

Long-term exclusion of folivorous mammals in two arctic-alpine plant communities: a test of the hypothesis of exploitation ecosystems

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During 1987–1994 we monitored changes in vegetation in exclosures and permanent open plots established in two contrasting habitats: a productive hemiarctic tall herb meadow and a less productive alpine snow-bed. In addition, we studied the survival and growth of transplanted tall herbs, woody plants and arctic-alpine plants together with their seed germination and seedling survival in the same habitats. The primary objective of the study was to test the following prediction of the hypothesis of exploitation ecosystems: exclusion of herbivorous vertebrates from the snow-bed initiates radical changes in the vegetation of the snow-bed, whereas in the tall herb meadow, the impact of grazer exclusion on the vegetation is modest. The vegetation within the snow-bed exclosures changed from a grassland to a herbfield during the experimental period. Transplanted tall herbs and seedlings of erect woody plants had high rates of survival and growth in snow-bed exclosures. No such changes were seen in the open snow-bed plots. Survival rates of transplanted woody plants and tall herbs in open snow-bed plots were low and the net growth rates of the survivors were close to zero. In the productive tall herb meadow, vegetational changes were modest on open plots and within exclosures. No clear treatment effects on survival or growth of transplanted woody plants and tall herbs were observed. The results of the experiment thus conformed to the predictions of the hypothesis of exploitation ecosystems.

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In boreal latitudes, nutrient-rich and moist mountain slopes with thick snow cover are characterized by vegetational gradients, where herb-rich woodlands grade into willow thickets or tall herb meadows and into alpine meadows at higher elevations. Such alpine meadows are dominated by graminoids and prostrate dicotyledons, and, where the snow cover delays the onset of plant growth, they are customarily referred to as snow-beds (Selander 1950, Gjørevoll and Bringer 1965, Walter 1968, Ellenberg 1978). Even at lower altitudes, small snow-beds are encountered in depressions. However, the gradient from the timberline region, where snow-beds only occur in sites with exceptionally deep

snow, to alpine habitat complexes where snow-beds abound, is also governed by an altitudinal decline in summer temperatures. Due to cooler springs at higher altitudes, the same amount of snow, which at lower altitudes disappears before the onset of the thermal growing season, lasts well past midsummer in truly alpine areas. The impact of the lost days on primary productivity is not linear, because the daily rates of net photosynthesis are often highest in the early part of the growing season in these regions with long days, clear skies and intense solar radiation (Chapin 1987). Due to the loss of primary productivity during the early part of the growing season, the vegetation even in snow-beds

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that disappear early (where the onset of the growing season is delayed by about two weeks) are only about half as productive as that at corresponding sites without a snow-bed (Kjelvik and Kärenlampi 1975, Wielgolaski 1975a, b). As snow depths, wind directions and early summer temperatures vary from year to year, the duration of the delay is highly variable on an annual basis. Gjærevoll (1956) hypothesized that the main reason for the distinct characteristics of snow-bed vegetation does not lie in differences in average snow conditions but is the result of the heavy mortality of plants imposed by the worst years of snow accumulation on plants not adapted to snow-bed conditions.

According to the data produced by the International Biological Programme (IBP), the gradient from willow thickets and tall herb meadows to early-melting snow-beds is accompanied by drastic declines in above-ground biomass from the boreal level to the level typical of that for circumpolar tundra (Oksanen 1983). This pattern conforms to the predictions of the hypothesis of exploitation ecosystems (Fretwell 1977, Oksanen et al. 1981, Oksanen 1988), according to which predators control folivores in productive ecosystems, as proposed by Hairston et al. (1960). In relatively unproductive areas, however, the top-down control of grazing vertebrates is predicted to fail, because there grazer densities, although too low to be profitably exploited by predators, are sufficient to deplete vegetation. Hence, above-ground plant biomass of relatively unproductive habitats should stay at a level primarily determined by the nutritional needs of grazers or at least to be periodically depressed to this level. The relatively flat relationship between primary productivity and the above-ground standing crop of the vegetation along the gradient from middle arctic tundras to early, and relatively nutrient-rich, low arctic (low alpine) snow-beds (Oksanen 1983) is in striking contrast with the general rule of a linear, positive relation between primary productivity and above-ground biomass of the vegetation (Lieth 1975, Whittaker 1975).

Correspondence between observed and predicted patterns is no proof of causality. The sharp decline in above-ground plant biomass is associated with a change from a predominance of erect shrubs or tall herbs to a prevalence of graminoids and prostrate dicotyledons (Kjelvik and Kärenlampi 1975, Wielgolaski 1975b). It can thus be argued that the increasingly stressful physical environment accounts for the vegetational change by excluding erect woody plants and tall herbs from habitats with short and cool growing seasons (Gjærevoll 1956, Dahl 1957, Billings and Mooney 1968, Woodward and Pigott 1975, Grime 1977, 1979, Billings 1987, Callaghan 1987; but see Fraser and Grime 1997). The vegetational gradient from productive boreal habitats to alpine snow-

beds could thus reflect competitive hierarchies and a trade-off between competitiveness and stress-tolerance (Grime 1977, 1979, Keddy 1989). Another potential explanation for the vegetational changes is that nutrient uptake, decomposition, and chemical weathering proceed slowly in cold areas (Billings and Mooney 1968, Chapin 1983, Jonasson 1983, Callaghan and Emanuelsson 1985, Billings 1987, Callaghan 1989), which could increase the intensity of root competition and thus decrease the optimal shoot/root ratio (Tilman 1988). In either case, the biomass pattern yielded by the IBP data might be just a fortuitous consequence of vegetational changes which have nothing to do with natural herbivory.

If the biomass pattern reflects changing trophic dynamics, the rapid decline in above-ground plant biomass should be accompanied by the disappearance of resident predators and a drastic reduction of predator activity. This seems to be the case. The activity of mammalian predators, such as stoat (*Mustela erminea*) and weasels (*M. nivalis*), has been strongly concentrated in productive habitats at and below the timberline, whereas the snow-beds and alpine heaths at higher altitudes have been visited only occasionally (Oksanen et al. 1992, 1997, Oksanen and Schneider 1995). Avian predators also occurred sparsely; their breeding was concentrated in the most productive habitats of the forest-tundra ecotone (Oksanen and Oksanen 1992, Oksanen et al. 1997). Again, the correspondence between predictions and the biomass data can be coincidental. Mammalian predators may just happen to avoid habitats with poor cover. This would result in a positive correlation between increasing plant biomass and predator activity.

If the observed patterns of plant biomass and predator activity are generated by the mechanisms outlined by Oksanen et al. (1981), the following predictions may be made. (1) Herbivore densities in early-melting snow-beds should be on the same level as herbivore densities in more productive willow thickets, woodlands and tall herb meadows. (2) Removal of grazers from snow-beds that melt early should trigger a rapid increase in plant biomass, and prostrate plants should be replaced by broad-leaved herbs and erect woody plants. (3) Removal of predators from more productive habitats should result in a grazer outbreak, strong reduction of plant biomass, and replacement of shrubs and tall herbs by graminoids and prostrate dicotyledons. These predictions are summarized in Fig. 1. The scope of the present paper is to report a test of prediction (2) and to shed some light on prediction (1), whereas the more logistically demanding test of prediction (3) will be left to a later stage.

Methods

Study area and basic design of the experiment

The experiments were performed in the Joatka area, northern Norway (69°46'N, 23°58'E), where two geologically and vegetationally different landscapes meet. The southern part of the study area belongs to the vast hemiarctic tundra plateau with a relatively continental climate, encompassing the interior parts of northernmost Norway (Finnmarksvidda) and adjacent parts of Finland and Sweden (Ahti et al. 1968, Oksanen and Virtanen 1995). The dominating habitat is lichen tundra with a scanty layer of bilberry twigs (*Vaccinium myrtillus* L.), rarely taller than 5 cm, and scattered dwarf birch (*Betula nana* L.) shrubs. Woodland patches dominated by stunted mountain birches (*Betula pubescens* Ehrh. ssp. *tortuosa* (Led.) Nyman) are encountered on south-facing slopes. In habitats enriched by running water, herb-rich willow thickets are formed. Those few sites, where strong southern exposure coincides with moist and nutrient-rich conditions, support herb-rich birch forests. Within the study area, the altitudes of this plateau range from 380 to 450 m. North of Finnmarksvidda there is another type of plateau landscape, which occupies the peninsulas of the Norwegian Barents Sea coast. This plateau lies at higher altitudes (within our study area at 500–700 m) and is entirely treeless, thus belonging to the lower oroarctic, or low alpine, zone (Ahti et al. 1968), and sites with good snow cover have a clear snow-bed character. The two landscapes belong to two different geological formations: Finnmarksvidda belongs to the Precambrian Baltic Shield with primarily granitic rocks, whereas the peninsulas belong to the northernmost part of the Scandina-

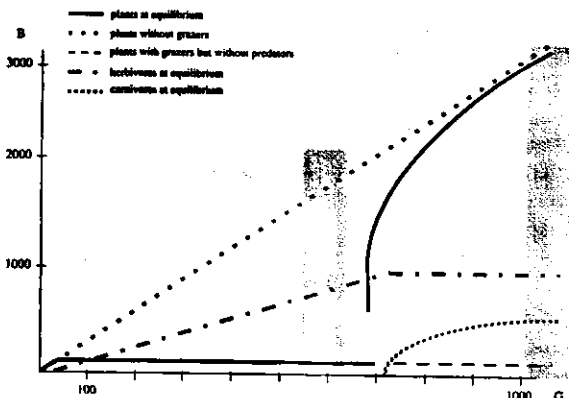


Fig. 1. Predicted relationships between primary productivity (G) and equilibrium standing crops (B) of plants, herbivorous vertebrates, and their predators according to Oksanen et al. (1981). The values on the vertical axis (based on Oksanen 1983) refer to plants only. The positions of relatively nutrient-rich, early snow-beds, and maximally productive habitats encountered in the timberline region, are represented by the shaded areas (based on Wielgolaski 1975a, b and Kjelvik and Kärenlampi 1975).

vian mountain formation, characterized by rather flat overthrusting nappes, consisting of hard and nutrient-poor rocks (NOU 1978, Lindström 1987).

The two habitat complexes meet in a steep, south-facing escarpment slope. The top part of the escarpment slope resembles the escarpments along the edges of the overthrusting nappes within the Scandinavian mountain formation, with rocky slopes and snow-beds. Nutrient-rich conditions occur locally, where the schists and dolomites sandwiched between the nappes become exposed, but oligotrophic habitats prevail. Below the escarpment, the Precambrian rocks of the Baltic Shield are covered by Cambro-Silurian sediments. All along the Scandinavian mountain chain, these sedimentary rocks are nutrient-rich and easily weathered rocks, creating exceptionally fertile soils (Anonymous 1953, NOU 1978). Immediately below the escarpment slope, edaphic conditions become even more favorable, because soils are moistened by subterranean drainage from the mountains. Even the microclimate is favorable, due to the southern exposure. Hence, the lower parts of the escarpment slope are occupied by exceptionally luxuriant hemiarctic habitats and show up as a bright red strands in a satellite image (see Oksanen and Virtanen 1995: p. 48). Willow thickets corresponding to the most productive Norwegian IBP sites abound, and at the lowest altitudes, there are substantial areas covered by herb-rich birch forest.

The most moist and nutrient-rich parts of the snow-bed complex on the top of the escarpment correspond vegetationally to the early-melting snow-bed sites of the Norwegian IBP project (Wielgolaski 1975a) which played a pivotal role for the biomass pattern predicted by Oksanen (1983). These snow-beds are dominated by graminoids (mostly *Carex bigelowii* Torr., *Festuca rubra* L. and *Agrostis mertensii* Trin.) and prostrate herbs (mainly *Sibbaldia procumbens* L. and *Gnaphalium supinum* L.). Broad-leaved herbs are relatively common, the dominating species being *Ranunculus acris* L. Abundances of other broad-leaved herbs (e.g. *Polygonum viviparum* L., *Viola biflora* L., *Gnaphalium norvegicum* Gunn.) vary locally. The only common woody plant is the creeping dwarf willow, *Salix herbacea* L. This habitat occurs mainly as narrow strands along creeks, but in one part of the study area, it forms a sufficiently large patch to be suitable for a replicated enclosure experiment.

The productive birch woodlands on the bottom of the slope serve as the main source of fuel for the Joatkanjävri tundra lodge. Hence, clearcuts are common. Within a few years after logging, the clearcuts develop into tall herb meadows, where the field layer is dominated by *Geranium sylvaticum* L., *Trollius europaeus* L., and *Cicerbita alpina* (L.) Wallr., together with a large number of smaller herbs and a few dwarf shrubs and graminoids (mostly *Deschampsia flexuosa* (L.) Trin. and *Festuca rubra*). Since the patches of

birch woodland lie above the general altitude of the timberline, the recovery of the woodland is slow. We checked the stages of recovery of different clear-cuts against the logging years given by the lodgekeeper (H. Romsdal pers. comm.) and found that clear-cuts less than 30 years old were practically open tall herb meadows, whereas older clear-cuts had been invaded by birch saplings to various degrees. Clear-cuts made 5–25 years ago could thus be regarded as semi-stable tall herb meadows, considerably more productive than the snow-beds on the upper part of the slope but equally strongly dominated by herbaceous plants.

As we wished to conduct parallel experiments in habitats which differ in primary productivity but are otherwise as similar as possible (equally little woody vegetation), we chose the largest patch of early-melting snow-bed and the tall herb meadow as our focal habitats. The size of the clear-cut was about 50 by 70 m. The snow-bed patch, which best corresponded to the Norwegian IBP sites was only 20 by 25 m. About 50 m west of this patch, there was another relatively similar patch of about 15 by 15 m. Six circular plots (diameters 9 m, areas 63.6 m²) were marked in each habitat in 1987. Three plots in each habitat were randomly assigned to exclosures and three were marked as open plots. They were chosen subjectively to represent vegetation typical for the habitat and they were placed at intervals across each entire habitat. In order to minimize the sensitivity of the plots in snow-bed patches to local variations in grazer impact, two of the paired snow-bed plots were chosen from the smaller patch. The exclosures were constructed from galvanized net with a mesh size of 1.2 × 1.2 cm. The net was 80 cm high and was dug down into the mineral soil, the depth varied between 10 cm and 30 cm. A 10-cm aluminum strip was put on the top of the fences to prevent rodents from climbing in. Snap-traps were placed in the exclosures at all times. The control plots were enclosed with the same net material along their eastern and western boundaries, whereas the southern and northern ends were left open to minimize differences in wind velocity and snow accumulation. (The slope is exposed to east and west winds, whereas a pocket of stagnant air is normally formed under the cliff during periods of southerly or northerly winds.) Snow depths were checked during snow-tracking periods in November–December (L. Oksanen unpubl.). No consistent differences in snow accumulation were seen either between exclosures and open plots or between the two habitats. Even the snowmelt proceeded at the same speed within exclosures and open plots.

The above design implies that we carried out replicated exclosure experiments in two different habitats. On the level of habitats, the experiment could not be replicated, because the two habitats belonged to two different habitat complexes with non-overlapping distributions within our study area. The nearest substantial

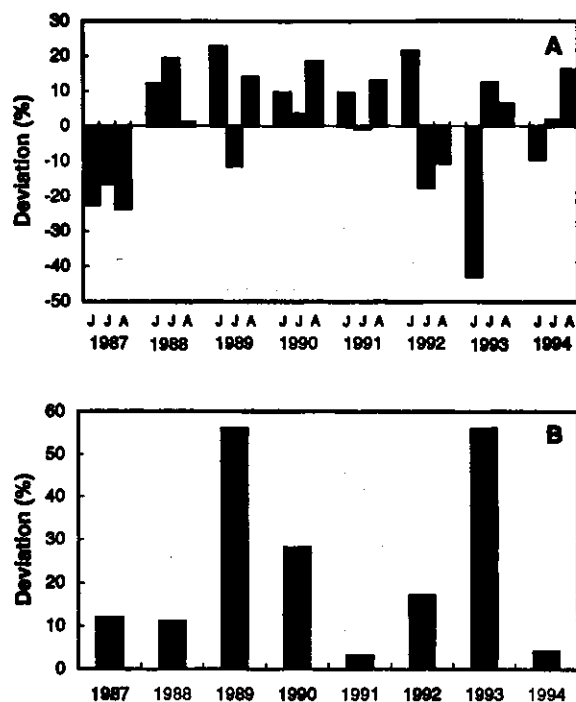


Fig. 2. A. Mean temperatures for June, July and August 1987–1994 at Suolovuobmi expressed as per cent deviances from the long-term averages (1961–1990; June + 8.4°C, July + 11.4°C, August + 9.3°C). B. Maximum snow depths at Joatka expressed as per cent deviances from the long-term average of the mean snow depth in the month with deepest snow (March, mean snow depth 76 cm).

patches of these habitats were tens of kilometers away, which exceeded our logistic capacity. Hence, the comparison between the two habitats was pseudoreplicated according to Hurlbert's (1984) terminology. In strictly statistical sense, our design thus does not allow inferences concerning between-habitat differences. It is up to the reader to judge how likely a result corroborating our a priori predictions could emerge as a consequence of random variation between grazing impacts on different habitat patches.

The essential weather parameters – mean temperatures for summer months at the nearest complete weather station (Suolovuobmi, 25 km SW of Joatka, at the same altitude) and maximum snow depths for Joatka during 1987–1994 – are presented in Fig. 2. Temperature data are presented as per cent deviations from the long-term average (data provided by Meteorologisk Institutt, Oslo), maximum snow depths (based on the primary data of Britta Romsdal, Joatkanjávri) are presented as per cent deviations from the long-term average for March (Anonymous 1949). The experiment was initiated in a cold summer. The next growing season was favorable, with a snow-poor winter followed by a warm summer. Snow-bed plots had melted out by 20th June and weather was periodically hot even in the snow-bed. In 1989 and 1990, the combination of copi-

ous snow and reasonably warm summers created average conditions, with snow-bed plots melting out in early July. Summer of 1991 was again relatively favorable. Conditions in 1992 and especially in 1993 were bad, as snow-rich winters were followed by cold summers. In our snow-bed site, 1992 was the worst year, because northeastern winds prevailed in the winter of 1991–1992, dumping snow from the higher plateau to the snow-bed. Our plots did not melt out until around 10th August in that year. In 1993, melting dates were about two weeks earlier. 1994 was again relatively favorable. We can thus conclude that our snow-bed site has been exposed to both benign and stressful conditions during the course of the experiment.

Plant community structure

In each plot, a 20-m line was permanently marked. As the diameter of the plot was only 9 m and we did not want to include the edges, the line was divided into four parallel sections of 7, 6, 4, and 3 m, respectively, located at equal distances from each other within the northern half of each plot. 250 points were randomly chosen along the line, with the constraint that a given point was at least 1 cm from any other point. The same points were used in all plots and all years. At each point a stick (diameter 3 mm) was lowered vertically and contacts with the stick were recorded, both the identity of the taxa and the height to the nearest centimeter (the height data will be presented in a separate paper). If the same taxon was in contact with the stick more than once at the same point, only one contact was registered and the mean height of contacts was noted (mean and maximum height in 1987 and 1994). The taxon was determined to species, or to genus in a few cases. Only vascular plants were recorded, except in 1994 when cryptogams (which only played a minor role in the two communities) also were recorded. The measurements were taken once each year during the first half of August from 1987 (when the enclosures were constructed) to 1994. The sampling dates were at roughly the time of peak vegetation development, which was determined phenologically based on when *Solidago virgaurea* L. was in full flower, except in 1993 when the snow-bed plots melted out so late that *Solidago* failed to flower. The 1993 analyses on the snow-bed were thus done at a phenologically earlier time than the other years, even though the calendar date was slightly later (mid-August).

The contacts in each plot were summed in three categories: woody plants, herbs, and graminoids. This was done to facilitate comparisons between plots and habitats, since the species composition varied. Moreover, this procedure reduced the risks of mass significance. In terms of the plant strategy scheme of Oksanen (1990) and Oksanen and Ranta (1992), almost all graminoids could be regarded as g-strategists (i.e. graz-

ing-adapted plants), due to a relatively low stature and narrow, basally attached leaves. Conversely, the vast majority of herbs and woody plants were assigned to K-strategists. (The main exception was *Ranunculus acris*, which has broad leaves only close to the ground and strong alkaloid defense, see Nordhagen 1943, Wielgolaski 1975c.) The numbers of contacts were tested with repeated measures ANOVAs for each category ($n = 3$ in each treatment combination). As a consequence of our a priori hypotheses, we paid special attention to the habitat \times fence \times time-interaction, which tests whether there are different time trends between enclosures and open plots in the patches representing the two habitats. Due to the low number of replicates, the assumption that the variance-covariance matrices are equal across all levels of the treatments (Crowder and Hand 1990) could not be tested. However, this condition can be assumed to be met when the different measurements have been taken at equal time intervals (C. Frampton pers. comm.).

In the snow-bed, the numbers of floral shoots of all reasonably abundant herbs and graminoids were censused as follows from 1988 to 1992, and again in 1994. In 1988, ten 25 \times 25 cm quadrats were randomly placed in each plot, and all floral shoots present in the quadrats were counted. In 1989, the number of quadrats in each plot was increased to 25, as the census work turned out to proceed quickly. The number was kept constant after this, except in 1994 when the number of plots varied between 8 and 23 (because many quadrats could not be located). The number of floral shoots in each category was pooled for each plot and scaled to numbers per m² for the subsequent repeated measures ANOVA. The quadrats were too small for censusing floral shoots of tall herbs. Hence, the numbers of floral shoots of *Trollius europaeus*, *Cicerbita alpina*, (tall herb meadow only) and *Gnaphalium norvegicum* (snow-bed only) were counted for each entire plot (i.e. 64 m²) in 1992 and 1994.

Survival of transplanted adult shoots

In August 1987, five shoots or ramets of nine different species regarded as K-strategists in the scheme of Oksanen (1990) and Oksanen and Ranta (1992) were transplanted into intact vegetation in each of the enclosures and open plots mentioned above (giving a total of 540 shoots). Six of these – *Alchemilla vulgaris* coll., *Angelica archangelica* L., *Epilobium angustifolium* L., *Geranium sylvaticum*, *Cicerbita alpina*, and *Veratrum album* L. – were tall herbs, and three – *Betula pubescens* ssp. *tortuosa*, *Salix glauca* L., and *Sorbus aucuparia* L. – were woody plants. Moreover, we conducted similar transplantations for six truly alpine plants: *Antennaria dioica* (L.) Gaertn., *Gnaphalium supinum* L. and *Viscaria alpina* (L.) G. Don (g-strategists according to the scheme of Oksanen 1990), and

Luzula confusa Lindeb., *Oxyria digyna* (L.) Hill, and *Ranunculus glacialis* (high alpine plants lying along the r-K axis; Oksanen and Ranta 1992, Oksanen and Virtanen 1995). For herbs, we took established but sterile individuals; for the woody plants, we chose established seedlings (about 10 cm tall). The plants to be transplanted were dug up with a soil core about 10 cm deep and 5 cm in diameter, stored in plastic bags and transferred to the new site within a few days. The plants had lost a substantial fraction of their fine roots, which probably had negative impact on their performance in the first years of growth. All shoots were transplanted by taking out a small plug of soil (ca 5 cm in diameter) and replacing it with the shoot to be transplanted thereby keeping the disturbance to the surrounding vegetation as low as possible.

The *Oxyria* and *Ranunculus* plants were collected from the mountain area Vuorasnjärhåldi ca 50 km NW from Joatka (850 m a.s.l., N69°56', E22°55'), the woody plants were collected from a roadside ca 20 km from Joatka (ca 300–400 m a.s.l.), the *Veratrum album* plants came from the Juovlatjohkka valley on the southeastern part of Várjatnjarga (Varangerhalvøya) (N70°29', E28°20', alt. 300 m a.s.l., slightly above the timberline), and the rest of the species were collected close to the experimental plots. *Veratrum*, which does not occur in the Joatka area, was included because it is considered to be toxic to livestock (Lid 1985, Nilsson 1986), in contrast to the other tall herbs in the experiment.

The transplanted plants were annually censused in August from 1988 to 1994. At the same time, the maximum lengths of tall herbs and woody plants were measured to the nearest millimeter by stretching the shoot gently along a ruler and checking the highest point touched by any plant organ. For the alpine rosette plants, the number of rosettes was used as an index of size. For *Ranunculus glacialis*, *Oxyria digyna*, and *Luzula confusa*, no measurements of size were taken. The proportions of surviving shoots in August 1994 were tested by multivariate ANOVAs with species from each classification category as variables and with habitat (tall herb meadow vs snow-bed) and fencing (exclosures vs open plots) as factors. The growth rate for the shoots that had survived until August 1994 was calculated as the difference between size in 1994 and size in 1988 divided by 6 to give an index of performance as mm per year or rosettes per year. A value > 0 thus indicates that the individual has increased in size. The indices were tested with multivariate ANOVAs with the same design as above except that a regression approach with type III sums-of-squares was adopted, since the number of replicates were unequal in the variables (Scheiner 1993). Residuals were checked in all MANOVAs to see if assumptions for the tests were met.

Seed germination and seedling survival

In August 1988, seeds of ten species were sown in each of the 12 plots mentioned above. The seeds were all collected in the Joatka area during the same summer. The ten species were: *Angelica archangelica*, *Epilobium angustifolium*, *Cicerbita alpina* (K-strategists, tall herbs), *Betula pubescens* ssp. *tortuosa*, *Salix glauca* (K-strategists, woody plants), *Antennaria dioica*, *Gnaphalium supinum*, *Viscaria alpina* (g-strategists), *Luzula confusa*, and *Oxyria digyna* (high alpine plants). In each plot, a square of 60 × 60 cm was cleared of all vegetation and 100 points were marked in a regular pattern. Each species was randomly assigned to ten points or microsites. At each point, a 'pinch' of 5 to 10 seeds depending on species was sown by placing them on the soil surface and covering them with soil. As we did not know the germinability of the seeds and as space was limited in the fenced areas, we did not sow just one seed at each point since that would have necessitated the use of many more points and plots. The plots were weeded annually of invading shoots, but no seedlings were removed.

The number of seedlings at each point was counted in August 1989 to 1991. In 1992 only the number of individuals that were flowering was counted. The proportion of points in each area where seeds had germinated in August 1989 was tested with multivariate ANOVAs with species from each classification category as variables and with habitat (meadow vs snow-bed) and fencing (exclosure vs open plots) as factors. The number of seedlings at each point that had emerged in August 1989 was tested with multivariate ANOVAs with the same design as above. The percentage mortality of the seedlings between 1989 and 1991 was tested with multivariate ANOVAs with the same design as above except that a regression approach with type III sums-of-squares was adopted since the number of replicates were unequal in the variables (Scheiner 1993).

The folivore community

The overwhelmingly dominating components of the folivore community in arctic-alpine and subarctic Fennoscandian habitats are the reindeer (*Rangifer tarandus* L.) and the microtine rodents (Wielgolaski 1975b). Willow grouse (*Lagopus lagopus* L.), mountain hares (*Lepus timidus* L.), and rock ptarmigan (*L. mutus* L.) are present but their standing crops only amount to a tiny fraction of the folivore standing crop. Folivorous insects are important consumers of mountain birches and tall willows, but in arctic and subarctic habitats without erect woody plants, the densities of folivorous insects are very low (Wielgolaski 1975b, Oksanen et al. 1997). Our observations are consistent with the data summarized by Wielgolaski. Moreover, we worked in

open meadow habitats, where there is no winter food for hares, grouse or reindeer. The impact of reindeer on habitats with primarily herbaceous vegetation in the study area was further reduced by the timing of their movements. The study area belongs to a migration route which is grazed in April–May and September–December, when herbaceous plants are withered and reindeer eat primarily lichens (Skjenneberg and Slagsvold 1968). However, there were some differences between the theory and the practice of reindeer husbandry. Reindeer herds, sometimes consisting of several hundred individuals, entered the area occasionally in August, in later years even in June. Grazing by reindeer was episodic, and there was no obvious pattern in their habitat use. Herbs with tall, flower-bearing shoots (e.g. *Cicerbita alpina*, *Geranium silvaticum* and *Trollius europaeus*) appeared to be especially sensitive to reindeer grazing because reindeer tend to move a lot and nibble small pieces of forage, and tall herbs tend to become severely trampled in the process (Skjenneberg and Slagsvold 1968, pers. obs.). The impact of reindeer could thus be expected to be especially pronounced in the tall herb meadow, dominated by these herbs.

The microtine community of the area consists of five species: grey-sided voles (*Clethrionomys rufocanus* Sund.), red voles (*C. rutilus* Pall.), field voles (*Microtus agrestis* L.), root voles (*M. oeconomus* Pall.), and lemmings (*Lemmus lemmus* L.). Since 1977, their densities in the area have been continuously monitored by snap trapping with the Small Quadrat Method (Myllymäki et al. 1971), where 12 traps are set in four clusters of three traps in the edges of a 15 by 15-m quadrat in order to counteract trap saturation. In order to obtain data maximally representative for winter conditions, trapping was conducted immediately after the snowmelt (approximately 10th–20th June) and in autumn when the tundra had turned red (approximately 5th–15th September) (Oksanen and Oksanen 1981, 1992, Ekerholm and Oksanen unpubl.). Snow-beds, which normally had not melted out by the spring trapping period, were represented by their margins during spring index trapping. (Comparisons between foraging signs and trapping results indicated that microtine rodents wintering in snow-beds move out when snow-beds are inundated by meltwater, see Kalela 1971, Oksanen and Oksanen 1981.)

As a background for the present study, we have compiled density indices (captures per 100 trap nights) from three habitat categories, each represented by five quadrats trapped for 48 h (i.e. the data are based on 120 trap nights per habitat and trapping occasion). The tall herb meadow is included in the trapping program as a separate habitat, although its definition is broader in the context of small mammal trapping. Moist and herb-rich snow-beds were trapped on the upper plateau, but it turned out that the small mammal dynamics there were not representative for the snow-beds of the

escarpment slope, influenced by dispersal of voles and by 'spillover predation' from adjacent lowlands (Oksanen et al. 1992). Hence, the microtine community of the slope was vole-dominated with only low numbers of lemmings (Oksanen 1993). As an index of microtine density within our snow-bed habitat, we thus used the mean for the slope snow-beds, representing the driest and most late-melting parts of the habitat, and for the low herb meadow, representing the part where early melting was most pronounced. Data were provided by Ekerholm and Oksanen (unpublished).

Microtines had a population peak in autumn 1987 in both habitats (Fig. 3; see also Oksanen and Oksanen 1992). On the slope, the 1988 peak was characterized by relatively high numbers of *Microtus* spp. Grey-sided voles were co-dominants in both habitats. After the crash in 1989–1991, vole populations have fluctuated at moderate densities, but no pronounced population peak built up. During the 1990's grey-sided voles have predominated in the microtine guild. Overall, no persistent difference in microtine densities between the two habitats was observed.

Results

Plant community structure

The number of contacts were significantly different between the habitats for woody plants and herbs, and approaching significance for graminoids ($p = 0.074$), indicating that the plant community structure was different between the two habitats (Table 1). Herbs had a significant fence effect indicating that the enclosures by chance were initially more herb-rich than the open plots (Table 1). All groups had a significant time trend in both habitats, and this trend was also significantly different between the habitats (Fig. 4 and Table 1). However, the only category that showed a significant habitat \times fence \times time interaction, i.e. which had a dif-

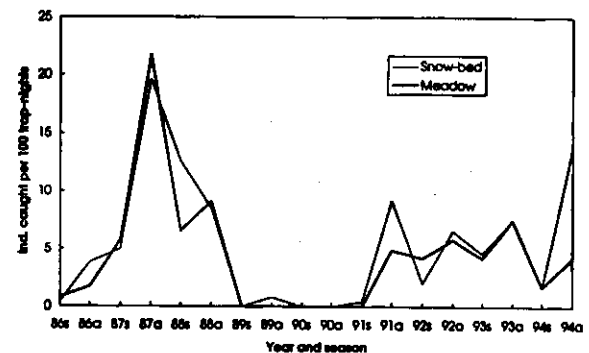


Fig. 3. Capture indices for microtine rodents in the area measured as the number of individuals caught per 100 trap-nights. 86s stand for spring 1986, 86a for autumn 1986 etc. (Data from Ekerholm and Oksanen unpubl.)

Table 1. Repeated measures ANOVAs on the number of contacts for woody plants, herbs and graminoids. Error(between) refers to the error term used for between-cases comparisons, while error(within) refers to the error term used for within-cases comparisons, i.e. comparisons involving time as a factor. "Habitat" refers to meadow vs snow-bed, and "Fence" refers to exclosures vs open plots.

Source	df	MS	F	p
A. Woody plants				
Habitat	1	83 898.37	13.29	0.007
Fence	1	5581.50	0.88	0.375
H × F	1	240.67	0.04	0.85
Error(between)	8	6311.58		
Time	7	2762.38	14.90	<0.001
H × T	7	403.33	2.18	0.05
F × T	7	150.02	0.81	0.583
H × F × T	7	138.00	0.74	0.635
Error(within)	56	185.33		
B. Herbs				
Habitat	1	1 985 763.00	222.14	<0.001
Fence	1	293 377.59	32.82	<0.001
H × F	1	16 880.51	1.89	0.207
Error(between)	8	8939.25		
Time	7	26 739.55	42.64	<0.001
H × T	7	2450.84	3.91	0.002
F × T	7	1816.33	2.90	0.012
H × F × T	7	3873.49	6.18	<0.001
Error(within)	56	627.05		
C. Graminoids				
Habitat	1	55 777.04	4.24	0.074
Fence	1	5046.00	0.38	0.553
H × F	1	9243.38	0.70	0.426
Error(between)	8	13 164.96		
Time	7	1043.14	2.19	0.048
H × T	7	5467.59	11.50	<0.001
F × T	7	638.60	1.34	0.248
H × F × T	7	586.40	1.23	0.300
Error(within)	56	475.42		

ferent response to exclusion of herbivores in the two habitats, was herbs which increased in the snow-bed exclosures (Fig. 4 and Table 1). No change was seen in the open plots on the snow-bed. Herbs in the tall herb meadow fluctuated over the years, but the trends were the same in both exclosures and open plots. A closer inspection of six of the most common herbs on the snow-bed showed that five species, *Gnaphalium norvegicum*, *Solidago virgaurea*, *Trollius europaeus*, *Polygonum viviparum* and *Viola biflora* (all of them also present in the tall herb meadow), had positive trends in the exclosures while abundances were relatively unchanged in the open plots (Fig. 5). However, the most common herb taxon, *Ranunculus* spp. (*R. acris* and *R. nivalis* L.), showed a similar trend in exclosures and open plots even though abundances were higher in the exclosures (Fig. 5).

The number of floral shoots per m² on the snow-bed showed significant time trends for both herbs and graminoids; herbs had a positive trend while graminoids showed a strong negative trend over time (Fig. 6; Table 2). Herbs also had a significant fence × time interaction, which reflected the increase in flower-

ing in the exclosures (Fig. 6). When the number of floral shoots of the most common tall species was counted over the entire plots (i.e. 64 m²), the number was consistently higher in exclosures than in open plots for *Trollius* and *Gnaphalium* (especially pronounced on the snow-bed), while *Cicerbita*, which grew in the tall herb meadow, showed little response to the establishment of the exclosures (Table 3).

Survival and growth of transplanted adult shoots

Survival was generally high, and all plants survived well when transplanted to their native habitat, indicating that transplantation itself was not a major stress factor (Table 4). The main exceptions were alpine plants in the tall herb meadow which survived poorly. All tall herbs and woody plants had over 45% survival in the fenced snow-bed plots, while the survival in open snow-bed plots was consistently lower (Table 4). Survival rates in the stressful year 1993 were as high as in other years, indicating that even plants typical of the most productive subarctic habitats can tolerate stress created by an exceptionally short growing season. The MANOVAs on the proportion of surviving shoots in August 1994 showed a significant fence effect for tall herbs and woody plants; there was a higher survival in exclosures (herbs: $F = 9.00$, $df = 6,3$, $p = 0.05$; woody plants: $F = 7.07$, $df = 3,6$, $p = 0.02$). Alpine plants had no significant effects, i.e. we cannot reject the null hypothesis that they had an equal survival in all treatments. How-

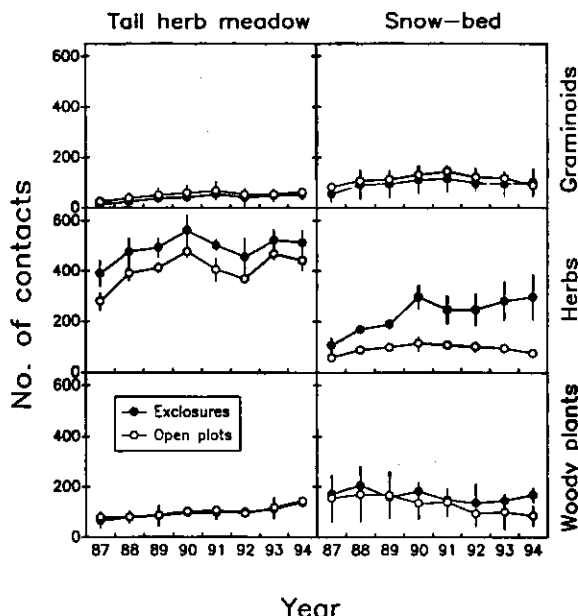


Fig. 4. The mean number of contacts (mean ± sd; $n = 3$) for woody plants (top), herbs (middle), and graminoids (bottom) from the tall herb meadow (left column) and the snow-bed (right column).

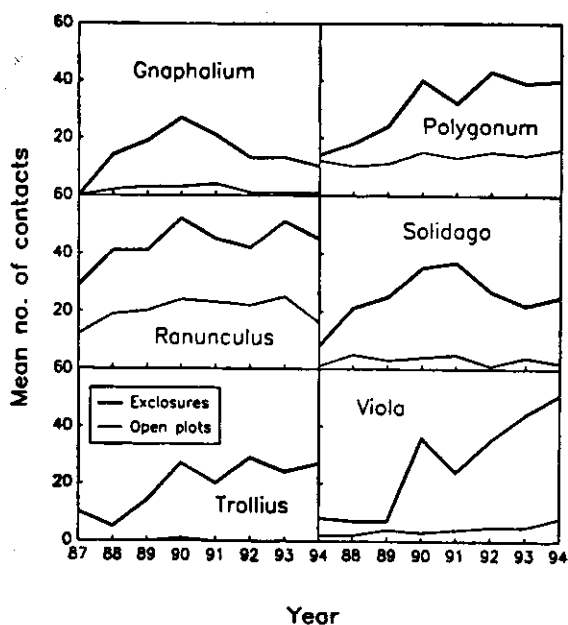


Fig. 5. The mean number of contacts for exclosures (thick line) and open plots (thin line) on the snow-bed for six of the most common herb taxa (*Gnaphalium norvegicum*, *Polygonum viviparum*, *Ranunculus* spp. [*R. acris* and *R. nivalis*], *Solidago virgaurea*, *Trollius europaeus*, *Viola biflora*). Note that all species were initially present although sometimes too infrequent to show up in the initial sampling.

ever, inspection of Table 4 shows that survival tended to be higher in the snow-bed.

The MANOVAs on the growth rates of surviving shoots showed a significant habitat \times fence interaction for herbs. There was a larger difference in survival between exclosures and open plots on the snow-bed as compared to the meadow (Wilks' lambda = 0.32, df = 6,14, $p = 0.007$). No significant effects were found for woody plants, while alpine plants could not be tested due to missing cells for some of the species. If the treatments are ranked according to the overall mean of the growth rates, the three categories of plants show the same order (from highest to lowest growth rate): fenced snow-bed > fenced meadow > open meadow > open snow-bed (Table 5), but this result must be regarded as tentative, due to the high variance within each category. A closer look at the growth rates of the surviving tall herbs and woody plants shows much variation between species and between individuals. Nevertheless, positive growth rates prevail in the tall herb meadow and in snow-bed exclosures, where the shoots have elongated by about a centimeter per year (Table 5). On open snow-bed plots, growth rates of surviving shoots varied from positive to negative values, but the long-term average for all species is close to zero. The surviving alpine plants show a weak decreasing trend in the number of rosettes (Table 5). A similar negative trend was visible even in the three non-rosette alpine plants

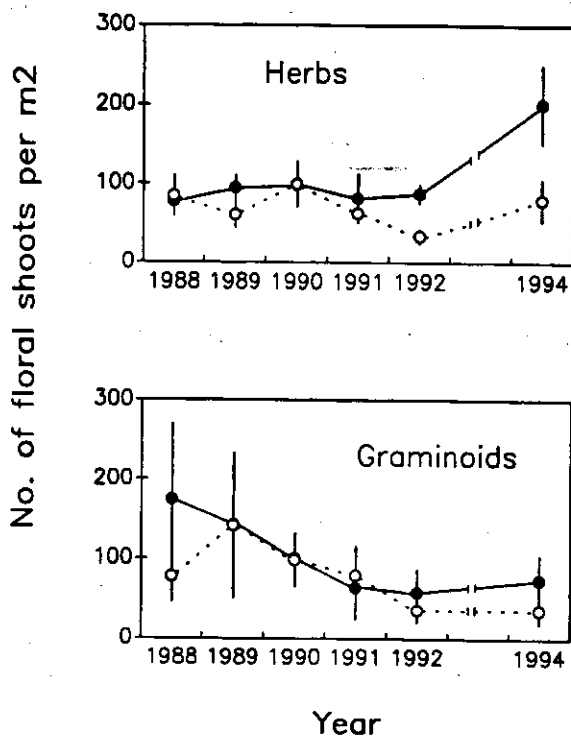


Fig. 6. The number of floral shoots per m^2 (mean \pm sd; $n = 3$) for herbs (top) and graminoids (bottom) on the snow-bed. Filled circles are for exclosures and open circles for open plots.

(*Luzula confusa*, *Oxyria digyna*, and *Ranunculus glacialis*). When transplanted, all shoots were at least a few centimeters tall, with normal-sized leaves, whereas at the end of the experiment, the surviving shoots looked like seedlings, with maximum leaf diameters of only a few millimeters.

In addition to the transplanted mountain birches, eight spontaneously dispersed *Betula* seedlings were found in the snow-bed exclosures, whereas none was found in the open plots or in the close surroundings, in spite of an extensive search. All eight birch seedlings

Table 2. Results from Repeated measures ANOVAs on the number of fertile shoots per m^2 in the exclosures and open plots on the snow-bed.

Source	df	MS	F	p
A. Herbs				
Fence	1	11 953.78	8.59	0.043
Error(between)	4	1391.94		
Time	5	4764.31	10.83	<0.001
Fence \times Time	5	3341.71	7.60	<0.001
Error(within)	20	439.98		
B. Graminoids				
Fence	1	5184.00	0.84	0.41
Error(between)	4	6168.89		
Time	5	8929.78	4.43	0.007
Fence \times Time	5	2369.13	1.18	0.36
Error(within)	20	2015.89		

Table 3. Number of floral shoots in the different treatments summed over the entire plot areas (i.e. 192 m² per treatment). A dash indicates that the species did not occur in those plots.

	Tall herb meadow		Snow-bed	
	Fence	Open	Fence	Open
1992				
<i>Trollius europaeus</i>	237	112	220	15
<i>Cicerbita alpina</i>	53	48	—	—
<i>Gnaphalium norvegicum</i>	—	—	577	186
1994				
<i>Trollius europaeus</i>	884	558	710	0
<i>Cicerbita alpina</i>	52	70	—	—
<i>Gnaphalium norvegicum</i>	—	—	768	123

were still present in 1994, and their sizes approached the sizes of the transplanted shoots.

Due to the combined effect of differential survival and growth of transplanted tall herbs and woody plants plus the spontaneous invasions and changes in the vegetation and in the densities of floral shoots, there was a pronounced difference in the appearances of the snow-bed exclosures and open snow-bed plots in 1994. The exclosures had the general appearance of a herbfield, and the transplanted tall herbs (especially *Veratrum* and *Cicerbita*) were visible over a long distance. So were the transplanted and spontaneous mountain birches. The open plots had remained grassy snowbeds, and the surviving transplants were difficult to find. The tall herb meadow, in turn, continued across the boundaries of exclosures without any visible change in the vegetation, and the transplanted shoots disappeared in the general luxuriance of the habitat.

Table 4. Survival of adult shoots transplanted in August 1987 (mean \pm sd; $n = 3$ replicates with 5 shoots in each). Survival is measured as the per cent alive shoots in August 1994. 'Fence' refers to exclosures, and 'Open' to open plots.

	Tall herb meadow		Snow-bed	
	Fence	Open	Fence	Open
A. Tall herbs				
<i>Alchemilla</i>	87 \pm 12	80 \pm 20	67 \pm 42	47 \pm 42
<i>Angelica</i>	73 \pm 23	80 \pm 0	47 \pm 50	33 \pm 12
<i>Epilobium</i>	27 \pm 23	47 \pm 42	53 \pm 12	33 \pm 42
<i>Geranium</i>	87 \pm 12	73 \pm 31	100 \pm 0	33 \pm 31
<i>Cicerbita</i>	80 \pm 20	60 \pm 20	67 \pm 23	33 \pm 12
<i>Veratrum</i>	93 \pm 12	53 \pm 12	100 \pm 0	87 \pm 12
B. Woody plants				
<i>Betula</i>	47 \pm 23	53 \pm 50	47 \pm 31	7 \pm 12
<i>Salix</i>	80 \pm 20	87 \pm 12	93 \pm 12	60 \pm 20
<i>Sorbus</i>	80 \pm 20	53 \pm 31	67 \pm 12	20 \pm 20
C. Alpine plants				
<i>Antennaria</i>	47 \pm 31	33 \pm 31	60 \pm 40	20 \pm 35
<i>Gnaphalium</i>	0 \pm 0	33 \pm 58	33 \pm 42	47 \pm 42
<i>Luzula</i>	7 \pm 12	0 \pm 0	13 \pm 23	13 \pm 12
<i>Oxyria</i>	7 \pm 12	7 \pm 12	20 \pm 35	47 \pm 50
<i>Ranunculus</i>	0 \pm 0	0 \pm 0	27 \pm 23	7 \pm 12
<i>Viscaria</i>	7 \pm 12	7 \pm 12	33 \pm 23	7 \pm 12

Seed germination and seedling survival

The seeding experiment was burdened by an unexpected technical problem. During the snowmelt, there was so much water running along the ground surface that the seeding plots where the humus had been removed became small pools for a period of 1–2 weeks (longer on the snow-bed). Nevertheless, germination success was generally high for all species, except for *Betula*, *Salix* and *Epilobium* in the snow-bed plots (Table 6). All these plants have seeds adapted to long-range wind dispersal and, hence, had structures which increase the likelihood of becoming washed away in spring. The MANOVAs showed a significant habitat effect for tall herbs and woody plants indicating a higher germination in the tall herb meadow plots (herbs: $F = 8.84$, $df = 3,6$, $p = 0.013$; woody plants: $F = 24.34$, $df = 2,7$, $p = 0.001$). No significant effects were found for the alpine plants.

The mean number of seedlings per microsite in 1989 was generally close to 2.0 with some exceptions: *Cicerbita*, *Betula* and *Antennaria* had generally lower germination, while *Viscaria* had generally higher germination (Table 7). All groups had a significantly higher germination in the tall herb meadow than on the snow-bed (herbs: $F = 4.14$, $df = 3,114$, $p = 0.008$; woody plants: $F = 15.97$, $df = 2,115$, $p < 0.001$; alpine plants: $F = 7.60$, $df = 5,112$, $p < 0.001$). Moreover, there was a significant fence effect for alpine plants, indicating a higher germination or early survival in fenced plots ($F = 6.20$, $df = 5,112$, $p < 0.001$).

The mean per cent mortality in each treatment varied between species, *Epilobium*, *Betula*, and *Salix* having the highest mortalities (Table 8). Note the plus signs in Table 8 indicating that the number of seedlings per microsite had increased for several alpine plants, i.e. some of the seeds probably stayed dormant for a few years. All *Betula* seedlings died during the period, and also all *Salix* seedlings on the snow-bed died. The MANOVAs showed no significant effects on tall herb or alpine plant mortality. Woody plants could not be tested due to missing cells.

Seedlings of only two species had reached a reproductive stage at the end of the experiment. These were *Gnaphalium supinum* and *Viscaria alpina*. *Gnaphalium* had a total of 15 floral shoots in the exclosures and 2 in the open plots in the tall herb meadow. No floral shoots were found on the snow-bed. *Viscaria* had a total of 9 and 18 floral shoots in exclosures and open plots, respectively, in the tall herb meadow, while the numbers were 17 and 1, respectively, on the snow-bed.

Discussion

Densities of microtine rodents did not increase along the gradient from the snow-bed to the luxuriant tall

Table 5. Growth rate (mean \pm sd; mm/yr except for alpine plants where growth is measured as no. of rosettes/yr) for transplanted shoots that had survived until August 1994. A dash indicates a missing value due to 100% mortality.

	Tall herb meadow		Snow-bed	
	Fence	Open	Fence	Open
A. Tall herbs	9	8	13	2
<i>Alchemilla</i>	4 \pm 13	10 \pm 4	6 \pm 10	-2 \pm 3
<i>Angelica</i>	9 \pm 21	4 \pm 4	8 \pm 17	3 \pm 6
<i>Epilobium</i>	1 \pm 8	-6 \pm 4	-1 \pm 10	-1 \pm 3
<i>Geranium</i>	6 \pm 12	11 \pm 13	15 \pm 13	2 \pm 4
<i>Cicerbita</i>	15 \pm 10	13 \pm 15	19 \pm 9	5 \pm 3
<i>Veratrum</i>	17 \pm 10	13 \pm 8	18 \pm 14	7 \pm 4
B. Woody plants	11	8	13	-3
<i>Betula</i>	14 \pm 10	16 \pm 6	22 \pm 16	7
<i>Salix</i>	16 \pm 12	10 \pm 13	13 \pm 11	-3 \pm 8
<i>Sorbus</i>	2 \pm 6	-2 \pm 8	5 \pm 2	-13 \pm 15
C. Alpine plants	-0.3	-0.5	-0.1	-1.0
<i>Antennaria</i>	-0.3 \pm 0.7	-0.6 \pm 0.6	-0.3 \pm 0.2	-0.8 \pm 0.9
<i>Gnaphalium</i>	—	-1.2 \pm 1.1	0.0	-2.0 \pm 2.3
<i>Viscaria</i>	—	0.3 \pm 1.0	0.0	-0.2

herb meadow, whereas the activities of specialist predators did (Oksanen et al. 1992, 1997). Hence, it seems reasonable to assume that intense predator activity in the latter habitat (Oksanen et al. 1992, 1997), had a regulatory impact on herbivores. Removal of herbivorous vertebrates from the tall herb meadow did not produce any drastic impacts on the structure of the vegetation or on the survival and growth rates of transplanted plants. No vole damage of transplants was observed after vole peaks, contrary to the hypothesis of Hansson (1987) according to which vole declines are initiated by acute resource depletion even in productive high latitude habitats. Alpine plants transplanted to the tall herb meadow perished in the shade of the tall herbs, although they germinated and grew well on the cleared plots. Hence, lack of tolerance of high temperatures, at least over the duration of the experiment, did not seem to be relevant for the lower limit of arctic-alpine plants in this

habitat gradient, contrary to the ideas of Dahl (1951) and Gauslaa (1984).

The above results are consistent with the predictions of the hypothesis of exploitation ecosystems (Fretwell 1977, Oksanen et al. 1981, Oksanen 1988, 1990), according to which productive habitats are characterized by a predation-controlled grazer community and competition-structured vegetation. Lack of strong grazer impacts on the vegetation is also consistent with the traditional bottom-up approach to plant ecology (Walter 1964, 1968, Ellenberg 1978). Even Grime (1977, 1979) and Tilman (1982, 1988) agree about the importance of light competition in a habitat with tall and dense vegetation.

In the snow-bed site, vegetationally corresponding to the snow-beds of the Norwegian IBP-project (Wielgolaski 1975a), erect, broad-leaved herbs rapidly gained dominance within exclosures. Explosive increase in the tallest (*Trollius europaeus*, *Gnaphalium norvegicum*) and

Table 6. Number of microsites where seeds had germinated in August 1989 (mean \pm sd, maximum number of microsites is 10; $n = 3$ in each treatment).

	Tall herb meadow		Snow-bed	
	Fence	Open	Fence	Open
A. Tall herbs				
<i>Angelica</i>	8.7 \pm 0.6	7.0 \pm 1.0	7.3 \pm 0.6	7.7 \pm 2.1
<i>Epilobium</i>	6.0 \pm 1.0	5.0 \pm 1.0	2.0 \pm 1.0	1.0 \pm 1.7
<i>Cicerbita</i>	6.0 \pm 1.7	6.3 \pm 3.8	4.0 \pm 1.0	4.3 \pm 1.2
B. Woody plants				
<i>Betula</i>	2.3 \pm 1.1	2.0 \pm 1.0	0.0 \pm 0	0.7 \pm 0.6
<i>Salix</i>	6.0 \pm 1.0	4.3 \pm 2.1	1.0 \pm 1.0	0.3 \pm 0.6
C. Alpine plants				
<i>Antennaria</i>	7.7 \pm 3.2	4.7 \pm 0.6	5.0 \pm 2.0	4.0 \pm 0
<i>Gnaphalium</i>	8.0 \pm 1.0	4.3 \pm 1.1	6.7 \pm 2.1	4.0 \pm 1.7
<i>Luzula</i>	8.0 \pm 1.7	7.0 \pm 2.6	6.3 \pm 2.1	3.7 \pm 1.5
<i>Oxyria</i>	8.7 \pm 2.3	7.3 \pm 1.5	9.3 \pm 0.6	8.0 \pm 1.0
<i>Viscaria</i>	9.3 \pm 1.1	10.0 \pm 0	8.0 \pm 1.7	7.0 \pm 2.6

Table 7. Number of seedlings per microsite (Mean \pm sd; $n = 30$ in each treatment) in August 1989.

	Tall herb meadow		Snow-bed	
	Fence	Open	Fence	Open
A. Tall herbs				
<i>Angelica</i>	2.0 \pm 1.1	1.5 \pm 1.4	1.9 \pm 1.5	1.8 \pm 1.4
<i>Epilobium</i>	2.0 \pm 2.6	2.0 \pm 3.1	1.1 \pm 2.7	0.1 \pm 0.4
<i>Cicerbita</i>	1.1 \pm 1.9	1.4 \pm 1.6	1.0 \pm 1.8	0.7 \pm 1.0
B. Woody plants				
<i>Betula</i>	0.2 \pm 0.4	0.3 \pm 0.7	0.0 \pm 0	0.1 \pm 0.2
<i>Salix</i>	2.1 \pm 2.9	1.1 \pm 1.7	0.2 \pm 0.5	0.03 \pm 0.2
C. Alpine plants				
<i>Antennaria</i>	1.7 \pm 1.5	1.2 \pm 1.7	1.0 \pm 1.4	0.7 \pm 1.2
<i>Gnaphalium</i>	3.5 \pm 3.1	1.2 \pm 1.7	2.2 \pm 3.0	0.7 \pm 1.0
<i>Luzula</i>	4.8 \pm 4.1	3.4 \pm 3.7	3.2 \pm 3.7	1.9 \pm 3.3
<i>Oxyria</i>	2.7 \pm 2.1	2.4 \pm 2.1	4.4 \pm 3.2	2.8 \pm 2.0
<i>Viscaria</i>	8.7 \pm 3.1	8.7 \pm 2.2	5.5 \pm 3.9	4.8 \pm 4.4

Table 8. Per cent mortality of seedlings summed per plot between autumn 1989 and autumn 1991 (Mean \pm sd, $n = 3$ except where otherwise noted). A plus indicates that the mean number of seedlings increased during the time period.

	Tall herb meadow		Snow-bed	
	Fence	Open	Fence	Open
A. Tall herbs				
<i>Angelica</i>	2 \pm 14	18 \pm 7	40 \pm 53	41 \pm 51
<i>Epilobium</i>	68 \pm 17	84 \pm 18	95 \pm 8	75 ^b
<i>Cicerbita</i>	55 \pm 37	61 \pm 31	63 \pm 34	29 \pm 29
B. Woody plants				
<i>Betula</i>	100 \pm 0	100 \pm 0	—	100 \pm 0 ^a
<i>Salix</i>	55 \pm 22	77 \pm 39	100 \pm 0 ^a	100 ^b
C. Alpine plants				
<i>Antennaria</i>	+24 \pm 29	14 \pm 33	22 \pm 52	52 \pm 14
<i>Gnaphalium</i>	+11 \pm 32	30 \pm 64	31 \pm 45	+21 \pm 75
<i>Luzula</i>	23 \pm 33	+1 \pm 37	+14 \pm 66	+6 \pm 39
<i>Oxyria</i>	10 \pm 12	13 \pm 43	18 \pm 54	27 \pm 40
<i>Viscaria</i>	+1 \pm 3	13 \pm 11	25 \pm 23	+2 \pm 32

^a $n = 2$.

^b $n = 1$.

most broad-leaved (*Viola biflora*) herbs largely accounted for this change. Conversely, the initially abundant buttercups (primarily *Ranunculus acris*) did not respond positively to the exclusion of grazers. *R. acris* thrives on mountain pastures (Nordhagen 1943, Wielgolaski 1975c), contains enough alkaloids to deter even reindeer (Skjenneberg and Slagsvold 1968, Nilsson 1986), and has finely lobed and relatively basal leaves. Hence, it is a g-strategist (i.e. a grazing-adapted plant) in the scheme of Oksanen and Ranta (1992) and its failure to respond to the treatment was expected on a priori grounds. An even more striking contrast was observed between the performances of transplanted tall herbs and woody plants between open snow-bed plots and exclosures. In open plots, survival rates were low and the survivors had shown little if any net growth during the course of the experiment. After microtine peaks, there were obvious gnawing signs in transplanted woody plants. In exclosures, in turn, survival rates were high and growth rates were normally higher than those in the tall herb meadow, suggesting that the more relaxed competition in the snow-bed more than compensated for the negative effects of a shorter growing season and lower summer temperatures. Woody plants invaded the exclosures spontaneously; in effect transplantations speeded up the invasion process.

Our data thus suggest that the vegetation of the early-melting snow-bed site is structured by grazing vertebrates, as predicted by Oksanen et al. (1981). Results of exclosure experiments performed in other Fennoscandian snow-bed sites by (Oksanen 1988, 1990, Moen et al. 1993, Oksanen and Moen 1994, Virtanen et al. 1997a, Virtanen 1998) differ with respect to the identity of plants reacting positively to the exclusion of grazers, but in all experiments, the winners were the

tallest species initially present in the community. In more extreme arctic-alpine habitats, exclusion of herbivorous vertebrates appears to favor robust cryptogams, capable of building compact carpets and pre-emptively competing for nutrients provided by precipitation (Batzli 1975, Virtanen et al. 1997a).

While the results of arctic-alpine exclosure experiments corroborate the general prediction of Fretwell (1977) and Oksanen et al. (1981) that herbivores of unproductive areas are resource-limited and exert strong influence on the vegetation, some more specific ideas of Fretwell (1977) and Oksanen (1980) have been thoroughly falsified. Fretwell claimed that extremely barren habitats, where herbivores cannot survive, are dominated by strong competitors. Accordingly, Oksanen interpreted Fennoscandian high alpine plants as pronounced K-strategists, more competitive than species typical for snow-beds with continuous vegetation. According to our results, however, the three pronouncedly high alpine plants (*Luzula confusa*, *Oxyria digyna* and *Ranunculus glacialis*) were weaker competitors than the dominating plants of early-melting snow-beds. Fretwell's idea that woody plants are always competitively superior to herbaceous plants is consistent with our results. However, Virtanen (1998), working in a more extreme snow-bed, found that the transplanted bilberry twigs (*Vaccinium myrtillus*) declined even in exclosures, although at a slower rate than in open plots. Vegetational patterns of arctic islands without grazing mammals (Virtanen et al. 1997b) further reduce the credibility of Fretwell's (1977) and Oksanen's (1980) plant ecological ideas. The warmest habitats on these islands are dominated by broad-leaved herbs, whereas other habitats with continuous plant cover are covered by thick moss banks. Erect, woody plants are absent, and high alpine and high arctic herbs (e.g. *R. glacialis*) are only encountered in blockfields and other disturbed habitats.

The failure of Fretwell (1977) and Oksanen (1980) to predict the characteristics of competitively superior plants in cold environments has its roots in shallow analysis and partially circular empirical reasoning. Woody stems inevitably contain some live tissue. In habitats with long winters but above-zero ground temperatures, woody plants suffer heavy respiratory losses (Havas and Mäenpää 1972). In such habitats, it can be more cost-efficient to construct new stems every summer. In still more extreme arctic-alpine habitats the terms of competition change (see Tilman 1988): light is superabundant and plants are likely to be nutrient-limited (Billings 1987, Chapin 1983, 1987). As the rate of mineralization is very low, cryptogams obtaining their nutrients directly from rain and snowmelt gain competitive dominance. The prevalence of herbaceous plants in the most extreme arctic-alpine habitats is, in turn, probably primarily a consequence of intense physical disturbance, which increases the nutrient content of the

soil (Jonasson 1986) and prevents the formation of cryptogam banks.

The collective message of arctic-alpine enclosure experiments is that the population dynamical core of the hypothesis of exploitation ecosystems (Fretwell 1977, Oksanen et al. 1981) is sound in the context of arctic-alpine productivity gradients. Impacts of grazing vertebrates may have been even more profound in the Pleistocene (Zimov et al. 1995), but at least in habitats with good snow cover, the role of natural herbivory is profound even today. Neither Fretwell (1977) nor Oksanen et al. (1981) can claim credit for discovering the importance of animal-plant interactions in the arctic. Lack (1954) interpreted lemming fluctuations as a predator-prey cycle with lemmings as predators and plants as prey, and similar ideas on arctic ungulates have been presented by Caughley and Lawton (1981; see also Caughley and Gunn 1993, Crête and Manseau 1996). Moreover, Tihomirov (1959) argued that the tundra as we know it is shaped by interactions between herbivores and plants. The role of the hypothesis of exploitation ecosystems is merely to place the arguments concerning unproductive arctic, alpine and arid environments into a broader picture.

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