

Plant defences at no cost? The recovery of tundra scrubland following heavy grazing by grey-sided voles, *Myodes rufocanus*

Jonas Dahlgren^{1,2}, Lauri Oksanen^{3,4}, Johan Olofsson¹
and Tarja Oksanen¹

¹Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden,
²Department of Forest Resource Management, Swedish University of Agricultural Sciences,
Uppsala, Sweden, ³Department of Biology, Section of Ecology, University of Turku,
Turku, Finland and ⁴Department of Natural Sciences, Finnmark University College,
Alta, Norway

ABSTRACT

Background: Evergreen ericaceous dwarf shrubs form a dominating component of low arctic and low alpine vegetation. They typically produce high contents of secondary chemicals such as phenolics. The primary function of these chemicals may be to defend the shrubs by making them less palatable to herbivores.

Question: Does the production of secondary chemicals carry a fitness cost in terms of low growth rate and, therefore, low capacity to recover from past herbivory?

Methods: In 2000, we constructed vole-proof exclosures on low arctic islands where vegetation had, since 1991, been heavily impacted by grey-sided voles. In 2000 and 2003, we surveyed the vegetation of the exclosures, of unfenced plots on the same islands, and of control plots on a vole-free island. We used the point-frequency method for vegetation surveys.

Results: In the exclosures, the biomasses of most plant species increased, by and large, at the same pace. The two woody species, which increased most rapidly, were the maximally palatable bilberry (*Vaccinium myrtillus*) and the phenolics-laden, maximally unpalatable northern crowberry (*Empetrum nigrum* ssp. *hermaprhoditum*). The recovery rates of these species were similar.

Conclusions: The high concentrations of phenolics typical for evergreen arctic dwarf shrubs do not carry any obvious cost in the form of reduced capacity for compensatory growth. The principle of trade-offs does not help to explain the variation in plant palatability.

Keywords: arctic, herbivory, multiple benefits, *Myodes rufocanus*, resistance, tolerance, trade-offs, tundra, vegetation recovery, voles.

INTRODUCTION

A characteristic feature of northern tundra and mountain areas is the abundance of evergreen ericoids in nutrient-poor upland habitats (Nordhagen, 1928; Kalliola, 1939; Dahl, 1957; Oksanen and Virtanen, 1995; Virtanen *et al.*, 1999a, 1999b; Nilsson *et al.*, 2002). These plants accumulate phenolics, which constitute about 15–20% of the dry weight of their leaves (Jonasson *et al.*, 1986; Nilsson *et al.*, 1998, 2000; Gallet *et al.*, 1999; Shetsova *et al.*, 2005; Hansen *et al.*, 2006). Similar dry weight percentages have also been reported for co-existing deciduous dwarf shrubs (Jonasson *et al.*, 1986; Oksanen *et al.*, 1987; Graglia *et al.*, 2001; Hansen *et al.*, 2006), but the values for evergreen ericoids imply much higher amounts of phenolics per leaf area unit and per unit weight of palatable mesophyll material. Much of the dry weight of evergreen ericoid leaves consists of other poorly palatable material, such as cuticles and internal support structures, increasing their weight-to-area ratio (Woodward, 1986; Van Wijk *et al.*, 2005) (see also Table 1) and reducing their palatability. Therefore, herbivores seldom forage on evergreen ericoids, unless facing an acute risk of starvation (Kalela, 1957; Aleksandrova *et al.*, 1964; Skjenneberg and Slagsvold, 1968; Emanuelsson, 1984; Moen *et al.*, 1993a; Hambäck and Ekerholm, 1997; Rammul *et al.*, 2007).

Nutrient-poor low arctic and low alpine heaths are characterized by periodically intense impacts of arvicoline rodents and migratory reindeer/caribou on the vegetation (Nordhagen, 1928; Tihomirov, 1959; Kalela, 1971; Oksanen and Oksanen, 1981; Emanuelsson, 1984; Moen *et al.*, 1993b; Crête and Doucet, 1998; Olofsson *et al.*, 2001, 2004a, 2005; Bråthen *et al.*, 2007), which could conceivably favour inedible plants (Harper, 1969; Crawley, 1983, 1990; Pastor and Naiman, 1992; Schmitz, 1994, 2006; Polis and Strong, 1996; Schmitz *et al.*, 2000; Rausher, 2001). The other option – tolerance and a capacity for rapid compensatory growth (McNaughton, 1979; Oosterheld and McNaughton, 1991; Strauss and Agrawal, 1999; Rausher, 2001; Del-Val and Crawley, 2005) – should be less advantageous in nutrient-poor tundra habitats, where plants cannot grow rapidly anyway (Grime, 1979) and where a surplus of reduced carbon therefore often accumulates (Bryant *et al.*, 1983; Oksanen, 1990; Honkanen and Haukioja, 1998; Jones and Hartley, 1999).

Nevertheless, resistance and tolerance represent two alternative strategies to tackle herbivory and alternative uses of reduced carbon, making a trade-off likely (Van der Meijden *et al.*, 1988; Herms and Mattson, 1992; Rosenthal and Kotanen, 1994). Moreover, the high content of phenolics in evergreen ericoids does not emerge as a passive consequence of a nutrient shortage and the subsequent shunting of the surplus carbon to phenolics, as proposed by Bryant *et al.* (1983). Contrary to the predictions of their carbon–nutrient balance hypothesis, evergreen ericoids do not respond to shading by reducing the concentration of phenolics in their leaves (Hansen *et al.*, 2006). Moreover, the northern crowberry, *Empetrum nigrum* ssp. *hermaphroditum*, starts to accumulate phenolics in the current year's leaves by early summer (Nilsson *et al.*, 1998), when conditions for growth are optimal (Chapin, 1987). These observations indicate an active and potentially costly synthesis of phenolics. The trade-off between defence and compensatory growth should become acute when herbivory has speeded up nutrient circulation, thus increasing the marginal costs of reduced carbon (Zimov *et al.*, 1995; Olofsson *et al.*, 2001, 2004b).

To test the hypothesis of a trade-off between defence (resistance) and capacity for compensatory growth (tolerance), we thus excluded herbivorous vertebrates from parts of low arctic islands that had for a decade been strongly impacted by food-limited voles (Hambäck *et al.*, 2004; Dahlgren *et al.*, 2009). The vegetation of these islands consisted of both unpalatable evergreen ericoids and palatable herbs and deciduous dwarf shrubs. According to the predictions of the trade-off hypothesis, the palatable plants with low defensive budgets should recover rapidly, while the heavily defended evergreens should increase slowly, if at all.

METHODS

The study was conducted in the freshwater archipelago of Lake Iešjávri, Norwegian Lapland, where in 1991 we had introduced grey-sided voles (*Myodes rufocanus* Pall.) on four two-trophic-level islands, isolated enough to be practically predator-free (Hambäck *et al.*, 2004; Dahlgren *et al.*, 2007, 2009; Aunapuu *et al.*, 2008). A fifth island, to be referred to as the one-trophic-level island, did not show any signs of past rodent activity in 1991 and has since remained rodent free owing to continual trapping, including intensive snap-trapping when needed. For the composition of the vegetation and the characteristics of the common species, see Table 1. For a detailed description of the system, see Dahlgren *et al.* (2009) and Aunapuu *et al.* (2008).

In spring 2000, we built a vole enclosure of 2×2 m on each two-trophic-level island. We used galvanized hardware netting with a mesh size of 1.2×1.2 cm. The net was 1 m high and was dug down into the mineral soil. Two poison-baited vole traps were placed in each enclosure to ensure that they would remain free from voles. The composition of the vegetation was recorded annually within the four permanent plots in each enclosure, and within eight unfenced permanent plots on the experimental islands (plot size 0.5×0.5 m, laid out in a fixed pattern), using the point-frequency method (Jonasson, 1988), with 100 sampling points per plot (pin diameter 2 mm). The one-trophic-level island had a similar set of unfenced plots, studied as above. All contacts between the green parts of vascular plants and the pin were recorded separately, except for the crowberry and other microphyllous plants (*Phyllodoce caerulea*, and club mosses) for which branches were treated as units. The point-frequency data were transformed to biomasses by undertaking separate point-frequency censuses on 90 additional plots in July 2003, followed by harvesting all shoots of vascular plants, sorting by species, drying for 48 h at 60°C , and weighing. Linear regressions between the point-frequencies and dry weights were thereafter computed for all species.

We computed the effects of vole exclusion on plant biomass in two ways: (1) by comparing changes in enclosures to changes on open plots within the same islands (the enclosure index, E); and (2) by comparing enclosure changes to changes on the one-trophic-level island (the recovery index, R). The strength of the enclosure index lies in the physical vicinity of the plots that are to be compared; its problem is that the dynamics on open plots are still far from asymptotic (Dahlgren *et al.*, 2009). The recovery index relates changes in enclosures to the impacts of the physical environment on each species in a habitat free from herbivore impacts. Because we were working with a piece of inland tundra with low and variable winter precipitation, creating unpredictable variation in snow melt (Anonymous, 1978; Oksanen and Virtanen, 1995; Lippstad, 2007), it was important to control the experiment for the impacts of premature snow melt (see Dahl, 1957; Kullman, 1989) by having a reference island that was as exposed to the winds and late winter sunshine as were the two-trophic-level islands.

Eight plant species, to be referred to as the 'common species', were initially present in both enclosures and open plots on at least three two-trophic-level islands. For these species and for the community-level plant biomass, we first computed island-specific indices of relative biomass change (CB_{ij}) as ratios of final (2003) to initial (2000) biomass on each island and in both treatments. (Note that we use i to refer to the identity of the island and j to the treatments. For enclosures, $j = e$; for open plots on two-trophic-level islands, $j = o$; for the one-trophic-level island, $j = v$.) Island-specific enclosure indices, E_i , were then computed as $E_i = \ln(CB_{ie}/CB_{io})$. The island-specific recovery index, R_i , was computed as

Table 1. Mean biomass ($\text{g} \cdot \text{m}^{-2}$) of common plant species (present on at least three experimental islands) at the start and the end of the experiment on open and enclosure plots and on the one-trophic-level island, together with mean biomasses of all common plants and whole vascular vegetation at the start and the end of the experiment

Common species	Leaf mass ($\text{g} \cdot \text{m}^{-2}$)	Characteristics		One-trophic level		Two-trophic level, open		Two-trophic level, enclosure	
		Edible	Chionophilic	Start	End	Start	End	Start	End
Dwarf cornel, <i>Cornus suecica</i>	—	+	+	2	2	15	16	10	18
Cloudberry, <i>Rubus chamaemorus</i>	—	+++	++	12	6	49	32	48	71
Bilberry, <i>Vaccinium myrtillus</i>	60	+++	+++	49	21	13	8	30	89
Arctic blueberry, <i>Vaccinium uliginosum</i>	80	+	—	52	39	13	8	12	19
Dwarf birch, <i>Betula nana</i>	85	+	0	353	248	144	89	159	262
Twinflower, <i>Linnaea borealis</i>	—	+	+	0	0	<1	<1	<1	<1
Lingonberry, <i>Vaccinium vitis-idaea</i>	190	—	—	41	36	26	12	13	24
Crowberry, <i>Empetrum nigrum</i>	240	—	—	184	212	75	71	59	204
Common species biomass				693	564	335	246	331	687
Total vascular biomass				707	565	385	256	392	781

Note: The leaf mass column provides leaf dry weights of low arctic dwarf shrubs per square metre of leaf area (to an accuracy of 5 g), according to Woodward (1986), Nilsson *et al.* (2000), and Van Wijk *et al.* (2005). For species studied in several habitats, we present the average value. The three 'characteristics' columns provide information about: the edibility of the plants (Edible: +++ = maximally edible; --- = maximally inedible); their relation to snow cover (Chionophilic: +++ = maximally chionophilic, i.e. depends on snow lasting until summer; 0 = snow neutral; --- = maximally chionophobic, i.e. strongly favoured by early snow melt); and their growth forms (Form).

$R_i = \ln(CB_{ie}/CB_v)$. Species-specific indices were calculated directly from point-frequency scores without converting them to biomass. To avoid divisions by zero, we replaced zeros with 0.5. For the twinflower, *Linnaea borealis*, which was not recorded on the one-trophic-level island, we set $CB_v = 1$.

Treatment effects on the community- and species-level biomasses were examined with a *t*-test. The species-specific E_i and R_i values were analysed using analysis of variance (ANOVA) and Tukey's *post hoc* test, which is controlled for mass significance and thus minimizes the risk of type I error. However, it is based on the assumption of statistical independence between the units that are to be compared, which is not the case in plant communities containing plants with similar responses to external factors. Therefore, all standard *post hoc* tests create a high risk of type II error when applied to plant communities: real interspecific differences tend to be obscured by the in-built Bonferroni-type corrections in large materials containing ecologically similar species. In our material, Tukey's *post hoc* test yields a *P*-value of 0.4 for the same contrast for which a *t*-test yields $P = 0.1$.

To ameliorate the problem with type II error, we also conducted a principal components analysis (PCA) on the changes in the vegetation. In this analysis, we first standardized the sums of point-frequency scores of the eight common species in 2000 and in 2003 to unity for each island \times treatment combination, to ensure that abundance changes of all common species had equal impact on the result, ran the PCA, and used a *t*-test to determine whether the enclosure and open plots moved in different directions with respect to the first and second principal components. By combining changes in mutually correlated species to two principal components, both type I and type II errors are avoided, but the species-specific information is lost.

The PCA was carried out using SAS version 9.1. All other statistical tests were performed in SPSS (version 12-0 for Windows). Latin nomenclature was based on Lid (1987), Mitchell Jones *et al.* (1999), and DelHoyo *et al.* (1992), except that *Clethrionomys* was replaced by *Myodes* (Pall.), which has priority (Pavlinov, 2006). For the Latin names of the common plant species, see Table 1.

RESULTS

When the experiment began, community-level plant biomass on the enclosures of the two-trophic-level islands was only 55% of the community-level plant biomass on the one-trophic-level island, indicating strong suppression by vole herbivory and thus much potential for recovery. In fact, after the exclusion of voles, the community-level plant biomass doubled in 3 years. At the same time, the community-level plant biomass continued to decline on the open plots (Table 2). The enclosure and recovery indices for community-level plant biomass differed significantly from zero (enclosure index: $t_6 = 5.382$, $P = 0.013$; recovery index: $t_6 = 12.667$, $P = 0.001$). The increases in community-level plant biomass varied little between islands (Figs. 1 and 2).

The recovery rates of individual species were more variable (Figs. 1 and 2). The results of ANOVA implied significant interspecific heterogeneity in recovery rates (enclosure index: $F_{7,19} = 3.556$, $P = 0.014$; recovery index: $F_{7,19} = 3.313$, $P = 0.012$), but in pairwise comparisons significant differences emerged only in those comparisons involving either the tiny (mean biomass in 2000 $< 1 \text{ g} \cdot \text{m}^{-2}$; see Table 1) and even initially sparse twinflower or the lingonberry, which recovered weakly, if at all (Fig. 1, Tables 2 and 3). All other species

Table 2. Probability values for obtaining the observed interspecific differences under the null hypothesis ‘no interspecific difference in the exclusion (*E*) index’, yielded by Tukey’s *post hoc* test (below diagonal), and corresponding probability values for the null hypothesis ‘no interspecific difference in the recovery (*R*) index’ (above diagonal)

	<i>Rcha</i>	<i>Csue</i>	<i>Vmyr</i>	<i>Vuli</i>	<i>Bnan</i>	<i>Lbor</i>	<i>Vvit</i>	<i>Enig</i>
<i>Rubus chamaemorus</i>		0.99	0.98	0.96	0.89	0.03	0.39	1.00
<i>Cornus suecica</i>	1.00		0.69	1.00	1.00	0.22	0.92	1.00
<i>Vaccinium myrtillus</i>	0.55	0.52		0.57	0.41	0.01	0.08	0.85
<i>Vaccinium uliginosum</i>	1.00	1.00	0.89		1.00	0.29	0.97	1.00
<i>Betula nana</i>	1.00	1.00	0.38	0.99		0.42	0.99	1.00
<i>Linnaea borealis</i>	0.11	0.22	0.00	0.07	0.31		0.77	0.13
<i>Vaccinium vitis-idaea</i>	1.00	1.00	0.75	1.00	0.99	0.06		0.79
<i>Empetrum nigrum</i>	0.99	1.00	0.91	1.00	0.98	0.06	1.00	

Note: Probability values < 0.1 are shown in **bold** font.

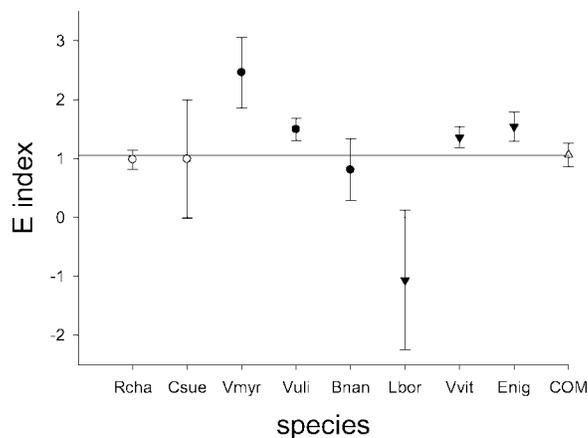


Fig. 1. Responses of the common vascular plants to the exclusion of grey-sided voles, as indicated by the exclusion index (*Rcha* = cloudberry, *Rubus chamaemorus*; *Csue* = dwarf cornel, *Cornus suecica*; *Vmyr* = bilberry, *Vaccinium myrtillus*; *Vuli* = arctic blueberry, *Vaccinium uliginosum*; *Bnan* = dwarf birch, *Betula nana*; *Lbor* = twinflower, *Linnaea borealis*; *Vvit* = lingonberry, *Vaccinium vitis-idaea*; *Enig* = crowberry, *Empetrum nigrum*). Open circles refer to herbs, solid circles to deciduous dwarf shrubs, and black triangles to evergreens. The response of the community-level plant biomass (COM) to the exclusion of grey-sided voles is denoted by a white triangle and a horizontal line. Error bars represent standard errors. Responses are measured as natural logarithms of response ratios (lnRR), with open plots on the same islands as points of reference.

recovered vigorously and, on average, largely at a similar pace to each other. But there were differences between islands (Fig. 2, Table 3).

Two species, bilberry and northern crowberry, appeared to respond to the exclusion of voles more positively than other plants. Their exclusion and their recovery indices were more than a standard error above the averages for community-level plant biomass (Figs. 1 and 2). For these species, the *P*-values for the null hypotheses of no interspecific difference in exclusion and recovery indices were high (> 0.8; Table 2).

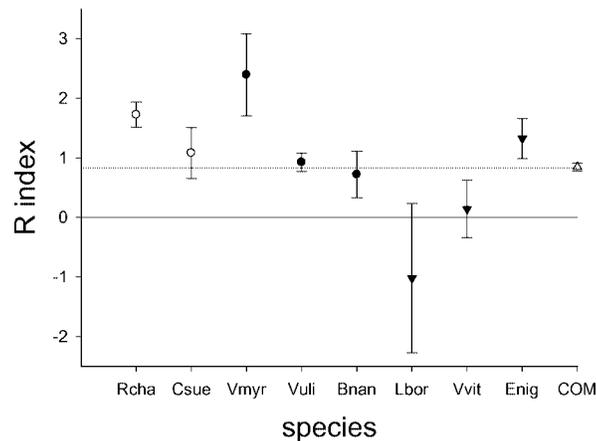


Fig. 2. Responses of the common vascular plants to the exclusion of grey-sided voles, as indicated by the recovery index (Rcha = cloudberry, *Rubus chamaemorus*; Csue = dwarf cornel, *Cornus suecica*; Vmyr = bilberry, *Vaccinium myrtillus*; Vuli = arctic blueberry, *Vaccinium uliginosum*; Bnan = dwarf birch, *Betula nana*; Lbor = twinflower, *Linnaea borealis*; Vvit = lingonberry, *Vaccinium vitis-idaea*; Enig = crowberry, *Empetrum nigrum*). Open circles refer to herbs, solid circles to deciduous dwarf shrubs, and black triangles to evergreens. The response of the community-level plant biomass (COM) to the exclusion of grey-sided voles is denoted by a white triangle and a horizontal line. Error bars represent standard errors. Responses are measured as natural logarithms of response ratios (lnRR), with the plots on the one-trophic-level island as points of reference.

Table 3. Changes in the positions of the open plots and exclosures in the coordinate space defined by the first two principal components from 2000 to 2003 (islands are used as replicates; i.e. $n = 4$)

	PC1	PC2
Exclosures	-0.003 ± 0.283	$+0.311 \pm 0.090$
Open plots	-1.033 ± 0.862	-0.317 ± 0.278

The first two principal components explained 64% of the variation in the vegetation. The first axis (eigenvalue 3.28, explaining 41%) was related to snow melt and palatability: poorly palatable, chionophobic (strongly favoured by early snow melt) ericaceous dwarf shrubs obtained high positive loadings (crowberry: 0.49; arctic blueberry: 0.43; lingonberry: 0.40), whereas the highest negative loadings were recorded for two herbs (dwarf cornel: -0.48 ; cloudberry: -0.40). The second axis (eigenvalue 1.82, explaining 23% of the variation) was related to the abundance relationships between bilberry (loading: $+0.52$) and dwarf birch (loading: -0.57).

With respect to the first axis, the exclosures changed very little during the experiment (Table 3), and the small movements of plots along this axis have no statistical relationship to the treatment ($t_6 = 1.136$, $P = 0.299$). Along the second axis, the exclosures and open plots moved in different directions and the difference was marginally significant ($t_6 = 2.153$, $P = 0.075$), indicating that bilberry recovered more rapidly than the comparatively tall dwarf birch.

DISCUSSION

The exclusion of voles resulted in a vigorous increase in community-level plant biomass. The increase was spatially consistent at the community level but the results of ANOVA highlighted significant differences in the responses of different species. Pairwise tests indicated that the aberrant behaviour of two species, the twinflower and the lingonberry, accounted for the heterogeneity revealed by the ANOVAs. The principal components analysis nuanced this picture by indicating that the tallest woody plant in our material, the dwarf birch, recovered slowly, as it has done in areas subjected to intense grazing by caribou (Crête and Doucet, 1998).

Contrary to the predictions of the trade-off hypothesis, the maximally unpalatable northern crowberry recovered at the same pace as the highly palatable bilberry. The physical conditions (low snowfall resulting in early snow melts) were favourable for the chionophobic crowberry and stressful for the chionophilic (depends on snow lasting until summer) bilberry (Table 1) (see also Dahl, 1957), but the indices were controlled for this source of bias (see Methods). Note also that the plots did not move along the first principal component, reflecting the relationship to snow cover.

The negative treatment response of the tiny, trailing twinflower (foliage height < 1 cm) does not provide evidence that defence is costly. Belonging to the Caprifoliaceae, the twinflower is taxonomically unrelated to ericoids and is moderately palatable to grey-sided voles (Ericson and Oksanen, 1987; Moen *et al.*, 1993a). Its low stature and consequent poor ability to compete for light provide a plausible explanation for its poor performance in exclosures and for its absence from comparable scrublands on the one-trophic-level island.

The trade-off hypothesis is more plausible for the other poorly recovering evergreen, the lingonberry, but other results contradict this interpretation. In the studies of Tolvanen (1994) and Olofsson *et al.* (2004a, 2005), in which they examined the impacts of an intermittent disturbance, the lingonberry recovered as fast as the bilberry or even faster. It is therefore likely that the poor recovery of the lingonberry in our exclosures reflects the accumulated impacts of its heavy losses during the 1990s (Dahlgren *et al.*, 2009), which have presumably drained its resources.

Our results are thus in line with the conclusion of Leimu and Koricheva (2006) that there is no consistent trade-off between resistance and tolerance. Whatever the metabolic costs of producing phenolics, they do not appear to result in a lower capacity to recover from past herbivory in this habitat (see also Riipi *et al.*, 2002). On balance, accumulation of phenolics does not provide an efficient defence against small herbivorous vertebrates either. In late winter, when food is running out, arctic herbivores take whatever they can get, including phenolics-laden evergreen ericoids (Pulliainen, 1970; Dahlgren *et al.*, 2009). Instead of having a primarily defensive function, the phenolics of evergreen arctic ericoids may have evolved as weapons in plant–plant chemical warfare (Nilsson *et al.*, 1998, 2000; Gallet *et al.*, 1999; Shetsova *et al.*, 2005). Phenolics also protect against physical stresses, such as photo-oxidation (Close and McArthur, 2002), which is probably more relevant than chemical warfare when a plant community is recovering from heavy herbivory.

Although the principle of trade-offs (Levins, 1968) is intellectually appealing and serves as a point of departure, it nevertheless only generates hypotheses – to be tested and exposed to the risk of refutation. Traits can provide multiple benefits. Hence adaptation need not be a zero sum game.

ACKNOWLEDGEMENTS

We thank the Swedish Natural Science Research Council, Swedish Council for Forestry and Agricultural Research, European Commission (projects 'DART', grant ENV4-CT97-0586 and 'LACOPE', grant EVK-2-CT_2002-00150) and the Academy of Finland for financial support, and the Norwegian authorities for the necessary permits. Marie Charlotte Nilsson helped us in formulating the manuscript. We also wish to thank N.R. Johnsen, O. Eriksen for technical assistance, and the many field workers for their devoted work.

REFERENCES

- Aleksandrova, V.D., Andreev, V.N., Vahtina, T.V., Dydina, R.A., Kareva, G.I., Petrovskij, V.V. *et al.* 1964. *Kormovaja harakteristika rostemij Krajnego Severa SSSR*. Moscow: Nauka.
- Anonymous. 1978. *Fimmarksvidda: Natur og kultur*. Oslo: Norges Statlige Utredninger.
- Aunapuu, M., Dahlgren, J., Oksanen, T., Grellmann, D., Oksanen, L., Olofsson, J. *et al.* 2008. Spatial patterns and dynamic responses of arctic food webs corroborate the Exploitation Ecosystems Hypothesis (EEH). *Am. Nat.*, **171**: 249–262.
- Bråthen, K.A., Ims, R.A., Yoccoz, N.G., Fauchald, P., Tveraa, T. and Hausner, V.H. 2007. Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems*, **10**: 773–789.
- Bryant, J.P., Chapin, F.S. and Klein, D.J. 1983. Carbon/nutrient balance of boreal plants in relation to herbivory. *Oikos*, **40**: 357–368.
- Chapin, F.S., III. 1987. Environmental control over growth of tundra plants. *Ecol. Bull.*, **38**: 69–79.
- Close, D.C. and McArthur, C. 2002. Rethinking the role of many plant phenolics – protection from photodamage not herbivores? *Oikos*, **99**: 166–172.
- Crawley, M.J. 1983. *Herbivory: The Dynamics of Animal–Plant Interactions*. Oxford: Blackwell Science.
- Crawley, M.J. 1990. Rabbit grazing, plant competition and seedling recruitment in acid grassland. *J. Appl. Ecol.*, **27**: 803–820.
- Crête, M. and Doucet, D.J. 1998. Persistent suppression in dwarf birch after release from heavy summer browsing by caribou. *Arctic Alpine Res.*, **30**: 126–132.
- Dahl, E. 1957. Rondane: Mountain vegetation in South Norway and its relation to the environment. *Skrifter av den Norske Videnskaps-Akademin, Oslo, I: Matematisk-Naturvidenskaplig Klasse*, **1956(3)**: 1–374.
- Dahlgren, J., Oksanen, L., Sjödin, M. and Olofsson, J. 2007. Interactions between gray-sided voles (*Clethrionomys rufocanus*) and bilberry (*Vaccinium myrtillus*), their main winter food plant. *Oecologia*, **152**: 525–532.
- Dahlgren, J., Oksanen, L., Oksanen, T., Olofsson, J., Hambäck, P.A. and Lindgren, Å. 2009. Plant defences to no avail? Responses of plants of varying edibility to food web manipulations in a low arctic scrubland. *Evol. Ecol. Res.*, **11**: 1189–1203.
- DelHoyo, J., Elliott, A. and Sargatal, J. 1992. *Handbook of the Birds of the World*. Barcelona: Lynx edicion.
- Del-Val, E.K. and Crawley, M.J. 2005. Are grazing increaser species better tolerators than decreaseers? An experimental assessment of defoliation tolerance in eight British grassland species. *J. Ecol.*, **93**: 1005–1016.
- Emanuelsson, U. 1984. *Ecological effects of grazing and trampling on mountain vegetation in northern Sweden*. PhD dissertation, Lund University, Lund, Sweden.
- Ericson, L. and Oksanen, L. 1987. The impact of controlled grazing by *Clethrionomys rufocanus* on experimental guilds of boreal forest floor herbs. *Oikos*, **50**: 403–416.
- Gallet, C., Nilsson, M.-C. and Zachrisson, O. 1999. Phenolic metabolites of ecological significance in *Empetrum hermaphroditum* leaves and associated humus. *Plant Soil*, **210**: 1–9.

- Graglia, E., Julkunen-Titto, R., Shaver, G.R., Schmidt, I.K., Jonasson, S. and Michelsen, A. 2001. Environmental control and intersite variations of phenolics in *Betula nana* in tundra ecosystems. *New Phytol.*, **151**: 227–236.
- Grime, J.P. 1979. *Plant Strategies and Vegetation Processes*. Chichester, UK: Wiley.
- Hambäck, P.A. and Ekerholm, P. 1997. Mechanisms of apparent competition in seasonal environments: An example with vole herbivory. *Oikos*, **80**: 276–288.
- Hambäck, P.A., Oksanen, L., Ekerholm, P., Lindgren, Å., Oksanen, T. and Schneider, M. 2004. Predators indirectly protect tundra plants by reducing herbivore abundance. *Oikos*, **106**: 85–92.
- Hansen, A.H., Jonasson, S., Michelsen, A. and Julkunen-Titto, R. 2006. Long-term experimental warming, shading and nutrient addition affect the concentration of phenolic compounds in arctic-alpine deciduous and evergreen dwarf shrubs. *Oecologia*, **147**: 1–11.
- Harper, J.L. 1969. The role of predation in vegetational diversity. *Brookhaven Symp. Biol.*, **22**: 48–62.
- Herms, D.A. and Mattson, W.J. 1992. The dilemma of plants: to grow or to defend? *Q. Rev. Biol.*, **67**: 283–335.
- Honkanen, T. and Haukioja, E. 1998. Intra-plant regulation of growth and plant–herbivore interactions. *Ecoscience*, **5**: 470–479.
- Jonasson, S. 1988. Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, **52**: 101–106.
- Jonasson, S., Bryant, J.P., Chapin, F.S., III, and Andersson, M. 1986. Plant phenolics and nutrients in relation to variations in climate and rodent grazing. *Am. Nat.*, **128**: 394–408.
- Jones, C.G. and Hartley, S.E. 1999. A protein competition model of phenolic allocation. *Oikos*, **86**: 27–44.
- Kalela, O. 1957. Regulation of reproduction rate in subarctic populations of the vole *Clethrionomys rufocanus* (Sund.). *Ann. Acad. Sci. Fenn. A IV 'Biol.'*, **55**: 1–72.
- Kalela, O. 1971. Seasonal differences in the habitat of the Norwegian lemming, *Lemmus lemmus*, in 1959 and 1960 at Kilpisjärvi, Finnish Lapland. *Ann. Acad. Sci. Fenn. A IV 'Biol.'*, **178**: 1–22.
- Kalliola, R. 1939. Pflanzesoziologische Untersuchungen in der alpinen Stufe Finnisch-Lapplands. *Ann. Bot. Soc. 'Vanamo'*, **13**(2): 1–321.
- Kullman, L. 1989. Cold induced dieback of montane spruce forests in the Swedish Scandes – a modern analogy of paleoenvironmental processes. *New Phytol.*, **113**: 377–389.
- Leimu, R. and Koricheva, J. 2006. A meta-analysis of tradeoffs between plant tolerance and resistance to herbivores: combining the evidence from ecological and agricultural studies. *Oikos*, **112**: 1–9.
- Levins, R. 1968. *Evolution in Changing Environments*. Princeton, NJ: Princeton University Press.
- Lid, J. 1987. *Norsk, Svensk og Finsk Flora*, 2nd edn. Oslo: Norske Samlaget.
- Lippestad, H. 2007. *Klimaet i Norge* (accessed at: http://retro.met.klima_norge/nrr_r5s4.html). Oslo: Meteorologisk institutt.
- McNaughton, S.J. 1979. Grazing as an optimization process: grass–ungulate relationships in the Serengeti. *Am. Nat.*, **113**: 691–703.
- Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger, F. *et al.* 1999. *The Atlas of European Mammals*. San Diego, CA: Academic Press.
- Moen, J., Gardfjell, H., Oksanen, L. and Ericson, L. 1993a. Grazing by food-limited microtine rodents on a productive, experimental plant community: does the green desert exist? *Oikos*, **68**: 401–413.
- Moen, J., Lundberg, P.A. and Oksanen, L. 1993b. Lemming grazing on snowbed vegetation during a population peak, northern Norway. *Arctic Alpine Res.*, **25**: 130–135.
- Nilsson, M.-C., Gallett, C. and Wallstedt, A. 1998. Temporal variability of phenolics and bantasin-III in *Empetrum hermaphroditum* leaves over an eight year period: interpretation of ecological function *Oikos*, **81**: 6–16.
- Nilsson, M.-C., Zackrisson, O., Stwerner, O. and Wallstedt, A. 2000. Characterisation of the differential interference effects of two boreal dwarf shrub species. *Oecologia*, **123**: 122–128.

- Nilsson, M.-C., Wardle, D.A., Zackrisson, O. and Järnelund, A. 2002. Effects of alleviation of ecological stresses on an alpine tundra community over an eight-year period. *Oikos*, **97**: 3–17.
- Nordhagen, R. 1928. Die Vegetation und Flora des Sylenegebietes. I. Die Vegetation. *Skrifter av den Norske Videnskaps-Akademi, Oslo, I: Matematisk-Naturvidenskaplig Klasse*, **1927**: 1–612.
- Oosterheld, M. and McNaughton, S.J. 1991. Interactive effects of flooding and grazing on the growth of Serengeti grasses. *Oecologia*, **88**: 153–156.
- Oksanen, L. 1990. Predation, herbivory, and plant strategies along gradients of primary productivity. In *Perspectives on Plant Competition* (D. Tilman and J. Grace, eds.), pp. 445–474. New York: Academic Press.
- Oksanen, L. and Oksanen, T. 1981. Lemmings (*Lemmus lemmus*) and grey-sided voles (*Clethrionomys rufocanus*) in interaction with their resources and predators on Finnmarksvidda, northern Norway. *Rep. Kevo Subarctic Res. Station*, **17**: 7–31.
- Oksanen, L. and Virtanen, R. 1995. Topographic, altitudinal and regional patterns in North Fennoscandian continental and suboceanic heath vegetation. *Acta Bot. Fenn.*, **153**: 1–80.
- Oksanen, L., Oksanen, T., Lukkari, A. and Sirén, S. 1987. The role of phenol-based inducible defense in the interaction between tundra populations of the vole *Clethrionomys rufocanus* and the dwarf shrub *Vaccinium myrtillus*. *Oikos*, **50**: 371–380.
- Olofsson, J., Kitti, H., Rautiainen, P., Stark, S. and Oksanen, L. 2001. Impact of summer grazing by reindeer on vegetation structure, productivity and nutrient cycling in the North Fennoscandian tundra. *Ecography*, **24**: 13–24.
- Olofsson, J., Hulme, P.E., Suominen, O. and Oksanen, L. 2004a. Importance of large and small herbivores for the plant community structure in the forest–tundra ecotone. *Oikos*, **106**: 324–334.
- Olofsson, J., Stark, S. and Oksanen, L. 2004b. Reindeer influence ecosystem processes on the tundra. *Oikos*, **105**: 386–396.
- Olofsson, J., Hulme, P.E., Oksanen, L. and Suominen, O. 2005. Effects of mammalian herbivores on revegetation of disturbed areas in the forest–tundra ecotone in northern Fennoscandia. *Landscape Ecol.*, **20**: 351–359.
- Pastor, J.B. and Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forests. *Am. Nat.*, **139**: 690–705.
- Pavlinov, I.Y. 2006. *Myodes* Pallas 1811 is a valid name for the genus of red-backed voles (Critecidae). *Zoologičeskij Žurnal*, **86**: 667–669.
- Polis, G.A. and Strong, D.R. 1996. Food web complexity and community dynamics. *Am. Nat.*, **147**: 813–846.
- Pulliainen, E. 1970. Winter nutrition of the rock ptarmigan, *Lagopus mutus* (Montin) in northern Finland. *Ann. Zool. Fenn.*, **7**: 95–302.
- Rammul, Ü., Oksanen, T., Oksanen, L., Lehtelä, J., Virtanen, R., Olofsson, J. *et al.* 2007. Vole–vegetation interactions in an experimental, enemy-free taiga floor system. *Oikos*, **116**: 1501–1513.
- Rausher, M.D. 2001. Co-evolution and plant resistance to natural enemies. *Nature*, **411**: 857–864.
- Riipi, M., Ossipov, V., Lempa, K., Haukioja, E., Koricheva, J., Ossipova, S. *et al.* 2002. Seasonal changes in birch leaf chemistry: are there trade-offs between leaf growth and accumulation of phenolics? *Oecologia*, **130**: 380–390.
- Rosenthal, J.P. and Kotanen, P.M. 1994. Terrestrial plant tolerance to herbivory. *Trends Ecol. Evol.*, **9**: 145–148.
- Schmitz, O.J. 1994. Resource edibility and trophic exploitation in an old field food web. *Proc. Natl. Acad. Sci. USA*, **91**: 5364–5367.
- Schmitz, O.J. 2006. Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology*, **87**: 1432–1437.
- Schmitz, O.J., Hambäck, P.A. and Beckerman, A.P. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.*, **155**: 141–153.

- Shevtsova, A., Nilsson, M.-C., Gallet, C., Zackrisson, O. and Jäderlund, A. 2005. Effects of long-term alleviation of nutrient limitation on shoot growth and foliar phenolics of *Empetrum hermaphroditum*. *Oikos*, **111**: 445–458.
- Skjenneberg, S. and Slagsvold, L. 1968. *Reindriften og dens naturgrunnlag*. Oslo: Universitetsforlaget.
- Strauss, S.Y. and Agrawal, A.A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.*, **14**: 179–185.
- Tihomirov, B.A. 1959. *Vzajmosvjazi životnogo mira i rastitel'nogo pokrova tundry*. Moscow: Botaničeskij Institut V.L. Komarova, Akademija Nauk SSSR.
- Tolvanen, A. 1994. Differences in recovery between a deciduous and an evergreen ericaceous clonal dwarf shrub after simulated above-ground herbivory and belowground damage. *Can. J. Bot.*, **75**: 656–666.
- Van der Meijden, E., Wijn, M. and Verkaar, J. 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos*, **51**: 355–363.
- Van Wijk, M.T., Williams, M. and Shaver, G.R. 2005. Tight coupling between leaf area index and foliage N content in arctic plant communities. *Oecologia*, **142**: 421–427.
- Virtanen, R., Oksanen, L. and Razzhvin, V. 1999a. Topographic and regional patterns in tundra heath vegetation from northern Fennoscandia to Taymyr Peninsula. *Acta Bot. Fenn.*, **167**: 29–83.
- Virtanen, R., Pöyhtäri, P. and Oksanen, L. 1999b. Topographic and altitudinal patterns of heath vegetation on Vannøya and northern Varanger Peninsula, northern Norway. *Acta Bot. Fenn.*, **167**: 3–28.
- Woodward, F.I. 1986. Ecophysiological studies on the shrub *Vaccinium myrtillus* L. taken from a wide altitudinal range. *Oecologia*, **70**: 580–586.
- Zimov, S.A., Chuprynin, V.I., Oreshko, A.P., Chapin, F.S., Reynolds, J.F. and Chapin, M.C. 1995. Steppe–tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. *Am. Nat.*, **146**: 765–794.