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RISTO HEIKKILÄ & TIMO MIKKONEN

EFFECTS OF DENSITY OF YOUNG SCOTS PINE (*PINUS SYLVESTRIS*) STAND ON MOOSE (*ALCES ALCES*) BROWSING

MÄNNYNTAIMIKON TIHEYDEN VAIKUTUS HIRVEN RAVINNONKÄYTTÖÖN

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ACTA FORESTALIA FENNICA 231

EFFECTS OF DENSITY OF YOUNG SCOTS PINE (*PINUS SYLVESTRIS*) STAND ON MOOSE (*ALCES ALCES*) BROWSING

Männyntaimikon tiheyden vaikutus hirven ravinnonkäyttöön

Risto Heikkilä & Timo Mikkonen

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The study was carried out at Padasjoki, southern Finland, where moose density on the winter range had been over 1.5 individuals/km². Moose browsing intensity, expressed in terms of the number of twigs eaten and biomass used, increased with stand density (biomass). Total biomass consumption (dry weight) per sample plot and per sapling increased with greater total food availability, or per sapling. The number of bites increased, but the percentage biomass removed did not differ when stand density increased. We observed a relatively large bite size on the plots of low stand density. The quantity of food, which on average was of relatively low quality, was obviously important due to the benefit gained through reducing the search time.

The nutritive value of the browse, expressed in terms of chemical compounds indicating low food digestibility, was lower in the dense than in the sparse stand. However, the amount of crude protein and arginine were relatively high in the dense stand. We concluded that shading affected the nutritional status of saplings on high density plots.

Although the biomass removed by moose per sapling was high for low density plots, the remaining biomass was larger than that on the high density plots, owing to the relatively large twig biomass of saplings. The number of saplings per hectare without main stem breakage increased significantly as stand density increased.

Tutkimus tehtiin Padasjoella alueella, jolla hirven talvikannan tiheys oli ollut yli 1,5 yksilöä/km². Hirven syömien oksien lukumäärä ja oksabiomassan kulutus lisääntyi, kun männyntaimikon tiheys kasvoi. Biomassan kulutus mitattuna kuiva-aineen painona ja taimikohtainen kulutus oli sitä suurempi, mitä enemmän ravintoa oli tarjolla kaikkiaan tai tainta kohti laskettuna. Syötyjen oksien osuus saatavilla olevista lisääntyi taimikon tiheyden kasvaessa. Kulutetun biomassan osuudessa ei sensijaan ollut eroa, koska syödyt oksat olivat olleet suurempia harvassa kuin tiheässä taimikossa.

Tiheässä taimikossa oksien ravinteisuus, mitattuna sulavuutta osoittavilla tunnuksilla, oli alhaisempi kuin harvassa taimikossa. Raakaproteiinin ja arginiinin pitoisuudet olivat kuitenkin korkeampia tiheässä kuin harvassa taimikossa, mikä johtui ilmeisesti varjostuksesta. Tiheässä taimikossa ravinnon helppo saatavuus vähentää liikkumiseen kuluvaa aikaa ja saattaa sen tähden lisätä syöntiä.

Vaikka hirven tainta kohti kuluttama biomassa oli suurempi harvassa kuin tiheässä taimikossa, jäljelle jäänyt oksabiomassa oli kuitenkin suurempi harvassa taimikossa. Tämä johtui harvassa kasvaneiden taimien suhteellisen suuresta oksabiomassasta. Hehtaaria kohti laskettuna tiheässä taimikossa oli enemmän latvatuhoilta säästyneitä taimia kuin harvassa taimikossa.

Keywords: moose browsing, feeding behaviour, *Alces alces, Pinus sylvestris,* stand density, plant phenology.
FDC 174.7 *Pinus sylvestris* + 451 + 23

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Contents

1 Introduction

Forest management has greatly influenced moose feeding habitat by establishing young stands containing large amounts of suitable browse (Ahlén 1975, Cederlund & Markgren 1987). Scots pine (*Pinus sylvestris*) is highly used by the moose as a winter food because of its high availability (Bergström & Hjeljord 1987). According to Löyttyniemi & Piisilä (1983), Scots pine was the tree species most commonly used by moose in young pine stands in southern Finland. However, for Scots pine the relation of use to availability was about one half that of deciduous tree species. Morow (1976) reported, that 89 % of moose winter browse consisted of Scots pine.

The moose is a large generalist herbivore, adapted to using food items that are abundantly available but that have relatively low nutritional value. Consequently, food with a high content of easily digestible material has great value in food intake (Westoby 1974, Belovsky 1981). The nutritional value of browse in terms of quantity as well as quality (chemical content and digestibility) varies between plant species, and with plant phenology and environmental factors (Oldemeyer 1974). There is considerable seasonal variation in the quality of browse available for moose (Oldemeyer et al. 1977, Eastman 1983). The relatively low quality of winter foods emphasizes the importance of diversity for net energy intake. Allocating resources to defensive chemical compounds to reduce the nutritive value for herbivores is the means primarily used by plants adapted to poor growing conditions to affect plant-animal interaction (Coley et al 1985).

An increase in food abundance is suggested to lead to higher selectivity in the feeding behaviour of herbivores (Stenseth 1981). Studies on birch (Vivås & Saether 1987) showed, that an increase in food availability led to increased use of twig biomass and greater selectivity of twigs by moose.

It has been reported that the damage caused by moose to young coniferous trees depends on stand density, and is hence also related to silvicultural thinning (Thompson 1988). Moose often break the main stems of young trees that are of a thickness making them unsuitable for feeding. Stem breakage lowers the economic value of the trees (Heikkilä & Löyttyniemi 1992). The young pine stands that are in poor condition due to e.g. insufficient tree density, are exposed to moose damage (Lääperi & Löyttyniemi 1988, Heikkilä 1990)

From a silvicultural perspective, more information is needed about moose browsing and the characteristics of young pine stands to enable development of management strategies on moose ranges.

The purpose of this study was to obtain information about moose feeding behaviour in young Scots pine stands in relation to tree density. This paper examins the following aspects: 1. The response of moose browsing to quantitative differences in food supply in terms of varying tree density, 2. Moose feeding preferences in relation to the nutritional status of food at low and high tree density, 3. The effect of browsing in the young pine stand with respect to stem damage.

2 Material and methods

2.1 Field sampling

The study area was located at Padasjoki, southern Finland (25°00'–25°30'E, 61°15'–61°30'N). The field work was done in 1989–90. The average moose winter density per forest land area in the municipality was 0.76/km^2 in 1985–89 and the density on the winter range area was estimated to have exceeded 1.5/km^2 during several winters (unpublished information from the Game Management Association). We chose a 4 ha stand that had been regenerated naturally, growing on a dry forest site type. The plantation had been thinned in 1984 to stand density classes ranging from 2000 to 10000 trees/ha using ten squares of 0.25 ha (two per class). In addition,

two squares remained unthinned with densities of 12–15000. The density classes used were < 3600, 3601–5600, 5601–7600, 7601–9600 and > 9600 trees/ha. Nine sample plots (50 m^2 circles) were placed systematically per square at intervals of 12.5 m, for a total of 108 plots.

Moose had used the area unevenly, evidently because of variation in topography and distance of a forest road junction (cf. Repo & Löyttyniemi 1985, Heikkilä 1990). Thus, in order to exclude the effects of other characteristics than tree density, one over-browsed square situated on a hill, as well as one under-used square situated lowest and close to the road junction at the edge of the area, were omitted. Saplings were unevenly distributed on 27 of the sample plots the open, treeless area being more than one quarter of the total area. These plots were omitted in order to avoid the effect of uneveness on food quality and moose feeding behaviour (cf. Rosvall & Friberg 1989, Heikkilä 1990). Most of the latter plots had a relatively high tree density.

Sixty-three sample plots were examined and the number of trees included in the study was 2563. The total number of browsed twigs was counted on each plot for all saplings the height of which was one meter or more. Height (cm) of the saplings was measured. The total number of fecal pellet groups on the plots was counted.

2.2 Estimation of twig biomass

In order to measure twig biomass removed by moose, a subsample of 363 trees was systematically chosen among eight different stand densities. Regression equations calculated for total twig consumption and increasing stand density were compared between the total sample and subsample plots (y = 1110.9 + 14.6 x and y = 459.6 + 32.1 x). There was no significant difference between regression coefficients (the analysis of variance, df = 39, F = 1.19, p = 0.31). The diameter of all moose bites were measured separately on lateral tip shoots (the last shoots of main branches) and side shoots of these trees. To avoid the effect of drying of the twig end, the diameter was measured at about 1 cm from the biting point. The number of shoots available per tree for moose was counted over a height range of 50–250 cm.

Biomass consumed was determined using the twig diameter/weight method (Telfer 1969). The dry weight (g) (70 °C for 24 hours) for each bite diameter class was first calculated using ten randomly chosen twigs from three saplings in each stand density. The number of twigs eaten in each diameter class was then multiplied by the dry weights of the sample twigs. Available twig biomass was calculated by weighing twigs (equal or less than 5 mm) in each density class per one sapling of average height and average number of shoots available.

Stem damage was defined as 'serious' for trees repeatedly broken, or if the breakage was located below the current year leader shoot (cf. Heikkilä & Löyttyniemi 1992). The height (cm) and diameter (mm) of the breakages were measured. All the browsed shoots as well as otherwise broken stems were included when analysing the stem defects.

2.3 Chemical analyses

Chemical analyses were made in order to compare the nutritional status of the trees growing in sparse and dense position. Analyses included compounds related with nutritive value and digestibility. Twig material for chemical analyses was collected from low density (less than 3600 trees/ha) and high density (more than 9600 trees/ha) plots in March. Twenty lateral tip shoots and 40 side shoots were taken from both density classes for analysis from randomly sampled trees (2–3 shoots per tree). The shoots were cut at a height of ca. 1,5 m, corresponding to the typical feeding height of moose.

Crude protein was determined with the Brilliant Blue G method (Bradford 1976). The arginine was determined, because the occurrence of this amino acid, which is an important storage of nitrogen, is related to phenological aspects (Durzan 1970). The arginine concentration was determined accordingly with the method presented by Sakaguchi (1951) and Messineo (1966). The neutral detergent fiber (NDF) and acid detergent fiber (ADF) were determined using the method presented by Van Soest (1963) and Van Soest & Wine (1967).

Acid insoluble lignin (AIL) was determined from the ADF according to Van Soest (1965). The foliar nutrients were determined according to the out lines of Halonen and Tulkki (1981)

The data were statistically analysed using the multiple linear regression analyses, one-way analysis of variance and the Student t-test (BMDP-programs).

3 Results

3.1 Consumption of twig biomass

The average height of the saplings was 282 ± 7 cm, and there was no significant differences in height among the five stand density classes. The number of saplings browsed by moose increased significantly with increasing stand density (Fig. 1 a). On average 87 % (± 1 S.E.) of the trees had been browsed to some extent, showing that moose had frequently visited the plots. The percentage of browsed saplings remained constant irrespective of stand density (Fig. 1 b). The total number of fecal pellet groups averaged 1974/ha (± 90 S.E.) and it increased along with increasing stand density ($n = 63$, $r = 0.37$, $r^2 = 0.13$, $p < 0.01$).

Twig biomass per plot available to moose increased significantly with stand density ($n = 8$, $y = 8598.67 + 0.67x$, $r^2 = 0.62$, $p < 0.05$). Saplings on the low density plots had more shoots ($n = 8$, $y = 321.46 - 0.02x$, $r = -0.86$), a larger individual biomass and larger shoots than those on the high density plots (Table 1, Fig. 5). The total number of twigs used by moose increased with stand density, but the number of bites per sapling decreased (Fig. 2 a, b). Moose ingested more dry weight twig biomass when the total available biomass increased. The corresponding decrease in biomass consumption per sapling was relatively steep (Fig. 2 c, d). This is because the moose took larger bites of trees growing in a low-density position (Fig. 3). Consequently, the food intake per sapling increased significantly, as the biomass available per sapling increased (Fig. 4).

The moose browsed a higher proportion of available twigs on plots with greater stand density (Fig. 5 a). The browsed biomass as a percentage of total biomass (54.8 % ± 2.2 S.E.) was not dependent on the amount of biomass available. Consequently, owing to the larger than average biomass per sapling on the sparse plots, the biomass remaining per sapling after browsing was still relatively large (Fig. 5 b).

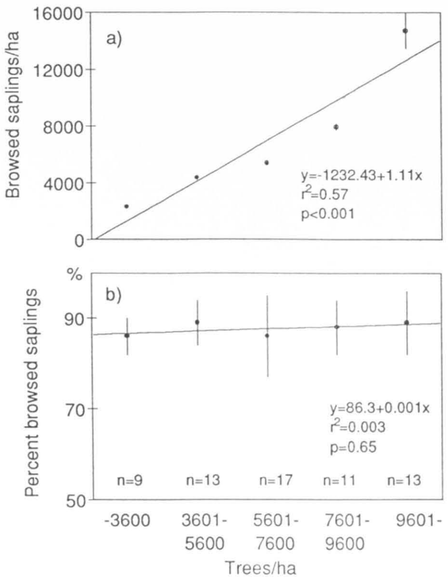

Fig. 1. a) Number of browsed saplings/ha (±S.E.) in relation to stand density ($df = 4$, $F = 63.58$, $p < 0.001$), b) percent browsed saplings (±S.E) in relation to stand density ($df = 4$, $F = 0.53$, $p = 0.71$).

Table 1. Size and dry weight of lateral tip shoots collected at 1.5 m height of saplings in sparse (< 3600 trees/ha) and dense (> 9600 trees/ha) stand (t-test).

	Shoot length cm ± S.E.	Shoot diameter mm ± S.E.	Shoot axis weight g ± S.E.
Sparse	21.3 ± 0.8	5.3 ± 0.2	0.9 ± 0.07
Dense	15.0 ± 0.5	3.7 ± 0.1	0.4 ± 0.03
p	< 0.001	< 0.001	< 0.001
n	40	40	40
	Needle length mm ± S.E.	**Needle weight g ± S.E.**	**Needle weight /shoot weight**
Sparse	40.6 ± 0.3	2.9 ± 0.2	3.4 ± 0.1
Dense	32.7 ± 0.3	1.4 ± 0.1	4.1 ± 0.2
p	< 0.001	< 0.001	< 0.05
n	400	40	40

3.2 Utilization of lateral and side shoots

The average diameter of the bites was 3.8 mm (± 0.025 mm S.E.) for the 363 trees representing different stand densities. Bite diameter reduced on denser stands (Fig. 3), where the proportion of bites with a diameter greater than 5 mm was 9.5 %. Thus the moose browsed little on the old parts of the branches.

The diameter of bites on the lateral tip shoots (5.4 mm ± 0.2 S.E.) was on average greater than the bites on the side shoots (3.7 mm ± 0.1 S.E.) ($df = 14$, $t = 8.20$, $p < 0.001$). The diameter of bites on the lateral tip shoots averaged 5.9 mm ± 0.2 S.E. in the low density stand (< 3600 trees/ha). This did not differ significantly from the base diameter of the lateral tip shoots (5.3 mm ± 0.2 S.E., $t = 1.88$, $p = 0.10$). On the contrary, the bite diameter of lateral tips in the dense stand (4.6 ± 0.1 S.E.) was significantly thicker than the twig base diameter (3.7 ± 0.1 S.E., $t = 5.06$, $p < 0.001$). Thus the moose utilized more of the older shoots in the dense stand compared to the sparse one.

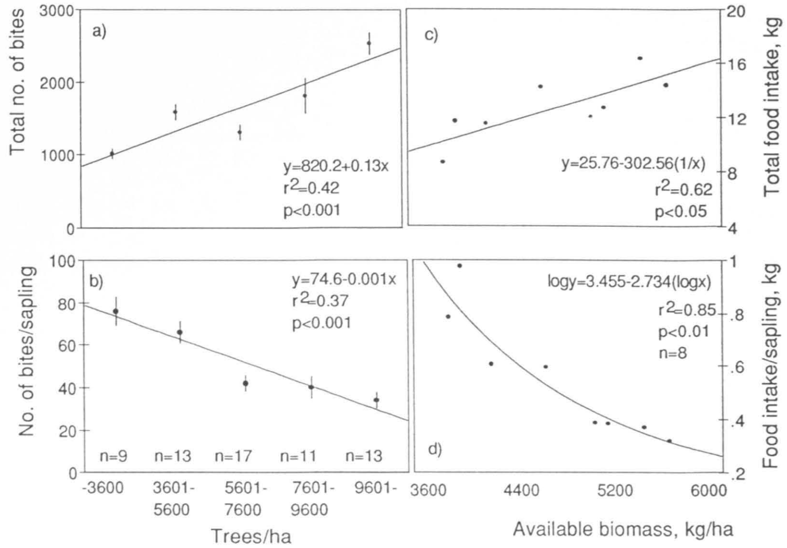

Fig. 2. a) total number of bites (±S.E.) in relation to stand density ($df = 4$, $F = 15{,}69$, $p < 0.001$) b) number of bites/sapling in relation to stand density ($df = 4$, $F = 13.34$, $p < 0.001$), c) food intake as dry weight in relation to total available biomass, measured from a subsample following the regression presented in Fig. 2a, d) food intake as dry weight/sapling in relation to total available biomass.

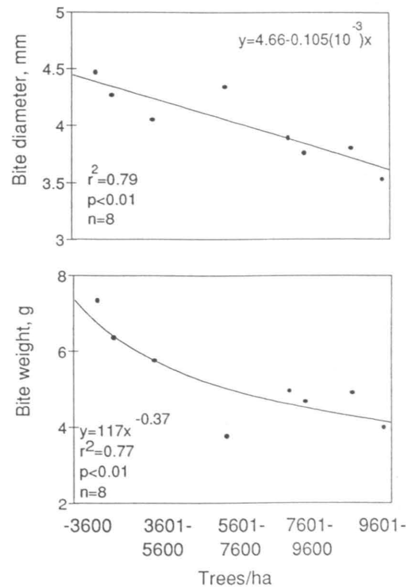

Fig. 3. Diameter and size (dry weight) of moose bites in relation to stand density.

The lateral tip shoots had been browsed more frequently (43.1 % ± 1.4 S.E., n = 8) than side shoots (35.3 % ± 1.0 S.E., n = 8)(t = 4.61, p < 0.01). The percentage of shoots used of shoots available was significantly greater for lateral tips (1.2 ± 0.1 S.E.), compared to side shoots (0.9 ± 0.02 S.E.) (t = 4.18, p < 0.01, n = 8), suggesting a preference for the former.

The number of available shoots/plot (6588 ± 689 S.E., n = 8, $r^2 = 0.87$, p < 0.001), as well as the proportion of lateral tips (14 % ± 1 S.E., n = 8, $r^2 = 0.73$, p < 0.01), increased with stand density. Thus the possibility of lateral tips being browsed was relatively high in the dense stand compared with the sparse one. The proportion of browsed lateral tips out of the total number of used twigs increased consistently with stand density (17 % ± 1 S.E., n = 8, $r^2 = 0.54$, p < 0.01). However, the ratio percentage lateral tips eaten/percentage available decreased slightly (n = 8, $r^2 = 0.59$, p < 0.05), indicating no increased preference for lateral tip shoots with increased stand density.

Lateral tip shoots on the least dense stand were larger than those on the densest stand (Table 1). The relationship between the needle weight and shoot axis weight was significantly higher in dense stand than in sparse stand. This indicates that a higher proportion of the food ingested by the moose consisted of needle biomass in the dense stand compared to the low density stand.

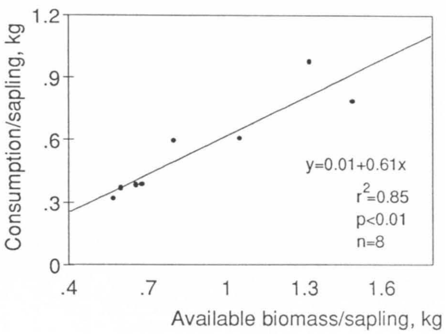

Fig. 4. Food intake as dry weight/sapling by moose in relation to biomass available/sapling.

3.3 Chemical analyses

The differences in the chemical composition of the lateral tip shoots were smaller than those of the side shoots (Table 2). The phosphorus and potassium content of shoots in the sparse stand were higher, and the sodium content higher in the dense stand. The lateral tip shoots in the dense stand contained more crude protein than those in the sparse stand. The arginine contents were significantly higher in both the lateral tips and side shoots in the dense stand. When comparing all shoots, also the contents of crude protein (n = 60, df = 118, t = 3.42, p < 0.001), ADF fiber (n = 60, df = 118, t = 2.81, p < 0.01) and lignin (n = 60, df = 118, t = 3.11, p < 0.01) were highest in the dense stand.

Several chemical components of side shoots from the sparse stand differed significantly from those in the dense stand. The acid detergent fiber and lignin contents of the side shoots in the dense stand were higher. The crude protein contents were the same, but the phosphorus and potassium contents of the low density class were higher.

The lateral tip shoots of the sparse stand contained less fiber (ADF) than the side shoots (df = 58, t = 3.94, p < 0.001), and also less lignin (df = 58, t = 2.56, p < 0.05) (Table 2). Corresponding differences for fiber (df = 58, t = 3.44, p < 0.01) and lignin (df = 58, t = 3.73, p < 0.001) in the dense stand were also significant.

The ratio (K · Ca)/Mg was greater for the lateral tip shoots in the sparse stand (16.1 ± 1.1 S.E.) than for those in the dense one (13.2 ± 0.7 S.E.)(df = 38, t = 2.27, p < 0.05) and also greater for the side twigs in the sparse stand (14.5 ± 0.7 S.E. and 11.5 ± 0.5 S.E.) (df = 78, t = 3.42, p < 0.01). No difference was found in the Ca/P ratio between either the sparse and dense stand, or between the lateral and side shoots.

Table 2. Chemical content (% dry weight) of lateral tip (n = 20) and side twig (n = 40) shoots collected from sparse (< 3600 trees/ha) and dense (> 9600 trees/ha) stands.

	Lateral tip shoots		Significance (t-test)		Side twig shoots		Significance (t-test)	
	Sparse	Dense	t	p	Sparse	Dense	t	p
	%				%			
Ash	2.0	1.9	2.06	NS	1.7	1.6	1.02	NS
Dry matter (%105°)	94.0	94.0	0.59	NS	95.8	94.6	6.01	0.000
P	0.16	0.14	3.46	0.002	0.14	0.11	4.97	0.000
K	0.52	0.46	2.92	0.006	0.52	0.40	6.22	0.000
Ca	0.11	0.11	0.68	NS	0.10	0.09	2.53	NS
Na	0.0013	0.0014	–2.15	0.04	0.0017	0.0015	0.99	NS
Crude protein	4.3	5.3	–3.86	0.001	4.8	5.0	1.39	NS
Arginine	0.26	0.42	–3.42	0.002	0.34	0.48	–5.79	0.000
Fibre NDF	55.0	57.5	–2.56	NS	56.5	56.6	–0.08	NS
Fibre ADF	41.1	42.6	–1.86	NS	43.7	45.0	–2.48	0.01
Lignin	15.5	16.4	–1.71	NS	17.0	18.5	–3.00	0.004

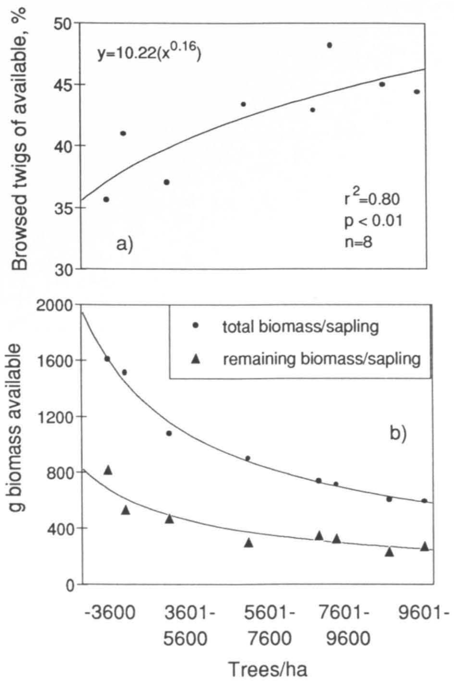

Fig. 5. a) proportion available browsed twigs of in relation to stand density, b) total biomass available per sapling (n = 8, $y = 632411.06 \cdot x^{-0.76}$, $r^2 = 0.85$) and biomass left after moose browsing (n = 8, $y = 254917.53 \cdot x^{-0.75}$, $r^2 = 0.73$) in relation to stand density.

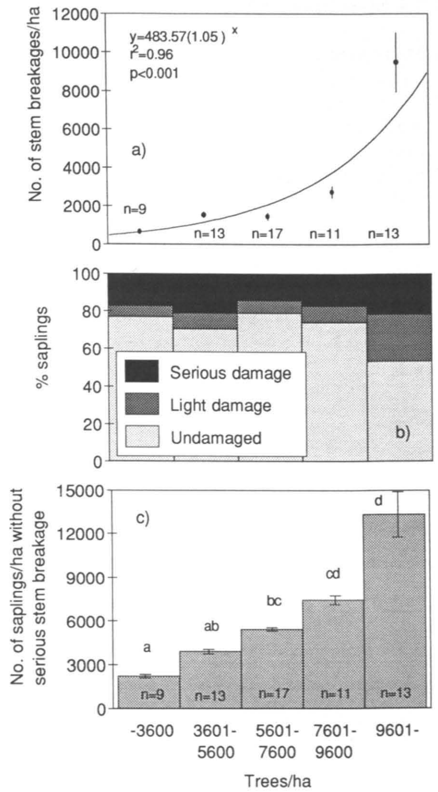

Fig. 6. a) number of stem breakages (±S.E.) caused by moose in relation to stand density, b) proportion of different damage classes, c) number of trees/ha (±S.E.) without serious stem breakage in relation to stand density. Different letters = significant difference (df = 4, Kruskal-Vallis Z = 2.81, p < 0.05).

3.4 Stem breakages

Main stem breakage occurred commonly, and on average 35 % of the saplings had been broken at least once by moose. The number of stem breakages/ha increased significantly with stand density (Fig. 6 a). The trees broken repeatedly or those broken at the points older than current leader shoot, and thus regarded as seriously damaged, were in equal proportions in different stand density classes (Fig. 6 b). Thus the number of saplings with no serious stem damage increased with stand density (Fig. 6 c).

The average height of the broken trees (190 cm ± 2 S.E., n = 886) was significantly smaller than that of unaffected trees (257 cm ± 2 S.E., n = 1677)(df = 2561, t = –20.20, $p < 0.001$). The height of the trees broken only once (29 % of total) was 191 cm (± 2 S.E., n = 745) and the height of those broken twice (5 % of total) was 183 cm (± 4 S.E., n = 137). Trees were broken three times in only four cases and they were incapable of further development.

The average thickness at the point of stem breakage was 11 mm (± 3 S.E., n = 885). The thickness of the breakage point on current leader shoots was 7 mm (± 0.1 S.E., n = 323) and that for one-year old main stem shoots 16 mm (± 0.4 S.E., n = 87). The thickest breakage point was 45 mm.

4 Discussion

Feeding behaviour. According to Belovsky (1978) moose can be characterized as energy maximizers rather than as time minimizers with foraging being predictable in a quantitative manner. Thus the quantity of readily available food is the primary influence on choice of food intake, provided that the constraints set by limitations in quality are low enough.

In the present study, the increase in food availability in terms of stand density (biomass) led to an increased food intake. This foraging pattern, implying that patches with high food availability are intensively browsed, suggests that moose used the available food resource in a manner which shortens the search time. In addition, the possibility that moose ingested large bites resulted in declined harvest rate, but in increased dry matter intake rate (Risenhoover 1987). An increase in tree biomass resulted in increased handling time per tree, and the amount of food consumed became relatively large along with greater available biomass (Åström et al. 1990). Increased bite rate of black-tailed deer, as a result of high bite density, led to reduced proportion of rumen processing time and thus intake rate declined (Spalinger et al. 1988).

According to Vivås & Saether (1987), moose select browse primarily for quality when feeding on saplings of the same size in a dense position, compared to in a sparse position. Assessing bite diameter is of importance, because an increase in the bite diameter leads to lower digestibility of food (Hjeljord et al. 1982). Selective browsing in relation to food availability leads to decreasing diet handling time in rumen processing (Spalinger et al. 1986).

In the present study, a decrease in bite diameter along with increasing stand density did not indicate improved food quality, because saplings growing in a dense position had relatively small twigs. Owing to high fiber and lignin content of twigs and the location of the bite-off points on older parts of branches, food ingested on the densest plots was of relatively low quality with respect to digestibility (Hjeljord et al. 1982, Renecker & Hudson 1985, Hoffmann 1989). Our results did not support the concept of more selective feeding behaviour by moose with an increase in young stand density.

Thompson et al (1990) reported that moose showed a high preference for thinned stands of *Abies balsamea* over the unthinned ones. Their thinned stands had larger twigs of significantly better quality than in dense stands, based on relatively good digestibility and high nutrient content. The stand density was substantially higher (three times those in the present study) in their unthinned stand.

Shading has a strong effect on the metabolism of soluble nitrogen especially in shade intolerant pine (*Pinus ponderosa*) compared to white spruce (*Picea glauca*) (Durzan (1970). For instance, shading results in the accumulation of amino acids, especially arginine, which is known to be a storage compound of nitrogen. The amount of arginine varies seasonally, and the highest concentration occurs during winter (Lähdesmäki & Pietiläinen 1988). Nitrogen content has been reported to be at high level consistently with high protein and arginine concentration (Pietilä et al. 1991, Pietiläinen et al. 1991). The importance of these changes for feeding behaviour and digestion, (e.g. possible benefits for the nitrogen metabolism of moose due to the increased amino acid/protein ratio) are not well known.

Crude protein content (Scwartz et al. 1987), was highest in the shoots of trees in our most dense stand. We believe that this resulted from the shading effect, which has been reported to increase not only crude protein, but also the fiber and lignin contents of plants (Blair et al. 1983). Thus, digestibility of the food in shade was reduced, making it more difficult for moose to derive benefit from the high protein content. The larger (K · Ca)/Mg ratio of the sparse stand indicates a possibility for higher Ca intake (cf. Lindlöf et al. 1978). Nitrogen fertilization, but not shading, is reported to increase the use by moose of young pines (Edenius 1992).

Plant secondary compounds, such as resins, influence optimal food choice (Freeland & Janzen 1974, Bryant et al. 1983, Coley et al. 1985). According to Löyttyniemi & Hiltunen (1978) and Haukioja et al. (1983) no marked differences in secondary compounds are to be expected within Scots pines of the same origin. Thompson et al. (1990) did not find correlation between some secondary compounds and moose browsing intensity, when comparing different stand densities. Pinifolic acid has been reported to correlate negatively with moose browsing intensity (Danell & Yazdani 1990). The concentration of pinifolic acid is higher in sun needles than in shade needles (Gref & Tenow 1987). Relatively high biomass consumption by moose in the dense stand possibly reflects a lowered carbon-based defense as a result of low light intensity (Bryant et al. 1983).

Our results suggested that the nutritive value of the Scots pines is low. The content of crude protein was lower than a reported minimum dietary value for moose (Schwartz et al. 1987), and also lower than those reported for pine in other studies (Löyttyniemi 1981, Salonen 1982). The values for P, K, Ca, and especially Na were also lower than required for ruminants (Van Soest 1982). The forest site types in the experimental area were slightly less fertile than average. Moose using a low quality diet should increase their intake as we observed in our study (Schwartz et al. 1988), compared to moose in good condition using a high quality diet. This implies that the browsing pressure per tree is relatively small in moose winter ranges with a high food supply of sufficient quality.

The relatively intensive use of lateral tip shoots probably reflects their higher quality compared to side shoots. However, their large size as well as position on the branches may also influence use (Danell et al. 1985). In the sparse stand lateral shoots were prominently available, which obviously affected the feeding rate. Löyttyniemi (1985) suggested that large needle size, rather than chemical composition, explained rebrowsing of Scots pine. In addition, Niemelä & Danell (1988) have reported moose derive benefit by collecting more biomass if they choose large shoots. The effects of quantitative and qualitative aspects on food choice are difficult to distinguish (Owen-Smith & Novellie 1982). In our study, preference for lateral tip shoots was not correlated with stand density.

Effect of browsing. The amount of browsing per sapling, calculated in terms of number of twigs removed, as well as biomass taken, was highest on the low-density plots. However, owing to the large biomass of saplings on sparse plots, the browsing pressure per sapling (percent biomass removed) did not cause a significant depletion of twig biomass (cf. Danell & al. 1992). On the contrary, the recovery capacity was best for trees growing in a less dense position. This result agreed with evidence presented by Lundberg & Danell (1990), who suggested that moose showed a decelerated functional response to both increasing tree density and total available biomass.

According to Danell et al. (1991), the pines growing on low productive soil suffer more of browsing due to the relatively large number of moose bites. The biomass consumed, however, is the largest on well-grown pines, which are relatively rich in mineral nutrients as well as easily digestible. The results of our study emphasize the effect of tree density on biomass availability. Owing to the small difference in the percentage of biomass removed per tree, a dense stand is suggested to be relatively resistant against browsing. According to Edenius et al. (1992) densely-grown pines compensate more intensively than open-grown pines for lost biomass.

Thompson (1988) reported stem breakage in high density stands to be significantly less than in low density stands. Compensative height growth after stem breakage is considerable in the young pines broken at current leader or second main stem shoot (Heikkilä & Löyttyniemi (1992). Our results for stem breakage supported those obtained in a young Scots pine stand with an admixture of deciduous trees (Heikkilä 1991), suggesting that a dense stand is relatively resistant against moose damage.

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