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Does Slow Tree Growth Reduce Browsing Risk by Moose?

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Abstract

Genotypic or phenotypic factors affect the growth of trees which can change the palatability of plants to herbivores. In a self-regenerating clear-cut forest stand in eastern Finland, we compared the growth of four boreal deciduous tree species that were browsed by moose with those which had been left unbrowsed. Diameter growth of young sapling trees of *Betula pendula*, *Populus tremula*, *Salix caprea* and *Sorbus aucuparia* was studied based on the width of the annual growth rings. Moderately browsed *B. pendula* showed higher radial growth than unbrowsed trees. Heavily browsed *S. aucuparia* and *S. caprea* initially had higher radial growth than unbrowsed trees although the radial growth increment decreased after consecutive years of repeated browsing. Moose browsing resulted in reduced height and stunted growth of the studied tree species. The results suggest that moose selects fast growing individuals and trees characterised by slow growth may have a higher probability of remaining unbrowsed.

Keywords: *Alces alces*, annual increment, boreal forest, deciduous trees, selective feeding

Introduction

Growth rates of boreal deciduous trees can be highly variable and these differences can be genotypic or phenotypic (Stern 1979, Crawley 1986). It is well known that microclimatic factors such as hydrology, soil conditions, light and nutrient availability greatly affect the growth of trees (Crawley 1986). By altering the carbon/nutrient balance, slow growth of trees may result in higher concentrations of secondary metabolites, lignin, lower water content and a thick cuticle, which, in turn makes plants less attractive to herbivores (Bryant *et al.* 1983 and references therein). Previous studies have provided evidence that growth rate sometimes correlates with the palatability of plants to a variety of herbivores such as insects (Prittinen *et al.* 2003), voles (Pusenius *et al.* 2002) and hares (Tahvanainen *et al.* 1985) although there are no indications for a clear trade-off between seedling defence and growth (Rousi *et al.* 1991, 1993, 1996, 1997).

In young boreal forest stands, deciduous trees face a high risk of being browsed by moose (Puttock *et al.* 1996, Ericsson *et al.* 2001) and these browsed trees often have a high probability of being rebrowsed in subsequent years (Bergqvist *et al.* 2003). It is remarkable that in a stand some saplings can remain unbrowsed for many years, even under relatively high browsing pressure. If these unbrowsed plants were equally as desirable as browsed plants, there is no logical reason why they would not get some browsing. We suspect that these unbrowsed plants have been growing in unfavourable conditions or they have an inherent slow growth rate and are therefore less attractive to moose. In this paper we will try to find evidence if the reason why some plants remain unbrowsed can be explained by a slow growth rate. Our hypothesis is that deciduous trees which remained unbrowsed should have a lower growth rate than browsed trees.

Dendrochronological analysis yields relatively easily obtainable data on long-term tree growth. We sampled trees of four different deciduous species, silver birch *Betula pendula* Roth., European aspen *Populus tremula* L., great sallow *Salix caprea* L. and rowan *Sorbus aucuparia* L., in a clear-cut forest area in eastern Finland. All four species rank high on the moose's diet list (Cederlund *et al.* 1980, Hörnberg 2001). For each tree species, we sampled browsed trees and trees with no signs of browsing so that the annual radial growth of browsed and unbrowsed trees could be compared.

Material and methods

Study area

Our study was carried out in eastern Finland (62°36′ N, 30°01′ E), 20 km's east of the city of Joensuu, in a young sapling stand established on a naturally-regenerating clear-cut which had been harvested 11 years before the start of our investigation. The area lies in the northernmost range of the southern boreal vegetation zone (Ahti *et al.* 1968). The size of our study site was about 8 ha. After clear-cutting in 1988, large numbers of seedlings appeared and in 1999 saplings of Scots pine *Pinus sylvestris* L., *B. pendula*, *S. caprea*, *S. aucuparia* and *P. tremula* dominated the stand. Dwarf shrubs, mainly heather *Calluna vulgaris* (L.) Hull, bilberry *Vaccinium myrtillus* L. and cowberry *Vaccinium vitis-idaea* L., dominated the field layer. The study site was surrounded by mature *Myrtillus*-type pine forest mixed with birch and was commercially managed. In the county of North Karelia, to which our study area belongs, the density of the moose population varied during 1980-1998 between 0.2 and 0.4 moose

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per km^2 (Vesa Ruusila, personal communication).

Experimental design

In spring 1999, at our study site, we randomly selected young sapling trees of four species: *B. pendula*, *P. tremula*, *S. caprea* and *S. aucuparia*. For each tree species, we selected browsed trees and trees that had no signs of browsing. For each tree, we recorded the diameter at the base, the height and the level of moose damage by estimating the proportion of browsed annual shoots of the total number of annual shoots. Estimation of the level of browsing damage by moose was only made for the winter season (1998/1999) preceding our assessment. However, most trees, which were damaged during the previous winter, also had signs of heavy moose browsing during previous years. The trees, which were not damaged during the winter of 1998/1999, did not show signs of previous damages either. After the field measurements, the trees were cut at ground level and transported to the laboratory for further analysis of the annual radial growth.

Measurements of the ring-width

For each sample tree, we took a horizontal disk by crosscutting the stem at about 10 cm above ground level. In each disk we measured the annual growth rings in three lines in a 120° angle of each other. Widths of the annual rings were measured to the nearest 0.01 mm using a Kutschenreiter Type I digital positiometer connected to a stereomicroscope and a desktop computer that registered the measurements. The advantage of analysing disks instead of increment cores is that missing rings can be easily detected by inspecting the whole disk under the microscope. In our samples, we were able to trace all annual rings. We calculated the trees' mean annual increment using the means of the three measured increment lines of each disk.

Statistical analysis

Only sample trees between 6 and 10 years old were included in the statistical analysis. Thus, all sample trees used in this study, appeared on the site after clear-cutting. This selection was made in order to create two treatment groups with an age structure which was as similar as possible. This was necessary since growth rates of trees may change as they grow older. Since not all sample trees originated from seed or rootstocks at the same time it was necessary to determine whether there were any major differences in age between browsed and unbrowsed trees. The mean age was slightly greater for browsed sample trees than for unbrowsed trees but this difference was, for each tree species, less than one year. Therefore, we considered these small age differences unlikely to cause differences in growth patterns. The radial increment data were analysed with analysis of variance with repeated measures (ANOVAR). Heavy browsing pressure made it difficult to find equal numbers of browsed and unbrowsed trees, especially for *S. caprea*, *S. aucuparia* and *P. tremula* (Table 1). Although the ANOVAR procedure is also robust in analysing unbalanced models, the low number of unbrowsed samples has, in case of the above-mentioned species, reduced the power of the test. In the statistical analysis we used 'browsing' (browsed versus unbrowsed) as a factor, 'year' as the repeated factor and radial increment for each year as the within-subject variable (SPSS for windows 10.0 standard version, 1999). Browsed trees were pooled regardless of the level of moose damage. Since the ANOVAR procedure does not allow missing data and there were not so many trees older than 6 years, analyses were performed only with the data from 1993-1998 to keep a sufficient amount of data for the statistical test. Therefore, no trees younger than six years were included in the analyses. Mauchly's test for sphericity was used to detect sphericity in the data. This test was significant for all four species and thus Huynh-Feldt corrected degrees of freedom and significance levels were applied for the within subject variables. Radial increment data were ln $(x+1)$ transformed to improve for homogeneity of variances.

Table 1. Sample size of browsed and unbrowsed sapling trees.

Species	Browsed	Unbrowsed (n)
B. pendula	52	30
S. caprea	46	6
S. aucuparia	32	3
P. tremula	35	11

The difference in damage caused by moose between the four tree species was tested using univariate analysis of variance with species (*B. pendula*, *S. caprea*, *S. aucuparia* or *P. tremula*) as a factor. A post-hoc test (Tukey's-b multiple comparison test, $p < 0.05$) was used to determine how damage indices differed between tree species. Damage index data were arcsine($\sqrt{x}$) transformed. The relation between the diameter at the base, age, and the height of browsed and unbrowsed sample trees was analysed using linear regressions.

Results

Browsing intensity

Browsing intensity was relatively low on *B. pendula* with 19 % of the total number of available shoots browsed (Fig. 1). Browsing was more intense on the other deciduous species; *P. tremula*, *S. caprea* and *S. aucuparia* had 58, 59 and 63 % of the total number of available shoots browsed, respectively (Fig. 1).

Effects of browsing on annual diameter growth

During 1993-1998, the annual diameter increment of browsed *B. pendula* and *S. caprea* was significantly higher than in unbrowsed trees (Fig. 2, Table 2). Although not significant, a p-value approaching significance indicates that browsed *S. aucuparia* also had a greater annual increment than unbrowsed trees. *P. tremula* showed the same trend, although the difference in radial increment between browsed and

unbrowsed trees was smaller and not significant. Three out of four species (*B. pendula*, *S. caprea* and *P. tremula*) showed significant differences in annual increment among years (Fig. 2, Table 2). Browsed *S. caprea* and *S. aucuparia* showed a clear decrease in radial growth during 1993-1998 (Fig. 2).

Moose browsing had marked effects on tree architecture. Unbrowsed *B. pendula* and *P. tremula* were taller than browsed trees of the same diameter (Fig. 3a-d). Unbrowsed *B. pendula* and *P. tremula* trees were also taller than browsed trees of the same age (Fig. 3e-h).

Fig. 1. Browsing intensity by moose on different deciduous trees expressed as the "moose damage index". The damage index was based on the proportion of browsed shoots of the total number of available previous year's shoots per tree. Error bars denote one standard error. A post-hoc test (Tukey's-b multiple comparison test, $p < 0.05$) was used to determine which damage indices were different between tree species and are indicated in the figure by a small 'a' or 'b'.

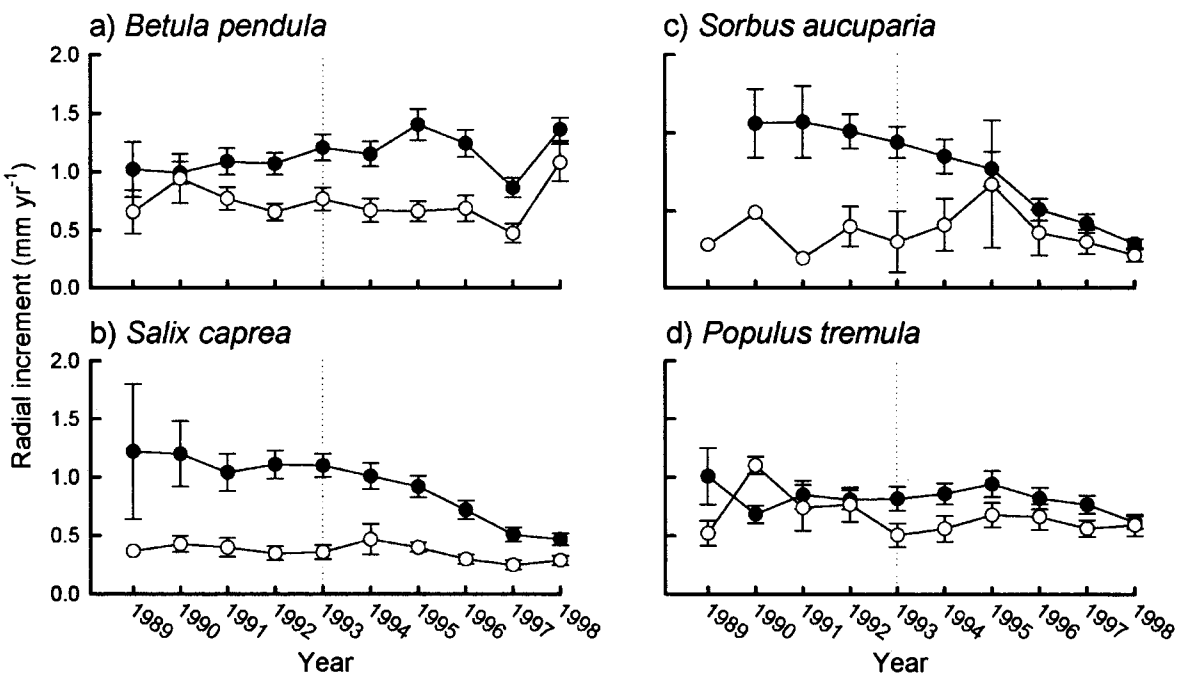

Fig. 2. Radial increment (mm yr^{-1}) during the period 1980-1998 of a) *Betula pendula*, b) *Salix caprea*, c) *Sorbus aucuparia* and d) *Populus tremula*. Filled circles (•) represent trees browsed by moose, open circles (o) those which have been left unbrowsed. The dotted line shows the start of the period included in the statistical analysis (1993-1998).

Table 2. Univariate analysis of variance with repeated measures for differences in radial increment of four tree species between browsed and unbrowsed trees during 1993-1998. A bold F and p value indicates a significant difference in radial growth between browsed and unbrowsed trees.

Species	Source	DF	F	p
	Browsing	1	**15.36**	**<0.001**
	Error	80		
	Year*	3.8	21.16	<0.001
	Year × browsing*	3.8	1.54	0.192
	Error*	300.4		
	Browsing	1	**6.08**	**0.017**
	Error	49		
	Year*	3.4	4.58	0.003
	Year × browsing*	3.4	1.98	0.112
	Error*	165.1		
	Browsing	1	2	0.167
	Error	32		
	Year*	3.7	1.93	0.115
	Year × browsing*	3.7	1.54	0.199
	Error*	119.8		
	Browsing	1	0.34	0.275
	Error	41		
	Year*	4.1	2.92	0.022
	Year × browsing*	4.1	1	0.413
	Error*	168.2		

*Huynh-Feldt corrected degrees of freedom and significance levels

Discussion

Browsed *B. pendula* and *S. caprea* showed higher annual radial increment throughout the study period compared to unbrowsed trees of the same species (Fig. 2). The radial growth of browsed *S. aucuparia*, which were severely damaged, was initially higher but decreased after consecutive years of repeated browsing (Fig. 1, 2). There was no significant effect on the radial growth of *P. tremula*, which were also severely damaged. The results for *B. pendula* and *S. caprea* provide evidence which support our hypothesis that moose prefer to browse fast-growing trees. Due to very high browsing pressure we were unable to find sufficient numbers of unbrowsed *S. aucuparia* and *P. tremula*. This reduced the probability of finding a significant difference in growth rate between browsed and unbrowsed trees of the latter two species. It would be good to do more studies examining the effect of growth rate of trees on forage selection of moose, especially for *S. aucuparia* and *P. tremula*. Previous studies confirm that moose prefer more productive tree species (Danell *et al.* 1985), genotypes (Danell *et al.* 1990) or phenotypes (Danell *et al.* 1991) over less productive ones. Slow-growing trees may be characterized by high fibre content, low water content and a thick cuticle and may produce secondary chemicals, which make them less attractive to herbivores (Bryant *et al.* 1983 and references therein). However, higher radial growth in trees browsed by moose may have resulted from compensatory growth responses of the trees. Unfortunately, in our data we cannot fully differentiate between these two factors. Nevertheless, Bergström and Danell (1987) observed that radial growth of *B. pendula* and *B. pubescens* decreased with artificial clipping. More precisely, the decrease in diameter growth was greatest at the most intense clipping regimes and even in the more moderate clipping regimes there was no indication of compensatory growth. Therefore, we suspect compensatory responses in diameter growth to be unlikely and we suggest that the observed greater radial growth in browsed trees in our data is mainly due to the preference of moose for fast-growing individuals. Continuous rebrowsing of fast-growing individuals may eventually slow down radial growth as the growth pattern of browsed *S. caprea* and *S. aucuparia* suggest (Fig. 2). After several rebrowsing events fast-growing browsed trees seem to end up with about the same growth rate as slow-growing unbrowsed trees.

Since moose possibly preferred fast-growing trees in our study, one can argue that unbrowsed trees were not equally accessible to the moose due to their slow growth. However, Figs. 3a-h suggest that unbrowsed trees grew taller than browsed trees of the same

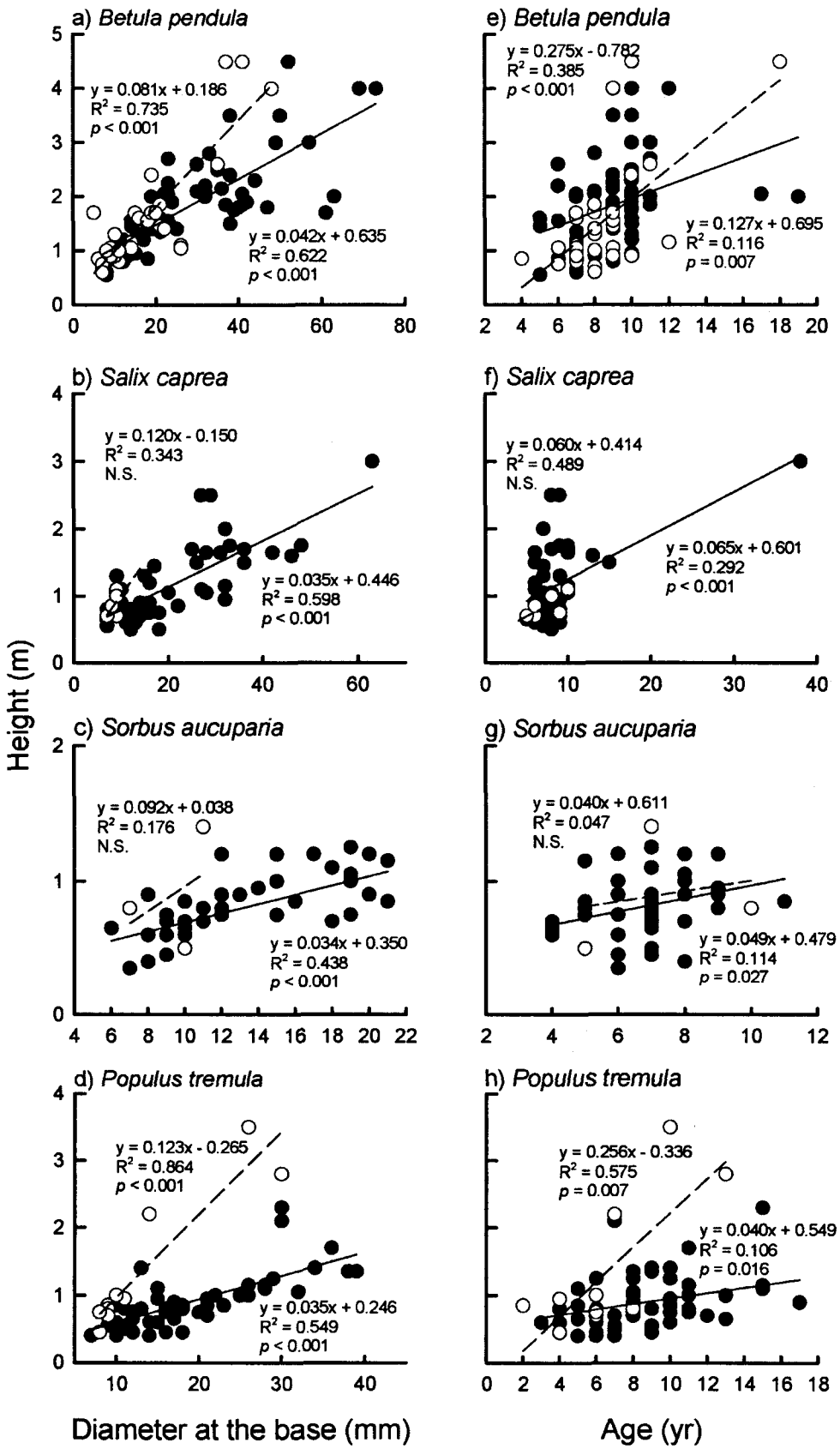

Fig. 3. Linear regressions between the diameter at the base (a-d), age of the trees (e-f) and tree height of four deciduous tree species. Filled circles (•) and continuous lines are browsed trees, open circles (o) and dashed lines are trees that were left unbrowsed.

diameter or age. This suggests that unbrowsed trees were easily accessible to moose and supports the explanation that moose can distinguish between fast and slow-growing trees. From our results it is clear that moose limited the height of trees and resulted in stunted tree growth.

Recently, conservationists have expressed concern that high moose densities may endanger the long-term persistence of deciduous species in Fennoscandia. Uneven browsing on different tree species may change competitive interactions between them (see e.g. Risenhoover and Maass 1987). Although other factors such as forest management also cause large-scale changes in forage species composition, a study by Angelstam *et al.* (2000) confirms that the occurrence of aspen, rowan and sallow was negatively related to increasing moose density going from Russian Karelia (low moose density) to Finland (intermediate moose density) and Sweden (high moose density). However, forest management, favouring pine and spruce and effectively reducing the abundance of sallow, aspen and rowan in most Fennoscandian forests, was not fully considered leaving still some questions with the deleterious effects of moose on the distribution of deciduous species. Kouki *et al.* (2004) found that small aspen saplings (dbh < 5 cm) occur in most protected old-growth forests in eastern Finland but they survive poorly and the larger aspen cohorts (5 cm < dbh < 15 cm) were lacking or very rare. One logical reason for poor sapling survival was high browsing pressure by moose although the lack of natural disturbance (e.g. forest fires) in protected areas, leading to spruce dominance, may also play a role. Besides a reduction in the size of the moose population, Kouki *et al.* (2004) suggested that aspen should also be promoted in the surrounding managed forest, for instance, by leaving all large aspen as retention trees and promoting aspen regeneration in clear-cut areas. Studies such as ours show that in clear-cut areas, moose heavily utilize deciduous trees such as aspen. Nevertheless, apart from rowan which may show high mortality due to browsing, their resilience to browsing is great and they may tolerate high browsing levels for many years. A small fraction of the individuals may actually remain unbrowsed or are only lightly browsed because they are protected by an inherent slow-growth rate or unfavourable microclimatic conditions which inhibit their growth. Eventually, these trees may grow out of the browsing limit and become part of the canopy.

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