The impact of the timing of brush management on the nutritional value of woody browse for moose *Alces alces*

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Summary

1. We examined how the removal of above-ground biomass (mechanical brushing) at different times of the year affected the nutritional value of regenerating shoots of Scouler's willow *Salix scouleriana* for moose for two winters after brushing.

2. Brushing trials were conducted throughout the 1996 and 1997 growing seasons in central British Columbia on a 10-year-old regenerating clear-cut replanted in lodgepole pine *Pinus contorta* var. *latifolia*.

3. We assessed the nutritional value of the browse in relation to length, diameter, mass, digestible energy, digestible protein, tannin and lignin content of current annual growth shoots in winter, as well as the phenology of plant leafing.

4. One winter after brushing, willows brushed in early July had shoots that were lower in lignin, higher in digestible protein and lower or not different in tannin content compared with shoots from earlier brushed or unbrushed willows. Willows brushed in early July also had long, heavy, shoots that were high in digestible energy and delayed leaf senescence.

5. In the second winter after brushing, willows that were brushed in July had larger shoots that were lower in digestible energy, digestible protein, tannin and lignin content and delayed leaf senescence compared with several other treatments. Willows brushed after July regenerated negligible shoot material in the first year after brushing. Willows brushed in September delayed leaf flush in the first post-brushing spring.

6. To increase the nutritional value of woody browse for cervids, we suggest that brushing should be performed in early to mid-July (mid-summer).

7. Reductions in browse quality and quantity may negatively affect many mammalian species. Therefore, we recommend that the needs of other fauna potentially affected by changes in shrub architecture, shoot morphology and shoot chemistry be considered when planning the timing of brush management activities.

Key-words: browse quality, herbivory, mechanical brushing, plant response, plant secondary compounds, *Salix scouleriana*, ungulate.

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Introduction

Early successional plants such as birch *Betula* spp. and willow *Salix* spp. dominate the diets of moose *Alces alces* L. and other ungulates in autumn and winter (Regelin, Schwartz & Franzmann 1987; Shipley, Blomquist & Danell 1998). Despite their importance to moose, however, such plants are often cleared from young forest stands by foresters managing for the production of conifers such as pine *Pinus* spp. and spruce *Picea* spp. Clearing reduces interspecific competition among shrubs and conifer seedlings and is generally accomplished with the use of forest herbicides and/or mechanical brushing (Lautenschlager *et al*. 1998).

The impacts of herbicides on browse production and quality have been studied (Hjeljord 1994; Raymond *et al*. 1996) but little work has addressed the effects of mechanical brushing on browse quality (Lautenschlager *et al*. 1998). Mechanical brushing is becoming increasingly common throughout the circumpolar distribution of moose, and is carried out throughout the growing season. The effects of mechanical brushing on the nutritional value of browse are, however, likely to vary with the timing of mechanical damage. For example,

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the nutritive quality of red stem ceanothus *Ceanothus sanguineus*, ninebark *Physocarpus malvaceus*, rose *Rosa* spp. and snowberry *Symphoricarpus* spp. for wild ungulates increases after simulated early summer browsing by sheep *Ovis aries*, but decreases if browsing occurs late in summer (Alpe, Kingery & Mosley 1999). Mechanical damage may also influence the timing of leaf flush and leaf senescence (Larson 1975; Kindschy 1989).

Moose select the largest available current annual shoots (hereafter referred to as shoots) when browsing (Danell, Huss-Danell & Bergström 1985) and choose forages that are relatively high in digestible energy and protein (Regelin, Schwartz & Franzmann 1987). Moose and other ungulates also avoid a variety of phenolic compounds such as lignin (Risenhoover 1987) and tannins, which can contribute to reductions in dry matter digestibility (Bryant & Kuropat 1980). The selection of browse in the early spring and late autumn is influenced by the presence or absence of leaves (Renecker & Hudson 1986; Danell, Bergström & Edenius 1994); moose tend to select early greening plants during spring and late-senescing plants during autumn (Schwartz, Hubert & Franzmann 1988; Danell, Bergström & Edenius 1994). Such plants are important to moose because they provide a readily accessible pool of nutrients during times of the year when nutritious foods are difficult to locate (Chapin 1980).

Any changes in plant morphology, chemistry or leafing phenology caused by mechanical brushing are likely to affect moose, as well as other herbivores such as hares *Lepus* spp. and microtine rodents that utilize willow in managed forests during winter. Consequently, we investigated how the timing of mechanical brushing affected the nutritional value of willow browse in the first 2 years following brushing. We determined the nutritional value of willow browse on the basis of size, digestible energy, digestible protein, and tannin and lignin content of dormant shoots. Willows that delayed leaf senescence in the autumn or flushed leaves prematurely in the spring were considered to be of better quality than those that did not. We chose Scouler's willow *Salix scouleriana* Barratt *ex* Hook. for our study because it is a predominant upland willow on clear-cuts in central British Columbia, and because of its importance as winter browse for moose (Porter 1990; Stein *et al.* 1992). We examined whether the timing of brushing affected: (i) the morphology and chemistry of regenerating or compensatory shoots in the first two winters following brushing; (ii) leaf senescence and the amount of time that willow leaves were available in the first two autumns following brushing; and (iii) the timing of the emergence of willow leaves in the spring following brushing.

Materials and methods

Our study area was located approximately 20 km north-east of Vanderhoof, British Columbia, Canada (54°05′ N, 123°55′ W) in the subboreal spruce forest ecotype (Meidinger & Pojar 1991). The topography is rolling and the site elevation is approximately 800 m a.s.l. The climate is continental and characterized by seasonal extremes, with cold winters and warm, moist, summers. Mean annual precipitation is approximately 46 cm, snow fall averages approximately 200 cm and mean annual temperatures range from 1·7 to 5 °C (Atmospheric Environment Service 1993). The landscape is dominated by coniferous forests of hybrid white spruce *Picea engelmannii × glauca* and subalpine fir *Abies lasiocarpa*. Lodgepole pine *Pinus contorta* var. *latifolia* and trembling aspen *Populus tremuloides* pioneer secondary successional sites (Meidinger & Pojar 1991), as do several species of upland willows (Porter 1990).

Our experiments were conducted on an approximately 14-ha 10-year-old regenerating clear-cut replanted in pine *Pinus contorta* var. *latifolia* Engelm. *ex* S. Wats. This site had abundant Scouler's willow saplings (all 2·0–2·5 m) and it was close to an active ranching operation and recreational trailhead; the moderate human activity minimized site use and browsing by moose. Moose density in the surrounding area at the time of the study was approximately 0·5 animals km^{-2} (Rea 1999).

We identified willows according to leaf characters, shoot morphology and catkin anatomy following Argus (1992). Each willow contained approximately 10–15 codominant main stems; willows were easy to delineate from one another because groups of main stems were well spaced. We randomly selected, numbered and tagged 120 willows in the spring of 1996 and subsequently divided the willows into one of four brushing treatments spaced at 6-week intervals: 14 June, 30 July, 15 September and a control. Recognizing that plant phenology follows the onset of spring rather than Julian date, we did not treat on the same dates in 1997 as 1996. Instead, we addressed the effects of timing at a finer scale by selecting 150 willows in the spring of 1997 according to the above procedures but by dividing the willows into one of five, rather than four, brushing treatments: 1 June, 1 July, 1 August, 1 September and unbrushed 1997 controls. We used a swing saw to brush willows approximately 10–15 cm above the ground. Disk samples were collected from the five largest main stems on all 1996-brushed willows. Based on our counts of the annuli, experimental plants were 7·30 ± 1·21 (mean ± SD; range 4–9) years of age.

SHOOT COLLECTIONS AND ANALYSIS

During the first 2 weeks of December 1996, we collected shoots from 15 of the 30 willows (randomly chosen) from the 14 June 1996 treatment and from the unbrushed 1996 controls. During the first 2 weeks of December 1997, we collected shoots from all 30 of the 1 June 1997, 1 July 1997 and unbrushed 1997 control willows. Shoots from the 30 July 1996, 15 September 1996, 1 August 1997 and 1 September 1997 treatments were considered to have grown insufficiently to be available as winter

browse for moose and were therefore not collected in the first winter after brushing. In the second winter after brushing, we collected shoots from the 15 previously unanalysed 14 June and 1996 controls and shoots from all 30 of the 30 July and 15 September 1996-brushed willows.

We collected our samples by selecting every third shoot from randomly selected willow main stems until we had approximately 150 g for analysis. Any snow-cover present (< 10 cm during both collections) was removed from around the plant and all shoots were exposed for selection. To inhibit shoot metabolic activities following clipping, shoots were collected during the first 2 weeks of December of both years, in subzero weather. Approximately one-quarter of the shoot material collected from each willow was randomly separated out for tannin analysis. All samples were sealed in plastic bags and stored at –20 °C until analysis.

Measures of mass, length, basal and tip diameters were taken in the laboratory for all collected shoots. If more than 30 shoots were collected from a particular willow, we randomly subsampled 30 shoots for these morphometric measures. Following the measurements, all shoot material for each plant was combined, cut to approximately 10-cm lengths, and dried to a constant mass ($\pm\,0\cdot1$ g) at 39 °C in a forced-draft drying oven (Despatch LAD series 2-24-3, Minneapolis, MN). We then milled the dried material with a Thomas-Wiley mill (Swedesboro, NJ) using a 0·5-mm sieve screen, and hand-mixed the samples to homogenize them. Gross energy was determined with a bomb calorimeter (Parr model 1341, Moline, IL) using 0·75–1·0 g of material and procedures outlined by the manufacturer. Gross energy values were corrected to dry mass by desiccating with anhydrous $CaSO_4$ (WA Hammond Drierite Co., Xenia, OH) for 24 h.

We determined elemental nitrogen using an elemental CHN analyser (Carlo Erba, Na Series 2, Milano, Italy) following procedures outlined by the manufacturer and Pella & Colombo (1973). The elemental analyser was calibrated using atropine (4·84% N) and the National Institute of Standards and Technology standard number 1573a (3·03% N). Because elemental nitrogen approximates the nitrogen content of a sample with the same accuracy and precision as total Kjeldahl nitrogen (TKN; Hellinga, Oftedal & Henen 1998), we substituted elemental nitrogen for TKN in equations outlined in Hanley *et al.* (1992) for estimating digestible protein. Digestible dry matter was used to compute *in vitro* digestible energy (gross energy × digestible dry matter). We computed digestible dry matter using equations developed for deer *Odocoileus* spp. and other cervids that secrete salivary tannin-binding proteins, as described in Hanley *et al.* (1992).

We used a fibre refluxing/distillation apparatus (Labconco model 30006, Kansas City, MO) and procedures outlined in Goering & Van Soest (1970) to estimate the fibre fractions in our samples for use in determining digestible dry matter. We omitted sodium sulphite from the neutral detergent fibre (NDF) procedure as recommended by Hanley *et al.* (1992) for the determination of NDF from browse stems. We also omitted the optional wash with hexane from the acid detergent fibre (ADF) procedure (Goering & Van Soest 1970). We did not use asbestos in the determination of acid detergent lignin (Goering & Van Soest 1970). We standardized NDF and ADF protocols by using standard forage mix samples from Norwest Labs (Lethbridge, Canada).

Although acid detergent lignin is used to calculate digestible dry matter, we also separated out and reported this fraction alone because lignin is the main cell wall component limiting digestion (Robbins 1993) and moose are known to select forages lower in lignin (Risenhoover 1987). We followed the recommendation of Hanley *et al.* (1992) and did not apply the tannin correction factor in calculations for either digestible protein or digestible dry matter because dormant twigs contain relatively small amounts of tannin (Palo 1984). Although crude tannin content was not quantified for use in digestibility determinations, we did determine the relative differences in tannin content between samples from the different brushing treatments in order to help understand changes to one of the chemical characteristics known to influence winter browse selection by moose. We assessed tannin content using a radial diffusion protein precipitation assay that we modified from Hagerman (1987) (Rea 1999).

MEASURING LEAFING PHENOLOGY

We estimated differences in autumn leaf senescence by determining the predominant leaf colour of each willow within each brushing treatment in both the autumns of 1996 and 1997. We classified plants as having predominantly green, yellow, brown or no leaves and we then compared the proportion of plants having predominantly green leaves among brushing treatments. Differences in leaf senescence between 1996 treatments were estimated once in the first autumn after brushing on 8 October 1996. To determine treatment effects on senescence at a finer scale, we analysed differences in leaf colour between treatments from both our 1996 and 1997 experiments weekly, from 5 September to 17 October in 1997.

To examine differences in spring leaf flush for all willows from the 1996 treatment year, we examined the willows every 3 days in the spring of 1997 and compared the proportion of willows in each brushing treatment bearing newly flushed leaves on each day. Willows were scored as leaf bearing when the bud scales of at least one bud had separated and the expanding foliage was visible. We collected data from 11 May, at the first signs of bud break, to 28 May, when all willows within each brushing treatment had flushed the majority of their leaves. Most of the shoots were removed from all willows in the final winter (1997–98) of the study for analysis so no measurements were made in spring 1998.

STATISTICAL ANALYSES

We used linear regression (Sokal & Rohlf 1995) to test the effect of age of willows brushed in 1996 on shoot morphological and chemical attributes in the first two winters following brushing treatments. To test the differences in shoot morphology and chemistry in the first two winters post-brushing among treatments, we used an analysis of variance (ANOVA; Sokal & Rohlf 1995) with treatment time as a fixed factor. Data were transformed as appropriate to meet the assumptions of the analyses.

Homogeneity of variances was tested using a Levene's test (Milliken & Johnson 1984); a Kolmogorov–Smirnov test (Zar 1984) was used to test for normality. Tukey's Honestly Significantly Different (HSD) test (Zar 1984) was used for post-hoc comparisons for ANOVAS. We used a *z*-test (Zar 1984) to analyse the differences in the proportions of willows bearing predominantly green leaves on specific dates in the autumns of 1996 and 1997. We also used a *z*-test to analyse the differences in the proportions of willows leafing within each brushing treatment

every third day during the spring of 1997. All analyses were conducted using Statistica (StatSoft Inc. 1997).

Results

Overall, mechanical brushing altered the nutritional value of willows. The specific plant attributes affected and the degree to which the value of browse was altered, however, depended on when willows were brushed. Plant age had no effect on morphological or chemical changes in nutritional value after treatment (all $P \geq 0.135$).

SHOOT MORPHOLOGY

Willows brushed on 14 June 1996 had longer and heavier shoots with thicker basal diameters, but thinner shoot tips, than unbrushed willows in the first winter after brushing (Table 1). Willows brushed on 1 June 1997 and 1 July 1997 also had longer, heavier and thicker shoots with thinner tip diameters than unbrushed willows in the first post-treatment winter (Table 2). In the second winter following brushing, willows brushed in

Table 1. Comparison of morphological and chemical attributes of shoots between Scouler's willow brushed on 14 June 1996 ($n = 15$) and unbrushed controls ($n = 11$) measured in the first winter following brushing. %DM indicates that values are expressed as a percentage of dry matter

Shoot attribute	Brushed		Unbrushed			
	Mean	SE	Mean	SE	*F*	*P*
Length (cm)	49·8	2·7	13·3	1·6	113·9	< 0·001
Mass (g)	4·93	0·54	0·75	0·12	137·3	< 0·001
Basal diameter (mm)	4·2	0·2	2·8	0·1	59·3	< 0·001
Tip diameter (mm)	1·5	0·1	2·0	0·1	27·1	< 0·001
Lignin (%DM)	0·11	0·01	0·13	0·01	12·3	0·002
Tannin content*	82·3	3·6	96·1	4·2	6·3	0·019
Digestible energy (kcal g^{-1})	2·885	0·028	3·327	0·309	111·0	< 0·001
Digestible protein (%DM)	0·53	0·10	1·76	0·33	16·0	< 0·001

*Tannin content is based on tannin reactivity to bovine serum albumin and quantified using a radial diffusion assay modified from Hagerman (1987; see the Materials and Methods).

Table 2. Comparison of morphological and chemical attributes of shoots of Scouler's willow brushed on 1 June or 1 July 1997 as well as unbrushed controls measured in the first winter after brushing ($n = 30$ for all morphological attributes and $n = 15$ for all chemical attributes). $P < 0.001$ for overall comparisons among brushed and unbrushed willows for all attributes. Means sharing a common superscript are not significantly different from each other, as determined by Tukey's HSD post-hoc comparisons

Shoot attribute	Brushed				Unbrushed		
	1 June		1 July				
	Mean	SE	Mean	SE	Mean	SE	*F*
Length (cm)	54·4	2·2	25·5	1·6	9·9	0·8	211·1
Mass (g)	4·59	0·38	1·31	0·15	0·42	0·06	163·3
Basal diameter (mm)	4·1	0·1	2·8	0·1	2·2	0·1	128·8
Tip diameter (mm)	1·3[a]	0·04	1·2[a]	0·02	1·6	0·04	26·9
Lignin (%DM)	0·12	0·01	0·10	0·01	0·16	0·01	84·7
Tannin content*	78·9[b]	4·8	80·8[b]	6·8	130·7	10·2	44·3
Digestible energy (kcal g^{-1})	2·821	0·009	3·168	0·052	3·254	0·105	39·4
Digestible protein (%DM)	1·37[c]	0·57	2·78	0·25	1·74[c]	0·58	20·5

*Tannin content is based on tannin reactivity to bovine serum albumin and quantified using a radial diffusion assay modified from Hagerman (1987; see the Materials and Methods).

Table 3. Comparison of morphological and chemical attributes of shoots of Scouler's willow brushed in June, July or September 1996, measured two winters after brushing, and unbrushed controls. *n* = 15, 28, 28 and 18 for morphometric attributes of June-, July-, September-brushed and unbrushed willows, respectively; *n* = 15 for all other attributes. *P* < 0·001 for overall comparisons between brushed and unbrushed willows for all attributes. Means sharing a common superscript are not significantly different from each other, as determined by Tukey's HSD post-hoc comparisons

| | Brushed | | | | | | Unbrushed | | |
| | 14 June | | 30 July | | 15 September | | | | |
Shoot attribute	Mean	SE	Mean	SE	Mean	SE	Mean	SE	*F*
Length (cm)	20·6	1·9	54·8	2·6	80·5	2·9	13·8	1·6	165·1
Mass (g)	1·17	0·19	6·70	0·54	12·82	0·84	0·63	0·10	164·6
Basal diameter (mm)	2·7[a]	0·2	4·5	0·2	6·0	0·2	2·5[a]	0·1	112·5
Tip diameter (mm)	1·4[a]	0·1	1·5[a]	0·1	1·6[b]	0·03	1·7[b]	0·1	6·2
Lignin (%DM)	0·15[a]	0·01	0·13[b]	0·003	0·13[b]	0·003	0·15[a]	0·003	12·2
Tannin content*	92·8	2·4	80·4[a]	2·5	78·3[a]	2·8	107·1	4·1	19·3
Digestible energy (kcal g^{-1})	2·962	0·035	2·796[a]	0·030	2·726[a]	0·028	3·178	0·033	40·5
Digestible protein (%DM)	1·87[ab]	1·36	0·68[c]	0·10	0·10[bc]	0·34	2·00[a]	0·32	5·5

*Tannin content is based on tannin reactivity to bovine serum albumin and quantified using a radial diffusion assay modified from Hagerman (1987; see the Materials and methods).

1996 continued to have shoots that were longer, heavier and thicker with thinner tips than unbrushed willows (Table 3). Although the shoot morphology of brushed and unbrushed plants differed in the first two winters after brushing, the magnitude of difference in shoot morphology between brushed and unbrushed plants depended on the timing of brushing. Willows brushed earliest (1 June) in the 1997 growing season had the largest shoots in the winter of 1997 (Table 2). Following a full season of post-treatment growth, willows brushed earliest (14 June) in the summer of 1996 no longer had the largest browse shoots in the second winter after brushing. Instead, willows brushed later (30 July, 15 September) in the 1996 season had larger shoots in the winter of 1997 (Table 3).

SHOOT CHEMISTRY

Lignin, tannin, digestible energy and digestible protein content were lower in the shoots of brushed compared with unbrushed willows in the first winter after brushing (1996; Table 1). Plants brushed during the 1997 growing season also had shoots in the winter after brushing that were lower in lignin, tannin and digestible energy content, but higher or not significantly different in digestible protein than the shoots of unbrushed controls (Table 2). Plants brushed in July 1997 had shoots that were lower in lignin but higher in digestible energy and digestible protein than the shoots of plants brushed in June of the same year (Table 2). Although plants brushed in July 1997 had shoots with significantly lower tannin content than the shoots of unbrushed willows, the tannin content of these shoots was not significantly different than that found in the shoots of June-brushed plants (Table 2).

In the second winter after brushing, the shoots of 1996-brushed willows (all treatment times) were lower in tannin content and digestible energy than the shoots of unbrushed controls, although July and September brushing treatments had shoots lowest in these chemical attributes (Table 3). Furthermore, in the second winter after brushing, shoots produced following July and September brushing treatments had significantly lower concentrations of lignin and digestible protein than the shoots of unbrushed willows. There were no significant differences between shoots from the June-brushed and unbrushed willows with respect to lignin and digestible protein (Table 3).

LEAFING PHENOLOGY

A higher proportion of willows brushed in 1996 and 1997 retained green leaves in the first autumn after brushing relative to unbrushed controls. This trend was apparent when measured once (1996 treatments; see statistics below) or when measured on a weekly basis (19 September to 10 October for 1997 treatments; Table 4). Additionally, a higher proportion of willows brushed on 30 July 1996 (*n* = 28) had green leaves relative to willows brushed on 14 June 1996 (*n* = 28; $\hat{p} = 0.857$, $z = -3.055$, $P = 0.001$), while a higher proportion of those brushed on 14 June retained green leaves relative to unbrushed 1996 controls (*n* = 30; $\hat{p} = 0.466$, $z = -3.669$, $P < 0.001$). Delays in senescence with later brushing times were also apparent when measured weekly in the first autumn for plants brushed in 1997 (Table 4). Although willows brushed later in the year had more green leaves on 17 October 1997, plants brushed in July and August of the same year showed no significant differences in patterns of leaf senescence from 5 September to 10 October (Table 4). Plants brushed in July and August 1997, however, delayed leaf senescence compared with June brushing treatments, from 3 October to 17 October (Table 4).

In the second autumn after treatment, brushed plants delayed leaf senescence longer than unbrushed plants from 5 to 19 September 1997, and plants brushed in July

Table 4. Proportion of Scouler's willow in each brushing treatment bearing predominantly green leaves during autumn 1997. Proportions sharing common superscripts are not significantly different from each other, as determined by separate z-tests

Measurement date	Date of brushing							
	1997				1996			
	1 June $n = 32$	1 July $n = 33$	1 August $n = 20$	Control $n = 32$	14 June $n = 15$	30 July $n = 30$	15 September $n = 30$	Control $n = 18$
5 September	1·00[a]	1·00[a]	1·00[a]	0·94[a]	1·00[x]	1·00[x]	1·00[x]	0·67
12 September	1·00[a]	1·00[a]	1·00[ab]	0·91[b]	0·97[xy]	1·00[x]	0·87[y]	0·43
19 September	0·91[a]	1·00[b]	1·00[ab]	0·75	0·57	0·93[x]	0·83[x]	0·30
28 September	0·91[a]	1·00[b]	1·00[ab]	0·59	0·37[x]	0·70[y]	0·60[y]	0·23[x]
3 October	0·82	0·97[a]	1·00[a]	0·44	0·23[x]	0·53[y]	0·57[y]	0·20[x]
10 October	0·50	0·91[a]	1·00[a]	0·18	0·07[x]	0·30[y]	0·33[y]	0·03[x]
17 October	0·32[a]	0·88	1·00	0·19[a]	0·03[x]	0·23[y]	0·33[y]	0·03[x]

and September delayed leaf senescence longer than plants brushed in June (measured on 19 September 1997; Table 4). In the second autumn after brushing, willows brushed in July and September of 1996 delayed leaf senescence longer than June-brushed and unbrushed willows from 28 September to 17 October. Willows brushed in July and September of 1996, however, did not show any differences in leaf senescence from 28 September to 17 October 1997; neither did June-brushed and control willows (Table 4).

The timing of brushing affected leaf flush in the spring following treatment: leaf flush was delayed when brushing was performed late in the previous growing season, but there was no effect on spring leaf flush when brushing was carried out earlier in the year. Although all plants brushed on 14 June ($n = 15$) and 30 July ($n = 30$) as well as all of the 1996 controls ($n = 17$) had flushed leaves by 14 May 1997, only 20% of the willows brushed on 15 September of the previous year ($n = 30$) had flushed leaves ($\hat{p} = 0·6$, $z = -4·472$, $P < 0·001$). By 20 May 1997, 80% of willows brushed during the previous September had flushed leaves ($\hat{p} = 0·9$, $z = -1·826$, $P < 0·034$). By 23 May all plants in the September treatment group had flushed leaves. During the spring of 1996, willows on this site flushed leaves between 21 May and 25 May.

Discussion

SHOOT MORPHOLOGY

The morphology of regenerating browse shoots varied with treatment time for at least 2 years after brushing. Shoots produced by plants cut early in the growing season were the largest in the first winter, but smallest in the second winter, after brushing relative to plants cut later in the year. Generally, plants respond to mechanical damage by allocating resources away from reproduction and into vegetative growth; resources are directed to proportionately fewer growing points and cause the plant to reassume a more juvenile form of growth (Bryant *et al*. 1991). More specifically, the differences in plant response due to the timing of brushing were probably

related to root to shoot ratios (Willard & McKell 1978) and concentrations of root reserves at the time of cutting (Kays & Canham 1991).

Although stump shoots produced following cutting may contain higher concentrations of defensive compounds, making them less palatable to smaller herbivores (Bryant 1981), ungulates such as moose and elk preferentially browse these large shoots (Bergström & Hjeljord 1987; Stein *et al*. 1992; Romme *et al*. 1995). Cropping larger shoots allows ungulates to spend less time and energy on cropping and more time on processing their bites (Shipley & Spalinger 1992). Additionally, browsing larger shoots reduces the incidental intake of older, less nutritious, stem materials, which can occur when smaller shoots are cropped (Hjeljord, Sundstol & Haagenrund 1982).

The large shoots of willows produced in the first year after early brushing and in the second year after late brushing are likely to be more valuable to large-sized cervids compared with the shoots of willows brushed at other times or to the shoots of unbrushed willows. Smaller shoots regenerating from plants brushed later in the year are probably less valuable to moose in the first winter after brushing, particularly as smaller sprouts are more difficult to reach in winter (Romme *et al*. 1995).

As the length, mass and basal diameter of browse shoots increased, the diameter of the shoot tip decreased (Tables 1–3). These changes in shoot morphology following mechanical damage may have resulted from an allocation of plant resources to shoot cortex rather than meristem and bark tissues (Danell & Bergström 1985). Such re-allocations may explain some of the changes in plant chemistry that we detected in plants brushed at different times of the year.

SHOOT CHEMISTRY

Diet selection is generally believed to be based on trade-offs between bite quantity and quality (Shipley, Blomquist & Danell 1998). Protein and energy are important factors influencing diet selection by cervids (Regelin, Schwartz & Franzmann 1987), as is the content of lignin (Risenhoover 1987) and tannins (Bryant & Kuropat

1980). Changes in shoot chemistry following brushing are, therefore, likely to influence the nutritional value of shoots and the selection of regenerating browse by moose.

Although the energy and protein content of shoots from unbrushed willows were comparable with other studies (Bergström & Danell 1987; Risenhoover 1987), the large shoots of brushed willows were generally lower in digestible energy and digestible protein for 2 years after brushing. The shoots of willows brushed in July, however, were higher in digestible protein and relatively high in digestible energy, compared with the shoots of willows brushed at other times during the growing season or unbrushed controls in the first winter after brushing. Because the large shoots produced by willows brushed in July were high in digestible energy and digestible protein, these shoots were high in nutritional value for moose, especially when the associated decreases in the lignin and tannin content of these shoots and increases in leaf senescence were considered.

The concentration of lignin in the shoots of unbrushed willows was similar to the concentration of lignin reported for other species of willow (Bryant *et al.* 1985; Schwartz, Regelin & Franzmann 1988). Our results, however, indicate that the shoots of brushed willows were significantly lower in lignin than those of unbrushed willows. Other willows regenerating from mechanical cutting in summer were found to produce winter browse that was lower in lignin than undamaged willows (Nellemann 1990). Furthermore, the timing of brushing appears to cause plants brushed later in the year to have shoots that are lower or equal in lignin content to earlier-brushed plants when analysed in both the first and second winters following brushing. Considering that the selection of browse by most vertebrate herbivores is determined more by the nature and quantity of phenolic compounds (specifically lignin and tannins; Coley, Bryant & Chapin 1985; Robbins *et al.* 1987) than overall energy and protein content (Chapin 1980), such changes increase the relative quality of browse for moose.

Tannins, unlike lignin, may not affect handling time or intake rates but constrain animal performance through a variety of mechanisms (Risenhoover, Renecker & Morgantini 1985). Although our results do not indicate that tannin content was always different between the shoots of willows brushed at different times, the shoots of brushed plants were always lower in tannin content than the shoots of unbrushed willows. Similar reductions in tannin content with increases in shoot size following mechanical damage have been reported previously (Dutoit, Bryant & Frisby 1990; Suter 1993; Singer, Mark & Cates 1994).

Although moose and other ungulates possess salivary tannin-binding proteins to help neutralize the effects of dietary tannins (Hagerman & Robbins 1993; Juntheikki 1996), moose avoid browsing shoots higher in tannin content (Suter 1993; Singer, Mark & Cates 1994). This type of foraging strategy presumably helps to reduce costs associated with the production of tannin-binding proteins that become quickly bound by tannins in winter browse shoots (Juntheikki 1996). Such costs are probably inconsequential, however, if trade-offs for reduced tannin intake come at the expense of digestible energy and protein intake (Hagerman & Robbins 1993).

Chemical concentrations in shoots tend to decrease with increases in shoot size (Danell & Bergström 1985). Not all of our results, however, are consistent with this finding. In the first winter after brushing, willows brushed on 1 July 1997 showed elevated levels of digestible protein and digestible energy when compared with other brushing treatments from that year. These abnormal levels were a result of elevated digestible dry matter, gross energy and elemental nitrogen, and were higher than what would be expected from corresponding shoot sizes. The relatively high digestible protein and energy for the size of shoots produced by willows brushed in July could not be explained by the age of willows at the time of brushing. Our analyses suggest that no changes in plant chemistry were explained by plant age. These changes, instead, were probably related to differences in active meristem numbers and root reserve levels (Kays & Canham 1991) or perhaps differences in the degree of pre-abscission nutrient translocation at the time of brushing (Bryant *et al.* 1991) between willows brushed at different times.

LEAFING PHENOLOGY

Brushed willows delayed leaf senescence as long as, or longer, than unbrushed plants in both the first and second autumns after brushing. Willows brushed latest in the growing season delayed leaf senescence as long as, or longer, than plants brushed earlier in the growing season. Such delays have been attributed to more nutrients being supplied to a relatively smaller number of extant shoots following tissue removal (Millington 1963; Danell, Haukioja & Huss-Danell 1997). Delayed senescence generally lasts only as long as there is recurrent damage to the plant or until the root–shoot ratio has been re-established (Willard & McKell 1978).

Moose avoid browsing shoots as long as autumn leaves persist (Regelin, Schwartz & Franzmann 1987) and will even select and forage on leaf litter despite the availability of woody browse (Renecker & Hudson 1986). This behaviour demonstrates the nutritional importance of leaves in the autumn diet of moose and suggests that delays in leaf senescence with later brushing dates may provide an increase in the nutritional value of available browse. Such increases would benefit ungulates during the autumn, when tannins and lignin begin to concentrate in bark and senescing leaves (Palo 1984) and nutritious foods are generally difficult to locate (Chapin 1980).

Premature leaf flush could likewise increase the availability of leaves for ungulates foraging in the early spring. Our results suggest that brushing plants in the early to mid-summer has no effect on leaf emergence in the first post-treatment spring. Autumn brushing,

however, did cause delays in leaf emergence in the spring following brushing, thereby reducing leaf availability and the overall value of browse for moose.

IMPLICATIONS FOR MOOSE AND OTHER HERBIVORES

Overall, our results indicate that the nutritional value of Scouler's willow is altered in relation to the timing of mechanical brushing. Because we located our study in an area that minimized any confounding effects of browsing, however, we did not detect or measure any moose preferences for plants brushed at different times. Although moose preferences with respect to brushing time remains unknown, moose and other cervids are known to select browses according to shoot morphology and chemistry (Bryant 1981; Stein *et al.* 1992; Romme *et al.* 1995; Ball, Danell & Sunesson 2000). This suggests that moose will discriminate between willows brushed at different times of the year and that willows brushed in July are likely to be of most value to moose for the first 2 years post-brushing. Willow brushed in July delayed leaf senescence into early winter and had large winter shoots that were low in tannin and lignin and relatively high in digestible energy and protein. In stands that are deemed important for moose in winter, we therefore recommend brushing in July, which corresponds well with the time recommended by vegetation managers for conifer release (Kays & Canham 1991).

Although moose are known to browse the largest available shoots (Bryant *et al.* 1991), some limits are imposed by mouth morphology (Shipley & Spalinger 1992). Mouth size prevents moose from cropping extremely large shoots. Because shoot quality decreases from the tip to the base of the shoot (Danell & Bergström 1985; Rea 1999), constraints on bite size may reduce the intake of the less nutritious, basal, parts of the shoot. Therefore, for very large shoots, our analysis of the entire shoot may have underestimated the quality of browse actually consumed by moose if they only consume the distal portion of the shoot. Despite this potential bias, however, we still observed that entire large shoots were of higher value to moose relative to small shoots.

Because reductions in browse quantity and/or quality negatively affect cervids (Oldemeyer *et al.* 1977; Schwartz, Hubert & Franzmann 1988), the timing of brushing should be considered where ungulate management is an objective. In such areas, retaining unbrushed leave-strips within stands and maintaining unbrushed stands across the landscape should be considered (Rea 1999). Such management strategies are important because brushing can alter plant architecture and aspects of shoot quality for at least 5 years (Rea 1999). Browse plants produce shoots that are more nutritious, succulent and accessible to ungulates for up to 3 years after fire (Stein *et al.* 1992) and can restore reserves lost to cutting within 2 years (Kays & Canham 1991). Presumably, then, brushing could be performed on 3–4-year rotations where concerns for ungulates exist and allowances in

the silvicultural prescriptions can be made. Determining how long the effects of brushing persist beyond this amount of time and, furthermore, how plants (both brushed and residual; Härkönen 1998) are affected by multiple brushings needs to be addressed before we can understand how frequently brushing treatments should be applied with respect to ungulate management.

Although our investigation primarily focused on the effects of brushing time on the quality of winter shoots, such changes presumably result from changes taking place in the growing shoots. Influences of cutting time on the morphology and chemistry of summer browse shoots extend the implications of brushing to multiple seasons that can, in turn, affect a variety of organisms using these plants for both forage and non-forage values (Lautenschlager *et al.* 1998). Recognizing a broad range of potential impacts underscores the need to incorporate the effects of brushing time into land-use planning decisions at many different levels.

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