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# Effects of reindeer browsing on tundra willow and its associated insect herbivores

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**Summary**

**1.** Browsing by large mammals may strongly constrain the growth and reproduction of woody plants, and may alter the food quality and resource availability for herbivorous insects. The response of the plants may vary between different growth stages, and the preference of herbivores may be related to plant age. Understanding the effects of reindeer *Rangifer tarandus* browsing on the growth of woody forage plants is important in formulating guidelines for reindeer grazing management, especially in low productivity subarctic environments.

**2.** We studied the effects of summer browsing by reindeer on the growth and reproduction of willow *Salix phylicifolia* and on the abundance of its insect herbivores, by studying plants inside and outside exclosures over a period of 6 years.

**3.** The experiment was run in northern Finland and included 80 willow genets in an area near the timberline formed by mountain birch *Betula pubescens*. At the beginning of the experiment, half of the willows were cut at ground level to rejuvenate ramets.

**4.** Reindeer feeding was more intense on rejuvenated willow compared with old willow, and the effects of browsing were more pronounced on rejuvenated plants.

**5.** Reindeer browsing reduced the height of willow by *c.* 50%, shoot length by *c.* 30% and accelerated dieback of the shoots by *c.* 50%. Browsed willow produced fewer shoots, with fewer buds and floral catkins, than unbrowsed willow. Browsing also reduced the densities of the most common insect herbivores: leaf beetles of the genus *Gonioctena* (Coleoptera: Chrysomelidae) and gall-inducing sawflies (Hymenoptera: Tenthredinidae) belonging to the genera *Phyllocolpa*, *Eupontania* and *Euura*.

**6.** *Synthesis and applications.* We show that reindeer browsing in summer reduces biomass and diminishes reproductive success of willow; it also lowers the numbers of its associated insect herbivores. Our results suggest that this effect will be most evident in low-productivity tundra heaths where alternative forage plants, such as relatively palatable and productive graminoids, are scarce. We advise that reindeer should be maintained below the present levels of 2–3 reindeer km$^{-2}$ to sustain the long-term persistence of important forage plants such as willow in these low productivity habitats.

*Key-words*: browsing, food preference, leaf beetles, plant growth, sawflies, tundra, willow

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## Introduction

Grazing and browsing by ungulates have marked effects on the abundance of deciduous scrubs and other plants in tundra ecosystems (Henry & Svoboda 1994). Manseau, Huot & Crête (1996) reported higher abundance of *Salix planifolia* in ungrazed areas than in areas with caribou *Rangifer tarandus caribou* (reindeer) grazing, noting that this willow was absent from some grazed areas. Long-term experiments on the Fennoscandian tundra have suggested that exclusion of grazers leads to increased abundance of woody plants (Moen & Oksanen 1998), whereas intense summer grazing by reindeer *Rangifer t. tarandus* virtually eliminates woody plants (Olofsson *et al.* 2001). There are several studies from

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other ecosystems showing that wild ungulates and domestic livestock can affect growth, plant structure and reproduction of willow *Salix* spp. (Maschinski 2001; Peinetti, Menezes & Coughenour 2001; Brookshire *et al.* 2002).

Ungulate browsing may cause a variety of morphological and physiological changes in plants, which depend on browsing intensity and frequency, the type of herbivory and the time of year when browsing occurs (Danell, Huss-Danell & Bergström 1985; Danell, Bergström & Edenius 1994). For instance, winter browsing by moose *Alces alces* may stimulate shoot growth in the next growing season (Danell, Bergström & Edenius 1994; Bergman 2002), while leaf-stripping in summer by moose or reindeer generally has the opposite effect (Danell, Bergström & Edenius 1994). Simulated browsing experiments have shown that clipping reduced the growth of willow *Salix lanata* (Ouellet, Boutin & Heard 1994), demonstrating that effects of browsing can be particularly pronounced in low productivity habitats. However, there are few studies showing how growth of willow is affected when it is exposed to long-term mammal browsing. Responses may also vary between different plant species, growing conditions and growth stage (Edenius, Danell & Bergström 1993). Swihart & Bryant (2001) found that winter herbivory is heavier on mature plants. Unfortunately, there are no experimental studies examining the effects of summer feeding by reindeer *Rangifer tarandus* L. on willow at different stages of development. Martinsen, Driebe & Whitham (1998) found that resprouting juvenile cottonwoods *Populus fremontii* × *Populus angustifolia* not only had a high nitrogen content but also contained high levels of compounds that defend against mammalian herbivores. Similarly, Tahvanainen *et al.* (1985) found increased levels of defensive compounds in juvenile willow, and hare *Lepus timidus* preferred mature willow shoots to juvenile ones. We might thus expect that reindeer would not heavily browse resprouting juvenile willow.

It has been proposed that browsing by ungulates affects the reproduction of plants in different ways (Mulder 1999). Loss of foliage leads to restricted carbon and nitrogen gain (Ouellet, Boutin & Heard 1994) and fewer resources are left for flower production. Bergström & Danell (1987) found that moose browsing reduced the production of female catkins in birch *Betula pendula* and *Betula pubescens*, and Elmqvist *et al.* (1987) showed that moderately browsed willow maintained flower production. In addition, reindeer may browse flower buds and developing catkins. There are no detailed studies in northern systems, but we expect reindeer to have a negative effect on flowering and seed production because resource limitation may prevent compensatory responses (Bryant, Chapin & Klein 1983).

The effects of browsing on the insect guild utilizing willows can operate in several ways. Induced-chemical responses of the plant to herbivory may change the nutritional quality of the plant, and therefore the quality of the plant as food (Bryant *et al.* 1991; Martinsen, Driebe & Whitham 1998). Many of these induced responses are long lasting (Bryant *et al.* 1991 and references therein). Browsing may reduce foliage available for leaf-feeding insects (leaf-gallers and leaf-beetles) and reduce buds available to bud-galling sawflies. Alternatively, browsing may stimulate development of long shoots, leading to increased resources for these insects (Price 1991). Winter browsing by moose improves the food quality for herbivorous insects, as indicated by higher insect densities on previously browsed trees (Danell & Huss-Danell 1985; Roininen, Price & Bryant 1997). In general, moose browsing leads to an improvement in leaf quality (Danell & Bergström 1989; Bryant *et al.* 1991) and growth of longer and more vigorous shoots (Bryant *et al.* 1991). For shoot- and leaf-galling sawflies in the genera *Euura* and *Eupontania*, shoot length has been found to correlate positively with the number of ovipositing females and survival of the larvae (Price, Craig & Roininen 1995; Roininen, Price & Bryant 1997), and galls were more common on browsed trees or ramets. Compared with the moose–woody plant–insect system, there is little information on the reindeer–woody plant–insect system. However, Olofsson & Strengbom (2000) found more gall-forming insects on reindeer-browsed willow *S. lanata*, even though shoot length was reduced by leaf-stripping.

In northern Fennoscandia, *Salix phylicifolia* L. is one of the common willow species browsed by reindeer (Haukioja & Heino 1974; Nieminen & Heiskari 1989). The objective of our study was to compare the growth and reproductive response of *S. phylicifolia* to summer browsing by reindeer. We measured several growth characteristics inside and outside exclosures 4 and 5 years after establishment of the experiment. Furthermore, we examined the impact of reindeer feeding on herbivorous insects on willows, in order to test the hypothesis that summer browsing would adversely affect both willow and its associated insect herbivores.

## Materials and methods

### STUDY AREA

The study was performed near Mt Muotkatakkavaara (68°55′N, 20°59′E), 20 km south of the village of Kilpisjärvi in north-western Finnish Lapland. The area belongs to Fjeld Lapland and lies in the orohemiarctic zone (Ahti, Hämet-Ahti & Jalas 1968). Continental subalpine birch woodland is the predominant vegetation (Hämet-Ahti 1963) below the timberline, while treeless heath prevails at the higher altitudes (Oksanen & Virtanen 1995). The forests are dominated by mountain birch *Betula pubescens* ssp. *czerepanovii* (N. I. Orlova) Hämet-Ahti. On drier sites, subarctic heath vegetation is more frequent, dominated by *Betula nana* L. On moister sites thickets of willow scrub *Salix* spp. are common. Here, *S. phylicifolia* is common, when not subjected to flooding, while *Salix lapponum* L. is dominant on sites subjected to spring flooding

after snowmelt. In our study area, *S. phylicifolia* may hybridize with *Salix myrsinifolia* Salisb. Phytochemical analysis of the experimental willows has revealed characteristics of *S. myrsinifolia* (P. Hallgren & R. Julkunen-Tiitto, unpublished data).

Reindeer, which are semi-domesticated in Finland, are the dominant large herbivores. Both wild and domestic reindeer have remarkably different summer and winter diets. In winter, they mainly feed on terrestrial lichens (Helle 1984; Danell *et al*. 1994), which they dig up from under the snow. In summer, they feed on a wide variety of forage plants, mainly the leaves of willow and birch, herbs and grasses (Kelsall 1968; Haukioja & Heino 1974; Nieminen & Heiskari 1989). The number of reindeer managed by the Käsivarsi reindeer herders' co-operative, to which our study area belongs, decreased between 1994 and 1998 from 7609 to 7489 animals (*c*. 1·6 reindeer km$^{-2}$) (Kumpula *et al*. 1997; Kumpula, Colpaert & Nieminen 1999). However, the local reindeer owner has maintained an above-average stocking rate of approximately 2–3 animals km$^{-2}$. Willow grouse *Lagopus lagopus* L. is fairly common in the study area and may show large fluctuations in population density. The last peak population density occurred during the winter of 1995–96 (R. Virtanen & H. Roininen, personal observations). Mountain hare *Lepus timidus* L. populations vary and occasionally they can be abundant. However, during the period of this study hare densities were very low. Moose *Alces alces* L. are important browsers, feeding on woody plants year round (Cederlund *et al*. 1980). However, moose are uncommon in the study area, although they occasionally migrate through it.

The most common folivorous insects are leaf beetles (Coleoptera: Chrysomelidae) belonging to the genus *Gonioctena* Chevrolat. There were three gall-inducing sawflies (Hymenoptera: Tenthredinidae) on our experimental plants: a leaf-folder belonging to the genus *Phyllocolpa* Benson, the leaf-galler *Eupontania arcticornis* Konow and the bud-galler *Euura mucronata* Hartig.

### EXPERIMENTAL DESIGN

In the study area, 20 blocks with four willow genets in each were established in 1997–98 on two sites of similar habitat type (10 blocks in each). The two sites were 2 km apart and there was a small altitudinal difference (±10 m) between sites. In each block of four willow genets, two randomly chosen genets were cut at ground level in 1997 to stimulate vegetative growth (young), and the remaining two genets were left without any pre-treatment (old). In each block, one of the young and one of the old willow genets were fenced, protecting a single willow genet from browsing, while the unfenced willows were open for browsing. The fences measured 2 × 2 m square and 2 m in height and were constructed from commercially available reindeer fence attached to four fence posts. The fences did not prevent access by insects, small mammals (such as *Microtus* and *Clethrionomys* voles and lemmings *Lemmus lemmus*) or willow grouse. Consequently, each block consisted of four subplots with different treatments: Young/fenced, young/open to reindeer and old/fenced, old/open to reindeer. Plants that were cut at ground level in 1997 started rejuvenating by forming new basal sprouts in 1998 and are hereafter referred to as rejuvenated. Plants that remained untouched are hereafter referred to as old. In each fenced or open plot, four ramets belonging to the same genet were selected at random and permanently identified with a long-lasting tag. All measurements were taken on these ramets throughout the study period.

### MEASUREMENTS ON EFFECTS OF HERBIVORY

Effects of reindeer summer browsing on willows were examined from spring 2001 to early autumn 2002. We measured the height of marked ramets in late August to early September 2001 and 2002. Plants were measured at the end of the growing season prior to leaf-fall, so representing maximum annual growth. During the same period, we measured the length of the leading shoots to quantify the growth of the main stem of the plant. In willow, annual internodes are clearly visible. By measuring the distance between the internodes, we were able to measure the annual shoot lengths back to 1998. Some parts of the shoots may not survive until the next year and show dieback due to severe frost, drought, disease or herbivores. In 2001, we measured the dieback of the annual shoots back to 1998. In 2002, we measured the dieback of the shoots grown in 2001. Based on these measurements, we were able to reconstruct the development of the height of the plants from 1997 onwards. Furthermore, we counted the number of shoots, the number of buds per shoot and the number of leaves eaten by reindeer per shoot. Reindeer feed on the leaves of willow throughout the growing season and leave characteristic marks as a consequence of their tendency to rip off the leaves. According to our own observations, utilization of willows was highest in August and had stopped almost completely by the date the measurements were initiated.

To give an estimate of the feeding by folivorous insects, we used a herbivory index. Each leaf of the three leading shoots was given an index number based on the proportion of leaf area removed by insects. Index numbers ranged from 0 to 4, where 0 = no damage, 1 = 0–1%, 2 = 1–5%, 3 = 5–25% and 4 = 25–100% of the leaf area eaten by insects. By calculating the mean herbivory index of the three leading shoots, we could give a mean herbivory index number for the whole ramet. We also counted the number of *Gonioctena* spp. on ramets in 2001. In 2001 and 2002, we counted the number of galls of three different sawfly species: *Phyllocolpa* spp., *Eupontania arcticornis* and *Euura mucronata*.

In 2001 and 2002, we took measurements on the reproductive capacity of the marked ramets to assess the response to herbivory. In the third week of June, we counted the number of catkins on each ramet as a measure of plant reproduction.

### STATISTICAL ANALYSIS

We tested the effects of reindeer exclusion on willow growth, reproduction and insect herbivory using repeated measures analysis of variance (ANOVAR). We used habitat (site), block, browsing (fenced vs. open to reindeer) and rejuvenation (rejuvenated plants vs. old plants) as factors and year as the within-subject variable (SPSS version 10·0; Anonymous 1999). Because the numbers of leaves eaten by reindeer were counted in open plots only, the preference of reindeer for rejuvenated or old plants was analysed with repeated measures analysis of variance (ANOVAR) using habitat, block and rejuvenation as factors and year as the within-subject variable. For all the variables there was no significant effect for the factors block and habitat, indicating that growth responses of the willows were more or less uniform and independent of any small variation in the landscape. Analyses were carried out in the univariate mode. Mauchly's test for sphericity was used to detect any violations against this assumption (Potvin, Lechowicz & Tardif 1990). This test was significant on a few occasions and where necessary Huynh–Feldt corrected degrees of freedom were used. Analyses were conducted using genet means from four ramets for each treatment ($n$ = 10 for each browsing and rejuvenation treatment) rather than individual plants. Shoot length and height data were transformed with a natural logarithm + 1 to improve the homogeneity of variances. The proportion of available leaves eaten by reindeer was arcsine transformed.

To test whether browsing, the growth stage of willows or sampling year had effects on the occurrence of insects on the plants, generalized linear interactive modelling was used. A model was constructed where the number of counted observations in four ramets was the response variable, and browsing (with levels fenced vs. open), growth stage of the willow (rejuvenated vs. old) and year (2001 vs. 2002) were explanatory variables (factors with all their interaction terms in the initial model). The response variable contained counts of items and the data included many zeroes. Thus, it was assumed that a Poisson-error structure would best approximate the distribution of the response variable. In addition, log-link is appropriate when dealing with positive integer values. To take overdispersion into account, a 'quasi-Poisson' error structure was used in final modelling. The quasi-Poisson family differs from the Poisson families only in that the dispersion parameter is not fixed at 1, allowing the modelling of overdispersion (McCullagh & Nelder 1989). Although the distributions of residuals revealed that the data had many rather extreme values, the residuals' distributions appeared satisfactory. Similar models were constructed for the leaf-galling sawflies *Phyllocolpa* spp. and *Eupontania arcticornis*, the bud-galling sawfly *Euura mucronata* and also *Gonioctena* spp. Significance of explanatory variables was tested by deletion ($F$-tests), starting from the higher order interaction terms. Non-significant terms were removed so that the minimum adequate model contained only significant explanatory variables. Analyses were run using R version 1·6·1 (Crawley 2002).

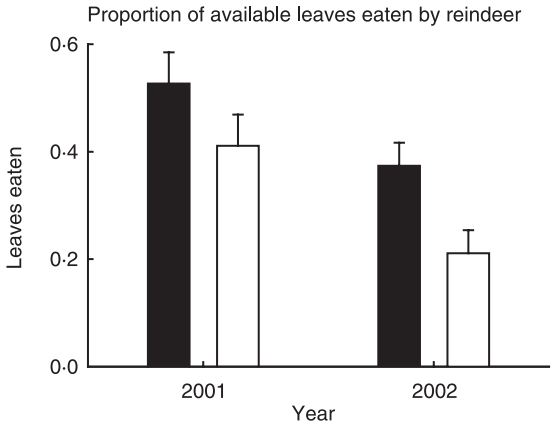


**Fig. 1.** Feeding intensity on rejuvenated and old bushes of *Salix phylicifolia* expressed as the proportion of available leaves eaten by reindeer. Error bars are one standard error. Rejuvenated bushes (filled bars) were cut at ground level in 1997 and old bushes (open bars) had no pre-treatment.

## Results

### REINDEER HERBIVORY

Reindeer ate a higher proportion of available leaves from young rejuvenated bushes compared with old bushes ($F_{1,19}$ = 6·48, $P$ = 0·02; Fig. 1). Furthermore, in 2002 the feeding intensity was lower than in 2001 ($F_{1,19}$ = 14·24, $P$ = 0·001). We did not observe any damage from mountain hare.

### EFFECTS OF HERBIVORY ON PLANT GROWTH CHARACTERISTICS

The height of the willows increased significantly during the study period ($F_{4\cdot6,178\cdot9}$* = 432·74, $P$ < 0·001; *Huynh–Feldt corrected degrees of freedom; Fig. 2). In addition, there were large differences in height between fenced plots and plots open to reindeer ($F_{1,39}$ = 13·62, $P$ = 0·001). A significant year × browsing interaction indicated that the effect of fencing increased over time due to continued willow growth in fenced plots ($F_{4\cdot6,178\cdot9}$* = 10·47, $P$ < 0·001). At the start of the experiment in 1997, the mean height of rejuvenated plants was lower and there was no difference in the height of willows inside and outside exclosures. From 1997 to 2002, reindeer exclusion resulted in a large increase in height of rejuvenated plants (significant browsing × rejuvenation interaction, $F_{1,39}$ = 7·19, $P$ = 0·011), and in 2002 rejuvenated plants reached the same height as the old plants. In contrast, rejuvenated plants not protected against reindeer browsing showed a height increase of less than half of that of the fenced plants.

Shoot length decreased significantly during the study period ($F_{4,144}$ = 195·12, $P$ < 0·001; Fig. 3a) and there was a significant difference in shoot length between fenced and open plots ($F_{1,36}$ = 23·33, $P$ < 0·001). Initially, rejuvenated plants had much longer annual shoots compared

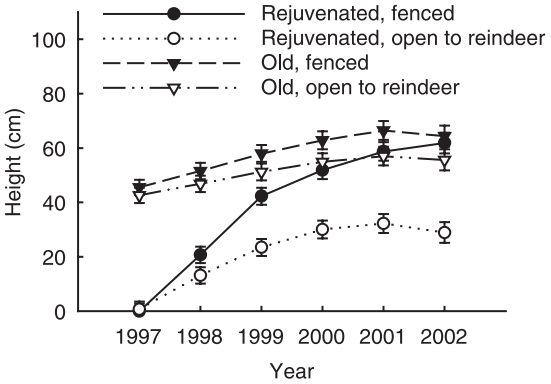


**Fig. 2.** Mean height of willows inside and outside fenced areas with different rejuvenation treatments (rejuvenated vs. old bushes). Error bars are one standard error. Differences between plant heights inside and outside the fenced areas were not significantly different in 1997, but were different for all subsequent years.

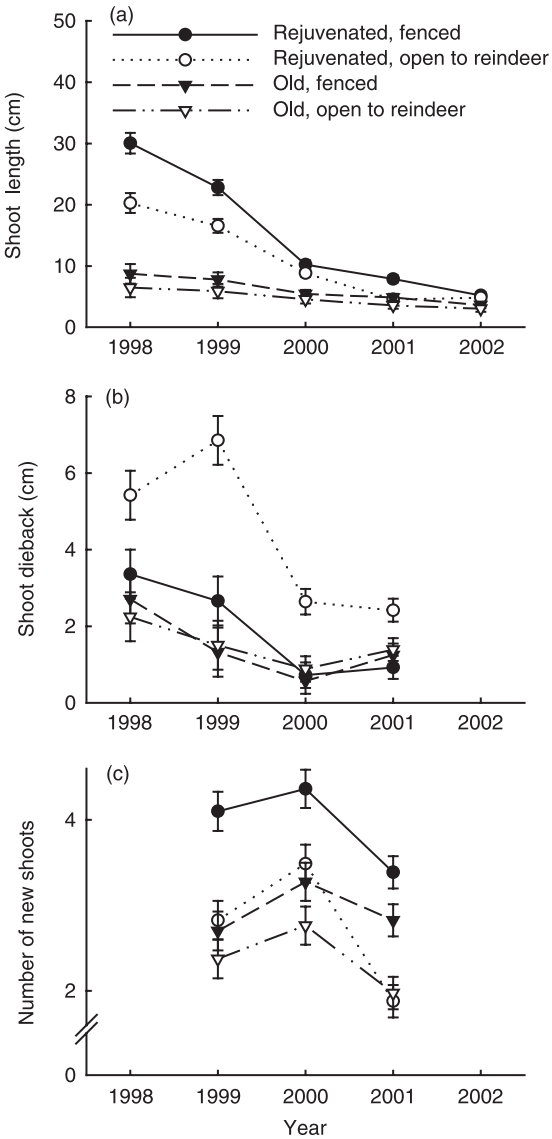


**Fig. 3.** (a) Current annual shoot length, (b) dieback and (c) number of new shoots of the leading shoot of willows inside and outside fenced areas with different rejuvenation treatments.

with old plants ($F_{1,36}$ = 148·96, $P$ < 0·001). A significant year × browsing interaction ($F_{4,144}$ = 2·71, $P$ < 0·032) indicated that the initially large effect of browsing (i.e. in 1998–99) on shoot length levelled off with increasing age of the plants (i.e. in 2000–02).

With decreasing shoot length, dieback of the leading shoot decreased equally over time ($F_{3,117}$ = 22·87, $P$ < 0·001; Fig. 3b). Furthermore, reindeer browsing increased dieback of the shoots ($F_{1,39}$ = 17·06, $P$ < 0·001). More specifically, a significant browsing × rejuvenation interaction suggested that rejuvenated plants showed much greater dieback compared with old plants ($F_{1,39}$ = 12·5, $P$ = 0·001).

The number of shoots emanating from the previous year's leading shoot increased from 1999 to 2000, and decreased from 2000 to 2001 ($F_{2,78}$ = 28·11, $P$ < 0·001; Fig. 3c). Reindeer browsing decreased branching ($F_{1,39}$ = 42·25, $P$ < 0·001) and the leading shoots of rejuvenated plants produced significantly more newly grown shoots ($F_{1,39}$ = 16·1, $P$ < 0·001). A significant year × browsing interaction ($F_{2,78}$ = 5·06, $P$ = 0·009) suggested that the effect of reindeer browsing on branching increased during the period 1999–2001. A browsing × rejuvenation interaction approaching significance ($F_{1,39}$ = 3·951, $P$ < 0·054) suggested that rejuvenated willows protected from browsing supported more branches than those browsed by reindeer.

Reindeer browsing markedly decreased the number of buds per shoot ($F_{1,39}$ = 11·03, $P$ = 0·002) and rejuvenated plants had significantly more buds per shoot ($F_{1,39}$ = 11·26, $P$ = 0·002; Fig. 4a). However, the initial difference

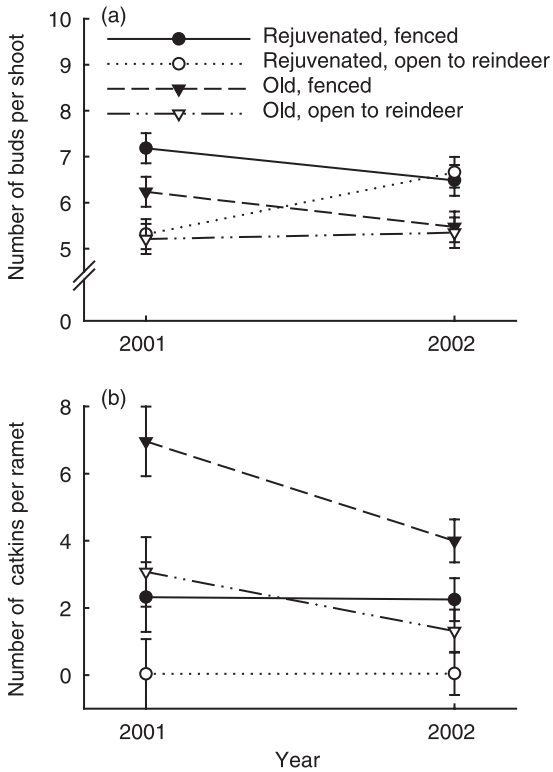


**Fig. 4.** (a) The mean number of buds of the leading shoot and (b) the mean number of catkins per ramet of willows inside and outside fenced areas with different rejuvenation treatments.

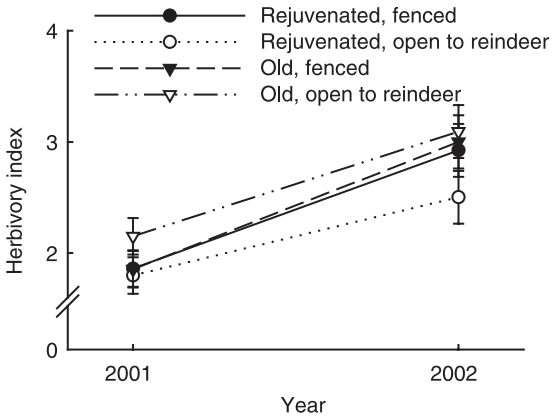


**Fig. 5.** Herbivory index to express the amount of defoliation by folivorous insects of willows inside and outside fenced areas with different rejuvenation treatments. Each leaf of the three leading shoots was given an index number based on the proportion of leaf area removed by insects. Index numbers ranged from 0 to 4 where 0 = no damage, 1 = 0–1%, 2 = 1–5%, 3 = 5–25% and 4 = 25–100% of the leaf area eaten by insects. Herbivory index numbers are based on the means for the whole ramet.

in 2001 between browsed and open plots levelled off in 2002 (year × browsing, $F_{1,39} = 13{\cdot}06$, $P = 0{\cdot}001$).

Flowering decreased during the period 2001–02 ($F_{1,39} = 5{\cdot}07$, $P < 0{\cdot}03$; Fig. 4b). Reindeer browsing also significantly decreased the number of catkins per ramet ($F_{1,39} = 20{\cdot}65$, $P < 0{\cdot}001$). Old ramets had more catkins compared with rejuvenated ramets ($F_{1,39} = 14{\cdot}18$, $P = 0{\cdot}001$) and hardly any rejuvenated bushes that were browsed by reindeer flowered.

### INSECT HERBIVORY AND ABUNDANCE

We found no difference in the amount of defoliation by folivorous insects between fenced blocks and blocks browsed by reindeer or between rejuvenated and old bushes (Fig. 5). There was, however, a great spatio-temporal variation in insect herbivory. From 2001 to 2002 the amount of insect-feeding on willows increased markedly ($F_{1,39} = 51{\cdot}58$, $P < 0{\cdot}001$) and there was considerable variation between different habitats and blocks.

In 2001, there were fewer *Gonioctena* leaf beetles on browsed willows ($F_{1,79} = 7{\cdot}34$, $P = 0{\cdot}008$) and there was no significant difference between rejuvenated and old bushes (Fig. 6). The number of *Eupontania arcticornis* galls was much higher in 2001 than in 2002 ($F_{1,157} = 12{\cdot}64$, $P < 0{\cdot}001$) and also decreased strongly through reindeer browsing ($F_{1,157} = 14{\cdot}44$, $P < 0{\cdot}001$; Fig. 7a). The number of *Phyllocolpa* galls was higher on old willows ($F_{1,155} = 7{\cdot}03$, $P = 0{\cdot}008$; Fig. 7b). A significant interaction term for year × browsing showed that the effect of browsing differed between the 2 years ($F_{1,156} = 4{\cdot}62$, $P = 0{\cdot}033$). Nevertheless, browsing reduced the number of *Phyllocolpa*, as indicated by a significant main effect for browsing (parameter estimate $t = 2{\cdot}74$, $P = 0{\cdot}007$). There were more *Euura mucronata* galls in 2002 than in

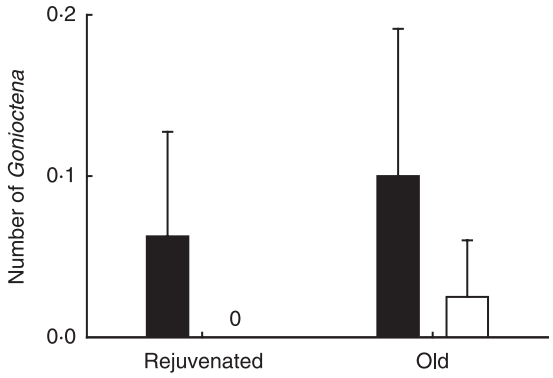


**Fig. 6.** The number of leaf beetles *Gonioctena* spp. per ramet of willows inside (filled bars) and outside fenced areas (open bars) with different rejuvenation treatments.

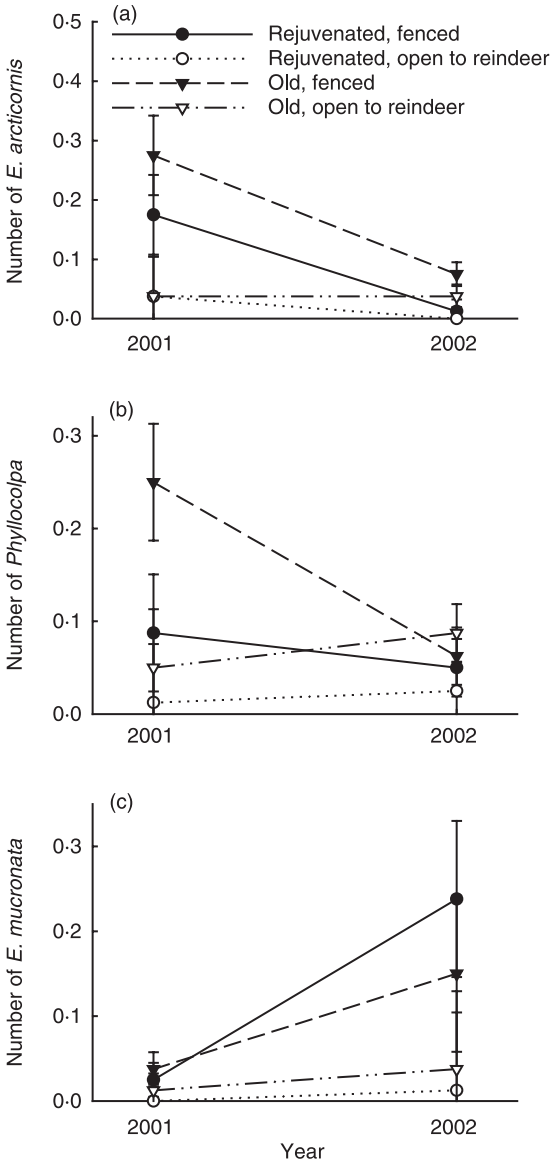


**Fig. 7.** The number of sawfly galls per ramet of willows inside and outside fenced areas with different rejuvenation treatments. There was (a) one leaf-galler *Eupontania arcticornis*, (b) one leaf-folder *Phyllocolpa* spp. and (c) the bud-galler *Euura mucronata*.

2001 ($F_{1,158}$ = 8·48, $P$ = 0·004; Fig. 7c). Furthermore, browsed willows had fewer *Euura mucronata* galls than those in the exclosures ($F_{1,158}$ = 9·87, $P$ = 0·002).

## Discussion

### EFFECTS OF HERBIVORY ON PLANT GROWTH CHARACTERISTICS

This experimental study, spanning several years, showed that browsing by reindeer strongly affects willow growth and reproduction, as well as densities of herbivorous insects utilizing willows. A major implication of this study is that browsing by large mammals reduces the abundance and performance of their food plants in northern ecosystems. This also implies that compensatory responses of plants are not sufficient to replace biomass losses, contrasting with evidence from more southerly ecosystems (Danell & Huss-Danell 1985; Danell, Huss-Danell & Bergström 1985; Bergström & Danell 1987; Oba, Mengistu & Stenseth 2000).

An important result was that the effects of reindeer browsing depended on the developmental stage of willows. Reindeer feeding was more severe on rejuvenated willows, and the growth and survival of these juvenile plants was significantly more affected by browsing than non-rejuvenated old plants. To our knowledge this is one of the few experimental demonstrations that frequent and heavy browsing on juvenile willows results in strong dieback of browsed shoots and a reduction in height growth (Peinetti, Menezes & Coughenour 2001). In general, mammalian herbivores select their food on the basis of its quality and quantity (Ball, Danell & Sunesson 2000). Heavy reindeer feeding on rejuvenated willow suggests that vigorous growth, possibly associated with higher nutritional value (Martinsen, Driebe & Whitham 1998), may prevail over the deterring effects of increased levels of secondary compounds (Julkunen-Tiitto 1989; Ruuhola *et al*. 2001).

It is obvious that the effects of winter and summer browsing differ. It could be that summer browsing on leaves has more detrimental consequences for the plants compared with pruning of shoots in winter. For instance, Bergman (2002) found that simulated winter browsing on *Salix caprea* by artificial tearing with a moose jaw and added moose saliva led to an increase in the number of branches. Moreover, Bergström & Danell (1987) and Bryant *et al*. (1991) demonstrated that winter browsing releases apical dominance and reduces the competition among growing points for nutrients, which results in enhanced shoot growth, an increased frequency of branched shoots and a higher number of buds. In a recent study in a riparian mountain habitat, Peinetti, Menezes & Coughenour (2001) not only found that winter and summer browsing by elk *Cervus elaphus* on *Salix monticola* decreased the number of shoots, but also reported that browsed willows produced longer and thicker shoots. In contrast, our results showed that reindeer browsing both decreased the number of willow shoots and reduced their length. We found no evidence of compensatory responses, where summer browsing would stimulate shoot production. Therefore, in this kind of low productivity habitat, the growth of *S. phylicifolia* is strongly constrained by heavy repeated browsing. The timing of browsing could be important, as leaf-stripping in summer and browsing of shoots and twigs in winter apparently have different effects on plant growth and chemistry. In contrast to winter browsing, which may release apical dominance, ripping of leaves during the growing season directly affects the photosynthetic capacity of the plant.

The flowering data for the 2 years of observation suggest that reindeer browsing may reduce the reproductive output of willow. A similar reduction in flower numbers of browsed plants in the year preceding this study was reported by Pajunen (2001). In our experiment, rejuvenated bushes browsed by reindeer hardly flowered, while rejuvenated bushes protected from reindeer flowered as much or even more than old protected bushes. Peinetti, Menezes & Coughenour (2001) found similar results on elk browsing on *S. monticola*, and Maschinski (2001) and Brookshire *et al*. (2002) found that the combined effects of wild ungulates and livestock totally prevented *Salix arizonica*, *Salix boothii* and *Salix geyeriana* from flowering. The latter also observed a threshold height of 70 cm, below which willows did not flower. Old bushes seemed to be less affected, probably because they have been less intensively browsed for a longer time and hence their stored energy reserves are greater. It is still doubtful whether decreased reproductive output affects the persistence of willow. den Herder & Niemelä (2003) showed that immigrant *S. phylicifolia* seeds germinate even under heavy reindeer browsing pressure. It is possible that willow establishment is microsite limited, i.e. trampling, drought, poor nutrient availability and a dense layer of scrubs and dwarf scrubs may significantly limit seedling establishment.

### THE RESPONSE OF ASSOCIATED INSECT HERBIVORES

There is growing interest in how browsers might affect abundances of other herbivores feeding on the same target plant, but there are few studies presenting data from well-replicated experiments. The outcome from this experiment was surprisingly clear: browsing by reindeer had consistent negative effects on the densities of galling and leaf-feeding insects. This is surprising because most studies on comparable systems suggest that browsing has a positive effect on insect densities (Danell & Huss-Danell 1985; Roininen, Price & Bryant 1997). Olofsson & Strengbom (2000) showed more galling insects on reindeer-browsed *S. lanata*, even though browsing reduced the shoot length. However, in their study browsed plants contained higher nitrogen as an effect of reindeer urine and faeces. We cannot explain why browsing reduced insect abundance in our study, but we suspect that a severe loss of plant foliage

and vigour, coupled with changes in foliage chemistry, are involved (P. Hallgren & R. Julkunen-Tiitto, unpublished data). We suggest that under extreme summer browsing, levels of photosynthesis might be so much reduced that nitrogen uptake or its transportation to the leaves is hindered, in contrast to situations in more productive habitats (Peinetti, Menezes & Coughenour 2001). Our results are in line with those of Bailey & Whitham (2003), who found that elk browsing reduced average leaf area in aspen and thereby reduced sawfly gall abundance, such that 90% of the galls were found on unbrowsed aspen ramets.

The herbivory index (Fig. 5) suggests that there were no differences in the preference of *Gonioctena* beetles to browsed or rejuvenated willows. Contrary to our results, previous studies showed a preference of herbivorous insects for browsed trees (Danell & Huss-Danell 1985; Roininen, Price & Bryant 1997). This also contrasts with the results of Ikonen (2002), who found that four leaf beetle species preferred leaves of young *S. phylicifolia* plants, despite higher contents of defensive secondary compounds. Such positive effects are mostly attributed to increased leaf size, leaf nitrogen, shoot length and overall plant vigour (Danell & Huss-Danell 1985; Price 1991; Price, Craig & Roininen 1995; Roininen, Price & Bryant 1997; Ikonen 2002).

### IMPLICATIONS FOR REINDEER GRAZING MANAGEMENT

If reindeer management allows high densities of reindeer, this may lead to a reduction of summer forage in unproductive nutrient-poor habitats. Our data show that growth, number of new shoots and reproduction of willows are severely limited by heavy reindeer browsing. With 2–3 reindeer km$^{-2}$, our study area was more heavily browsed than other areas belonging to the neighbouring reindeer herders' co-operative, where the average stocking rate was maintained at *c*. 1·6 reindeer km$^{-2}$. Intense grazing and browsing may lead to changes in vegetation patterns (Leader-Williams, Smith & Rothery 1987; Oksanen, Moen & Helle 1995; Suominen & Olofsson 2000; Augustine & McNaughton 2004) and, in the worst case, a loss of productivity of the most preferred food plants. Preferred food plants may eventually become replaced by less preferred food plants (e.g. ericoids) and may become less abundant. It seems unlikely that heavy grazing can actually increase plant community productivity by turning a low productive tundra heath into more productive tundra dominated by graminoids, as observed, for example, by Olofsson *et al*. (2001). Instead, heavy browsing would probably lead to a transition from relatively productive willow–scrub to a low productive tundra heath dominated by *Betula nana* and ericaceous scrub. Manseau, Huot & Crête (1996) observed similar negative effects on plant community productivity when caribou browsing led to a persistent decrease in the carrying capacity of their summer range. One year later, heavily browsed *Betula glandulosa* stands within the same summer range did not show signs of vigorous and rapid recovery after release from heavy caribou browsing (Crête & Doucet 1998). In their regional survey, Kumpula, Colpaert & Nieminen (1999) found that our study site belongs to the area with the lowest summer food resources per hectare and per reindeer in Lapland. The amount of summer pasture available per reindeer, as well as the quantity and quality of food, are known to affect the growth, condition, autumn weights and productivity of caribou and reindeer (Huot 1989; Crête & Huot 1993). The effects of heavy summer browsing may also have cascade effects on other members of the food web. For instance, reindeer browsing may reduce the food resources of willow grouse (Pajunen 2001). To optimize reindeer husbandry in a sustainable way, the growth responses of their food plants need to be understood. This is particularly important under the extremely harsh and unfavourable climatic conditions that prevail in northernmost Fennoscandia. We therefore suggest that, in these low productivity tundra habitats where graminoids are not abundant and where willow is an important summer food resource, the number of reindeer should be maintained at low levels in order to allow the long-term persistence of willow.

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