

Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity

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The effects of long-term (11 yr) exclusion of vertebrate herbivores on competition intensity and plant community structure were studied using manipulative field experiments in two arctic-alpine plant communities with contrasting productivity: an unproductive snowbed and a considerably more productive tall herb meadow. In the snowbed, the exclusion of herbivorous mammals resulted in a significant increase in the biomasses of vascular plants and cryptogams, whereas no corresponding response was observed on the tall herb meadow. The intensity of competition, measured with a neighbour removal experiment, did not differ significantly between three of the four habitat × treatment combinations – snowbed exclosures, meadow exclosures and open meadow plots – but was significantly lower on open snowbed plots. Our results thus suggest that the low competition intensity in the unproductive snowbed is caused by herbivorous mammals, which tend to depress plant biomass in relatively unproductive habitats. When herbivorous mammals have been excluded for a sufficiently long time to allow the build-up of plant biomass even in unproductive habitats, between-habitat differences in competition intensity disappear.

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A central question in community ecology is whether and how the importance of herbivory and competition varies along productivity gradients (Grime 1977, 1979, Oksanen et al. 1981, Ellison 1987, Bonser and Reader 1995, Oksanen and Oksanen 2000). The importance of herbivory along gradients has been the subject of several experimental studies, but no clear consensus has been reached. Some review articles even suggest that there is no relationship between productivity and the intensity of herbivory (McNaughton et al. 1989, Cyr and Pace 1992). Cebrián and Duarte (1994) found evidence that intensity in grazing pressure is positively correlated with plant growth rate, and thus herbivory should be more intense on fast-growing than on slow-growing plants. Because plant growth rate and community primary production were not correlated in their data set, intensity of herbivory and primary production were not correlated either. However, quite a few terres-

trial experiments conducted in productivity gradients indicate that the intensity of herbivory is positively correlated with plant biomass (Rice 1987, Boyd 1988, Reader 1992, Bonser and Reader 1995).

One reason for these inconsistent findings might be that trophic dynamics have not been considered in these studies. According to the exploitation ecosystems hypothesis (Fretwell 1977, Oksanen et al. 1981, Oksanen and Oksanen 2000), the correlation between productivity and the importance of herbivory may range from positive to negative depending on the range of productivity covered in the study, because changes in primary productivity are predicted to be accompanied by changes in trophic dynamics. Mammalian herbivory is predicted to be most important in moderately productive areas, where the vegetation can support a fairly high density of food-limited herbivores. In more productive areas, herbivory should be less important as

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carnivores limit the abundance of herbivores. In extremely barren areas, herbivory should be of minor importance as there are not enough plants to support a resident population of herbivorous endotherms.

How the importance and intensity of competition between plants changes along productivity gradients has been an even more controversial question. There is empirical evidence indicating that competition intensity should be similar, regardless of primary productivity (Wilson and Tilman 1991, Gurevitch et al. 1992, Reader et al. 1994, Blecher et al. 1995, Peltzer et al. 1998). However, several other studies indicate that plant competition should increase with increasing plant biomass (Wilson and Keddy 1986, Reader and Best 1989, Keddy 1990, Campell and Grime 1992, Bonser and Reader 1995, Twolan-Strutt and Keddy 1996, Sammul et al. 2000). Tilman (1988) argues that competition should be equally important in all environments at equilibrium, but change from below-ground to above-ground competition along gradients of increasing productivity. Conversely, Grime (1977, 1979) proposed that the relative importance of competition should be inversely proportional to the levels of stress within an environment, which leads to increasing competition intensity along a gradient of increasing productivity.

The importances of competition and herbivory are likely to interact. Gurevitch et al. (2000) showed that competitor removal had positive effects on the focal organisms both with and without predation, but that it was more intense when predators were excluded. In this study, we investigated whether differences in the importance of herbivory between a low-productive and a productive habitat are influencing the importance of competition intensity in these two habitats. As arctic-alpine plant communities respond slowly, and thus it takes time before the impacts of past grazing on the intensity of competition disappear, competition intensity was measured inside 11-yr-old herbivore exclosures and on open plots in a low-productive snowbed and in a more productive tall herb meadow.

Based on the theoretical arguments (Oksanen et al. 1981, Oksanen and Oksanen 2000) and empirical results (Moen and Oksanen 1998) outlined above we predict that:

1. Plant biomass will be higher inside exclosures than in open plots in the snowbed, but similar in both treatments in the tall herb meadow.
2. The higher plant biomass will cause higher competition intensity in exclosures than in open plots in the snowbed, but competition intensity will be similar in both treatments in the tall herb meadow.
3. The increased competition intensity will result in lower species diversity in exclosures than in open plots on the snowbed, but species diversity will be similar in both treatments in the tall herb meadow.

Method

The study site is situated in Finnmark, northern Norway near the lake Joatkanjávri (69°46'N, 23°58'E). The area belongs to the hemiarctic zone (Ahti et al. 1968, Oksanen and Virtanen 1995), where tundra prevails but patches of forest are found in sites with warm microclimate. The experiment was conducted on a south-facing slope. The lower parts of the slope harbour mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest. Willow thickets dominate the middle part of the slope. Heathland or snowbed, depending upon duration of the snow cover, dominates the upper part of the slope. The two habitats used for this experiment are a tall herb meadow (450 m a.s.l.) and a snowbed (600 m a.s.l.) (see Moen and Oksanen 1998 for a more detailed description).

The tall herb meadow consists of a 30-yr-old clear-cutting in a forest patch. The forest recovers very slowly in this area and only scattered, small saplings and some basal sprouts of trees are found after 30 yr. The lush vegetation consists mainly of tall herbs such as *Cicerbita alpina*, *Cirsium helenioides*, *Geranium sylvaticum* and *Trollius europaeus*. There are also numerous small herbs and graminoids as well as some willow shrubs. The vegetation in the snowbed consists mainly of graminoids, such as *Anthoxanthum odoratum* and *Carex bigelowii*, and a few small herbs like *Bistorta vivipara*, *Gnaphalium supinum* and *Viola biflora*. Patches of *Salix herbacea* are also abundant. The time of snowmelt varies substantially between years, ranging from early June to mid-August. The closest counterpart to the tall herb meadow studied in the Norwegian IBP project (Wielgolaski 1975), is the low alpine willow thicket, with annual above- and below-ground primary productivity of 884 g/m². Tall herb meadows are successional stages of willow thickets or herb-rich birch woodlands (Kalliola 1939). The snowbed corresponds vegetationally to Wielgolaski's dry meadow with an annual above- and below-ground primary production of 534 g/m².

The important herbivores in this system are mainly microtine rodents of five species: grey-sided voles (*Clethrionomys rufocanus*), red voles (*C. rutilus*), field voles (*Microtus agrestis*), root voles (*M. oeconomus*) and lemmings (*Lemmus lemmus*). Long-term trapping data in the area show that vole peaks occurred in the area in 1987, 1992 and 1998, and that there was a lemming peak in 1988 (Ekerholm et al. 2001). The vole densities were similar in both areas, indicating greater consumption/productivity ratio on the less productive snowbed (Moen and Oksanen 1998). Willow grouse (*Lagopus lagopus*), rock ptarmigan (*L. mutus*) and mountain hares (*Lepus timidus*) have been present, but their influence on the vegetation is probably minor. Reindeer (*Rangifer tarandus*) migrate through the areas mostly in April–May and September–December, when

vascular plants are dormant. However, reindeer occasionally enter the area in June and August.

In 1987, six circular plots (diameter 9 m, area 63.6 m²) were marked in both habitats. Three plots in each habitat were randomly assigned to be exclosures and three were marked as open plots. The exclosures were constructed from galvanised net with a mesh size of 1.2 × 1.2 cm. The net was 80 cm high, which is sufficient to keep reindeer out, and was dug down into the mineral soil, between 10 and 30 cm deep. A 10-cm aluminium strip was put on the top of the fence to prevent rodents from climbing in, and the fences have been kept in good condition. Snap-traps were placed in the exclosures at all times. A lemming entered one of the snowbed exclosures during the snowmelt 1998 and severely damaged a portion of the vegetation. However, the area influenced by the lemming had clear boundaries. Biomass sampling and competition intensity measuring were conducted in the undamaged part of that plot. Dummy fences surrounding half of the plots were built around the open plots, and were maintained until 1995. No effect of the dummy fences on vegetation was observed (Moen and Oksanen 1998), and no differences in snow accumulation or snow melting have been observed between exclosures and open plots.

Plant biomass samples from all plots were collected in early August 1998, to study the long-term effect of excluding herbivores. Eight 0.1-m² circles were randomly placed inside each plot and above-ground biomass was clipped. The plant material was sorted to species or genus, dried to constant weight (48 h, 60°C), and weighed with an accuracy of 0.001 g.

To test whether the long-term exclusion of herbivores had changed competition intensity between individuals in the snowbed and the tall herb meadow, we marked ten equally sized plants of two different species inside each treatment and control plot. As the vegetation in these two habitats were dominated by graminoids and herbs, one graminoid species, *Carex bigelowii*, and one herb species, *Solidago virgaurea*, present in both habitats were chosen as target plants. The *S. virgaurea* plants had six to eight leaves, of which the longest leaf was about 50 mm. The *C. bigelowii* plants had four or five leaves. Five of the plants were randomly assigned to the competitor removal treatment and the other five were unmanipulated controls. In the middle of June 1999, all vegetation except the target plant was removed by hand-weeding from an area of 0.25 × 0.25 m, with the target plant in the middle. The vegetation was left intact around the control plants. All roots were cut with a spade around the edges of the 25 × 25 cm wide manipulated area, to prevent below-ground competition. The roots were cut around the edges of the unmanipulated controls in the same way, to assure that both treatments were receiving the same input of nutrients from dead decaying roots. The manipulated plots

were kept free of neighbouring plants by hand-weeding and the roots were cut around both manipulative and control plots every third week. At the end of August, the above-ground parts of all target plants were harvested, dried at 60° for 48 h and weighed with an accuracy of 0.001 g.

To compare the intensity of competition (CI) between the different sites and treatments, relative competition intensity was calculated for each exclosure or open plot, based on Grace (1995):

$$CI = (W_R - W_I) / W_R$$

where W_R is mean shoot weight of target plants with neighbours removed and W_I is the mean shoot weight of target plants with neighbours left intact. We analysed competition as relative competition intensity since relative values tend to be more useful for questions concerning the consequences of competition (Goldberg and Scheiner 1993).

Differences in plant biomass and species diversity were tested with two-way ANOVA, with habitat and herbivore treatment as fixed factors. The eight subplots harvested within each exclosure and open plot were pooled before statistical analysis. Variation in competition intensity was tested with habitat and herbivore treatment as fixed factors. The five shoots of each species, within each exclosure or open plot, were pooled before the statistical analysis. The data fulfilled the assumptions of normality and homoscedasticity, except for some of the plant growth forms. As analysis of variance is quite robust for minor divergence from these assumptions, no transformation of the data was made, as the interpretation of the test is clearer if all growth forms are tested with data in the same form as the total biomass.

Results

Biomass of vascular plants on open plots was more than two times greater in the tall herb meadow than in the snowbed (Fig. 1, Table 1). The significant treatment × site term indicates that plant biomass was significantly higher inside exclosures than in the open plots in the snowbed but not in the tall herb meadow. Graminoids and *Salix herbacea* were more abundant in the snowbed, while tall herbs, ericoids and shrubs were more abundant in the tall herb meadow (Table 2). The only group of vascular plants that responded significantly to the herbivore exclusion was erect herbs, which increased in the snowbed exclosures and accounted for most of the differences observed in total biomass of vascular plants. Biomass of cryptogams was substantially higher on the open plots in the tall herb meadow than in the snowbed (Fig. 1, Table 1). Cryptogams were

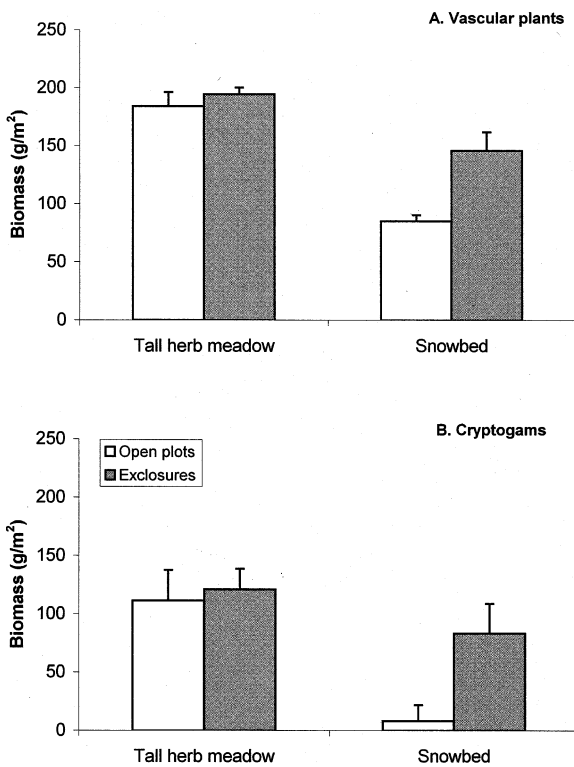


Fig. 1. Above-ground biomass of A. vascular plants and B. cryptogams in exclosures and open plots on the tall herb meadow and on the snowbed.

more abundant inside exclosures on the snowbed, but did not differ between treatments in the tall herb meadow. Bryophytes accounted for most of the pattern observed for total cryptogam biomass. Hepatics and lichens did not differ significantly, neither between the treatments nor between the sites.

The relative competition intensity (CI) on *Carex bigelowii* was significantly different between treatments and sites, and there was a significant exclosure \times site interaction (Fig. 2, Table 3), indicating that competi-

Table 1. Results from two-way ANOVAs on the amount of biomass of vascular plants and cryptogams per square meter in open plots and exclosures on the snowbed and the tall herb meadow. Statistically significant differences are marked in bold.

Source	DF	MS	F	p
Vascular plants				
habitat	1	2433.51	12.94	0.007
exclosure	1	10 445.09	55.56	<0.001
exclosure \times site	1	1210.83	6.44	0.035
error	8	187.98		
Cryptogams				
habitat	1	14 936.89	32.48	<0.001
exclosure	1	5403.78	11.75	0.009
exclosure \times site	1	3203.40	6.96	0.030
error	8	459.92		

tion intensity was higher in exclosures in the snowbed but not in exclosures in the tall herb meadow. The relative competition intensity in open plots was much lower in the snowbed than in the tall herb meadow. The relative competition intensity did not differ between the snowbed exclosures and the two treatments in the tall herb meadow. The competition intensity on *Solidago virgaurea* followed the same pattern as the competition intensity on *C. bigelowii*, but the exclosure \times site interaction was not significant (Fig. 2, Table 3).

The number of species was higher in the tall herb meadow than in the snowbed ($F = 27.5$, $p = 0.001$, Fig. 3). The number of species was nearly significantly higher inside the exclosures than in the open plots ($F = 5.19$, $p = 0.052$, Fig. 3). To illustrate the species-specific responses to herbivory and competition, the ten species which differed most between exclosures and open plots in the snowbed, where herbivory had a substantial impact, are listed in Table 4. The ten species that had the largest negative difference between exclosures and open plots were all species typical for the snowbed vegetation and the ten species that had the largest positive difference between exclosures and open plots were all, except *S. herbacea*, species typical for the tall herb meadow vegetation (Table 4).

Discussion

Mammalian herbivory influenced biomass and competition intensity more on the unproductive snowbed than in the tall herb meadow. Mammalian herbivores depressed the standing crop of vegetation to less than half the levels found inside herbivore exclosures in the snowbed. Excluding herbivores had no substantial effect on standing crop in the tall herb meadow. As we predicted, competition intensity was higher in the tall herb meadow than in the open plots on the snowbed, but rather similar in the snowbed and in the tall herb meadow inside the exclosures. Competition intensity was only reduced by herbivory in the snowbed where herbivores limited the standing crop.

As predicted by the exploitation ecosystem hypothesis, above-ground plant biomass after 11 yr of experimental manipulation was higher in exclosures than in open plots in the snowbed, while plant biomass in the tall herb meadow did not differ between exclosures and open plots. This is in accordance with the previous study in the same exclosures by Moen and Oksanen (1998), who reported radical changes in vegetation, from a grassland to a herbfield, inside exclosures within the snowbed, while the changes in vegetation inside exclosures on the tall herb meadow were modest after 7 yr. Moreover, the higher abundance of erect herbs primarily accounts for the higher vascular plant biomass found in snowbed exclosures. This was the

Table 2. Comparison of biomass of different growth forms or taxonomic groups of plants between the two different treatments in the two different sites. Results from two-way ANOVAs are presented as *p*-values. Statistically significant differences are marked in bold.

	g/m ² ± SE				<i>p</i> -value		
	tall herb meadow		snowbed		site	exc	Site × exc
	open plot	exclosure	Open plot	exclosure			
Vascular plants							
graminoids	10.65 ± 1.89	11.13 ± 3.53	19.02 ± 2.33	25.30 ± 1.59	0.002	0.205	0.271
erect herbs	70.53 ± 11.72	88.11 ± 13.36	16.68 ± 1.80	49.04 ± 7.72	0.001	0.033	0.459
prostrate herbs	5.30 ± 3.93	3.87 ± 1.32	3.17 ± 1.05	4.08 ± 1.36	0.681	0.912	0.616
ericoids	24.84 ± 7.09	21.34 ± 5.96	2.87 ± 2.87	3.90 ± 3.90	0.005	0.820	0.677
<i>Salix herbacea</i>	0.01 ± 0.01	0 ± 0	26.44 ± 1.48	31.52 ± 13.14	0.002	0.711	0.711
shrubs	35.95 ± 17.75	3.20 ± 15.77	0 ± 0	2.91 ± 2.83	0.028	0.940	0.757
Cryptogams							
mosses	105.57 ± 10.26	111.26 ± 3.30	8.16 ± 8.00	82.99 ± 14.84	< 0.001	0.004	0.009
hepatics	5.35 ± 5.09	9.03 ± 7.62	0 ± 0	0 ± 0	0.155	0.699	0.699
lichens	0.51 ± 0.16	0.87 ± 0.80	0.03 ± 0.03	0.31 ± 0.16	0.248	0.453	0.926

same category of plants that increased most in abundance during the first 7 yr of herbivore exclusion (Moen and Oksanen 1998). However, mosses had almost ten times higher biomass in the exclosures than in the open plots in the snowbed. Thus, mosses constituted more than a third of the total plant biomass in the snowbed when herbivores had been excluded for 11 yr. Decreased abundance of mosses in the presence of herbivores has been reported in several tundra studies (Oksanen and Oksanen 1981, Moen et al. 1993, Oksanen and Moen 1994, Virtanen et al. 1997a, Virtanen 2000). In the long run, it seems unlikely that both erect herbs and mosses can continually increase in the absence of herbivores, as both are competition-adapted plants, but with totally different strategies. Studies of the vegetation pattern on grazing-free islands suggest that the asymptotic outcome of herbivore-free dynamics depends upon thermal conditions (Virtanen et al. 1997a). Tall herbs achieve dominance over mosses in nutrient-rich sites with a relatively warm microclimate, whereas mosses out-compete herbs in cold and nutrient-poor sites. The main reason for the competitiveness of mosses in more extreme conditions appears to lie in their ability to take up nutrients directly from precipitation and thus decrease the nutrient availability in the soil (Jónsdóttir et al. 1995). Moreover, expanding moss banks decrease the nutrient mineralization rate by cooling the ground (Longton 1988, During and van Tooren 1990, van Breemen 1995, Zimov et al. 1995, Olofsson et al. 2001).

Moen and Oksanen (1998) suggested that the herbivory is more important in the snowbed than in the tall herb meadow, as predators regulate the herbivores in the tall herb meadow. The activity of mustelids, which are the main vole predators in this area, is strongly concentrated in the productive meadow woodland and scrubland habitats whereas barren areas such as the snowbeds are only occasionally visited by preda-

tors (Oksanen 1992, Aunapuu 1998). This conclusion is consistent with the exploitation ecosystem hypothesis (Fretwell 1977, Oksanen et al. 1981, Oksanen and Oksanen 2000), which characterizes productive habitats as predation-controlled grazer communities with competition-structured vegetation.

Competition intensity was lower in the relatively unproductive snowbed than in the more productive tall herb meadow in the open plots, and therefore vegetation is most likely more structured by competition in the more productive habitat as proposed by Grime (1977, 1979). However, after 11 yr of exclusion of

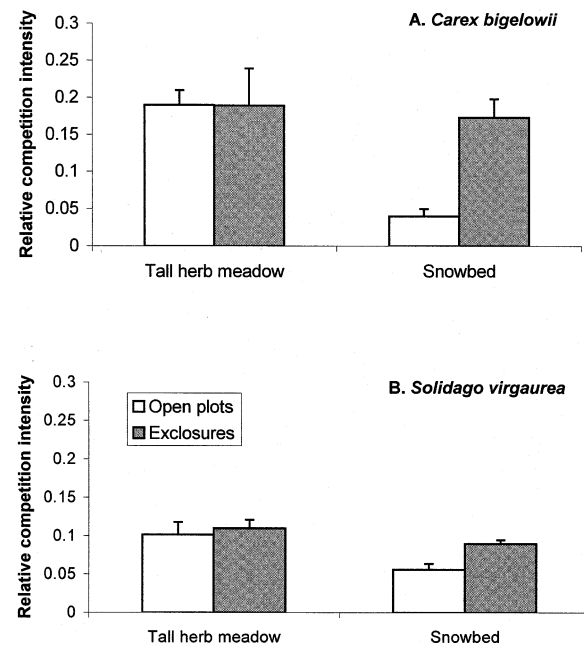


Fig. 2. Relative competition intensity of A. *Carex bigelowii* and B. *Solidago virgaurea* in exclosures and open plots on the tall herb meadow and on the snowbed.

Table 3. Results from two-way ANOVAs on relative competition intensity of *Carex bigelowii* and *Solidago virgaurea* in open plots and exclosures on the snowbed and the tall herb meadow. Statistically significant differences are marked in bold.

Source	DF	MS	F	P
<i>Carex bigelowii</i>				
habitat	1	0.021	5.240	0.050
exclosure	1	0.013	8.378	0.020
exclosure × site	1	0.013	5.524	0.048
error	8	0.002		
<i>Solidago virgaurea</i>				
habitat	1	0.0032	5.345	0.050
exclosure	1	0.0015	11.647	0.009
exclosure × site	1	0.0005	1.924	0.203
error	8	0.0003		

herbivorous mammals, competition intensity did not differ between the two sites with contrasting productivity, thus suggesting that productivity per se has no impact on the intensity of competition, as suggested by Tilman (1988). Differences in grazing pressure appear to account for the positive relationship between productivity and intensity of competition. The lower competition intensity in the open plots in the snowbed, where herbivores had lowered the amount of standing crop, supports the hypothesis that competition intensity should decrease with increasing herbivory or disturbance (Grime 1977, 1979, Taylor et al. 1990). Reduced competition intensity with increasing disturbance is also consistent with other experiments (Lubchenco and Gaines 1981, Campell and Grime 1992, Turkington et al. 1993). As it is difficult to measure the intensity of disturbance along natural gradients, it may often be difficult to separate the effect of productivity and disturbance on competition intensity (Wilson and Keddy 1986, Campell and Grime 1992, Turkington et al. 1993, Wilson and Tilman 1995).

The inconsistent results between different studies, regarding the relationship between competition intensity and productivity are difficult to explain, especially as each study considered a relatively small range of productivities, and these ranges frequently did not overlap (Gurevitch et al. 1992, Grace 1993, Bonser and

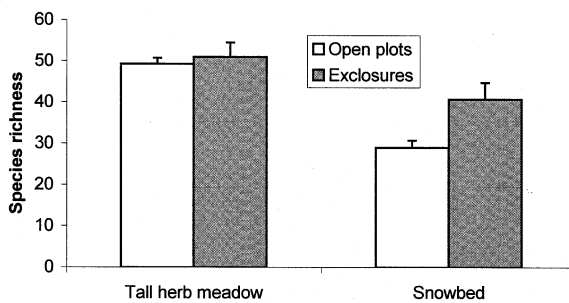


Fig. 3. Number of species in exclosures and open plots on the tall herb meadow and on the snowbed.

Reader 1995, Goldberg and Barton 1997). Different methods of calculating competition intensity have also contributed to the inconsistency. Calculating competition intensity with absolute measurements instead of relative measurements more often results in a positive correlation between competition and productivity (Grace 1993, 1995, Turkington et al. 1993). Relative and absolute values give the same result in this study, but only relative values are presented as they are considered to be more useful for questions concerning the consequences of competition (Goldberg and Scheiner 1993). Goldberg and Novoplansky (1995) have proposed that some of the inconsistency between different experiments on competition intensity along productivity gradients may be caused by different mechanisms of competition for different resources. This study indicates that changing the intensity of herbivory may cause the positive correlation between plant competition intensity and productivity found in tundra habitats (Sammul et al. 2000). Thus, differences in herbivory or disturbance regimes may partly explain why plant competition intensity is independent of productivity in some environments, and positively correlated with productivity in other environments. It is notable that even if both target plants responded in the same way to competition, the effect of competition was more pronounced on *C. bigelowii* than on *S. virgaurea*. It is possible that the taller herb *S. virgaurea* is less influenced by competition, as it is a more competition-adapted species than the graminoid *C. bigelowii* (Grime 1977, 1979, Oksanen 1990).

The increase of species diversity in the snowbed exclosures is in contrast with other studies that have found decreased species diversity when voles and lemmings are excluded (Fox 1979, 1985, Virtanen et al. 1997b). Species richness is generally thought to be highest at intermediate grazing pressure (Paine 1966, Grime 1973, Lubchenco 1978, Fox 1979, Milchunas et al. 1988). However, intense herbivory does not just mean relaxation of competition, but also replacement of resource competition by apparent competition (Holt 1977). Whether species richness will increase or decrease in the long run depends on the number of species that can coexist in a plant community structured by resource competition or apparent competition and on the species pool of competition-adapted and herbivory-adapted plants (Chapin and Facelli 1991, Olff and Ritchie 1998). Moreover, the increase in the number of species in the snowbed exclosures could be a feature of transient dynamics as the vegetation is still changing inside the exclosure. The ten most strongly decreasing species in the snowbed exclosure all were typical snowbed species, characterized by high initial abundance and weak competitive ability according to Grime (1979) and Oksanen (1990). Conversely, competition would reduce species richness in the long run, when competitive plants have had sufficiently long time to

Table 4. The ten most increasing and the ten most decreasing species in the snowbed. Plant type refers to growth form or taxonomic group used in Table 2. The species belongs to: m = mosses, eh = erect herbs, g = graminoids, ph = prostrate herbs, sh = *Salix herbacea*. The difference was calculated as biomass in enclosure-biomass in controls. The ten species that decreased most in the enclosures were all species typical for the snowbed vegetation and the ten species that increased most in enclosures were species typical for the tall herb meadow vegetation, except *Salix herbacea*. *Salix lapponum* and *Pleurozium schreberi* were not present in the control. Thus, the relative difference can not be calculated. Nomenclature follows Mossberg et al. (1992) for vascular plants and Hallingbäck and Holmäsén (1981) for mosses.

The ten species with the largest positive difference				The ten species with the largest negative difference			
	plant type	difference (g/m ²)	difference (%)		plant type	difference (g/m ²)	difference (%)
<i>Sanionia uncinata</i>	m	47.3	584	<i>Carex bigelowii</i>	g	-3.4	40
<i>Polytrichum juniperinum</i>	m	23.9	113 584	<i>Taraxacum</i> sp.	eh	-1.6	48
<i>Geranium sylvaticum</i>	eh	8.4	7439	<i>Sibbaldia procumbens</i>	ph	-1.4	80
<i>Anthoxanthum odoratum</i>	g	7.5	343	<i>Calamagrostis lapponica</i>	g	-1.1	98
<i>Solidago virgaurea</i>	eh	5.8	245	<i>Hieracium</i> sp.	eh	-1.1	90
<i>Salix herbacea</i>	sh	5.1	19	<i>Gnaphalium supinum</i>	ph	-0.9	92
<i>Trollius europaeus</i>	eh	5.0	1845	<i>Hierochloe hirta</i>	g	-0.7	100
<i>Bistorta vivipara</i>	eh	4.3	114	<i>Carex lachenalii</i>	g	-0.4	77
<i>Salix lapponum</i>	s	2.9	-	<i>Equisetum arvense</i>	eh	-0.3	100
<i>Pleurozium schreberi</i>	m	2.7	-	<i>Trisetum spicatum</i>	g	-0.1	87

obtain dominance and exclude typical snowbed plants. Even if herbivores were excluded for 11 yr in this study, a period generally considered as a long-term experiment, we still only observe transient dynamics. If the scope is to infer asymptotic dynamics in the Arctic, it appears to be necessary to combine experiments with comparative studies of natural experimental situations, such as grazer-free islands (Virtanen et al. 1997a).

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