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ORIGINAL ARTICLE

Paper birch (*Betula papyrifera*) shoot selection by moose (*Alces alces*) following a forest-cleaning experiment

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Abstract
In order to maximize food intake per harvesting effort and minimize energy expenditures required to move between feeding patches in nature, herbivores such as moose (*Alces alces* L.) generally select large plant shoots when browsing in winter. To determine moose preferences for shoots of different morphologies, an experiment was conducted in northern British Columbia in which shoots from birches cut at different times of the growing season were fed in 2 consecutive years to eight human-habituated moose in cafeteria-style feeding trials. The results indicate that moose preferred smaller winter shoots of birches regardless of when the parent plant was cut and also appeared to reject larger shoots containing sylleptic branches. It is argued that the preferences for smaller shoots by moose detected in these trials should be observable under natural conditions, but are generally only supported by literature from some parts of Scandinavia. The findings underscore the importance that factors such as mouth filling per harvesting effort, snow depth and consistency, predators and browse patch distribution must have on foraging decisions made by moose while browsing in the wild. Implications of the findings include the significance of cutting time on the size of shoots produced by birch after cutting, how this affects moose browsing birch and, subsequently, how managers can theoretically use cutting time as a tool in forest cleaning operations to direct the foraging efforts of moose towards or away from forest plantations.

Keywords: *Forage, plant–animal interaction, plantation, plant response, rangeland, ungulate.*

Introduction

Large herbivores such as moose are often reported to preferentially select resprouts of plants that have been previously cut or browsed (broken) rather than the shoots of undamaged plants (Danell et al., 1985; Hessl & Graumlich, 2002). Resprouts are generally larger than the shoots of undamaged plants and when eaten allow larger intake rates per cropping effort (Danell et al., 1985; Renecker & Schwartz, 1998; Gross et al., 1993). Resprouts are also widely reported to have fewer phenolic anti-herbivore chemicals (tannins/lignins). However, large shoots may also contain fewer minerals and more fiber than smaller shoots (Danell & Bergström, 1989; Rea & Gillingham, 2001),

making them less attractive to moose throughout various parts of their range (Hagen, 1983; Vivås & Sæther, 1987; Histøl & Hjeljord, 1993).

Conclusions about the nutritive value of shoots growing from plants cut at different times have been assessed using laboratory analyses. Fiber, energy, protein, tannin and other such indicators have been quantified in the laboratory (Rea & Gillingham, 2001) and field studies have allowed for the determination of proportions of cropped stems from different plants cut at various times of the growing season (R. V. Rea, unpublished data). However, no cafeteria-style trials to determine why herbivores consume resprouts from plants cut at different times of the year seem to have been conducted or published.

This study sought to determine whether moose selected shoots in cafeteria-style feeding trials similar to how they are reported to select shoots in nature. The objectives were: (1) to ascertain whether shoots selected by moose in such trials were of a certain size and diameter and were produced exclusively from plants cut earlier or later in the year; and (2) to determine preferences that may help natural resource managers to decide how plants producing such shoots should be managed both on and off winter rangelands and forest plantations.

Materials and methods

Field studies

In April 2003, 210 paper birch saplings were selected from a 9-year old pine plantation in the John Prince Research Forest in north-central British Columbia (54°39′10.49″ N, 124°30′12.61″ W, 900 m a.s.l.). The saplings were of the size that were observed to be typically used by local moose in winter and ranged in size from between 2 and 5 m tall. The birches were randomly divided into groups with 30 saplings per treatment category. A total of seven treatment categories were each marked with a specific color of flagging ribbon based on the month of the year that each was to be cut down. One group of 30 was left as a control and the other birches within all other groupings were separately cut: one group each within the first 2 days of May, June, July, August and October. Uncontrollable events prevented cutting treatments from being performed that were planned for September and, therefore, plants tagged for treatment in September remained uncut and the shoots subsequently unharvested. All treated plants were cut with a brush saw at between 20 and 30 cm above the ground.

In the first winter after cutting, all resprouts from 15 randomly selected plants of each of the May, June and July treatments that had resprouted following cutting and current shoots from 15 random control plants were collected on 21 February 2004. Shoots from plants cut in August and October had not resprouted at all or insufficiently (i.e. August-cut plant shoots were between 1 and 3 cm long) for the purposes of the experiment and were, therefore, considered unavailable for collection in 2004. Shoots from plants were collected in composite by treatment category, bagged in large plastic bags and weighed to the nearest 100 g, then transported at ambient temperatures (−5 to +3°C) to the Northern Lights Wildlife Shelter in Smithers, British Columbia, Canada (54°51′00.63″ N 127°05′47.16″ W, 680 m a.s.l.).

The Northern Lights Wildlife Shelter has raised moose since 1990 and each year, on average, raises between two and six moose calves that have been orphaned or abandoned by their mothers. Moose are brought to the shelter from all over the province of British Columbia and bottle-raised until the age of 4 months. Calves generally begin eating plant materials at 4–6 weeks old and are housed in an outdoor electrified enclosure to protect them from predators. At around 4 months of age, the moose calves are released from the pens and are free to roam around in the surrounding woodlands of the shelter as well as the provincial park that borders the property of the shelter. Although moose have free access to natural forage, supplemental feeding of plant matter is provided for moose twice per day throughout the winter months from November/December to April each year. Calves that are raised at the shelter are known to return to the shelter up to 10 years of age.

Of all the composite shoot materials collected and bagged by treatment category, about 20% of shoots from each treatment were randomly selected and retained for prefeeding measurements of shoot morphometrics. The remainder of all the materials collected from each treatment was then presented on 22 February 2004 to six moose (9–33 months of age) residing at the wildlife shelter. All of these shoots from the 15 replicate birches from each treatment category were placed into one composite feeding pile per treatment category. Piles were distributed between 5 and 10 m apart in random order around the feeding grounds at the shelter and presented in a cafeteria-style similar to that described in Renecker and Schwartz (1998). Ten shoots of various sizes that were randomly selected from the piles were weighed and kept outdoors at the exclosure during the trial and monitored for loss of water mass due to evaporation to the nearest one-hundredth of a gram. However, losses were negligible so a correction factor for water loss was not applied to the experimental results.

Moose followed the researchers, carefully and systematically inspecting each pile as the materials were distributed on the feeding grounds. Once the materials were in place, moose were allowed to feed on the piles of shoots for approximately 24 h, moving between feeding piles and in and out of the surrounding woodlands at will. After 24 h, all shoots and shoot portions left in and around the piles were meticulously collected and bagged, then the bags were weighed (to nearest 100 g) and transported to the laboratory at the University of Northern British Columbia, Prince George, BC (53°53′ N, 122°40′W, 780 m a.s.l.). On the shoots that were not presented to moose, the length of shoots was measured to the nearest centimeter and the basal diameter of each shoot was measured to the nearest millimeter. Because after the first year of the study

there was reason to believe that supplementary or sylleptic branches arising from the main current annual shoots (and growing from the lateral buds that were formed in the current growing season; *sensu* Cline & Dong-Il, 2002) played a role in forage selection, the number of sylleptic branches arising from second year shoots from all treatments was also measured. On shoots that were recovered from the feeding trial, shoot diameter at the point of browsing and the length of shoots from the basal diameter to point of browsing or shoot tip were measured.

The same procedures were repeated for year 2 of the study, clipping the second year current annual shoots of the remaining 15 plants (15 random plants in the case of August- and October-treated birch) per treatment category that remained unclipped from year 1 trials. Clippings were made on 19 February 2005 at around $-5°C$ and transported to the animal shelter the following day at between $-1°C$ and $-14°C$ for cafeteria trials. In year 2, three moose were present during the feeding trials. During this period, shoots left over from the feeding trials were used to determine shoot length, basal diameters and browse diameters, as well as the average number of sylleptic branches per shoot from different treatment categories.

Statistical analyses

Analysis of variance (ANOVA; Tabachnick & Fidell, 2007) was used to determine differences in length, basal and bite diameter between shoots, as well as the differences in the degree of sylleptic branching from different cleaning treatment times and controls. Homogeneity of variances for all ANOVA comparisons was tested using Levene's test (Milliken & Johnson, 1984). A Kolmogorov–Smirnov test was used to test assumptions of normality (Gotelli & Ellison, 2004). When samples sizes were approximately equal, Tukey's HSD test was used for *post hoc* comparisons (Gotelli & Ellison, 2004); otherwise, a Spjotvoll/ Stoline for unequal sample sizes test was used for *post hoc* comparisons (Zar, 1984). To test differences in the percentage of shoot biomass consumed by moose from different treatment types and between treatment types, in the first and second years after the cleaning experiment, a two-proportion z test (Zar, 1984) was used, as previously used to test the differences in plant response variables to forest cleaning (brush-cutting) experiments (Rea & Gillingham, 2001).

Results

Year 1

In the first winter after cutting, shoots from birches in different treatment categories were significantly different in length ($F_{1,3} = 18.677$, $p \leq 0.001$) and basal diameter ($F_{1,3} = 8.141$, $p \leq 0.001$). Shoots from plants cut earlier in the year were longer, with larger basal diameters than those cut later in the season and controls (Figure 1).

Of the shoots produced in the first year after cutting, moose consumed less shoot biomass from plants cut in May (71.3%) than from plants cut in June (86.7%) and July (86.7%) ($\hat{p} = 0.795$, $z = -2.978$, $p = 0.001$) or controls (80.9%) ($\hat{p} = 0.765$, $z = -1.834$, $p = 0.033$). No differences existed in the proportion of shoot biomass that was consumed by moose from birches cut in June and July and from controls ($\hat{p} = 0.850$, $z = -1.188$, $p = 0.117$).

A significant difference existed in bite diameters on first year shoots from different treatment categories ($F_{1,2} = 11.137$, $p \leq 0.001$). Bite diameters measured on the shoots of birches following the feeding trials in year 1 indicate that moose took larger bites from plants cut in May ($p \leq 0.001$) and June ($p = 0.050$) (Figure 2) than from controls. Shoots from plants cut in June did not sustain larger bite diameters than shoots from May-cut birches ($p > 0.05$).

Year 2

Significant differences existed in shoot length between shoots collected from birches in the second year after cutting ($F_{1,5} = 78.822$, $p \leq 0.001$) and were longest from plants cut in October (the only treatment category to produce its first full season resprouts in the year after cutting) and May (Figure 3). No differences in shoot length existed between
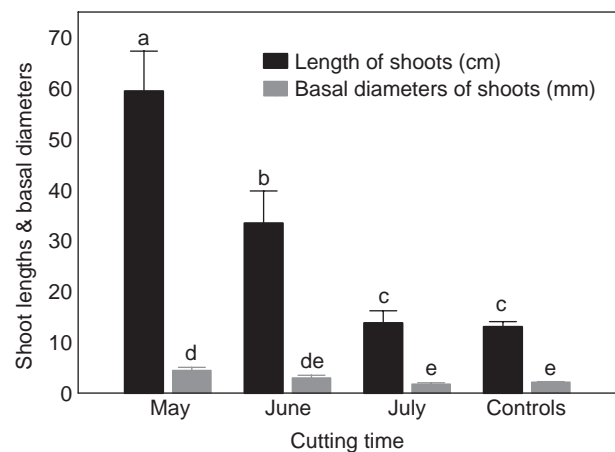

Figure 1. Average ($\pm$ 1 SE) length and basal diameter of winter shoots from controls and plants cut at various times during the previous (2003) growing season. Measurements were taken in the first winter (2004) after cutting and resprouting. $n = 15$ shoots per treatment category. Bars with common letter designations are not significantly different from one another as determined by Tukey's *post hoc* comparisons.
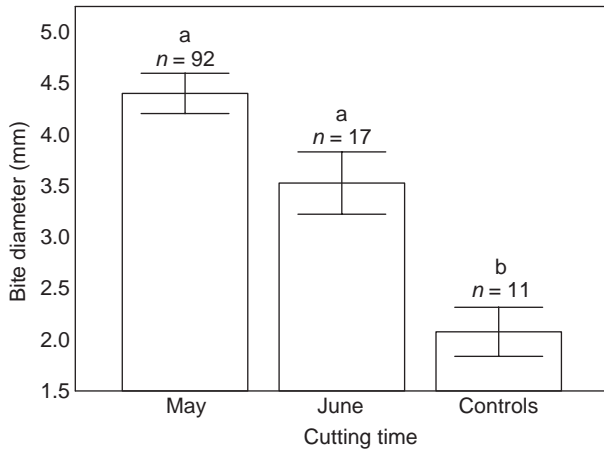
Figure 2. Average ($\pm$ 1 SE) bite diameters measured on shoots collected from birches cut at different times of the 2003 growing season and left over by moose following feeding trials in February 2004. July shoots that were eaten by moose were fully consumed so those that were left over had no bite marks on them available to measure. Bars with common letter designations are not significantly different from one another as determined by Spjotvoll/Stoline *post hoc* comparisons.

birches cut in June, July and August ($p > 0.050$), while controls had the smallest shoots. Basal diameters of shoots from different treatment categories were also significantly different from one another ($F_{1,5} = 38.306$, $p \leq 0.001$). Diameters of shoots were largest from plants cut in October, followed by shoots from May and June cuttings and then August, July and control treatments (Figure 3).

In the second year after cutting, moose consumed significantly more shoot biomass taken from control birches (34.5%) than birches cut in May (3.3%), June (7.7%), July (6.9%) August (3.1%) or October (4.0%),
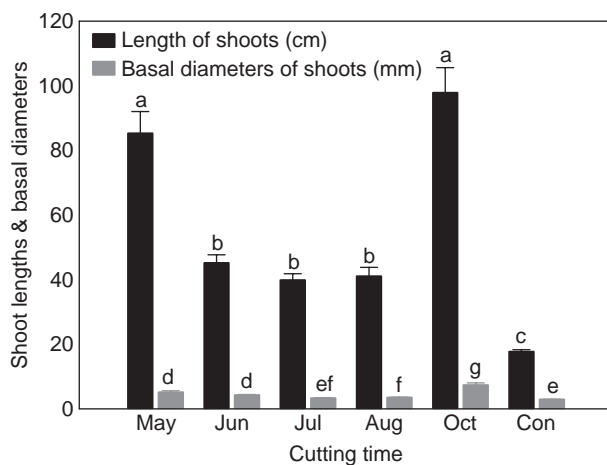
as determined by z tests ($p \leq 0.001$). There was no significant difference between the amounts of biomass consumed by moose from plants experimentally cut at various times of the year.

Bite diameters varied on shoots from different treatments ($F_{1,5} = 4.485$, $p \leq 0.001$) (Figure 4) and were largest on May- and smallest on July-cut plants, although the bite diameters on the shoots of July-cut birches were not significantly different from August- or October-cut birches or controls.

The degree of sylleptic branching differed between shoots from different treatment categories ($F_{1,5} = 51.766$, $p \leq 0.001$); sylleptic branches were found in higher densities on the second year shoots collected from May- and October-cut birches, and were effectively absent from shoots taken from July-cut and control shoots (Figure 5). Shoots from June-cut birches had a higher number of sylleptic shoots than controls, July- and August-cut plants, but not as many as those from May- and October-cut plants.

Discussion

Moose preferred small (controls and July-cut) and medium-sized (June-cut) shoots of birches relative to those that were available in the cafeteria trials when fed shoots collected in the first winter after cutting. No statistical significance was present for overall biomass consumption by moose in year 1 between shoots of plants cut in June and July. However, the findings indicate that when moose consumed shoots from July-cut, in comparison to June-cut birches, shoots from July-cut birches, when eaten, were entirely consumed, resulting in a lack of available
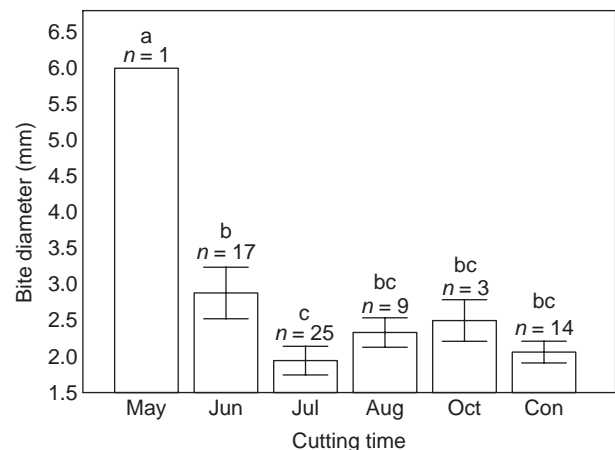

Figure 3. Average ($\pm$ 1 SE) length and basal diameter of shoots produced by birches during the second (2004) postcutting growing season. Measurements were taken in February 2005; $n = 15$ birches per treatment category. Bars with common letter designations are not significantly different from one another as determined by Tukey's *post hoc* comparisons.

Figure 4. Average ($\pm$ 1 SE) bite diameters taken by moose in February 2005 on shoots produced by birches during the 2004 growing season following cutting at different times in 2003. $n =$ number of shoots left over from trials from which bite diameters were measured. Bars with common letter designations are not significantly different from one another as determined by Spjotvoll/Stoline *post hoc* comparisons.
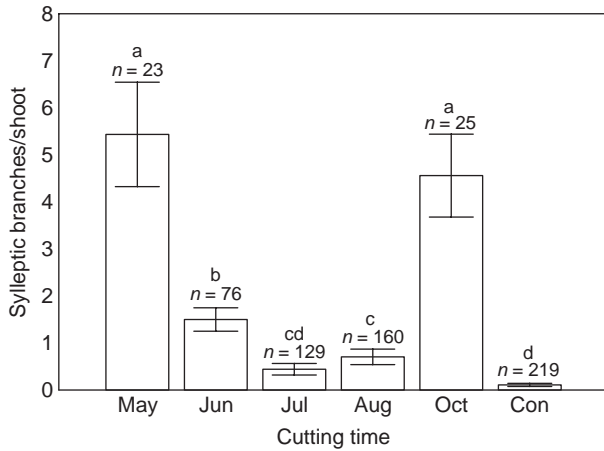
Figure 5. Average ($\pm$ 1 SE) number of sylleptic branches found on second year current annual shoots of birches from different treatment categories. n =number of shoots of the 15 plants per treatment category upon which sylleptic branches were detected. Bars with common letter designations are not significantly different from one another as determined by Tukey's *post hoc* comparisons.

Figure 6. Moose selecting from various piles of birch shoots during the cafeteria-style feeding trial were able to move between piles unimpeded by deep snow.

shoots from which bite diameters could be determined (see Figure 2 caption). This finding suggests that moose may be showing a slight preference for whole shoots from July-cut compared with June-cut birches. In the second winter after cutting, moose preferred to browse on the smallest available, non-compensatory shoots, i.e. those that were from the uncut control plants.

Free-ranging moose select large over small resprouts when browsing (Penner, 1978; Danell et al., 1985; Risenhoover, 1987; Bowyer & Bowyer, 1997) in an effort to increase intake rates per cropping effort (Shipley & Spalinger, 1992). Such selective browsing is likely to be a response by moose to increase biomass consumption per amount of energy expended in moving through their environment, and fits optimal foraging models for moose proposed by Vivås and Sæther (1987). An energy-maximizing foraging strategy by moose is particularly advantageous in winter when snows are deep and energy expenditures rise exponentially with increasing snow depth (Renecker & Schwartz, 1998).

Although these experiments were performed in winter when snows were deep, the animals recruited for the experiments did not appear food limited and were contained within a feeding area of the wildlife shelter where snow was trampled and movements were unimpeded (Figure 6). Presumably, operating principles that govern foraging behaviors in the wild were of little consequence for moose feeding on these birch shoots, and may help to explain choices made by these human-habituated moose when choosing some of the smallest shoots available in the trials.

Because most nutrients in shoots are stored in and just under the bark and because smaller shoots have a higher bark to woody cortex ratio than larger shoots, smaller shoots are considered more nutritious (Hjeljord et al., 1982). The selection of smaller shoots by moose has been documented in Norway where moose engage in winter consumption of the shoots of understory blueberry (*Vaccinium* spp.) (Hagen, 1983, Histøl & Hjeljord, 1993) and shoots of birch trees that were densely concentrated in the forest, making shoot availability high (Vivås & Sæther, 1987). Few such cases have been reported, but suggest, in combination with the present data, that when an abundance of small shoots is present and movement between patches of required food items can be minimized, moose will select smaller rather than larger shoots.

Although intake rates could not be measured in this experiment, it was observed that moose feeding on shoots from the trials were able to obtain more shoot material per bite than when browsing on shrubs and trees in the forested areas surrounding the feeding grounds to which they had free access. This was true when moose were eating from piles containing large or small shoots. This behavior suggests that if a mouthful of 100 small shoots could be obtained as easily as 25 large shoots, that higher quality, small shoots would be preferred to larger shoots which require more sorting and chewing to process as well as more energy to digest in the rumen (Renecker & Schwartz, 1998).

Despite the fact that free-ranging moose appear to select predominantly large resprouts, our results suggest that if equally available, or at least where browse patches are dense and shoot availability is high (Vivås & Sæther, 1987), smaller shoots are likely to be preferred by moose. These findings highlight the importance of local ecological conditions as they relate to animal foraging behavior in the wild such

as reducing energy expenditure in snow, avoiding predators and maintaining a neutral thermal balance.

Winter shoots of willows that had been cut at different times in the growing season 2 years before winter collections were of poorer quality (higher tannin and lignin and lower digestibility) in year 2 than those analyzed in the first year after cutting (Rea & Gillingham, 2001), and may partially explain why fewer birch shoots from cut plants were eaten by moose in year 2 than in year 1. Another possibility to consider is that first year resprouts from plants cut in early to mid-summer may contain attributes preferred by moose that cannot be found in the growth of shoots from plants cut late in the previous autumn or the second year shoots of plants cut earlier during the previous summer. Kays and Canham (1991) reported significantly smaller autumn root reserves for plants cut during early to mid-summer compared with those cut later in the autumn. If higher levels of root reserves facilitate the production of shoots that are more chemically defended from herbivory (Bryant et al., 1985), then overconsumption of year 1 shoots (from plants cut early in the year with smaller reserves available for plant regrowth and defense), relative to shoots of plants cut in autumn or year 2 shoots, appears reasonable.

The fact that three (instead of six from year 1) moose fed on year 2 shoots may also help to explain an overall reduced consumption of shoots from both treated and control birches. It is probable that a combination of several factors resulted in the differences detected in consumption levels between years. Regardless, it seems clear from the data that small shoots of control plants in year 2 were by far the most preferred.

Remaining unexplained is the fact that moose did not eat much of the first year shoots from birches cut in October (in the second year of the study). This is surprising because they consumed close to 90% of the first year shoots from June- and July-cut birches in year 1. Part of the reason may be that the October shoots are coarser, with a larger average basal diameter (7 mm) than shoots from June and July treatments (3–4 mm) (Figure 3). This is supported by the lower consumption of first year shoots from browse cut in May compared with browse cut in June and July; shoots from May also have a larger basal diameter (4–5 mm) than shoots from birches cut in June and July (1–3 mm) (Figure 1).

In the first year feeding trials it appeared that sylleptic branches may have had some influence upon shoot selection by moose. Therefore, we decided to collect data on sylleptic branching in year 2. The findings from analyzing these data suggest that birches cut in early spring and late summer/autumn produce significantly more sylleptic branching than those cut in mid-summer and controls, probably due to a larger imbalance of root to shoot ratios incurred as a result of cutting before leaf flush or after leaf abscission (Kays & Canham, 1991). Because such shoots were selected less by moose than controls without sylleptic growth and not preferred over June-, July- and August-cut birches that also lacked sylleptic growth (Figure 5), it is assumed that such shoots somehow acted to deter browsing. These findings appear counterintuitive because sylleptic shoots are generally of medium size and concentrated and arranged in such a way on resprouts that forage intake would be high had moose elected to feed upon them. However, this kind of first year resprout may contain high concentrations of inducible antiherbivore chemicals similar to those found by Bryant et al. (1985) in feltleaf willow, which in combination with the larger and coarser parent resprouts may deter browsing by moose.

Cafeteria-style feeding trials have limited applications due to the artificial circumstances in which moose are given to select shoot types, but are nonetheless valuable tools for understanding food preferences and the relationship between moose and their environment (Renecker & Hudson, 1998). Recent experiments using anchored whole birch and willow plants showed that moose unequivocally select for the smallest shoots from plants first and subsequently move down shoots and branches, cropping larger and larger bite diameters as smaller shoots become scarce (Rea & Hjeljord, unpublished data). These recent findings and those presented here, together with the results of other studies from Norway (Hagen 1983; Vivås & Sæther, 1987; Histøl & Hjeljord, 1993), suggest that where small shoots are produced by plants growing under natural conditions or regenerating from forest cleaning operations at particular times of the year, plants with small shoots are likely to be preferentially sought out by moose.

The authors do not contend that moose do not select large shoots when browsing, but that large bite diameters may be the result of refined cropping efforts by moose that started by cropping more preferred, smaller shoots, but then took progressively bigger bites from the same plant in a single or return bout of feeding. If this is true (as it appears to be in areas of high food availability; Sæther & Andersen, 1990), then birches and other plants containing multiple branches with many small shoots may get more use and be selected by moose more than plants with large shoots that contain fewer bites.

In conclusion, these findings suggest that (1) the timing of forest cleaning affects the size of shoots produced by birches after cutting, and (2) moose select shoots in winter from treatments that promote the growth of smaller shoots, rejecting larger shoots

that contain sylleptic branches. Although shoot selection in more natural settings will be moderated by environmental factors that drive foraging behavior, this study found moose showing a clear preference for smaller shoots when such factors were artificially controlled.

The types of shoots preferred by moose and the ways in which plants can be managed to produce certain shoot types are of likely interest to forest resource managers interested in providing improved (e.g. ungulate winter range) or poorer quality (e.g. some forest plantations or roadside areas) habitats for moose. As such, these findings may be of use to those attempting to determine how moose inhabiting their management areas utilize browse and how experimenting with the timing of forest cleaning may be used as a tool to alter those food resources sought by moose in winter.

Acknowledgements

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