SHOOT GROWTH OF BETULA PENDULA AND B. PUBESCENS IN RELATION TO MOOSE BROWSING

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Abstract: Birches are important food plants for moose in Sweden. Of the two closely-related species Betula pendula Roth and B. pubescens Ehrh. moose prefer B. pendula during the winter. This study compared the shoot growth and architecture of the two species for both unbrowsed and browsed birches. Unbrowsed B. pendula generally produced heavier current annual shoots than unbrowsed B. pubescens. After browsing both species responded by producing shoots which were longer, thicker, heavier and more often branched. In addition, browsing, caused shoot growth to occur at lower heights. The responses to browsing were more pronounced in B. pendula. Moose bites occured most frequently between 1.0-2.0 m in height. Within this interval moose encountered on previously browsed B. pendula, about three times more biomass of current annual shoots, than on unbrowsed trees of the same age.

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Birches (Betula spp.) constitute an important food for moose (Alces alces (L.)) in Sweden (Ahlén 1971, 1975, Bergström 1980, Cederlund et al. 1980). The consumption by moose consists of twigs in winter and leaves and young shoots in summer.

The two tree-like birch species, Betula pendula Roth and B. pubescens Ehrh., are very similar in appearence and are often found growing side by side. In the northern part of Sweden moose show a preference for B. pendula during winter (Bergström 1980, Danell, unpublished observation), and apparently distinguish between the two species.

The moose-birch complex was chosen to study the relationship between a large herbivore and its food plants. As a first step I examined the shoot growth pattern of the two birches and especially their growth responses following browsing during the winter period.

MATERIALS AND METHODS

Forty single-stemmed plants each of Betula pendula and B. pubescens were collected during 19-22 October 1981 (at the first snowfall), in an area located about 30 km NE of Umeå in northern Sweden. Of each species 20 unbrowsed and 20 browsed specimens were taken. The birches were chosen so that their ages and habitats (mixed pine-spruce forest; mainly along logging roads) were as similar as possible. The browsing pressure by moose in the area can be regarded as light to moderate. The browsed birches had been browsed mainly during the last winter. The height, stem diameter at 0.20 m above ground level, age (annual rings in a cross-section of the stem at ground level) and number of bites are given in Table 1.

Table 1. Characteristics of harvested birches ($\bar{X}$±S.E., N=20)

	Betula pendula		Betula pubescens	
	Unbrowsed	Browsed	Unbrowsed	Browsed
Height (m)	2.88±0.06	2.64±0.04	2.82±0.05	2.78±0.06
Stem diameter (mm) at 0.2 m height	32 ±1	35 ±1	32 ±1	35 ±1
Age (years)	9 ±0	9 ±0	9 ±1	10 ±0
Number of bites	0	77 ±6	0	76 ±8

Until February 1982 the birches were kept outdoors and protected from browsing animals. They were then taken into the laboratory for analyses. The 1981 annual long-shoots (herein called current annual shoots) were collected for the following height layers: 0-0.5, 0.5-1.0 and 1.0-1.5...m above ground level. If a shoot was found within two layers it was assigned to the layer where its main part was located. The total number of current annual shoots within each layer was counted and the shoots were classified as either branched (proleptic) or unbranched shoots.

For each height layer 20 shoots (or all available) from each specimen were treated individually. The fresh weight was measured to the nearest mg and the shoot length and diameter (at 1.0 cm from the base) measured to the nearest mm and 0.1 mm, respectively. Within the respective layers the dry weight (constant weight at 70°C) of all the collected shoots was measured for each tree. The diameter of each twig at point of browsing (DPB), layer for layer, was measured to the nearest 0.1 mm. Furthermore, the bites were classified as either bites by moose or hare (Lepus timidus L.). The bites were mainly from the winter 1980/1981. None of the trees had been browsed during the summer of 1981.

The statistical tests used were the Mann-Whitney U-test and the Wilcoxon matched-pairs signed-ranks test (Siegel 1956).

RESULTS

Moose Bites

Moose bites occurred more frequently than bites by hare. Only 0.1 and 2.9% of the bites on B. pendula and B. pubescens, respectively, were classified as hare bites. The majority of the moose bites were found between 1.0 and 2.0 m in height for both species (Figure 1).

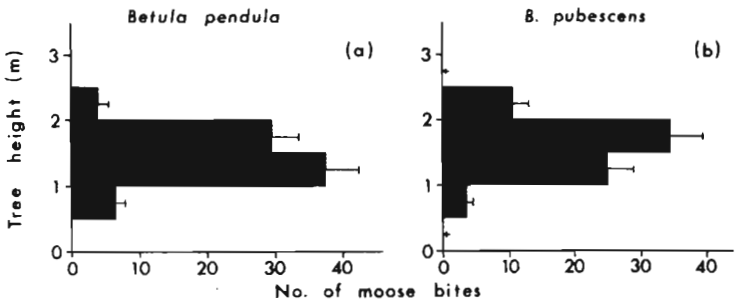

Figure 1. Distribution of moose bites on different height levels in Betula pendula and B. pubescens ($\bar{x} \pm$ S.E., N=20; +=less than 1 bite per tree).

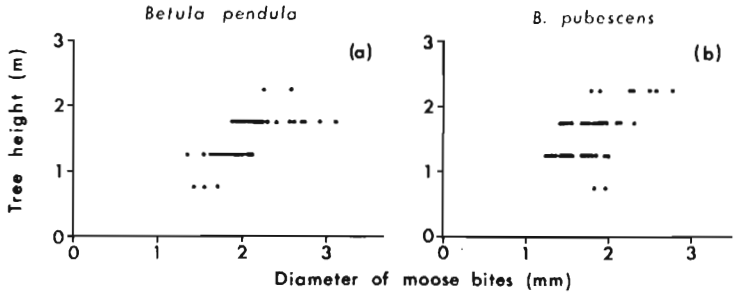

Figure 2. Diameters of moose bites on different height levels in Betula pendula and B. pubescens (each point represents the mean for ≥10 bites on a tree).

The mean DPB of moose bites on B. pendula was greater than on B. pubescens (Mann-Whitney U-test, $P<0.02$ at 1.0-1.5 m and $P<0.002$ at 1.5-2.0 m height). The mean DPB increased with the height of the trees (Figure 2). For both species of birch and on the same tree the DPB's were greater at 1.5-2.0 m, than at 1.0-1.5 m. (Wilcoxon matched-pairs signed-ranks test, N=18 and 14, $P<0.01$). Furthermore, for B. pubescens the bites were greater at 2.0-2.5 m than at the preceeding level (N=7, P=0.02).

Numbers of Current Annual Shoots

There were no significant differences in the total number of current annual shoots on unbrowsed B. pendula or B. pubescens (Mann-Whitney U-test, $P>0.05$) (Table 2). For both species, 55-60% of the shoots were found within the 1.0-2.0 m height classes. (Figure 3). On browsed B. pubescens there were fewer current annual shoots than on unbrowsed trees ($P<0.02$), however, no such difference was observed for B. pendula there ($P>0.05$) (Table 2).

Browsed B. pendula showed a marked tendency, and B. pubescens only a slight, to produce their shoots at a lower level than unbrowsed trees did (Figure 3). In browsed B. pendula about 80% of the current annual shoots were distributed between 1.0-2.0 m, while about only 55% of the shoots were found within this level on unbrowsed trees.

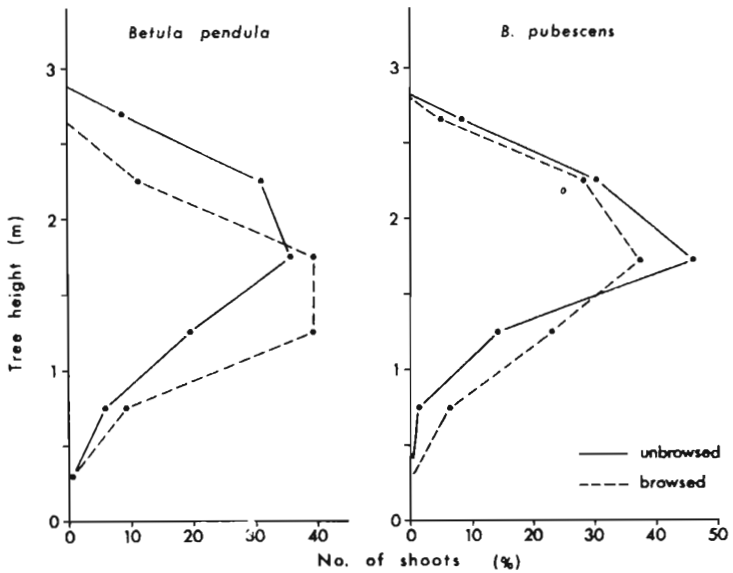

Figure 3. Relative distribution of current annual shoot numbers at different height levels in unbrowsed and browsed Betula pendula and B. pubescens.

Individual Current Annual Shoots

The mean base diameter and fresh weight of unbrowsed shoots of B. pendula, between 1.0-1.5 m, was greater than unbrowsed shoots of B. pubescens (Mann-Whitney U-test, $P<0.05$) (Figure 4). Above this level the differences were even greater. The browsed B. pendula and B. pubescens had greater length, base diameter and fresh weight of the mean current annual shoot from the height interval 1.0-2.0 m than the corresponding shoots from unbrowsed trees had ($P<0.05$).

Table 2. Current annual shoots on unbrowsed and browsed Betula pendula and B. pubescens ($\bar{x}$±S.E., N=20).

	Betula pendula		Betula pubescens	
	Unbrowsed	Browsed	Unbrowsed	Browsed
No. of shoots	110±17	97±9	104±9	72±7
Frequency of branched shoots (%)	0	5±1	0±0	3±1
Dry weight of shoots (g)	31±4	52±5	24±2	24±2

For both species of birches there was a higher frequency of branched shoots on the browsed trees ($P<0.002$ and $P<0.02$ for B. pendula and B. pubescens, respectively) (Table 2).

Biomass of Current Annual Shoots

Within the height interval 1.0-2.0 m the total dry weight of shoots was about 25% greater for unbrowsed B. pendula than for unbrowsed B. pubescens. However, on a whole tree basis there were no significant differences in shoot dry weight between the two species (Mann-Whitney U-test, $P>0.05$) (Table 2).

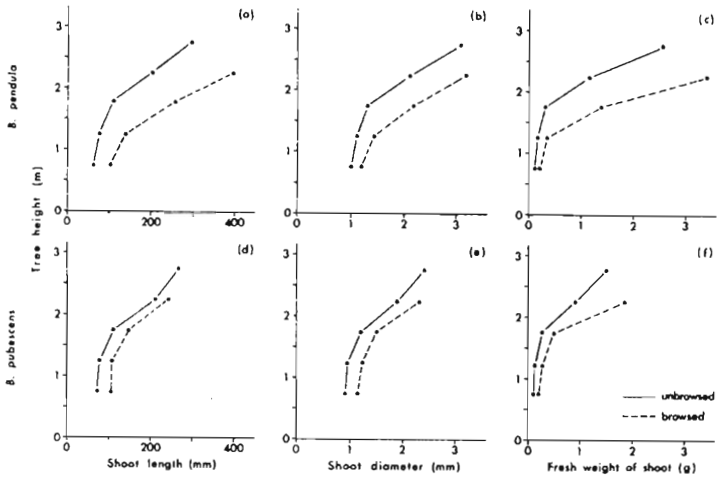

Figure 4. Characteristics of individual current annual shoots of unbrowsed and browsed Betula pendula and B. pubescens. Shoot length (a&d), shoot diameter at base (b&e) and fresh weight of shoot (c&f) given as mean of ≥ 10 trees.

Browsed B. pendula had a higher total dry weight of current annual shoots than unbrowsed trees of the same species ($P<0.02$), but for B. pubescens there was no significant difference between the corresponding groups ($P>0.05$) (Table 2).

The browsed trees of B. pendula had about 65 % of their current annual shoot dry weight distributed between 1.0-2.0 m, while the unbrowsed trees there had only about 35% of the current growth in that

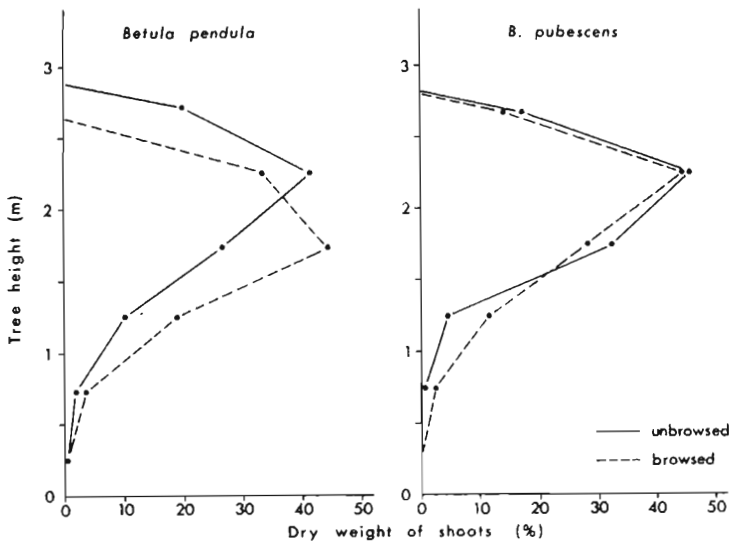

Figure 5. Relative distribution of current annual shoot dry weight at different height levels in unbrowsed and browsed Betula pendula and B. pubescens.

height interval (Figure 5). Conversely, on browsed and unbrowsed B. pubescens there was no such difference and both groups had about 40% of the shoot dry weight in the 1.0-2.0 m height interval. In terms of absolute dry weight the browsed B. pendula carried about three times more current annual shoots between 1.0-2.0 m than unbrowsed trees did. For B. pubescens the figures for the two groups of trees are almost equal.

DISCUSSION

It seems that moose closely adjust their bite size to the size of the current annual shoots. In unbrowsed birches the shoots were generally thicker and heavier for B. pendula than for B. pubescens (Figure 4). Consequently moose bites were larger when recorded on B. pendula than on B. pubescens (Figure 2). For both species of birch moose also took larger bites from the upper part of the trees, where the shoots were generally thicker, than from the lower part where the shoots were more slender.

Browsing affects shoot morphology (e.g. Aldous 1952, Krefting et al. 1966, Metzger 1977, Bergström 1980). In this study of the current shoots of birches the shoots become longer, thicker and heavier after browsing (Figure 4). At least at the studied browsing pressure (about 80 bites per tree) the growth responses of B. pendula seemed more favourable to the moose than the response by B. pubescens, i.e. larger individual shoots and greater dry weight of shoots within 1.0-2.0 m of height.

In addition to the differences in shoot morphology and architecture between the two species there may be differences in their chemical content. There is now an increasing amount of evidence that plant secondary compounds play an important role in the food selection of browsers (see review by Bryant & Kuropat 1980). Studies on inter- as well as intraspecific differences in the digestibility and chemical content of the two birches are in progress.

Without these chemical data it seems possible to simply explain the preference for unbrowsed B. pendula over unbrowsed B. pubescens as "food-density selection". Winter browsing on intact birches changes their appearance to the following winter. Because browsed birches produce larger shoots and a higher "food-density" we can expect: (1) a greater consumption and (2) larger bite sizes by moose from/on these browsed trees. Some preliminary data from field experiments supports these predictions, at least for B. pubescens (Danell & Huss-Danell, unpublished observations). Another explanation is that moose select fast-growing shoots. However, these observations do not disprove the importance of secondary compounds in the birch-moose interface, they merely stress the importance of studies involving both shoot morphology/architecture and chemistry.

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