

## Effects of simulated winter browsing on mountain birch foliar chemistry and on the performance of insect herbivores

M. Riipi, K. Lempa, E. Haukioja, V. Ossipov and K. Pihlaja

Riipi, M., Lempa, K., Haukioja, E., Ossipov, V. and Pihlaja, K. 2005. Effects of simulated winter browsing on mountain birch foliar chemistry and on the performance of insect herbivores. – *Oikos* 111: 221–234.

Winter browsing by mammalian herbivores is known to induce a variety of morphological and physiological changes in plants. Browsing has been suggested to decrease the carbohydrate reserves in woody plants, which might lead to reduced tannin production in leaves during the following summer, and consequently, to increased herbivore damage on leaves. We conducted a clipping experiment with mature mountain birch trees and measured the effects of clipping on birch growth, leaf chemistry and toughness, as well as on the performance of insect herbivores. Leaves grew larger and heavier per unit area in the clipped ramets and had a higher content of proteins than leaves in the control trees. Clipping treatment did not affect the total content of sugars in the leaves ( $\text{mg g}^{-1}$ ), suggesting that a moderate level of clipping did not significantly reduce the carbohydrate pools of fully-grown mountain birch trees. Furthermore, the contents of proanthocyanidins (condensed tannins) and gallotannins were slightly higher in the leaves of clipped ramets, contrary to the hypothesis of reduced tannin production. The effects of clipping treatment on leaf and shoot growth and on foliar chemistry were mainly restricted to the clipped ramets, without spreading to untreated ramets within the same tree individual. The effects of clipping on leaf characters varied during the growing season; for instance, leaf toughness in clipped ramets was higher than toughness in control trees and ramets only when leaves were mature. Accordingly, clipping had inconsistent effects on insect herbivores feeding at different times of the growing season. The generally small impact of clipping on herbivore performance suggests that the low intensity of natural browsing at the study area, simulated by our clipping treatment, does not have strong consequences for the population dynamics of insect herbivores on mountain birch via enhanced population growth caused by browsing-induced changes in food quality.

*M. Riipi, K. Lempa and E. Haukioja, Dept of Biology and Kevo Subarctic Research Station, Univ. of Turku, FIN-20014 Turku, Finland (mariipi@utu.fi). – V. Ossipov and K. Pihlaja, Dept of Chemistry, Univ. of Turku, FIN-20014 Turku, Finland.*

Browsing by mammalian herbivores is known to induce a variety of morphological and physiological changes in plants, depending on the type of herbivory, its intensity, and the time of the year when it occurs (reviewed by Bryant et al. 1991, Danell et al. 1994). Changes in the morphology and chemistry of plants may then affect the level of future herbivory, either by the same species (Bergström 1984, Löyttyniemi 1985) or by other herbivores belonging to a variety of feeding guilds and

taxonomic units. For instance, natural or simulated browsing may induce susceptibility for leaf mining, galling and chewing, sap sucking and stem galling (Danell and Huss-Danell 1985, Karban and Niiho 1995, Hjältén and Price 1996, Roininen et al. 1997), although negative relationships between browsing and insect herbivory have also been reported (Hjältén 1999, Bergström et al. 2000, Olofsson and Strengbom 2000, Shimazaki and Miyashita 2002). The indirect

Accepted 12 April 2005

Copyright © OIKOS 2005  
ISSN 0030-1299

interactions between herbivores feeding at different times of the season are interesting because they may influence the population dynamics of the herbivores (Hjältén and Price 1996) and the evolution of plant resistance traits.

The effects of mammal browsing on woody plants are believed to be mainly due to the removal of apical buds, which leads to the release of apical dominance and reduced competition for nutrients among the remaining buds (Haukioja et al. 1990, Bryant et al. 1991, Lehtilä et al. 2000). Previous studies have shown that the removal of dormant or swollen apical buds from mountain birch (*Betula pubescens* subsp. *czerepanovii* (N.I. Orlova) Hämet-Ahti) in the winter or spring increases the size, water percent and nutrient content of leaves (Senn and Haukioja 1994, Danell et al. 1997). This may be caused by the redistribution of resources among fewer, but larger leaves, without a significant difference in the total biomass of leaves between clipped and control trees (Lehtilä et al. 2000). On the other hand, winter browsing has been suggested to decrease shoot carbohydrate reserves in woody plants (Bryant 1987). Since carbohydrates can be used for the production of condensed tannins, Bryant (2003) suggests that winter browsing might lead to reduced tannin production in leaves during the following summer.

Water and protein are generally considered important nutritive factors for insects feeding on woody plants (Scriber and Slansky 1981, Mattson and Scriber 1987, Slansky 1993, Haukioja 2003), while condensed tannins may act as resistance compounds (reviewed by Bernays et al. 1989, Harborne 1991). In accordance with the detected changes in leaf nutritive traits and the proposed changes in the content of condensed tannins after winter browsing, birch leaves tend to become more suitable for insect herbivores after natural or simulated winter browsing (Danell and Huss-Danell 1985, Haukioja et al. 1990, Martel et al. 1999). However, the effects of winter browsing on the carbohydrate and tannin contents in the leaves of mountain birch have not been directly measured.

The performance of different species of herbivorous insects, or even different larval stages of a single species, may be affected by different leaf traits (Kause et al. 1999, Haukioja et al. 2002). Therefore, winter browsing may have different effects on different herbivore species. For instance, the proposed decrease in the content of carbohydrates may have negative effects on certain herbivores, since sugars (e.g. glucose and fructose) are known feeding stimulants (Bernays and Chapman 1994) and have also been related to an increased growth rate of a birch-feeding herbivore (Henriksson et al. 2003). Furthermore, many herbivore species display compensatory responses to low leaf quality (Slansky 1993), which means that even though the growth rates of insects may not differ between trees, leaf consumption rates (and

thereby the amount of damage suffered by the plant) may vary.

To increase our understanding of the indirect interactions between mammalian browsers and herbivorous insects sharing a common host plant species, we studied the effects of simulated winter browsing on a variety of leaf characteristics of mountain birch throughout the growing season. We monitored changes both in the nutritive compounds of birch leaves (sugars and amino acids) and in two classes of tannins (proanthocyanidins and gallotannins) which have been connected with decreased suitability for some herbivorous insects both in mountain birch (Kause et al. 1999, Ossipov et al. 2001, Haukioja et al. 2002) and in other plant–herbivore systems (Bernays et al. 1989, Ayres et al. 1997). In addition, we studied the growth and consumption rates of five species of insect herbivores fed with leaves from the experimental trees, to determine whether species feeding at different times of the growing season respond similarly to browsing-induced changes in leaf quality.

## Material and methods

### The study species

Mountain birch is a polycormic, clonal tree that forms extensive tree line forests in northwestern Europe. In northernmost Finland, mountain birch budburst usually takes place in early June and the leaves fall in mid to late September. Mountain birch, like other birches, produces two types of shoots (Macdonald and Mothersill 1983, Macdonald et al. 1984). In mature trees, short shoots form the main part of the canopy and their leaves flush simultaneously in the spring. Canopy expansion takes place through the growth of long shoots that grow and form new leaves throughout the summer. Mountain birch is well known ecologically and a wide range of biochemical compounds has been identified from its leaves in previous years (Nurmi et al. 1996, Ossipov et al. 1997, 2001). Phenolics are common secondary compounds in mountain birch leaves, and their total content may reach 20% of leaf dry mass, while proteins and sugars constitute between 5–20% and 4–16% of leaf dry mass, respectively, depending on the time of the growing season (calculated from the data in Riipi et al. 2002).

In northern Finland, reindeer (*Rangifer tarandus* L.) and moose (i.e. European elk, *Alces alces* L.) consume the twigs of mountain birch during the winter and in the spring. During the summer, reindeer also feed on leaves and growing long shoots. In the study area, mountain birch is a host plant for more than 55 leaf-feeding species of lepidopterans and sawflies (Koponen 1973, Hanhimäki 1993). In terms of potential damage to trees, the most important insect herbivore of mountain birch is *Epirrita autumnata* (Borkhausen) (Lepidoptera: Geometriidae), a flush-feeding moth, which in northern

Fennoscandia has outbreaks with a cycle of 9–11 years (Tenow 1972, Ruohomäki et al. 2000).

In addition to *E. autumnata*, we chose for this study four common sawfly species whose larval periods form a gradient and altogether cover the whole summer. The early season species (*Amauronematus amplus* Konow) mainly consumes growing leaves, the mid-season species (*Nematus brevipalpis* Thomson) consumes both growing and mature leaves, and from the two late-season species *Arge* sp. Shrank feeds on mature leaves, whereas *Dineura pullior* Schmidt and Walter also encounters senescing leaves. The sawfly species belong to family Tenthredinidae, except for *Arge* sp., which belongs to Argidae and is a member of the *A. ustulata-clavicornis* group. Larvae of all the species are solitary external feeders; *D. pullior* is a leaf skeletoniser and the other species, including *E. autumnata*, are leaf-chewers.

## The experiments

The study was conducted in 1999 at the Kevo Subarctic Research Institute of University of Turku (69°45'N, 27°01'E). The study trees had a minimum of seven ramets (stems), and grew in a natural mountain birch stand near the tree line (230 m asl.). Twenty trees were randomly selected from 30 trees for which the biochemistry of leaves had been previously studied (Riipi et al. 2002). Three ramets were assigned for the experiment in each of the ten control trees. In the browsing trees, three ramets were randomly assigned for clipping, which simulated winter browsing by mammals, and three became control ramets. The within-tree controls were included in the design to study if the effects of clipping spread through a tree into other than the damaged ramets. Clipping treatment was conducted during snow-melt at the end of May, when buds were swollen but not yet open. We cut off all long shoots grown in the previous year and approximately 5 cm of the older growth of all branches in the browsing ramets. This represented less than 15% of the total aboveground biomass of the ramets.

Short shoot leaves were collected at seven sampling dates during the summer of 1999, starting from young developing leaves at June 16 and ending at August 24 before leaf senescence. Leaves were collected randomly from the marked ramets into plastic vials that were closed immediately and put into a cooler for transportation into the laboratory. Seven to nine leaves from each tree were collected for the measurements of toughness (Chatillon Digital Force Gauge penetrometer), area (Analytical Imaging Station, Imaging Research Inc., Canada), fresh and dry mass, and water percent of leaves. Each leaf was closed into a paper envelope, pressed for at least 24 h and then dried at +60°C for 2 days before determination of dry weight. At five of the

seven sampling dates (June 20, June 24, June 29, July 15, and August 24), 10–15 short shoot leaves were collected for chemical analysis and vacuum-dried for at least 48 h. The leaves were kept in sealed vials at +4°C until the time for analysis. The methods for chemical analysis are described in Ossipov et al. (2001), Ossipova et al. (2001) and Riipi et al. (2002). In addition to leaf growth and chemistry, we measured the length of six long shoots per tree (or set of ramets) at three dates during the summer.

At all of the sampling dates, five to ten leaves per tree were collected for laboratory bioassays with herbivore larvae. *E. autumnata* larvae were bioassayed four times during their larval development (once during each instar from second to last) and each of the sawfly species was tested once (at the beginning of the final instar). The bioassay of *A. amplus*, which in nature feeds at the same time of a season as the late instars of *E. autumnata*, was conducted on July 1, two days after the bioassay of *E. autumnata*. The results of both of these bioassays are associated with the same leaf and chemistry data (June 29) in the statistical analyses.

The larvae used in the bioassays were descendants of laboratory populations, with new individuals collected from nature each year to avoid inbreeding. *E. autumnata* larvae were kept outdoors, and reared individually in transparent plastic vials (48 ml) for the whole larval period and fed every two to three days with fresh leaves of the experimental trees. Each larva received leaves from only one tree, or from only one set of ramets within the browsing trees, throughout its whole development. Originally, there were 10 larvae per each tree or set of ramets (300 larvae altogether), but numbers at the end of the experiment were lower in some trees due to mortality. Adults of the studied sawfly species were enclosed in mesh bags in branches of non-experimental trees at the time of their natural occurrence, and let to oviposit on the leaves. A few days before the experiments, 5–10 larvae per each set of ramets (altogether 150–300 larvae for each species) were transferred into plastic vials and randomised into treatments.

The bioassays lasted for 24 h at +12°C with 24 h light; settings that approximated the average environmental conditions in the area during the summer. For all the species, larger larvae were synchronised with the others by keeping them at +1°C for no longer than three days, following a practice that has been used in several previous experiments (Kause et al. 1999, 2001, Henriksen et al. 2003). Larvae were weighed in the beginning and in the end of the bioassay. Each larva received one leaf, which was pressed and dried after the experiment. The eaten area was measured (Analytical Imaging Station, Imaging Research Inc., Canada), and transformed into dry mass with tree-specific area–biomass regressions, based on the leaves that were collected at the time of the bioassays. In the case of the leaf skeletoniser, *D. pullior*, leaf fresh weight was measured before the

bioassay, and the eaten dry mass was calculated by subtracting the mass of dried leaf remnants from the original dry mass of the leaf, estimated with regressions based on the fresh and dry masses of the leaves collected from the study trees at the time of the bioassay.

## Data analysis

Physical and chemical leaf traits and the length of long shoots were tested with repeated measures analysis of variance, time as the repeated factor, tree as the subject, and treatment as a fixed factor (Procedure MIXED, SAS vs. 8.02). Procedure MIXED was used because it allows the modelling of covariance structure in repeated measures analysis. Multivariate analysis for the different leaf traits was not used because the assumptions of the analysis were not fulfilled. Tree means (separately for the clipped ramets and control ramets in the trees with a browsing treatment) were calculated for all the leaf traits. Since the dependency between the clipped and control ramets from the same trees needed to be taken into account, different statistical models were used for the within-tree comparison (clipped ramets vs control ramets in the “browsed” trees), and for the between-trees comparison (control ramets vs control trees). Note that due to the use of separate models for the within-tree and between-tree comparisons, the standard errors for means are different for the control ramets in the two models. In the figures, the standard errors for the control ramets are from the between-tree comparisons, which usually produced larger SEs than the within-tree comparisons.

Heterogeneous first-order autoregressive (ARH(1)) covariance structure was chosen a priori, to account for the usually decreasing correlations among measurements from the same trees with increasing time between samplings. Model fit was ensured by comparing the Akaike's information criterion (AIC) values for models with unstructured or ARH(1) covariance structures. Kolmogorov–Smirnov tests were used to study whether the distribution of model residuals differed from normal. The following variables were analysed (transformation in parentheses): leaf dry mass (log), leaf area (log), leaf dry mass per unit area (square root), water percent of leaves, leaf toughness (log), the length of long shoots (log), the total content of gallotannins in leaves (log), the contents of proanthocyanidins (log), protein-bound amino acids (hereafter protein), soluble carbohydrates (sum of sucrose, glucose and fructose, galactose and inositol), nutritive sugars (sum of sucrose, glucose and fructose; log), galactose (square root) and inositol.

Larval growth and leaf consumption on dry mass and fresh mass basis were tested with repeated measures models with unstructured covariances, separately for *E. autumnata* and for the sawfly species. To improve the accuracy for the estimation of treatment effects on larval

performance, least squares means for each tree (or set of ramets within a tree in the browsing treatment) were first calculated for each larval trait by taking into account the initial mass and brood of the larvae and the exact time in the experiment. As with the physical and chemical leaf traits, different models were used for the between-tree and within-tree comparisons. All larval traits were log-transformed to ensure normality of residuals. The pupal mass of *E. autumnata* was tested with a mixed model analysis of variance (with Satterthwaite approximation for the denominator degrees of freedom), by using treatment and the sex of the larvae as fixed factors and tree as a random effect; in the within-tree comparison also tree  $\times$  treatment interaction was included as a random effect. The number of larvae surviving until the measurement of pupal mass was 70 for clipped ramets, 58 for control ramets and 64 for control trees.

Finally, we correlated (with Spearman rank-order correlation) leaf traits and larval performance, both separately for each treatment and over all trees, to determine which leaf traits were related to the performance of each species. We report only the strongest correlations and those that may help in explaining the results of the analyses of variance on larval performance. Since leaf chemistry data was not available for the date when the bioassay with the second instar larvae of *E. autumnata* was conducted, and considering the rapid change in leaf composition in the spring, we did not run correlations for the performance of second instar *E. autumnata*. For *Arge* sp., we used chemistry data from two weeks before the bioassay (the same chemistry sample that was used in the correlations with larval performance of *N. brevicollis*). Although the seasonal change in leaf quality is relatively slow in these mature leaves, the correlations between leaf traits and the performance of *Arge* should be viewed with caution.

## Results

### Leaf and shoot growth, leaf water content and toughness

Leaves grew faster in the clipped ramets and their final dry mass was larger than in control ramets of the same trees or in the control trees (Table 1, Fig. 1a). Leaves of control ramets and control trees had somewhat different seasonal trends in growth, as indicated by the significant interaction between time and treatment (Table 1); leaves in the control trees appear to have reached their final size earlier than leaves in the control ramets of browsed trees (Fig. 1a). Leaf areas displayed a similar pattern to dry masses (Table 1). Leaf dry mass per area (LMA) was slightly higher in clipped ramets than in control ramets, while the control ramets and control trees did not differ in LMA (Table 1, Fig. 1b). Leaf toughness was higher in

Table 1. Effects of simulated winter browsing on leaf and shoot growth, and on leaf toughness and water content.

Variable	Effect	Clipped vs control ramets				Control trees vs control ramets			
		F	Num df	Den df	P	F	Num df	Den df	P
Dry mass of leaves	treatment	256.2	1	9	<0.001	0.0	1	18	0.855
	time	67.7	6	54	<0.001	115.4	6	108	<0.001
	interaction	6.6	6	54	<0.001	4.3	6	108	0.001
Leaf area	treatment	146.2	1	9	<0.001	0.2	1	18	0.705
	time	32.4	5	45	<0.001	100.6	5	90	<0.001
	interaction	2.9	5	45	0.023	6.1	5	90	<0.001
Leaf mass per area	treatment	20.8	1	9	0.001	0.5	1	18	0.493
	time	35.3	5	45	<0.001	144.7	5	90	<0.001
	interaction	2.2	5	45	0.070	0.3	5	90	0.916
Toughness	treatment	13.8	1	9	0.005	0.0	1	18	0.940
	time	100.8	5	45	<0.001	307.1	5	90	<0.001
	interaction	3.9	5	45	0.005	1.4	5	90	0.234
Water	treatment	60.2	1	9	<0.001	0.2	1	18	0.656
	time	113.3	6	54	<0.001	365.1	6	108	<0.001
	interaction	2.3	6	54	0.047	3.2	6	108	0.006
Shoot growth	treatment	24.7	1	9	0.001	0.3	1	18	0.616
	time	19.2	2	18	<0.001	39.9	2	36	<0.001
	interaction	1.1	2	18	0.364	0.6	2	36	0.576

the clipped ramets than in control ramets, but only when leaves were mature (Table 1, Fig. 1c). Control trees and control ramets did not differ in leaf toughness (Table 1, Fig. 1c), indicating ramet-specific response to browsing. The seasonal trends of LMA in each treatment were quite similar to the trends in leaf toughness, suggesting that these variables measure the same trait. Accordingly, leaf toughness and leaf mass per area at each sampling date correlated quite strongly: correlation coefficients for the clipped ramets varied between 0.22 and 0.83, for the control ramets between 0.59 and 0.81, and for the control trees between 0.37 and 0.92. Water percent was highest in leaves from the clipped ramets, especially in the late season (Table 1, Fig. 1d). In the spring, water percent was higher in the control ramets from clipped trees than in control trees, suggesting that the browsing treatment had some effects also in the undamaged ramets within the browsed tree (Table 1, Fig. 1d). Long shoots grew longer in the clipped ramets than in the control ramets, while control ramets and trees did not differ in long shoot growth (Table 1, Fig. 1e).

## Leaf chemistry

The content of protein-bound amino acids was higher in the leaves of clipped ramets than in the leaves of control ramets (Table 2, Fig. 2a). Control ramets and control trees did not differ in the content of protein in their leaves (Table 2, Fig. 2a). The treatments did not differ in the total content of sugars (Table 2), but the seasonal trends in the sum contents of 'nutritive' sugars (glucose, fructose and sucrose) and in the contents of inositol varied between the control trees and the control ramets of clipped trees (Table 2, Fig. 2b, 2c). The content of galactose was lower in the leaves of clipped ramets than in the leaves of control ramets in the early season, but control trees and control ramets did not differ in their contents of galactose (Table 2, Fig. 2d).

The leaves from clipped ramets had a higher content of proanthocyanidins than control ramets and control trees (Table 2, Fig. 2e), indicating a ramet-specific effect of browsing on the content of proanthocyanidins. The leaves from clipped ramets had a higher content of gallotannins during the spring peak than the leaves from control ramets in the same trees (Table 2, Fig. 2f). However, the leaves from control trees had even higher content of gallotannins, but the difference between control trees and control ramets was not significant (Table 2). Since the number of trees per treatment was only ten, there could have been some differences between the control trees and browsing trees before the treatment by chance alone. Therefore, we tested the between-tree models (control ramets vs control trees) of leaf chemistry, water content, toughness and dry mass using values from corresponding sampling dates in 1997 as

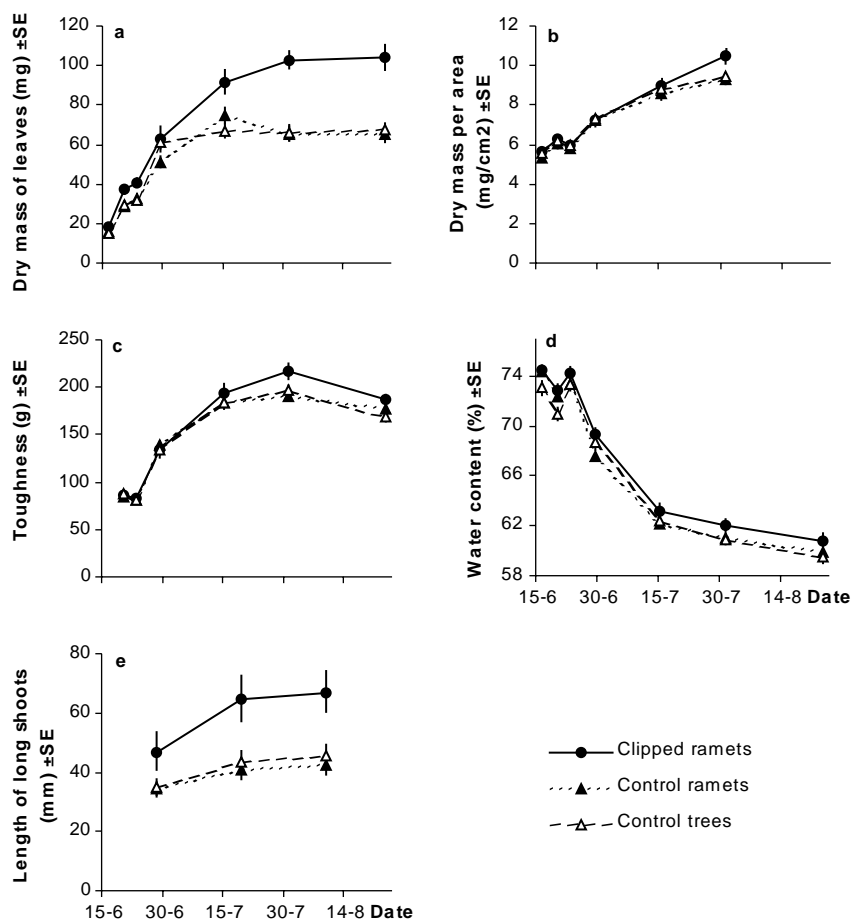


Fig. 1. Seasonal trends (with standard errors of means) in the (a) dry mass (mg), (b) dry mass per unit area ( $\text{mg}/\text{cm}^2$ ), (c) toughness and (d) water content of leaves, and in the (e) length of long shoots. Solid lines with dots represent clipped ramets, dotted lines with filled triangles represent control ramets in the trees where part of the ramets were clipped, and dashed lines with empty triangles represent control trees.

covariates. The only change in the results was that the interaction between time and treatment in the content of gallotannins became significant (interaction  $F(4, 71) = 3.08$ ,  $P = 0.021$ , main effect for treatment  $F(1, 18) = 4.22$ ,  $P = 0.055$ ), indicating that the spring peak in gallotannins was higher in the control trees than in the control ramets of browsed trees (Fig. 2f).

### Larval performance

A significant interaction between the growth rate and the instar of *Epirrita autumnata* suggests that the effects of clipping on the growth rate varied during the larval development (Table 3, Fig. 3a). The pupal masses of *E. autumnata* did not differ between control treatments (LS mean for control ramets: 72.0 mg and for control trees: 72.6 mg,  $F(1, 18.1) = 0.07$ ,  $P = 0.790$ ), but larvae fed with leaves from clipped ramets developed into slightly heavier pupae than larvae fed with leaves from control ramets (LS mean for clipped ramets: 74.8 mg and for control ramets 72.0 mg,  $F(1, 8.6) = 6.01$ ,  $P = 0.038$ ). Larval growth rate of sawflies was not strongly affected by the clipping treatment, nor were there

significant differences in larval growth rates between control trees and control ramets (Table 3, Fig. 3b).

Consumption rates of leaf dry mass by *E. autumnata* did not differ between clipped ramets and control ramets, or between control trees and control ramets (Table 3, Fig. 3c). In contrast, for the sawfly species the consumption rate of leaf dry mass was higher for the control trees than for the control ramets of clipped trees (Table 3, Fig. 3d). The difference between the clipped and control ramets was not significant in terms of dry mass consumption (Table 3, Fig. 3d). When consumption was measured on fresh mass basis, sawflies consumed more when fed with leaves from the clipped ramets than from the control ramets, due to the higher water content of leaves in the clipped ramets (Table 3).

### Correlations between leaf traits and larval performance

The performance of *E. autumnata* was related to different leaf traits at different stages of its larval development. The fact that larval growth rates did not differ between treatments at the third instar (Fig. 3a)

Table 2. Effects of simulated winter browsing on leaf chemistry.

Variable	Effect	Clipped vs control ramets				Control trees vs control ramets			
		F	Num df	Den df	P	F	Num df	Den df	P
Protein	treatment	7.4	1	9	0.024	0.3	1	18	0.569
	time	81.5	4	36	<0.001	58.6	4	72	<0.001
	interaction	1.2	4	36	0.344	0.4	4	72	0.839
Soluble carbohydrates	treatment	0.4	1	9	0.534	0.0	1	18	0.980
	time	22.1	4	36	<0.001	27.6	4	72	<0.001
	interaction	1.6	4	36	0.204	1.8	4	72	0.140
Nutritive sugars	treatment	0.8	1	9	0.407	0.3	1	18	0.591
	time	34.8	4	36	<0.001	59.9	4	72	<0.001
	interaction	1.0	4	36	0.419	6.1	4	72	<0.001
Inositol	treatment	0.3	1	9	0.606	0.6	1	18	0.443
	time	50.6	4	36	<0.001	74.8	4	72	<0.001
	interaction	1.1	4	36	0.370	4.6	4	72	0.002
Galactose	treatment	11.1	1	9	0.009	0.5	1	18	0.472
	time	60.5	4	36	<0.001	102.4	4	72	<0.001
	interaction	4.3	4	36	0.006	1.0	4	72	0.425
Proanthocyanidins	treatment	11.3	1	9	0.008	0.0	1	18	0.993
	time	7.5	4	36	<0.001	17.5	4	72	<0.001
	interaction	0.9	4	36	0.453	0.8	4	72	0.515
Gallotannins	treatment	8.6	1	9	0.017	2.7	1	18	0.117
	time	5.3	4	36	0.002	19.4	4	72	<0.001
	interaction	1.1	4	36	0.357	2.4	4	72	0.060

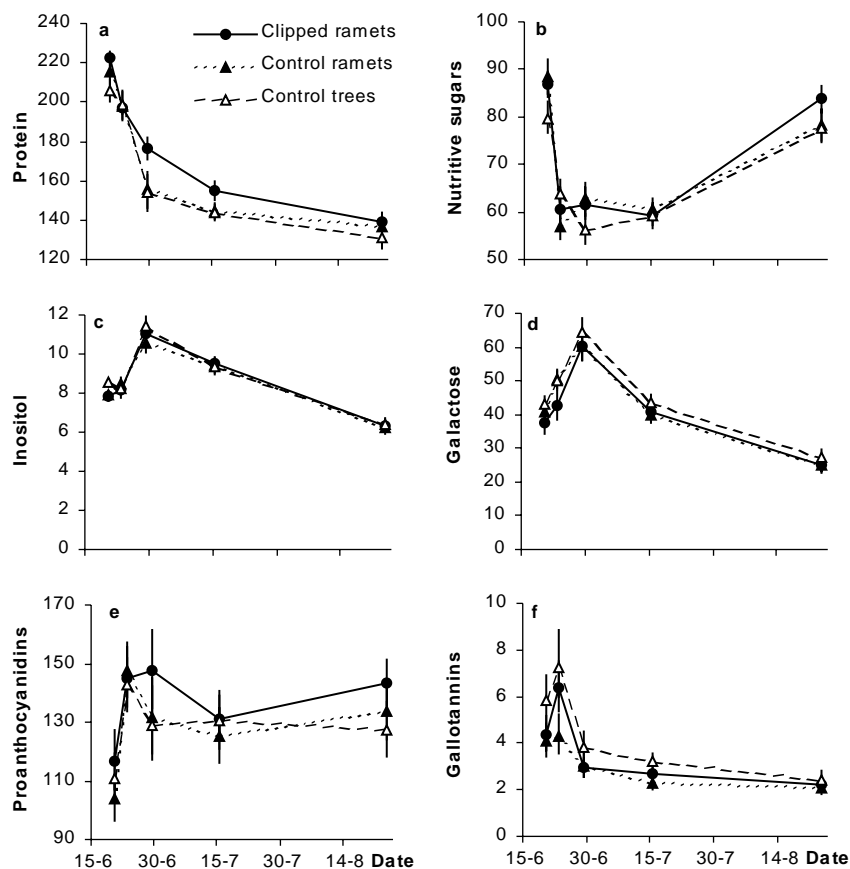


Fig. 2. Seasonal trends in the contents ( $\text{mg g}^{-1} \pm \text{SE}$ ) of protein, sugars, and tannins in leaves. (a) protein, (b) sum of nutritive sugars, (c) inositol, (d) galactose, (e) proanthocyanidins, and (f) gallotannins. Symbols as in Fig. 1.

although the level of proteins was slightly higher in the clipped ramets than in the control ramets (first sampling date in Fig. 2a) suggests that some other factors were affecting larval growth in the clipped ramets. Since leaf dry mass correlated strongly and negatively with larval growth in the clipped ramets ( $r = -0.64$ ,  $P = 0.048$ ,  $N = 10$ ) but not in the control treatments (control ramets:  $r = -0.18$ ,  $P = 0.627$ ; control trees:  $r = -0.16$ ,  $P = 0.652$ ), it seems likely that some unmeasured trait related to fast growth or maturation of leaves was limiting larval growth in the clipped ramets.

At the fourth instar of *E. autumnata*, larval growth rate tended to be higher in the clipped ramets than in the control trees or ramets (Fig. 3a). Water content of leaves correlated positively with larval growth in the control ramets ( $r = 0.82$ ,  $P = 0.004$ ,  $N = 10$ ) and a similar trend was found for control trees ( $r = 0.54$ ,  $P = 0.117$ ), but water content was not related to larval growth in the clipped ramets ( $r = -0.04$ ,  $P = 0.907$ ). This suggests that water was limiting larval growth in the control treatments but the higher leaf water content in clipped ramets (see third sampling date in Fig. 1d) allowed the higher growth rate of larvae on the leaves of these ramets. Leaf consumption rate correlated negatively with the protein content of leaves over all treatments ( $r = -0.45$ ,  $P =$

$0.012$ ,  $N = 30$ ), probably indicating compensatory consumption on low protein diet, since the correlation with larval growth was to the opposite direction ( $r = 0.18$ ,  $P = 0.338$ ,  $N = 30$ ). However, since the protein contents of leaves in different treatments did not differ during this bioassay (Fig. 2a), correlations between larval growth and protein content of leaves cannot explain the among-treatment difference in larval growth. Interestingly, the content of gallotannins was not related either to the growth rate or consumption rate of *E. autumnata* at this stage of larval development, despite the high variation among treatments (second sampling date in Fig. 2f).

At fifth instar, the larval growth rate of *E. autumnata* correlated negatively with leaf toughness over all treatments ( $r = -0.39$ ,  $P = 0.031$ ,  $N = 30$ ). In the clipped ramets, where the content of proanthocyanidins was higher than in the control treatments (Fig. 2e), consumption rate of larvae correlated positively with the content of proanthocyanidins ( $r = 0.65$ ,  $P = 0.043$ ,  $N = 10$ ), but the relationship between larval growth and the content of these tannins was weaker ( $r = 0.36$ ,  $P = 0.310$ ,  $N = 10$ ), suggesting that high consumption rate did not always lead to high growth rate.

The relationships between leaf traits and larval performance of sawflies were different for each species.



Table 3. Effects of simulated winter browsing on larval growth and leaf consumption.

Variable	Effect	Clipped vs control ramets				Control trees vs control ramets			
		F	Num df	Den df	P	F	Num df	Den df	P
Larval growth									
<i>E. autumnata</i>	treatment	0.2	1	9	0.640	0.1	1	18	0.712
	instar	5779.0	3	9	<0.001	4185.9	3	18	<0.001
	interaction	5.2	3	9	0.023	1.1	3	18	0.392
Sawflies	treatment	0.8	1	9	0.407	2.0	1	18	0.176
	species	106.7	3	9	<0.001	144.0	3	18	<0.001
	interaction	0.3	3	9	0.830	1.7	3	18	0.214
Consumption (dry mass)									
<i>E. autumnata</i>	treatment	1.6	1	9	0.238	0.8	1	18	0.391
	instar	1952.5	3	9	<0.001	3258.8	3	18	<0.001
	interaction	0.4	3	9	0.730	0.5	3	18	0.710
Sawflies	treatment	3.6	1	9	0.089	15.2	1	18	0.001
	species	23.1	3	9	<0.001	26.3	3	18	<0.001
	interaction	0.3	3	9	0.853	1.0	3	18	0.413
Consumption (fresh mass)									
<i>E. autumnata</i>	treatment	0.0	1	9	0.857	0.1	1	18	0.738
	instar	2263.2	3	9	<0.001	3543.2	3	18	<0.001
	interaction	0.7	3	9	0.604	0.3	3	18	0.841
Sawflies	treatment	8.8	1	9	0.016	21.1	1	18	<0.001
	species	16.7	3	9	0.001	24.6	3	18	<0.001
	interaction	0.3	3	9	0.848	0.7	3	18	0.564

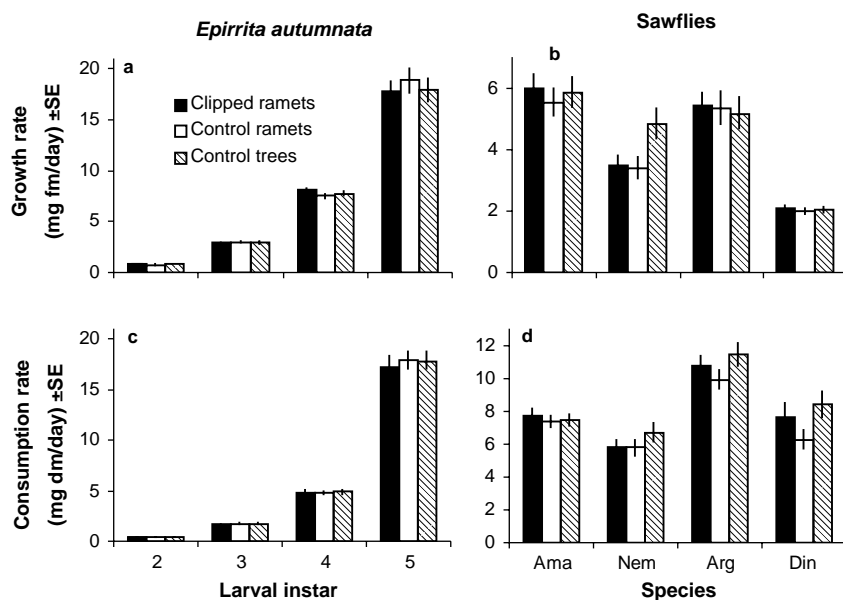


Fig. 3. Larval growth rates (in fresh mass) and leaf consumption rates (in dry mass) on leaves from clipped ramets (black bars), control ramets (white bars) and control trees (hatched bars). For *Epirrita autumnata*, instars 2 to 5 on x-axis indicate the timing of the bioassay during the larval development. For sawflies, abbreviations for the species are Ama: *Amauronematus amplus*, Nem: *Nematus brevisvalvis*, Arg: *Arge* sp. and Din: *Dineura pullior*.

The growth rate of *A. amplus*, the seasonally earliest species, correlated negatively with leaf toughness ( $r = -0.69$ ,  $P < 0.001$ ,  $N = 30$ ), while a positive relationship was displayed between leaf water content and larval growth ( $r = 0.67$ ,  $P < 0.001$ ,  $N = 30$ ). The results were similar for each treatment. Thus, the explanation for the similar growth rates in all treatments for this species seems to be the fact that toughness did not differ between treatments in the early season (third sampling date in Fig. 1d). This result implies that the contents of proanthocyanidins, proteins or water in the leaves were of minor importance for this species, or the positive effects of water and proteins in the clipped ramets counteracted the negative effects of proanthocyanidins. Leaf consumption was not clearly related to any single leaf trait.

When all treatments were tested together, the larval performance of *N. brevisvalvis* did not correlate with any of the measured leaf variables. Even when different treatments were tested separately, none of the measured leaf traits explained why the growth rate of *N. brevisvalvis* was higher in the control trees than in the browsed trees (Fig. 3b).

The growth rates of *Arge* sp. and *D. pullior*, which feed on mature leaves, were negatively related to the content of proanthocyanidins in the leaves ( $r = -0.55$ ,  $P = 0.002$ ;  $r = -0.37$ ,  $P = 0.046$ , respectively;  $N = 30$  in both). The growth rate of *Arge* was positively related to the contents of nutritive sugars ( $r = 0.57$ ,  $P = 0.001$ ), while the growth rate of *D. pullior* was positively related to the content of fructose ( $r = 0.56$ ,  $P = 0.001$ ). However, these relationships did not lead to differences among treatments in larval growth or leaf consumption, probably because some other unmeasured factors affected

performance in different treatments. In addition, during the last sampling date, both the content of nutritive sugars and the content of proanthocyanidins were higher in the clipped ramets, and thus their effects may have countered each other.

## Discussion

Simulated winter browsing had large effects on leaf and shoot growth of mountain birch in the following growing season, but its influence on leaf chemistry was much smaller in magnitude. In addition, different responses were shown at different parts of the season. For most leaf traits, the effects of clipping did not spread to the control ramets within the same individual, but for leaf water content and the content of nutritive sugars, small changes in seasonal trends were detected in the control ramets compared to control trees. The effects of winter browsing on the larval performance of insect herbivores during the following season were relatively weak and inconsistent. Our results suggest that the developmental change in leaf quality during the growing season may be a stronger factor affecting larval performance than the changes in leaf quality caused by moderate levels of winter browsing.

Our results contrast with some earlier findings indicating preference of herbivores for browsed trees (Danell and Huss-Danell 1985, Hjaltn and Price 1996, Roininen et al. 1997). Since our treatment had equally strong effects on leaf growth as many earlier studies on winter browsing (Haukioja et al. 1990, Hjaltn et al. 1993, Senn and Haukioja 1994, Danell et al. 1997), it is unlikely that the clipping treatment was not intensive enough to

cause biologically relevant changes in leaf quality. The difference between our results and others may thus be caused by arthropod behaviour in the field, since in most experiments herbivore abundance on naturally colonised trees has been measured instead of laboratory performance of herbivores. On the other hand, an earlier study on mountain birch reported only a weak tendency towards higher damage by herbivorous insects on browsed trees, which was evident on some study sites but not on all (Danell et al. 1997). Furthermore, in a recent meta-analysis by Nykänen and Koricheva (2004), simulated mammal browsing was found to significantly increase the pupal weight of insect herbivores, but the increase in insect growth and survival was not significant, suggesting that the positive effects of browsing on insect herbivores may not be as strong as previously thought.

### Effects of simulated winter browsing on leaf growth and chemical composition

Clipping increased the growth of long shoots and short shoot leaves, confirming the results by Danell and co-authors (1997). This was most likely due to the removal of apical buds, which freed the lower buds to grow more vigorously by breaking the hormonal control of apical buds and decreasing competition for resources among the remaining leaves (Haukioja et al. 1990, Bryant et al. 1991). The effects caused by the treatment were similar to those caused by natural moose browsing (Danell and Huss-Danell 1985). Most of the treatment effects (increased growth of long shoots, increased toughness of leaves in late season and higher content of protein and proanthocyanidins in leaves) did not spread from the clipped ramets to the control ramets within the trees, indicating that resource allocation in mountain birch ramets is relatively independent. This is in line with the level of branch independence found in a study of partial shading of mountain birch trees (Henriksson 2001). On the other hand, there were significant treatment  $\times$  time interactions between control trees and control ramets in leaf growth and water content, and in the content of nutritive sugars and inositol, suggesting that clipping treatment may have influenced the timing of leaf development in the control ramets of the clipped trees.

Simulated winter browsing did not lead to decreased levels of carbohydrates in the leaves, when the sum of soluble carbohydrates was considered. This is in contrast with the findings indicating that severe browsing of willows in winter leads to reduced levels of shoot carbohydrates (Bryant 1987). Different results may be explained by differences in the severity and duration of treatments in these studies. Moreover, we used mature birch trees that probably had extensive carbohydrate reserves in their trunks, allowing compensation for the

removed biomass. Since there was no decline in the level of carbohydrates in the leaves of clipped ramets, it is not surprising that we found no evidence for the hypothesis that winter browsing leads to decreased content of condensed tannins (Bryant 2003). In fact, the content of proanthocyanidins was slightly higher in the clipped ramets than in the control ramets and control trees. Thus, the amount of condensed tannins per leaf increased along with the increased dry mass of leaves in the clipped ramets, indicating that the clipping treatment did not change the positive relationship between leaf growth and accumulation of proanthocyanidins that has been found in mountain birch (Riipi et al. 2002).

These results appear to be in contrast with a previous study on feltleaf willows, where the content of condensed tannins was lower in the leaves of such willows that had been heavily browsed in the previous years compared to the leaves of willows protected from mammalian herbivory (Bryant 2003). On the other hand, simulated winter browsing has been shown to increase the content of proanthocyanidins in the twigs of feltleaf willow in the following winter, despite a decline in the content of soluble carbohydrates in the twigs (Bryant 1987). It thus appears that the level of proanthocyanidins may not be directly related to the content of sugars in the twigs or in the leaves of woody plants. Although the metabolism of carbohydrates and the biosynthesis of proanthocyanidins are connected, there are many steps of control in the biosynthesis of proanthocyanidins (Dixon et al. 2005), which obscure the relationship between sugars and proanthocyanidins at the level of their foliar contents.

Our results suggest that the content of gallotannins in browsed trees was reduced compared to control trees, but within the browsed trees, gallotannins accumulated more in the leaves of clipped ramets than in the leaves of control ramets. Since gallotannins are typical of young leaves, their higher content in the leaves of clipped ramets may be related to the increased activity of leaf growth in these ramets compared to leaves in control ramets. At the level of whole trees, the result partly corresponds to the findings of Danell and co-authors (1997), who report decreased protein precipitation capacity (PPC) in browsed mountain birch trees in comparison to control trees. However, it is problematic to compare the total PPC of leaves to the content of gallotannins, although the content of gallotannins explains most of the PPC in birch leaves (Ossipova et al. 2001).

Deer browsing has been suggested to increase leaf toughness in a deciduous shrub *Viburnum dilatatum* (Shimazaki and Miyashita 2002), but in a previous experiment with mountain birch, simulated winter browsing did not affect leaf toughness significantly (Danell et al. 1997). On the other hand, an increase in leaf mass per area, which correlated with leaf toughness

in this study, has been detected on *Betula pubescens* after simulated winter browsing (Danell and Huss-Danell 1985), and on *Salix lanata* after summer browsing (Olofsson and Strengbom 2000). No clear correlations between leaf toughness and the measured chemical compounds could be found, although some phenolics are known to be involved in the process of leaf hardening (Ossipov et al. 2001).

## Larval performance

Winter browsing by moose or reindeer may change the composition of mountain birch leaves into more favourable for herbivores through higher contents of nitrogen and water (Danell et al. 1997). The weak responses of the herbivore species to clipping treatment in this experiment were rather unexpected, because the effect of simulated browsing was quite evident on the growth of the leaves. Vigorously growing leaves have been suggested to be better food for some herbivores (Price 1991), and we also found an increase in the content of protein and water in the leaves of clipped ramets. The increased toughness in the clipped ramets might be one explanation for the lack of a positive effect on the larvae, because toughness is often negatively correlated with herbivore performance (Coley and Barone 1996). However, toughness was only increased in the later season, and during this time, toughness did not correlate negatively with larval performance in the clipping treatment in any of the sawfly species (*N. brevisvalvis*, *Arge* sp. and *D. pullior*). Both for leaf toughness and water percent, the changes during natural leaf development were much larger than the changes caused by the cutting treatment. It is probable that the larvae of the birch specialists encounter variation of this magnitude during their larval development and are at least partially adapted for it. For instance, the skeletonising feeding mode of the latest species, *D. pullior*, may be an adaptation to the toughness of mature leaves. Toughness seemed to be most important for the early-season species, *E. autumnata* and *A. amplius*, but the negative relationships were similar in all treatments since leaf toughness did not differ between clipped ramets and control ramets or trees in the early season.

Another possible explanation for the lack of improved performance on clipped ramets is the higher content of proanthocyanidins in the leaves. These tannins may have interacted with the beneficial effects of the higher protein and water contents. There was also an increased level of gallotannins in clipped ramets (compared to control ramets) during the early season, but we did not find any relationship between the content of gallotannins during the peak phase and the larval performance of fourth instar *E. autumnata*. In fact, the growth rate of larvae was higher on the leaves of clipped ramets than on other

treatments at the time when the content of gallotannins was highest. This increase in larval growth rate was probably due to the higher water content of leaves in clipped ramets.

In this experiment, clipping did not increase leaf quality for the sawfly species. The main positive effect of the clipping treatment on larval performance was a small (3.9%) increase in the pupal mass (a correlate of female fecundity; Tammaru et al. 1996) of *E. autumnata*. This result agrees with earlier findings reporting weak positive (non-significant) effects of clipping on the pupal mass (Neuvonen and Danell 1987) and on the growth rate (Haukioja et al. 1990) of *E. autumnata*. Thus, the degree of simulated browsing used in this experiment, which corresponds to the natural level of winter browsing by mammalian herbivores in our study area, is not likely to strongly affect the population dynamics of insect folivores on mountain birch via browsing-induced changes in leaf quality affecting population growth. It remains possible that other traits, such as the oviposition preference of sawfly females could be affected by the clipping treatment. The increased shoot growth could also benefit stem galls, as has been shown for *Euura lasiolepis* on browsed *Salix lasiolepis* (Hjältén and Price 1996).

Although an increase in the suitability of browsed trees for insect herbivores is a predominant result in the studies of winter browsing, some negative effects have also been reported (Hjältén 1999, Bergström et al. 2000). Lack of response by herbivores, such as was shown in this study, may be partially explained by temporal variation in the responses of leaf chemistry to the clipping treatment and by variable responses of different herbivore species to clipping. In addition, variation in the intensity and duration of browsing, in combination with the size and ontogenetic age of the plants, is likely to affect the consequences of winter browsing for the chemistry and morphology of the plants, and for the insect herbivores feeding on the plants during summer.

**Acknowledgements** – We are grateful to Eija Asikainen, Henrik Heinilä, Annika Parantainen, Satu Ramula, Paula Salminen and Teija Turunen for their assistance in the field and in the laboratory. We thank Lauri Kapari for helpful discussions and Julia Koricheva, Tapio van Ooik and Stig Larsson for valuable comments on earlier versions of the manuscript. This work was supported by a grant from the Academy of Finland to E.H (project number 43518) and by the Graduate School of Biological Interactions.

## References

- Ayres, M. P., Clausen, T. P., MacLean, S. F. Jr. et al. 1997. Diversity of structure and antiherbivore activity in condensed tannins. – *Ecology* 78: 1696–1712.
- Bergström, R. 1984. Rebrowsing on birch (*Betula pendula* and *B. pubescens*) stems by moose. – *Alces* 9: 3–13.
- Bergström, R., Skarpe, C. and Danell, K. 2000. Plant responses and herbivory following simulated browsing and stem

- cutting of *Combretum apiculatum*. – J. Veg. Sci. 11: 409–414.
- Bernays, E. A. and Chapman, R. F. 1994. Host-plant selection by phytophagous insects. – Chapman and Hall.
- Bernays, E. A., Cooper Driver, G. and Bilgener, M. 1989. Herbivores and plant tannins. – Adv. Ecol. Res. 19: 263–302.
- Bryant, J. P. 1987. Feltleaf willow–snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. – Ecology 68: 1319–1327.
- Bryant, J. P. 2003. Winter browsing on Alaska feltleaf willow twigs improves leaf nutritional value for snowshoe hares in summer. – Oikos 102: 25–32.
- Bryant, J. P., Danell, K., Provenza, F. et al. 1991. Effects of mammal browsing on the chemistry of deciduous woody plants. – In: Tallamy, D. W. and Raupp, M. J. (eds), Phytochemical induction by herbivores. John Wiley and Sons, pp. 135–154.
- Coley, P. D. and Barone, J. A. 1996. Herbivory and plant defenses in tropical forests. – Annu. Rev. Ecol. Syst. 27: 305–335.
- Danell, K. and Huss-Danell, K. 1985. Feeding by insects and hares on birches earlier affected by moose browsing. – Oikos 44: 75–81.
- Danell, K., Bergström, R. and Edenius, L. 1994. Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. – J. Mammal. 75: 833–844.
- Danell, K., Haukioja, E. and Huss-Danell, K. 1997. Morphological and chemical responses of mountain birch leaves and shoots to winter browsing along a gradient of plant productivity. – Ecoscience 4: 296–303.
- Dixon, R. A., Xie, D.-Y. and Sharma, S. B. 2005. Proanthocyanidins – a final frontier in flavonoid research? – New Phytol. 165: 9–28.
- Hanhimäki, S. 1993. Leaf quality and leaf chewers: an experimental approach to variation in the mountain birch-insect herbivore system. PhD thesis. Rep. Dept of Biology, Univ. of Turku, No. 31.
- Harborne, J. B. 1991. The chemical basis of plant defense. – In: Palo, R. T. and Robbins, C. T. (eds), Plant defenses against mammalian herbivory. CRC Press, pp. 45–59.
- Haukioja, E. 2003. Putting the insect into the birch-insect interaction. – Oecologia 136: 161–168.
- Haukioja, E., Ruohomäki, K., Senn, J. et al. 1990. Consequences of herbivory in the mountain birch (*Betula pubescens* ssp. *tortuosa*): importance of the functional organization of the tree. – Oecologia 82: 238–247.
- Haukioja, E., Ossipov, V. and Lempa, K. 2002. Interactive effects of leaf maturation and phenolics on consumption and growth of a geometrid moth. – Entomol. Exp. Appl. 104: 125–136.
- Henriksson, J. 2001. Differential shading of branches or whole trees: survival, growth, and reproduction. – Oecologia 126: 482–486.
- Henriksson, J., Haukioja, E., Ossipov, V. et al. 2003. Effects of host shading on consumption and growth of the geometrid *Epirrita autumnata*: interactive roles of water, primary and secondary compounds. – Oikos 103: 3–16.
- Hjältén, J. 1999. Willow response to pruning: the effect on plant growth, survival and susceptibility to leaf galls. – Ecoscience 6: 62–67.
- Hjältén, J. and Price, P. W. 1996. The effect of pruning on willow growth and sawfly population densities. – Oikos 77: 549–555.
- Hjältén, J., Danell, K. and Ericson, L. 1993. Effects of simulated herbivory and intraspecific competition on the compensatory ability of birches. – Ecology 74: 1136–1142.
- Karban, R. and Niiho, C. 1995. Induced resistance and susceptibility to herbivory: plant memory and altered plant development. – Ecology 76: 1220–1225.
- Kause, A., Ossipov, V., Haukioja, E. et al. 1999. Multiplicity of biochemical factors determining quality of growing birch leaves. – Oecologia 120: 102–112.
- Kause, A., Saloniemi, I., Morin, J.-P. et al. 2001. Seasonally varying diet quality and the quantitative genetics of development time and body size in birch feeding insects. – Evolution 55: 1992–2001.
- Koponen, S. 1973. Herbivorous invertebrates of the mountain birch at Kevo, Finnish Lapland. – Rep. Kevo Subarctic. Res. Stat. 10: 20–28.
- Lehtilä, K., Haukioja, E., Kaitaniemi, P. et al. 2000. Allocation of resources within mountain birch canopy after simulated winter browsing. – Oikos 90: 160–170.
- Löyttyäniemi, K. 1985. On repeated browsing of Scots pine saplings by moose (*Alces alces*). – Silva Fenn. 19: 387–391.
- Macdonald, A. D. and Mothersill, D. H. 1983. Shoot development in *Betula papyrifera*. I. Short-shoot organogenesis. – Can. J. Bot. 61: 3049–3065.
- Macdonald, A. D., Mothersill, D. H. and Caesar, J. C. 1984. Shoot development in *Betula papyrifera*. III. Long-shoot organogenesis. – Can. J. Bot. 62: 437–445.
- Martel, J., Lempa, K. and Haukioja, E. 1999. Effects of stress and rapid growth on fluctuating asymmetry and insect damage in birch leaves. – Oikos 86: 208–216.
- Mattson, W. J. and Scriber, J. M. 1987. Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral nutrients. – In: Slansky, F. Jr. and Rodriguez, J. G. (eds), Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley-Interscience, pp. 105–146.
- Neuvonen, S. and Danell, K. 1987. Does browsing modify the quality of birch foliage for *Epirrita autumnata* larvae? – Oikos 49: 156–160.
- Nurmi, K., Ossipov, V., Haukioja, E. et al. 1996. Variation of total phenolic content and individual low-molecular-weight phenolics in foliage of mountain birch trees. – J. Chem. Ecol. 22: 2023–2040.
- Nykänen, H. and Koricheva, J. 2004. Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis. – Oikos 104: 247–268.
- Olofsson, J. and Strengbom, J. 2000. Response of galling invertebrates on *Salix lanata* to reindeer herbivory. – Oikos 91: 493–498.
- Ossipov, V., Loponen, J., Ossipova, S. et al. 1997. Gallotannins of birch *Betula pubescens* leaves: HPLC separation and quantification. – Biochem. Syst. Ecol. 25: 493–504.
- Ossipov, V., Haukioja, E., Ossipova, S. et al. 2001. Phenolic and phenolic-related factors as determinants of suitability of mountain birch leaves to an herbivorous insect. – Biochem. Syst. Ecol. 29: 223–240.
- Ossipova, S., Ossipov, V., Haukioja, E. et al. 2001. Proanthocyanidins of mountain birch leaves: quantification and properties. – Phytochem. Anal. 12: 128–133.
- Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. – Oikos 62: 244–251.
- Riipi, M., Ossipov, V., Lempa, K. et al. 2002. Seasonal changes in birch leaf chemistry: are there trade-offs between leaf growth and accumulation of phenolics? – Oecologia 130: 380–390.
- Roininen, H., Price, P. W. and Bryant, J. P. 1997. Response of galling insects to natural browsing by mammals in Alaska. – Oikos 80: 481–486.
- Ruohomäki, K., Tanhuanpää, M., Ayres, M. P. et al. 2000. Causes of cyclicity of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice. – Popul. Ecol. 42: 211–223.
- Scriber, J. M. and Slansky, F., Jr. 1981. The nutritional ecology of immature insects. – Annu. Rev. Entomol. 26: 183–211.
- Senn, J. and Haukioja, E. 1994. Reactions of the mountain birch to bud removal: effects of severity and timing, and implications for herbivores. – Funct. Ecol. 8: 494–501.
- Shimazaki, A. and Miyashita, T. 2002. Deer browsing reduces leaf damage by herbivorous insects through an induced response of the host plant. – Ecol. Res. 17: 527–533.

- Slansky, F., Jr. 1993. Nutritional ecology: the fundamental quest for nutrients. – In: Stamp, N. E. and Casey, T. M. (eds), Caterpillars, ecological and evolutionary constraints on foraging. Chapman and Hall, pp. 29–91.
- Tammaru, T., Kaitaniemi, P. and Ruohomäki, K. 1996. Realized fecundity in *Epirrita autumnata* (Lepidoptera: Geometridae): relation to body size and consequences to population dynamics. – *Oikos* 77: 407–416.
- Tenow, O. 1972. The outbreaks of *Oporinia autumnata* Bkh. and *Operophtera* spp. (Lep., Geometridae) in the Scandinavian mountain chain and northern Finland 1862-1968. PhD thesis. Zool. Bidr. Uppsala, Suppl 2:1–107.

*Subject Editor: Lauri Oksanen*