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RESEARCH

Influence of Cutting Time on Brush Response: Implications for Herbivory in Linear (Transportation) Corridors

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Abstract An experiment was conducted to determine the influence the time of brush-cutting can have on plant regrowth and attractiveness to herbivores that browse in linear corridors. The influence of cutting time on leaf flush and senescence, shoot morphometry, and biomass was measured for 3 consecutive years after initial brush-cutting. Results indicate that morphological and phenological attributes of three woody deciduous plants were influenced by the timing of brush-cutting for up to 3 years after initial cutting. Brush-cutting generally stimulated plants to produce larger than normal shoots and delay leaf senescence. The degree to which plants were affected, however, varied with the timing of initial cutting and the species in question. Generally, plants cut later in the year resprouted more vigorously and were taller in the third year after cutting but produced less overall biomass than when cut earlier. In the years following brush-cutting, plants cut earlier flushed leaves earlier in the spring but delayed leaf senescence in the fall when compared to uncut controls. Results of these trials suggest that brush-cutting time influences plant response and several plant attributes known to influence plant attractiveness to moose and other herbivores. We therefore recommend that roadside and railside vegetation management plans consider the influence of cutting time on plant regrowth. Such considerations can ensure that brush is cut to reduce the attractiveness of plant regrowth in these linear corridors, reduce the utilization of such brush by herbivores, and, as such, mitigate collision risk between motorists and herbivores such as moose.

Keywords Browse · Brush-cutting · Collision · Herbivore · Resprouts · Vegetation management

Introduction

Brush-cutting is a popular method of vegetation management used to control woody deciduous shrubs and trees in areas such as conifer plantations and utility and transportation corridors. Brush-cutting is becoming increasingly popular in some jurisdictions due to public outcry against herbicide applications and because species richness is known to be better maintained on brush-cut rather than herbicide-treated areas (Lautenschlager and others 1998; Mallik and others 2002). Additionally, mechanical cutting of brush is used in watercourse setbacks and is often used in areas occupied by First Nations due to objections against the use of herbicides (Brodie and others 2001).

Although some of the more generalized responses of shrubs and trees to cutting are known (Kozlowski and Pallardy 1997), how various plant species specifically respond to the time or season of cutting in the years after cutting is poorly documented. Generally, plants cut during

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the growing season are not as equipped to compensate for loss of aboveground biomass as plants cut during the dormant period (Buell 1940; Kays and Canham 1991; Mallik and others 2002). The amount of root carbohydrate reserves in below-ground biomass determines compensatory ability, and plants cut immediately following the flush of these reserves into new shoots and leaves cannot produce resprouts and suckers during the next growing season with the same vigor as plants cut during the dormant period (Kays and Canham 1991; LePage and others 1991).

Determining just how shrubs and trees respond to the time of cutting is of potential interest to a variety of resource managers interested in the relationship of cutting time to vegetation maintenance, silviculture, and range management. Changes in plant phenology and biomass production following cutting influence the length of the vegetation control cycle, conifer competition for resources (Peterson and others 1997), and browse attractiveness and availability (Anderson 1991; Bozzo and others 1992; Hardesty and others 1988; Hobbs and others 1981; Kelsall and Simpson 1987; Renecker and Schwartz 1998).

As part of a 3-year-long study on the effects of brush-cutting time and the use of brush-cut plants by moose (*Alces alces* L; Rea 2005), we recorded changes to shoot morphometrics and leafing phenology of several deciduous shrubs and trees that were brush-cut at different times of the year. Our objective was to determine how brush-cutting plants in different seasons could influence plant regrowth and attractiveness to herbivores that feed on resprouts of brush-cut plants growing in transportation corridors. Another of our goals was to be able to prescribe cutting times for roadside and railside vegetation management to reduce corridor brush attractiveness and herbivore use and concomitantly reduce the odds of vehicle encounters with moose and other large herbivores. Our working hypotheses were the following: H1: Brush-cutting time significantly influences morphological and phenological attributes of woody plant regrowth in a way that can influence the use of plant parts by herbivores such as moose; H2: The effects of cutting time on plants is species-specific and impacts plant growth for several years after cutting.

Methods

Study Area

We conducted our research at the Tabor Mountain Wildlife Viewing Area in the Grove Burn (53°54’35.98’’N, 122°19’39.36’’W), 30 km east of Prince George, British Columbia, Canada, near Tabor Mountain Ski Resort. The site contains a wildlife viewing tower surrounded by six ~1-ha strips of forest that were cut away from the platform using a hydroaxe in 1979 (strips range in their orientation away from the platform from between 80°NE to 330°NW; Fig. 1). The terrain at the site is predominantly even, sloping down and away from the viewing platform at an ~5% grade in all directions.

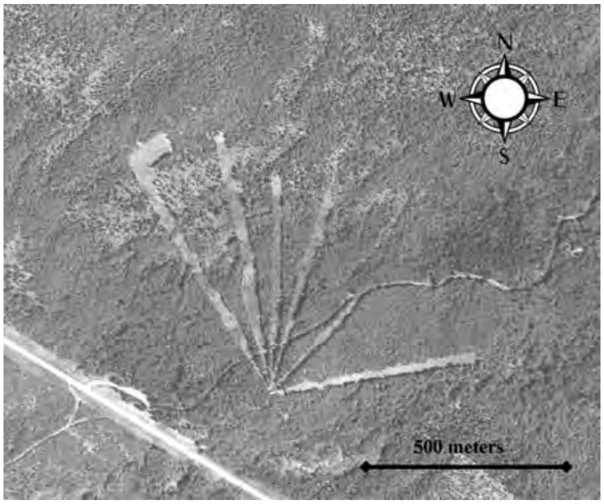

Fig. 1 The Tabor Mountain Wildlife Viewing Area established in 1979 provided a unique study area for the project. Strips of vegetation radiating away from the viewing tower were randomized and cut at different times of the year in 2001. Moose and other animals browsing in any of the strips could be monitored simultaneously by one observer

The site is located in the subboreal spruce forest ecotype (Meidinger and Pojar 1991). The climate is continental and characterized by seasonal extremes with cold winters and warm, moist summers. Mean annual precipitation is ~46 cm; snow fall averages ~200 cm, and mean annual temperatures range from 1.7°C to 5°C (from 1961 to 1990; Atmospheric Environment Service 1993). The landscape is dominated by coniferous forests of hybrid White Spruce (*Picea engelmannii* Parry ex Engelm. x *glauca* (Moench) Voss) and Subalpine Fir (*Abies lasiocarpa* (Hook.) Nutt.). Lodgepole Pine (*Pinus contorta* Dougl. Ex Loud. var. *latifolia* Engelm.) and Trembling Aspen (*Populus tremuloides* Michx.) pioneer secondary successional sites (Meidinger and Pojar 1991) as do several species of upland willows.

In May 2001, we randomized these six hyrdoaxed strips at our research site and assigned each one a cutting date. Randomized strips were brush-cut at the beginning of June, July, August, September, and October, and one remained uncut to serve as a control. All plants were cut ~10 cm above the ground with brush saws. Within the strips, we monitored plant response to cutting. For 3 years after cutting, we specifically examined the effects of cutting time on plant shoot morphometry and leafing phenology. For the purpose of our larger study (Rea 2005) but not reported here, we also assessed the frequency with which moose consumed resprouts through direct observations, track counts, pellet counts, and browse surveys.

Field Surveys

In the first spring (2002) after cutting treatments were applied, we made an attempt to survey all deciduous shrubs and trees that had been brush-cut in each of the strips. The plants, however, were surveyed only within 250 m of the observation tower within each strip because extensive leaf flush and shoot growth by the fifth week of our surveys obscured determination of the previous year's browsing intensity. In the springs of 2003 and 2004, we started surveys a week earlier on all plants within 2-m-wide belt transects that ran diagonally down the length of each strip. Each year we randomly selected and laid out specific areas in which to establish the transects in each strip; the 3000–6000 plants surveyed each year, therefore, were not individually tagged, and we did not follow the progress of plants on an individual basis. This design prevented us from performing repeated measures on individual plants but allowed us to assess the average response of plants and how often moose browsed those plants in different strips on a sequential year-to-year basis following initial cutting.

Each spring, we surveyed plants to determine shoot length, the total number of current annual shoots produced during the preceding year, and the degree of leaf flush on each plant. In the final (third) spring, we also recorded total plant height for each plant surveyed. Because browsing of shoots continued into the spring and the degree of leaf flush progressed daily during spring, we designed surveys so that plants from ~25 m of each strip per day could be measured throughout the spring survey period. Here we report our results for the effects of cutting time on three important browse species: Scouler's Willow (*Salix scouleriana* Barratt in Hooker), Black Twinberry (*Lonicera involucrata* Banks ex Spreng.), and Paper Birch (*Betula papyrifera* Marsh.).

Morphometric Measurements

We measured shoot length (to the nearest centimeter) on 10 randomly selected shoots from each plant in the areas surveyed in each strip. We measured length from the previous year's terminal or lateral bud scar (depending on whether shoots were determinant or indeterminant) and considered the length in total whether or not the shoot had been browsed.

We calculated an index of biomass production (hereafter referred to simply as biomass) for each of the three spring surveys for plants surveyed in each strip by multiplying the average shoot length measured for each plant each spring by the total number of shoots counted on each plant each spring. Occasionally, we estimated (usually on some of the larger uncut plants in the control strip) the total number of shoots on the plant by counting all shoots on one-third or one-half of the plant and multiplying that number by 3 or 2, respectively.

We measured plant height (to the nearest centimeter) in the third spring after cutting for each plant found in belt transects in each strip. By measuring the length of the dominant stem on each plant from the ground to the apex of the stem, we were able to assess the total plant height.

We assessed leaf flush for willows and twinberry plants surveyed during each spring period (2002–2004) by measuring the amount of leaf expansion along the length of a representative leaf (including the petiole and leaf blade) from each plant evaluated in each strip. Due to the duration of our spring survey periods (4–5 weeks) and the fact that we were assessing individual plants from multiple species, plants specimens early in the spring were often assessed prior to leaf flush; unflushed leaf buds were recorded as zero. Over the spring periods, leaf length measurements ranged from zero to ~15 cm.

Leaf Senescence Surveys

We assessed leaf senescence by comparing plant leaf coloring among plants (twinberry and willow) growing in different strips during each autumn (2001–2003) of the study. Each autumn, we conducted surveys three times, 1 week apart, to ensure that we captured the peak in leaf coloring in our measurements for comparison. We assessed leaf coloring by comparing the predominant leaf color from each study plant with Munsell®-style color chips for plant tissues using a technique modified from Rea and Gillingham (2001). We recorded color chip codes in the field for each plant. Chips used were then organized in the lab into a spectrum from green through yellow to brown and assigned a number between 0.1 and 5.0 in 1/10 increments. The greenest color recorded was assigned a value of 0.1; 5.0 was the brownest. We then compared differences in plant colors among treatment categories (month of cutting or uncut controls) during each weekly survey period.

The use of this simple leaf color assessment procedure is not a conventional method for measuring progression to leaf abscission. The technique, however, allows for an approximation of the degree of chlorophyll disintegration and formation of anthocyanin pigments within leaves. Because chlorophyll disintegration is related to the amount of time remaining to autumn leaf abscission (Kozlowski and Pallardy 1997), we used the technique to determine how long leaves would remain on particular plants relative to other plants occupying the same site.

Statistical Analyses

We compared differences in shoot length, plant shoot biomass, total plant height, leaf flush, and leaf senescence of the regrowth from plants brush-cut at different times of the year and uncut controls in the first 3 years after brush-cutting treatments were applied (2001) using analysis of variance (ANOVA; Sokal and Rohlf 1995). We tested homogeneity of variances in all plant attributes analysed using a Levene's test (Milliken and Johnson 1984). We employed a Kolmogorov–Smirnov test to verify assumptions of normality for each attribute compared (Zar 1999). When sample sizes between treatments within a species were approximately equal, we used a Tukey's HSD test for post hoc comparisons; otherwise a Spjotvoll/Stoline for unequal sample sizes test was used for post hocs (Zar 1999). We neither assessed nor expressed changes in plant species attributes in relation to cutting time as a ratio against controls. We did not use ratios because our primary objective was to determine the relationship of plant responses from one cutting time to another—not to compare plant responses to uncut plants.

Results

Shoot Length

Year 1

The resprouts of all species cut in June were consistently larger when measured in the first spring (2002) after cutting than the shoots of plants cut at any other time during 2001 or uncut controls (Table 1; YEAR 1). In the case of willows, shoots from plants cut in July were shorter than those on June-cut plants but longer than the shoots on control plants when measured in the first spring after cutting; otherwise there were no significant differences in shoots from July-cut plants and controls (i.e., birch) or shoots from July-cut plants were shorter than those found on controls. Shoots from plants cut in August were generally (with the exception of birch) shorter than shoots from any other treatment category (Table 1; YEAR 1).

Year 2

In the second spring (2003) after cutting, shoots were longer in willows cut in October of 2001 than uncut controls and those cut at any other time in 2001 (Table 1; YEAR 2). June- and July-cut willows had shorter shoots than willows cut at any other time but were still longer than uncut controls. Shoots of willows cut in September were shorter than shoots from October- and August-cut plants. September-cut plants had the longest and uncut controls had the shortest shoots of twinberry. August-, June-, and October-cut birches contained longer shoots than uncut controls (Table 1; YEAR 2).

Table 1 Differences between treatments in mean length (cm) of resprouting current annual shoots of three different browse plants as measured in the first (2002), second (2003), and third (2004) springs after initial brush-cutting in 2001

Species	Cutting time												F_{stat}
	June		July		August		September		October		Control		
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
YEAR 1													
Willow	${}^{271}28.1$	0.4	${}^{174}16.7$	0.5	${}^{615}5.3$	0.2					${}^{134}13.0$	0.5	909.04
Twinberry	${}^{110}21.9$	0.6	${}^{70}7.7$	0.7	${}^{21}5.6$	1.3					${}^{156}12.7$	0.5	107.37
Birch	${}^{13}19.4$	1.6	${}^{13}12.4$	1.6	${}^{51}12.3$	0.8					${}^{13}11.3$	1.6	6.18
YEAR 2													
Willow	${}^{479}18.7^{a}$	0.5	${}^{350}16.7^{a}$	0.6	${}^{441}25.2$	0.5	${}^{465}22.0$	0.5	${}^{428}37.9$	0.5	${}^{443}12.5$	0.5	301.66
Twinberry	${}^{327}13.0$	0.6	${}^{350}17.6$	0.5	${}^{289}25.7$	0.6	${}^{463}29.5$	0.5	${}^{324}22.3$	0.6	${}^{336}10.3$	0.5	204.20
Birch	${}^{9}17.3$	2.8	${}^{12}11.9$	2.4	${}^{37}14.9$	1.4	${}^{11}13.8$	2.6	${}^{24}17.2$	1.7	${}^{54}7.8$	3.2	6.10
YEAR 3													
Willow	${}^{434}9.0^{ade}$	0.3	${}^{411}8.9^{cef}$	0.3	${}^{395}13.1$	0.3	${}^{422}9.3^{bdf}$	0.3	${}^{420}11.7$	0.3	${}^{393}8.4^{abc}$	0.3	38.49
Twinberry	${}^{333}9.1^{cd}$	0.3	${}^{320}9.8^{acef}$	0.3	${}^{328}10.7^{bfg}$	0.3	${}^{325}13.2$	0.3	${}^{318}9.5^{deg}$	0.3	${}^{331}10.9^{ab}$	0.3	23.10
Birch	${}^{21}18.3$	1.6	${}^{9}13.5$	2.5	${}^{121}20.3$	0.7	${}^{28}15.1$	1.4	${}^{34}13.6$	1.3	${}^{64}11.1$	0.9	14.7

Note: Plants that were cut in the fall of 2001 did not produce sprouts until the following growing season. Superscripted prefixes indicate sample sizes. In year 1, all treatment means are significantly different from one another for willows. For twinberry, July is not significantly different than August. For birch, only June is significantly different than all other treatments. In year 2, means sharing a common superscripted suffix across a species (willow and twinberry) are *not* significantly different from one another. In the case of birch, controls are significantly different than June-, August- and October-cut plants. In year 3, means sharing a common superscripted suffix across a species (willow and twinberry) are *not* significantly different from one another. In the case of birch, control plants are significantly different than June- and August-cut plants and October-cut plants are significantly different than August-cut plants. A Tukey's HSD or a Spjotvoll/Stoline for unequal sample sizes test was performed for post hocs. Note: All p-values for all tests <0.001

Year 3

In the third spring (2004) after cutting, August-cut plants had the longest and October-cut plants had the second longest shoots of all shoots produced by willows in all the other treatment categories (Table 1; YEAR 3). Control, June-, July-, and September-cut willows had the shortest shoots. September-cut twinberry had the longest shoots of all treatments. Shoots of all other twinberry plants were close to the same size. August- and June-cut plants had the longest and controls had the shortest shoots of brush-cut birches (Table 1; YEAR 3).

Biomass

Year 1

For willows and twinberry, June-cut plants possessed the most current annual shoot biomass in the first spring (2002) after cutting treatments, whereas August- and/or July-cut plants had the least biomass (Table 2; YEAR 1). June-cut and control birches had the most and August- and July-cut had the least biomass (Table 2: YEAR 1).

Year 2

In the second spring (2003) after cutting, the June-cut willows had the most shoot biomass followed by October-cut, August-cut, controls, July-, and September-cut plants (Table 2; YEAR 2). September- and August-cut twinberry plants had the most shoot biomass, whereas October-cut, June-cut and controls had the least biomass. Birch showed no significant difference in biomass between treatments in the second spring after cutting (Table 2; YEAR 2).

Year 3

In the third spring (2004) after cutting, June-cut willows had the highest and October-, September-, and July-cut plants the lowest biomass values, respectively (Table 2; YEAR 3). September-cut and control twinberry had the highest and October-cut twinberry the least amount of biomass. August-cut birches had the highest and July-cut the lowest biomass values (Table 2; YEAR 3).

Total Plant Height

By the third spring after cutting, uncut controls were as tall or taller than any other treatment categories for all plants

Table 2 Differences between treatments in mean biomass (average plant current annual shoot length (cm) x number of shoots) of 3 different browse plants measured in the first (2002), second (2003) and third (2004) springs after initial brush-cutting

Species	Cutting time												F_{stat}
	June		July		August		September		October		Control		
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
YEAR 1													
Willow	$^{271}643.3$	17.0	$^{174}209.2$	21.2	$^{615}33.0$	11.3					$^{134}327.7$	24.2	304.17
Twinberry	$^{110}425.7$	20.5	$^{70}97.4$	25.8	$^{21}21.8$	47.0					$^{156}302.6$	17.3	44.10
Birch	$^{13}350.9$	42.0	$^{13}110.4$	42.0	$^{51}90.5$	21.2					$^{13}251.7$	42.0	12.49
YEAR 2													
Willow	$^{479}639.5$	28.8	$^{350}228.0^{bd}$	33.7	$^{441}385.4^{ce}$	30.0	$^{465}224.7^{ad}$	29.3	$^{428}449.6^{e}$	30.5	$^{443}318.7^{abc}$	30.0	27.81
Twinberry	$^{327}297.3^{bc}$	28.4	$^{350}442.3^{e}$	27.5	$^{289}527.0^{de}$	30.2	$^{463}631.0^{d}$	23.9	$^{324}225.3^{ac}$	28.5	$^{336}244.0^{ab}$	28.0	38.90
Birch	$^{9}152.8$	38.7	$^{12}91.8$	33.6	$^{37}140.7$	19.1	$^{11}126.4$	35.0	$^{24}107.6$	23.7	$^{54}67.7$	15.8	2.22
YEAR 3													
Willow	$^{434}388.5$	15.3	$^{411}125.1^{ac}$	15.8	$^{395}254.3$	16.1	$^{422}144.1^{ab}$	15.5	$^{420}175.6^{bc}$	15.6	$^{392}321.7$	16.1	45.60
Twinberry	$^{333}255.9^{bc}$	38.9	$^{320}295.8^{bd}$	38.6	$^{328}351.4^{cd}$	38.2	$^{325}609.3^{a}$	38.4	$^{318}98.1$	38.8	$^{331}530.6^{a}$	38.0	23.67
Birch	$^{21}167.1$	34.9	$^{9}99.0$	53.4	$^{121}215.1$	14.6	$^{28}110.8$	30.3	$^{34}103.1$	27.5	$^{64}103.3$	20.0	6.12

Note: Plants that were cut in the fall of 2001 did not produce sprouts until the following growing season. Superscripted prefixes indicate sample sizes. In year 1, all treatment means are significantly different from one another for willow. For twinberry, the July treatment is not significantly different from the August treatment. For birch, the June treatment is significantly different from the July and August treatments, and the control mean is significantly different than the August mean. In year 2, means sharing a common superscripted suffix across a species (willow and twinberry) are *not* significantly different from one another. In year 3, means sharing a common superscripted suffix across a species (willow and twinberry) are *not* significantly different from one another. In the case of birch, August- and July-cut plants are significantly different than one another. Tukey's HSD or a Spjotvoll/Stoline for unequal sample sizes tests were performed for post hocs. All p-values for all tests <0.001, except for birch in year 2, for which $p = 0.055$

Table 3 Differences between treatments in mean overall height (cm) of plants measured at the end of the study in the spring of 2004 for three different woody browse plants

Species	Cutting time												F_{stat}
	June		July		August		September		October		Control		
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Willow	$^{424}68.2^{a}$	1.4	$^{410}49.4^{b}$	1.5	$^{363}60.2$	1.6	$^{409}46.2^{b}$	1.5	$^{381}71.8^{a}$	1.5	$^{418}106.7$	1.5	222.43
Twinberry	$^{332}55.6^{abc}$	1.3	$^{319}52.1^{ade}$	1.3	$^{332}54.2^{bef}$	1.3	$^{321}71.4$	1.3	$^{330}51.6^{cdf}$	1.3	$^{331}95.4$	1.3	175.74
Birch	$^{20}43.6$	3.7	$^{9}35.3$	5.6	$^{127}36.9$	1.5	$^{27}30.5$	3.2	$^{32}32.5$	3.0	$^{70}47.5$	2.0	6.76

Note: Superscripted prefixes indicate sample sizes. Means sharing a common superscripted suffix across a species (willow and twinberry) are *not* significantly different from one another. In the case of birch, control plants are only significantly different than August-, September-, and October-cut plants. Tukey's HSD or a Spjotvoll/Stoline for unequal sample sizes tests were performed for post hocs. All *p*-values for all tests <0.001

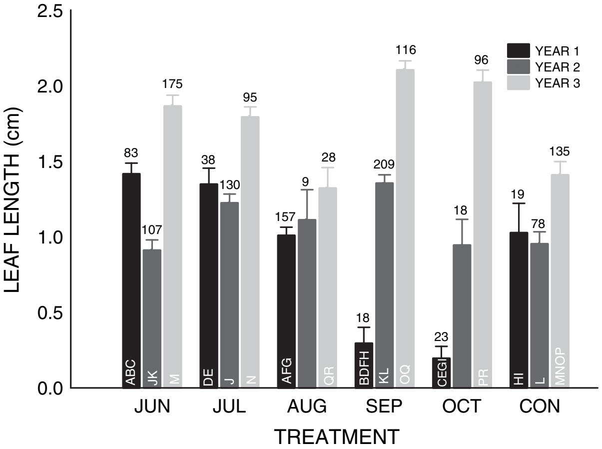

Fig. 2 Differences (± 1 SE) in onset of leaf flush between willows cut at different times during 2001 (treatment) as measured by average leaf length during the springs of 2002, 2003, and 2004. Note: Treatments sharing a common letter assignment within a survey year are the only treatments significantly different than one another as determined by a Spjotvoll/Stoline for unequal sample sizes test. Numbers atop error bars indicate sample sizes

sampled (Table 3). Which plants were smaller than controls but tallest among brush-cut plants varied by species. The tallest brush-cut willows were those cut in October and June 2001. The tallest brush-cut twinberry plants were those cut in September. There were no significant differences in plant height after 3 years of growth among birches cut at different times of the year (Table 3); birches are the preferred browse species in our research area and were vertically suppressed by heavy browsing in each of our treatment strips.

Leaf Flush

Year 1

The average degree of bud break and leaf expansion (usually the third week of May in northern British Columbia) varied in the first spring (2002) after brush-cutting between willow treatments, $F(1, 5) = 19.136$, $p \leq 0.001$. Leaf expansion was most advanced in willows that had been cut during the previous June and July (but also controls) and least advanced in October- and September-cut willows (Fig. 2; black bars). Similarly, differences existed in the degree of leaf expansion in twinberry plants in the first spring, $F(1, 5) = 20.978$, $p \leq 0.001$, after brush-cutting, with plants cut in June and August flushing leaves earlier in spring than those cut at other times of the year but not earlier than uncut controls.

Year 2

Differences in the degree of willow leaf flush also existed in the second year, $F(1, 5) = 7.044$, $p \leq 0.001$, after cutting (Fig. 2; dark gray bars). September-cut plants were the most advanced, and controls the least, in leaf expansion during the peak in flush (Fig. 2). Twinberry also displayed differences in leaf expansion in the second spring, $F(1, 5) = 8.529$, $p \leq 0.001$, after brush-cutting, with plants cut in August being the most advanced and those cut in June the least advanced in leaf expansion during leaf flush.

Year 3

Leaf expansion continued to be significantly different between willow treatments when measured in the third spring after brush-cutting, $F(1, 5) = 11.721$, $p = 0.001$ (Fig. 2; light gray bars). Leaf expansion was most advanced for September-cut willows and least advanced for August-cut willows during the spring of 2004 (Fig. 2). Once again, twinberry plants revealed differences relative to treatment in the third spring, $F(1, 5) = 20.840$, $p \leq 0.001$, after brush-cutting, with August- and October-cut plants showing more advanced leaf flush than uncut controls or plants cut at other times of the year.

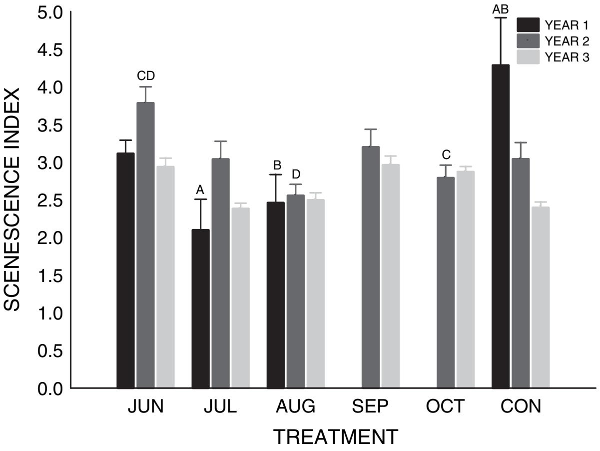

Fig. 3 Differences (± 1 SE) in progression to senescence of twinberry plants brush-cut at different times during 2001 (treatment) as measured by a senescence index (0 = least senescent; 5 = most senescent; see text) during the autumns of 2001, 2002, and 2003. Note: Treatments sharing a common letter assignment within a survey year are the only treatments significantly different than one another as determined by a Tukey's HSD test; $n = 35$ for each treatment category for years 1 and 3 and $n = 32$ for each category for year 2

Leaf Senescence

Time of cutting influenced the senescence of twinberry and willow leaves as measured by leaf greenness (senescence index) in fall for at least 3 years after cutting. The specific influence depended on the brush species in question and the number of years after cutting.

Year 1

During the peak of leaf coloring (October 11) in the autumn of 2001, twinberry plants cut in July and August were greener than uncut controls ($p \leq 0.001$; Fig. 3; black bars). Cut willows were greener than leaves on uncut control plants ($p \leq 0.001$), but no significant differences in leaf coloration and senescence existed between plants cut at different times of the year.

Year 2

In the second year after cutting, twinberry plants that had been cut in July and August of 2001 were greenest and June-cut twinberry most advanced in senescence (most yellow) on October 19, 2002 ($p \leq 0.001$; Fig. 3; dark gray bars). No significant differences in leaf coloration were apparent for willow in the second postcutting year.

Year 3

In the third autumn after cutting, there was no significant difference in leaf color for twinberry plants cut at different times when measured during the peak in fall leaf coloring (October 9, 2003; Fig. 3; light gray bars). Willows cut in August of 2001, however, had leaves that were significantly greener than willows cut in September, July, and October and uncut controls. Willows cut in June and July were greener than October-cut plants ($p \leq 0.001$).

Discussion

Brush Response

Overall, our data suggest that the season of brush-cutting consistently affects plant growth response, both within and among species for several years after brush-cutting. These results agree with those of Cremer (1973), who suggested that the ability of plants to recover or compensate for damage depends strongly on season of cutting. Kays and Canham (1991) demonstrated that fall root starch reserves as well as resprouting vigor were related to season of cutting in several species of deciduous hardwood shrubs and trees. Plant attributes such as shoot morphometry and leafing phenology, which are known to influence selection of plant parts by herbivores, were among those attributes altered by our cutting treatments.

In agreement with the findings of Hardesty and others (1988), various patterns in brush response to our cutting times were most pronounced in the first year after brush-cutting but persisted for several years following cutting. Although some variation existed between species, measurements on shoot morphometrics and leafing phenology taken in the first year after brush-cutting indicate that brush that is cut earlier in the year generally produces the largest resprouts and the most resprout biomass after cutting. Leaf flush in the spring after cutting treatments also occurred earliest for willows cut earlier during the previous growing season and earliest for twinberry cut in June and August.

Our finding that plants cut earlier in the year produced larger shoots and more biomass in the year after brush-cutting is predictable and has been demonstrated by others (Babeux and Mauffette 1994; Belanger 1979; Kays and Canham 1991; LePage and others 1991) and can be attributed to the fact that these plants had a longer growing season available to respond to cutting treatments before becoming dormant. This form of plant compensation in response to damage is also known to delay leaf senescence in the fall (Danell and Bergstöm 1985; Hardesty and others 1988), albeit the degree to which plants delay senescence in relation to plant cutting time is rarely reported (Rea and

Gillingham 2001). Such delays appear to be related to shifts in the root-to- shoot ratio following an interruption in the plant's growing cycle, which shifts relatively more nutrients to the remaining biomass of damaged relative to undamaged plants (Millington 1963), thus causing an extension of the growing season (Danell and Bergstöm 1985). Because cutting at various times of the growing season can influence root-to-shoot nutrient exchanges relative to available root reserves (Kays and Canham 1991), changes in leaf senescence relative to cutting time are not surprising.

Leaf development can be affected by pruning in different seasons (Zeng 2003). Delays in leaf flush are also known to occur in response to terminal bud decapitation (Chaar and others 1997) and are likely to be driven by similar physiological processes. Chaar and others (1997) reported an effect of induced simulated herbivore damage on bud burst and leaf flush in sessile oak and attributed such changes to the degree to which buds are formed and/or are under the influence of apical inhibition at the time of damage. Changes in leaf flush might also occur as a result of stem and leaf materials being removed before they are able to complete the export of nutrients and other factors required for spring leaf flush to below ground structures in the late fall (Larson 1978; Tuomi and others 1989).

Cutting plants at different times of the growing season removes apical influences differentially relative to season and results in remaining stump buds at different phenological stages being activated. How such stump buds and leaf buds produced on resprouts that arise from these buds over winter could presumably influence patterns of leaf flush. Stored reserves of nitrogen, which facilitate leaf flush and development in the spring, are stored in stem and bark materials (Millard and others 2001). In this respect, earlier leaf flushing in the resprouts of plants cut earlier during the previous growing season might be explained by the fact that early-cut plants had more time to resprout and produce biomass where nitrogen could be stored and subsequently influence leaf flush in the following spring. Interestingly, uncut controls had more aboveground biomass than any of the brush-cut plants, yet the degree of leaf flush on control shoots was not proportionately represented as such. This somewhat counterintuitive finding appears to suggest that in brush-cut plants, nitrogen and other factors required for leaf flush might be stored disproportionately in newer versus older growth (where it is typically stored; Millard and others 2001) due to plant rejuvenation from cutting.

Although trends in plant response were clearest in the first postcutting year, plant biomass and leafing phenology remained different between treatments and were detectable in posttreatment regrowth in the second and third year after cutting. Much of the difference in plant response among treatment categories can be attributed to the number of buds released and the timing of their release, as described earlier. Plants able to compensate and regrow following damage in the same growing season were able to produce new shoots with buds before winter dormancy, whereas plants cut later in the year (September and October) were unable to resprout until the following spring. Plants cut earlier in the treatment year produce larger shoots and more biomass (as illustrated in our findings) that contain more buds (Rea unpublished data) in relation to resprouts of plants cut later in the year. A higher density of buds in resprouts of earlier-cut plants results in a condition in which shoots contain more growing points from which new shoot materials can emerge the following spring; in the spring that follows, more root resources are directed into more growing points relative to late-cut plants, which have smaller shoots and fewer buds. When resources are directed to several growing points, shoots are proportionately smaller than when resources are distributed among fewer growing points (Haukioja and Lehtilä 1992).

Patterns of plant response in the years following brush-cutting are influenced by resource allocation to growing points (Kays and Canham 1991). The quantity of shoot material removed by browsing animals also determines plant architecture and the number of buds available to produce shoots in the year after browsing (Danell and others 1994). Browse removal by moose and Snowshoe Hare (*Lepus americanus* Erxl.) at our research site approached 70% of current annual shoots on average in some of our treatment categories in some years (Rea 2005) and likely contributed to less distinct patterns of plant responses being detectable in the second and third year after brush-cutting. Removal of apical dominance through shoot removal by browsing also likely affected brush response (Chaar and others 1997).

In summary, regrowth in the years after brush cutting appeared to be influenced by resource availability at the time of year that brush-cutting took place, whether or not plant hormone cues for growth were present at time of cutting and what the available resource:bud ratio was for directing plant response. Moreover, shoot removal from browsers likely modulated plant response by removing apical dominance and growing points and influencing the available resource:bud ratios.

Brush Attributes and Herbivore Preferences

Herbivores select browse shoots based on many of the plant attributes that changed in response to our cutting treatments. Shoot size is the most important determinant of edible digestible dry matter (Oppong and others 2002) and is of particular importance to large ungulates such as moose and elk, which select the largest shoots available (Danell and others 1994) and select stump sprouts when available (Bergström and Hjeljord 1987). Cropping large shoots allows for increases in intake rates per cropping effort (Gross and others 1993; Shipley and others 1994) and facilitates maximizing energy intake per foraging bout (Renecker and Schwartz 1998). This feeding strategy helps explain why overall plant biomass is also important in the foraging ecology of large ungulates that tend to concentrate feeding efforts at individual plants with greater absolute quantities of biomass (Danell and others 1991). More time spent visiting plants with more abundant shoot biomass, regardless of shoot quality, reduces time spent moving between feeding patches (Renecker and Schwartz 1998).

Because plant height determines shoot accessibility for mammalian herbivores that feed from the ground (Danell and others 1987; Rooke and others 2004), plant height influences plant attractiveness, particularly where snow pack can obscure shorter plants (Schwab and Pitt 1987). Although none of the plants in our treatments was too tall for moose to access, smaller herbivores, such as deer, might be deterred from, or at least expend more energy when, browsing on plants as tall as those measured in our control strip (twinberry and willows were on average ~1 m tall).

In the absence of snow, most of the shoots of brush-cut plants would be easily available to moose and other ungulates. However, because most shoot browsing occurs during the winter when most other forage items are less available, the quantity of shoot material remaining above the snow pack can influence accessibility and attractiveness. Our findings and winter observations indicate that plants cut at certain times of the year are more likely to be available above the snowline than those cut at other times. In particular, plants cut in the early spring and late fall appeared to be most available at maximum snow pack in mid-winter; plants cut at these times of the year contain relatively more root reserves at the time of cutting, which facilitates vigorous resprout production and shoot elongation (Kays and Canham 1991). Brush cut in spring and fall is most likely to be selected by herbivores on the basis of accessibility; browse protruding above the snowline costs less to access than browse buried under the snow.

Greener foliage is more attractive to herbivores (Bergerud and Manuel 1968), and although cafeteria style feeding trials for testing herbivore preferences for greener versus more senescent vegetation does not appear to have been conducted, herbivore preference for greener leaves has been implied (Hardesty and others 1988; Rea and Gillingham 2001). Moose are known to eat leaves as long as leaves are available (Hobbs and others 1981, Renecker and Schwartz 1998), which suggests that plants bearing leaves and delaying leaf senescence into the early winter months would be more attractive to browsers. Such a preference by herbivores for greener plants suggests that regrowth from brush-cut plants is likely to be more attractive in the late autumn and early winter due to delays in leaf senescence from cutting relative to uncut controls. In this respect, brush-cutting makes plants more attractive, although cutting time appears to have a less significant effect.

Nutritious forages are sparse and difficult for herbivores to locate in the late winter and early spring (Blair and others 1980). At this time of year, ungulates are attracted to deciduous trees flushing leaves (Danell and others 1994; Chaar and others 1997) and to early greening spring vegetation in general (Schwartz and others 1988). Schwartz and others (1988) in fact argued that availability of early greening vegetation in spring might play an important role in the survival of ungulates emaciated following long, hard winters. Consequently, brush-cutting treatments that result in the production of resprouts, which flush leaves relatively early in the spring, are likely to be most attractive to herbivores. Therefore, in the first spring after brush-cutting, brush that is cut earlier in the year is likely to be more attractive to moose and deer than brush cut later in the year. Plants cut in late summer and early fall, however, are likely to be most attractive to herbivores in the second and third spring after cutting.

The attributes known to change in response to cutting time are many, as are the possible ways in which animals consuming such regrowth might perceive these changes. One area of research in the field or foraging ecology that is receiving increasing amounts of attention—but not discussed here—is the multitude of chemical responses plants can have as a result of tissue damage (Bryant and others 1991; Danell and others 1994). Undoubtedly, investigating plant chemical response to cutting time could have enhanced our study. Such experiments, however, have been previously conducted, with only small changes in shoot chemical deterrents being reported from plants cut at different times of the year (Rea and Gillingham 2001). In fact, browse shoots in general appear to be poorly defended by chemical deterrents (Hanley and others 1992) and appear to be of little consequence to browsing moose and other ungulates that produce salivary binding proteins to inactivate such chemicals (Hagerman and others 1993). As such, we considered changes in shoot chemistry to be of secondary importance relative to changes in accessibility, morphometrics, and the phenology of leafing.

Conclusions and Recommendations

Although no particular cutting treatment resulted in the production of larger resprouts, more biomass, earlier leaf flush, and delayed leaf senescence in all species in all years tested, some treatments produced resprouts that are

Table 4 Matrix highlighting cutting times that produced regrowth possessing the plant traits most likely to be attractive to ungulates at various times (spring, fall or winter) of the year

Postcutting year	Spring	Fall	Winter		
	Earlier leaf flush	Later senescence	More shoot biomass	Larger shoots	Taller plants
1	JUN^{W}	JUL^{T}	JUN^{TWB}	JUN^{TWB}	
2	SEP^{W}	AUG^{T}	JUN^{W}SEP^{T}	JUN^{B}SEP^{T}OCT^{W}	
3	SEP^{W}	AUG^{W}	JUN^{W}AUG^{B}SEP^{T}	AUG^{WB}SEP^{T}	JUN^{B}SEP^{T}OCT^{W}

Note: T = twinberry; W = willow; B = birch. Plant height was only measured in year 3. More than one treatment time per cell indicates differences among willow, twinberry and birch. Treatments included in the matrix are those showing the most extreme mean (regardless of SE or *p*-values) for each plant attribute analyzed where differences existed between cutting treatments and presented in tables and figures in the Results section. The matrix represents a simplification of how such data could be analyzed to produce an operational matrix for use in vegetation maintenance planning where browse quality is being considered

likely—according to our review of the literature—to be perceived as relatively more attractive to ungulates in the years after brush-cutting. Identifying brush attributes targeted by foraging ungulates and constructing a matrix (as illustrated in Table 4) to demonstrate which cutting treatments produced resprouts containing those attributes in the years after brush-cutting is one approach to determining which plants are most and least likely to be attractive to ungulates.

Analysis of our matrix reveals that there is no single treatment time that appears most suited to producing unattractive browse, albeit July-cuttings rarely appear in our ‘‘preference matrix’’ or appear to produce regrowth that would be considered attractive to ungulates regardless of the seasonal category inspected (Table 4). Specifically, if increasing the quality of spring range is the desired outcome, June- and September-cuttings are likely to provide the best treatment option. July- and August-cuttings will provide the best autumn range, whereas June-cuttings are most likely to produce the best winter range. Autumn-cuttings are also an alternative option for producing attractive winter browse in the second and third year after cutting (Table 4).

Summer range is not listed as a matrix category because summer leaf and shoot quality were not analyzed in our study. We chose not to undertake tracking and analysis of summer shoot quality as part of this study because consumption of shoots by ungulates happens predominantly between fall and spring and not as intensively during summer, when other forage items such as grasses, forbs, and aquatics are more readily available. Specifically, our objectives were to analyze browse quality in fall and winter, when moose focus feeding efforts on brush.

The predominant activity of deer and other ungulates in transportation corridors is feeding (Groot Bruinderink and Hazebroek 1996; Peek and Bellis 1969; Puglisi and others 1974). Such linear rights-of-way often provide forest edge, which is preferred habitat for moose and other ungulates (Child 1998) and increased browse availability relative to adjacent woodlands (Lunseth 1988). Because increased animal activity in corridors is correlated with the odds of colliding with animals, determining ways to reduce activity is currently the subject of much debate.

It is the opinion of several authors (Gundersen and others 1998; Jaren and others 1991; Lavsund and Sandegren 1991) that reducing browse attractiveness and accessibility within transportation corridors can reduce animal activity along road and rail lines and subsequently reduce the odds of animals encountering traffic. Because ungulate use of transportation corridors and the occurrence of ungulate–vehicle collisions appears to peak in fall and winter in British Columbia and many other parts of North America (Allen and McCullough 1976; Puglisi and others 1974; Sielecki 2004), determining a brush-cutting time that results in plants producing less attractive fall and winter browse could conceivably facilitate a reduction in roadside browsing and vehicle encounters. Indeed, our findings demonstrate that brush-cutting plants in July appears to result in the production of such growth.

Obviously, the influence that brush-cutting time has on plant attributes and subsequently on the influence that such changes can have on how herbivores perceive and consume brush is species- and likely region-specific. Our study was not replicated outside of our study area and is, therefore, not likely to be broadly generalizable to other regions where variations in soil nutrients, moisture, leaching, and plant population genetics might differently influence plant response to cutting. Obviously, more field and laboratory research is needed to understand better how cutting time is related to animal consumption of specific brush species in various areas, both within and outside transportation corridors.

It is important for managers to begin to understand that cutting time does influence plant response. Such an understanding gives transportation corridor managers an appreciation of the potential effects of vegetation maintenance activities on vegetation response and how herbivores might perceive and utilize that vegetation. Equipped with such information, managers can experiment in their operating areas and begin to plan the timing of vegetation maintenance activities in a more deliberate fashion, particularly in areas where concerns for the extensive use of roadside and railside plants by herbivores exist.

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