Effects of reindeer on the re-establishment of *Betula pubescens* subsp. *czerepanovii* and *Salix phylicifolia* in a subarctic meadow

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Abstract: The effect of reindeer browsing on the regeneration of *Betula pubescens* subsp. *czerepanovii* and *Salix phylicifolia* was studied in a subarctic meadow in Finnish Lapland. The aim of the study was to see whether tree recovery from seeds is possible under heavy reindeer-browsing pressure. After removal of the ground and field layer vegetation in 1986, two exclosures were established so that the effect of reindeer on the secondary succession, starting from seeds, could be studied. The size and the number of *B. pubescens* and *S. phylicifolia* were recorded in 1994, 1996, 1997 and 1999. Reindeer significantly reduced the height and the number of saplings (plants > 10 cm high) of *B. pubescens* and *S. phylicifolia* but the number of seedlings (plants < 10 cm high) did not differ between browsed and unbrowsed plots. Furthermore the height-class distribution of saplings was different inside the exlosures compared to control areas. Over time browsed plots continued to have high densities of small saplings while in protected plots an increasing number of larger saplings appeared. In our study site, regeneration from seeds seemed possible although the height of *B. pubescens* and *S. phylicifolia* was limited by reindeer.

Key words: browsing, height-class distribution, plant growth, seedling establishment, succession.

Rangifer, 23 (1): 3-12

Introduction

Reindeer husbandry has often been cited as one of the major biotic factors affecting the natural vegetation in Finnish Lapland (Ahti, 1961; Hämet-Ahti, 1963; Helle, 1966; Kallio *et al.*, 1969; Oksanen, 1978; Oksanen *et al.*, 1995). Especially the depletion of the lichen carpet due to high grazing pressure has received a lot of scientific attention (Helle & Aspi, 1983; Väre *et al.*, 1995, 1996; Kumpula *et al.*, 1997). Nowadays reindeer *Rangifer tarandus* (L.) densities are kept at an artificially high level since supplementary winter-feeding started in the early 1970s. Not only grazing on lichens or browsing of woody species may change the development of the vegetation. Trampling also may cause a severe reduction of the lichen carpet (Helle & Aspi, 1983; Väre *et al.*, 1996; Cooper & Wookey, 2001) or may inhibit the establishment and growth of shrubs and trees (Väre *et al.*, 1996). Leaves of shrubs and deciduous trees, mainly birch *Betula* spp. and willows *Salix* spp., are important summer forage for reindeer (Haukioja & Heino, 1974; Tenow, 1996). In heavily grazed areas, reindeer and caribou can suppress the abundance and productivity of shrubs, dwarf shrubs, tall herbs and ericoids while graminoids and bryophytes might increase due to grazing (Manseau *et al.*, 1996; Crête & Doucet, 1998; Olofsson *et al.*, 2001). Furthermore, from previous studies reindeer browsing has been known to be a significant factor in reducing the height growth of deciduous trees (Lehtonen & Heikkinen, 1995; Oksanen *et al.*, 1995). By feeding on them, reindeer may prevent the recruitment of deciduous trees into the overstorey. Moreover, grazing by reindeer is a significant factor in slowing down, or in some areas even preventing, the renewal of mountain birch *Betula pubescens* subsp. *czerepanovii* (Orlova) Hämet-Ahti after defoliation *e.g.* by the larvae of the autumn moth *Epirrita autumnata* (Bkh.) (Kallio, 1975; Lehtonen & Heikkinen, 1995; Oksanen *et al.*, 1995; Helle *et al.*, 1998). In 1964-65 in Utsjoki, *E. autumnata* defoliated 1350 km^2 of the forests (Kallio & Lehtonen, 1973; Lehtonen & Yli-Rekola, 1979). The recovery of the damaged trees and the reforestation of the defoliated mountain birch forests can take place by the germination of seedlings from seeds and the resprouting of buds on the damaged stumps (Lehtonen & Heikkinen, 1995). The resprouting of dormant basal buds in damaged trees is not so greatly affected by reindeer grazing. Results from previous studies indicate that tree recovery from seeds is in theory possible in the damaged birch forests almost everywhere in the mountain birch forest zone (Lehtonen & Heikkinen, 1995). However, the establishment of new seedlings from seeds may be prevented by reindeer browsing, leaving the recovery of *Betula pubescens* subsp. *czerepanovii* (hereafter called *B. pubescens*) mostly to resprouting of dormant basal buds on damaged stems.

Leaves of deciduous trees (*e.g.* birch *Betula* spp. and arctic willows *Salix* spp.) are important summer food for reindeer and caribou (Kelsall, 1968 and references therein; Haukioja & Heino, 1974; Tenow, 1996). Hare *Lepus timidus* (L.) feeds on the shoots and twigs in winter (Tahvanainen *et al.*, 1991 and references therein). Compared to other plants in arctic and subarctic environments, *Betula* spp. and *Salix* spp. are relatively fast growing. Moreover, browsing by mammals, equivalent to pruning by humans, may cause a growth reaction in willows, resulting in longer and normally fewer, more vigorous shoots (Bryant *et al.*, 1991). The fast growth of willows and ability to overcompensate (Bryant *et al.*, 1991), are likely to be important factors in the resilience mechanism of *Salix* spp. after reindeer browsing. However, the effect of reindeer browsing on *Salix* spp. has been little studied. This makes it interesting to compare the re-establishment of *Salix phylicifolia* (L.), the most common willow species in our meadow, and *Betula pubescens*.

The aim of this study was to analyse the effect of reindeer browsing on the height growth of *B. pubescens* and *S. phylicifolia*. In particular, this study aims to investigate the effect of reindeer on the regeneration of *B. pubescens* and *S. phylicifolia* and the abundance of seedlings originating from seeds.

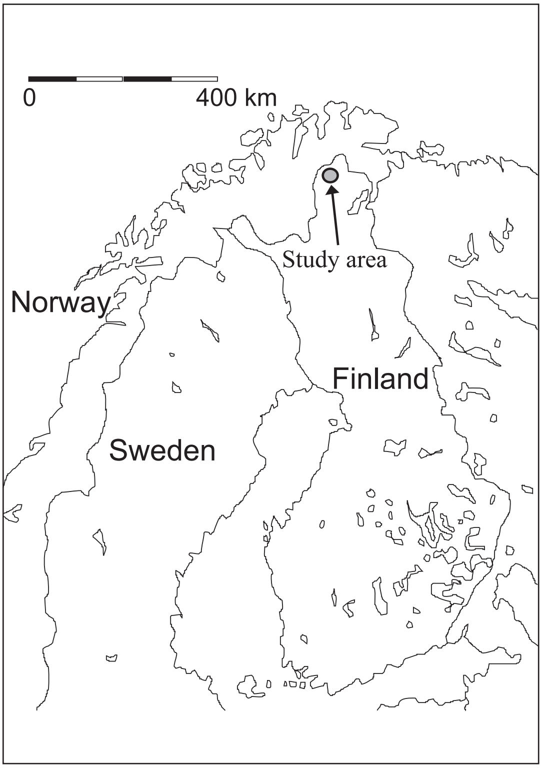


Fig. 1. The study area in northernmost Lapland.

Material and methods

Study site

The study area was situated in the Kevo Nature Reserve in the community of Utsjoki in the northwest part of Inari Lapland, northernmost Finland (Fig. 1). The area belongs to Fell Lapland, characterised by large subalpine mountain birch forest and gently sloping low fells. It lies in the subarctic zone north of the northern limit of the continuous pine forest (Kallio *et al.*, 1969), or in the orohemiarctic zone according to Ahti *et al.* (1968). The forest belongs to the continental subzone of the subalpine mountain birch forest zone (Hämet-Ahti, 1963).

The Kevo Nature Reserve was subjected to relatively intense grazing over the past few decades. Two cooperatives of reindeer owners (Paistunturi and Kaldoaivi) have their grazing pastures in the community of Utsjoki. Between 1994 and 1998 the number of reindeer owned by these two cooperatives together remained more or less stable, about 14 000 (Kumpula *et al.*, 1997; 1999). Even in protected areas like the Kevo Nature Reserve overgrazed areas can be found (Heikkinen & Kalliola, 1989).

Our experimental site was situated in an abandoned meadow on the west-bank of the river Kevojoki close to the Kevo Subarctic Research Station (69°45'N, 27°01'E). The experimentally manipulated area is part of an old semi-natural mesic grassland, inhabiting, according to Hinneri's (1975) classification, an eutrophic riverbank. The grassland has been farmed more or less continuously since the mid-19th century (Hustich, 1942). Birch and Scots pine (*Pinus sylvestris*) forest surrounds the grassland.

The climate is quite severe, and the duration of the growing season is only 110-120 days. The snow depth varies between 40 and 70 cm (Ohlson, 1981).

Site preparation

The study site was treated with herbicide (Roundup) in the autumn of two successive years before sod cutting (1986, 1987) to destroy perennial vegetation. This was done in order to create uniform initial conditions. The extensive moss layer was removed carefully in 1988 to facilitate recruitment from the soil seed bank. Thus, secondary succession began on bare ground in 1988 and re-colonisation of *Betula pubescens* and *Salix* spp. started from the local soil seed bank and immigrant propagules (Zobel *et al.*, 1997). Fences were established in the summer of 1989 so that the effect of reindeer and hare feeding on the secondary succession could be studied from the seed bank. Reindeer frequently visited our site since the establishment of the exclosure.

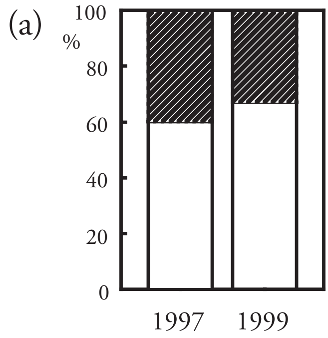
Experimental design

The experimental site of 405 m^2 was divided into 45 3 m × 3 m plots. These were divided into 4 blocks (2 × 2). Two blocks (diagonally opposite), measuring 7.5 m × 13.5 m were fenced so that in total an area of 202.5 m^2 was excluded to prevent herbivory of large and medium-sized mammals (reindeer, mountain hare) (Zobel *et al.*, 1997). Moose (*Alces alces*), the other major herbivore, is rare in the study area but can occasionally be observed. Both *Betula* spp. and *Salix* spp. rank high on the moose's winter-diet list. However, the plants in our experimental site were still quite small and probably not available to the moose because of a thick layer of snow. Furthermore, no moose droppings were observed in the experimental site neither were there signs of moose browsing on the plants. Next to the fenced blocks were control areas of the same dimensions where reindeer and hare were able to move freely. As the 45 plots were divided into 4 blocks, a certain degree of pseudoreplication was inevitable. True replication of the experiment would have been too costly and laborious and is at this stage impossible. However, since measurements were carried out in four different years, we do have replication in time. The number and height of *Betula pubescens* and *Salix phylicifolia* was recorded during the summers of 1994, 1996, 1997 and 1999. Hereafter, plants smaller than 10 cm will be referred to as seedling, plants larger than 10 cm will be referred to as sapling. In all four years, only the height was recorded for saplings taller than 10 cm, because of the large number of plants. Furthermore, in 1997 and 1999 the cause of damage was identified (hare or reindeer) if a plant was browsed. Only plants with clear signs of browsing were recorded as browsed plants. Reindeer rips off the leaves while hare makes a sharp and angled cut. The feeding preference of reindeer and hare was calculated as the proportion of browsed plants of the total number of *Salix phylicifolia* or *Betula pubescens*. Seedlings of *B. pubescens* and *S. phylicifolia* smaller than 10 cm were counted in 1997 and 1999. Due to very high seedling numbers a grid (0.5 m × 0.5 m) was used. In 1997 the coverage of graminoids and bryophytes was estimated visually.

The data were analysed with SPSS (version 10.0) statistical software. The number of *B. pubescens* and *S. phylicifolia* saplings browsed by either reindeer or hare was analysed by χ^2 -test. Differences in height-class distribution of *B. pubescens* and *S. phylicifolia* between the two browsing treatments and the four sampling years were also tested using a χ^2 -test. The difference in density of seedlings and saplings between browsing treatment were tested with a repeated-measure ANOVA where the browsing treatment was used as a between-subject factor and sampling year as a within subject factor. The number of saplings of *Salix phylicifolia* in 1996 was excluded from the analysis since for this species only a small number of plots were measured during this year. For *Betula pubescens* the data for all four years were analysed. Differences in sapling height were tested with ANOVA, with browsing treatment as a fixed factor, year as a repeated fixed factor and plot as a random factor. To improve the homogeneity of variance, height data were transformed by a natural logarithm.

Results

In our study site reindeer had a marked effect on the vegetation. *B. pubescens* was in both browsing treatment the dominant plant and had thus the highest availability to reindeer and hare (60.2% of the total number of saplings > 10 cm in 1997 and 67.1% in 1999) (Fig. 2a). However, reindeer browsed *S. phylicifolia* more frequently compared to *B. pubescens*



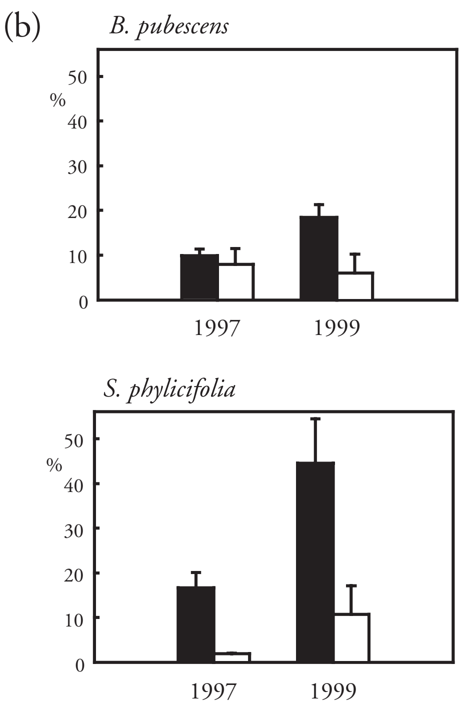


Fig. 2. (a) Proportion of *Betula pubescens* subsp. *czerepanovii* □ and *Salix phylicifolia* ▨ (% of the number of plants > 10 cm high) available to the herbivores and (b) proportions of *B. pubescens* and *S. phylicifolia* saplings browsed by reindeer ■ or hare □ .

(Fig. 2b). In 1997, reindeer browsed 9.7% of the number of *B. pubescens* and 16.7% of *S. phylicifolia* (χ^2 = 30.2, *df.* = 1, P < 0.001). In 1999, reindeer browsed 18.4% of *B. pubescens* and 44.5% of *S. phylicifolia* (χ^2 = 207.1, *df.* = 1, P < 0.001). Hare, the other browser, affected a smaller number of plants and had no clear preference for *B. pubescens* or *S. phylicifolia*. In 1997, hare browsed 7.9% of *B. pubescens* and 1.9% of *S. phylicifolia* (χ^2 = 51.2, *df.* = 1, P < 0.001). In 1999 the proportion of browsed *B. pubescens* and *S. phylicifolia* was 6.1 and 10.9%, respectively (χ^2 = 21.4, *df.* = 1, P < 0.001).

Browsing reduced the density (number of saplings per m^2) of *B. pubescens* and *S. phylicifolia* (Fig. 3, Table 1). During 1994-1999 the number of *B. pubescens* saplings (plants > 10 cm high) increased while the number of *S. phylicifolia* saplings decreased. The same trend was observed in both browsing treatments. The number of seedlings (plants < 10 cm high) was not affected by browsing (Fig. 4, Table 2). In 1997 high densities of *B. pubescens* seedlings were found which decreased remarkably during the period 1997-1999. Seedlings of *S. phylicifolia* occurred at much lower densities and their numbers stayed more or less stable throughout the study period. Reindeer grazing did not affect the grass/moss ground-cover ratio and there were no signs of exposed soil.

Reindeer browsing affected the height-class distribution of both *B. pubescens* (χ^2 = 714.2, *df.* = 18, P < 0.001) and *S. phylicifolia* (χ^2 = 402.8, *df.* = 14, P < 0.001) (Fig. 5). Furthermore, the height-class distribution of both *B. pubescens* (χ^2 = 1600.5, *df.* = 54, P < 0.001) and *S. phylicifolia* (χ^2 = 1269.6, *df.* = 42, P < 0.001) changed during vegetation succession over the period 1994-1999. Browsed plots continued to have great numbers of small saplings while in protected plots more and more larger plants appeared. Therefore, the mean height of *B. pubescens* and *S. phylicifolia* was lower in browsed plots (Fig. 6, Table 3). However, during the period 1994-1999 an increase in height was observed in both browsing treatments.

Discussion

Results from previous studies on the ripening and germination rate of *B. pubescens* subsp. *czerepanovii* seeds are contradictory. Mikola (1942) refers to studies suggesting that seedling formation has no role in the birch forest zone. On the other hand, Kalliola (1941) reported large numbers of seedlings in birch forests, especially in those damaged by *E. autumnata*. Heikkinen & Kalliola (1989) observed abundant seedling stands at a few sites (*e.g.* riversides, mesic forests), but the plants were usually many years old. This is indicated by their thick, bent structure, which is probably caused by mammalian herbivores. In areas with stronger abiotic stress, *e.g.* in the upper fell areas and xeric forests, seedlings are rare (Kallio *et al.*, 1983).

Kullman (1981, 1993) found that birch seeds are effectively spread in the Swedish part of the Scandes, even in high elevation habitats where tree line trees are unable to produce viable seeds. So, in principle, even in mountain birch forests damaged by *E. autumnata* seeds could disperse from the surrounding undamaged areas. This leads to a great surplus of seeds and creates an effective potential seed bank in most areas within the birch forest. Kullman (1993) found that the mortality of seedlings was relatively high in different birch forest habitats, even far below the tree line. In most cases, the reasons for the die-

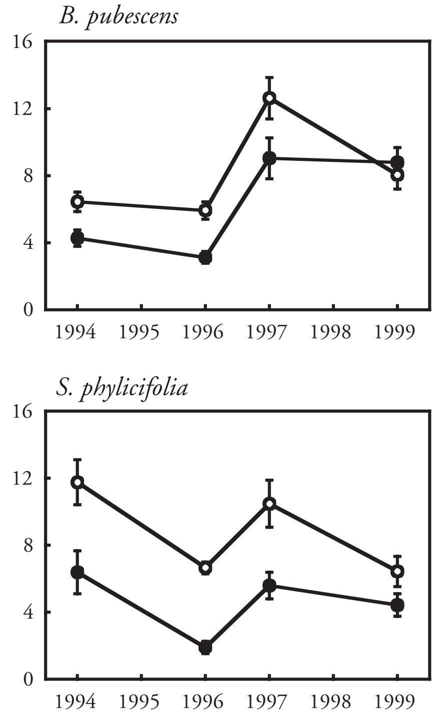


Fig. 3. Sapling densities (plants > 10 cm high) (mean number per m^2 ± SE) in browsed ● and unbrowsed ○ plots.

Table 1. Analysis of variance with repeated measures for differences in sapling (plants > 10 cm high) densities between browsing treatments and sampling years. Bold *F* and *P*-values indicate a significant difference between browsing treatments.

		df.	*F*	*P*
B. pubescens	treatment	1	**4.31**	**0.048**
	year	3	52.47	<0.001
	year × treatment	3	5.60	0.006
S. phylicifolia	treatment	1	**11.18**	**0.003**
	year	2	24.72	<0.001
	year × treatment	2	5.80	0.005

back or lack of seedlings seems to be either the occurrence of dry periods or a too dense ground-layer vegetation during the first growing season of the seedlings (Kallio & Lehtonen, 1973; Kullman, 1981). Holm (1993) states that patches of disturbed ground are necessary for successful seedling establishment of both *Betula pendula* and *B. pubescens* apart from a high amount of viable seeds.

Kallio & Lehtonen (1973) found that seedlings in *E. autumnata* deforested areas were often severely damaged by reindeer or voles. Moreover, Lehtonen & Heikkinen (1995) found that reindeer grazing led to statistically significant differences in the number of seedlings and they considered reindeer grazing in Finnish Lapland as an important factor limiting the regeneration of mountain birch. This is only partly supported by our data. We demonstrated that excluding reindeer had no effect on the number of seedlings smaller than 10 cm (Fig. 4). Neither was an effect found on the number of seedlings of *S. phylicifolia*. The larger saplings (plants > 10 cm high), on the contrary, were affected by reindeer browsing and both *B. pubescens* and *S. phylicifolia* occurred in lower densities in browsed plots. More specifically, reindeer feeding altered their height-class distribution (Fig. 5). As time progressed browsed plots continued to have high densities of small saplings while an increasing number of larger saplings appeared in protected plots.

The contribution of plant nutrients from faeces and urine of large herbivores may be trivial in preferred foraging areas (Persson *et al.*, 2000). Faeces and urine offer easily available plant nutrients and may enhance plant growth. Increased nutrient levels in the browsed plots might have contributed to a more vigorous growth and more seedlings and saplings, which is the opposite effect of browsing. There is however a feedback: Higher nutrient levels followed by increased and more vigorous growth also leads to more feeding (Ball *et al.*, 2000) which in turn will decrease plant densities.

Our results showed a lower average height of both *B. pubescens* and *S. phylicifolia* due to reindeer browsing. However, growth was observed even in plots subjected to browsing. The regeneration of *B. pubescens* from seeds was limited only to a minor extent by reindeer. So reindeer browsing is indeed a factor limiting the regeneration of *B. pubescens*, but the extent of the effect of reindeer may be dependent on other biotic and abiotic factors such as elevation, climatic conditions, vegetation type and ground layer vegetation. Our results demonstrate, however, that regeneration of *B. pubescens* from seeds is possible even under relatively heavy reindeer browsing pressure in our relatively fertile study site in the river valley. As reviewed by Persson *et al.* (2000), also trampling can have substantial effects on the ground vegetation and might affect the growth and regeneration of woody plants. In our study it is hard to estimate the effect of trampling since only plants with clear signs of browsing were recorded as browsed plants. Other characteristics which might be caused by trampling,

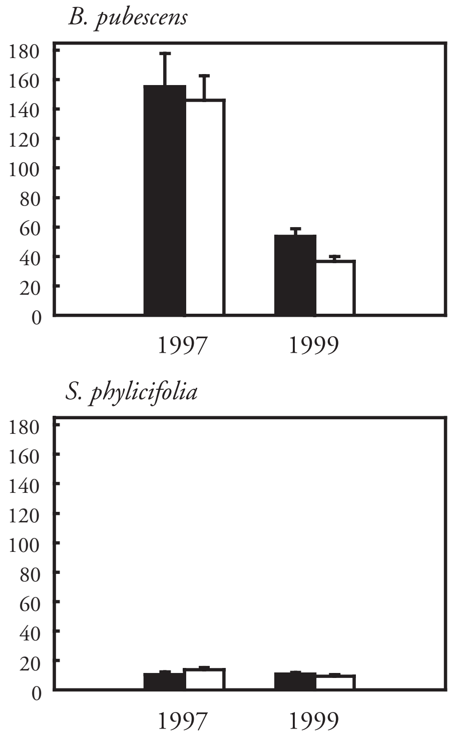


Fig. 4. Seedlings densities (plants < 10 cm high) (mean number per m^2 + SE) in browsed ■ and unbrowsed □ plots.

Table 2. Analysis of variance with repeated measures for differences in seedling (plants < 10 cm high) densities between browsing treatments and sampling years.

		df.	*F*	*P*
B. pubescens	treatment	1	0.15	0.699
	year	1	43.68	<0.001
	year × treatment	1	2.31	0.135
S. phylicifolia	treatment	1	0.34	0.564
	year	1	2.88	0.096
	year × treatment	1	3.97	0.051

Table 3. Analysis of variance for differences in sapling height between browsing treatments and sampling years. Bold *F* and *P*-values indicate a significant difference between browsing treatments.

		df.	*F*	*P*
B. pubescens	treatment	1	**80.45**	**<0.001**
	year	3	193.39	<0.001
	year × treatment	2	1.98	0.169
S. phylicifolia	treatment	1	**74.45**	**<0.001**
	year	3	74.71	<0.001
	year × treatment	2	6.83	0.007

e.g. broken plants or plants with a bent structure, were not recorded.

It must be noted that fencing only excluded reindeer and hares, not voles or lemmings, which use small seedlings and dwarf shrubs as winter food (Kalela, 1957; Oksanen & Oksanen, 1981). On islands where predation pressure is low, these small mammals can cause up to 100% shoot mortality on all woody plants (Oksanen & Oksanen, 1981). It can be speculated that reindeer and hare feeding indeed has an effect on seedling density, but that this effect is not observed due to other external factors. These factors can be biotic *e.g.* voles (Kalela, 1957; Oksanen & Oksanen, 1981; Oksanen *et al.*, 1987) or climatic (Kulmann, 1993). These factors are not affected by fencing and may equally reduce the seedling establishment on both sides of the fence. Predation on the seeds of *B. pubescens* and *S. phylicifolia* by small mammals might have a very small ecological effect. The small seeds are largely protected from predation because of their size (Crawley, 1997).

Competition with other plants may also cause a set back in seedling survival on both sides of the fence. Before the establishment of the exclosure in 1988 the moss and the herb layer was removed. This resembles a natural disturbance, which greatly enhances the establishment of seedlings (Holm, 1993). The high number of seedlings observed in 1997 supports this. In 1999 a four-fold decrease on both sides of the fence in the number of seedlings was observed compared to 1997. This may be due to the shading effect of the larger *B. pubescens* and *S. phylicifolia*. Furthermore, the development of a more dense and continuous herb and moss layer might lower the germination and survival of seedlings (Brown & Mikola, 1974). There are reports that the herb (especially graminoids) and moss layer are affected by reindeer grazing (Leader-Williams *et al.*, 1987; Broll, 2000; Virtanen, 2000; Olofsson *et al.*, 2001). However, grazing did not affect the coverage of graminoids and bryophytes in our site.

Reindeer clearly seemed to prefer *S. phylicifolia* over *B. pubescens*. Compared to *B. pubescens*, *S. phylicifolia* was less abundant at the end of the study period (Fig. 2a, 3) and still this plant was more frequently browsed (Fig. 2b). Several studies support the hypothesis that for large ungulates the amount of available plant biomass for browsing rather than

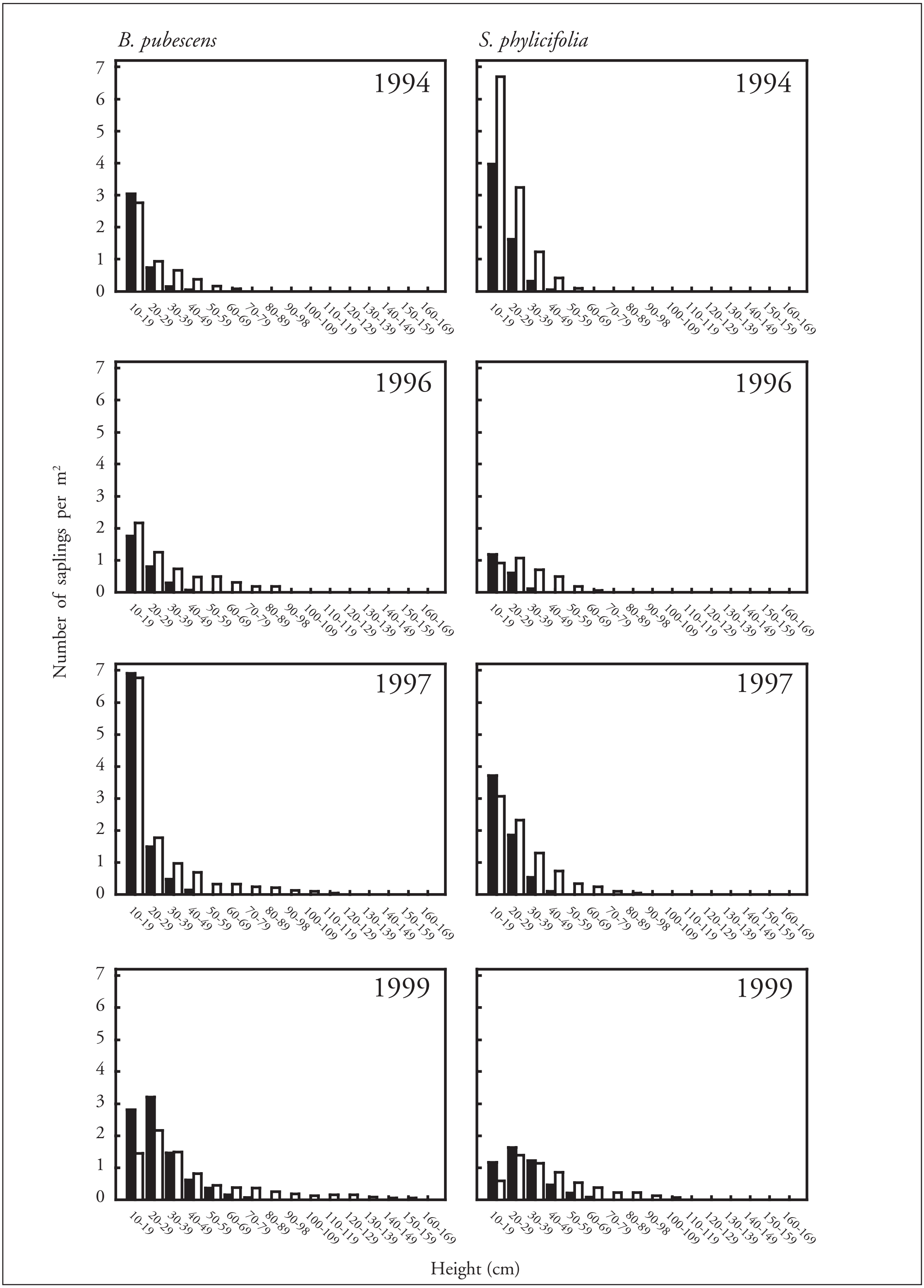


Fig. 5. Height distribution of *Betula pubescens* subsp. *czerepanovii* and *Salix phylicifolia* in the period 1994-1999 in browsed ■ and unbrowsed ☐ plots.

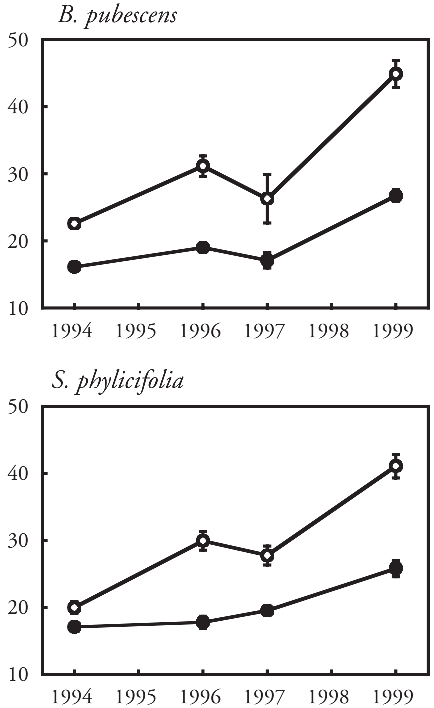


Fig. 6. Height in cm (mean + SE) of *Betula pubescens* subsp. *czerepanovii* and *Salix phylicifolia* in browsed ● and unbrowsed ○ plots.

secondary chemicals seems to be the key factor in selecting their food plants (Tahvanainen *et al.*, 1991). Belovsky (1981) found that moose feeding was predicted by the nutrient contents of plants, the size of the food items and their relative abundance. Mårell *et al.* (2002) found that reindeer selected sites with higher green biomass of *Betula* spp. and *Salix* spp. In our study reindeer browsed more frequently on the less abundant *S. phylicifolia*. This indicates that reindeer did not choose its food on basis of the highest abundance but rather selected food of a higher palatability. Only small amounts of phenolic glycosides, the major components in herbivore resistance of willows, have been found in the leaves of *S. phylicifolia* (Julkunen-Tiitto, 1989). However, the leaves contain considerable amounts of some other phenolics, including a flavonoid and condensed tannins (Julkunen-Tiitto, 1989). In general it can be said that the leaves of this mild tasting willow are palatable food for a variety of generalist herbivores and in some places *S. phylicifolia* suffers from heavy defoliation (Sipura, 1999; 2000). The leaves of *B. pubescens* contain relatively high levels of phenols compared to *S. phylicifolia* (Tuomi *et al.*, 1984). However, the levels of secondary compounds in both *S. phylicifolia* and *B.* pendula are subjected to large spatial and temporal variation and are dependent on the browsing intensity and the type of herbivore (insects or mammals) (Bryant *et al.*, 1991; Danell & Bergström, 2002). Even browsing on different parts of the plants (leaves, twigs, shoots or flowers) may cause a different chemical reaction (Bryant *et al.*, 1991). Insect defoliation of *B. pubescens* is followed in the subsequent growing season by increased levels of foliage phenols and reduced nitrogen contents (Tuomi *et al.*, 1984). These wound-induced changes in the foliage of *B. pubescens* can influence the food preference of at least some birch feeding insects (Neuvonen & Haukioja, 1991) and possibly also reindeer. However, such effects are far from universal and some insects might actually perform better on damaged leaves (Haukioja & Niemelä, 1979). Browsing by mammals can also affect the food value of woody plants. The palatability and/or nutritional value may decrease or increase in response to browsing (Danell *et al.*, 1985; Danell & Huss-Danell, 1985; Bryant *et al.*, 1991). However, in our study no chemical analysis has been carried out so the mechanism behind the preference of *S. phylicifolia* over *B. pubescens* (less secondary metabolites, higher nutritional value) remains speculative. It must be noted that higher preference for *S. phylicifolia* in our study is based on feeding frequency. In terms of absolute biomass, the preference is not necessarily the same. Reindeer can adjust their bite size and may feed on different parts of the plant. However, with our experimental design the amount of biomass removed would be impossible to measure.

There were surprisingly few plants that were browsed by both reindeer and hare. The feeding behaviour of hares and reindeer is different. Hares browse the twigs in winter, while reindeer feed on the fresh leaves in spring and summer. The plants in our study area were all quite small and a deep snow cover in winter covered most of them. So only the tallest plants were available to hares. If the experiment would have continued, hare browsing might have become more important with increasing seedling height during succession.

Acknowledgements

We are grateful to the staff of the Kevo Subarctic Research Station for providing excellent facilities. We thank Jari Pohtila for collecting the data in 1997 and Michael Theijsmeijer for his invaluable help during the fieldwork in 1999. The Centre of International Mobility (CIMO), the Ministry of Agriculture and Forestry of Finland and the Maj and Tor Nessling Foundation financed the study.

We thank Seppo Neuvonen, Jorma Tahvanainen and Olli-Pekka Tikkanen for their valuable comments on the manuscript.

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Manuscript received 5 March, 2002
accepted 12 December, 2002