



Vole–vegetation interactions in an experimental, enemy free taiga floor system

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Vole–vegetation interactions in a predation-free taiga environment of northern Fennoscandia were studied by transferring vegetation from natural *Microtus* habitats into a greenhouse, where three habitat islands of about 30 m² were created. The ‘islands’ were subjected to simulated summer conditions and a paired female field vole, *Microtus agrestis*, was introduced to each ‘island’. The development of the female and her young was followed by recurrent live trapping. The development of the vegetation was followed by recurrent marking and censusing of plant shoots at intervals of five days. In the next growing season, two ‘islands’ were subjected to a new grazing treatment to study the impacts of repeated grazing on the vegetation and on the growth and reproduction of voles. Plant biomasses were harvested at the end of each trial. In all trials, the biomasses of graminoids and non-toxic herbs other than ferns, fireweeds and rosaceous plants were profoundly decimated. Even the biomass of a toxic herb *Aconitum lycoctonum* decreased largely at pace with the palatable herbs. The least preferred plant categories maintained their biomasses at control levels. Their neutral collective response was created by opposite species-level trends. Species typical for moist and nutrient-rich forests suffered from vole grazing, whereas the biomass of species adapted to disturbed habitats increased.

In spite of the dramatic changes in the vegetation, the introduced female voles survived throughout the trials and reproduced normally. The young of their first litters survived well and reached the final weights typical for individuals starting to winter as immatures. We conclude that most of the plant biomass found on productive boreal forest floors is potential food for field voles and remains palatable for them even when subjected to recurrent, severe grazing. If nothing else than summer resources were limiting the growth of the field vole populations, the plants currently dominating moist and nutrient-rich taiga floors could not survive in this habitat.

The importance of strong trophic cascades has been debated during the last decades. Hairston et al. (1960) hypothesized that the collective density of herbivores is controlled by the collective action of predators. Strong, community-level trophic cascades, involving three trophic levels, should thus characterize terrestrial ecosystems. Experimental tests of this conjecture have supported the idea that predation has profound impacts on the dynamics of folivorous insects, and the impact of predation cascades or at least trickles down to plant

communities. However, the changed dynamics of folivorous insects appears to influence primarily the composition of the plant community, whereas strong impacts on community-level biomass have only been found in homogeneous agro-ecosystems (Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002, Schmitz 2003, Borer et al. 2005).

Even herbivorous mammals seem to be regulated frequently by predators (Hanski et al. 1991, 1993, 2001, Korpimäki et al. 1991, 2005a, Krebs et al. 1992,

1995, Korpimäki and Krebs 1996, Korpimäki and Norrdahl 1998, Wilson et al. 1999, Klemola et al. 2000a, b, Gilg et al. 2003, Ekerholm et al. 2004) and severe devastation of woody vegetation by mammalian herbivores has been documented on islands with impoverished predator communities (McLaren and Peterson 1994, Terborgh et al. 2001, Hambäck et al. 2004). Conversely, the cascading impacts of predation on the biomass of herbaceous vegetation have been weak (Norrdahl et al. 2002, Hambäck et al. 2004). In systems with intense natural herbivory, the exclusion of herbivorous mammals has influenced the composition of herbaceous vegetation but not its total biomass (Chase et al. 2000). This supports Leibold's (1989, 1996) conjecture of dynamics in food webs with heterogeneous trophic levels. Hambäck (1998) and Norrdahl et al. (2002) proposed that the ultimate reason for the contrasting responses of woody and herbaceous plants is seasonality. Woody plants are accessible in the limiting season, when herbivorous mammals are compelled to use even the marginal forage, whereas herbaceous plants are only accessible in the growing season, when grazers are literally wading in forage and can thus be expected to be maximally selective.

To disentangle the roles of inherent non-palatability and seasonality, we constructed "islands" of natural, productive northern boreal forest floor vegetation in a greenhouse. The "islands" thus constructed were about 30 m² large, corresponding the vegetated areas of the outermost islands at Tvärminne, Finland, where invasions lead to extremely high (>2000 voles ha⁻¹) densities (Pokki 1981). Technically, the experiment followed the approach pioneered by Moen et al. (1993), but this time with sufficient space to allow the population growth of voles to start from levels that actually occur in nature.

According to conjectures, which regard the vegetation as an essentially homogeneous resource (Hairston et al. 1960, Oksanen et al. 1981, Oksanen and Oksanen 2000), the recovering vegetation should consist primarily of the most resilient species and ruderals with high reproductive output. Herbivores should grow and reproduce normally when introduced to this community. Conversely, Leibold's (1989, 1996) conjecture of dynamics in food webs with heterogeneous trophic levels predicts, that the recovering vegetation should be dominated by unpalatable plants, whose expansion should at least partially restore plant biomass, reducing the difference between treatment and control plots. Herbivores introduced to the community should perform poorly. Even the third group of hypotheses, emphasizing the induction of chemical defenses (Haukioja and Hakala 1975, Rhoades 1985, Karban and Myers 1989, Seldal et al. 1994) predicts that previous grazing should make the vegetation unsuitable

for grazers, but instead of changes in the composition of the vegetation, these hypotheses emphasize changes in individual plants. To provide a test for the contesting conjectures, we repeated the experiment of Moen et al. (1993) by using vegetation, which was recovering from the past impacts of grazing.

As for the interpretation of the results, there is one caveat. We did not allow dispersal out of the "islands" and thus, did not control the fence effect in the experiment (Krebs et al. 1969, Boonstra and Krebs 1977). The choice was intentional. Predator exclusion experiments controlling the fence effect have been conducted e.g. by Desy and Batzli (1989), Klemola et al. (2000a, b), and Korpimäki and Norrdahl (1998); the problems of interpreting the fence effect have been discussed by Ostfeld (1994). The goal of the present study was to find out how strongly field voles influence the vegetation of a moist and nutrient-rich taiga floor, if nothing else than summer forage limits their population growth. Mixing in other questions would only have increased the risk of obtaining ambiguous results.

Material and methods

Over-all design

The experiment consisted of three trials, two conducted in Oulu, Finland, 65°00'N, during two subsequent years (1997 and 1998) and one in Umeå, Sweden, 63°50'N, in 1998. Each trial was planned to consist of two phases, so that in the 1st phase, voles were interacting with vegetation that had been only lightly grazed in the recent past. In the 2nd phase, they interacted with vegetation recovering from the impacts of the 1st phase. The experimental vegetation was excavated from herb-rich taiga floor habitats of northern Fennoscandia in 25 × 25 cm blocks in years when rodent densities had been low. To include the entire range of palatability encountered in the vegetation, we excavated an equal number of blocks containing remains of floral shoots of the following three species: of *Solidago virgaurea* (a palatable rosette herb), *Geranium sylvaticum* (a moderately palatable herb with elevated foliage, Moen et al. 1993) or *Aconitum lycoctonum* (morphologically similar to *G. sylvaticum* but strongly toxic, Gutser et al. 1998), which indicated the presence of a mature and physiologically independent plant in a block. All other species growing in these blocks were included. Excluding the plants, which were missing from our enclosure plots in some of the three trials, the material thus obtained (Appendix 1) contained 31 vascular species with variable morphological and chemical properties. The blocks were excavated in late fall (October–November), when all herbaceous plants had withered and the topsoil was frozen. The

blocks included the organic and mixed organic–inorganic layers (where the plant roots were situated). The *Geranium* and *Solidago* blocks were taken from a lime-rich site in Kiiminki, northern Finland (65°09'N, 25°50'E). The *Aconitum* blocks were taken from Kvikkjokk, Swedish Lapland (66°52'N, 18°10'E). (Finnish material could not be used for *Aconitum lycoctonum* is red-listed and strictly protected in Finland.)

To ensure bud activation in the greenhouse, the blocks were initially stored outdoors. In early December, when the plants had received a necessary cold treatment, the blocks were taken to a greenhouse where they were randomly assigned to vole enclosures and controls. The blocks were arranged as 75 × 75 cm plots on greenhouse tables, which were covered with gravel to ensure drainage. Each plot consisted of three *Solidago* blocks, three *Geranium* blocks and three *Aconitum* blocks in a Latin square arrangement, with covered runways between the plots (Moen et al. 1993). Each trial included one experimental table and a paired control table. The experimental tables (sizes about 30 m², Table 1) were surrounded by galvanized mink cage net (mesh size 1.2 × 1.2 cm) with flashings along the top to prevent voles from escaping. The control tables (sizes about 6 to 8 m²) had a similar layout (Table 1).

After the construction of the habitat islands, the vegetation was exposed to conditions corresponding to spring and summer in moist northern taiga. The tables were kept continuously moist by daily irrigation. As blocks contained plenty of nutrient-rich soil, no fertilizers were applied in the 1st phase. Before the beginning of the 2nd phase, 1.6% commercial fertilizer (Keikkilä's Superex in 1997, Kemira's 14-5-21 NPK in 1998) was applied twice to replace the nutrients leached out of the soil with vole excrements. The temperature

was initially kept between +5°C and +10°C. When the plots started to green, the temperature was increased to around +10°C. When spring plants (e.g. *Maianthemum bifolium*) started to flower, the temperature was raised to +20°C at daytime and +15°C night-time. On sunny days, the temperature was allowed to rise to +25°C (a value seldom exceeded in northern Fennoscandia); further increase was prevented by ventilation. Simultaneously, a newly mated field vole female was introduced. The photoperiod was initially 20 h, increasing to 24 h and gradually declining to 15 h to match the photoperiods of spring, summer and early fall. The 1st phase experiment was scheduled to last 77 days from the introduction to the removal of voles (+1 to 2 days if day 77 was during a weekend), unless the young of the first litter would start to lose weight, which we regard as an indication of acute shortage of edible plants. This happened in the 1998 Umeå trial, which was terminated on day 71. After the end of the 1st phase, voles were removed and the temperature was decreased to +15°C daytime and +10°C night-time to mimic the normal cooling process in fall.

When the plants had turned into fall colors, the vegetation blocks were transferred to an outdoor table, surrounded by a temporary plastic greenhouse to keep its maximum temperature slightly above zero and minima at about –5°C, as normal in late fall. After withering, the plastic greenhouse was removed, allowing the temperature first to drop to the prevailing April levels and to rise again in a natural way the following spring. The vegetation was also allowed to develop under natural thermal conditions. In the 2nd phase of the experiment, the control vegetation was again allowed to grow undisturbed. Majority of the previously grazed plots were placed to an outdoor enclosure, but five plots were transferred to a control table to allow the

Table 1. Total and vegetated areas of the enclosures and controls, total numbers of vegetation plots, and numbers of censused and harvested enclosure, control and 2nd phase control plots.

		Oulu 1st 1997	Oulu 1st 1998	Umeå 1st 1998	Oulu 2nd 1997	Oulu 2nd 1998
Enclosure	Total area m ²	32.0	32.0	33.6	28.4	28.4
	Vegetated area m ²	24.8	24.8	27	21.9	21.9
	No. of plots. total	44	44	48	39	39
	No. of censused plots	15	8	8	15	4
	No. of harvested plots	0	14	15	21	8
Control	Total area m ²	6.1	8.3	8	5.9	4.5
	Vegetated area m ²	4.5	6.2	4.5	4.5	3.4
	No. of plots. total	8	11	8	8	6
	No. of censused plots	0	4	4	0	2
	No. of harvested plots	0	5	4	8	6
2nd phase control	Total area m ²	–	–	–	3.6	3.6
	Vegetated area m ²	–	–	–	2.8	2.8
	No. of plots. total	–	–	–	5	5
	No. of harvested plots	–	–	–	5	5

evaluation of vole impacts in the 1st and 2nd phases (Table 1).

Studying vole–vegetation interactions

The experiment consisted of three replicate trials. In each trial, the vole population was initiated using a field vole, which had not been mated before and had started to winter as immature. The voles were captured in late fall at Konnevesi Biological Station, central Finland. The females were mated in cages 3–8 days prior to their introduction to the enclosures. To minimize stress from switching from laboratory food to green plants (Ranson 1934, Moen et al. 1993), we used plants growing on surplus plots to feed the voles while they were in cages and provided them with some laboratory food (less than the daily energy need) during the first four days of the experiment. During the rest of the experiment, the only supplemental food obtained by the voles consisted of <1 g pieces of dried apple, which were used as baits in the traps. Due to uncertain success of mating in cages, the male accompanied the female in the enclosure. The male was removed after 1–3 days. After the female had given birth to the first litter, the male was again introduced into the enclosure and left there until evidence of successful pairing was obtained, but at most for five whole days. After the birth of the second litter, the male was introduced only once for one whole day (to minimize the risk of infanticide and the impacts of the male on the already scanty vegetation). Throughout the experiment we trapped the females and later also the juveniles with Ugglan special live traps (about 10 traps per enclosure) at intervals of 1–3 days. Traps were checked at least once per hour. For each capture, the female's weight, status of milk glands and vagina were recorded. Juveniles were marked individually and weighed after every trapping.

In the enclosures, a set of census plots was sampled randomly from the plots along the perimeter of the table (because of accessibility). The number of census plots in the first trial (Oulu 1997) was 15. As the variance of vole impact turned out to be small, we reduced the number to eight in the subsequent trials (Table 1). For the less abundant plants, the census areas were extended to adjacent plots to provide fair sample sizes. Immediately before the beginning of the experiment, all shoots present on the census plots were identified to species (except for *Poa* spp., which were pooled), counted and marked with armored plastic ribbons. For bunch grasses and rosette plants, both the clusters and individual leaves were marked (leaves with ink or thread) to allow studies of shoot dynamics at both levels. For *Deschampsia flexuosa* with large numbers of thread-fine leaves, marking and counting

individual leaves turned out to be unreasonably tedious. Hence, leaf level data for this species were based on numbers of crossings between leaves and index lines laid across the plots. On the census plots, we counted all surviving shoots and marked all emerging ones at 5-day intervals, except that in the 1997 Oulu trial, the interval between the 10th, 11th and the 12th plant census was 10 days. Different colors were used for different shoot cohorts. For trailing plants, the number of shoot tips was counted. Partially grazed shoots were regarded alive if at least 5% of the leaf area remained.

The experimental procedure during the 2nd phase was conducted as above, except for the following differences. First, we obtained only two replicates because the second phase failed in Umeå, where April temperatures were not low enough to provide the cold treatment necessary for the bud break of many northern forbs. Second, both the thermal conditions and the duration of the experiment were this time determined by natural conditions. The experiment was terminated when first night frosts induced the turn into fall colors, which happened on day 72 in the 1997 Oulu trial and on day 62 in the 1998 Oulu trial.

We have only two replicates of the 2nd phase, and they were conducted under very different conditions. In 1998, thermal conditions were normal in the summer, and the spring was even cooler than in our simulations. Conversely, the spring and summer of 1997 were exceptionally hot. The sum of effective temperatures was 1236 dd, (normally 1107 dd). Precipitation during the growing season (reflecting cloudiness) was only 222 mm (normally 321 mm; source: official statistics of Finnish Meteorological Institute, Helsinki, Finland). The sunny and warm weather made the summer of 1997 extraordinarily favorable for plant growth, whereas for field voles, high temperature and intense sunshine were probably stressful and even resulted to trap mortality of two juveniles.

Estimating grazing impacts

Plant biomass was harvested in the end of the 1st phase in the 1998 trials, but not less in 1997 (Table 1). The plots harvested in the 1st phase were excluded from shoot censuses and harvesting in the 2nd phase. On the harvested plots, the shoots standing above ground were clipped, counted, collected and sorted by species, except for *Poa* spp. Grazed but still more than 50% green stumps were included in the aboveground biomass. Before weighing, all biomass samples were dried to constant weight (at 60°C).

The shoot census data provide a way to follow the development of the vegetation during the trials. To make the data tractable, we pooled the plants into five

functional groups, weighing all 31 species found in at least one plot in all trials with their average shoot weights, which were obtained by computing a regression line between shoot numbers and harvested biomasses. Since only a few species were present in the enclosures at the end of the trials, conversions from numbers to biomass were based on the control and recovery plots. For common species, conversion factors were computed separately for both phases of each trial. For rare species, we pooled the data. Conversion factors for rosette herbs and bunchgrasses were based on leaf censuses.

The plants were divided into the following five categories:

- 1) ericoids and evergreens: dwarf shrubs, club mosses, and members of the family Pyrolaceae,
- 2) strongly toxic herbs (the only common species being *Aconitum lycoctonum*),
- 3) 3 non-preferred herbs and woody plants: woody and non-woody rosaceous plants, birch seedlings, ferns, fireweed,
- 4) other herbs (primarily: *Geranium sylvaticum*, *Cirsium helenioides*, *Luzula pilosa*, *Solidago virgaurea*, *Maianthemum bifolium* and *Oxalis acetosella*),
- 5) graminoids (families Poaceae and Cyperaceae, primarily: *Deschampsia flexuosa*, *Melica nutans*, *Carex vaginata* and *C. digitata*).

Categories 1–3 consisted of relatively unpalatable plants, whereas categories 4 and 5 consisted of highly to moderately palatable plants (Stenseth et al. 1977, Moen et al. 1993). The rationale for including woody deciduous plants in the same category with non-preferred herbs was that the deciduous woody species were almost exclusively represented by seedlings with non-lignified stems.

In addition, we divided the species in accordance to the habitat where they were most abundant into four habitat preference categories: moist and mature taiga, dry woodlands, mid-successional habitats and recently disturbed (ruderal) habitats (sources: Hämet-Ahti 1963, Holmen 1965, Kalliola 1973).

Vole impacts on harvested plant biomasses in the end of the 1st phases were computed as $VI_i = 100(B_{ei} - B_{ci})/B_{ci}$, where B_{ei} is the final biomass of category i in the enclosure and B_{ci} is the final biomass of the category i in the control plots. In the end of the 2nd phases, we used the above formula to estimate the gross impact of voles (GVI_i). In addition, we estimated the immediate vole impacts (IVI_i) as $IVI_i = 100(B_{ei} - B_{ri})/B_{ri}$, where B_{ri} is the final biomass of category i in the recovery plots.

Estimating growth and biomass production of voles

For data presentation, vole biomasses were estimated for each of the plant census day on the basis of linear interpolations from the nearest weighing records. The weights of the newborn were estimated on the basis of the female's weight loss; range 2.0 to 2.5 grams (Frank 1956, Rychnovsky 1983). The growth rates of individual voles were estimated using non-linear regression with the logistic function as a model (SSlogis function, Anonymous 2000). The two juveniles, which disappeared in the 1st phase of the Oulu 1997 trial and the three victims of handling/trap mortality (Table 2) were excluded from the analyses of growth and biomass production of voles. The parameter values describing maximum growth rates of the first litters were compared between the 1st and 2nd phases with a t-test, using the averages of each litter as input variables (growth rates of all the young are influenced by the same mother). Moreover, we compared the mean asymptotes (wintering weights predicted by the regression) of the first litter young between the 1st and 2nd phases, and with the weights of the 21 immature and wintering voles originally trapped at Konnevesi, using ANOVA. We compared the maximum growth rate parameter with the biomass of forage plants (categories 4 + 5) 19 days after the birth of the first litter, when the growth rates of juveniles were at their highest. The asymptotes of the growth curves were compared to the estimated biomasses of forage plants 35 days after the birth of the first litter.

Table 2. Sizes of first litters in 1st and 2nd phases of the three replicate trials, mean values of the parameters referring to maximum growth rates and asymptotes, obtained from the non-linear regressions (model: the logistic curve) for each juvenile.

	Size of 1st litter (no.)	Parameter for maximal growth rate	Asymptotic weight (g)
1st phase 97 Oulu	6	8.02	19.24
1st phase 98 Oulu	6	6.50	21.72
1st phase 98 Umeå	4	8.87	21.74
1st phase, mean	5.3	7.80	20.90
2nd phase 97 Oulu	5	11.01	18.07
2nd phase 98 Oulu	5	8.60	18.62
2nd phase, mean	5.0	9.81	18.35

Results

Vole survival, reproduction and growth

The first reproduction was successful in all trials. The estimated day of birth for the first litters in Oulu was day 22 or 23 in both phases of the Oulu trials. In Umeå, the first litter was born already on day 13. After the first reproduction, the female became estrous and mating resulted in a new pregnancy in the 1st phases of all trials. The birth times of the second litters ranged from day 41 (Umeå 1998) to day 46 (Oulu 1997). In the 2nd phase of the 1997 Oulu trial, the weight of the female dropped on day 38, indicating abortion. After a new mating, the second litter was born on day 58. The third mating was only successful in the 2nd phase of the 1997 Oulu trial. The third litter was born in a cage after the trial. In the 2nd phase of the 1998 Oulu trial, the second mating failed. The male in question turned out to be unsuccessful even in cage tests.

The numbers of the first litter juveniles reaching trappable age varied from 4 to 6, means being similar for the two phases (Table 2). One juvenile was lost as a consequence of a handling mistake in the 1st phase of the 1998 Oulu trial. In the 2nd phase of the 1997 Oulu trial, the weather was periodically so hot that two juveniles were lost as victims of trap mortality, in spite of the frequent checking of traps. Disappearance of the first litter juveniles for unknown reasons only occurred in the 1st phase of the 1997 Oulu trial, where two juveniles disappeared after having been captured once. The weights of the first litter juveniles never decreased in Oulu trials. In Umeå, a decreasing trend was observed after day 68, and the experiment was terminated on day 71. There were no statistically significant differences in either the maximum growth rates ($t = 1.589$, $p = 0.21$) or the asymptotes of growth curves ($t = 2.345$, $p = 0.101$) between the two phases, although there was a tendency for higher maximum growth rates and lower asymptotes in the 2nd phases (Table 2). The ANOVA comparing the asymptotes of the two phases with each other and with the weights of the wintering immatures captured at Konnevesi in late autumn 1996 and 1997 (mean = 19.55 g, SD = 1.68 g, $n = 21$) gave a non-significant result ($F = 1.534$, $p = 0.235$). Regressions for the connection between the growth rate parameters and food quantity when the first litters were 19 and 35 days old did not reveal any indications of a statistical connection.

The second litters had low survival rates. In the 1st phase of the 1998 Oulu trial and in the 2nd phase of the 1997 Oulu trial, the births could only be inferred from a sudden drop in the weight of the female. No second litter voles reached trappable size. In the 1998 Umeå trial, two second litter juveniles had apparently escaped through a crack in the table and were captured

from the greenhouse floor on day 59. They survived until the end of the 1st phase, but no other 2nd litter juveniles were found. Fair survival of the second litter juveniles was only found in the 1st phase of the 1997 Oulu trial, where seven second litter juveniles reached trappable age and 4 survived to the final days of the 1st phase. (Two started to lose weight in the end and were removed two days early.) The second litter young grew slowly. In the 1997 Oulu trial, the final weights of the second litter young which survived, ranged from 8.5 g to 9.5 g (ages from 29 to 31 days). In Umeå 1998, the final weights of the two survivors were 8.0 g and 10.5 (both 28 days old). For the sake of comparison, the mean weights of 30 days old first litter juveniles of the same females were 17.0 g for Oulu 1997 and 16.5 g for Umeå 1998.

The collective mass of the surviving voles grew continuously in the 1st phases of Oulu trials (Fig. 1A–B). The short-term fluctuations in vole biomass reflected normal reproductive biology, and the slowing down of the growth curve for the first litter followed the growth pattern of voles wintering as immatures (Myllymäki 1977). Even in Umeå, the biomass development followed the same pattern, except for a slight decline in the end (Fig. 1C). The development of vole biomass in the 2nd phases of the Oulu trials followed approximately the same pattern seen in the 1st phases, except that the absolute biomass was lower in 1997, when two voles were accidentally lost (Fig. 1D–E). No indications on the impact of past grazing on growth or survival of voles could be observed.

Development of plant shoot populations and plant biomass

The development of plant communities in the vole enclosures followed the same general pattern in both phases of all trials (Fig. 2A–C, 2F–G). In both the simulated and the actual spring, shoot densities of all functional groups increased. The preferred graminoids started to decline between days 25 and 35. The shoot densities of moderately preferred herbs started to decline between days 35 and 50. Simultaneously or a few days after, *Aconitum* disappeared roughly in pace with equally tall but palatable species (*Geranium silvaticum*, *Cirsium helenoides*). The two groups of non-toxic but relatively unpalatable plants mostly stood their ground, except for the 1st phase of the Umeå trial, when clear signs of resource-limitation were observed in the end. In this trial, even marginal forage plants like *Vaccinium vitis-idaea* and *Phegopteris thelypteris* became strongly depleted during the last ten days. Only *Epilobium angustifolium* managed to produce new shoots at the same rate the old ones were consumed. In the controls, the expansion continued throughout

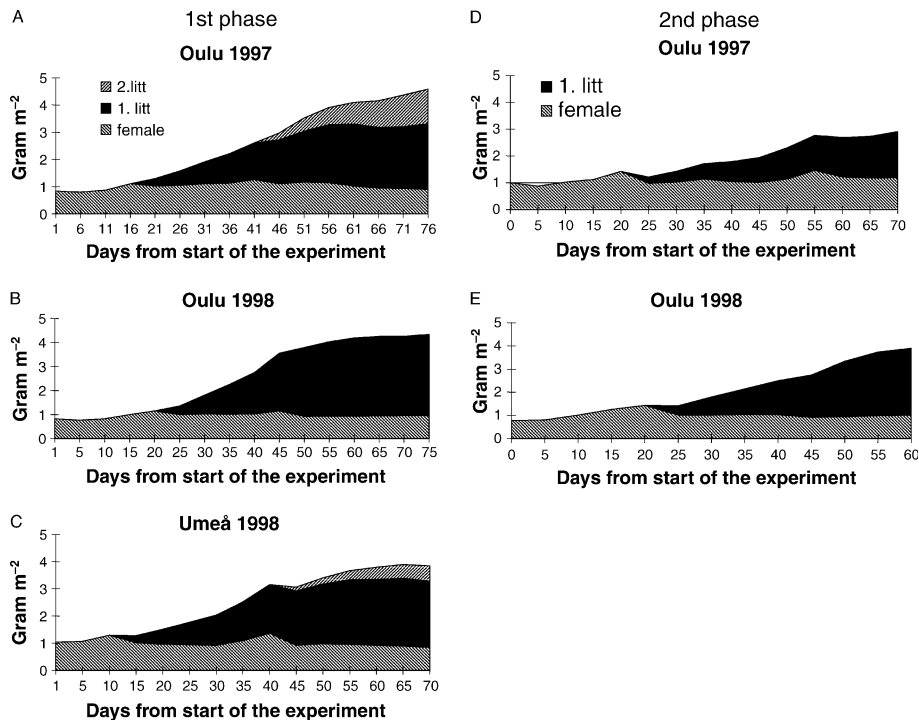


Fig. 1. Development of vole biomass (g^{-2} , fresh wt) during the three trials. (A) Oulu 1997, 1st phase. (B) Oulu 1998, 1st phase. (C) Umeå 1998, 1st phase. (D) Oulu 1997, 2nd phase. (E) Oulu 1998, 2nd phase. To facilitate comparison with plant biomasses, vole biomasses have been presented for the plant census days. For individuals not captured these days, weights were interpolated from nearest records. For the period between birth and trappability, juveniles were assumed to grow linearly. For the sake of graphical clarity, the biomass of the litter was connected to the last pre-parturition weighing record of the female. Hence, birth dates seem a bit earlier than they really were.

the 1st phase (Fig. 2D–E) and in the 2nd phase, shoot densities stayed largely at the level they had obtained in the end of the 1st phase (Fig. 2H; compare with Fig. 2D). The data for the 1998 trials, where a fraction of plots was harvested already in the end of the 1st phase, show that the regression method worked well in this phase, especially considering that census and harvest data came from different plots.

The impacts inferred by the shoot census method were verified by harvesting (Fig. 3, 4). The impacts of voles on the collective biomasses of graminoids, ‘other herbs’ and on the toxic *Aconitum lycoctonum* were strong and negative (Fig. 1, 3, 4, Table 3, Appendix 1). For the preferred graminoids, the impacts of intense grazing persisted even after a growing season without grazing. Their collective biomass in the recovery plots was only 20 to 25% from the control level (Fig. 4). Equally consistent and dramatic recovery failures were recorded even for some species belonging to other functional groups (*Linnaea borealis*, *Luzula pilosa*, *Oxalis acetosella*, *Solidago virgaurea*; Appendix 1), and the carry-over impacts on ‘other herbs’ were substantial even at the level of the functional group, whose biomass in the recovery plots was only 60% from

the control level in both trials. In the summer of 1997, the favorable growing conditions and the accidental loss of two voles ameliorated the effects of the voles on *Aconitum* and on the collective biomass of other herbs (Fig. 2F, 4). This was largely due to a fairly high final biomass of the tallest herbs with robust shoots (*Geranium silvaticum*, *Cirsium helenoides*, Appendix 1), which were among the last to be depleted in other trials, too.

At a collective level, ericoids and evergreens stood their ground in both phases of all trials and non-preferred herbs and woody plants gained more ground (Table 3, Fig. 2–4, Appendix 1). However, these two functional categories were heterogeneous, including both grazing-sensitive plants (e.g. *Linnaea borealis*, *Phegopteris thelypteris*) and plants which reacted positively to grazing in both trials (*Vaccinium vitis-idaea*, *Epilobium angustifolium*, *Fragaria vesca*, *Rubus idaeus*; Appendix 1). The differences in the response were related to habitat preferences. All species typical for moist, mature taiga suffered from vole grazing. The winners were primarily found among successional plants and ruderals (Fig. 4B, Appendix 1).

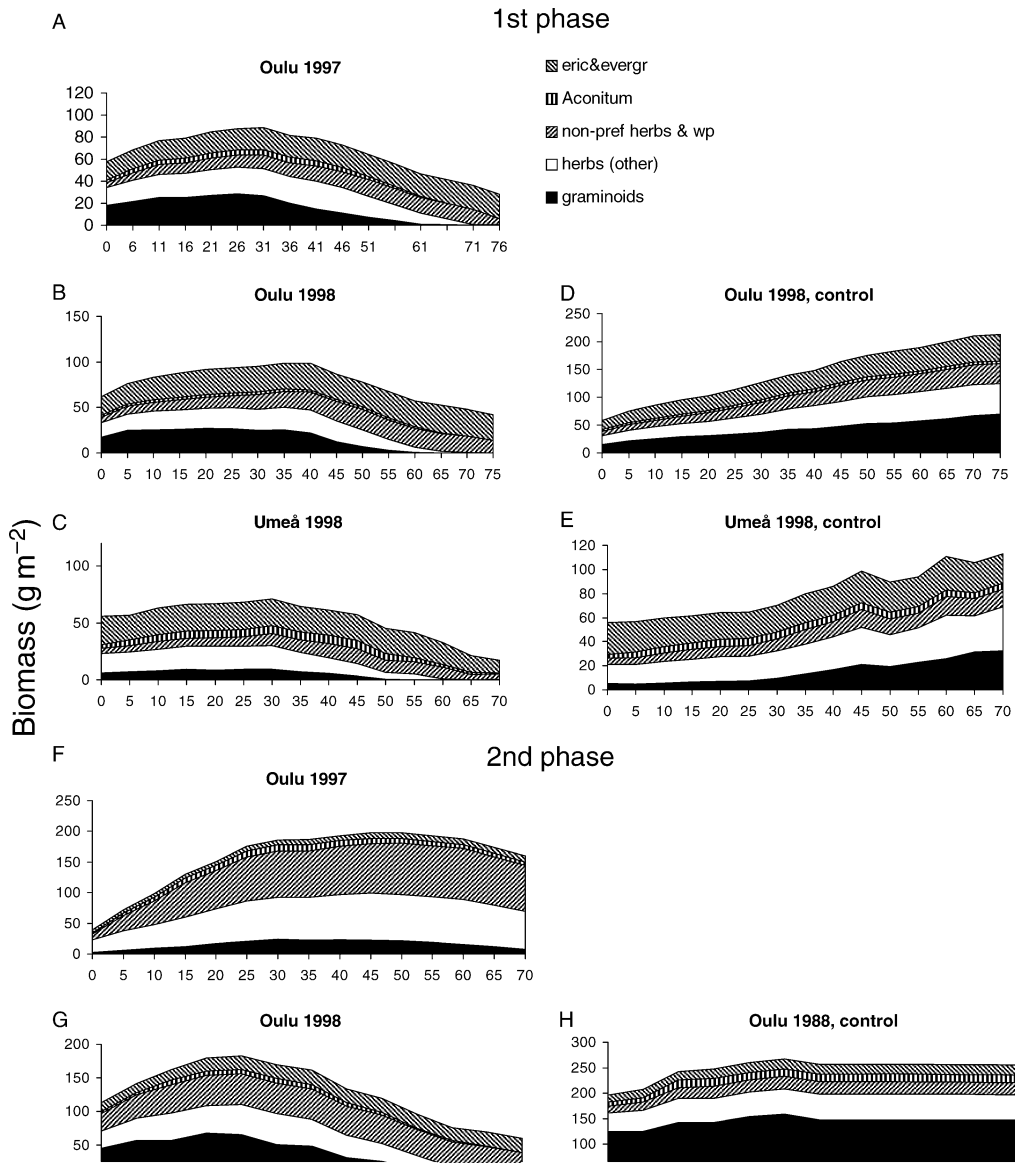


Fig. 2. Development of estimated biomass (g m^{-2} , dry wt) of main plant categories during the three trials. (A) Oulu 1997, enclosure, 1st phase. (B) Oulu 1998, enclosure, 1st phase. (C) Umeå 1998, enclosure, 1st phase. (D) Oulu 1998, control 1st phase. (E) Umeå 1998, control 1st phase. (F) Oulu 1997, enclosure, 2nd phase. (G) Oulu 1998, enclosure, 2nd phase. (H) Oulu 1998, control 2nd phase. wp refers to non-ericaceous woody plants.

Discussion

Seldal et al. (1994) argued that graminoids respond to grazing by producing trypsinases, which make it impossible for rodents to maintain positive protein balance. The consequent net loss of proteins was proposed to account for the summer declines of northern rodent populations, characterized by low survival rates, especially for juveniles (Viitala 1977, Hansson and Henttonen 1985, Korpimäki et al. 1991, Klemola et al. 2000a). Plant ecological studies con-

ducted in the peak phase show that the impact of voles on the growing vegetation is modest in *Microtus* habitats (Ericson 1977, Oksanen and Ericson 1987, Moen and Oksanen 1998, Klemola et al. 2000a, Olofsson et al. 2002). Therefore, this conjecture requires that modest grazing impacts suffice to trigger chemical responses, strong enough to cause the summer decline syndrome. Exactly the opposite was seen in our experiment. In both phases of the trials, graminoid shoots became eliminated at a fairly early stage, but the introduced females survived and reproduced and the

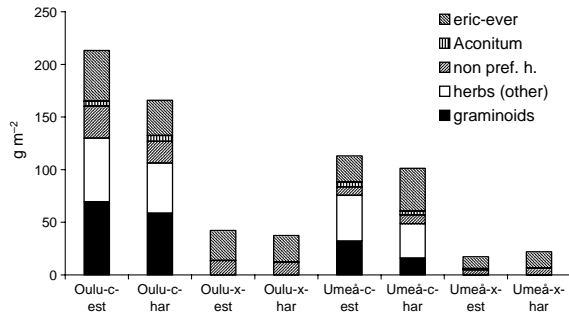


Fig. 3. Estimated (est) and harvested (har) biomass of different functional groups in the experimental enclosures (x) and on control tables (c) in the end of the 1st phases of 1998 trials in Oulu and Umeå. “non pref. h.” refers to non preferred herbs and non-ericaceous woody plants.

first litter juveniles grew normally as long as any herbs, generally included in the summer diet of field voles, were present. Our results are consistent with those obtained by Klemola et al. (2000a, b). Notice that our voles were not interacting with semi-agricultural grasses but with the natural vegetation of northern field vole

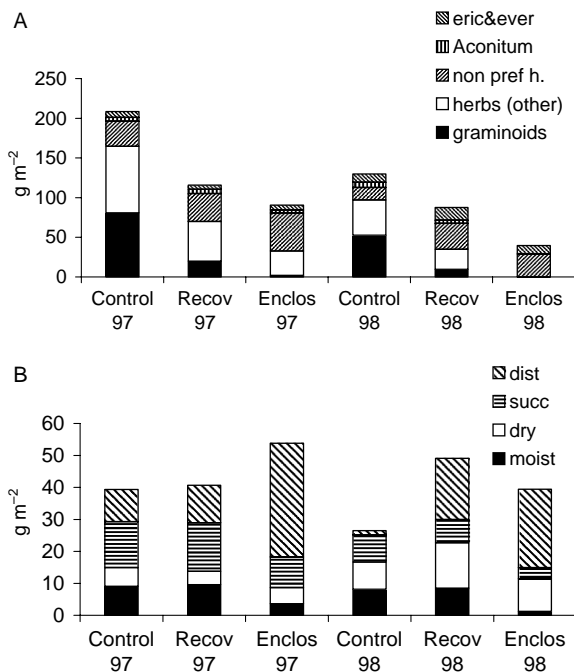


Fig. 4. Harvested biomass of different functional groups in the end of the 2nd phase of the 1997 and 1998 trials in Oulu on control and recovery plots and in enclosures. (A) Biomasses divided into functional categories. (B) Biomasses of non-preferred herbs and woody plants, divided in accordance habitat preference of species. “dist” refers to recently disturbed sites, “succ” refers to successional habitats, “dry” and “moist” refer to dry and moist climax habitats, respectively.

habitats, where plants have a long co-evolutionary history with cyclic vole populations.

Conversely, our results were consistent with the conjecture of Leibold (1996) and Chase et al. (2000) concerning the tradeoffs between competitiveness and grazing-tolerance and with the related ideas of Grime (1979). Adaptations relevant for tolerating shade and competing with other plants on a moist taiga floor turned out to be incompatible with adaptations required for coping with the intense grazing pressure created by food limited field voles. However, these tradeoffs were not just a matter of palatability. The ferns, normally avoided by field voles, suffered from grazing. The highly toxic *Aconitum* did not survive any better than the equally tall but non-toxic *Cirsium helenoides*. Conversely, those few plants, which clearly gained from recurrent, intense grazing of field voles – fireweed (*Epilobium angustifolium*), strawberry (*Fragaria vesca*) and raspberry (*Rubus idaeus*) – did not belong to the normal taiga floor vegetation but prevailed in adjacent, disturbed habitats (early successional stages, scree slopes) and were initially recorded in only a few plots. When the vegetation started to be depleted, their seedlings started to abound, indicating that they were primarily recruited from the seed bank.

The grazing-favored species have defensive features (milk veins in fireweed, coarse leaf texture in strawberry and raspberry, spines in raspberry), but they are, nevertheless, moderately palatable for field voles (Gebczynska et al. 1989, Moen et al. 1993). Moreover, none of them turned out to be entirely grazing resistant. In the final phases of each trial, a decline was usually observed (Table 3, Appendix 1). Thus, the resilience and high reproductive output of these species seem to be the most important traits accounting for their ability to cope with heavy vole impact.

Our results also revealed that ideas derived from interactions between plants and larger grazers need not apply to vole-vegetation interactions. Graminoids, which coevolved with grazing mammals (Stebbins 1981), turned out to be especially sensitive to grazing by field voles, which are small enough to selectively graze their basal intercalary meristems (Norrdahl et al. 2002). Other unexpected losers were the rosette forming goldenrod, *Solidago virgaurea*, and the trailing twinflower, *Linnaea borealis*, for which already the 1st phase turned out to be fatal, in contrast to the results of our previous experiment (Moen et al. 1993). The “sledgehammer” design of Moen et al. (1993), who introduced voles to tables of only 7 m², probably contributed to these contrasting results. In our experiment, where grazing pressure increased gradually, voles had time to learn to exploit especially nutritious plant parts, such as the leaf-producing buds in the middle of goldenrod rosettes and the growing tips of twinflower shoots. Also the trailing twinflowers suffered

Table 3. Indices of immediate vole impacts in 1st and 2nd phases of the trials, excluding the 1st phase of the Oulu 1997 trial for which this index could not be computed. Indices for 1st trials were computed as $VI = 100(Be - Bc)/Bc$, where Be is the harvested biomass of the category in enclosure and Bc is the harvested biomass on control plots. For the 2nd phase, the index was computed as $VI = 100(Be - Br)/Br$, where Br is the harvested biomass on recovery plots.

	Ericoids and evergreens	Non-preferred herbs and wp	<i>Aconitum lycoctonum</i>	Other herbs	Graminoids
1st Oulu 1998	-24.9	-49.5	-100.0	-99.9	-100.0
1st Umeå 1998	-63.4	-46.7	-97.9	-99.4	-99.6
2nd Oulu 1997	+15.7	+34.9	-24.1	-38.4	-90.1
2nd Oulu 1998	-33.7	-13.0	-100.0	-99.2	-100.0

from collateral damage when voles were making runways and digging for rhizomes.

In addition to their tolerance for disturbance and their copious seed production, the grazing-tolerant plants were even characterized by fairly low palatability. In this respect, our results differ from the results reported by Hambäck et al. (2004) and Dahlgren (2006) who found that the least palatable species were especially vulnerable to grazing. This contrast probably reflects the differential impacts of summer and winter grazing. Compared to summer conditions, selective grazing is much more costly in winter, when the vegetation is snow-covered. Even mechanical collateral damage is likely to be more widespread in winter. Moreover, the primary goal of a wintering herbivore is to survive, whereas in summer, the goal is to accumulate resources for reproduction. This requires more selective foraging.

According to the conjecture of the dynamics in food webs with heterogeneous trophic levels (Leibold 1989, 1996), the expanding unpalatable plants should at least partially restore the community level plant biomass. In accordance with Leibold's predictions, the biomass of fireweed, strawberry and raspberry increased from the 1st to the 2nd phase. The ability of the three dicotyledonous species to expand should, however, be related to the small size of our enclosures, which forced us to work with a single vole species. As we chose to work with the grass-adapted field vole, our enclosures became analogous to pastures grazed only by cattle, which can lead to invasions of relatively unpalatable dicots (Walter 1964, 1968). In nature, corresponding habitats even harbor *Clethrionomys* species (Henttonen et al. 1977, 1987, Viitala 1977, Oksanen et al. 2000) adapted to exploit dicots (Kalela 1957). Considering the strong impact of gray-sided voles, *C. rufocanus*, on both the herbaceous and woody dicots in the previous experiments conducted by our team (Moen et al. 1993, Hambäck et al. 2004), it seems obvious, that interaction with a complete microtine guild would put even more priority to ruderal characteristics and further reduce the importance of palatability.

Indeed, while the details can be debated, the main conclusions are clear. The floor of a northern taiga is

not a "green desert" (White 1978), where field voles would depend on some rare species, on high-quality plant organs or on the temporary relaxation of plant defenses due to masting (Selås 1997). Most of the plant biomass is edible and qualitatively sufficient to support growth and reproduction of field voles, and this applies even to shoots produced after heavy grazing, contrary to the conjectures of Haukioja and Hakala (1975), Karban and Myers (1989), Rhoades (1985), and Seldal et al. (1994). On the other hand, sustained summer declines are a diagnostic feature of the boreal vole cycle (Hansson and Henttonen 1985, Hanski et al. 2001, Hanski and Henttonen 2002) and these declines can be quite dramatic even in herb-rich forests, where rodent densities are an order of magnitude lower than in our experimental enclosures, and where rodents do not have a detectable impact on the vegetation (Viitala 1977). Our results imply that the lack of adequate forage is an unlikely cause for these declines but they do not rule out any other conjectures. The basic idea of our experimental design was to eliminate negative animal-animal and pathogen-animal interactions by creating a situation, where the experimental populations consisted of a laboratory reared mother and her young. This enabled us to test the potential of animal-plant interactions to account for the observed summer declines but, simultaneously, denied us the possibility to discriminate between other hypotheses concerning the causes of boreal rodent cycles.

Out of the interactions which were not tested in this study, interspecific competition seems an unlikely explanation for rodent cycles, because the cycles are interspecifically synchronous from the northernmost agricultural areas through the taiga to low arctic scrublands (Henttonen et al. 1987, Korpimäki et al. 1991, 2005b, Ekerholm et al. 2001, Hörnfeldt 2004). We regard it as likely that these cycles are driven by predation (Oksanen 1990, Hanski et al. 1991), because experimental reduction of predator densities has reversed ongoing vole declines (Korpimäki and Norrdahl 1998, Korpimäki et al. 2005a). One should notice, however, that the predation hypothesis is inherently multi-factorial. All formal models of predator-prey limit cycles include a source of direct

density-dependence, reducing per capita rate of prey population growth at high prey densities. Our results imply that shortage of adequate summer forage is not a likely source for such direct density-dependence in the natural *Microtus* habitats of the taiga. Interference between rodents appears more plausible (Stenseth 1986). Even pathogens, which spread rapidly in dense rodent populations, can have a substantial impact on population dynamics (Soveri et al. 2000).

Our results indicate, that seasonality can contribute to the lack of herbivore impact on the peak biomass of herbaceous vegetation in communities, where herbivory is intense enough to have a strong impact on the species composition (Hambäck 1998, Chase et al. 2000). By mammalian standards, field voles have a spectacular reproductive capacity and an introduced vole in an enclosure of 33 m² corresponds to a density of 300 voles ha⁻¹. Yet, severe devastation of the vegetation has not been recorded before the end of the growing season, and signs of acute resource limitation have been observed only once (in the Umeå trial). In nature, an acute depletion of the herbaceous vegetation should thus only occur in extreme situations, such as on small islands, where the vegetated area corresponds to the size of our enclosures (Pokki 1981). In mainland areas, seasonality per se should normally suffice to protect herbaceous vegetation against the pronounced impact of resident herbivores (Norrdahl et al. 2002, Hambäck et al. 2004, Dahlgren 2006). If, however, summer resources become limiting in herb-rich taiga habitats, this should be observed as a total devastation of the vegetation. In this habitat, subtle changes in the vegetation composition or the reproductive performance of the dominating plants do not seem to influence growth, reproduction or survival of field voles.

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Appendix 1 can be found as electronic Online Appendix O14981 at www.oikos.ekol.lu.se/Appendix