

# ACTA FORESTALIA FENNICA 224

RISTO HEIKKILÄ

MOOSE BROWSING IN A SCOTS PINE PLANTATION  
MIXED WITH DECIDUOUS TREE SPECIES

HIRVEN RAVINNONKÄYTTÖ LEHTIPUU-  
SEKOITTEISESSA MÄNTYTAIMIKOSSA

THE SOCIETY OF FORESTRY IN FINLAND  
THE FINNISH FOREST RESEARCH INSTITUTE

Acta Forestalia Fennica was established in 1913 by the Society of Forestry in Finland. It was published by the Society alone until 1989, when it was merged with Communicationes Instituti Forestalis Fenniae, started in 1917 by the Finnish Forest Research Institute. In the merger, the Society and Forest Research Institute became co-publishers of Acta Forestalia Fennica.

Prior of the merger, 204 volumes had appeared in Acta Forestalia Fennica, and 145 volumes in Communicationes.

---

**EDITORS – TOIMITUS**

**Editors-in-chief** Eeva Korpilahti, the Society of Forestry in Finland  
**Vastaavat toimittajat** Erkki Annila, the Finnish Forest Research Institute

**Editors – Toimittajat** Seppo Oja, Tommi Salonen

---

**EDITORIAL BOARD – TOIMITUSKUNTA**

**The Society of Forestry in Finland**  
Matti Keltikangas, Erkki Annila, Seppo Kellomäki, Antti Korpilahti, and Liisa Saarenmaa.

**The Finnish Forest Research Institute**  
Erkki Annila, Pentti Hakkila, Seppo Kainisto, Jari Kuuluvainen, Juha Lappi, and Eino Mälkönen.

---

**PUBLISHERS – JULKAISIJAT**

**The Society of Forestry in Finland**  
**Suomen Metsätieteellinen Seura r.y.**  
Unioninkatu 40 B, 00170 Helsinki  
Tel. +358-0-658 707 Fax: +358-0-1917 619  
Telex: 125181 hyfor sf

**The Finnish Forest Research Institute**  
**Metsäntutkimuslaitos**  
Unioninkatu 40 A, 00170 Helsinki  
Tel. +358-0-857 051 Fax: +358-0-625 308  
Telex: 121286 metla sf

---

**AIM AND SCOPE – TAVOITTEET JA TARKOITUS**

Acta Forestalia Fennica publishes dissertations and other monographs. The series accepts papers with a theoretical approach and/or of international interest. The series covers all fields of forest research.

Acta Forestalia Fennicassa julkaistaan väitöskirjoja ja muita monografiatyypisiä kirjoituksia. Kirjoitusten tulee olla luonteeltaan teoreettisia ja/tai kansainvälisesti merkittäviä. Sarja kattaa metsäntutkimuksen kaikki osa-alueet.

---

**SUBSCRIPTIONS AND EXCHANGE – TILAUKSET**

Subscriptions and orders for back issues should be addressed to Academic Bookstore, P.O.Box 128, SF-00101 Helsinki, Finland. Subscription price is FIM 70 per issue. Exchange inquiries should be addressed to the Society of Forestry in Finland.

Tilaukset ja tiedustelut pyydetään osoittamaan Suomen Metsätieteelliselle Seuralle. Tilaushinta Suomeen on 50 mk/numero. Seuran jäsenille sarja lähetetään jäsenmaksua vastaan.

**MOOSE BROWSING IN A SCOTS PINE PLANTATION  
MIXED WITH DECIDUOUS TREE SPECIES**

Hirven ravinnonkäyttö lehtipuusekoitteisessa mäntytaimikossa

Risto Heikkilä

*Approved on 4.12.1991*

Heikkilä, R. 1991. Moose browsing in a Scots pine plantation mixed with deciduous tree species. Tiivistelmä: Hirven ravinnonkäyttö lehtipuusekoitteisessa mäntytaimikossa. Acta Forestalia Fennica 224. 13 p.

The utilization of available food resources by the moose was studied in a Scots pine (*Pinus sylvestris*) plantation containing an admixture of deciduous species. Rowan (*Sorbus aucuparia*) and aspen (*Populus tremula*) were highly utilized compared to pine and both silver birch (*Betula pendula*) and pubescent birch (*B. pubescens*). However, they were not capable of withstanding continuous browsing by moose owing to their diminished biomass. In total, the browsing intensity (number of browsed twigs/tree) on pine and birch was about double that on rowan and aspen.

The number of browsed twigs per tree increased as the amount of available main branches increased. The number of bites per available branch, as well as the maximum diameter of the bites, decreased as the density of the plantation increased. Silver birch was more used by moose than pubescent birch as well as planted silver birch compared with naturally regenerated trees.

Main stem breakage was especially common in winter 1988, the average height of the pine and birch trees being over two meters. The tops of broken stems were commonly utilized as food. The increase in moose density and the relatively deep snow cover evidently promoted the incidence of serious damage. The number of undamaged trees/ha was greater in dense than in sparse parts of the stand.

Keywords: moose browsing, mixed plantation, feeding behaviour, *Alces alces*.  
FDC 451 + 232.4

Author's address: Finnish Forest Research Institute, Box 18, SF-01301 Vantaa, Finland.

ISBN 951-40-1184-8  
ISSN 0001-5636

Tampere 1991. Tammer-Paino Oy

## Contents

1. INTRODUCTION .....	4
2. MATERIAL AND METHODS .....	4
3. RESULTS .....	5
4. DISCUSSION AND CONCLUSIONS .....	11
REFERENCES .....	12

## 1. Introduction

During the winter young forest plantations provide a considerable amount of food for the moose. In the winter ranges of moose especially, continual browsing on young trees year after year has an effect on food availability (Bedard & al. 1978), as well as on the occurrence of damage in the plantations. Plantations established with Scots pine (*Pinus sylvestris*) or birch (*Betula pendula*, *B. pubescens*) often also include other tree species, a high proportion of which consists of the deciduous plants commonly utilized by moose. Pine is eaten almost only during the winter, but birch, rowan (*Sorbus aucuparia*) and aspen (*Populus tremula*) also during the summer. The feeding preferences of moose in relation to the quantity and quality of the food resources can be expected to affect the rate of consumption (Belovsky 1981).

Selective browsing by a dense moose population influences the growth rate of forest tree plants and alters the composition of plantations.

Repeated browsing year after year may considerably alter the forest community succession for a long period (Snyder & Janke 1976, Risenhoover & Maass 1987). Utilization of the tree species preferred by moose may also release the less palatable conifers, such as Norway spruce, from the strong competition caused by hardwoods (Hjeljord & Groenvold 1988). When subjected to a long-term, intensive browsing pressure, a young pine stand is gradually converted into a spruce-hardwoods mixed stand (Kuznetsov 1987). On the other hand, in the Nordic countries aspen and rowan are highly preferred by the moose compared to pine (Bergström & Hjeljord 1987). These two deciduous species occur commonly in pine plantations.

The aims of the study were to obtain information about moose browsing patterns in Scots pine plantation containing an admixture of deciduous species, and to evaluate the short-term effect of browsing on silvicultural practices.

## 2. Material and methods

The study area was situated at Lapinjärvi in southern Finland (60°30'–60°40'N, 26°00'–26°30'E). According to information provided by the Uusimaa Game Management District, moose utilize the area especially during the winter, the summer ranges being located to the south near the coast. The area of the plantation was ca. 5 ha, and it had originally been established by planting with Scots pine, but later on with silver birch during 1978–82. According to studies made in southern Finland (Löytyniemi & Piisilä 1983, Repo & Löytyniemi 1985, Heikkilä 1990), the characteristics of the plantation were typical of feeding sites preferred by moose: soil fertility better than average for Scots pine, grassy vegetation, sloping terrain, high proportion of deciduous saplings in the undergrowth and a high proportion of mature spruce forests in the surroundings.

The other tree species growing in the plantation were naturally regenerated *Betula pendula* and *B. pubescens*, *Sorbus aucuparia* and *Popu-*

*lus tremula*. The moose winter density in the total land area of the municipality during 1985–87 averaged 0.26/km<sup>2</sup> (T. Nygrén, Finnish Game and Fisheries Institute, pers. commun.). In 1988 the density increased to 0.39/km<sup>2</sup>, which is an increase of 33 % compared to the density in 1987. When calculated per forest land, the moose density averaged 0.40/km<sup>2</sup> during 1985–87, and 0.62/km<sup>2</sup> in winter 1988. The density in the experimental forest area was obviously higher than the average due to concentration of the moose population in winter after migration from the coast (information from the Game Management District). The maximum snow cover, 60–70 cm, occurred in the study area in 1984 and 1988 (Monthly report... 1984–1988). The snow depth was generally at a level that is considered to have no marked effect on the mobility of moose (Coady 1974). Snow frequently decreases the accessibility of low vegetation, e.g. dwarf shrubs.

A total of 55 plots (50 m<sup>2</sup> in size) were sys-

tematically marked out in the plantation at distances of 18–25 m. Five saplings of every tree species on each plot were inspected, starting systematically from the same direction and point on each plot. Stand density (trees/ha) and tree height (cm) were measured on each plot. The total number of browsed twigs was counted per tree. Moose biting was also recorded per main branch growing from the stem. The maximum diameter of bites per plant was recorded. The maximum bite diameter has been found to correlate significantly with the mean diameter of bites (S. Härkönen, Finnish Forest Research Institute, unpublished), which has been reported to be a good measure of browsing intensity (Vivås & Saether 1987). Broken main stems were counted separately because the moose do not always use them as food down to the breaking point. Classification of the severity of stem breakage was done according to the results of Heikkilä & Löytyniemi (1991). The trees with a breakage point of diameter > 1 cm on pine and > 0.5 cm on birch, as well as repeatedly broken stems, were considered as severely damaged. Only plants over 50 cm high were included in the sample.

## 3. Results

During the initial development of the plantation up to spring 1987, the proportion of browsed stems of aspen and rowan was higher than that on any of the other tree species (Fig. 1). Browsing, including stripping off the leaves, was less common on pubescent birch than on the other deciduous tree species during the following summer.

In 1988 the proportion of browsed pubescent birch saplings was significantly lower than that of the other species. In total, the average proportion of browsed trees for spring 1987 was 62 % ( $\pm 2$  S.E.), summer 1987 17 % ( $\pm 1$  S.E.) and winter 1988 53 % ( $\pm 2$  S.E.).

A high proportion of the rowan and aspen saplings had been repeatedly browsed and become bushy with no clear main stem. In autumn 1987 the average height of the pine saplings was 189 cm ( $\pm 6$  S.E.), silver birch 256 cm ( $\pm 7$  S.E.), pubescent birch 210 cm ( $\pm 6$  S.E.), aspen 144 cm ( $\pm 6$  S.E.) and rowan 115 cm ( $\pm 3$  S.E.).

In winter 1988 the browsing pressure on the

The first inventory was made in May 1987, when all signs of browsing were recorded. The work was continued the following September and again in May 1988 in order to evaluate the progress of moose browsing. Only new bites were recorded in the last two inventories. New bites were recognized on the basis of the position of the shoots on branches and changes in the breakage point. The total number of plants inspected was 821; 204 Scots pine (*Pinus sylvestris*), 212 silver birch (*Betula pendula*), 110 pubescent birch (*B. pubescens*), 65 aspen (*Populus tremula*) and 230 rowan (*Sorbus aucuparia*). The average density of the plantation was 6300 trees/ha, the figures for pine being 1120, silver birch 1580, pubescent birch 760, aspen 280 and rowan 2560/ha. Pellet group counting was done in spring 1987. Only pellets lying on ground vegetation that had withered during the previous autumn were counted. Only new pellet groups were included in subsequent countings. Statistical analysis was done using the Kruskal-Wallis one-way analysis of variance, the Mann-Whitney (rank sum) test, the Wilcoxon test, the Pearson chi-square test, and linear regression analysis.

plantation was intensive because of the increased number of moose in the area. The number of pellet groups (476/ha) found on the sample plots in spring 1988 was about three times greater than that during the previous spring (164/ha).

Up to spring 1987 the total number of twigs utilized per sapling on aspen and rowan was 1.5–2 times greater than that on the other tree species (Fig. 2). Twigs of silver birch were also significantly more utilized than those of pubescent birch. In summer silver birch was more browsed per sapling than either pubescent birch or rowan. In addition to biting, leaf stripping occurred commonly and its proportion out of the total number of browsing cases was 40 % for silver birch, 42 % for pubescens birch, 38 % for aspen and 21 % for rowan. Leaf stripping done in the early summer is not easy to detect in the autumn, and thus the recorded cases mainly represent browsing on the new shoots.

During the following winter, when moose browsing in the study area intensified, the number

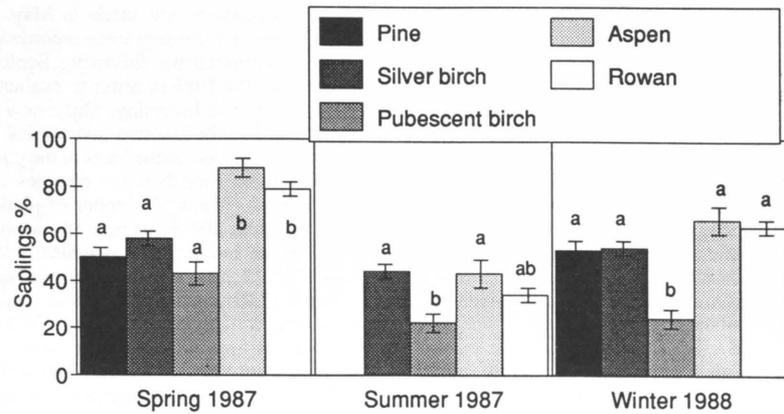


Figure 1. Average proportion of browsed saplings out of the total ( $n = 821$ ,  $p < 0.05$ , Kruskal-Wallis-test = 77.86, 69.29 and 51.10). Different letters = significant difference.

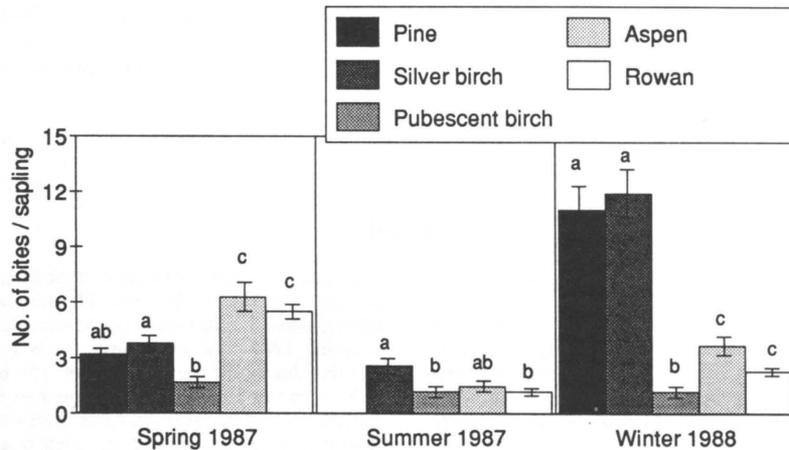


Figure 2. Number of bites per sapling in successive inspections ( $n = 821$ ,  $p < 0.05$ , Kruskal-Wallis-test = 80.77, 62.87 and 53.45). Further explanation in Fig. 1.

of bites was highest on pine and silver birch. The number of bites per pubescent birch sapling was lower than that for any other tree species. The average total number of bites per sapling was  $4.0 (\pm 0.2 \text{ S.E.})$  in spring 1987 and  $6.9 (\pm 0.5 \text{ S.E.})$  in 1988, the increase being significant ( $n = 821$ ,  $p < 0.05$ , Wilcoxon).

Aspen and rowan were heavily used and the number of bites per available branch was con-

siderably high at the first inspection, compared with the other species (Fig. 3). These species had remained relatively small and the number of main branches growing from the main stem was low. Differences in the number of bites per branch were not significant between pine and the two birch species. In summer pubescent birch was less browsed than other tree species. No other differences were found. No difference was

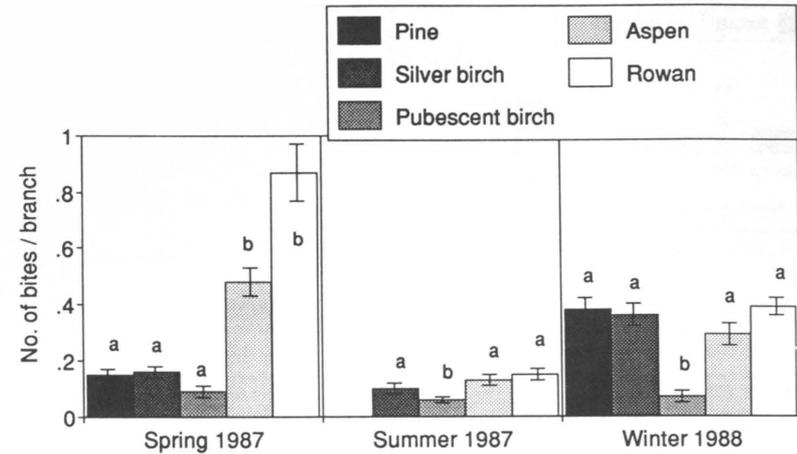


Figure 3. Number of bites per branch in successive inspections. Stripping off the leaves in summer included ( $n = 821$ ,  $p < 0.05$ , Kruskal-Wallis-test = 215.70, 70.22 and 60.20). Further explanation in Fig. 1.

found in summer between naturally regenerated saplings of the two birch species. In 1988 the number of bites per branch for aspen and rowan was at about the same level as for pine and silver birch. No marked difference was found between pine and silver birch; consumption of these species intensified as a result of stronger browsing pressure. Only pubescent birch, which was browsed to a small extent, differed significantly from the other species. The total average number of bites per branch was  $0.4 (\pm 0.03 \text{ S.E.})$  in spring 1987 and  $0.3 (\pm 0.02 \text{ S.E.})$  in 1988. The significant decrease ( $n = 821$ ,  $p < 0.05$ , Wilcoxon) was evidently due to the diminished utilization of aspen and rowan.

The difference between the two birch species was not significant up to 1987. However, the planted silver birch saplings were more browsed ( $0.17 \pm 0.02 \text{ S.E. bites/branch}$ ) than naturally regenerated pubescent birch saplings ( $0.09 \pm 0.02 \text{ S.E. bites/branch}$ ) ( $n = 197$ ,  $p < 0.01$ , Mann-Whitney-test = 3195.0). The difference in height was also considerable ( $254 \text{ cm} (\pm 9 \text{ S.E.})$  and  $182 \text{ cm} (\pm 8 \text{ S.E.})$  in spring 1987).

Overall the naturally regenerated silver birch saplings were browsed ( $0.42 \pm 0.04 \text{ S.E. bites/branch}$ ) to a significantly greater extent than those of pubescent birch ( $0.16 \pm 0.02 \text{ S.E. bites/branch}$ ) ( $n = 235$ ,  $p < 0.01$ , Mann-Whitney-test = 9182.0). However, the difference was not sig-

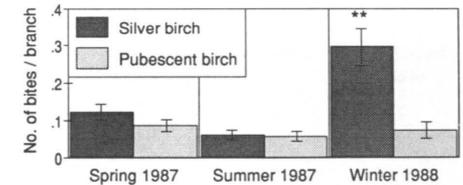


Figure 4. Number of bites per branch in naturally regenerated saplings of silver birch and pubescent birch ( $n = 235$ , Mann-Whitney-test = 7423.00, 6942.50 and 8814.50). Significance of results: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ .

nificant until 1988 (Fig. 4). The height of both species was about the same ( $216 \text{ cm} \pm 9 \text{ S.E.}$  and  $211 \text{ cm} \pm 8 \text{ S.E.}$ ), and there was no marked difference in the height distributions (63 % of the former and 69 % of the latter species were less than 250 cm high). Stem breakages occurred commonly especially on silver birch; 71 % of the tops of browsed natural silver birch and 46 % of pubescent birch saplings were broken.

Planted silver birch saplings were significantly more browsed than naturally regenerated ones at all inspections (Fig. 5). The difference in height (in spring 1987  $254 \text{ cm} \pm 9 \text{ S.E.}$  and  $190 \text{ cm} \pm 8 \text{ S.E.}$ , respectively) was considerable. In summer 1987 the annual height growth of natu-

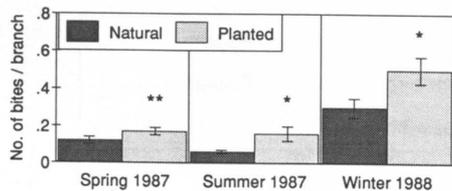


Figure 5. Number of bites per branch in natural and planted silver birch ( $n = 212$ , Mann-Whitney-test = 2952.00, 3307.50 and 3190.50). Further explanation in Fig. 4.

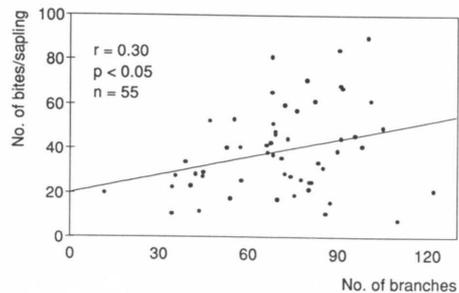


Figure 6. Number of bites per sapling in relation to branches available.

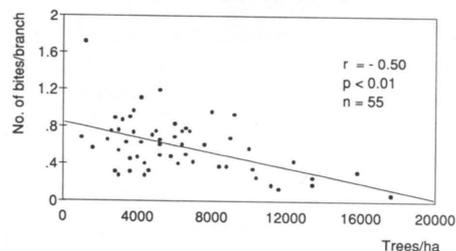


Figure 7. Number of bites per branch in relation to stand density.

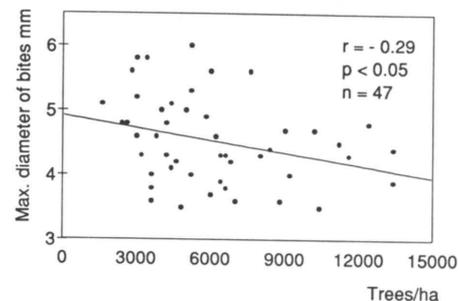


Figure 8. Maximum diameter of bites in relation to stand density.

rally regenerated saplings was 78% that of the planted ones.

When the results of the two successive inspections in spring 1987 and 1988 were summarized, the average number of bites per tree was greatest on pine ( $14.2 \pm 1.4$  S.E.) and silver birch ( $15.7 \pm 1.3$  S.E.). The number was also considerable on aspen ( $9.9 \pm 1.0$  S.E.) and rowan ( $7.8 \pm 0.5$  S.E.). Only pubescent birch ( $2.9 \pm 0.5$  S.E.) differed significantly from the other tree species ( $n = 821$ ,  $p < 0.05$ , Kruskal-Wallis-test = 75.75). Aspen ( $0.8 \pm 0.07$  S.E.) and rowan ( $1.3 \pm 0.1$  S.E.) were clearly the most intensively utilized tree species per available branch, pubescent birch ( $0.2 \pm 0.03$  S.E.) being browsed to a significantly lower extent than the other species. No difference was found between pine ( $0.5 \pm 0.05$  S.E.) and silver birch ( $0.5 \pm 0.04$  S.E.) ( $n = 821$ ,  $p < 0.05$ , Kruskal-Wallis-test = 117.13).

32% of the pines browsed earlier were rebrowsed in winter 1988, the proportion of unbrowsed ones being 18%. The proportion of

earlier unbrowsed, but browsed in 1988, was 21% and that of totally unbrowsed pines 29%. Thus rebrowsing of pine occurred significantly ( $n = 204$ , Pearson Chi-square 10.5,  $p < 0.01$ ). Especially those pines intensively ( $> 10$  bites) browsed earlier, were commonly browsed again (79% of saplings). Rebrowsing did not occur significantly on silver birch. However, 42% of the intensively browsed saplings were affected again.

The number of bites per tree increased as the number of available branches increased (Fig. 6). Thus the degree of browsing was the higher, the greater was the amount of food available. With an increase in stand density, the number of bites per branch as well as the maximum diameter of bites decreased (Figs. 7 and 8), showing selective utilization of the food resource.

The average maximum diameter of the bites was highest in pine (Fig. 9); even the young shoots of this species are relatively thick. The differences in maximum diameter in deciduous

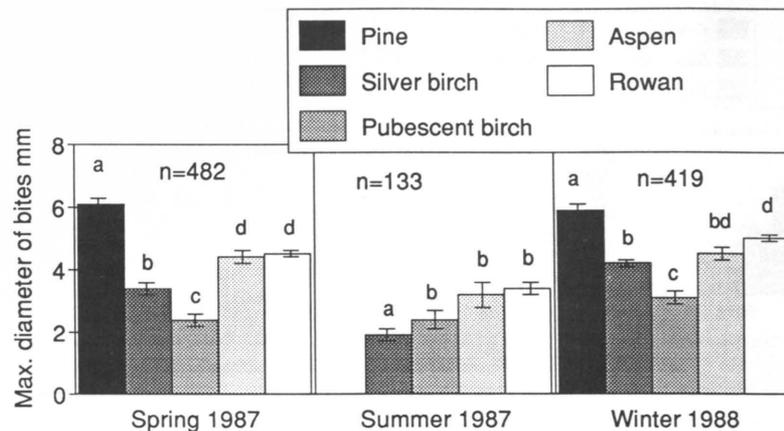


Figure 9. Maximum diameter of bites in different tree species ( $p < 0.05$ , Kruskal-Wallis-test = 191.12, 44.42 and 101.83).

species correlated better with the number of twigs consumed than in pine. The highest values occurred on rowan, the difference between rowan and aspen being insignificant. Silver birch and aspen no longer differed to any great extent in 1988, browsing having increased on silver birch and aspen already having been heavily utilized. The values were lowest for pubescent birch. When the browsing pressure intensified, the differences in maximum diameter tended to decrease. Compared with spring 1987, the moose appeared to continue using twigs of rowan and silver birch of relatively thick diameter in 1988.

The intensified browsing pressure in 1988 also resulted in a higher value for the average maximum diameter of bites (1987  $4.7$  mm  $\pm 0.1$  S.E., 1988  $4.9$  mm  $\pm 0.1$  S.E.,  $n = 278$ ,  $p < 0.01$ , Wilcoxon). As the number of bites per available branch increased, the moose utilized twigs of thicker maximum diameter (Fig. 10).

The number of main stem breakages increased considerably in winter 1988; 17% of the pines, 32% of the silver birch and 9% of pubescent birch saplings were broken. Obviously the thick snow cover in 1988 promoted the frequency of stem breakage by reducing the mobility of moose. In total 37% of the pines, 50% of the silver birch and 17% of the pubescent birch saplings had been broken at least once by moose. Thus the number of saplings with unbroken main stems for pine was 706/ha, for silver birch 790/ha and for pubescens birch 631/ha. In 1988, 34

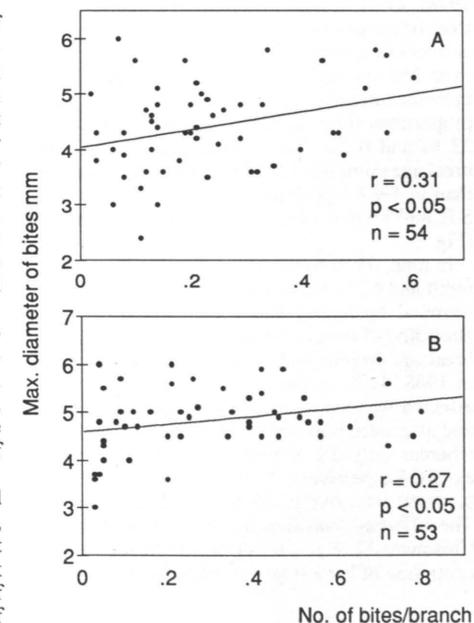


Figure 10. Maximum diameter of bites in spring 1987 (A) and winter 1988 (B) in relation to the number of bites per available branch.

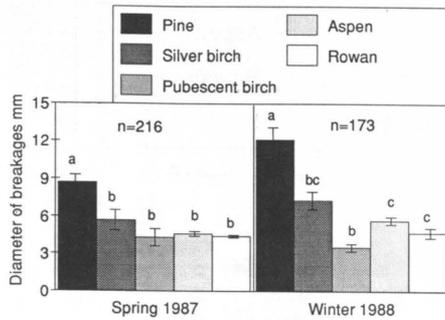


Figure 11. Diameter of main stem breakages of different tree species ( $p < 0.05$ , Kruskal-Wallis-test = 52.56, 8.61 and 52.57).

% of all stem breakages occurred in the saplings over 250 cm high, which is a height that moose rarely exceeds while feeding (cf. Telfer & Cairns 1978). 41 % of the stem breakages in browsed trees occurred in those over 250 cm high. In the case of silver birch, 77 % of the broken saplings over 250 cm high and used for feeding were browsed intensively (> 10 bites). The respective proportions for pine and pubescent birch were 33 % and 0 %. The average diameter of the breakage point was in 1988 significantly greater than in 1987 especially on pine ( $8.0 \text{ mm} \pm 0.5 \text{ S.E.}$  and  $5.5 \text{ mm} \pm 0.2 \text{ S.E.}$ ,  $p < 0.05$ , Wilcoxon) (Fig. 11).

In total, 55 % of the pines, 73 % of the silver birch and 62 % of the pubescent birch saplings browsed by moose had main stem breakage. Browsing of twigs occurred in all cases of stem breakage on pine and both of the birch species in 1988. 49 % of the 114 silver birch saplings affected by moose in 1988 had stem breakage and also were browsed intensively (> 10 bites), whereas only 18 % was browsed to a lesser extent. Respectively, 12 % were unbroken and browsed intensively, 20 % to a lesser extent. The difference was significant ( $n = 114$ , Pearson Chisquare 12.8,  $p < 0.01$ ) thus indicating concentration of browsing on broken trees.

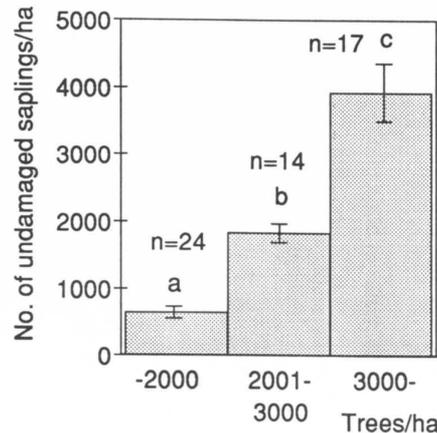


Figure 12. Number of undamaged saplings/ha in relation to stand density ( $p < 0.05$ , Kruskal-Wallis-test = 42.56).

Table 1. Occurrence of stem defects in different stand density classes ( $n = 55$ ,  $p < 0.05$ , Kruskal-Wallis-test = 42.56). Different letters = significant difference.

Stand density trees/ha	Trees with stem defect ( $\pm$ S.E.)/ha	Proportion of damaged pine and silver birch %
< 2000	500 $\pm$ 81 a	43
2001-3000	757 $\pm$ 134 ab	29
> 3000	1058 $\pm$ 130 b	23

The number of undamaged or slightly damaged pine saplings was 952/ha and for silver birch 1343/ha. The number of pine and silver birch saplings with a stem defect increased with increasing stand density (Table 1). However, the proportion of damaged saplings decreased. Thus the number of undamaged saplings per ha was significantly greater in the dense part of the stand compared with the sparse one (Fig. 12).

## 4. Discussion and conclusions

**Feeding behaviour.** According to the optimal foraging strategy of large generalist herbivores, browsing intensity is highly affected by the digestibility, size and availability of the food item (Westoby 1974, Belovsky 1981). The digestibility of the tree species available in the present study has been reported as the best for rowan and aspen, relatively good for pine and at a lower, similar level for the birch species (Hjeljord et al. 1982, Salonen 1982, Bergström & Danell 1987). According to the present results, the utilization of the best digestible species in mixed young stands is intensive leading to a considerable reduce in their availability during the initial development of young stands. To what extent this leads to an increased use of other tree species evidently depends on moose density.

The browsing pattern observed in the present study shows that selective behaviour is pronounced when the amount of available food increases. The result is in accordance with the pattern of resource utilization by the moose found in experimental studies in which pubescent birch was used (Vivås & Saether 1987, Lundberg & Danell 1990). In addition, the mobility of moose in highly productive winter ranges has been reported to be greater than that on relatively unproductive ones, which is also associated with differences in the exploitation of food resources (Saether, Engen & Andersen 1989). The daily length of the moose track has been found to be smaller in conditions where mainly pine saplings are available, compared with mixed stands with great number of deciduous species (K. Nygrén, Finnish Game and Fisheries Institute, unpublished).

In the present study silver birch was found to be significantly more browsed than pubescent birch. Such a result has also been reported earlier (Danell et al. 1985, Danell & Ericson 1986), but not by Löytyniemi & Piisilä (1983). One possible reason for the differences between the birch species is the higher growth rate of silver birch, which increases the palatability and physical accessibility of plants (Bryant et al. 1983, Danell 1983, Danell et al. 1985). The difference in the present study was significant especially during the last winter. According to Danell & Ericson (1986), the preference of moose for silver birch is more distinct in the

case of relatively tall saplings. The reason for the preference for planted saplings compared with naturally regenerated ones may also lie in their different growth rate.

The total number of bites was greatest in pine and silver birch. The difference in biomass consumed was not estimated on the basis of weight. If it had been, the difference would evidently have been even more distinct. This is because the dry weight of pine and birch twigs of the same diameter has been estimated to weigh 2–2.5 times that of aspen and rowan (Bergström & Danell 1987, S. Härkönen, Finnish Forest Research Institute, unpublished). However, the number of bites well explains the biomass utilized within a single species (Vivås & Saether 1987).

The decrease in maximum bite diameter along with increasing food availability means that the digestibility of food eaten is correspondingly higher. The digestibility of e.g. rowan twigs of relatively thick diameter has been estimated to be better than that of silver birch twigs of very small bite diameter, which explains differences in the use of tree species (Hjeljord et al. 1982).

Rebrowsing of saplings occurred significantly on pine, but not on the birch species. According to Löytyniemi (1985), rebrowsing on pine can be explained by induced lush growth as well as by improved accessibility during the recovery, which presumably increase the probability of browsing. According to several years' monitoring in a moose pen, both of the birch species are significantly rebrowsed (Bergström 1984). The intensified growth rate after browsing leads to a greater likelihood of rebrowsing and *B. pendula* especially has a strong capacity for reproductive growth (Danell 1983). The observations made in the present study covered only a short period and the tendency of moose to break the main stems before or after starting to feed was prominent. Thus it was not possible to evaluate rebrowsing on birch using criteria totally comparable with earlier studies.

When the food supply on a winter range is abundant, the selective feeding behaviour by moose is pronounced. In this sense the removal of preferred broadleaved species from plantations in order to avoid intensive damage on pine or birch appears to be detrimental if it is not

compensated by a higher density of other species. However, considerable pine damage has been reported in plantations containing admixtures of preferred broadleaved trees (Lääperi & Löyttyniemi 1988, Heikkilä 1991). The presence of aspen has been reported to increase browsing intensity at the edges of planted areas (Edenius 1990). In conditions where there is abundant alternative food in mature forests, moose browsing in plantation areas is smaller (Thompson & Vukelich 1981).

*Stem breakage.* The habit of the moose to break off main stems of a relatively large diameter was a common occurrence in the present study. The moose also utilized to a great extent the twigs of saplings with earlier stem breakage. This phenomenon has been reported to be especially common during late winter, when the moose gather on winter ranges and their mobility is low (Sweaner & Sandegren 1989). Stem breakage is common even when a lot of smaller saplings are available. By breaking taller saplings the moose can considerably increase the availability of food and the breaking behaviour is probably innate or at least quickly learnt by the young calves (Telfer & Cairns 1978). Bryant & Kuropat (1980) assume that moose have adapted to utilizing the tops of taller trees because

of their low concentration of relatively indigestible secondary compounds.

Reducing the incidence of main stem breakage is an important goal from the silvicultural point of view. According to extensive inspection in young stands (Löyttyniemi & Piisilä 1983) the stem of every second pine browsed by moose is broken. In the present study the corresponding proportion on both pine and birches was over 60 %, showing relatively great browsing pressure. The distribution of breakage was related to stand density. The possibility of attaining a relatively large number of undamaged saplings is thus evident in a dense stand. The average number of pine and silver birch saplings without any serious damage in the present study was over 2200/ha. Continuing damage in subsequent years was, however, likely. According to Dinesman (1957), serious damage is to be expected if the area of available young and older plantations is below 30 ha/moose. In the present study the amount of plantations in the municipality in question was about 30 ha/moose during the last year of the study. Congregation of the moose population in their winter ranges, where the density may considerably exceed the average, was evidently the reason for the high level of damage.

## References

- Bedard, J., Crete, M. & Audy, E. 1978. Short-term influence of moose upon woody plants of an early seral wintering site in Gaspé Peninsula, Quebec. *Canadian Journal of Forest Research* 8: 407–415.
- Belovsky, G.E. 1978. The time-energy budget of a moose. *Theoretical Population Biology* 14: 76–104.
- 1981. Food plant selection by a generalist herbivore: the moose. *Ecology* 62: 1020–1030.
- Bergström, R. 1984. Re-browsing on birch (*Betula pendula* and *B. pubescens*) stems by moose. *Alces* 19: 3–13.
- & Danell, K. 1987. Moose winter feeding in relation to morphology and chemistry of six tree species. *Alces* 22: 91–112.
- & Hjeljord, O. 1987. Moose and vegetation interactions in Northwestern Europe and Poland. *Swedish Wildlife Research, supplement 1*: 213–228.
- Bryant, J.P. & Kuropat, P.J. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics* 11: 261–285.
- & Chapin III, F.S. & Klein, D.R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357–368.
- Coady, J.W. 1974. Influence of snow on behaviour of moose. *Le Naturaliste Canadien* 101: 417–436.
- Danell, K. 1983. Shoot growth of *Betula pendula* and *B. pubescens* in relation to moose browsing. *Alces* 18: 197–209.
- Huss-Danell, K. & Bergström, R. 1985. Interactions between browsing moose and two species of birch in Sweden. *Ecology* 66(6): 1867–1878.
- & Ericson, L. 1986. Foraging by moose on two species of birch when these occur in different proportions. *Holarctic Ecology* 9: 79–84.
- & Bergström, R. 1989. Winter browsing by moose on two birch species: impact on food resources. *Oikos* 54: 11–18.
- Dinesman, L.G. 1957. Materialy k lechohozjaistvennomu znatseniju losja v Evropeiskoi tsasti SSSP. Summary: Data on the importance of the elk to forestry in the European part of the USSR. *Bulletin Moskovskogo Obscestva Isp. Prirody, Otd. Biologii* 62: 5–12.
- Edenius, L. 1990. Moose browsing in relation to the spatial distribution of items. *Third International Moose Symposium, Abstracts*. p 63.
- Freeland, W.J. & Janzen, D.H. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *The American Naturalist* 108: 269–289.
- Heikkilä, R. 1990. The effect of plantation characteristics on moose browsing in Scots pine. *Silva Fennica* 24(4): 341–351.
- & Löyttyniemi, K. 1991. The effect of simulated moose damage on the development of young Scots pines. [Subm. for *Silva Fennica*].
- Hjeljord, O., Sundstøl, E. & Haagenrud, H. 1982. The nutritional value of browse to moose. *Journal of Wildlife Management* 46(2): 333–343.
- & Groenvold, S. 1988. Glyphosate application in forest-ecological aspects. *Scandinavian Journal of Forest Research* 3: 115–121.
- Kuznetsov, G.V. 1987. Habitats, movements and interactions of moose with forest vegetation in USSR. *Swedish Wildlife Research, supplement 1*: 201–211.
- Lundberg, P. & Danell, K. 1990. Functional response of browsers: tree exploitation by moose. *Oikos* 58: 378–384.
- Lääperi, A. & Löyttyniemi, K. 1988. Hirvituhot vuosina 1973–1982 perustetuissa männyn viljelytaimikoissa Uudenmaan-Hämeen metsälautakunnan alueella. Summary: Moose (*Alces alces*) damage in pine plantations established during 1973–1982 in the Uusimaa-Häme Forestry Board District. *Folia Forestalia* 719. 13 s.
- Löyttyniemi, K. & Piisilä, N. 1983. Hirvivahingot männyn viljelytaimikoissa Uudenmaan-Hämeen piiri-metsälautakunnan alueella. Summary: Moose (*Alces alces*) damage in young pine plantations in the Forestry Board District Uusimaa-Häme. *Folia Forestalia* 553. 23 s.
- 1985. On repeated browsing of Scots pine saplings by moose (*Alces alces*). *Silva Fennica* 19(4): 387–391.
- Monthly report of the climate in Finland. 1984–1988. Meteorological Institute.
- Repo, S. & Löyttyniemi, K. 1985. Lähiympäristön vaikutus männyn viljelytaimikon hirvivahinkoalttiuteen. Summary: The effect of immediate environment on moose (*Alces alces*) damage in young scots pine plantations. *Folia Forestalia* 626. 14 s.
- Risenhoover, K.L. & Maass, S.A. 1987. The influence of moose on the composition and structure of Isle Royale forests. *Canadian Journal of Forest Research* 17: 357–364.
- Saether, B-E., Engen, S. & Andersen, E. 1989. Resource utilization of moose *Alces alces* during winter. *Finnish Game Research* 46: 79–86.
- Salonen, J. 1982. Hirven talviravinnon ravintoarvo. Summary: Nutritional value of moose winter browsing plants. *Suomen Riista* 29: 40–45.
- Snyder, J.D. & Janke, R.A. 1976. Impact of moose browsing on boreal-type forests of Isle Royal National Park. *American Midland Naturalist* 95: 79–92.
- Sweaner, P.Y. & Sandegren, F. 1989. Winter-range philopatry of seasonally migratory moose. *Journal of Applied Ecology* 26: 25–33.
- Telfer, E.S. & Cairns, A. 1978. Stem breakage by moose. *Journal of Wildlife Management* 42(3): 639–643.
- Thompson, I.D. & Vukelich, M.F. 1981. Use of logged habitats in winter by moose with calves in north-eastern Ontario. *Can. J. Zool.* 59: 2103–2114.
- Vivås, H. & Saether, B-E. 1987. Interactions between a generalist herbivore, the moose *Alces alces*, and its food resources: an experimental study of winter foraging behaviour in relation to browse availability. *Journal of Animal Ecology* 56: 509–520.
- Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. *The American Naturalist* 108: 290–304.

Total of 36 references

## Instructions to authors — Ohjeita kirjoittajille

### Submission of manuscripts

Manuscripts should be sent to the editors of the Society of Forestry as three full, completely finished copies, including copies of all figures and tables. Original material should not be sent at this stage.

The editor-in-chief will forward the manuscript to referees for examination. The author must take into account any revision suggested by the referees or the editorial board. Revision should be made within a year from the return of the manuscript. If the author finds the suggested changes unacceptable, he can inform the editor-in-chief of his differing opinion, so that the matter may be reconsidered if necessary.

Decision whether to publish the manuscript will be made by the editorial board within three months after the editors have received the revised manuscript.

Following final acceptance, no fundamental changes may be made to manuscript without the permission of the editor-in-chief. Major changes will necessitate a new submission for acceptance.

The author is responsible for the scientific content and linguistic standard of the manuscript. The author may not have the manuscript published elsewhere without the permission of the publishers of Acta Forestalia Fennica. The series accepts only manuscripts that have not earlier been published.

The author should forward the final manuscript and original figures to the editors within two months from acceptance. The text is best submitted on a floppy disc, together with a printout. The covering letter must clearly state that the manuscript is the final version, ready for printing.

### Form and style

For matters of form and style, authors are referred to the full instructions available from the editors.

### Käsikirjoitusten hyväksyminen

Metsäntutkimuslaitoksesta lähtöisin olevien käsikirjoitusten hyväksymismenettelystä on ohjeet Metsäntutkimuslaitoksen julkaisuohjesäännössä.

Muista käsikirjoituksista lähetetään Suomen Metsätieteellisen Seuran toimitukselle kolme täydellistä, viimeisteltyä kopiota, joihin sisältyvät myös kopiot kaikista kuvista ja taulukoista. Originaaliaineistoa ei tässä vaiheessa lähetetä.

Vastaava toimittaja lähettää käsikirjoituksen valitsemilleen ennakotarkastajille. Tekijän on otettava huomioon ennakotarkastajien ja toimituskunnan korjausesitykset. Korjaukset on tehtävä vuoden kuluessa siitä, kun käsikirjoitus on palautettu tekijälle. Jos tekijä ei voi hyväksyä korjausesityksiä, hänen on ilmoitettava eriävä mielipiteensä vastaavalle toimittajalle tai toimituskunnalle, joka tarvittaessa ottaa asian uudelleen käsittelyyn.

Acta Forestalia Fennican toimituskunta päättää kirjoituksen julkaisemisesta ennakotarkastajien lausuntojen ja muiden ilmenneiden seikkojen perusteella. Päätös tehdään kolmen kuukauden kuluessa siitä, kun käsikirjoituksen lopullinen korjattu versio on saapunut toimitukselle.

Hyväksymisen jälkeen käsikirjoitukseen ei saa tehdä olennaisia muutoksia ilman vastaavan toimittajan lupaa. Suuret muutokset edellyttävät uutta hyväksymistä.

Tekijä vastaa kirjoituksen tieteellisestä asiasisällöstä ja kieliasusta. Tekijä ei saa julkaista kirjoitusta muualla ilman Acta Forestalia Fennican julkaisijoiden suostumusta. Acta Forestalia Fennicaan hyväksytään vain aiemmin julkaisemattomia kirjoituksia.

Tekijän tulee antaa lopullinen käsikirjoitus ja kuvaoriginaalit toimitukselle kahden kuukauden kuluessa hyväksymispäätöksestä. Käsikirjoituksen saatteesta pitää selvästi ilmetä, että käsikirjoitus on lopullinen, painoon tarkoitettu kappale. Teksti otetaan mieluiten vastaan mikrotietokoneen levykkeellä, jonka lisäksi tarvitaan paperituloste.

### Käsikirjoitusten ulkoasu

Käsikirjoituksen asun tulee noudattaa sarjan kirjoitusohjeita, joita saa toimituksesta.



- 219 Heliövaara, Kari, Väisänen, Rauno & Immonen, Auli.** Quantitative biogeography of the bark beetles (Coleoptera, Scolytidae) in northern Europe. Seloste: Pohjois-Euroopan kaarnakuoriaisten kvantitatiivinen eliömaantieteellinen analyysi.
- 220 Kuusela, Kullervo & Salminen, Sakari.** Suomen metsävarat 1977–1984 ja niiden kehittyminen 1952–1980. Summary: Forest resources of Finland in 1977–1984 and their development in 1952–1980.
- 221 Pohjonen, Veli.** Selection of species and clones for biomass willow forestry in Finland. Tiivistelmä: Biomassan viljelyyn sopivien pajulajien ja -kloonien valinta Suomessa.
- 222 Häme, Tuomas.** Spectral interpretation of changes in forest using satellite scanner images. Seloste: Metsän muutosten spektrinen tulkinta satelliittikelaikuvien avulla.
- 223 Finér, Leena.** Effect of fertilization on dry mass accumulation and nutrient cycling in Scots pine on an ombrotrophic bog. Seloste: Lannoituksen vaikutus männyn kuivamassan kertymään ja ravinteiden kiertoon ombrotrofisella rämeellä.
- 224 Heikkilä, Risto.** Moose browsing in a Scots pine plantation mixed with deciduous tree species. Tiivistelmä: Hirven ravinnonkäyttö lehtipuusekoitteisessa mäntytaimikossa.