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Summer foraging on Scots pine *Pinus sylvestris* by moose *Alces alces* in Sweden - patterns and mechanisms

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Scots pine *Pinus sylvestris* is a dominant winter food species to moose *Alces alces* in Fennoscandia but reports of its use during the growing season are limited. Browsing by moose on current-growth, terminal shoots of Scots pine (CGTS) during summer was studied in three areas in southern and central Sweden to quantify this seasonal feeding habit. Dynamics of nutrient content in CGTS were also studied to relate the timing of consumption to the changing qualitative value of this forage. To determine the temporal pattern of browsing by moose, data were taken in young pine stands of two separate areas during the growing seasons of two different years, 1980 and 1995. In the former year use of terminal shoots peaked in mid-June while in the latter year it peaked some two weeks earlier. Nutrient analyses, made only in 1995, showed that peak use of pine terminal shoots coincided with seasonal highs in magnesium (Mg), potassium (K), crude protein (CP), phosphorus (P), starch and total carbohydrates, and seasonal lows in acid detergent fibre (ADF) and acid detergent lignin (ADL). *In vitro* dry matter disappearance (IVDMD), a measure of digestibility, in terminal shoots in June was found to be significantly higher than in two other important moose browse species, birch *Betula* spp. and bilberry *Vaccinium myrtillus*. To determine frequencies of use of CGTS and heights of recently browsed trees, young pine stands in a third area were surveyed in July 1985. All browsed pine trees were between 30 and 230 cm in height, and 14% were browsed on some occasion during the growing season. Our results are discussed with respect to the potential mechanisms underlying summer use of CGTS by moose. Further research on the impact this feeding habit may have on forestry is suggested.

Key words: Alces alces, browsing, conifers, feeding habits, nutrients, summer, terminal shoots

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Moose *Alces alces* have been shown to use a wide array of plant species (LeResche & Davis 1973, Peek 1974, Cederlund, Ljungqvist, Markgren & Stålfelt 1980, Renecker & Schwartz 1997), and the importance of diversity in their diet has been suggested (Oldemeyer, Franzmann, Brundage, Arneson &

Flynn 1977, Miquelle & Jordan 1979). Studies of moose food habits especially concerning winter range have been reported (see reviews by Peek 1974, Bergström & Hjeljord 1987) as it has traditionally been assumed that the availability of winter forage is probably the most critical factor for moose populations (LeResche & Davis 1973, Peek 1974). More recently, however, Schwartz, Hubbert & Franzmann (1988) suggested that summer and transitional fall and spring ranges that provide high-quality, abundant forage for moose may play an important role in the survival of individuals, and ultimately, populations.

Many studies have reported on the great variety of plant species and parts thereof taken by moose in summer (Murie 1934, Peterson 1955, Knorre 1959, Peek, Urich & Mackie 1976, Cederlund et al. 1980, Lautenschlager, Crawford, Stokes & Stone 1997). However, few have documented or discussed mechanisms underlying summer use of conifers, whereas Scots pine *Pinus sylvestris* has been found to be an important winter forage for moose in Fennoscandia (Cederlund et al. 1980, Bergström & Hjeljord 1987). In southern Sweden, Dietrichson & Karlsson (1979) and Lavsund (1980) reported that moose browsed on pine in early summer and clearly preferred terminal shoots. More recently, Faber (1996) documented use of pine bark by moose in spring and summer in central Sweden. From other regions, Murie (1934) described summer use of ground hemlock *Taxus canadensis* by moose on Isle Royale, Michigan, USA; Knorre (1959) reported that in parts of Siberia feeding on conifers occurred throughout the year, even in areas where sufficient quantities of deciduous browse were available. In other cervids, spring and summer use has been reported: Columbian black-tailed deer *Odocoileus hemionus columbianus* using Douglas fir *Pseudotsuga menziesii* (Browning & Lauppe 1964) and California mule deer *O. h. californicus* using white fir *Abies concolor* (Jordan 1967), both in California, USA; red deer *Cervus elaphus* using Scots pine in the Netherlands (van de Veen 1979), and red deer and roe deer *Capreolus capreolus* using Sitka spruce *Picea sitchensis* in Scotland (Welch, Chambers, Scott & Staines 1988, Welch, Staines, Scott, French & Catt 1991). In Sweden, Cederlund et al. (1980) reported that Scots pine is the major component of the winter diet of moose, whereas in summer, pine comprises <2% of the forage.

The purpose of this study was to confirm the reported use of current-growth, terminal shoots of pine (CGTS) by moose during the growing season (Dietrichson & Karlsson 1979, Lavsund 1980) and establish the temporal pattern. Also characteristics of recently browsed pine trees and frequencies of use of CGTS were determined. Additionally, the qualitative value of pine terminal shoots as summer browse to moose compared to other commonly used browse species is examined. Finally, potential mechanisms underlying summer use of pine terminal shoots are discussed in relation to nutrient content and palatability in an attempt to explain this moose feeding pattern.

Study area

The study was conducted in the southern part of the boreal forest zone in southern and central Sweden (Ahti, Hämet-Ahti & Jalas 1968), and consists of three segments. One segment was conducted in the county of Kronoberg (57°00'N, 15°17'E) in 1980, the second at Halleberg-Hunneberg (58°20'N, 12°29'E) in 1985, and the third at the 140-km² Grimsö Wildlife Research Area (GWRA) (59°05'N, 15°05'E) in 1995 (Fig. 1). These areas are relatively similar in their

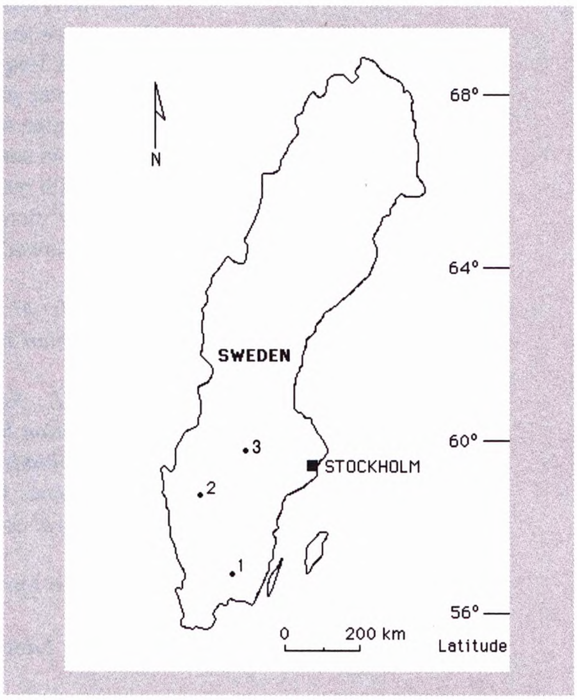


Figure 1. Location of the three study areas in Sweden with year of study (given in parentheses); 1) the county of Kronoberg (1980); 2) Halleberg-Hunneberg (1985); and 3) Grimsö Wildlife Research Area (GWRA)(1995).

general vegetational characteristics and climate (Sveriges Nationalatlas 1992, Sand, Cederlund & Danell 1995), as reported by Dietrichson & Karlsson (1979) for the county of Kronoberg, Gustafsson & Tyrland (1976) for Halleberg-Hunneberg, and Cederlund et al. (1980) and Cederlund, Sand & Pehrson (1991) for GWRA. They are all relatively flat and forested with elevations of 75-200 m a.s.l. Forests are dominated by Scots pine and Norway spruce *Picea abies* with a varying intermixture of birch *Betula* spp. and aspen *Populus tremula*. The ground layer is dominated by dwarf shrubs, mainly bilberry *Vaccinium myrtillus*, lowbush cowberry *Vaccinium vitis-idaea*, and heather *Calluna vulgaris*. There is a small to moderate interspersion (18% at GWRA) of boggy, swampy wetlands and farmlands in the three areas. Forest management is intensive, with mature stands harvested by clear-cutting of 3- to 15-ha patches, then either replanted with conifers or allowed to regenerate naturally.

The climate is typical of inland, southern and central Sweden with some variation from south to north; winter minimum temperatures are seldom <-25°C and summer maximum temperatures seldom >30°C. Snow cover is usually present from mid-December to mid-March (mid-April at GWRA), with the greatest depths, 40-50 cm, at GWRA during February and early March. Mean monthly summer precipitation (May-August) ranges within 55-75 mm, while the length of the growing season (number of days ≥6°C) ranges from ca 183 days in the south to 167 at GWRA (Sand et al. 1995). Mean annual density of moose in winter, after hunting, during the study periods were ca 1.0/km² in Kronoberg (Dietrichson & Karlsson 1979, Statens Naturvårdsverk Rapporter 1982), ca 2.0/km² at Halleberg-Hunneberg (S. Lavsund, unpubl. data), and ca 1.4/km² at GWRA (G. Cederlund, unpubl. data).

Material and methods

Temporal pattern of browsing

In Kronoberg, four stands of young Scots pine were systematically surveyed for signs of current browsing during the growing season in 1980. The stands selected had a mean size of 3.5 ha (range: 2.0-5.0 ha) and were within 5 km of each other, and all had pine with signs of previous summer browsing by moose (S. Lavsund, pers. obs.). The surveys were made every 9-11 days during 22 May - 23 July, with additional surveys performed on 10 August and 10 September to document if browsing of terminal shoots continued over the entire summer. There were eight recording intervals. At each stand, 50 young pine trees varying in height within 1-2.5 m were chosen along a random line transect and individually numbered with plastic tags.

Current-growth of the terminal and lateral shoots was checked for signs of recent (i.e. this growing season's) moose browsing at the described intervals, and browsing activity, i.e. number of trees and type of newly browsed shoots, was recorded. In this paper, the definition of CGTS encompasses the newly sprouting 'clump' of shoots (Fig. 2), i.e. the true terminal shoot plus laterals directly surrounding it, extending from the tip of the previous year's terminal shoot; all other side shoots are considered laterals. On pine trees with more than a single dominant terminal (see below), all shoots on the upper crown portion of such stems were counted as terminals.

At GWRA, five stands of young pine were systematically surveyed for signs of current browsing between April and August 1995. The stands selected had a mean size of 7.4 ha (range: 2.6-10.5 ha) and were 1-7 km apart. These stands were dominated by young pines 1-2.5 m high, and were chosen because earlier investigations (Dietrichson & Karlsson 1979, this study) and preliminary field data at GWRA from 1994 had shown that during the growing season moose use pine with terminal shoots in this height range. Each stand was surveyed for signs of recent

Figure 2. Unbrowsed (left) and newly browsed (right) current-growth, terminal shoots of Scots pine in late May 1998. The photos were taken at a study stand in the Grimsö Wildlife Research Area.

Table 1. Size and shapes of Scots pines chosen for observation of browsing by moose during the 1995 growing season at Grimsö Wildlife Research Area, Sweden.

Trees	N	Height (cm)	SD	Min.	Max.	DBH[1] (mm)	SD	Min.	Max.
All trees combined	250	165.2	22.9	110	235	12.4	4.3	5.1	37.8
Normal[2]	208	167.5	22.3	112	235	12.4	3.9	5.9	23.1
Bush-like[2]	42	154.1	23.0	110	197	12.7	6.1	5.1	37.8
Shoot growth trees	25	168.2	15.6	134	200	11.7	3.5	6.1	21.2

[1] DBH: Diameter at breast height
[2] For definition, see the section 'Characteristics of browsed trees and frequency of use' below.

terminal and lateral shoot browsing every 9-11 days during 24 April - 4 July. A final survey was made one month later on 7 August to document if the rate of terminal shoot browsing had changed after early July, as had been found in Kronoberg in 1980. There were eight recording intervals.

In the GWRA study, 50 young pine trees varying in height within 1-2.5 m (Table 1) were chosen at each stand; the trees were distributed along a random line transect and each was marked with a plastic number tag. The CGTS and lateral shoots of the tagged trees were checked for signs of recent moose browsing, and browsing activity, i.e. the number of trees newly browsed and the number of shoots removed per browsed tree, was recorded. During each survey, newly browsed terminal and lateral shoots were marked at their base with a small piece of copper wire for future identification of possible re-browsing within summer.

Temporal pattern of terminal shoot development

To compare browsing activity to terminal shoot development, growth of new terminal shoots of pine was estimated. In Kronoberg in 1980, growth was measured to the nearest 1 cm on each survey day throughout the study period on 15 randomly chosen pine in an adjacent stand which had similar age and stand characteristics compared to the survey stands.

At GWRA in 1995, growth of terminal shoots was measured to the nearest 1 cm on each survey day throughout the study period on five randomly chosen 'normal' pine within each survey stand (see Table 1). Each of these trees was given a plastic number tag and equipped with a cylinder of chicken wire around the terminal shoot to protect them from moose browsing, and consequently measured during the study period, to compare browsing activity and shoot growth.

Samples of CGTS were collected from 10 random pine within each stand during each survey at GWRA in 1995. Each sample consisted of current-growth shoots including both needles and shoot axis, 1) to measure average weight gain of terminal shoots, and 2) for analyses of mineral nutrients, fibre and sugar content, and determination of *in vitro* dry matter disappearance (IVDMD). Shoot samples were oven-dried immediately after collection at 50°C for at least 48 hours to reach constant weight and weighed to the nearest 0.01 g. Mean weight of shoots for each stand was calculated from a single weighing of each set of 10 shoots.

Characteristics of browsed trees and frequency of use

At Halleberg-Hunneberg, an area long known as a site of moose damage (Klementsson & Schärnell 1984, S. Lavsund, pers. obs.), 10 stands of young pine were surveyed for signs of recent terminal shoot browsing in early and mid-July 1985. The stands selected had a mean size of 7.6 ha (range: 5.0-10.3 ha) and were chosen to contain a wide range of heights (i.e. 10-440 cm) of young pine. Ten sample plots (in total 100 m^2) were systematically distributed across each stand. All pine were measured for total height to the nearest 10 cm and signs of recent moose browsing on CGTS were recorded. Signs of summer browsing in previous years (Dietrichson & Karlsson 1979) were also recorded in order to determine if earlier browsing increased the likelihood of future summer browsing, since it has been found for winter browsing that moose prefer to re-browse pine previously browsed (Marcström 1973, Löyttyniemi & Piisilä 1983, Löyttyniemi 1985).

A similar determination of the likelihood of future browsing was made at GWRA in 1995; stem diameter at breast height (DBH, mm) and a subjective visual classification of each study tree was made when they were being chosen and individually marked. Trees were either classified as normal, having a single dominant terminal shoot, or as bush-like, when the crown of the tree was multiple-leadered and it was not possible to distinguish any single dominant terminal shoot (Gross 1983; see Table 1). Earlier observations have shown that these latter trees are bush-like due to summer browsing by moose in previous years (Westman 1958, Dietrichson & Karlsson 1979).

Chemical analyses

Terminal shoot samples were analysed at the Department for Production Ecology, Swedish University of Agricultural Sciences (SLU) in Uppsala, Sweden. Levels of the macroelements calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), and phosphorus (P), and the trace elements aluminium (Al), boron (B), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) were determined by a standard Inductively Coupled Plasma-Atomic Emission Spectroscopy (ICP-AES) technique using a JY 70 Plus Spectroanalyser. Total nitrogen (N) content was determined by elemental analysis using a Carlo Erba NA 1500 Elemental Analyser, and crude protein (CP) was expressed as $6.25 \times N$. Simple sugar and starch concentrations were measured with a Hitachi U1100 spectrophotometer using a slightly modified version of the enzymatic method developed by Steen & Larsson (1986). This enzymatic method is a two-step extraction procedure applied for non-structural (available) carbohydrates, with total soluble sugars determined in the first extract, and starch in the second extract. Total carbohydrates was defined as the sum of simple sugar concentrations of glucose, fructose, sucrose, fructan, maltodextrin and starch. Fibre fraction acid detergent fibre (ADF) and acid detergent lignin (ADL) concentrations were determined at Grimsö Wildlife Research Station using the sequential techniques of Van Soest (1963) and Van Soest & Wine (1967). Concentrations of macroelements, fibre and sugar contents were expressed as percent of dry weight (%-d.w.), and trace elements on a dry weight basis were expressed in parts per million (ppm).

In vitro dry matter disappearance analyses

To compare the apparent digestibility of CGTS vs two other typical summer forage species at GWRA, bilberry and birch (Cederlund et al. 1980), an IVDMD trial was run according to the modified method of Tilley & Terry (1963). Our IVDMD method was originally developed at the Swedish University of Agricultural Sciences (SLU) (den Braver & Eriksson 1967), and is described completely by Pehrson & Faber (1994). A finely ground, 0.5 g forage sample is incubated with 1 ml of rumen fluid and 50 ml of buffer solution for 72 hours. This procedure has been used at Grimsö for studies on the digestibility of browse in moose and roe deer (Cederlund & Nyström 1981, Pehrson & Faber 1994). A subsample of the CGTS used for forage analyses was used as substrate and tested against birch and bilberry, both including leaves and twigs, collected during the same period within the GWRA. Although earlier research has found that moose prefer silver birch *Betula pendula* over pubescent birch *B. pubescens* (Danell, Huss-Danell & Bergström 1985), in this study these two species were combined. Rumen inoculum was from a yearling moose harvested at the GWRA in June 1996, less than one hour before the incubation was initiated. Results are expressed as percent disappearance (%-d.w.) of the forage sample.

Statistical analyses

Moose browsing on CGTS and the temporal pattern of growth of pine terminal shoots in Kronoberg in 1980 were tested for using a Friedman (χ^2_r) test. At GWRA, browsing observations and terminal shoot growth, both in length and weight, were individually tested for using a Friedman (χ^2_r) test. For Halleberg-Hunneberg and GWRA, a χ^2-test was used to test whether CGTS with terminals previously browsed during the growing season in years past incurred a higher likelihood of being browsed than those of pine with terminals previously unbrowsed. The changes over time in the amounts of macroelements, fibre fractions, and sugar content in the pine samples were each tested for using one-way factorial ANOVA, which was also used to test the IVDMD values. Statistics were computed using StatView™ SE+$^{\text{Graphics}}$, and for each ANOVA test used, all means were tested but only significant differences (Fisher's protected least significant difference or PLSD) are presented.

Results

Temporal pattern of browsing

For nine stands where moose density varied within 1.0-1.4/km^2, some feeding on CGTS was recorded (see Fig. 2). The temporal patterns found, which in 1980 peaked in June and in 1995 peaked in late May, are shown in Figure 3. The pattern found in 1980 varied significantly (χ^2_r = 16.6, df = 8, N = 4, P =

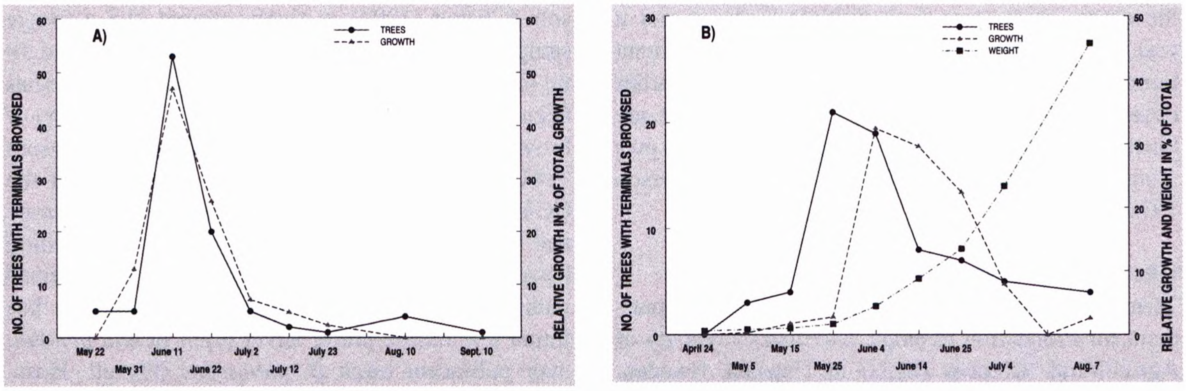


Figure 3. Temporal pattern of browsing on current-growth, terminal shoots and of shoot growth. A) Number of trees of the total observed (N = 200) with current-growth, terminal shoots newly browsed and relative growth of pine terminal shoots (N = 15) in percent of total growth, from four pine stands during May-September, 1980, in Kronoberg; and B) number of trees of the total observed (N = 250) with newly browsed current-growth, terminal shoots and relative growth and relative weight of pine terminal shoots (N = 5) in percent of total growth and weight, for five pine stands during April-August, 1995, at Grimsö Wildlife Research Area.

0.0345) during the growing season (see Fig. 3a). Only a low amount of browsing occurred at the start of the growing season during the interval 22 May - 31 May. Browsing on terminal shoots showed a sudden increase between 31 May and 11 June and a similarly sharp decrease afterwards until 2 July. Little or no activity was observed for the remainder of the summer (see Fig. 3a).

In 1995, the pattern of feeding on CGTS also varied but not significantly (χ^2_r = 9.68, df = 8, N = 5, P = 0.2884) during the growing season (see Fig. 3b). There was no browsing on terminal shoots prior to the start of the growing season in late April which was followed by a low use in early to mid-May. During the interval from 15 May to 25 May terminal shoot browsing showed a sudden increase followed by a slight decline during the next interval to 4 June, and then a sharper decrease in the interval ending on 14 June. The remainder of the growing season showed a declining amount of browsing on CGTS until early July, and then virtually no activity, i.e. four trees were browsed during the last 34-day interval ending on 7 August (see Fig. 3b). During the 1995 study period, there were 71 records of CGTS browsed by moose; 50 trees with terminal shoots browsed once, six trees were terminally browsed twice (i.e. 12 observations), and three trees were browsed three times (i.e. 9 observations). Of the 71 total terminals browsed, 46 of the trees had only terminals browsed, whereas 25 had laterals browsed as well. In addition, 39 trees had only had current-growth laterals browsed; hence a total of 64 trees had laterals browsed.

Temporal pattern of terminal shoot development

The temporal pattern of growth of pine terminal shoots in 1980 in Kronoberg varied significantly during the growing season (χ^2_r = 102.77, df = 7, N = 15, P < 0.0001) and the most intensive growth, coinciding with the peak in browsing, was found to occur from the end of May to the beginning of July (see Fig. 3a). The growth rate peaked between 31 May and 22 June, was followed by a levelling off of the growth rate curve and by mid-July terminal shoot growth had ceased (see Fig. 3a).

The temporal growth pattern of terminal shoots in 1995 at GWRA also varied significantly during the

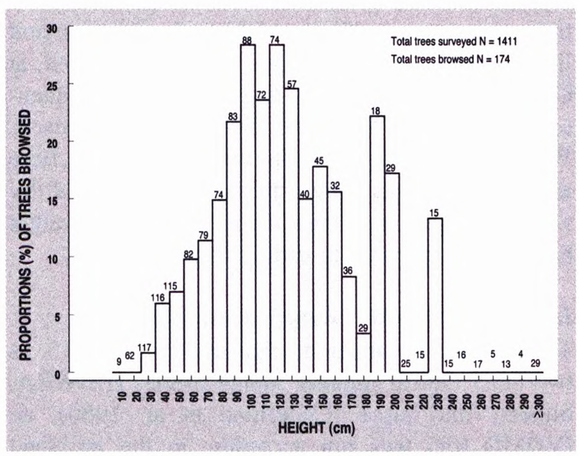
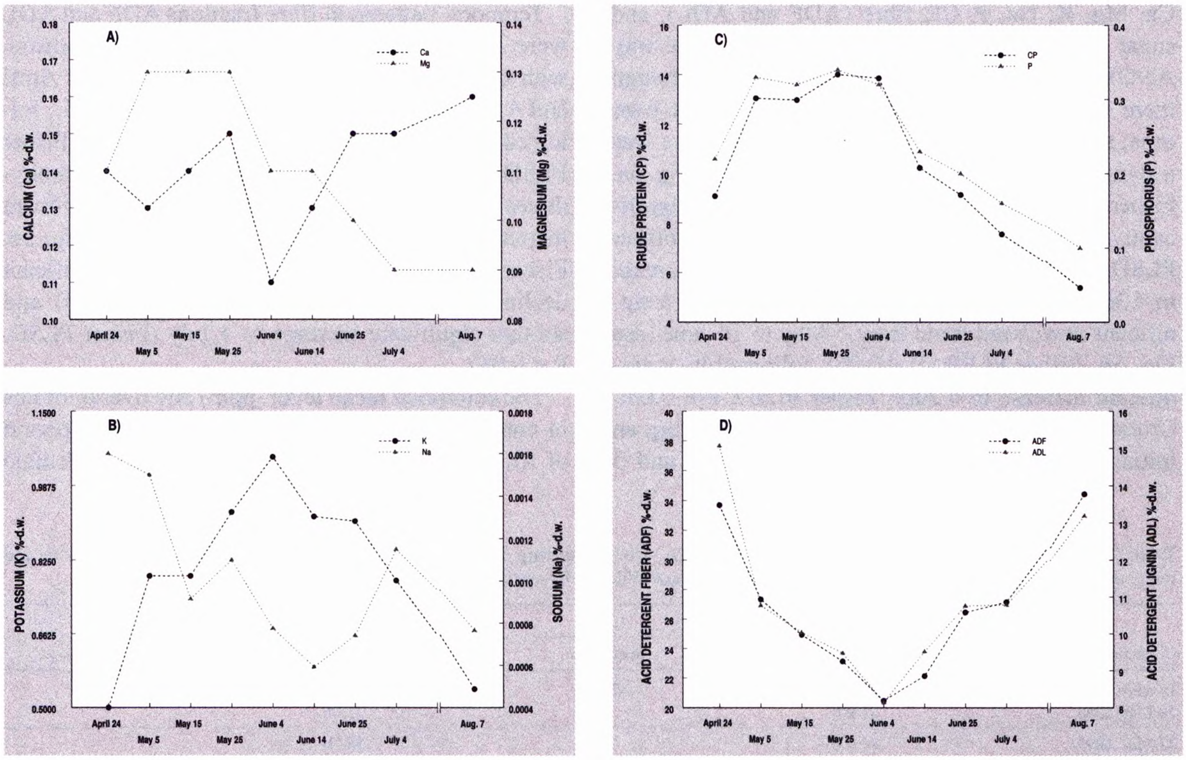


Figure 4. Height distribution of pine trees with current-growth, terminal shoots browsed within 10 stands in early and mid-July 1985 at Halleberg-Hunneberg in the counties of Älvsborg and Skaraborg. Respective total sample sizes (N) are given above each tree height column.

growing season (χ^2_r = 175.4, df = 8, N = 25, P < 0.0001) and showed that the greatest growth occurred from the end of May to the end of June. This increase was slightly delayed when compared to the peak in browsing seen between 15 May and 25 June (see Fig. 3b). The majority of growth occurred between 25 May and 25 June. This was followed by a levelling off of the growth rate curve by early July, and by 7 August terminal shoot growth had nearly ceased (see Fig. 3b). Weight development of terminal shoots varied significantly during the growing season (χ^2_r = 40, df = 8, N = 5, P < 0.0001) with the greatest increase in weight occurring after the elongation of terminals had occurred (see Fig. 3b). The greatest weight gain occurred from early June to early August.

Characteristics of browsed trees and frequency of use

At Halleberg-Hunneberg in 1985 moose browsed pine trees within a limited height range during summer. A total of 1,411 trees were surveyed (height: mean = 106.3 ± 72.1 (SD) cm) on 100 sample plots, and 174 (12%) had terminal shoots with current-growth recently browsed by moose. The 174 browsed pine trees had a mean height of 108.1 ± 40.1 cm and all of the trees were between 30 and 230 cm in height (Fig. 4). Of trees within the height-range



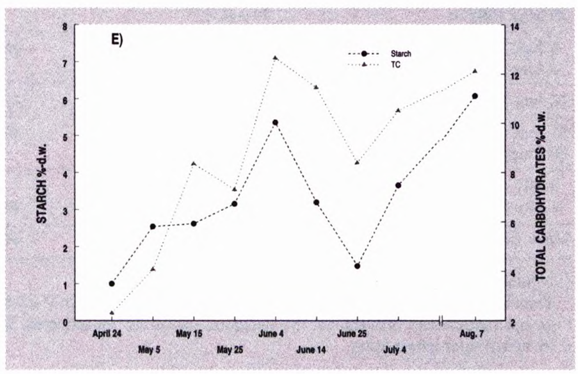


Figure 5. Concentrations in percent of dry weight (%-d.w.) of mineral nutrients, fibre fractions and sugars analysed from current-growth Scots pine terminal shoots collected between April and August 1995 at Grimsö Wildlife Research Area, Sweden. A) calcium (Ca) and magnesium (Mg); B) potassium (K) and sodium (Na); C) crude protein (CP) and phosphorus (P); D) the fibre fractions acid detergent fibre (ADF) and acid detergent lignin (ADL); and E) starch and total carbohydrates (TC; the sum of the simple sugars glucose, fructose, sucrose, fructan, maltodextrin and starch).

browsed by moose, i.e. 30-230 cm (see Fig. 4), 14% had been recently browsed. There was an apparent central tendency with trees between 90 and 160 cm in height being preferred while no trees over 230 cm were chosen (see Fig. 4).

Further, there was a significantly higher chance for trees browsed in earlier years to be re-browsed (χ^2 = 101.9, df = 1, P < 0.0001). This was also the case at GWRA in 1995 as CGTS of bush-like, previously browsed pines incurred a significantly higher chance of being re-browsed (χ^2 = 14.59, df = 1, P < 0.0001) than previously unbrowsed pines.

Table 2. Mean trace element levels (ppm) combined for April-August, 1995, collections (N = 45) and overall trend in concentrations during the growing season of aluminium (Al), boron (B), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) in current-growth of Scots pine terminal shoots at the Grimsö Wildlife Research Area.

	Mean	SD	Trend
Al	142.0	44.8	Increasing
B	13.4	2.8	Decreasing
Cu	6.3	2.3	Decreasing
Fe	88.7	80.7	Decreasing
Mn	320.0	100.0	Variable
Zn	43.9	9.4	Decreasing

Chemical analyses

CGTS collected in 1995 showed significant variation throughout the growing period in concentrations of Ca, Mg, K, Na, P, CP, fibre (ADF and ADL), and sugar (starch and total carbohydrates) (one-way ANOVA, P < 0.0001 in all cases) (Fig. 5). Although there were significant changes in Ca content over time, no clear pattern was seen; but for Mg there was a significant drop from 25 May to 4 July (see Fig. 5a, Fisher PLSD, P < 0.05). Potassium increased significantly from 24 April to 4 June (see Fig. 5b, Fisher PLSD, P < 0.05), followed by a significant decrease to 4 July (Fisher PLSD, P < 0.05). Na showed a significant downward trend from 5 May to 14 June (see Fig. 5b, Fisher PLSD, P < 0.05), followed by a significant increase to 4 July (Fisher PLSD, P < 0.05). Crude protein and P were similar, both showing an initial significant increase between 24 April and 5 May (see Fig. 5c, Fisher PLSD, P < 0.05) and, the greatest change, a significantly decreasing content (Fisher PLSD, P < 0.05) from 4 June to 4 July.

Temporal patterns in fibre fractions ADF and ADL were almost identical during the growing season, with both significantly decreasing between 24 April and 4 June (see Fig. 5d, Fisher PLSD, P < 0.05), followed by significant increases to 4 July (Fisher PLSD, P < 0.05). Levels of starch and total carbohydrates showed similar patterns with a significant increase between 24 April and 4 June (see Fig. 5e, Fisher PLSD, P < 0.05), followed by a significant decline to 25 June (Fisher PLSD, P < 0.05) and another significant increase to 4 July (Fisher PLSD, P < 0.05).

The combined mean level (ppm) and overall trends in concentrations for the April-August study period of Al, B, Cu, Fe, Mn, and Zn showed considerable

Table 3. *In vitro* dry matter disappearance (IVDMD, %-d.w.) trial comparing current-growth, terminal shoots of Scots pine to leaves and twigs of birch and bilberry, using moose inoculum at Grimsö Wildlife Research Area.

		Species		
Collection date	Sample size[1]	Scots pine	Birch	Bilberry
15 May 1995	N = 6	42.3[2]a		
16 May 1995	N = 6		31.6b	
22 May 1995	N = 6		33.7b	
25 May 1995	N = 9	40.9a		
29 May 1995	N = 6; 6		37.1b	38.5a
4 June 1995	N = 6	46.8a		
6 June 1995	N = 5			41.6b
14 June 1995	N = 6	47.7		
25 June 1995	N = 9	46.0a		
26 June 1995	N = 6; 6		41.7b	41.8b
3 July 1995	N = 6; 6		42.7a	41.0a
4 July 1995	N = 6	44.7a		
Mean IVDMD		44.5a	37.4b	40.7b

[1] Number of replicate tubes
[2] Tests for significant differences (one-way ANOVA, Fisher PLSD, P < 0.05) were run for pine vs each of the two deciduous species within each of the six groups. Differences between the two deciduous items are not reflected. Differences between pine and either or both of the deciduous species are indicated by non-similar letters (a,b).

variation through time as indicated by large standard deviations (Table 2). B, Cu, Fe and Zn decreased in concentration during the study period, whereas Al increased and Mn was variable (see Table 2).

In vitro dry matter disappearance analyses

For all sets of plant material collected during May-July, IVDMD was higher for pine shoots than for two deciduous species commonly used by moose during these months (one-way ANOVA, $P < 0.063$ in all cases), and in six of nine cases the differences found were significant (Fisher PLSD, $P < 0.05$, Table 3). The average IVDMD for pine shoots was ca 4 and 7% higher than the average for birch and bilberry, respectively (see Table 3), and these differences were also significant (one-way ANOVA, $F = 25.04$, $df_1 = 2$, $df_2 = 92$, $P < 0.0001$). The differences were greatest in the early part of the growing season, i.e. May to mid-June, when CGTS had an IVDMD on average 17% higher than birch and bilberry. By the end of June and the beginning of July, IVDMD of pine remained higher than the other two browse species, but the average difference was reduced to ca 8.5%.

Discussion

Our findings confirm that moose in forest land of southern and central Sweden use CGTS in summer. Knorre (1959) reported that moose in parts of Siberia consume conifers throughout the year. This contrasts with reports from North America that have documented little or no use of conifers by moose in summer (Peterson 1955, Peek et al. 1976, Lautenschlager et al. 1997).

The peak in browsing on CGTS in 1980 coincided with the greatest increase in growth of the terminal shoots, while in 1995 the peak in browsing slightly preceded the peak in growth. It has been shown previously that forage biomass is one important factor determining forage choice and selectivity in moose, in addition to bite rate and bite size; this is in turn related to and affected by forage quality and availability (Renecker & Hudson 1986, Vivås & Sæther 1987, Sæther & Andersen 1990, Heikkilä & Mikkonen 1992, Renecker & Schwartz 1997). In the present study direct measures of biomass removed by moose were not made and this makes a detailed comparison difficult. However, we made a rough estimate of the maximum amount of CGTS removed by moose from pine within GWRA during summer 1995; the total dry weight removed daily by a moose over the 100-day study period was ca 0.5-1 kg (W. Faber, unpubl. data). This is far less than the 11.5 kg dry weight requirement based on Renecker & Hudson (1985)(Faber 1996). We therefore suggest that the amounts of CGTS consumed by moose during the growing season seems too limited to be of any major importance from an energetic standpoint, both on an individual and a population level. Faber (1996) made a similar suggestion concerning bark stripping of pine by moose during spring and summer in Sweden. Since only 12% of all pine trees up to 4.4 m and 14% of pine 30-230 cm high had CGTS browsed during the growing season, the availability of terminal shoots is much greater than that used by moose. These values of 12 and 14% are from an area known for its moose damage (Klementsson & Schärnell 1984, S. Lavsund, pers. obs.) and probably are higher than would be expected in other areas of Sweden. Therefore, this difference between browsed vs available pines would arguably be even greater in other regions. Thus, in our study factors other than forage biomass and availability were also investigated to elucidate the mechanisms underlying moose use of CGTS during summer. Specifically, nutrient content and palatability was determined, since these plant characteristics appear to be related to moose selection and consumption of individual woody plants and plant parts (Risenhoover 1987, 1989, see Renecker & Schwartz 1997).

Chemical and IVDMD analyses of CGTS reported in our study show that its qualitative value is equal to or better than that of the most utilised alternative forage (Cederlund et al. 1980), birches and bilberry. The greatest amounts of CP, ca 13-14%, and P, found in CGTS (see Fig. 5c) coincided with the period of greatest use, i.e. from mid-May to mid-June (see Fig. 3b). Schwartz, Regelin & Franzmann (1985) showed that a formulated ration for moose containing 12.7% CP is suitable for maintenance of moose including costs of growth, reproduction and lactation during summer. Thus, values for pine early in the growing season are at or above this level suggesting it is a good quality browse for moose. Early in the growing season birch had slightly lower amounts of CP than those found in terminal shoots of pine, and the peak in birch CP of ca 18% (Å. Pehrson, unpubl. data) occurs after the peak in pine. Starch and total carbohydrates also peaked (see Fig. 5e) at the same time as CP, whereas the fibre fractions ADF and ADL declined (see Fig. 5d). In addition, IVDMD values of pine were higher throughout the growing season when compared to birch and bilberry (see Table 3). Therefore, we would argue that the overall qualitative value of CGTS in terms of nutrients and palatability are such that moose select this readily available browse as a transitional forage when levels of CP, P, starch and total carbohydrates are highest, and digestibility is favourable. Further, this use peaks prior to when the peak in CP levels in birch occurs, which remains considerably higher than for CGTS during the remainder of the growing season (Å. Pehrson, unpubl. data), and may help explain the greater use of birch by moose throughout the growing season.

At GWRA, little research has been done concerning trace elements, making detailed comparisons difficult. However, concentrations of the trace elements Mn and Zn found in CGTS are similar to amounts found in pine during winter at GWRA, whereas CGTS in summer have less Al and more Cu and Fe than in winter (Pehrson & Faber 1993). Also, concentrations found in our study for all six trace elements (Al, B, Cu, Fe, Mn and Zn) were comparable to values found in pine in both winter (Salonen 1982) and summer in Finland (Helmisaari 1990). Concerning Al and B, neither have been shown to be essential to animals (National Research Council 1980) and thus it is not likely that moose should be utilising CGTS to meet any physiological requirements for either of these trace elements. When compared to the normal requirements given for domestic sheep *Ovis aries* and cattle *Bos taurus* (National Research Council 1985, 1996), results presented here would suggest that CGTS should contain sufficient amounts of Fe, Mn and Zn to meet requirements whereas Cu is somewhat below requirement. This latter finding may have implications in relation to a previously unknown disease in moose, a wasting syndrome (Rehbinder, Gimeno, Belák, Belák, Stéen, Rivera & Nikkilä, 1991, Stéen, Diaz & Faber 1993), that has been occurring since 1985 in an area of southwestern Sweden. Trace element imbalance along with secondary Cu deficiency due to elevated molybdenum (Mo) levels, as well as chromium (Cr) deficiency, has been suggested as a potential cause of this disease (Frank, Galgan & Petersson 1994, Frank 1998). However, at present, moose browsing on CGTS cannot be linked to a deficiency of any of the trace elements analysed here.

When suggesting why moose browse pine terminal shoots in summer, one should also consider the availability of alternative forage species, e.g. deciduous browse, in areas adjacent to the study sites. Therefore, we looked at data from surveys made in 1996 and 1997 in the same portion of GWRA as the one in which the 1995 study was done. When combining the availability and recent moose browsing pressure on the most preferred species (i.e. birch, willow *Salix* spp., aspen and rowan *Sorbus aucuparia*; Å. Pehrson, unpubl. data), it is clear that moose have available and utilise these to a much greater degree during the growing period. However, our results still suggest that moose actively select CGTS and lateral shoots of pine to some extent in early summer.

Since use of CGTS by moose is not directly related to energetic factors or trace element imbalance, then other mechanisms influencing this selectivity (Risenhoover 1987) need to be explored. Therefore, another potential mechanism influencing moose forage choice concerns the importance of diversity in the diet and has been suggested by Oldemeyer et al. (1977) and Miquelle & Jordan (1979). They suggested that moose need to incorporate more than one plant species in their diet to meet their nutritional demands, and that assemblages of five or more species could better meet the needs of moose than any one. We suggest that the need for diversity in the diet could underlie moose use of CGTS during the growing season, a period when the bulk of the diet for moose at GWRA consists of two species, birch and fireweed *Epilobium angustifolium* (Cederlund et al. 1980). Further, Risenhoover (1989) suggested that for moose any selective feeding, which results in even small improvements in diet quality, can greatly influence animal condition and productivity because of 'multiplier effects' (White 1983). Therefore, we found that the quality in terms of nutrients and palatability of CGTS was as good or better than for birch and bilberry, and suggest that inclusion of terminals improves the summer diet of moose.

The likelihood of being browsed is significantly higher for those CGTS of trees that have been previously browsed by moose. This is in agreement with previous work concerning winter browsing of Scots pine by moose in Finland (Löyttyniemi & Piisilä 1983, Löyttyniemi 1985). In Sweden, simulated winter top browsing of Scots pine also resulted in a much higher likelihood of re-browsing on the affected trees the following year by moose (Marcström 1973). In these studies, it is suggested that the initial browsing resulted in pine that were of a higher quality making them even more palatable to moose, thus increasing their likelihood for re-browsing. In Sweden, Danell et al. (1985) have suggested a similar mechanism for moose browsing on birch in winter. Bowyer & Bowyer (1997) found moose in interior Alaska to exhibit a similar pattern of preference for regrowth from willow *Salix glauca* stems that were browsed in the previous winter. Similar results have been found in Scotland for red deer and roe deer browsing on young Sitka spruce trees (Welch et al. 1991). However, Miquelle (1983) found that moose on Isle Royale avoided regrowth foliage of four deciduous browse species that had been browsed previously during the growing season. He suggested that this may be an important mechanism by which browse plants reduce the impact of herbivory. It was not, however, the scope of the present study to test whether terminal shoots of previously browsed pine were of higher quality than unbrowsed ones, but more research in this area is warranted.

It has been suggested elsewhere that moose seem to prefer terminals of balsam fir *Abies balsamea* to laterals during winter (Bergerud & Manuel 1968). However a thorough comparison of moose use of pine terminals vs laterals during the growing season was beyond the scope of the present study, although there are indications that moose did prefer terminals to laterals, especially on bush-like pine trees, i.e. previously browsed (Dietrichson & Karlsson 1979, Lavsund 1980, W. Faber, pers. obs.). In Norway, Hjeljord, Hövik & Pedersen (1990) found that moose prefer upper crown twigs of birch to side branches during summer, and in Scotland Welch et al. (1988) suggested that roe deer prefer terminal shoots of Sitka spruce to laterals during the early part of the growing season. Thus, further detailed studies comparing the qualitative and quantitative differences between CGTS and laterals of pine including more detailed measurements of amounts of biomass removed by moose vs available biomass are suggested.

Tree height seems to be a fundamental factor in determining which pine trees bear CGTS most susceptible to browsing by moose. Trees from 30 up to 230 cm were used and there was an apparent central tendency indicating moose preference for trees 90-160 cm high (see Fig. 4). This pattern is quite similar to that of winter browsed shoots of Scots pine reported in Finland (Löyttyniemi & Piisilä 1983). Faber & Thorson (1996) also found that height was an important factor in determining which pine trees are most susceptible to spring and summer bark stripping by moose in south-central Sweden. They found that 99% of bark-stripped pine trees were 1.5-4 m in height and that moose prefer to strip bark at heights from 100 to 170 cm.

Browsing frequency of CGTS was 14% of the most susceptible trees, i.e. 30-230 cm. In the same region where this damage was observed, observations of pine stands of varying older age classes clearly show this type of damage had been commonly occurring for at least the past 50 years (S. Lavsund, pers. obs.). Further, Dietrichson & Karlsson (1979) suggested that browsing damage to pine terminal shoots during the growing season would impair pine growth and quality, and measurable financial losses, depending on moose densities and browse availability, could result. In Sweden, forestry has a very high commercial value since forest products, to which Scots pine is a major contributor, are one of the main export articles, contributing 17% (Skogsstatistisk årsbok 1997: 287) of the export value for the country. Therefore, the impact that summer browsing on CGTS has on pine plantations in respect to forestry damage requires further investigation, and can be an important factor to consider during moose management discussions.

Although moose actively select CGTS early in the growing season, they seem to take only a limited amount of what is available. One possible mechanism limiting use could be the high K/Na ratio (see Fig. 5) found in the CGTS coinciding with the peak in browsing from mid-May to late June in 1995 (see Fig. 3b). Staaland & Jacobsen (1983) pointed out that a high K/Na ratio can drain the sodium pool of reindeer *Rangifer tarandus*, and as Faber, Pehrson, Cederlund & Jordan (1988) argued this may be the case for moose in summer at GWRA. Thus the high K/Na ratio found in pine terminal shoots as presented in the present study could be one factor involved in explaining the limited use of pine during the growing season. However, a similar argument would supposedly also be valid for other plant species, e.g. bilberry and birch, at GWRA (Pehrson & Faber 1993, Å. Pehrson, unpubl. data).

Another potential mechanism underlying this restricted use could lie in the amounts of secondary compounds present in CGTS. Such plant defences are suggested to limit the use of certain plant species in boreal forests (Bryant & Kuropat 1980, Bryant, Chapin, III & Klein 1983). Future studies focusing on levels and variation in secondary compounds of CGTS during the growing season are recommended.

Conclusions

We have confirmed that moose use CGTS during the growing season with a peak in early summer. The nutritive value of this forage is comparable to or better than that of important alternative food such as birch and bilberry. The qualitative value of CGTS may dictate its use by moose. The importance of diversity in the diet and the potential for 'multiplier effects' due to an inclusion of high-quality pine terminal shoots in the summer diet of moose are suggested as positive effects from this usage. On the other hand, since moose are using only a fraction of the pine terminal shoots available during summer, there must be other plant physiological factors, including an unfavourable K/Na ratio and levels of secondary compounds, which may be limiting this use. Moose prefer to browse CGTS of trees that have been browsed previously, and also seem to prefer terminals to laterals during the summer period.

Areas for further research have also been emphasised, including more detailed studies of the mechanisms limiting use of pine terminals by moose, determining the impact of moose summer browsing for forestry, and finally the importance of taking such damage into consideration when discussing moose management issues.

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