MOOSE WINTER FEEDING IN RELATION TO MORPHOLOGY AND CHEMISTRY OF SIX TREE SPECIES

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Abstract: The consumption and utilization of six deciduous tree species by moose were studied in relation to available browse biomass, shoot size and chemistry. Three-meter high trees of *Alnus glutinosa*, *Betula pendula*, *B. pubescens*, *Populus tremula*, *Salix caprea* and *Sorbus aucuparia* were presented to enclosed moose. After browsing by moose the number of bites and their diameters were recorded from different heights on the trees.

Bite diameter increased with increased height in the crown and was thereby correlated to the diameter of the annual shoots. Number of bites, total consumption, utilization and browsing time per tree differed between the tree species. The highest consumption of twigs was from *Populus tremula*, *Salix caprea* and *Sorbus aucuparia*, which corresponds to wild moose preferences. Large annual shoots were a common feature of the most preferred tree species.

The total consumption of browse was positively correlated to Mg and K concentrations in twigs.

The moose is a polyphagous herbivore which is known to rank food items by species, individuals, and parts of plants. (Miquelle and Jordan 1980, Danell et al. 1985 and review by Bergström and Hjeljord 1986). Reasons for selection among plant species have been studied and discussed by several authors (Penner 1978, Machida 1979, Bryant and Kuropat 1980, Belovsky 1981, Danell et al. 1985). No single factor has so far been identified as the governing factor although it appears that plant growth rate, measured as shoot length, is positively correlated to preference (Danell et al. 1985). Although larger shoots may physically make cropping easier it is probable that positive and negative chemical characteristics of the shoots are also involved (Bryant and Kuropat 1980, Danell et al. 1985). Whatever the reasons, we can hypothesize that differences in plant characteristics will result in different instantaneous feeding behavior and consumption rates by moose (Trudell and White 1981, Renecker and Hudson 1986). Better quality food will increase the intake rate, due mainly to a more rapid passage through the gut, which Crawley (1983) summarized as either an effect of higher food digestibility or lower levels of plant secondary compounds.

The aim of the present study was to evaluate moose feeding behavior, in terms of size of bites and mouthfuls, consumption rate and utilization in relation to food availability, shoot morphology and chemistry of six deciduous tree species.

MATERIAL AND METHODS

The experiment was conducted at Grimsö Research Station (59°40'N; 15°25'E) where moose were kept in a 17 ha enclosure with 3 paddocks. Four moose, one bull and three cows, each weighing 350-400 kg, were used for the study. The bull and two of the cows were 7 years old and were hand-reared in the enclosure. The third cow was 5 years old and had been raised in the pen by her mother. Usually all moose were daily offered natural food such as whole trees (2 - 5 m) of the evergreens Juniperus communis L. and Pinus sylvestris L., and the deciduous species Betula pendula Roth, B. pubescens Ehrh., Populus tremula L., Salix aurita L., S. caprea L., S. cinerea L., S. nigricans Sm. and Sorbus aucuparia L. In addition, each moose was daily offered 1.5-2 l of commercial cattle pellets. Ten days before the trial all tree species used in the experiment were exposed in equal amounts to the moose. No food was offered on the day of the trial.

A few days before the experiment we cut 50 stems each of Alnus glutinosa (L.) Gaertn (7.6±0.8 years old, $\bar{X}\pm SE$, N=9), Betula pendula (5.4±0.2, N=8), B. pubescens (6.9±0.3, N=9), Populus tremula (10.0±0.9, N=9), Salix caprea (5.7±0.2, N=9) and Sorbus aucuparia (9.1±0.7, N=9). Alnus glutinosa were taken along a riverside and Betula spp. and Sorbus aucuparia were cut in mixed Pinus sylvestris-Picea abies L. forests around the research station. Populus tremula and S. caprea were taken on abandoned arable land. We selected normal, unbrowsed trees that were 3 m high.

All trees were numbered and nine trees of each species were randomly selected for pre-trial non-destructive measurements. Those measurements included length (to the nearest mm) and diameter (10 mm from the base and to the nearest 0.1 mm) of three randomly chosen current annual long-shoots (shoots with elongated internodes between leaves) per each half meter interval (0.0-0.5........2.5-3.0 m). We also collected a varying number (n=6-21) of 3 m high trees of each species on which we measured the base diameter on each current annual long-shoot.

In order to calculate the consumption by moose on a weight basis from bite diameters we established regression equations, one for each species. From randomly selected trees we clipped 40 twigs at each 1 mm interval between 1.0 and 6.0 mm for the Betula species and 2.0 to 6.0 mm for the other species. The twigs were dried at 70°C and weighed individually. The values were converted to a logarithmic scale (base 10) and the equations took the form of log twig weight = a + b log twig diameter. The values for a and b respectively were -1.94 and 3.63 (A. glutinosa), -1.28 and 2.98 (B. pendula), -1.31 and 3.00 (B. pubescens), -1.64 and 3.22 (P. tremula), -1.96 and 3.48 (S. caprea) and -1.85 and 3.39 (Sorbus aucuparia). The relations between twig diameter and biomass for the different species are presented in Fig. 1.

Six trees of each species were presented to the moose in each of six replicate feeding trials. The trees were placed systematically in four rows in front of an observation tower (Fig. 2). The first row was 17 m from the tower. The distance between rows was 5 m and between trees within rows 3 m. After the 36 trees were placed in position one moose was given access to the trees. Usually the moose went up to the trees

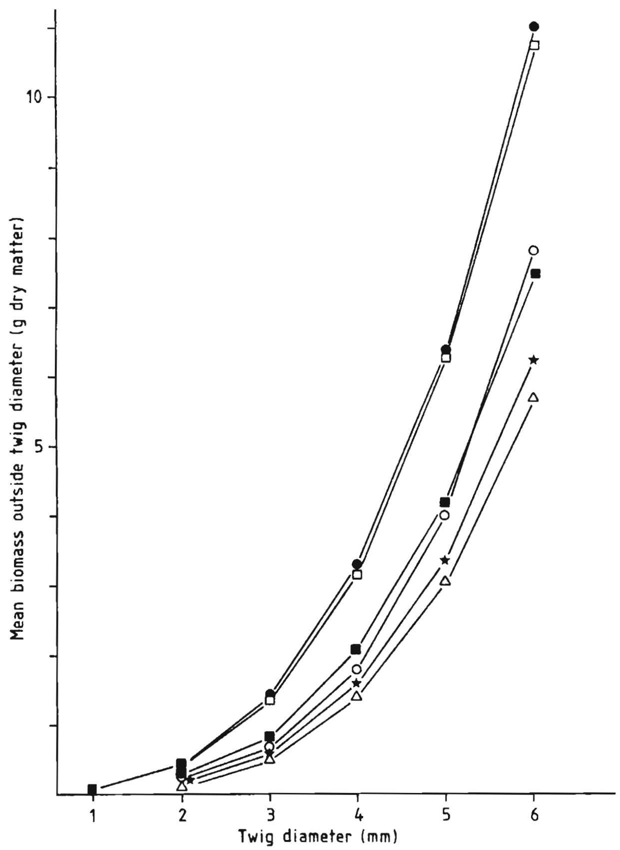

Fig 1. Curves showing the biomass found outside twig diameters for six deciduous tree species (○ = Alnus glutinosa, ● = Betula pendula, □ = B. pubescens, ■ = Populus tremula, △ = Salix caprea, ✱ = Sorbus aucuparia. Each value is a mean of forty twigs. Standard error of each mean was around 5%.

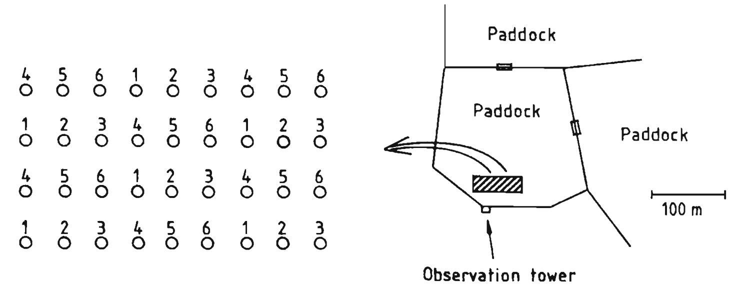

Fig. 2. Illustration of the observation tower and experiment arena within the moose pens (right) and position of the trees during feeding trials (left). The numbers 1-6 refer to the six tree species used in the study.

immediately and started browsing. On average each moose spent 42 minutes (range 20-63 minutes) feeding before we terminated the trial. During this time we recorded how the moose moved between the trees, the number of mouthfuls (each mouthful = one act when one or more twigs were taken) and time spent browsing at each tree (= time from start to end of browsing, including shorter breaks).

After termination of the experiments the trees were taken to the laboratory where we counted the number of bites (= number of browsed twigs) and measured each bite diameter (= diameter at point of browsing) for each 0.5 m height interval. With the equations established earlier we calculated consumed biomass in g dry weight per height interval. The remaining twig biomass up to a diameter of 4 mm (Betula spp.), 5 mm (A. glutinosa), 7 mm (P. tremula and Sorbus aucuparia) and 8 mm (S. caprea) was clipped off, dried at 70°C and weighed. These diameter limits were chosen by taking the diameter which included 90% of the number of bites (Telfer 1980) collected in ordinary browse surveys (R. Bergström unpubl.). We were thereby able to calculate the potential available forage for each species and also obtain estimates of the utilization by moose.

The values from the six replicates were combined for data analyses.

The material from three of the diameters (4, 5 and 6 mm) clipped for establishment of the regression equations were ground in a mill to pass through a 1 mm screen and analyzed colorimetrically for Kjeldahl-nitrogen (N) and phosphorus (P). An atomic absorption spectrophotometer was used to analyze sodium (Na), potassium (K), calcium (Ca) and magnesium (Mg). Ash content was determined after combustion in 600°C for 2 hours. Crude fat was determined by extraction in diethyl-ether for 16 h in a Soxhlet apparatus (Kungl. lantbruks- styrelsen 1966). In vitro organic matter digestion was analyzed according to den Braver and Eriksson (1967).

The statistical analyses included one-way analyses of variance and Spearman's rank correlation (correlation coefficient = r_s).

RESULTS

Morphology of trees

The amount of available twig biomass per tree differed significantly between species (P<0.022). Most of this variation was accounted for by _B. pendula_ which had only half the amount of twig

biomass (60.4 g) compared to other species (range: 120.0-126.3 g). Mean diameter of long-shoots from the whole tree varied from 1.1 mm (_B. pendula_) to 3.6 mm (_Sorbus aucuparia_) (Fig.3). Differences in shoot size were also recorded between height intervals within species (Table 1). Shoot diameter and length increased the higher up in the crown the shoots were measured. These size variables increased roughly 2-5 times from the lower to the upper part of the crown, except for _Sorbus aucuparia_, for which the size increases were less pronounced.

Moose browsing

Of the 36 trees per species that were presented in the trials, 18 trees were browsed of _A. glutinosa_, 10 of _B. pendula_, 18 of _B. pubescens_, 24 of _P. tremula_, 26 of _S. caprea_ and 19 of _Sorbus aucuparia_.

The bite diameter increased with higher position in the crown (Table 1). This increase was not of the same magnitude as the one for shoot diameter (Table 1). The frequency distribution of all shoot and bite diameters and their means are shown in Fig. 3. Generally the frequency distribution of moose bites was centered around larger diameters than the current annual shoots of the same species. Further, the frequency distribution of bites was broader. However, the correlation between shoot and bite diameters from all levels and all species together was highly significant (Fig. 4; P<0.001).

Number of mouthfuls (P<0.001) and number of a bites (P<0.017) differed significantly between species (Table 2). There were about two bites per mouthful for _A. glutinosa_ and the _Betula_ species while for the

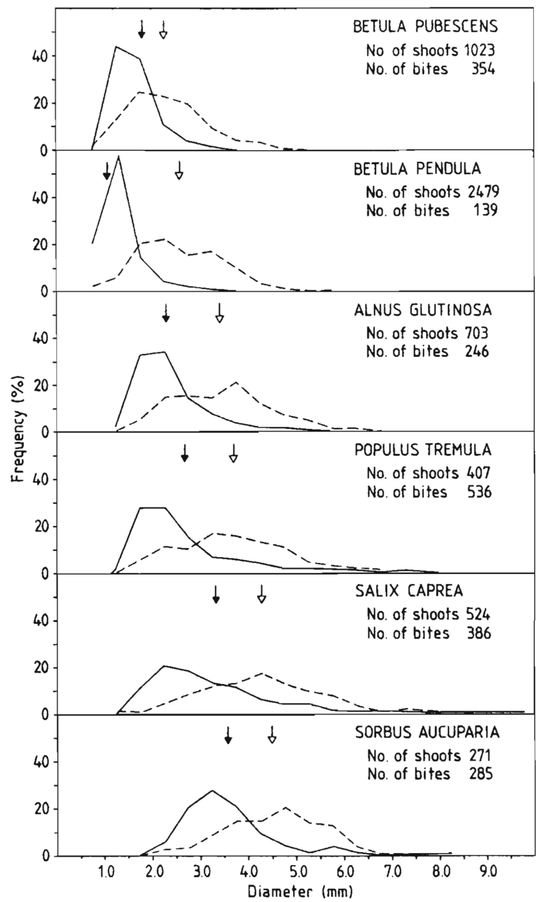

Fig. 3. Frequency distribution of bite diameters (---) and the base diameters of current annual long-shoots (——) for six tree species are given. Mean diameter of bites (↓) and long-shoots (↓) are also indicated.

Table 1. Length (mm) and base diamter (mm) of current annual long-shoots and diameter at point of browsing (dpb, mm) from different height intervals of six plant species.

Plant species	Height interval (m)					
	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0
Alnus glutinosa						
length	35.3	40.3	38.0	45.0	98.6	214.5
base diam.	1.8	1.9	1.9	2.0	2.7	3.9
dpb	-	3.5	3.3	3.4	3.6	3.5
Betula pendula						
length	86.0	92.2	72.5	100.3	181.0	538.4
base diam.	1.1	1.4	1.0	1.3	2.0	5.1
dpb	-	-	2.1	2.4	2.9	3.4
Betula pubescens						
length	-	47.2	69.0	68.8	114.0	211.7
base diam.	-	1.0	1.1	1.1	1.5	2.4
dpb	-	2.0	2.0	2.2	2.6	3.0
Populus tremula						
length	29.0	54.2	29.5	66.0	167.4	272.5
base diam.	2.2	1.9	1.8	2.0	2.7	4.0
dpb	-	3.6	3.5	3.7	3.8	3.9
Salix caprea						
length	70.3	104.6	114.1	198.0	264.8	508.8
base diam.	1.3	1.7	2.0	2.7	3.2	4.6
dpb	-	4.0	3.8	4.1	4.8	4.8
Sorbus aucuparia						
length	23.0	216.0	178.0	245.9	233.3	329.1
base diam.	3.5	3.5	3.7	3.9	3.8	4.9
dpb	-	4.5	4.2	4.6	4.6	4.5

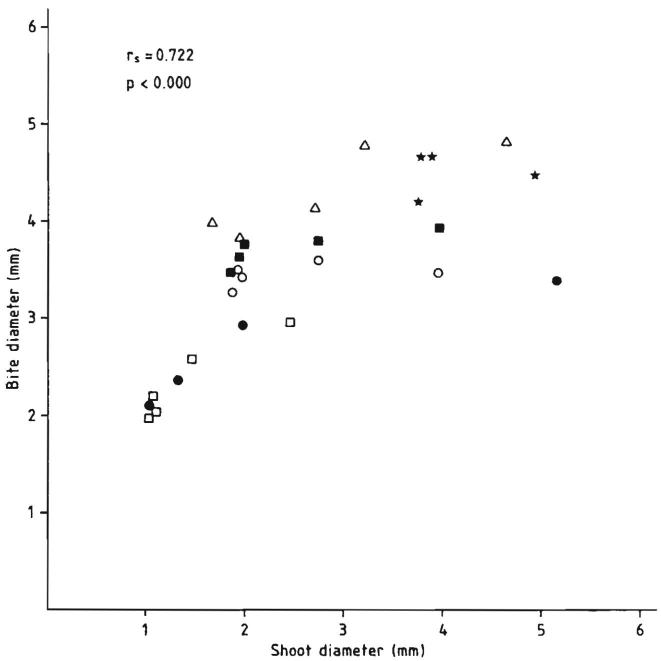

Fig. 4. Relationship between the average moose bite diameter and the base diameter of long-shoots produced during the last growing season. Each value represents one height interval for one species (○ = Alnus glutinosa, ● = Betula pendula, □ = B. pubescens, ■ = Populus tremula, △ = Salix caprea, ✱ = Sorbus aucuparia).

Table 2. Number of mouthfuls and bites, mean bite weight and consumed and utilized twig biomass on six deciduous tree species presented to moose. Means per tree and their standard errors are given.

Plant species	Number of mouthfuls	Number of bites	Mean[1] weight of bite (g)	Total consumption (g)	Utilization[2] (%)
Alnus glutinosa	6.5 (1.3)	13.7 (1.5)	1.61 (0.19)	20.4 (2.4)	17 (4.6)
Betula pendula	8.9 (1.9)	13.9 (3.0)	1.17 (0.18)	16.9 (3.6)	25 (5.4)
Betula pubescens	12.2 (2.5)	19.7 (3.2)	0.85 (0.10)	16.1 (3.0)	15 (3.7)
Populus tremula	17.5 (2.2)	22.3 (2.1)	2.39 (0.22)	49.5 (4.8)	36 (4.5)
Salix caprea	12.3 (1.3)	14.8 (1.5)	2.96 (0.32)	40.2 (5.7)	38 (5.4)
Sorbus aucuparia	14.6 (1.7)	15.0 (1.9)	2.93 (0.22)	43.3 (5.8)	38 (6.7)
F	4.29	2.90	13.17	8.76	4.36
P	<0.001	<0.017	<0.001	<0.001	<0.002
df	5/108	5/109	5/109	5/109	5/52

1) total consumed biomass per tree divided by number of bites per tree
2) based on available twig biomass within certain diameter limits (see Material and methods for further explanation)

other three species each mouthful equalled about one twig (Table 2). Taking the total consumption per tree (Table 2) and dividing it by the number of moose bites gives the mean bite weight. Mean bite weights of A. glutinosa and Betula spp. were considerably smaller than those of P. tremula, S. caprea and Sorbus aucuparia (Table 2).

The lowest consumption per tree was recorded for the two Betula species while the moose consumed slightly more per Alnus tree. Two to three times more biomass was consumed on P. tremula, S. caprea and Sorbus aucuparia than on Betula and Alnus. Consumption per height interval was also calculated (Table 3). In absolute values most biomass is consumed 1.5-2.5 m above ground. To test the hypothesis that consumption on a tree species is connected to shoot size on that particular species we used a rank correlation analysis. Both variables were expressed as mean per tree. The test did not show any significant correlation ($r_s=0.77$, $P<0.072$, n=6). However a significant correlation was found between consumption and bite size ($r_s=0.83$, $P<0.042$, n=6). The relative harvest of the available twig biomass (or utilization) showed a similar pattern as consumption with the exception that B. pendula had an intermediate position (Table 2). The data did not permit us to calculate utilization per height interval.

We observed the moose browsing for a total of 3 hours 14 min. During each trial the browsing time per tree was recorded (Table 4). Moose spent the shortest time with each A. glutinosa tree. Next came Betula spp. and a considerably longer time was devoted to each tree of the three remaining species. The differences between trees were

Table 3. Average consumption (g dry weight) per height interval of six deciduous tree species.

Plant species	Height interval (m)					
	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0
Alnus glutinosa	0.03	2.8	6.3	6.4	4.0	0.8
Betula pendula	-	0.1	1.8	4.9	5.8	4.3
Betula pubescens	0.1	0.3	3.1	6.0	3.7	2.7
Populus tremula	0.7	5.3	11.5	12.7	11.2	8.1
Salix caprea	0.5	2.5	6.8	8.1	12.1	10.1
Sorbus aucuparia	0.6	5.8	7.1	10.4	13.9	5.5

Table 4. Browsing time and consumption rate (g dry weight/min) by moose on six deciduous tree species. Means per tree and their standard errors are given.

Plant species	Total browsing time (min)	Browsing time per tree (min)	Consumption per time unit (g/min)
Alnus glutinosa	10.5	0.6	48.6
		(0.1)	(7.1)
Betula pendula	9.0	0.9	18.6
		(0.2)	(2.7)
Betula pubescens	16.4	0.9	21.6
		(0.2)	(3.4)
Populus tremula	57.8	2.4	31.2
		(0.4)	(5.4)
Salix caprea	56.4	2.2	19.8
		(0.3)	(1.3)
Sorbus aucuparia	43.7	2.3	19.8
		(0.3)	(1.9)
F		7.12	8.76
P	-	<0.001	<0.001
df		5/109	5/109

Table 5. Chemical composition and in vitro digestibility of three twig sizes (diameter: 4, 5 and 6 mm) from each of six tree species. All values, which are given as percent of dry matter, are means of duplicate analyses on composite samples.

Plant species	Item								
	N	P	Na	K	Ca	Mg	Ash	IVOMD	Crude fat
Alnus glutinosa									
4	1.385	0.078	0.009	0.40	0.349	0.096	1.8	25	5.5
5	1.185	0.059	0.009	0.25	0.364	0.093	1.7	23	5.5
6	1.275	0.070	0.006	0.24	0.278	0.083	1.6	24	5.2
Betula pendula									
4	0.926	0.107	0.015	0.25	0.230	0.077	1.4	22	5.4
5	1.021	0.104	0.012	0.25	0.239	0.066	1.4	26	4.9
6	0.879	0.104	0.013	0.24	0.250	0.065	1.3	24	4.0
Betula pubescens									
4	0.792	0.085	0.013	0.20	0.293	0.057	1.3	22	2.9
5	0.733	0.077	0.010	0.18	0.267	0.060	1.0	23	3.6
6	0.831	0.087	0.010	0.19	0.288	0.058	1.5	24	3.6
Populus tremula									
4	0.950	0.089	0.013	0.51	1.029	0.138	3.6	41	4.3
5	1.025	0.107	0.012	0.50	0.939	0.142	3.4	41	3.8
6	1.085	0.108	0.012	0.46	0.797	0.136	3.3	41	3.4
Salix caprea									
4	1.150	0.151	0.014	0.40	1.395	0.109	4.4	48	2.8
5	0.955	0.140	0.010	0.35	1.265	0.105	4.1	43	2.7
6	0.761	0.116	0.009	0.32	0.975	0.071	3.3	38	2.4
Sorbus aucuparia									
4	0.763	0.104	0.011	0.38	0.740	0.161	2.8	29	3.0
5	0.729	0.108	0.009	0.37	0.658	0.165	2.5	22	2.9
6	0.613	0.094	0.005	0.31	0.533	0.126	2.0	18	2.5

Table 6. Spearman's correlation coefficients between total consumption and chemical composition of three different twig diameters. Each correlation is based on values from six tree species. (**=P<0.01; ***=P<0.001)

Item	Twig diameter (mm)		
	4	5	6
N	0.086	0.203	-0.086
P	0.200	0.600	0.486
Na	-0.232	0.000	-0.257
K	0.812	1.000***	0.928**
Ca	0.771	0.771	0.657
Mg	0.943**	0.943**	0.943**
IVOMD	0.812	0.203	0.334
Crude fat	-0.029	-0.257	-0.543

significant (P<0.001), as also were the differences in consumption rate (Table 4; P<0.001).

Chemical composition and in vitro digestibility were determined for 4, 5 and 6 mm twigs of each tree species (Table 5). Four variables (number of bites, browsing time and absolute and relative total consumption), all recorded per tree, were tested in Spearman's rank correlation analyses against each chemical variable. Significant correlations were found only between total absolute consumption and K (diameters 5 and 6 mm) and Mg (diameters 4, 5 and 6 mm) (Table 6).

DISCUSSION

The six tree species used in our experiments ranged widely over the preference scale according to a literature review by Bergström and Hjeljord (1987). These authors ranked our species/genus in the following order: *Sorbus aucuparia* > *Salix* spp. > *P. tremula* > *Betula* spp. > *Alnus* spp. This ranking order has been established mainly after browse surveys and not in critical experiments. Grouping the species we could say that *Sorbus aucuparia*, *S. caprea* and *P. tremula* are highly preferred while *Betula* spp. and *A. glutinosa* are of moderate and low preference respectively. Thus, the trend in our material fits the results from various browse surveys in the Nordic countries and Poland. However, *A. glutinosa* was browsed more than expected and moose were also feeding on this species at the highest consumption rate.

In summary, we can say that at equal availability moose browse for a longer time on the preferred tree species. On such a species moose take more mouthfuls (each including fewer bites) and also increases the bite diameter (and thereby the bite weight), resulting in greater total consumption per tree of the preferred species. This relationship between consumption and bite size was also shown for browsing elk (Cervus elaphus nelsoni) (Wickstrom et al. 1984).

The idea presented earlier (Danell 1983, Danell et al. 1985), that moose biting is adjusted to base diameter of the annual shoots, is strongly supported by the results from this study. This relationship seems to hold both within (depending on where in the crown the biting takes place) and between plant species. The positive correlation between shoot- and bite-size can easiest be explained by a higher physical availability of large shoots (Danell et al. 1985). In general, tree species with large shoots often have a rapid growth while slow-growing species have small shoots. However, we cannot exclude chemical differences coupled to growth rate and/or shoot size although the presented chemical analyses give no strong support for this. However, a slight trend towards better digestibility and lower crude fat (ether extract) content for the preferred species is indicated in Table 5. Coley et al. (1985) also consider growth rates by plants in a general discussion of plant herbivore defences and they argue that low growth rates increase the possibility for the plant to allocate more resources for chemical defence. This will in turn decrease plant acceptability for herbivores. In the correlation analyses we found that the total consumption was significantly correlated to concentrations of Mg and K. At present we have no good explanation for those relationships. One function of Mg and K in plant cells is to activate enzymes and it is likely that high concentrations of these elements are occuring in

rapidly growing tissues. The high concentrations of Mg and K in the three preferred species is also supported by data presented by Ahlén (1975) and A. Nyström and R. Bergström (unpubl.).

Although we found a significant difference in moose feeding rate on the six tree species there were only two species that clearly diverged from the others. Populus tremula was well above the values of Betula spp, S. caprea and Sorbus aucuparia while A. glutinosa was considerably higher than all other species. Thus in this short-term perspective our data could not support the idea that intake rate increases with food preference.

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