially leading to seed limitation in populations of preferred plants, and increase when grazing pressure is relaxed (Eskelinen & Oksanen 2006). These results are also in agreement with other studies reporting a reduction in sexual reproduction of various plants in response to herbivory (Mulder & Ruess 1998; Van der Wal *et al.* 2000; Goheen *et al.* 2007). By suppressing plant growth, survival and sexual reproduction, grazers may impact the population dynamics of the preferred tall forbs and contribute to the observed plant distributions across tundra landscapes.

JOINT EFFECTS OF HERBIVORES AND PRODUCTIVITY ON NEIGHBOURHOOD INTERACTIONS

An unexpected result from my study was that plant–neighbourhood and plant–herbivore interactions operated independently, and the exclusion of mammal herbivores did not reinforce plant competition. This is contrary to predictions by Oksanen *et al.* (1981) and findings from other studies (Bonser & Reader 1995; Van der Wal *et al.* 2000; Olofsson *et al.* 2002; reviewed by Gurevitch *et al.* 2000). Nevertheless, the total above-ground biomass seemed to be greater inside fertilized exclosures, at least at non-acidic sites (my personal observation) and there was some indication (albeit not statistically significant) that the growth and flowering of transplants (Figs 2 and 3) were slightly increased by neighbour removal in these plots. As tundra vegetation generally reacts slowly to changed conditions it is possible that intensification of plant competition in the absence of herbivores may become significant after a time period longer than 2 years. Alternatively, the joint effect of herbivory and increased productivity on plant competition may operate via increased microsite limitation, with little effect on the performance of adult plants but with a profound impact on seedlings (Van der Wal *et al.* 2000; Stevens *et al.* 2004; Eskelinen & Virtanen 2005; Gough 2006).

Conclusions

My findings highlight that both abiotic environmental conditions and biotic interactions act to govern plant performance in low-productivity tundra ecosystems and that their effects are strongly interconnected. Soil nutrient availability and habitat type modify the direction and strength of plant–plant interactions, which vary from net neutral or positive responses in inherently nutrient-poor habitats and under natural nutrient concentrations, to net negative responses in fertile habitats and under nutrient-amended conditions. Similarly, plant–herbivore interactions are strongly contingent on soil resource availability and local environmental conditions. My results suggest that under nutrient-enriched conditions (e.g. increased nutrient mineralization and nutrient availability to plants under global warming; Nadelhoffer *et al.* 1991), individual plants preferred by mammal herbivores may not benefit from improved nutrient availability and subsequent growth, because added plant growth is counteracted by losses to grazers (see also Gough *et al.* 2007). In addition, in tundra landscapes with habitat patches of differing productivity, grazing pressure tends to be more intense in more productive patches, leading to a proportionally greater impact on the performance of preferred forbs in fertile habitats. By contrast, arctic–alpine specialists and low-statured forbs that are not preferred by grazers are limited by interspecific competition in productive habitats and fertilized conditions, and are prone to face population losses if global nutrient availabilities increase.

Acknowledgements

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