Moose Alces alces bite diameter selection in relation to twig quality on four phenotypes of Scots pine Pinus sylvestris

Authors: Jia, Jingbo, Niemelä, Pekka, and Danell, Kjell

Source: Wildlife Biology, 1(1) : 47-55

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1995.009

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 07 Jun 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Moose *Alces alces* bite diameter selection in relation to twig quality on four phenotypes of Scots pine *Pinus sylvestris*

Jingbo Jia, Pekka Niemelä & Kjell Danell

Jia, J., Niemelä, P. & Danell, K. 1995: Moose *Alces alces* bite diameter selection in relation to twig quality on four phenotypes of Scots pine *Pinus sylvestris*. - Wildl. Biol. 1: 47-55.

The bite diameter selection by moose in relation to twig quality on four phenotypes of Scots pine was studied on the basis of a field cafeteria experiment. Comparison of twig quality was made among: 1) phenotypes, 2) different twig diameters, and 3) mean moose bite diameters. Chemical and morphological analyses of the trees indicated that twig fibre and tree/shoot size strongly affected moose bite diameter choice. Sight and chewing sensation are suggested to be the main browsing strategies used by moose. Moose adjusted the bite diameter among phenotypes on the criterion of similar food quality. The factors involved may play a multiple role in affecting moose foraging. Quantitative features of trees had no significant effects on moose bite diameter selection.

Key words: Alces alces, bite diameter, feeding selection, moose, Pinus sylvestris, Scots pine, twig quality.

Jingbo Jia & Pekka Niemelä, Department of Forest Ecology, Finnish Forest Research Institute, SF-01301 Vantaa, Finland.
Kjell Danell, Department of Animal Ecology, Swedish University of Agricultural Science, S-901 83 Umeå, Sweden.

Received 10 August 1994, accepted 4 January 1995.

Associate Editor: Bernt-Erik Sæther

Food selection by free-ranging animals is based on the animals' perception of the cost-benefit constraints imposed when different foods are sought and ingested (Robbins 1983). The multiplicity of factors influencing food choice by ruminants has long been known (Arnold & Hill 1972). Determining the diameter at which to clip a shoot or twig (i.e. the bite diameter) is a decision which a herbivore must face each time it encounters a suitable woody plant. An optimal clipping diameter may maximise the benefit and minimise the cost (Vivås et al. 1991). The concept of trade-off between factors has been widely accepted (Stephens & Krebs 1986) and discussed, with different emphasis being placed on the chemical defence of the food plant (Palo et al. 1992) or on the time spent in browsing (Vivås et al. 1991).

It seems reasonable to assume that, if the browsed twig had an equal food quality in every part of the twig irrespective of diameter or if there was even higher quality in the thicker part of the twig, the animals would tend to clip as thick a twig as possible in order to satisfy their needs for nutrients/energy at a given time. However, food quality is generally lower in the thicker part of the twig (Hjeljord 1987, Vivås & Sæther 1987) and, therefore, there should be an optimal bite diameter at which the benefits of nutrition or energy obtained are balanced with the costs of time or the energy spent.

In an earlier paper (Danell et al. 1991), we reported that moose *Alces alces* took smaller diameters but more bites per tree from the Scots pine *Pinus sylvestris* phenotype with the lowest productivity, the converse being that fewer but larger bites per tree were taken from the phenotype with the highest productivity. This suggested that moose browsing was associated with bite diameter selection.

The aim of this study is to examine moose winter browsing on four phenotypes of Scots pine representing a gradient of plant productivity and to determine the relationship between bite diameter selection and the nutritional quality of twigs. Primarily we were interested in the following questions: 1) why do moose take different sized bites on different phenotypes of Scots pine, 2) are there chemical differences between twigs of different diameters and how do moose perceive twig quality, 3) do moose select bite diameter according to the same nutritional criteria and which factors affect selection?

Material and methods

Pine phenotypes

Two hundred and eighty unbrowsed, single-stemmed, 2-metre-high Scots pines of four different phenotypes (70 trees of each) were randomly cut from four habitat types on the northern coast of Sweden (63°45'N, 20°0'E) in late autumn, after the ground was frozen. Two hundred of these (50 of each phenotype) were exposed to moose browsing in a field cafeteria experiment from 12 November 1984 to 12 April 1985 in a study area of about 7 km^2. In total, 50 feeding stations were established at intervals of 150 metres. At each station, four pines (one of each phenotype) were "planted" in holes in the ground, one at each corner of a square with sides two metre long. Sixty of the pines (15 of each phenotype) were selected for analysis of mineral content, IVDMD (*in vitro* dry matter disappearance), and ether soluble fraction. Another 16 trees (4 of each phenotype) were selected for fibre and DMD (dry matter disappearance) analyses.

The four phenotypes of pine are referred to as 1) LP: low productivity (yield <1 $m^3.ha^{-1}.yr^{-1}$; mean age ± SD: 58 ± 14 years) growing in a mire habitat; 2) MPO: medium productivity (3 $m^3.ha^{-1}.yr^{-1}$; 38 ± 8 years) with competition from an overstory of mature pines in a sandy soil habitat; 3) MP: medium productivity (3 $m^3.ha^{-1}.yr^{-1}$; 9 ± 1 years) without overstory, also in sandy soil habitat (note that the labelling of MPO and MP is somewhat different from Danell et al. (1991), in which they were referred to as MPO^+ and MPO^-, respectively); 4) HP: high productivity (6 $m^3.ha^{-1}.yr^{-1}$; 6 ± 1 years) in a moraine habitat.

Morphology of different Scots pine phenotypes

Morphological characteristics were measured on samples of each phenotype (see Danell et al. 1991 for details). The average number of current annual shoots (CAS) per tree in the four phenotypes was counted. As 90% of moose bites involved twigs with a diameter of less than 4.8 mm, all twigs with a diameter of less than 4.8 mm were regarded as biomass available to moose.

Chemical analysis

Three twigs in each millimetre-class of 2 to 6 (3 to 5 mm in most cases) were taken randomly from three parts (0-66 cm, 67-133 cm, and 134-200 cm above the ground, respectively) of the tree. The twigs were dried at 70°C for 24 hours and milled to pass through a 1.0 mm screen.

The content of nitrogen (N) was determined by the Kjeldahl method. Sodium (Na), potassium (K), calcium (Ca) and magnesium (Mg) contents were determined using an atomic absorption spectrophotometer. Total nutrient concentration was calculated by summing up the concentrations of all five minerals. The ether soluble fraction was extracted in petroleum ether for four hours in a Soxhlet apparatus. Dry matter disappearance (DMD) was measured at the end of 24, 48 and 96 hour periods using the nylon bag technique in a non-lactating cow, using 4 mm twigs (Danell et al. 1991). In order to test the difference in digestibility of different diameters, IVDMD was measured at the end of a 24-hour period on 3 and 4 mm diameter twigs using the one-step method as described by Den Braver and Eriksson (1967). We used sheep rumen liquor in the IVDMD analysis because Hjeljord et al. (1982) concluded that the relative quality of different species of browse for moose can be accurately sampled using *in vitro* techniques with sheep rumen liquor. Neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin were determined according to Van Soest (1963) and Van Soest & Wine (1967, 1968).

The inhibitory effect of defensive materials on digestibility (Palo et al. 1992) was calculated by the formula: Inhibition = 100% - (UDM% + DMD%), where UDM is indigestible material such as NDF, ADF or lignin, and DMD is the dry matter disappearance.

Factors, comparisons and statistical tests

The factors used in the analysis include the nutrient and defensive chemicals, the DMD and IVDMD, the biomass availability and several morphological features of the tree (see Table 5).

We compared chemical concentrations or twig digestibility between the four pine phenotypes in three aspects: 1) the difference in the whole twig by using the pooled diameter classes of 3 to 5 mm to reveal phenotypic variation in twig quality; 2) the linear trend between twig diameters to reveal the diameter variation of twig quality; and 3) the difference in the content value at the mean moose bite diameters (i.e. LP 2.80 mm, MPO 2.78 mm, MP 3.49 mm and HP 4.17 mm, see Fig. 1) to reveal the difference in the amount of nutrients or plant defensive materials consumed, or the digestibility of twigs consumed by moose when they browsed different phenotypes.

The linear trend between diameters and the trend variation among phenotypes were examined using the Gurevitch & Chester (1986) method, in which a positive trend (+) with $P<0.05$ shows that the chemical content increases significantly, while a negative trend (-) means that the

Table 1. Numbers of moose bites per tree, numbers of current annual shoots (CAS) per tree and available biomass recorded on the four phenotypes of Scots pine*.

Phenotype	No of moose bites/tree (N = 43)	No of CAS/tree (N = 15)	Available biomass (g) (N = 42)
LP	79_a ± 66	322_a ± 160	289_a ± 21
MPO	36_b ± 28	83_b ± 62	113_b ± 16
MP	38_b ± 28	205_c ± 101	209c ± 15
HP	31_b ± 20	187_c ± 83	238_d ± 18

* Means and standard deviations are presented. Means with the same letter do not differ statistically (Wilcoxon test, P<0.05). The four phenotypes are low productivity (LP), medium productivity with overstory (MPO), medium productivity without overstory (MP), and high productivity (HP). N = sample size.

chemical content decreases significantly, with increasing twig diameter.

Results

Number of moose bites and bite diameter distributions

The mean number of moose bites per tree recorded was significantly higher on phenotype LP than on the other three phenotypes among which no differences were registered (Table 1).

Mean moose bite diameters were larger in the phenotypes of higher productivity, HP and MP, (χ^2-test, P<0.001) than in the phenotypes of lower productivity, LP and MPO, (Fig. 1), where smaller means were found (P<0.001).

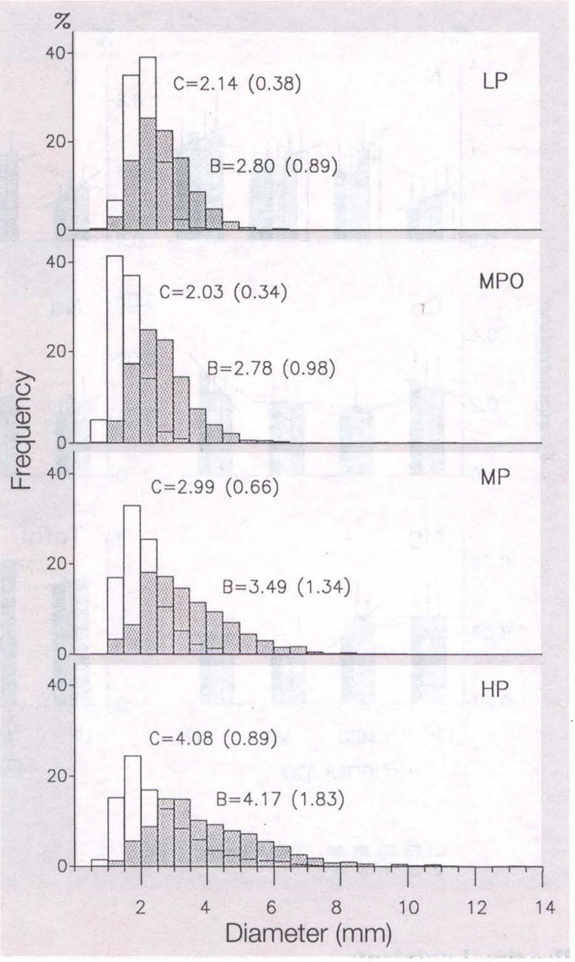

Figure 1. Frequency distributions of moose bite diameters (B, shaded bars) and current annual shoot diameters (C, open bars) in the four Scots pine phenotypes, LP, MPO, MP and HP (see Table 1 for definitions). Means and SD (in brackets) are given in mm.

Table 2. Linear trends and ANOVAs of twig quality parameters among different diameters. For explanation of the method see the text and Gurevitch & Chester (1986). "Interaction" tests the hypothesis of equal linear trends in the four phenotypes; n.s. = P>0.05

Parameter	Linear trend	F	P	Interaction F	P
Nitrogen (N)	-0.202	20.82	<0.001	0.50	n.s.
Potassium (K)	-0.093	21.95	<0.0001	0.11	n.s.
Sodium (Na)	+0.002	1.44	n.s.	1.21	n.s.
Calcium (Ca)	-0.011	0.06	n.s.	1.62	n.s.
Magnesium (Mg)	-0.008	2.58	n.s.	0.57	n.s.
Total nutrients	-2.039	23.72	<0.001	0.74	n.s.
Dry matter	+0.157	0.12	n.s.	0.38	n.s.
Ether sol. fraction	+0.685	5.82	<0.05	0.37	n.s.
IVDMD*	-1.51	14.56	<0.001	0.98	n.s.
Fibre (NDF)**	+3.237	13.42	<0.001	0.34	n.s.

* IVDMD: *in vitro* dry matter disappearance, ** Only tested in two phenotypes, MP and HP (see Fig. 4)

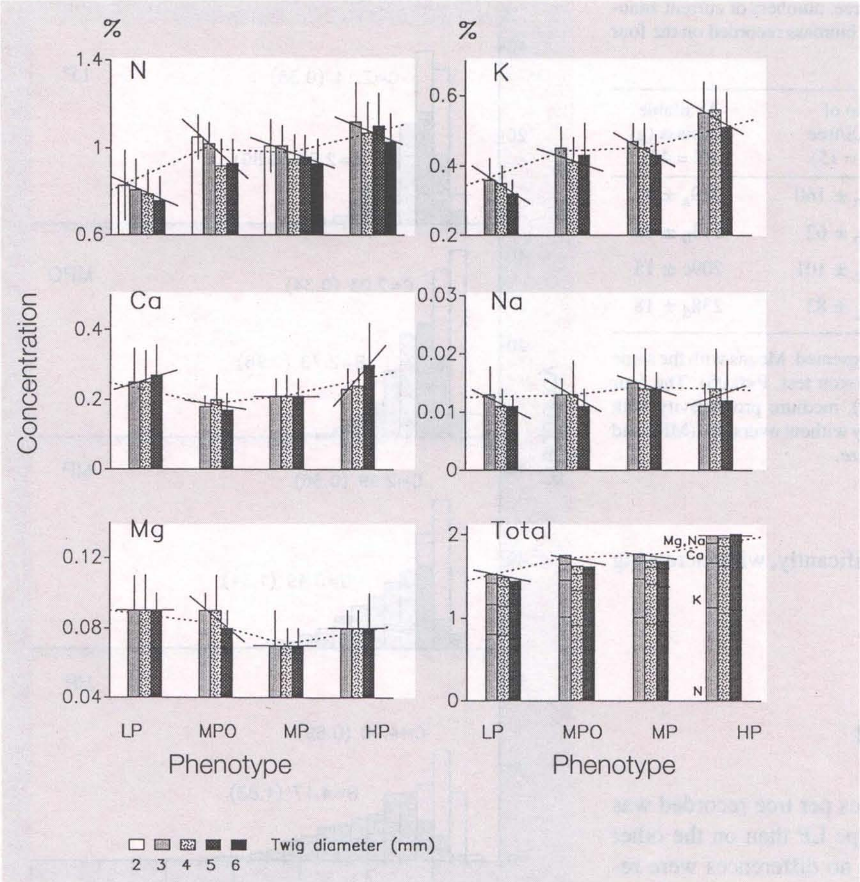

Figure 2. Mean mineral nutrient concentrations (% of dry matter) according to twig diameter classes (2-6 mm) for the four Scots pine phenotypes. Broken lines indicate concentrations at mean moose bite diameters. Standard deviations are indicated by the vertical line.

Proximal nutrients

Of the five nutrients, N and K concentrations increased significantly (ANOVA, $F = 27.0$, $P<0.001$ and $F = 40.49$, $P<0.001$ respectively) with phenotype productivity (Fig. 2); Ca and Na did not increase significantly ($P>0.05$), and Mg was higher in phenotypes of low productivity ($F = 13.42$, $P<0.001$). Significant increase was seen in the concentration of total mineral nutrients according to phenotype productivity from LP to HP ($F = 37.22$, $P<0.001$).

While the N and K concentrations decreased significantly as the twigs became thicker (Table 2, Fig. 2), concentrations of Ca, Na and Mg did not. The total mineral nutrients showed a significant decreasing trend (except for HP) with increasing twig thickness. The interaction component used to test the hypothesis that linear trends in the four phenotypes are equal showed no significant difference in the trend among phenotypes in any case (Table 2). Thus the four phenotypes behave in similar ways in relation to twig diameter.

When comparing the content value at the mean moose bite diameters, all mineral nutrients showed similar concentrations among phenotypes (Fig. 2); N ($\chi^2 = 0.045$, $P>0.99$), K ($\chi^2 = 0.033$, $P>0.99$), Ca ($\chi^2 = 0.014$, $P>0.99$), Na ($\chi^2 = 0.00013$, $P>0.99$), Mg ($\chi^2 = 0.00255$, $P>0.99$), and total mineral nutrients ($\chi^2 = 0.067$, $P>0.99$).

Dry matter

The dry matter content of twigs differed significantly between the four phenotypes (ANOVA, $F = 12.31$, $P<0.001$); the highest content was found in MPO and LP (Fig. 3). No difference was found in the different twig diameters (Table 2). When compared at the mean moose bite diameters, the four phenotypes showed no difference ($\chi^2 = 0.178$, $P>0.98$) though a slightly higher dry matter content was found in the phenotypes of low productivity, LP and MPO.

The declining relationship found between the dry matter content (D) and the bite diameter (B) of the four phenotypes ($D = 54.08B^{-0.18}$, $r = -0.93$, $P<0.01$) might be a reflection of water and/or fibre content.

Ether soluble fraction

The ether soluble fraction did not differ significantly (ANOVA, $P>0.05$) between phenotypes (Fig. 3), but an

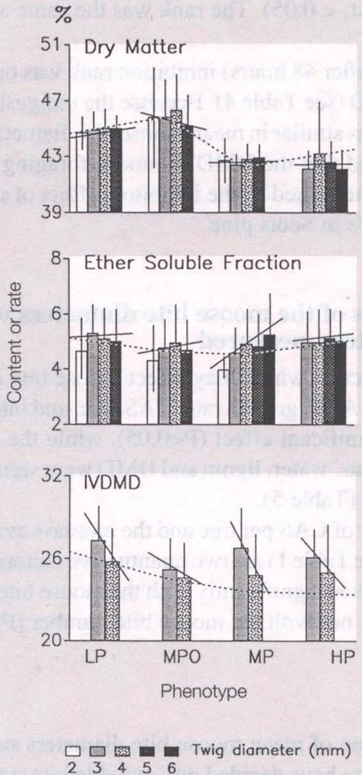

Figure 3. Mean contents of dry matter (%), ether soluble fraction (% of dry matter) and IVDMD (%) according to twig diameter classes (2-6 mm) for the four Scots pine phenotypes. Broken lines indicate contents at mean moose bite diameters. Standard deviations are indicated by the vertical line.

increase trend was observed in general (except for LP) as the twig diameter increased (Table 2, Fig. 3). When compared at the mean moose bite diameters, the concentration of ether soluble fractions did not differ among phenotypes ($\chi^2 = 0.079$, $P>0.99$), but was slightly higher in LP and HP and lower in MPO and MP.

IVDMD

The IVDMD values were similar between phenotypes (ANOVA, $P>0.05$) when comparing pooled diameters of only 3 and 4 mm (Fig. 3), but decreased in larger twigs (Table 2, Fig. 3). The IVDMD at the mean moose bite diameters was similar ($\chi^2 = 0.1499$, $P>0.98$) among the four phenotypes.

IVDMD was positively correlated with a number of chemical parameters in all phenotypes but HP (Table 3). Unexpectedly, the ether soluble fraction had a positive effect on IVDMD in all phenotypes and significantly in LP and MPO.

Fibre and lignin

Neither NDF, nor ADF, nor lignin content differed significantly between the four phenotypes (ANOVA, $P>0.05$) in the 4 mm diameter twigs (Table 4). However, the lignin content in phenotype HP where the mean moose bite diameter was the largest, was obviously lower than in the other three phenotypes LP, MPO and MP.

Although we did not analyse the fibre contents of individual diameter classes in LP and MPO, the results from MP and HP indicate that the NDF content increased significantly with increasing twig diameter (Table 2, Fig. 4) and was mainly determined by the NDF content of twig stems rather than that of needles (Fig. 4). Comparison at the mean moose bite diameters in these two phenotypes also showed similar NDF content (χ^2-test, $P>0.99$), which suggested that the moose browsed the different Scots pine phenotypes at the same level of fibre content as well.

DMD and inhibitory effect

As in IVDMD, the DMD showed no significant difference between phenotypes after 24 hours (Table 4; ANOVA, $P>0.05$). At this time, the NDF% + DMD% was over 100%, but the ADF% + DMD% was below 100% in all phenotypes. The inhibitory effect based on the ADF

Table 3. Correlations between IVDMD and chemical parameters of the four phenotypes of Scots pine (see Table 1 for definition). The twig diameter classes, 2 and 3 mm, were pooled. The Pearson correlation coefficient (r) and N = sample size of twigs, are given. *P<0.05, **P<0.01.

Phenotypes/	LP		MPO		MP		HP	
Parameters	r	N	r	N	r	N	r	N
Nitrogen (N)	0.142	33	0.251	26	0.393*	28	0.037	31
Potassium (K)	0.342*	32	0.457*	26	0.487**	28	-0.241	31
Sodium (Na)	0.377*	33	-0.037	26	0.169	28	-0.163	31
Calcium (Ca)	0.069	33	-0.174	26	0.123	28	0.171	31
Magnesium (Mg)	0.024	33	0.198	26	0.551**	28	-0.031	31
Dry matter	-0.246	27	-0.342	24	-0.41	19	-0.091	23
Ether sol. fract.	0.354*	33	0.474*	26	0.137	26	0.172	31

Table 4. Mean contents (% of dry matter) of neutral detergent fibre (NDF), acid detergent fibre (ADF), and lignin, as well as percentage of dry matter disappearance (DMD) at three different times for each of the four pine phenotypes (see Table 1 for definitions) at twig diameter 4 mm. Sample size: N = 4 in all cases; n.s. = P>0.05; * = P<0.05: h = hours.

Parameter/ Phenotypes	NDF	ADF	Lignin	DMD 24 h	DMD 48 h	DMD 96 h
LP	53.7	40.6	12.8	48.3	57.4	61.0
MPO	55.0	40.9	12.6	50.4	56.8	59.3
MP	54.1	40.3	12.7	48.7	58.2	61.8
HP	52.8	39.2	10.8	50.0	60.4	64.3
ANOVA	n.s.	n.s.	n.s.	n.s.	*	*

ranked as LP (11.1%) > MP (11%) > HP (10.8%) > MPO (8.7%) with no significant difference (χ^2-test, P>0.05).

However, after 48 hours, DMD differed significantly between phenotypes (Table 4). The ADF% + DMD% was still below 100%, but the inhibition rank changed to MPO (2.3%) > LP (2%) > MP (1.5%) > HP (0.4%) also with significant difference (χ^2-test, P<0.05).

After 96 hours, DMD also differed significantly between phenotypes (Table 4). At this time the ADF% + DMD% was over 100% but lignin% + DMD% was below 100% in all phenotypes. The inhibitory effect based on the lignin content ranked as MPO (28.1%) > LP (26.2%) > MP (25.5%) > HP (24.9%) with significant difference (χ^2-test, < 0.05). The rank was the same as at 48 hours.

This final (after 48 hours) inhibition rank was opposite to that of DMD (see Table 4). Because the indigestible fibre content was similar in mean moose bite diameter (Fig. 4), this implied that the DMD in moose foraging would be strongly determined by the inhibitory effect of secondary compounds in Scots pine.

Correlations of the moose bite diameters with the parameters measured

Among the factors which may affect moose bite diameter choice, the ADF, growth rate, CAS size, and internode length had significant effect (P<0.05), while the effects of total nutrients, water, lignin and DMD were significant at P<0.1 level (Table 5).

The number of CAS per tree and the biomass availability per tree (see Table 1) are two quantitative factors. They neither correlated significantly with the moose bite diameter (Table 5), nor with the moose bite number (P>0.1).

Discussion

Our comparison of mean moose bite diameters suggests that once moose have decided on a suitable bite size from different pine phenotypes, they consume the same amount of nutrients and plant defensive chemicals, i.e.

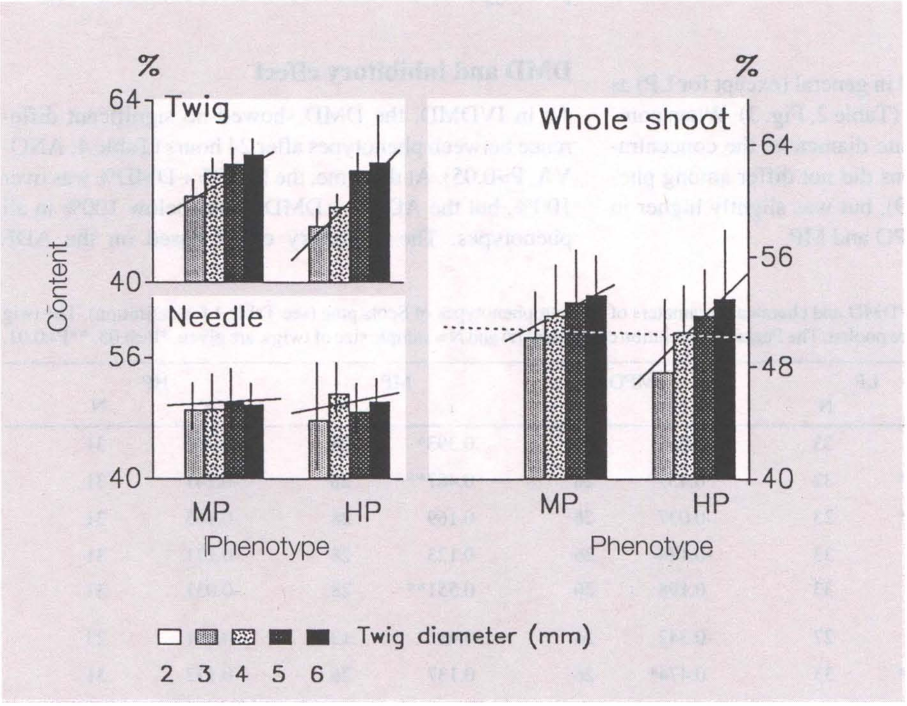

Figure 4. Mean fibre (NDF) contents in twigs, needles and in total for the two Scots pine phenotypes, MP and HP. Broken lines indicate contents at mean moose bite diameters. Standard deviations are indicated by the vertical line.

Table 5. Factors possibly affecting the bite diameter selection by moose on the four phenotypes of Scots pine (see Table 1 for definitions). Nutrient concentrations are pooled for diameters of 2, 3 and 4 mm, except for fibre, lignin, DMD and inhibition which were based on diameters of 4 mm only, and for IVDMD which was based on pooled diameters of 3 and 4 mm; r = the Pearson correlation coefficient (df = 2).

Factors	r
Nitrogen (N)	0.83
Potassium (K)	0.89
Sodium (Na)	0.24
Calcium (Ca)	0.42
Magnesium (Mg)	-0.60
Total nutrient	0.91°
Water[1] (H$_2$O)	0.90°
Ether sol. fraction	-0.14
ADF	-0.96*
Lignin	-0.90°
DMD[2]	0.94°
IVDMD	-0.09
Inhibition[2]	-0.82
Growth rate	0.99**
CAS diameter	1.00***
CAS length	1.00***
CAS number	-0.05
Internode length	1.00***
Stem diameter	0.58
Available biomass	0.24

[1] Converted from dry matter content
[2] After 96 hours
° $P<0.1$; *$P<0.05$; **$P<0.01$; ***$P<0.001$

moose have a selection standard in choosing the right bite diameter according to their perception of food quality.

In phenotypes LP and MPO, moose had a similar bite diameter choice (Fig. 1). CAS diameters in LP and MPO were also basically the same (Fig. 1). However, proximal nutrient contents in LP and MPO were different, LP being lower in N, K and total nutrients than MPO (Fig. 2). On the other hand, MPO had a lower digestibility and lower water content (converse of dry matter, Fig. 3) than LP. This suggests that the food quality of LP and MPO was similar and therefore caused no difference between the bite diameters.

Our IVDMD and DMD analyses demonstrated that mammalian herbivores cannot quickly detect forage digestibility; therefore, the importance of forage digestibility and secondary compound defence (see inhibition calculation) for bite selection are reduced. On the other hand, further analyses of DMD and inhibition after 48 hours indicated that phenotypic variance in pine mobile defence (i.e. secondary compounds, Coley et al. 1985) does exist. However, we did not analyse the phenolics or terpenes directly and we did not find any such defensive effect of the ether soluble fraction on IVDMD (Table 3).

The ether soluble fraction has been considered as a measure of the deterrent secondary compound content of woody browse in boreal forests because they mainly consist of terpene and phenolic resins (Bryant & Kuropat 1980, Bryant 1981; Haukioja et al. 1983). However, this does not exclude the presence of other compounds that may affect the digestibility of twigs (Varvikko 1988), because the ether soluble fraction is a heterogeneous mixture of generally high-energy compounds such as glycerides, phospholipids, sterols, pigments, waxes, volatile oils and resins. The aromatic fragrance of evergreens consists of volatile oils that are easily lost during drying (Robbins 1983). Similarly, some of the compounds may be lost after cutting or during extraction (Van Soest 1982). The ether soluble fraction may also contain compounds that can be absorbed very efficiently by ruminants (Varvikko 1988, Moore & Christie 1984), if judged on the basis of their positive effect on IVDMD, as seen in our Table 3. Therefore, the ether soluble fraction may not be a suitable indicator of the toxin defence of plants. We recommend that Palo's inhibition would be a good calculation to evaluate the effect of defensive materials before precise information about the constituents become available.

According to Palo et al. (1992), the minimum deterrent effect of plant defensive materials may be estimated by calculating inhibition. In our results, the percentage of NDF (composed of ADF + hemicellulose) + DMD was over 100% after 24 hours. This means that the NDF had been partially digested, probably as a result of partial digestion of the hemicellulose by stomach acidity (Robbins 1983), which inflated the DMD value. Similarly, after 96 hours, the percentage of ADF (consisting of lignin + cellulose) + DMD was over 100%, indicating that the ADF may have been partially digested. Lignin is totally indigestible, however, cellulose could be digested by symbiotic gastro-intestinal microflora (Robbins 1983). Our results after 24 hours suggest that NDF as indigestible material should be used with caution, while using ADF to calculate the inhibition should be in a time limit, such as less than 96 hours in our case.

Lignin, which is known to be an effective defensive chemical (Robbins 1983), especially in slow-growing plants, may have dosage-dependent effects on herbivores (Coley et al. 1985). Previous lignin analysis showed that HP had a lower lignin content than the other three phenotypes in the 4 mm twig diameter class (Danell et al. 1991). This means that the cell rigidity of the twigs was lower in HP in this diameter class. Unfortunately, we did not analyse the lignin content in different twig diameters, and therefore, did not see the same lignin content among pine phenotypes at the mean moose bite diameters as expected.

Previous measurements showed that the four phenotypes differed in internode length, CAS length, CAS diameter, and the needle biomass of twigs (Danell et al. 1991). These properties reflect the growth rate of the pines. We suggest that these features are important in visual decision-making by moose and affect moose behaviour in bite diameter selection (Table 5). A very close positive relationship between moose bite diameter (B) and CAS diameter (C) ($C = -2.08 + 1.47B$, $r = .99$, $P<.001$) supports this. The size parameters of CAS appeared to have a strong effect on moose bite diameter selection (Table 5). CAS may be a very important visual signal for moose in forage selection.

In our study, the macro elements analysed include those nutrients important for animals (Robbins 1983). However, none of them could determine the bite diameter as such because it is impossible for moose to recognise them. They do not exist in the form of molecules that can be detected by an animal's taste or smell receptors. The correlations between these nutrients and bite diameters must relate to specific compounds or some physical property of plant, such as the morphological characteristics in our case. Arnold & Hill (1972) have demonstrated that the senses of touch, smell and taste are of the greatest importance for foraging selection in ruminants such as sheep. Our experiment suggests that the sense of sight is more important for moose bite diameter selection. In addition, fibre chewiness sensed in the mouth may also play a role for moose; in our results, fibre content was highly negatively correlated with bite diameter choice (Table 5). Even though the slender twigs in LP could stimulate browsing (more bites resulted), the high fibre content of twigs over 2.8 mm in diameter inhibited moose browsing. Chewing experience may also inform the moose that the least roughness existed only at the top of the twigs (i.e. CAS). If this is the case, moose would take more bites (this is not equal to more biomass) on trees with more CAS and have larger bite diameters on trees with bigger CAS. Both features were well demonstrated in our results.

Plant quantitative features may affect moose browsing (Sæther 1990, Vivås & Sæther 1987, Bergström & Danell 1986, Niemelä & Danell 1988). However, in our results, neither the number of CAS nor the available biomass significantly affected bite diameters (Table 5). Their weak effect on the numbers of bites per tree might be due to the overwhelming selection on the bite diameter by moose.

Moose feeding selection at the intraspecific food plant level has been demonstrated on Scots pine in several studies. Observations have been made on trees of different origins (Niemelä et al. 1989), clones (Haukioja et al. 1983), phenotypes (Danell et al. 1991), and morphological or nutritional characteristics (Laine & Mannerkoski 1980, Löyttyniemi 1981, 1985). Our results indicate that food quality of Scots pine varies also among twig diameters. Adapting to the intraspecific nutrient environment, moose should select the same kind of food in particular patterns. We suggest that the characteristics of this selection should include: 1) that browsing takes place in an immediate manner with the bite diameter selection under a criterion of similar nutrition and/or plant defence at the bite point; 2) that plant immobile defence, such as fibre or lignin, plays an important role in moose bite diameter choice; 3) that moose perception of food quality could be realised through visual detection of the tree's morphological features, especially those of CAS in our case.

Acknowledgements - We thank Tiina Vahala, Tuija Lojouder, Maria Carlsson, Ola Gärdemalm, Heikki Kuitunen, Åke Nordström, Monica Phillips, Seija Siren and Aila Vanhatalo for their assistance in the chemical analyses and other techniques. Permission by the landowners of Mo & Domsjö Company and Umeå Municipality to use their land and pine trees is gratefully acknowledged. We also thank two anonymous reviewers for their valuable comments on the manuscript, and Mr. John Derome for revising the English language. Financial support was provided by the Finnish Centre for International Mobility (CIMO) and grants from the Nordic Council for Wildlife Research to J. Jia, the Academy of Finland to P. Niemelä, and the Swedish National Environment Protection Board to K. Danell.

References

Arnold, G.W. & Hill, J.L. 1972: Chemical factors affecting selection of food plants by ruminants. - In: Harborne, J.B. (ed.); Phytochemical Ecology, Academic Press, New York, pp. 72-101.

Bergström, R. & Danell K. 1986: Moose winter feeding in relation to morphology and chemistry of six tree species. - Alces 22: 91-112.

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.

Bryant, J.P. 1981: Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. - Science 213: 889-890.

Coley, P.D., Bryant, J.P. & Chapin III, F.S. 1985: Resource availability and plant antiherbivore defense. - Science 230: 895-899.

Danell, K., Niemelä, P., Varvikko, T. & Vuorisalo T. 1991: Moose browsing on Scots pine along a gradient of plant productivity. - Ecology 72: 1624-1633.

Den Braver, E. & Eriksson S. 1967: Determination of energy in grass hay by in vitro methods. - Lantbrukshögskolans Annaler 33: 751-765.

Gurevitch, J. & Chester, Jr. S.T. 1986: Analysis of repeated measures experiments. - Ecology 67: 251-255.

Haukioja, E., Huopalahti, R., Kotiaho, J. & Nygren, K. 1983: Millaisia männyntaimia hirvi suosii (In Finnish with English summary: The kinds of pine preferred by moose). - Suomen Riista 30: 22-27.

Hjeljord, O., Sundstol, F. & Haagenrud H. 1982: The nutritional value of browse to moose. - Journal of Wildlife Management 46 (2): 333-343.

Hjeljord, O. 1987: Research on moose nutrition in the nordic countries. - Swedish Research Supplement. 1: 389-397.

Laine, J. & Mannerkoski, H. 1980: Lannoituksen vaikutus mänty taimikoiden kasvuun ja hirvituhoihin Karuilla ojitetuilla nevoilla (In Finnish with English summary: Effect of fertilization on tree growth and elk damage in young Scots pine stands planted on drained, nutrient-poor open bogs). - Acta Forestalia Fennica: 166, 1-45.

Löyttyniemi, K. 1981: Typpilannoituksen ja neulasten ravinnepitoisuuden vaikutus hirven mäntyravinnon valintaan (In Finnish with English summary: Nitrogen fertilization and nutrient contents in Scots pine in relation to the browsing preference by moose (Alces alces L.)). - Folia Forestalia 487, 14 pp.

Löyttyniemi, K. 1985: On repeated browsing of Scots pine saplings by moose Alces alces. - Silva Fennica 19: 387-391.

Moore, J.H. & Christie, W.W. 1984: Digestion, absorption and transport of fats in ruminant animals. - In: Wiseman, J. (ed.); Fats in animal nutrition. Butterworths, London, pp. 123-149.

Niemelä, P. & Danell K. 1988: Comparison of moose browsing on Scots pine (Pinus sylvestris) and lodgepole pine (P. contorta). - Journal of Applied Ecology 25: 761-775.

Niemelä, P., Hagman, M. & Lehtilä, K. 1989: Relationship between Pinus sylvestris L. origin and browsing preference by moose in Finland. - Scandinavian Journal of Forest Research 4: 239-246.

Palo, R.T., Bergström R. & Danell K. 1992: Digestibility, distribution of phenols, and fibre at different twig diameters of birch in winter. Implication for browsers. - Oikos 65: 450-454.

Robbins, C.T. 1983: Wildlife feeding and nutrition. - Academic Press, Inc. London, 343 pp.

Sæther, B.-E. 1990: The impact of different growth pattern on the utilization of tree species by a generalist herbivore, the moose Alces alces: implications of optimal foraging theory. - In: Hughes, R.N. (ed.); Behavioural Mechanisms of Food Selection. NATO ASI Series, Vol. G 20, Springer-Verlag Berlin Heidelberg, pp. 323-341

Stephens, D.W. & Krebs, J.R. 1986: Foraging theory. - Princeton University Press, Princeton, 247 pp.

Van Soest, P.J. 1963: Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fibre and lignin. - Journal of the Association of Official Analytical Chemists 46: 829-835.

Van Soest, P.J. 1982: Nutritional ecology of the ruminant. - O & B Books Inc. 374 pp.

Van Soest, P.J. & Wine, R.H. 1967: Use of detergents in the analysis of fibrous feeds. IV. Determination of plant cell-wall constituents. - Journal of the Association of Official Analytical Chemists 50: 50-55.

Van Soest, P.J. & Wine, R.H. 1968: Determination of lignin and cellulose in acid-detergent fibre with permanganate. - Journal of the Association of Official Analytical Chemists 51: 780-785.

Varvikko, T. 1988: Partition of feed nutrient digestion and utilization in the ruminant alimentary tract. - Agricultural Research Center, Department of Animal Husbandry, Jokioinen, (Dissertation), 104 pp.

Vivås, H.J. & Sæther 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.

Vivås, H.J., Sæther, B.-E. & Andersen, R. 1991: Optimal twig-size selection of a generalist herbivore, the Moose Alces alces: implications for plant-herbivore interactions. - Journal of Animal Ecology 60: 395-408.