



Counterbalancing effects of competition for resources and facilitation against grazing in alpine snowbed communities

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Alpine snowbeds are habitats where the major limiting factors for plant growth are herbivory and a small time window for growth due to late snowmelt. Despite these limitations, snowbed vegetation usually forms a dense carpet of palatable plants due to favourable abiotic conditions for plant growth within the short growing season. These environmental characteristics make snowbeds particularly interesting to study the interplay of facilitation and competition. We hypothesised an interplay between resource competition and facilitation against herbivory. Further, we investigated whether these predicted neighbour effects were species-specific and/or dependent on ontogeny, and whether the balance of positive and negative plant–plant interactions shifted along a snowmelt gradient. We determined the neighbour effects by means of neighbour removal experiments along the snowmelt gradient, and linear mixed model analyses. The results showed that the effects of neighbour removal were weak but generally consistent among species and snowmelt dates, and depended on whether biomass production or survival was considered. Higher total biomass and increased fruiting in removal plots indicated that plants competed for nutrients, water, and light, thereby supporting the hypothesis of prevailing competition for resources in snowbeds. However, the presence of neighbours reduced herbivory and thereby also facilitated survival. For plant growth the facilitative effects against herbivores in snowbeds counterbalanced competition for resources, leading to a weak negative net effect. Overall the neighbour effects were not species-specific and did not change with snowmelt date. Our finding of counterbalancing effects of competition and facilitation within a plant community is of special theoretical value for species distribution models and can explain the success of models that give primary importance to abiotic factors and tend to overlook interrelations between biotic and abiotic effects on plants.

Snowbed habitats are a common component of alpine areas, where they are usually found in depressions and hollows or lee sides of ridges. These habitats are characterised by a very long lasting snow cover of eight to ten months which limits plant biomass production due to the short time available for photosynthesis (Kammer and Möhl 2002). Consequently, following the definition by Grime (1977), the short growing season can be considered a factor of stress. These peculiar habitats are inhabited by a variety of highly specialised species that form a distinctive type of plant community (Choler 2005). Several species in snowbeds are even restricted to these habitats (Tomaselli 1991, Stanton et al. 1994). Consequently, snowbeds make up a unique component of alpine biodiversity. Another distinctive quality of snowbed habitats are the rather favourable environmental conditions for plant growth during the short growing season. The thick and long lasting snow pack in snowbeds is a large source of nitrogen (Bowman 1992), and since soils in snowbeds rarely experience temperatures below -1°C (Baptist and Choler 2008), they

allow for microbial activity even during wintertime (Schimel et al. 2004). This results in a high ratio of net nitrogen mineralisation to plant biomass nitrogen, indicating that plant growth in snowbeds is not nitrogen limited (Makarov et al. 2003). Further, water availability in snowbeds is typically rather high compared to other alpine habitats (Vonlanthen et al. 2006a). Other important factors limiting plant life in the alpine zone, namely wind effects and soil movement, are negligible (Kammer and Möhl 2002, Vonlanthen et al. 2006a). Damages caused by frost are also rare due to the protection by the snow pack and late flowering (Inouye 2008). Indeed, the time deficit is very often the single abiotic limiting factor for plant growth in snowbeds.

The stress-gradient hypothesis links environmental severity levels to plant–plant interactions. It predicts facilitation in stressful habitats due to an amelioration of environmental severity by stress-tolerant benefactor species, and competition under more favourable growth conditions (Bertness and Callaway 1994, Brooker and Callaghan 1998). Although plant

growth in snowbeds is environmentally limited by a very short growing season, this abiotic factor is hardly ameliorable by plants and may be difficult to reconcile with the stress-gradient hypothesis. Therefore, since the growth conditions within the very short growing season are rather favourable, we hypothesise that competition for resources predominates in snowbeds. Further, we hypothesised that the balance between competition and facilitation may not change along a gradient of growing season length, because plants occurring in snowbeds cannot impinge on this abiotic environmental constraint.

Snowbeds also provide a dense carpet of tiny and palatable plants on generally flat areas and are therefore frequently visited by different types of herbivores (Olofsson et al. 2002). Herbivory can affect the dynamic balance between competition and facilitation (Brooker and Callaghan 1998, Callaway 2007, Smit et al. 2009). Callaway (2007) distinguished two different types of indirect facilitative effects of neighbouring species against herbivory: shared defense (i.e. beneficiary species benefit from heavily defended plant neighbours) and associational resistance (i.e. beneficiary species benefit from being hidden in a crowd of other palatable plant neighbours). Plant species with anti-herbivore characteristics are very rarely found in snowbeds. However, we hypothesised that the dense carpet of tiny plants serves as a type of associational resistance for individual plants against herbivores.

Previous studies also showed that plant species experience different effects from their neighbours depending on their distributional optimum (Wang et al. 2008) and their strategy (Chen et al. 2009). In an alpine meadow community Wang et al. (2008) found that species showed weak facilitative responses at their distributional optimum, where they are most abundant and dominant. However, species at the periphery of their optimum showed strong facilitative responses (Choler et al. 2001). In particular the competitive species benefit from facilitative effects of neighbouring (stress-tolerant) species, whereas stress-tolerant species, generally acting as benefactors, most often suffer from their beneficiary competitive species (Liancourt et al. 2005, Michalet et al. 2006, Chen et al. 2009). Only under extremely severe environmental conditions stress-tolerators may benefit from facilitation by other stress-tolerant plants (Michalet et al. 2006, Chen et al. 2009). Based on this knowledge we hypothesised that species differing in their distribution and strategy may show species-specific responses to neighbour removal in snowbeds.

The abiotic and biotic characteristics and their peculiarities make snowbeds particularly interesting for studying plant-plant interactions to improve our understanding of the interplay between facilitation and competition. We measured plant-plant interactions by means of neighbour removal experiments set along a snowmelt gradient, and tested six target species with different ecological characteristics. Our specific aims were: (1) to test our prediction about the predominance of competition, (2) to test the presence of facilitative interactions protecting plants from grazing, (3) to test for species-specific responses of plants to neighbour removal, and (4) to test whether the balance of net plant-plant interactions changes along the snowmelt gradient. We measured plant responses to experimental manipulations

in terms of biomass accumulation, fruiting, mortality and effects of herbivores on biomass and mortality, and analysed the data with general and generalised linear mixed effects models.

Methods

Field site

Twenty-four spatially separated snowbeds were studied in the western part of the Central Alps at the Gemmi Pass, Leukerbad, Switzerland (2400 m a.s.l., 46°25'N, 7°37'E). They were located within an area of approximately 0.3 km² and had an average distance of 119 m ± 62 m SD between each other.

In the Gemmi Pass region, total annual precipitation amounts to 2100 mm, of which about two-thirds fall as snow (this and the following climatic data of the study area are from Döbeli 2000). The precipitation between July and September totals to 350 mm on average. The mean annual temperature is close to 0°C. The mean summer temperature from July to September is generally between 6°C and 9°C. Snowbeds were located in northeast/southwest-directed hollows where the predominating northwesterly winds accumulate snow during wintertime. Soil moisture conditions were mesic with low soil suction values (Vonlanthen et al. 2006a, Schöb unpubl.). Additional information on soil properties is provided in Schöb et al. (2009). The two main herbivores in the study area were occasionally grazing sheep and caterpillars of *Zygaena* sp.

Vegetation in the snowbeds under study belonged to the class of *Salicetea herbaceae*-snowbed communities (according to Ellenberg 1996). The three most abundant (by cover) vascular plant species were *Alchemilla pentaphylla*, *Salix herbacea* and *Gnaphalium supinum*. Vascular plant species covered 72% of the snowbed area and this cover was constant over the whole snowmelt gradient under study (Schöb et al. 2009). The remaining 28% of the snowbed area was covered by bryophytes (15%), lichens (3%), and bare ground (10%). Plant size of all species occurring in snowbeds was consistently low (mean canopy height approximately 5 cm). Peak standing biomass was 14.5 g m⁻² with a vegetation cover of 85% (Vonlanthen et al. 2006b).

Snowmelt gradient

During our weekly visits at the study site in 2003, we localised 40 plots with four different snowmelt dates within the snowbeds: 2 June (Julian day 153, six plots), 9 June (Julian day 160, 13 plots), 16 June (Julian day 167, 13 plots), and 23 June (Julian day 174, eight plots). Plots represent a defined area within a particular snowbed with a specific snowmelt date. During the experiment, the snowmelt dates were later on average compared to 2003, i.e. 15 days later in 2005, 17 days later in 2006, and eight days later in 2007. Nevertheless, the snowmelt regime, i.e. the chronological ranking of the plots becoming snow-free, was constant over these years. For convenience, we refer to the original snowmelt dates in 2003 when analysing the effect of snowmelt date.

Target species

We selected six frequent species in snowbeds that represent a range of relative abundances and different distribution patterns along the snowmelt gradient, but that occur over the whole snowmelt gradient under study. In previous studies we distinguished four species groups with distinct frequency and distribution patterns along the snowmelt gradient within snowbed communities (Schöb et al. 2008, 2009). Two species groups showed an even distribution in snowbeds along the snowmelt gradient: (1) dominant species showing high frequency and abundance with later snowmelt, thereby indicating a distributional optimum inside snowbeds and a relatively good competitive strength; (2) indifferent species showing high frequency but lower abundance, indicating no distributional optimum in snowbeds and less competitive strength compared to the dominant species. The other two species groups showed a distribution pattern that significantly changed along the snowmelt gradient: (3) mesic grassland species significantly decreasing in frequency and abundance with later snowmelt date, which is indicative of a distributional optimum outside snowbeds and lower stress tolerance compared to the other species groups, and (4) subordinate snowbed species showing the converse distribution pattern, indicative of a distributional optimum inside snowbeds and high stress tolerance (Fig. 1). To represent the group of dominant species in snowbeds, we selected *Alchemilla pentaphylla*. This species forms rosettes usually consisting of five leaves and offshoots by means of creeping shoots. The dominant species *Salix herbacea* was not used in the experiments because it was too difficult to find discrete individuals for this species. We selected *Poa alpina* to represent the indifferent species. It is an ubiquitous graminoid caespitose species forming dense tussocks. We selected *Ligusticum mutellina* and *Polygonum viviparum* from the group of grassland species, and *Cardamine alpina* and *Veronica alpina* from the group of subordinate snowbed species. We observed that *L. mutellina* and *P. viviparum* usually formed one basal leaf each year and they flowered in the year when the fourth leaf

was formed (Diggle 1997). *Cardamina alpina* forms leaves arranged like a rosette. *Veronica alpina* is the only species under study forming shoots without a basal leaf rosette.

We chose target individuals that were well established, but not flowering yet. We looked for distinct individuals to minimise the effects of clonal connections. However, we cannot absolutely exclude the possibility of belowground connections for the rhizomatous species (*C. alpina*, *L. mutellina*, *P. viviparum* and *V. alpina*).

Experimental design

For each species we chose 10 pairs of individuals for each snowmelt date. Individuals of each pair were chosen as similar as possible regarding leaf number and leaf length (shoot height for *V. alpina*). The two individuals of each pair were located within the same plot, far enough from each other to prevent physical connections between them, but close enough to disregard the effect of micro-environmental differences on individual performance. Each target individual was marked for retrieval with an insulated wire ring. In total 480 target individuals were investigated (six species \times two treatments (removal/control) \times four snowmelt dates \times 10 replicates).

To manipulate plant–plant interactions, we randomly applied a neighbour removal treatment to one individual of each pair, removing all aboveground biomass of the neighbouring vegetation around the target individual. The area clipped was 5 cm in radius around the target individual ($\approx 0.008 \text{ m}^2$). Target individual performance was compared to that of the respective control individual around which neighbouring plants were left intact. With this approach we could determine the effect of diffuse interaction (Wilson and Keddy 1986) rather than species-specific interactions. Since plants in snowbeds are very small, 5 cm is a sufficient clearance to prevent shading and contact of the target plant shoots with those of neighbouring plants. However, some interference through belowground resources cannot be excluded, because belowground manipulation was avoided to prevent

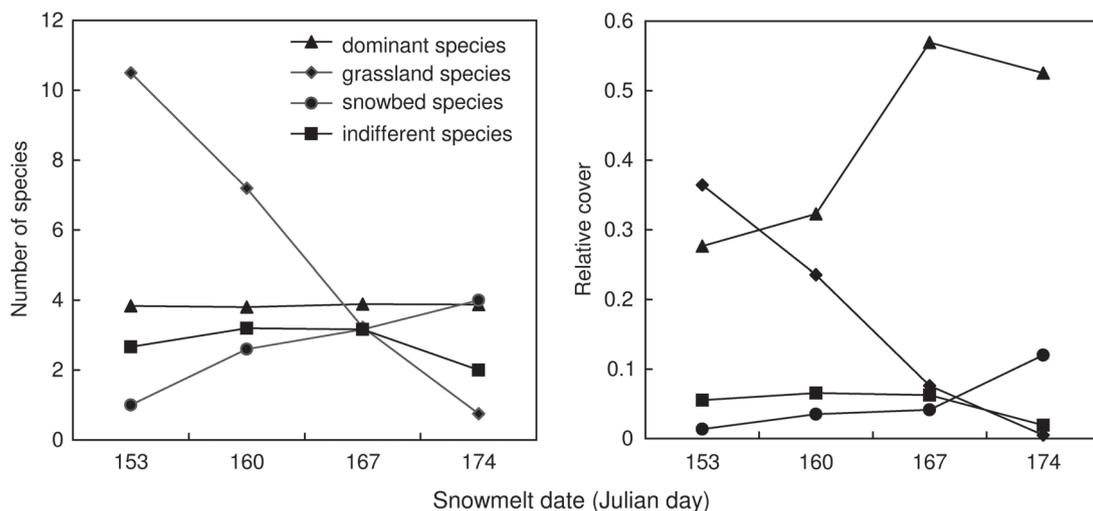


Figure 1. Number of species (left panel) and relative cover (right panel), determined by estimation of percentage cover, for dominant species, grassland species, subordinate snowbed species, and indifferent species along the snowmelt gradient within snowbeds. Data from Schöb et al. (2009).

disturbance to the roots of target individuals. This is particularly important since most of the species are assumed to be mycorrhizal (Vare et al. 1997), and infection by mycorrhizal mycelium can greatly affect plant performance (McLellan et al. 1995).

The removal experiments were set up during the growing season 2005 between 19 July and 8 August, about four weeks after snowmelt, i.e. just before peak biomass. The neighbour removal treatment was applied to plots according to the order of snowmelt date. The occasional regrowth in 2005 was removed again four weeks after the onset of the experiment. During each of the two following growing seasons, aboveground vegetation at the margins of each circle was cut back to the original radius twice to remove the sparse aboveground regrowth of previously clipped vegetation.

The number of leaves and leaf length (for *V. alpina* shoot height) was determined at the beginning of the experiment in 2005, when the treatments were established, and again in the two successive years at the time when peak biomass was estimated (8 to 10 August 2006 and 31 July to 1 August 2007). This corresponds to a growing period of about 50 days in the earliest melting sites and 30 days in the latest melting sites each year. Data were always collected in the order of snowmelt date. In 2006 and 2007 mortality, presence or absence of fruiting and herbivory, and the estimated biomass losses due to herbivory, particularly by caterpillars and sheep, were additionally recorded. To allow for the analyses of year-effects on herbivory and mortality, at the end of the growing season 2006 dead target plants were replaced by conspecific individuals. These replacement-plants were only used for the analyses of herbivory and mortality to get an equal sample size each year. They were omitted from the analyses of biomass, leaf morphometry and fruiting, since the performance of these variables in the second year of the experiment is assumed to depend on the first year. At the end of the experiment (13 and 14 August 2007) the aboveground parts of all original surviving targets were harvested before dissemination and biomass was determined for the non-flowering (i.e. vegetative) and the flowering (i.e. generative) parts of each individual separately after drying at 70°C for three days.

Data analyses

In some plots, we had to sample more than one pair of individuals of a particular target species due to the small number of plots for the first and latest snowmelt date and the fact that not all target species occurred in every plot. Therefore, the grouping structure of the data was as follows: 'snowmelt date' varied between plots, 'species' varied between pairs of individuals within plots and treatments varied between individuals within pairs. In all subsequent analyses we took this grouping structure into account by including plots and species within plots as random factors into the models. The random factor 'snowbed' was also tested but the results were very similar to the models with the random factor 'plot'. Therefore, we omitted the factor 'snowbed' from the grouping structure and tested in the subsequent models the factor 'species' on the 'plot × species' level ($n=183$), 'snowmelt date' on the 'plot' level ($n=42$) and 'treatment' on the residual level.

To analyse the effect of species, snowmelt date and treatment on aboveground biomass, linear mixed effects models (LMM) were run by the statistical software package R ver. 2.8.1 (R Development Core Team 2008) using the lmer function of the lme4 library (Bates et al. 2008). The model fit was calculated using the restricted maximum likelihood (REML) criterion. To select a model, we compared a number of models with one supplementary argument, selecting the model with the lowest AIC value (best fit). In addition, we calculated Akaike weights indicating the probability that the model is the best among the whole set of candidate models and evidence ratios resembling the extent to which the selected model is better than any of the competing models.

The repeated measures of the estimated biomass loss due to herbivory and of the leaf morphometry parameters (number of leaves and leaf length) were analysed using LMM with the same methods as mentioned above for the biomass data. Species, snowmelt date, treatment and additionally year were treated as fixed factors and each target individual (= subject identity) as an additional random factor nested within species within plots to take the repeated measures for each individual into account. For the analysis of the estimated biomass loss due to herbivory we excluded all individuals with no damage due to herbivory. For leaf morphometry parameters, we took potential effects of initial values of number of leaves and leaf length on the results obtained into account by subtracting the value of the leaf parameter measured at the onset of the experiment in 2005 from the measured values in 2006 and 2007 prior to analyses.

To analyse the repeated measures of binomial response variables such as mortality, presence/absence of herbivory, and fruiting we used generalized linear mixed effects models (GLMM) with a binomial distribution and a logit link function (lmer function of the lme4 library). The model fit was calculated using Laplace approximation under consideration of the same factors as mentioned above for LMM with repeated measures. Model selection was also performed according to the criteria described above for LMM.

Results

Biomass

Variation in total aboveground biomass could be attributed to species, snowmelt date and treatment effects. The best-supported model included these three main effects without interaction terms (Table 1). Mean aboveground biomass of the individuals in the removal plots was 22% higher than in the control plots (Fig. 2). However, differences in total aboveground biomass between control and removal plots were mostly due to the increased biomass allocation to the flowering parts of plants in the removal plots. Whereas the biomass of the flowering plant parts of individuals in the removal plots was 14% of their total aboveground biomass, it was only 7% of total aboveground biomass in the control plots.

Along the snowmelt gradient an increase in aboveground biomass of more than 72% from the first to the latest snowmelt date was observed (Fig. 2) despite significantly less time for growth with later snowmelt. However, the treatment effect did not significantly change along the snowmelt gradient,

Table 1. Model comparison for the effects of species, snowmelt date, and treatment on total aboveground biomass by Akaike's information criterion (AIC), Akaike weights (ω_i), and evidence ratios (E). Factors: treatment (Treat): removal and control; snowmelt date (Snow): Julian day 153, 160, 167, and 174; species (Spec): *Alchemilla pentaphyllea*, *Cardamine alpina*, *Ligusticum mutellina*, *Poa alpina*, *Polygonum viviparum* and *Veronica alpina*. The model with the lowest AIC and the highest probability to be the best model is in bold, additional models with $\Delta AIC \leq 2$ in italics. $n=382$ (dead plants omitted). Corresponding figures: Fig. 2 and 3.

Model	DF	Total aboveground biomass		
		AIC	ω_i	E
Intercept	4	-1910	<0.001	<0.001
Spec	9	-1941	0.074	0.162
Spec + Treat	10	-1944	0.255	0.557
Spec + Snow	12	-1943	0.135	0.295
Spec + Snow + Treat	13	-1945	0.458	1
Spec + Snow \times Treat	16	-1941	0.076	0.166
Spec \times Snow + Treat	28	-1931	<0.001	<0.001
Spec \times Snow \times Treat	51	-1905	<0.001	<0.001

i.e. an inclusion of the interaction term between snowmelt date and treatment did not improve the model. Accordingly, biomass_{control-removal} showed no significant differences between snowmelt dates (Fig. 3).

Species showed obvious differences in biomass (Fig. 2): aboveground biomass of the two grassland species (*L. mutellina* and *P. viviparum*) and the dominant species (*A. pentaphyllea*) was at least twice as much as the biomass of the two subordinate snowbed species (*C. alpina* and *V. alpina*). The mean individual biomass of all species was higher in the latest melting sites compared to the earliest ones (no species \times snowmelt date interaction).

The plants generally responded to neighbour removal by producing more leaves of smaller size (Supplementary material Appendix 1).

Mortality and herbivory

Mortality was different between species, snowmelt dates, treatments and years (Table 2a). In general, neighbour

removal increased mortality from 8.5% to 13.1% (Fig. 4). Along the snowmelt gradient, mortality increased from 3.8% in the earliest melting sites to 15.8% in the latest melting sites (Fig. 4), but the treatment effect was constant along the snowmelt gradient, i.e. the interaction term 'treatment \times snowmelt date' did not improve the model (Table 2a). Mortality was highest in subordinate snowbed species, intermediate in grassland species and lowest in the dominant species *A. pentaphyllea* (Fig. 4). Mortality was higher in 2007 than 2006. The difference between years was most pronounced for the subordinate snowbed species (8% in 2006, 33% in 2007), whereas for grassland species the difference was lower (9% in 2006, 17% in 2007).

Presence/absence of herbivory (Table 2b) as well as the estimated biomass loss due to herbivory (Table 3) differed between species, treatments and years, but did not differ along the snowmelt gradient. The presence of herbivory was 17% higher in removal plots compared to control plots (Fig. 5a) and the estimated biomass loss due to herbivory was 78% higher in removal plots (Fig. 5b). Further, the presence of herbivory was highest for the grassland species and *A. pentaphyllea*, and at least two times lower for *P. alpina* and the subordinate snowbed species (Fig. 5a). However, the estimated biomass loss due to herbivory was highest for the small growing *C. alpina*, followed by *V. alpina*, the other subordinate snowbed species (Fig. 5b). The presence of herbivory was slightly higher in 2006 (mean₂₀₀₆=0.26) than in 2007 (mean₂₀₀₇=0.21). However, the estimated biomass loss due to herbivory was markedly higher in 2007 (mean₂₀₀₆=0.09, mean₂₀₀₇=0.29).

If herbivory-induced mortality was excluded, survival was estimated as 0.94 for individuals in control plots but 0.93 for individuals in removal plots. Consequently, for mortality without herbivory-induced mortality a model without treatment was slightly better and indicated no significant treatment effect (Table 2c). Thus, the higher mortality in removal plots was particularly due to the increased herbivory in these plots.

Fruiting

The occurrence of fruiting was different between species, snowmelt dates, treatments and years (Table 4). In general,

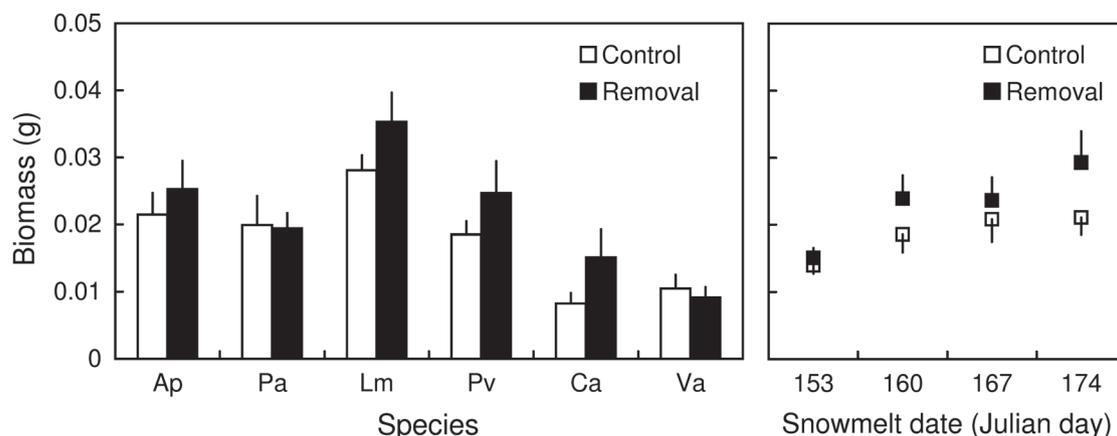


Figure 2. Mean individual aboveground biomass + 1 SE by treatment for the six study species (left panel) and the four snowmelt dates (right panel). $n=382$ (dead plants were excluded). The figure corresponds to Table 1. Dominant species: Ap = *Alchemilla pentaphyllea*; indifferent species: Pa = *Poa alpina*; grassland species: Lm = *Ligusticum mutellina*, Pv = *Polygonum viviparum*; subordinate snowbed species: Ca = *Cardamine alpina*, Va = *Veronica alpina*.

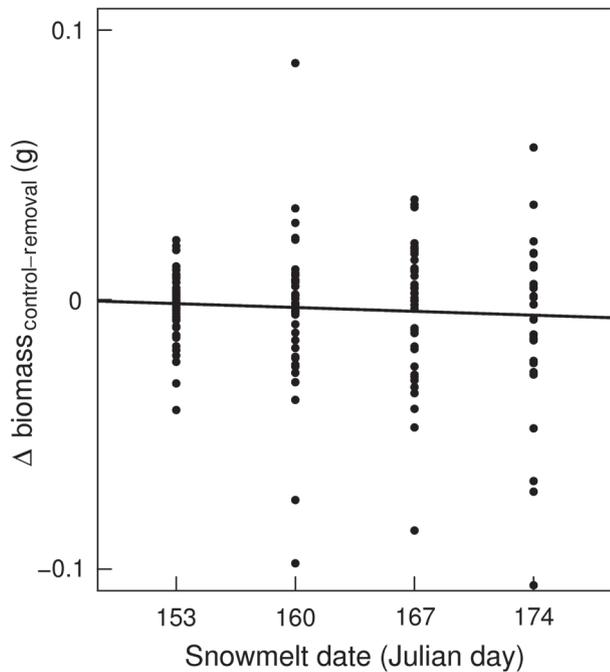


Figure 3. Differences (Δ) in biomass (of control individuals–removal individuals) for each treatment pair (treatment pairs with dead individuals were excluded). $n=158$. This figure corresponds to the treatment \times snowmelt date effect of the models presented in Table 1.

removal of neighbouring vegetation increased fruiting by 79% (Fig. 6). In addition, there was also a vague influence of the interaction between the snowmelt gradient and the treatment on fruiting observed. From the earliest to the latest snowmelt date, fruiting increased by more than three times. There were also significant differences in the fruiting occurrence between species: *L. mutellina* showed almost no fruiting, whereas for the other five species fruiting occurrence reached 20–23%.

The occurrence of fruiting was higher in 2006 ($\text{mean}_{2006}=0.22$) than in 2007 ($\text{mean}_{2007}=0.13$).

Discussion

Competition for resources

The effects of the neighbour removal treatment were generally weak and depended on the response variable considered. Our results for biomass accumulation and fruiting generally supported our hypothesis that competition is relatively intense compared to facilitation in alpine snowbed communities. These results are in line with the findings of Onipchenko et al. (2009) in alpine snowbed communities in the north-west Caucasus, Russia. Choler et al. (2001) and Michalet et al. (2002) also found less facilitation in snow rich or more mesic sites along topographical gradients at high elevations. Similarly, Wipf et al. (2006) detected a decrease in facilitation along an artificial snowmelt gradient in the subarctic tundra. This indicates that snowbed plants can tolerate a reduced length of the growing season, but they cannot ameliorate this type of growth limitation. Therefore, snowbeds are difficult to

Table 2. Model comparison for the effects of species, snowmelt date, treatment, and year on mortality (a), presence/absence of herbivory (b), and mortality without herbivory-induced mortality (c) by Akaike's information criterion (AIC), Akaike weights (ω_i), and evidence ratios (E). Factors: treatment (Treat): removal and control; snowmelt date (Snow): Julian day 153, 160, 167, and 174; species (Spec): *Alchemilla pentaphyllea*, *Cardamine alpina*, *Ligusticum mutellina*, *Poa alpina*, *Polygonum viviparum* and *Veronica alpina*; and year (2006 and 2007). The model with the lowest AIC and the highest probability to be the best model is in bold, additional models with $\Delta\text{AIC} \leq 2$ in italics. $n=960$. Corresponding figures: Fig. 4 (mortality), Fig. 5a (herbivory P/A).

Model	DF	AIC	ω_i	E
(a) Mortality				
Intercept	4	655	<0.001	<0.001
Spec	9	641	<0.001	<0.001
Spec + Treat	10	638	<0.001	<0.001
Spec + Snow	12	630	<0.001	<0.001
Spec + Snow + Treat	13	626	<0.001	<0.001
Spec + Snow + Year	13	615	0.117	0.145
Spec + Snow + Treat + Year	14	611	0.808	1
Spec + Snow \times Treat	16	631	<0.001	<0.001
Spec + Snow \times Treat + Year	17	615	0.073	0.091
Spec \times Snow + Treat + Year	29	626	<0.001	<0.001
Spec \times Snow \times Treat + Year	52	641	<0.001	<0.001
(b) Herbivory P/A				
Intercept	4	984	<0.001	<0.001
Spec	9	940	0.069	0.143
Spec + Treat	10	940	0.080	0.166
Spec + Treat + Year	11	936	0.483	1
Spec + Snow	12	943	0.019	0.039
Spec + Snow + Treat	13	942	0.022	0.045
Spec + Snow + Treat + Year	14	939	0.130	0.270
Spec \times Treat + Year	16	938	<i>0.164</i>	<i>0.340</i>
Spec + Snow \times Treat	16	947	0.002	0.004
Spec + Snow \times Treat + Year	17	944	0.011	0.023
Spec \times Snow + Treat + Year	29	943	0.019	0.040
Spec \times Snow \times Treat + Year	52	957	<0.001	<0.001
(c) Mortality (without herbivory-induced mortality)				
Intercept	4	512	<0.001	<0.001
Spec	9	499	0.052	0.16
Spec + Treat	10	500	0.026	0.078
Spec + Snow	12	495	<i>0.272</i>	<i>0.831</i>
Spec + Snow + Treat	13	497	<i>0.135</i>	<i>0.411</i>
Spec + Snow + Year	13	495	0.328	1
Spec + Snow + Treat + Year	14	496	<i>0.163</i>	<i>0.497</i>
Spec + Snow \times Treat	16	502	0.011	0.032
Spec + Snow \times Treat + Year	17	501	0.013	0.039
Spec \times Snow + Year	28	508	<0.001	0.001
Spec \times Snow + Treat + Year	29	510	<0.001	<0.001
Spec \times Snow \times Treat + Year	52	529	<0.001	<0.001

classify within current schemes of stress and have to be added to the cases for refinement of the stress-gradient hypothesis according to Maestre et al. (2009).

Plants in snowbeds probably compete for belowground resources. We did not directly manipulate root competition, but the sparse regrowth of previously clipped vegetation in the removal plots indicates that our treatment by clipping aboveground vegetation probably had a negative impact on belowground plant structures. Therefore, belowground competition of the clipped neighbours should have been considerably reduced (Pennings and Callaway 1992) and could, together with reduced aboveground competition, have led to

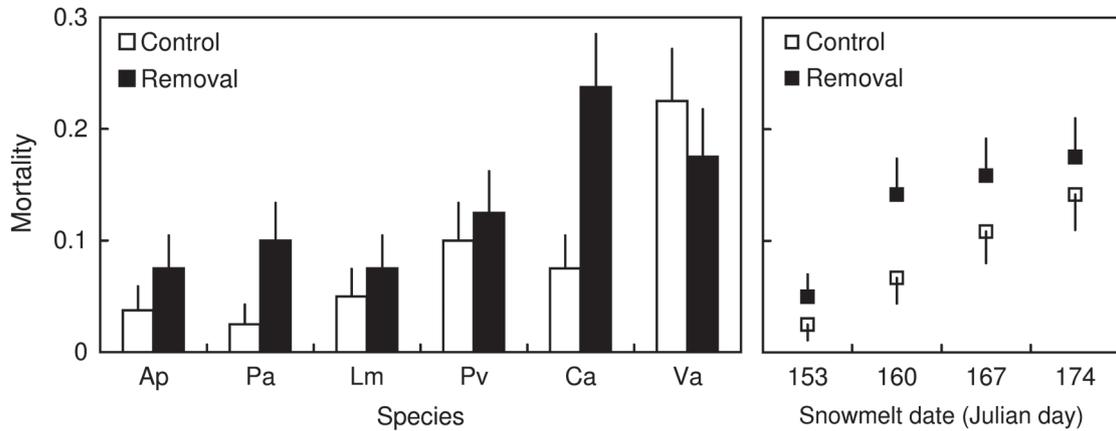


Figure 4. Mean mortality + 1 SE by treatment for the six study species (left panel) and the four snowmelt dates (right panel). $n=960$. The figure corresponds to Table 2. Dominant species: Ap = *Alchemilla pentaphylla*; indifferent species: Pa = *Poa alpina*; grassland species: Lm = *Ligusticum mutellina*, Pv = *Polygonum viviparum*; subordinate snowbed species: Ca = *Cardamine alpina*, Va = *Veronica alpina*.

increased biomass and fruiting of target individuals grown without neighbours. In addition, the long lasting snow results in a synchronous start of growth for all species in snowbeds. As a consequence, the amplified coincidence of species' resource demands may intensify competition due to the high capacity of resource acquisition and the accompanied high relative growth rate of snowbed species (Choler 2005). This short time period available for resource uptake was

also observed in water-limited ecosystems, where temporal pulses of resource supply are common and competition among species of similar life forms during these pulses is high (Novoplansky and Goldberg 2001). Further, the observed increase in leaf number and decrease in leaf length due to neighbour removal may indicate light competition. Our morphometric observations are consistent with the well-known response to better light quality: an increased red to far-red ratio usually

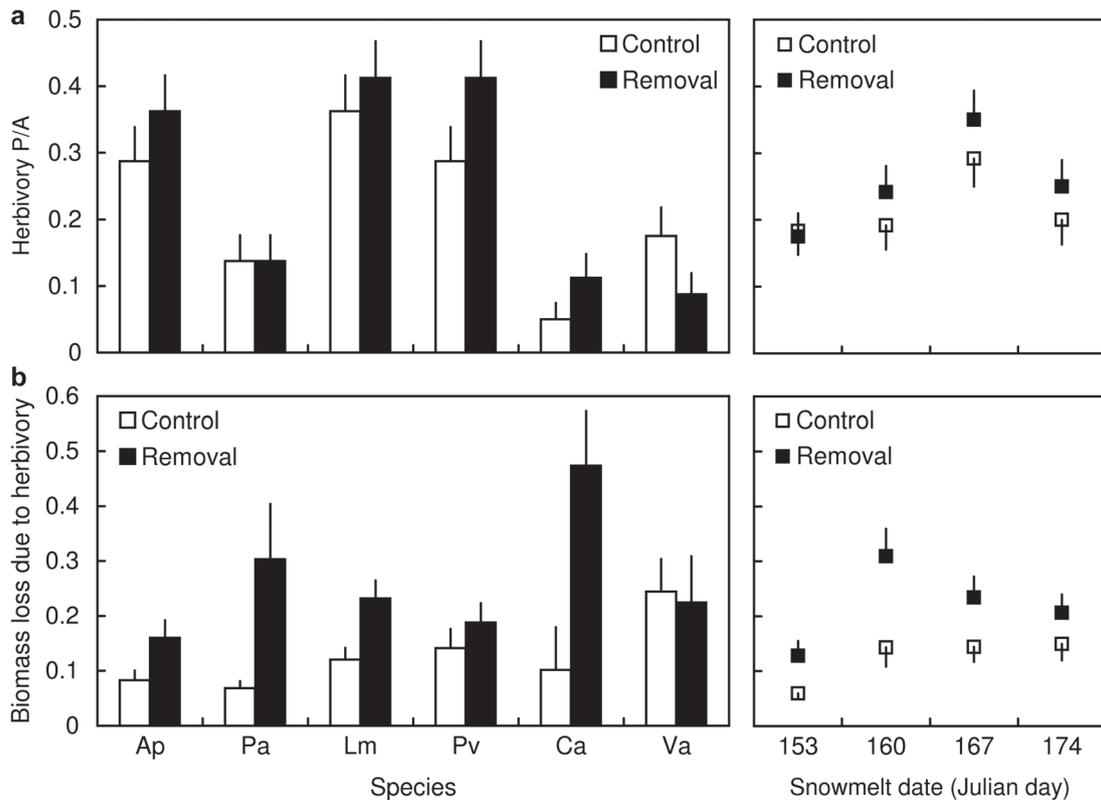


Figure 5. Mean presence/absence (P/A) of herbivory (a) and mean estimated biomass loss due to herbivory (b) + 1 SE by treatment for the six study species (left panel) and the four snowmelt dates (right panel). Biomass loss due to herbivory was determined by estimating shortage of aboveground biomass due to herbivory. $n=960$ for herbivory P/A, $n=226$ for biomass loss due to herbivory (only individuals with herbivory included). The figure corresponds to Table 2 for herbivory P/A and Table 3 for biomass loss due to herbivory. Dominant species: Ap = *Alchemilla pentaphylla*; indifferent species: Pa = *Poa alpina*; grassland species: Lm = *Ligusticum mutellina*, Pv = *Polygonum viviparum*; subordinate snowbed species: Ca = *Cardamine alpina*, Va = *Veronica alpina*.

Table 3. Model comparison for the effects of species, snowmelt date, treatment, and year on the estimated biomass loss due to herbivory by Akaike's information criterion (AIC), Akaike weights (ω_i), and evidence ratios (E). Factors: treatment (Treat): removal and control; snowmelt date (Snow): Julian day 153, 160, 167, and 174; species (Spec): *Alchemilla pentaphyllea*, *Cardamine alpina*, *Ligusticum mutellina*, *Poa alpina*, *Polygonum viviparum* and *Veronica alpina*; and year (2006 and 2007). The model with the lowest AIC and the highest probability to be the best model is in bold. n=226 (only individuals with herbivory included). Corresponding figure: Fig. 5b.

Model	DF	Biomass loss due to herbivory		
		AIC	ω_i	E
Intercept	5	-85	<0.001	<0.001
Spec	10	-93	<0.001	<0.001
Spec+Treat	11	-104	<0.001	<0.001
Spec+Treat+Year	12	-160	0.839	1
Spec+Snow	13	-92	<0.001	<0.001
Spec+Snow+Treat	14	-105	<0.001	<0.001
Spec+Snow+Treat+Year	15	-156	0.128	0.153
Spec+Snow×Treat	17	-102	<0.001	<0.001
Spec+Snow×Treat+Year	18	-153	0.032	0.039
Spec×Snow+Treat+Year	30	-135	<0.001	<0.001
Spec×Snow×Treat+Year	53	nc ¹	nc ¹	nc ¹

¹nc=not computable.

induces branching and inhibits leaf extension (Schmitt and Wulff 1993). This finding is supported by another study that found reduced growth and generative reproduction for arctic-alpine forbs due to light competition, especially when nutrient supply is adequate (Eskelinen 2008).

Overall, the detected competitive effects between plants were weak. Probably, interspecific plant interactions are not the dominant structuring force in snowbed communities. Several studies have stressed the overwhelming importance of the abiotic environment in alpine plant communities (reviewed by Körner 2003) and our results are in line with these findings considering the fact that the mean effect size of the snowmelt gradient is generally higher than that of the neighbour removal treatment. Furthermore, in steady 'climax' plant communities the current competition among plants may be reduced by past competitive exclusions that led to

Table 4. Model comparison for the effects of species, snowmelt date, treatment, and year on presence/absence of fruiting by Akaike's information criterion (AIC), Akaike weights (ω_i), and evidence ratios (E). Factors: treatment (Treat): removal and control; snowmelt date (Snow): Julian day 153, 160, 167, and 174; species (Spec): *Alchemilla pentaphyllea*, *Cardamine alpina*, *Ligusticum mutellina*, *Poa alpina*, *Polygonum viviparum* and *Veronica alpina*; and year (2006 and 2007). The model with the lowest AIC and the highest probability to be the best model is in bold, additional models with $\Delta AIC \leq 2$ in italics. n=788 (dead plants omitted). Corresponding figure: Fig. 6.

Model	DF	Fruiting P/A		
		AIC	ω_i	E
Intercept	4	690	<0.001	<0.001
Spec	9	674	<0.001	<0.001
Spec+Treat	10	662	<0.001	<0.001
Spec+Treat+Year	11	651	0.015	0.028
Spec+Snow	12	668	<0.001	<0.001
Spec+Snow+Treat	13	656	0.001	0.002
Spec+Snow+Treat+Year	14	<i>644</i>	<i>0.373</i>	<i>0.667</i>
Spec×Treat+Year	16	651	0.011	0.020
Spec+Snow×Treat	16	655	0.002	0.003
Spec+Snow×Treat+Year	17	644	0.559	1
Spec×Snow+Treat+Year	29	649	0.038	0.069
Spec×Snow×Treat+Year	52	662	<0.001	<0.001

a spatial segregation of species (Freckleton and Watkinson 1999). However, the treatment effect could have been stronger if we had manipulated belowground competition or excluded herbivores. Onipchenko et al. (1998) showed that belowground phytomass in snowbeds is about eight times higher than aboveground phytomass, suggesting strong belowground competition. However, as already mentioned above, aboveground clipping most probably also reduced belowground competition. Thus, neighbour removal generally decreases the effect of neighbours on a target species, even if some residual belowground competition may persist. Further, since herbivory was more frequent and the estimated biomass loss due to herbivory was significantly higher in removal plots, herbivory most probably reduced the observed effect of neighbour removal on biomass. Consequently, herbivory might have led to a conservative estimate of the neighbour effect regarding biomass.

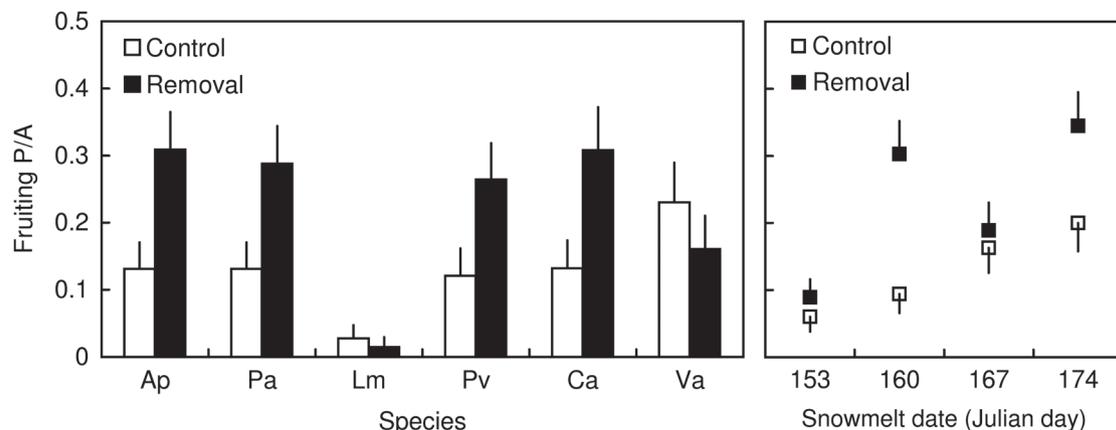


Figure 6. Mean presence/absence (P/A) of fruiting +1 SE by treatment for the six study species (left panel) and the four snowmelt dates (right panel). n=788 (dead plants were excluded). The figure corresponds to Table 4. Dominant species: Ap=*Alchemilla pentaphyllea*; indifferent species: Pa=*Poa alpina*; grassland species: Lm=*Ligusticum mutellina*, Pv=*Polygonum viviparum*; subordinate snowbed species: Ca=*Cardamine alpina*, Va=*Veronica alpina*.

Facilitation against grazing

Protection against herbivory was the most obvious facilitative effect of neighbouring plants on target individuals in our study. We could show that herbivory was significantly reduced in the presence of neighbours compared to isolated individuals in the removal plots. From other studies it is known that plant individuals may benefit from being hidden by the surrounding vegetation, even if they are not well defended, because they are more difficult for herbivores to locate (Milchunas and Noy-Meir 2002). Moreover, compared to the presence of herbivory, biomass loss due to herbivory was even more pronounced in removal plots than in control plots. There are two main herbivores on site: caterpillars and sheep. Since caterpillars generally only nibble from the edge of the plant leaves whereas sheep tend to eat the main part of such tiny plants, we suppose that sheep particularly grazed target individuals in removal plots.

In our study, the observed grazing shifted net interactions towards less negative in snowbeds. The associational resistance of co-occurring species could reduce damages due to herbivory thereby increasing individual fitness, and also could reduce mortality. However, since our biomass measurements already included biomass losses due to herbivory, the facilitative effect of associational resistance seems not to be able to completely shift the balance from net competition to net facilitation in snowbeds. These findings are in line with several other studies which showed that responses of plants to biotic interactions can vary depending on whether growth, i.e. biomass production, or survival will be measured (Goldberg et al. 1999, Liancourt et al. 2005).

Species specificity of plant interactions

Our results suggest that there are no differences of the prevailing type of plant interactions between the species considered, even if they show different distributional ranges along the snowmelt gradient in snowbeds (Schöb et al. 2009) and are assumed to show different plant strategies. Probably, given that all these species are obviously able to cope with the short growing season length and given that they cannot ameliorate this type of growth limitation, competition for all species may prevail in snowbeds due to the otherwise favourable growing season. However, a closer look at the results revealed minor, but consistent, deviations of *V. alpina* from the general trend. *V. alpina* seems to be the only species experiencing some facilitative effects from the neighbouring vegetation, apart from protection against herbivory.

Plant interactions along the snowmelt gradient

The balance of positive and negative interactions did not change along the snowmelt gradient within snowbeds, even though mean aboveground biomass of plants was higher in later melting sites. The higher biomass in sites with later snowmelt might be due to increased nutrient and water availability, i.e. two factors which seem to overcompensate for the increasingly shorter growing season. Later snowmelt is usually associated with an increased snow pack. Therefore, an increased reservoir of nutrients and water occurs in the latest melting sites (Bowman 1992). Further, increasing aboveground primary productivity in late-melting snowbeds might be associated

with a lower frequency of frost events since the number of days with frost negatively depends on the date of snowmelt (Inouye 2008). The increasing frequency of fruiting observed along the snowmelt gradient towards later snowmelt supports these conclusions. Thus, biomass and generative reproduction in snowbeds most probably depend indirectly on the snowmelt gradient, i.e. through its effects on nutrient and water availability, and protection against frost.

However, the fact that increasing biomass with later snowmelt did not translate into increasing competition is an unexpected finding. Therefore, either the increase in biomass production was not associated with increased competition or the importance of unknown facilitative effects in late melting sites concomitantly increased with the competitive interactions so that the balance of interactions remained constant. This question remains unanswered because neighbour removal experiments only reveal the net effect of plant interactions. In addition, even if the changes in biomass are rather high along the short snowmelt gradient considered within a single plant community, we have to admit that the absolute change in biomass was relatively small compared to biomass changes between different alpine plant communities (Vonlanthen et al. 2006b). Therefore, the productivity gradient (represented by biomass) in our study could have been too short to reveal a significant effect on the balance of positive and negative plant interactions.

Conclusions

In the present study, we showed that the observed weak net plant–plant interactions in alpine snowbeds were due to the simultaneous occurrence of competition for resources and facilitation against herbivores but not due to the low intensity of interactions per se. This finding, if confirmed in other plant communities, may explain the success of models of species distributions that give primary importance to abiotic factors and discount biotic interactions. Successful descriptions based on such models may give a delusive certainty about the overwhelming importance of abiotic factors and may be misleading if the counterbalancing effect of competition and facilitation will be cancelled out due to particular changes in the environment (e.g. removal of herbivores).

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References

- Baptist, F. and Choler, P. 2008. A simulation on the importance of growing season length and canopy functional properties on the seasonal gross primary production of temperate alpine meadows. – *Ann. Bot.* 101: 549–559.

- Bates, D. et al. 2008. lme4: Linear mixed-effects models using S4 classes. – R package ver. 0.999375-28. <<http://lme4.r-forge.r-project.org>>.
- Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. – *Trends Ecol. Evol.* 9: 191–193.
- Bowman, W.D. 1992. Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. – *Arct. Alp. Res.* 24: 211–215.
- Brooker, R. W. and Callaghan, T. V. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. – *Oikos* 81: 196–207.
- Callaway, R.M. 2007. Positive interactions and interdependence in plant communities. – Springer.
- Chen, S.-Y. et al. 2009. Beyond dual-lattice models: incorporating plant strategies when modeling the interplay between facilitation and competition along environmental severity gradients. – *J. Theor. Biol.* 258: 266–273.
- Choler, P. 2005. Consistent shifts in alpine plant traits along a mesotopographical gradient. – *Arct. Antarct. Alp. Res.* 37: 444–453.
- Choler, P. et al. 2001. Facilitation and competition on gradients in alpine plant communities. – *Ecology* 82: 3295–3308.
- Diggie, P. K. 1997. Extreme preformation in alpine *Polygonum viviparum*: an architectural and developmental analysis. – *Am. J. Bot.* 84: 154–169.
- Döbeli, C. 2000. Das hochalpine Geoökosystem der Gemmi (Walliser Alpen): Eine landschaftsökologische Charakterisierung und der Vergleich mit der arktischen Landschaft (Liefdefjorden, Nordwest-Spitzbergen). – *Physio-geographica* 28: 1–193.
- Ellenberg, H. 1996. Vegetation Mitteleuropas mit den Alpen. – UTB Eugen Ulmer.
- Eskelinen, A. 2008. Herbivore and neighbour effects on tundra plants depend on species identity, nutrient availability and local environmental conditions. – *J. Ecol.* 96: 155–165.
- Freckleton, R. P. and Watkinson, A. R. 1999. The mis-measurement of plant competition. – *Funct. Ecol.* 13: 285–287.
- Goldberg, D. E. et al. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. – *Ecology* 80: 1118–1131.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – *Am. Nat.* 111: 1169–1194.
- Inouye, D. W. 2008. Effect of climate change on phenology, frost damage and floral abundance of montane wildflowers. – *Ecology* 89: 353–362.
- Kammer, P. M. and Möhl, A. 2002. Factors controlling species richness in alpine plant communities: an assessment of the importance of stress and disturbance. – *Arct. Antarct. Alp. Res.* 34: 398–407.
- Körner, C. 2003. Alpine plant life: functional plant ecology of high mountain ecosystems. – Springer.
- Liancourt, P. et al. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. – *Ecology* 86: 1611–1618.
- Maestre, F. T. et al. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. – *J. Ecol.* 97: 199–205.
- Makarov, M. I. et al. 2003. Nitrogen dynamics in alpine ecosystems of the northern Caucasus. – *Plant Soil* 256: 389–402.
- McLellan, A.J. et al. 1995. On decaying roots, mycorrhizal colonisation and the design of removal experiments. – *J. Ecol.* 83: 225–230.
- Michalet, R. et al. 2002. Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: comparative effects of soil chemistry and water status. – *Arct. Antarct. Alp. Res.* 34: 102–113.
- Michalet, R. et al. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? – *Ecol. Lett.* 9: 767–773.
- Milchunas, D. G. and Noy-Meir, I. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. – *Oikos* 99: 113–130.
- Novoplansky, A. and Goldberg, D. E. 2001. Effects of water pulsing on individual performance and competitive hierarchies in plants. – *J. Veg. Sci.* 12: 199–208.
- Olofsson, J. et al. 2002. Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. – *Oikos* 96: 265–272.
- Onipchenko, V. G. et al. 1998. Population strategies in severe environments: alpine plants in the northwestern Caucasus. – *J. Veg. Sci.* 9: 27–40.
- Onipchenko, V. G. et al. 2009. Experimental comparison of competition and facilitation in alpine communities varying in productivity. – *J. Veg. Sci.* 20: 718–727.
- Pennings, S. C. and Callaway, R. M. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. – *Ecology* 73: 681–690.
- Schimel, J. P. et al. 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. – *Soil Biol. Biochem.* 36: 217–227.
- Schmitt, J. and Wulff, R. D. 1993. Light spectral quality, phytochrome and plant competition. – *Trends Ecol. Evol.* 8: 47–51.
- Schöb, C. et al. 2008. Changes in species composition in alpine snowbeds with climate change inferred from small-scale spatial patterns. – *Web Ecol.* 8: 142–159.
- Schöb, C. et al. 2009. Small scale vascular plant species distribution in snowbeds and its sensitivity to climate change. – *Plant Ecol.* 200: 91–104.
- Smit, C. et al. Inclusion of biotic stress (consumer pressure) alters predictions from the stress gradient hypothesis. – *J. Ecol.* 97: 1215–1219.
- Stanton, M. L. et al. 1994. Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, USA. – *Arct. Alp. Res.* 26: 364–374.
- Tomaselli, M. 1991. The snow-bed vegetation in the northern Apennines. – *Vegetatio* 94: 177–189.
- Vare, H. et al. 1997. Shifts in mycorrhiza and microbial activity along an oroarctic altitudinal gradient in northern Fennoscandia. – *Arct. Alp. Res.* 29: 93–104.
- Vonlanthen, C. M. et al. 2006a. Alpine plant communities: a statistical assessment of their relation to microclimatological, pedological, geomorphological, and other factors. – *Phys. Geogr.* 27: 137–154.
- Vonlanthen, C. M. et al. 2006b. Alpine vascular plant species richness: the importance of daily maximum temperature and pH. – *Plant Ecol.* 184: 13–25.
- Wang, Y. et al. 2008. On the relevance of facilitation in alpine meadow communities: an experimental assessment with multiple species differing in their ecological optimum. – *Acta Oecol.* 33: 108–113.
- Wilson, S. D. and Keddy, P. A. 1986. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. – *Am. Nat.* 127: 862–869.
- Wipf, S. et al. 2006. Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. – *Global Change Biol.* 12: 1496–1506.

Supplementary material (available as Appendix O18288 at <www.oikos.ekol.lu.se/appendix>). Appendix 1