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#### RESPONSE OF SCOULER'S WILLOW (Salix scouleriana)

## TO MECHANICAL BRUSHING: IMPLICATIONS TO THE QUALITY OF WINTER

#### BROWSE FOR MOOSE (Alces alces)

by

#### Roy V. Rea

B.S., California State University, Stanislaus, 1992

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### APPROVAL

Name:

Roy V. Rea

Master of Science

Degree:

Thesis Title:

RESPONSE OF SCOULER'S WILLOW (Salix scouleriana) TO MECHANICAL BRUSHING: IMPLICATIONS TO THE QUALITY OF WINTER BROWSE FOR MOOSE (Alces alces)

Examining Committee:

Chair: D. Max Blouw, Dean of Graduate Studies

bervisorl

Supervisor/ Michael P. Gillingham, Associate Professor

Katherine E. Parker, Associate Professor

Douglas C. Heard,

Adjunct Faculty

ALT F-

External Examiner: Arthur L. Fredeen, Assistant Professor

Date Approved:

26 April/99

#### ABSTRACT

We examined the effects of the timing of mechanical brushing on the nutritional value of Scouler's willow (Salix scouleriana) for moose (Alces alces) in winter. Brushing at different times during the growing season differentially altered morphological, chemical and phenological attributes of willows that are considered to be important determinants of the nutritional value of browse for moose. Willows brushed in July produced browse of higher value for moose (increased current annual shoot size with increased digestible protein, decreased tannin and lignin content and longer autumn leaf retention) in the first and second winter after brushing than willows brushed at other times during the growing season or unbrushed willows. We also investigated the effects of brushing (without a timing component) on the value of willow browse for moose for 2 to 5 winters post-brushing in relation to willows growing in unbrushed strips retained for wildlife food and cover. Many of the effects of brushing on the value of willows for moose were apparent for several years after brushing, although the degree to which brushing affected willows depended on site, year of brushing and sampling year. The winter shoots of brushed willows were larger for 5 years, lower in tannin for 2 years, lower in lignin for 3 years, and lower in digestible energy and digestible protein for 5 years post-brushing. Willows also delayed leaf senescence for 3 to 4 years after brushing. Additionally, we examined the effects of browsing and clipping on the value of willow shoots produced in the year after shoot removal. Shoots produced by some willows in the year after browsing/clipping were unaffected by the previous year's browsing/clipping intensity, but others increased in size when measured in the third to fifth winter after brushing. As the previous year's clipping/browsing intensity increased,

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willows often produced smaller shoots that were higher in lignin and tannin when analyzed in the second winter after brushing and produced shoots that were lower in digestible energy and digestible protein when analyzed in the third to fifth and fifth winter after brushing, respectively. Based on the results of a browse survey conducted in the third spring following brushing, moose browsed the shoots of brushed and unbrushed willows at similar diameters. Moose browsed past current-annual shoots and into older, less nutritious stem materials more often when browsing the shoots of unbrushed when compared to brushed willows. In areas being managed for the production of conifers and where concerns for the value of browse for moose exist, willows should be brushed in July. Because the effects of brushing alter the nutritional value of browse for moose for at least 5 years after brushing such changes should be considered in relation to managing wildlife strips and adjacent forest stands in moose wintering areas.

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#### PREFACE

1

Quickly transforming early seral forests into productive forest plantations is a primary goal of the forest vegetation manager. To meet this objective, managers often employ stand-tending measures, that although they may be advantageous to conifer crops, reduce the growth and maturation of other plant species. Brushing and weeding operations, for instance, are often used to eliminate or reduce the competitive effects of early-successional trees and shrubs on conifers such as pine (*Pinus spp.*) and spruce (*Picea spp.*) in the early stages of forest succession (Smith 1986).

Brushing and weeding operations in North America are typically accomplished through aerial applications of forest herbicides such as glyphosate (Roundup<sup>®</sup>, Monsanto Chemical Co. St. Louis, Mo.) and 2,4-D formulations (Biggs and Walmsley 1988). In areas where social objections relative to herbicide use exist, or where forest-worker unemployment is high, however, other means such as sheep (*Ovis aries*) grazing and motor/manual (mechanical) brushing operations may supplant the application of herbicides to reduce brush. Mechanical brushing operations, which employ crews of forest workers with handheld brushsaws, are particularly popular in some parts of British Columbia. Several forest-worker crews, for example, brush and weed an average of 1500 ha of regenerating forests each growing season in the Vanderhoof district of the British Columbia Forest Service (R.V. Rea, unpublished data)

By altering the vegetative composition of regenerating forests, mechanical brushing also alters the habitat suitability of these areas for a variety of animals in the years following treatment (Goodrum and Reid 1956). For example, such treatments reduce the abundance of important winter browses for moose (*Alces alces*) such as willow (*Salix* spp.) and birch (*Betula* spp.; Härkönen et al. 1998). Such compositional changes may be short-lived due to intense vegetative or compensatory sprouting following mechanical damage (Coates and Haeussler 1986). The value of compensatory growth for herbivores such as moose (*Alces alces*), however, is not completely understood because plants often respond to mechanical injury by altering their morphological and chemical composition (Rhoades 1985; Danell and Bergström 1989). Plants may also alter patterns of leaf senescence and leaf flush when damage is severe due to changes in plant physiochemistry (Millington 1963; Kindschy 1989).

How plants specifically respond to damage depends to a large extent on the timing of damage (Whitham et al. 1991; Ouellet et al. 1994). Because mechanical brushing operations are performed throughout the growing season, the morphology and chemistry of shoots in winter and/or the fall and spring leafing phenology of recently brushed plants could depend on when plants are brushed. Because moose tend to select browse based on shoot morphology and chemistry as well as leafing phenology (Danell et al. 1994), such changes will likely affect the value of browse for moose.

Although mechanical brushing affects browse production in the years following treatment (Hjeljord and Grønvold 1988), the effects of the timing of brushing on the overall value of browse for moose and how long these effects last are poorly understood. My thesis research, therefore, was designed to determine the effects of the timing of brushing on the value of browse for moose and to determine how long such effects last. I focused my investigation on the response of Scouler's willow because this upland species of willow is commonly eaten by moose in winter and is regularly brushed throughout central BC.

In chapter 1, I describe the results of an experiment designed to determine the effects of brushing time on the nutritional value of Scouler's willow for moose. I

compared nutritional value of willows (in terms of the morphology and chemistry of winter shoots and leaf phenology) from brushed willows for 1 to 2 years following brushing, with unbrushed willows, and compared the value of plants brushed at different times.

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In chapter 2, I examine the effects of mechanical brushing on these same plant attributes for 2 to 5 years post-brushing. Unlike chapter 1, however, my analysis did not include a time-of-brushing within season. Instead, I determined the effects of brushing among 6 sites that were brushed at more of an operational level throughout the growing season prior to the commencement of my study (3 in 1993 and 3 in 1995). I also examined the effects of clipping and browsing on the nutritional value of shoots produced during the following year and compared the shoot diameter at the point of browsing from shoots on brushed and unbrushed willows.

In Chapter 3, I summarize my findings from Chapters 1 and 2 and discuss the implications of these findings for managing brush in areas where concerns for the quality of browse for moose exist. I make specific recommendations on when to brush willows for moose while maintaining vegetation management objectives and discuss the long term effects of brushing on browse quality with respect to managing adjacent forest stands and unbrushed wildlife strips.

# CHAPTER 1. EFFECTS OF THE TIMING OF MECHANICAL BRUSHING ON THE NUTRITIONAL VALUE OF SCOULER'S WILLOW (Salix scouleriana): IMPLICATIONS FOR WINTER BROWSING BY MOOSE (Alces alces). Abstract

We<sup>1</sup> examined the effects of the timing of mechanical brushing on determinants of nutritional value of Scouler's willow (Salix scouleriana) for moose (Alces alces) in the first 2 winters after brushing. Brushing at different times in the growing season differentially altered morphological, chemical and phenological attributes known to affect the value of browse for moose. We determined nutritional value of browse on the basis of the size, digestible energy, digestible protein, tannin and lignin content of willow shoots in winter. Additionally, we included the phenology of plant leafing in our estimate of nutritional value. Willows brushed in July were of higher value for moose in the first 2 winters following brushing than willows brushed in June, August or September or unbrushed willows. In the first winter after brushing, plants that were brushed in early July had shoots that were lower in lignin content, higher in digestible protein, and lower or not different in tannin content than shoots from either earlier-brushed or unbrushed willows (all P < 0.001). Willows brushed in early July also had shoots that were large (in terms of basal diameter, length and mass), high in digestible energy, and displayed a longer delay in leaf senescence when compared to shoots from either earlier-brushed or unbrushed willows in the first winter after brushing. Willows brushed in late July, however, were not available in the first winter after brushing. In the second winter after

<sup>&</sup>lt;sup>1</sup> The first person plural is used in the context of the individual chapters of the thesis which have been written in manuscript format and prepared for journal submission. The first person plural indicates and acknowledges the contributions of my supervisor Mike Gillingham as co-author of these manuscripts and of those involved with the technical assistance required for field and lab work.

brushing, willows that were brushed in July had shoots that were lower in digestible energy and digestible protein but larger, and lower in tannin and lignin content and displayed a longer delay in leaf senescence when compared to shoots of either earlierbrushed or unbrushed willows. Willows brushed after July also produced nutritious shoots in the second post-treatment year, but did not regenerate sufficient growth to be available for moose in the first winter after brushing. In addition, willows brushed in September displayed a delay in leaf flush in the first post-brushing spring. We recommend that willows should be brushed in July in areas that are managed for conifer production and that are also important to moose in winter.

#### Introduction

Early-successional plants such as birch (*Betula* spp.) and willow (*Salix* spp.) comprise the majority of the diet of moose in fall and winter (Pierce 1983; Regelin et al. 1987; Härkönen et al. 1998). These deciduous shrubs and trees are highly palatable and nutritious for moose and other herbivores in relation to other plants that are available during winter (Chapin 1980; Salonen 1982; Pastor and Naiman 1992). Despite the importance of willows and other deciduous plants to moose, these species are often considered weedy competitors by foresters managing early seral forests for the production of conifers such as pine (*Pinus* spp.) and spruce (*Picea* spp.). Consequently, the growth of these plants in conifer plantations is suppressed through the application of herbicides and/or mechanical brushing. Although both herbicide applications and mechanical brushing affect browse production (Hjeljord and Grønvold 1988), most research has focused on determining the impacts of herbicides on the quality and abundance of browse for moose (Soper et al. 1993; Hjeljord 1994; Raymond et al. 1996).

Mechanical brushing, is used extensively in parts of northern Europe (S. Härkönen, South Savo Game Management District, Juva, Finland, personal communication) and in many parts of North America where the use of herbicides is unpopular (Bernstein 1978; Conard 1984). Mechanical brushing is extremely labour intensive and time consuming when compared to herbicide applications at comparable landscape scales. Consequently, plants growing in areas targeted for brushing treatments are not brushed simultaneously, but rather throughout the growing season. This constraint results in plants being brushed during different stages of phenological development and growth (Coates and Haeussler 1986) and likely influences the overall quality and availability of browse for moose.

Deciduous browse species such as willow and oak (*Quercus* spp.) respond to severe forms of mechanical damage through vegetative regeneration (Gysel 1957; Kauppi et al. 1988; Tschaplinski and Blake 1994; Sennerby-Forsse and Zsuffa 1995). The timing of damage and the ratio of retained nutrients to lost nutrients, however, often influence such responses (Kays and Canham 1991; Whitham et al. 1991; Ouellet et al. 1994). If current-annual-shoot (measured from the previous year's growth scar to the shoot tip and hereafter termed "shoot") loss occurs when nutrients are concentrated in the aboveground structures being removed, the ability of plants to respond in a compensatory manner (compensate for lost tissues through shoot regeneration; *sensu* Belsky 1986) may be weaker than if damage occurs when the majority of nutrients have been translocated to below-ground storage structures (Kays and Canham 1991). Yellowpoplar (*Liriodendron tulipifera*) and flowering dogwood (*Cornus florida*), for example, produce more shoot biomass when heavily pruned during plant dormancy than when pruned during summer (Harlow and Halls 1972). Birch produces larger, more fibrous compensatory shoots that

are lower in nutrients following winter rather than summer browsing by moose (Danell et al. 1994). 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 but decreases if browsing occurs late in summer (Alpe et al. 1999).

Nutrient losses that are associated with summer tissue damage may lead to fineroot mortality, which further decreases nutrient uptake from soils and alters plant carbon/nutrient ratios (Herms and Mattson 1992). Changes in carbon/nutrient ratios can alter the production of chemical deterrents and structural compounds such as tannins and lignin (Bryant and Kuropat 1980; Belovsky 1981; Herms and Mattson 1992) and may affect the digestibility of plant tissues for herbivores (Bryant and Kuropat 1980; Hanley et al. 1992). Changes in the production and distribution of plant hormones following damage at different times also accompany changing carbon/nutrient ratios (Wenger 1953; Phillips 1975). Such changes, acting alone or in concert, can affect the nutritional value of browse tissues for herbivores such as moose.

Because the phenology of plant leafing depends largely on hormonal activity and plant nutritional status (Millington 1963; and Kramer and Kozlowski 1979), changes to plant chemistry following mechanical damage are likely to alter patterns of leaf senescence and leaf flush in accordance with the timing of damage. For example, birch trees display a delay in spring leaf flush when defoliated early in the previous growing season, but trees defoliated later in the year are typically less affected (Tuomi et al. 1989; Raitio et al. 1994). Defoliating willows in early summer also stimulates the production of leaves later in the growing season that are higher in nitrogen, phosphorus and potassium (Chapin 1980). Late-summer and winter shoot removal may cause browse plants to

display premature leaf flush in the spring (Larson 1975; Kindschy 1989) and delayed leaf senescence in fall (Willard and McKell 1978; Kindschy 1989; Smith 1986); how the timing of shoot removal may affect such patterns is less clear.

Moose select browse shoots based on shoot morphology and chemistry (Danell et al. 1985*b*; Risenhoover 1987*b*). Moose select the largest available shoots when browsing and select compensatory growth originating from previously damaged versus undamaged plants (Penner 1978; Machida 1979; Danell et al. 1985*b*; Risenhoover 1987*a*). This selection is presumably due to morphological changes that allow for increased bite sizes and intake rates (Gross et al. 1993; Shipley et al. 1994) and/or chemical changes that make the shoots of damaged plants more palatable and easy to browse (Danell et al. 1985*b*; Suter 1993). Because the ratio of bark and buds (where most nutrients and chemical deterrents are stored) to woody cortex is relatively reduced in large shoots (Danell and Bergström 1985; Radwan and DeBell 1988; Schwartz 1992), moose may select shoots based on a trade-off between their nutritional requirements and chemical tolerance (Palo et al. 1992).

Although moose do not select forages based exclusively on palatability or nutritive quality (Risenhoover et al. 1985; Risenhoover 1987*b*: Jia et al. 1997), they tend to select forages that are relatively high in digestible energy and protein (Regelin et al. 1987; Schwartz et al. 1987). Moose also avoid a variety of phenolic compounds such as lignin (Risenhoover 1987*b*) and tannins (Bryant and Kuropat 1980; Bryant et al. 1983; Singer et al. 1994), which can contribute significantly to reductions in dry matter digestibility (Bryant and Kuropat 1980; Hanley et al. 1992). Selecting browses low in tannin and lignin content is particularly important to ruminants because tannins can chemically inhibit the proper functioning of rumen microbes (Risenhoover et al. 1985)

and lignin can reduce cropping and processing rates that regulate energy intake (Spalinger et al. 1986).

Although the selection of winter shoots by moose depends to a large extent on shoot morphology and chemistry, the selection of browse in the early spring and late fall is influenced by the presence or absence of leaves (Renecker and Hudson 1986; Danell et al. 1994). Moose tend to select early-greening forages and late-senescing plants during spring and fall, respectively (Schwartz et al. 1988*a*; Danell et al. 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 reduced (Blair et al. 1980; Chapin 1980). Understanding how the timing of brushing affects the phenology of leafing as well as the morphology and chemistry of shoots will help resource managers better understand and manage for the effects of brushing on forage quality and availability in important wintering areas for moose.

In this chapter, we investigate how the timing of mechanical brushing affects the nutritional value of Scouler's willow for moose in the first 2 years following brushing. We determined the nutritional value of willow shoots on the basis of size, digestible energy, digestible protein, tannin and lignin content of dormant shoots. Willows that displayed delays in leaf senescence in the fall or premature leaf flush in the spring were considered to be of better quality than those that did not. We chose Scouler's willow for our study because it is a predominant upland willow on clearcuts in central British Columbia and because of its local importance as winter browse for moose (Roberts 1986; Porter 1990). Specifically, we examined whether the timing of brushing affected: (1) the morphology and chemistry of regenerating or compensatory shoots for moose in the first 2 winters following treatment; (2) leaf senescence and the amount of time that willow

leaves were available to moose in the first 2 falls following treatment; and (3) the timing of the emergence of willow leaves for moose in the spring following brushing.

#### Methods

#### The study area

Our study area was located 20 km north-east of Vanderhoof, British Columbia, Canada ( $54^{\circ}05$ 'N,  $123^{\circ}55$ 'W) in the sub-boreal spruce forest ecotype (Meidinger and Pojar 1991). The topography is rolling and the site elevation is ~ 800 m. Soils are sandy loam (D. Sommerville, Vanderhoof Forest District, Vanderhoof, B.C., Canada, personal communication). 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 to 5 °C (from 1961-1990; Atmospheric Environment Service 1993). The landscape is dominated by coniferous forests of hybrid white spruce (*Picea engelmannii x glauca*) and subalpine fir (*Abies lasiocarpa*). Lodgepole pine (*Pinus contorta* var. *latifolia*) and trembling aspen (*Populus tremuloides*) pioneer secondary successional sites (Meidinger and Pojar 1991), as do several species of upland willows (Porter 1990).

Our experiments were conducted on a 10-year-old regenerating pine clearcut replanted in pine and ~ 14 ha in size. We selected this site because of the abundance of Scouler's willow saplings of similar size (2.0 to 2.5 m) and structure and because of the proximity of the site to an active ranching operation and recreational trailhead. Locating the site in an area of moderate human activity minimized site utilization and browsing by moose. Moose density in the surrounding area at the time of the study was ~ 0.5 animals per km<sup>2</sup> (D. Heard, Ministry of Environment Lands and Parks, Prince George, B.C., Canada, personal communication).

#### **Experimental Design**

We selected individual willows for our experiment on the basis of size (2 to 2.5 m tall) and form and identified them according to leaf characters, shoot morphology and catkin anatomy following Argus (1992). Each willow contained  $\sim 10$  to 15 co-dominant main stems; willows were easy to delineate from one another because groups of main stems were well spaced. We selected, numbered and tagged 120 willows in the spring of 1996 and another 150 willows in the spring of 1997. In the spring of 1996, 30 willows were randomly assigned to 1 of 4 brushing treatments spaced at 6-week intervals: 14 June, 30 July, 15 September and a control. In the spring of 1997, an additional 30 willows were randomly assigned to each of 5 brushing treatments: 1 June, 1 July, 1 August, 1 September and an unbrushed control. A swing saw was used to brush willows  $\sim 10$  to 15 cm above the ground. Disk samples were collected from the 5 largest main stems on all 1996-brushed willows. We then assessed the age of each willow from disk samples by counting the annuli to determine whether or not the age of willow affected the morphological and chemical response of plants to brushing. The growth response of each willow within each brushing treatment was determined 6 weeks after brushing by measuring the length of 5 randomly selected compensatory shoots and calculating their mean length.

#### Shoot Collections and Analysis

During the winter of 1996-97 we collected shoots from 15 randomly selected willows of the 14 June 1996 treatment and corresponding unbrushed controls. We also collected shoots from all 30 of the 1 June, 1 July, and 1997 control willows during the winter of 1997-98 to determine the effect of brushing on willow shoots in the first winter following brushing. Shoots from the 30 July 1996, 15 September 1996, 1 August 1997,

and 1 September 1997 treatments did not grow sufficiently following treatment to be visible above mid-December snows and were not collected.

In the second winter after brushing, we collected shoots from the 15 previously unanalyzed 14 June and 1996 controls as well as shoots from all 30 of the 30 July and 15 September 1996-brushed willows. We sampled by selecting every third shoot from a tree. If we did not obtain at least 150 g of material, we repeated the sampling procedure until we had ~ 150 g for analysis. To inhibit shoot metabolic activities following clipping, shoots were collected during the first 2 weeks of December of both years, in sub-zero weather. We separated collections from each willow in the field into 1 plastic freezer bag for tannin analysis and 1 bag for all other analyses. Bags were then sealed and all materials were stored at -20 °C until analysis.

Morphometric measures of mass, length, basal and tip diameters were taken for all shoots collected from willows. If more than 30 shoots were collected from a particular willow, we randomly sub-sampled 30 shoots for morphometric measures. Following morphometric measurements, all shoot material for each plant was combined, cut to  $\sim$  10-cm lengths and dried to a constant mass (±0.1 g) at 39 °C in a forced-draft drying oven (Despatch LAD series2-24-3 Minneapolis, MN). We then milled the dried material with a Thomas-Wiley (Swedesboro, NJ) mill 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 to 1.0 g of material and procedures outlined by the manufacturer. Gross energy values were corrected to dry mass by desiccating with anhydrous CaSO<sub>4</sub> (WA Hammond Drierite Co., Xenia, OH.) for 24 h.

Elemental nitrogen (EN) was determined with an elemental CHN analyzer (Carlo Erba, Na Series 2, Milano, Italy) following procedures outlined by the manufacturer and

Pella and Colombo (1973). The elemental analyzer was calibrated using atropine (4.84 %N) and the National Institute of Standards and Technology (NIST) standard #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 et al. 1998), we substituted elemental nitrogen for TKN in equations outlined in Hanley et al. (1992) for estimating digestible protein. Digestible dry matter (the fraction of plant dry matter that is digestible by ruminants such as moose after accounting for the content of structural compounds, e.g., cellulose, hemicellulose and lignin) was determined for use in computing *in vitro* digestible energy (gross energy × digestible dry matter). Digestible dry matter was computed using equations outlined in Hanley et al. (1992). Although equations for digestible protein and digestible dry matter were originally developed for deer (*Odocoileus* spp.), these equations can be used to provide useful approximations for large-sized cervids that secrete salivary tannin-binding proteins, such as moose (Hanley et al. 1992).

To estimate the fibre fractions in our samples for use in determining digestible dry matter, we used a fibre refluxing/distillation apparatus (Labconco model 30006, Kansas City, MO). We used the neutral detergent procedure to determine total plant fibre (neutral detergent fibre or NDF), the acid detergent procedure to determine cellulose and lignin content (acid detergent fibre or ADF), and the acid detergent lignin procedure to determine the lignin content (acid detergent lignin or ADL; including cutin) of our samples (Goering and Van Soest 1970). Sodium sulfite was omitted from the NDF procedure as recommended by Hanley et al. (1992) for the determination of NDF from browse stems. Because the filtrate did not congeal, we also omitted the optional wash with hexane from the ADF procedure (Goering and Van Soest 1970). Because there

were no problems with filtration, asbestos was not used in the determination of acid detergent lignin (Goering and Van Soest 1970). We standardized NDF and ADF protocols by using standard forage mix samples from Norwest Labs (Lethbridge, Alberta).

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 1987b). Because dormant twigs contain relatively small amounts of tannin (Palo 1984; Robbins et al. 1987b), 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. Although crude tannin content was not quantified for use in digestibility determinations, we did determine the relative differences in tannin content between brushing treatments in order to help understand changes to one of the chemical characteristics known to influence winter browse selection by moose.

Tannin content was assessed using a radial diffusion protein precipitation assay that we modified from Hagerman (1987). We altered the procedure to reduce chemical usage and concentrate the extract, because winter twigs are known to contain relatively little tannin (Hanley et al. 1992). Frozen samples were submersed in liquid nitrogen, and then ground with a Thomas-Wiley mill and a 1-mm sieve screen that had been cooled with liquid nitrogen to avoid gumming. We homogenized the material by hand mixing and dispensed 200  $\mu$ g into a 1.5-ml centrifuge tube. After the addition of 500  $\mu$ l of 70% acetone, the sample was vortexed for 1 min and centrifuged at 7500 g for 5 min. Subsequently, we pipetted 60  $\mu$ l of supernatant into a collection tube. We then

resuspended the sample pellet in an additional 100 µl of acetone, vortexed, centrifuged again and collected 100 µl of supernatant in the collection tube. This last step was repeated 2 additional times resulting in a 360-µl sample that was 2.5 times more concentrated than extracts obtained using Hagerman's (1987) original procedures. Finally, 4, 8-µl aliquots of extract were dispensed into agarose plates containing bovine serum albumin fraction V powder (BDH Chemical Co., Toronto, Ont.) following procedures outlined by Hagerman (1987). We prepared 3 replicate samples of 200 µg for each plant. Each replicate sample of extract was dispensed into 9 separate wells distributed across 3 separate plates. After incubating the plates for 96 h at 30 °C, we determined the diameter of the precipitation ring; to allow for non-circular rings, 3 ring measurements were made  $\sim 120^{\circ}$  apart with a digital calliper on each ring. The 3 replicate ring diameters were then averaged first across plates, then among the 3 replicate samples from each plant to determine the mean diameter for a plant. Because the square of the ring diameter is proportional to the amount of tannin in the sample (Hagerman 1987), we use the mean ring diameter squared as an index of the amount of tannin (hereafter referred to as "tannin content") contained in the shoots sampled from each willow. Because this modified technique uses plant extract 2.5 times more concentrated than extracts derived using the original technique, however, tannin content reported here cannot be directly compared to values reported by others using extracts that were not concentrated.

#### Measuring Leaf Senescence

Differences in fall-leaf senescence were estimated by determining the predominant leaf colour of each willow within each brushing treatment on a given date, in both the falls of 1996 and 1997. We classified plants as having predominantly green,

yellow, brown or no leaves. We then compared the proportion of plants having predominantly green leaves among brushing treatments. To assess stage of leaf senescence in the fall of 1996 for willows brushed in 1996, the predominant leaf colour of each willow was estimated on a single day in mid-fall (8 October). We estimated stage of senescence in the fall of 1997 for willows brushed in 1996 and 1997 by estimating the predominant leaf colour of each willow on a weekly basis from 5 September to 17 October, before fall frosts.

#### Measuring Leaf Flush

To examine differences in spring-leaf flush for all willows from the 1996treatment year, we monitored plants 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 1 bud had separated and the expanding foliage was visible (Suzuki et al. 1988). We collected data from 11 May, at the first signs of bud break, through 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 and Rohlf 1995) to test the effect of age of willows brushed in 1996 on shoot length 6 weeks after brushing, as well as shoot morphological and chemical attributes in the first 2 winters following brushing treatments. To test the differences in shoot length 6 weeks after brushing, as well as the differences in shoot morphology and chemistry in the first 2 winters post-brushing among treatments, we used an analysis of variance (ANOVA; Sokal and Rohlf 1995) with

treatment time as a fixed factor. When appropriate, square root, log or inverse transforms (Tabachnick and Fidell 1996) were applied to normalize and/or homogenize the variance of the shoot attribute being tested between treatments. If the marginal distributions were negatively skewed (as was the case for digestible protein), we reflected the variable before applying the appropriate transform (Tabachnick and Fidell 1996). To reflect the variable, we took the largest value in the distribution and added 1 to it to form a constant; a new variable was then created by subtracting each value from this constant (Tabachnick and Fidell 1996).

Homogeneity of variances were tested using a Levene's test (Milliken and Johnson 1984); a Kolmogorov-Smirnov test (Zar 1984) was used to test for normality. Tukey's HSD test (Zar 1984) was used for post-hoc comparisons for ANOVA's. We used a z test (Zar 1984) to analyze the differences in the proportions of willows bearing predominantly green leaves on specific dates in the falls of 1996 and 1997. We also used a z test to analyze 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

#### Shoot morphology

Willows brushed during the summer of 1996 had longer and heavier shoots with thicker basal diameters, but thinner shoot tips than unbrushed willows in the first winter after brushing (Table 1.1). Willows brushed during the summer of 1997 also had longer, heavier and thicker shoots with thinner tip diameters than unbrushed willows in the first post-treatment winter (Table 1.2). In the second winter following brushing, willows brushed in 1996 continued to have shoots that were longer, heavier and thicker with

Table 1.1. Comparison of morphological and chemical attributes of shoots from 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 percent of dry matter.

Shoot Attribute	Brus	hed	Unbrus	shed		
	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 <sup>†</sup>	82.3	3.6	96.1	4.2	6.3	0.019
Digestible Energy (kcal/g)	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

+ Content of tannin is the square of the diameter (in mm) of the precipitation ring (see text).

Table 1.2. Comparison of morphological and chemical attributes of shoots of Scouler's willow brushed in June or July of 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 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.

Shoot Attribute		Bru	shed	Unbru			
	1 Ju	ine	1 Jı	ıly			
	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 Diam. (mm)	4.1	0.1	2.8	0.1	2.2	0.1	128.8
Tip Diam. (mm)	1.3 <sup><i>a</i></sup>	0.04	1.2"	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 <sup>b</sup>	4.8	80.8 <sup>b</sup>	6.8	130.7	10.2	44.3
Digestible Energy (kcal/g)	2.821	0.009	3.168	0.052	3.254	0.105	39.4
Digestible Protein (%DM)	1.37 <sup>c</sup>	0.57	2.78	0.25	1.74 <sup>c</sup>	0.58	20.5

thinner tips than unbrushed willows (Table 1.3). Although the shoot morphology of brushed and unbrushed plants differed in the first 2 winters after brushing, the magnitude of difference in shoot morphology between brushed and unbrushed plants depended on the timing of brushing (Fig. 1.1 and Table 1.3). In the year following brushing, willows brushed earliest in the growing season produced the longest shoots as indicated by data collected 6 weeks following brushing (Fig. 1.1; 1996:  $F_{1,58} = 180.67$ ; P < 0.001; 1997:  $F_{2.90} = 252.20$ ; P < 0.001). Measurements taken from dormant shoots in the winter following the 1997 brushing treatments showed similar trends: willows brushed earliest in the previous growing season had the largest shoots in winter (Table 1.2). Following a full season of post-treatment growth, willows brushed earliest in the summer of 1996 no longer had the largest browse shoots in the second winter after brushing. Instead, willows brushed later in the 1996 season had larger shoots in the winter of 1997 (Table 1.3).

#### Shoot Chemistry

Lignin, tannin, digestible energy and digestible protein content were lower in the shoots of brushed when compared to unbrushed willows in the first winter after brushing in 1996 (Table 1.1). 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 1.2). 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 July 1997 had shoots with

**Table 1.3.** Comparison of morphological and chemical attributes of shoots of Scouler's willow brushed in June, July or September 1996, measured 2 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.

Shoot Attribute	Brushed							Unbrushed	
	14 Ju	une	30 July		15 Sep				
	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 Diam. (mm)	2.7 <sup><i>a</i></sup>	0.2	4.5	0.2	6.0	0.2	2.5 <sup><i>a</i></sup>	0.1	112.5
Tip Diam. (mm)	1.4 <sup><i>a</i></sup>	0.1	1.5 <sup>a</sup>	0.1	1.6 <sup>b</sup>	0.03	1.7 <sup>b</sup>	0.1	6.2
Lignin (%DM)	0.15"	0.01	0.13 <sup>b</sup>	0.003	0.13 <sup>b</sup>	0.003	0.15 <sup><i>a</i></sup>	0.003	12.2

## Table 1.3 (continued)

Shoot Attribute		Unbrushed							
	14 June		30 July		15 Sep				
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	F
Tannin Content	92.8	2.4	80.4 <sup><i>a</i></sup>	2,5	78.3 <sup><i>a</i></sup>	2.8	107.1	4.1	19.3
Digestible Energy (kcal/g)	2.962	0.035	2.796"	0.030	2.726 <sup>a</sup>	0.028	3.178	0.033	40.5
Digestible Protein (%DM)	1.87 <sup>ab</sup>	1.36	0.68 <sup>c</sup>	0.10	0.10 <sup>bc</sup>	0.34	2.00 <sup><i>a</i></sup>	0.32	5.5



Fig. 1.1. Comparison of the mean length of compensatory shoots 6 weeks following brushing, for willows mechanically brushed at different times in the 1996 and 1997 growing seasons. n = 31 for June and July 1997 brushing treatments; n = 30 for all other treatments. Willows brushed in September did not grow until the following growing season. Error bars indicate 1 SE.
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 1.2)

In the second winter after brushing, the shoots of plants brushed at different times during 1996 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 1.3). Shoots produced following July and September brushing treatments had significantly lower concentrations of lignin and digestible protein than the shoots of unbrushed willows in the second winter after brushing. There were, however, no significant differences between shoots from the June-brushing and unbrushed willows with respect to lignin and digestible protein (Table 1.3).

# Leaf Senescence

A higher proportion of plants brushed during the 1996 treatment year had greener, younger leaves than the unbrushed controls on 8 October, in the first fall after brushing (Fig. 1.2). Similarly, a higher proportion of plants brushed during the 1997 treatment year had greener leaves than unbrushed willows from 19 September through 10 October in the first post-treatment year (Table 1.4). Brushing treatments applied later in the growing season, during both years, retained the highest proportion of plants with predominantly green leaves in the first October following brushing (Table 1.4). Although brushing treatments applied later in the 1997 treatment year had increasingly higher proportions of plants with 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



**Fig. 1.2.** Proportion of Scouler's willow within each brushing treatment bearing predominantly green leaves on 8 October 1996. Error bars represent 1 SE. Because all willows in the 30 July treatment retained predominantly green leaves, there is no SE associated with this proportion.

Table 1.4. Proportion of Scouler's willow in each brushing treatment, in the 1996 and 1997treatment years, bearing predominantly green leaves during fall 1997. Proportions sharingcommon superscripts are not significantly different from each other.

Measurement	Date of Brushing										
Date		1	997			1996					
	1 June	1 July	July 1 Aug Co		14 June	30 July	15 Sep	Control			
	<i>n</i> = 32	<i>n</i> = 33	n = 20	<i>n</i> = 32	<i>n</i> = 15	<i>n</i> = 30	<i>n</i> = 30	<i>n</i> = 18			
5 Sep	1.00 <sup>a</sup>	1.00 <sup>a</sup>	1.00 <sup>a</sup>	0. <b>94</b> <sup>a</sup>	1.00 <sup>x</sup>	1.00 <sup>r</sup>	1.00 <sup>r</sup>	0.67			
12 Sep	1.00 <sup><i>a</i></sup>	1.00 <sup>a</sup>	1.00 <sup>ab</sup>	0.91 <sup>b</sup>	0.97 <sup>xy</sup>	1.00 <sup>r</sup>	0.87 <sup>.v</sup>	0.43			
19 Sep	0.91 <sup><i>a</i></sup>	1.00 <sup>6</sup>	1.00 <sup>ab</sup>	0.75	0.57	0.93 <sup>x</sup>	0.83 <sup>x</sup>	0.30			
28 Sep	0.91 <sup><i>a</i></sup>	1.00 <sup>b</sup>	1.00 <sup>ab</sup>	0.59	0.37 <sup>x</sup>	0.70 <sup>v</sup>	0.60 <sup>v</sup>	0.23 <sup>x</sup>			
3 Oct	0.82	0.97ª	1.00 <sup>a</sup>	0.44	0.23 <sup>x</sup>	0.53 <sup>v</sup>	0.57 <sup>y</sup>	0.20 <sup>r</sup>			
10 Oct	0.50	0.91 <sup>a</sup>	1.00 <sup>a</sup>	0.18	0.07 <sup>x</sup>	0.30 <sup>v</sup>	0.33 <sup>y</sup>	0.03 <sup>.r</sup>			
17 Oct	0.32 <sup>a</sup>	0.88	1.00	0.19 <sup>a</sup>	0.03 <sup>x</sup>	0. <b>2</b> 3 <sup>ν</sup>	0.33 <sup>y</sup>	0.03 <sup>x</sup>			

from 5 September through 10 October (Table 1.4). Plants brushed in July and August 1997, however, did show signs of delayed leaf senescence when compared to June brushing treatments from 3 October through 10 October (Table 1.4).

In the second fall after treatment, brushed plants displayed delays in leaf senescence longer than unbrushed plants from 5 to 19 September 1997 and plants brushed in July and September displayed delays in leaf senescence longer than plants brushed in June (measured on 19 September 1997; Table 1.4). In the second fall after brushing, willows brushed in July and September of 1996 displayed delays in 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 Junebrushed and control willows (Table 1.4).

# Leaf Flush

The timing of mechanical brushing affected patterns of leaf flush in the spring following treatment as evidenced by a delay in leaf flushing when brushing was performed late in the previous growing season (Table 1.5). In contrast, there was no effect on spring-leaf flush when brushing was carried out earlier in the year (Table 1.5). On 14 May 1997, willows brushed during the previous September had a smaller proportion of plants that displayed a break in dormancy than unbrushed controls or plants brushed earlier in the year. This late break in dormancy for September-brushed plants was different from all other brushing treatments and was apparent on 14 May ( $\hat{p} = 0.6, z$ = -4.472, P < 0.001), 17 May ( $\hat{p} = 0.7, z = -3.586, P < 0.001$ ), and 20 May 1997 ( $\hat{p} =$ 

Table 1.5. Proportion of willows in each of the 1996 brushingtreatments flushing new leaves as observed on 4 different days in thespring of 1997. Proportions sharing a common superscript are notsignificantly different from each other.

Proportion	Date of Brushing									
calculated on	14 June	30 July	15 Sep	Controls						
	<i>n</i> = 15	n = 30	<i>n</i> = 30	<i>n</i> = 17						
11 May	0.13 <sup><i>a</i></sup>	0.13 <sup><i>a</i></sup>	$0.00^{a}$	$0.00^{a}$						
14 May	1.00 <sup><i>a</i></sup>	1.00 <sup><i>a</i></sup>	0.20	1.00 <sup><i>a</i></sup>						
17 <b>Ma</b> y	1.00 <sup><i>a</i></sup>	1.00 <sup><i>a</i></sup>	0.40	1.00 <sup><i>a</i></sup>						
20 May	1.00 <sup><i>a</i></sup>	1.00 <sup><i>a</i></sup>	0.80	$1.00^{a}$						

0.9, z = -1.826, P < 0.034). No other plants from any other brushing treatments displayed significant differences in the timing of leaf flush due to brushing time. During the spring of 1996 willows on this site flushed leaves between 21 May and 25 May.

## Age Regressions

Based on our examination of disk annuli taken from plants brushed during the summer of 1996, we determined that the average age of willows in our study was  $7.3 \pm 1.21$  years (range: 4 to 9 years). The age of willows in the summer of 1996 did not predict the length of 6-week compensatory growth following brushing for the 14 June 1996 or 30 July 1996 brushing treatments (all  $P \ge 0.069$ ). In addition, age did not predict any morphological or chemical attributes of shoots from these brushing treatments in either the first or second winter following brushing (all  $P \ge 0.135$ ).

# Discussion

### Shoot morphology

Brushing affected the morphology of Scouler's willow shoots in the first 2 winters following brushing. Although we did not measure the effect of brushing time on the production of overall above-ground biomass, the most obvious effect of mechanical brushing was a complete lack of available browse immediately following treatment. The duration of this effect, when measured in terms of compensatory shoot size, appeared to depend on when brushing occurred within the growing season. Willows brushed in June produced compensatory shoots that averaged 38 cm in length by the sixth week following brushing and 50 (1996) to 54 (1997) cm by the onset of dormancy. In the first winter after brushing, the shoots of willows brushed in early July averaged 26 cm long while plants from later treatments produced relatively smaller (<10 cm), thinner shoots that were not visible above December snow packs. Therefore, depending on the timing of brushing, willows may produce shoots that are significantly longer than the average shoot size of unbrushed willows (9 cm; 1997 to 13 cm; 1996), or may have shoots too short to protrude above mid-winter snows to be accessible to moose in the first winter after brushing.

All brushed willows, regardless of when they were brushed, produced shoots in the second growing season after brushing that were larger (as measured in the second winter after brushing) than shoots produced by unbrushed willows during the same growing season. Plants brushed earliest in the previous year, however, produced the smallest of shoots from all brushing treatments; those brushed latest in the previous year produced increasingly larger shoots (>80 cm long). Similar responses to the timing of cutting occur in other early-successional trees and shrubs (DeBell and Alford 1972; Kays and Canham 1991) and are related to the concentration of root reserves at the time of damage and the number of remaining growing points to which those reserves can be allocated (Stafford 1990; Kays and Canham 1991). Changes in active meristem numbers and root reserves even appear to outweigh any changes in post-damage plant response due to the age at time of brushing (Kays and Canham 1991). Indeed, willow age at time of brushing (4 to 9 years) was not related to any of the morphological or chemical attributes altered by the timing of brushing in the present study.

Plants damaged later in the growing season have relatively higher concentrations of root reserves through fall and winter when compared to plants damaged earlier in the year (Gregory and Wargo 1986). Such plants will have less time to compensate for damage before dormancy onset, and will have fewer growing points in the following spring to which those resources may be allocated (Sennerby-Forsse and Zsuffa 1995). The allocation of resources to relatively few growing points leads to the production of

shoots in the year following damage that are larger than those of earlier-brushed and unbrushed plants (Harrington 1984; Kays and Canham 1991). Plants brushed early in the growing season, on the other hand, tend to exhaust remaining reserves in the treatment year attempting to compensate for earlier damage (Kays and Canham 1991), which may help explain differences in willow compensatory responses between the first and second post-treatment growing season.

As shoot length, mass and basal diameter increased in shoots following brushing, the diameter of the shoot tip (apical bud) decreased. Because large shoots have proportionately more woody cortex to bud material (Danell and Bergström 1985), the small shoot tips of large shoots may result from an allocation of plant resources to shoot cortex rather than meristem. This difference in morphology may be advantageous to moose browsing large shoots arising from brushed plants because many of the chemical deterrents produced by plants are concentrated in buds (Clausen et al. 1986; Herms and Mattson 1992) and a smaller bud at the shoot tip may have relatively smaller concentrations of these chemicals. Although plants may produce thinner apical buds due to the reallocation of resources to stem materials, the significance of a thinner apical bud for moose remains unclear.

Shoot size is one of the most important determinants of food selection by moose (Danell et al. 1985*b*; Risenhoover 1987*a*) because it influences bite size and consequently affects intake rates (Gross et al. 1993; Danell et al. 1994; Shipley et al. 1994). Cropping smaller bites requires more frequent interruptions of chewing to refill the mouth than consuming larger bites and requires moose to spend more time and energy on cropping than processing their bites (Shipley and Spalinger 1992; Gross et al. 1993). Minimizing cropping time by selecting larger shoots may allow moose to maximize energy intake and

fitness while minimizing the amount of time spent foraging away from mature forest cover. Reducing time spent away from cover is important to moose in areas where the threat from predators is high; minimizing the amount of time required minimizes the vulnerability to predation (Weixelman et al. 1998).

Reducing the time required to prehend forage may help explain why moose typically choose the largest stems (Danell et al. 1985b; Schwartz 1992; Bowyer and Bowyer 1997) with the thickest basal diameters available (Haukioja and Lehtila 1992; Bowyer and Bowyer 1997) and select large compensatory shoots, such as lower stump or basal shoots originating from mechanically-damaged trees (Wolff 1978; Danell et al. 1985b; Bergström and Danell 1987a; Bergström and Hjeljord 1987; Bevins 1989; Suter 1993). The prehension of large bites appears to be of such overriding importance that moose will select larger shoots even if such shoots are relatively high in fibre and low in protein (Jia et al. 1997). Moose in north-central British Columbia even browse past current-annual shoots into less digestible 2- and 3-year old stem materials when browsing the smaller shoots of unbrushed willows (see this study: Chapter 2), presumably in an effort to maintain larger bite diameters and higher intake rates (Shipley et al. 1994). Compromises between larger bite sizes and reductions in the protein and energy digestibility of large shoots become key to understanding how the overall nutritional value of browse for moose may change following brushing at different times during the growing season.

# Shoot Chemistry

Although the energy and protein content of shoots of unbrushed willows in this study are comparable to willows in other studies (Wolfe et al. 1983; Eastman 1984; Bergström and Danell 1987*b*; Risenhoover 1987*b*), 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 when compared to 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 tannin and lignin content of these shoots and increases in leaf senescence were considered. Estimating the overall nutritional value of large shoots with reduced digestible energy and digestible protein content from plants brushed at other times of the year requires considering changes to a larger suite of plant attributes altered by mechanical brushing.

Digestible energy and digestible protein are frequently reduced in larger shoots due to the high proportion of digestibility reducing structural materials such as cellulose contained within the shoot cortex (Eastman 1984). Reductions in digestible energy and digestible protein as well as mineral content are also known to occur with increasing shoot size in species such as birch, black cottonwood (*Populus trichocarpa*) and red alder (*Alnus rubra*). This "dilution of nutrients" (*sensu* Herms and Mattson 1992) appears to be a function of the ratio of bark and bud material where most nutrients are concentrated, to the woody, fibrous cortex (Danell and Huss-Danell 1985; Radwan and DeBell 1988; Schwartz 1992) and may exist not only in shoots of varying sizes but between different portions of the same shoot. For example, digestibility decreased in Scouler's willow (Appendix A) as well as other woody deciduous browse plants (Bailey 1967; Haveraaen and Hjeljord 1981; Palo et al. 1992; Shipley and Spalinger 1995) from the tip to the base of the shoot where there is relatively more cortex to bark and bud material. This change

in bark-to-cortex ratio highlights nutritional trade-offs often faced by moose when selecting for shoots of a larger size and is likely responsible, not only for decreased energy and protein digestibility, but for the reductions in tannin and lignin content we found in the shoots of brushed willows.

Concentrations of phenolic compounds such as lignin (Hanley 1982; Risenhoover 1987*b*; Nellemann 1990) and tannin (Singer et al. 1994) are known to be important factors influencing browse selection in ruminants and are suspected to influence selection more than digestible energy (Bryant et al. 1983; Coley et al. 1985; Robbins et al. 1987*a*). Indeed, the selection of browse by most vertebrate herbivores is determined more by the nature and quantity of phenolic compounds than overall energy and protein content (Chapin 1980). Shipley and Spalinger (1992) report that tannin and lignin are at least as important as other chemical or qualitative properties of shoots, and even the spatial distribution of browse. Such characteristics appear to determine the handling time of winter food items and can significantly affect the energy budget of the animal (Spalinger et al. 1986).

The concentration of lignin in the shoots of unbrushed willows was similar to the concentration of lignin reported for other species of willow (Oldemeyer et al. 1977; Eastman 1984; Bryant et al. 1985; Risenhoover 1987b; Schwartz et al. 1988b). Our results, however, indicate that mechanical brushing causes willows to produce shoots significantly lower in lignin than levels found in the shoots 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 lower or equal in lignin content to earlier-brushed plants when analyzed in both the first and second winters following brushing.

Brushing later in the growing season (i.e., 1 July versus 1 June) reduces the effective length of the growing season and consequently the amount of time required by plants to compensate for damages. This truncation of the growing season decreases the plants ability to form mature shoots and deposit structural materials such as lignin before the onset of dormancy (Danell and Bergström 1985; Raitio et al. 1994). Such reductions in lignin may be important to moose because lignin specifically determines plant fibrosity and is inversely related to the relative breakdown rate of plant material (Spalinger et al. 1986). Shoots with lower lignin may be more easily handled and processed by moose through a reduction of the chewing effort and may allow for higher cropping rates and increased intake (Gross et al. 1993).

Our index of tannin derived from a modified assay was used for comparative purposes and cannot be directly compared with values obtained by others using Hagerman's (1987) original technique. Despite the differences in methodology used to obtain data on changes in tannin content, our results agree with the findings of Dutoit et al. (1990), Suter (1993) and Singer et al. (1994) who reported overall reductions in tannin content associated with increases in shoot size following various forms of mechanical damage. For example, Suter (1993) demonstrated that large compensatory shoots originating from the stumps of willows contained less tannin content than the smaller crown shoots of plants on the same site.

Because the production of phenolic compounds such as tannins and lignin represent a competition with other cellular processes for common metabolic substrates (Herms and Mattson 1992), reductions in these compounds following plant damage and

rapid compensatory growth can be expected. Our results indicate that although tannin content was always lower in the winter shoots of brushed compared to unbrushed plants, tannin content was not always different between the shoots of willows brushed at different times. Such responses suggest that changes in tannin content may be less affected by the timing of brushing than by brushing itself.

Tannins, unlike lignin, may not affect handling time or intake rates but may inhibit animal performance through the chemical inhibition of rumen microbes (Risenhoover et al. 1985). Tannins can also reduce amino acid and iron bioavailability (Choo et al. 1981) and may work as toxins rather than digestion inhibitors (Mehansho et al. 1987). Moose possess salivary tannin-binding proteins to help neutralize the effects of dietary tannins (Hagerman and Robbins 1993; Juntheikki 1996). Despite this and the fact that winter browses contain relatively small amounts of tannins (Hanley et al. 1982), moose avoid browsing winter foods higher in tannin content (Bryant and Kuropat 1980; Bryant et al. 1983; Suter 1993; Singer et al. 1994).

Even the small amounts of tannins found in dormant browses tend to quickly bind all tannin-binding proteins in moose saliva (Junetheikki 1996). Although the metabolic costs associated with the production of these tannin-binding proteins are poorly understood, reductions in protein turnover are less costly. Additionally, because moose are not able to bind tannins from all winter browses equally well (i.e. *Salix pentandra*; Junetheikki 1996), the ingestion of unbound tannins could be costly for moose in terms of reduced rumen microbe functioning (Risenhoover et al. 1985) or other deleterious effects. If, however, the costs associated with neutralizing dietary tannins are insignificant compared to potential gains in energy and protein from browsing materials higher in tannins, but also higher in digestible energy and protein, the importance of lower tannin

content in the shoots of brushed plants may be inconsequential (Hagerman and Robbins 1993). In addition, winter browse is often much lower in absolute tannin content than summer forages (Hagerman and Robbins 1993). Consequently, the 15 to 60 percent reductions (depending on when willows were brushed) in tannin found in the shoots of willow in this study may be offset by the higher digestible energy of these shoots.

Although useful for understanding the effect of brushing on shoot tannin content, our index does not provide a quantitative measure of tannin that could be used to estimate the effect of decreased tannin content on dry matter digestibility, iron or amino acid bioavailability. Even in the event that such quantitative measures had been made and used to calculate reductions in dry matter digestibility for instance (Hanley et al. 1992), the biological significance of such measurements for moose would be suspect because not all tannins (as measured here with BSA) have physiological consequences for moose (Hagerman and Robbins 1993; Juntheikki 1996). Furthermore other phenolic compounds such as salicylic acids (SA; Raskin 1992) may be more important to the winter foraging ecology of herbivores than tannic acids (Danell et al. 1985*b*); just how concentrations of such compounds are altered by mechanical brushing or how moose respond to such changes are not presently understood.

The majority of our results agree with the findings of others and indicate decreases in shoot chemical concentrations, digestibility and a number of mineral elements (Appendix B) associated with increases in shoot size (Hjeljord et al. 1982; Owen-Smith and Novelli 1982; Vivås and Sæther 1987; Sæther et al. 1989; Haukioja and Lehtila 1992). Some of our results, however, contradict this relationship between shoot morphology and chemistry. In the first winter after brushing, willows brushed on 1 July showed high 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 were likely a result of damage-induced juvenile reversion and the relative age of the regenerating plants as they entered plant quiescence. The shoots of these plants appear to be effectively younger than shoots of earlier damaged or undamaged plants and appeared to subscribe to a lammas-form of growth. Lammas shoots, which are produced by the bursting and elongation of current-year terminal buds late in the growing season, (Kramer and Kozlowski 1979), are known to be relatively high in succulence and digestibility during the fall when compared with more mature shoots (Dietz 1971). Such shoots remain metabolically active, continue shoot production and elongation and continue to sequester nutrients from leaves late into the fall well past older plants (Kramer and Kozlowski 1979). Shoots growing from plants brushed later in the growing season, therefore, may not have had the time required to mature and deposit structural materials such as lignin or transport photosynthates to roots before fall frosts (Danell and Bergström 1985; Raitio et al. 1994), in contrast to plants brushed earlier in the year. Rapid freezing and the resultant trapping of nutrients in these pre-dormant lateseason shoots may help explain some of the chemical anomalies we detected when analyzing the dormant shoots of July-brushed plants.

### Leaf Senescence

Brushing resulted in a delay in leaf senescence as long as or longer than unbrushed plants in both the first and second falls after brushing. Plants brushed latest in the year showed a delay in leaf senescence in both the first and second post-treatment

falls as long as or longer than plants brushed earlier in the growing season. Such delays in leaf senescence following brushing, like patterns of extended shoot growth, are strongly influenced by chemical and hormonal changes brought about in the plant from cutting (Kramer and Kozlowski 1979). Changes in leaf senescence have been attributed to a richer supply of nutrients being supplied to a relatively smaller number of extant shoots (Millington 1963; Danell et al. 1997) and plant rejuvenation. Such changes may help to compensate for losses in translocating resources from shoots to roots due to earlier damage, but generally last only as long as there is recurrent damage to the plant or until the root-shoot ratio has been re-established (Willard and McKell 1978).

Because green, leafy forages are an important component of many ungulate diets (Blair et al. 1980; Hanley 1982; Schwartz et al. 1988*a*; Danell et al. 1994), changes in the patterns of leaf senescence following brushing may have important consequences for moose. The production and retention of greener, younger secondary leaves on the shoots of recently-brushed plants could be important for moose during the fall when tannins and lignin begin to concentrate in bark and senescing leaves (Palo 1984; Herms and Mattson 1992) and nutritious foods are generally reduced (Blair et al. 1980). Moose, as well as black-tailed deer (*Odocoileus hemionus columbianus*), will selectively forage on darker, greener foliage over lighter green or yellowing foliage (Cowan 1945; Bergerud and Manuel 1968), presumably because greener younger leaves are typically higher in nutrients than yellowing or older senescing leaves (Kramer and Kozlowski 1979; Chapin 1980).

Leaves are higher in nutritive quality than woody stems (Eastman 1984). Consequently, moose avoid browsing shoots as long as fall leaves persist (Regelin et al. 1987). Moose will even select and forage on leaf litter when twigs and other forages are

available in the fall landscape (Renecker and Hudson 1986), demonstrating the nutritional importance of leaves in the fall diet of moose. Because brushing from mid to latesummer delays leaf senescence in the first 2 falls after brushing, such treatments may provide moose with leafy materials late into the fall and help to enhance the quality of plants for moose on late fall and early winter ranges.

## Leaf Flush

Although plants cut during the winter are known to flush leaves early in the spring (Kindschy 1989), our results suggest that brushing plants in the early to mid-summer has no effect on leaf emergence in the first post-treatment spring. Fall brushing, however, may cause a delay in willows leaf emergence in the spring following brushing. Such delays can occur if stem and leaf material is removed before it is able to complete the export of nutrients and other factors, such as hormones, necessary for spring growth from above to below-ground structures in the late fall (Larson 1978; Tuomi et al. 1989). Delays in spring leaf flush may protect previously damaged plants from early spring frosts, but may also reduce the availability of leaves for moose foraging in the early spring.

Although willows brushed in July did not delay leaf flush and, overall, produced browse of better quality for moose in the first 2 winters following brushing, we did not measure the selection of such plants over others brushed during June, August, September or unbrushed controls by moose. The study site was selected in an area where browsing by moose was minimal (<5%); this was done to reduce the confounding effects of browsing on plant responses to brushing. Consequently, we were unable to determine the selection of shoots from plants brushed at different times by moose. We did, however, observe some browsing by deer (*Odocoileus* spp.) in late August of 1997; browsing was

directed predominantly to willows brushed in June 1997 (determined during winter collections; Appendix C).

Because the removal of a small percentage of shoots from a plant has a relatively small impact on overall plant response (Danell et al. 1994), we do not believe that browsing on experimental plants altered our results. Furthermore, browse damage by deer was unlikely to affect our results because deer browsed plants late in the final growing season of the study, beyond the time that willows were able to respond to damage with compensatory growth. Although the use of exclosures may have helped to reduce browsing on study plants, the percentages of shoots removed by browsing likely had no effect on our overall findings.

Although we do not present data on the relative use of shoots from brushed and unbrushed willows, moose do heavily utilize browse plants in the years immediately following mechanical brushing (Hjeljord and Grønvold 1988) often times browsing up to 100% of post-brushing current shoot growth (R.V. Rea, personal observations). Such selectivity for re-growth following mechanical brushing is also demonstrated by other ruminants such as cattle (*Bos taurus*) and deer (Powell and Box 1966; Siebert et al. 1980), presumably due to the increases in plant palatability, availability or accessibility associated with cutting; increases that, as the present work outlines, can be influenced by the timing of mechanical brushing.

#### Conclusions

Mechanical brushing significantly reduces the availability of deciduous biomass for herbivores such as moose. Although some vegetation managers retain unbrushed wildlife strips (see this study; Chapter 2) in areas being mechanically brushed in an effort to mitigate reductions in available biomass, other managers do not subscribe to such strategies. In areas where wildlife strips are not retained then, brushing operations should be performed in July to ensure a supply of nutritious browse for moose using these areas in winter.

Willows brushed in July produced shoots that were of higher value for moose in the first 2 years after brushing. Although brushing in late July did not allow willows to compensate sufficiently for shoots to be available in the first winter after brushing, the shoots of willows brushed in early July were available above first year snows and more nutritious than the shoots of earlier-brushed willows. Brushing in early July also corresponds well with the time suggested by vegetation managers to brush competing vegetation (i.e., willows) growing in conifer plantations because brushing at this time more effectively reduces the plants ability to compete for resources (Kays and Canham 1991).

Scouler's willow tended to show morphological responses to the timing of brushing that are consistent with the response of other browse plants to time of cutting (Kays and Canham 1991). How other important browse plants specifically respond to brushing time, however, should be investigated more thoroughly because plant response can be influenced by factors such as environment (site; see this study; Chapter 2), species genetics, life history traits and plant morphology (Whitham et al. 1991; Danell and Bergström, 1989; Borkowska and Konopko, 1994). Although the timing of brushing may affect some browse plants for no longer than 2 years after damage (Kays and Canham 1991), the long-term effects of brushing time on willows appears to last much longer (see this study; Chapter 2).

Mechanical brush control is practised on regenerating conifer plantations, utility rights-of-way, rail and/or roadsides as well as rangelands and unproductive forest areas

where vegetation control or browse production is desired. Although it has been a longheld belief that stimulating vegetative growth through cutting results in better browse for herbivores (Gysel 1957; Ferguson and Basile 1966; Roberts 1986), recent studies show that this is not invariably true (Bryant et al 1985; this study). Our results indicate that significant changes in the nutritional value of willow may occur for at least 2 winters post-treatment, depending on the timing of brushing. Although brushing time may affect different plant species to different degrees, determining the response of willows to brushing time, in combination with understanding the response of other species to time of cutting, may help delineate a more generalized pattern of plant response to damage. Understanding these patterns can then help to determine the consequences that such responses may have on the overall nutritional value of these plants for moose.

# CHAPTER 2. CHANGES IN THE NUTRITIONAL VALUE OF SCOULER'S WILLOW (Salix scouleriana) FOLLOWING MECHANICAL BRUSHING: IMPLICATIONS FOR MOOSE (Alces alces).

## Abstract

We examined the effects of mechanical brushing on the nutritional value of Scouler's willow (Salix scouleriana) browse for moose (Alces alces) for 2 to 5 winters after brushing in relation to willows growing in unbrushed strips of regenerating vegetation retained for wildlife food and cover. We also examined the effects of the previous year's clipping and browsing on browse quality and compared how moose utilized willows growing in brushed and unbrushed areas in the third winter after brushing. The nutritional value of willows varied among sites, but was altered by brushing for at least 5 winters post-brushing. The current annual shoots of brushed willows tended to be larger, although lower in digestible protein and digestible energy, than shoots of unbrushed willows for at least 5 years after brushing. Shoots of brushed willows were also lower in tannin and lignin content than the shoots of unbrushed plants for 2 and 3 years post-brushing, respectively. Furthermore, brushed willows displayed a delay in leaf senescence for up to 4 years post-brushing. The shoots produced by willows were often unaffected by the previous winter's clipping/browsing intensity, but increased in size when measured in the third to fifth winter after brushing. Shoot size decreased with an increase in the previous winter's clipping/browsing intensity when measured in the second winter after brushing. The tannin and lignin content of shoots increased with an increase in the previous winter's clipping/browsing in the second winter after shoot removals. With an increase in the previous winter's clipping/browsing intensity, digestible energy and protein decreased in the third to fifth and fifth winter after brushing,

respectively. The average shoot diameter at the point of browsing did not differ between the shoots of brushed and unbrushed willows; the shoots of unbrushed willows were browsed past current annual shoots and into older stem materials significantly more when compared to shoots from brushed willows.

#### Introduction

Releasing conifers from the competitive effects of deciduous trees and shrubs through the use of herbicides or by motor/manual removal (i.e., mechanical brushing) leads to changes in forest stands that can reduce browse biomass and cover for wildlife (Goodrum and Reid 1956; Conard 1984; Lautenschlager 1993). To reduce these impacts, resource managers occasionally retain strips of regenerating forest within stands being managed for conifer growth that allow for some of the needs of wildlife (hereafter termed "wildlife strips"; Gysel 1957; Santillo 1994). Because the application of systemic herbicides such as glyphosate (Roundup<sup>®</sup>, Monsanto Chemical Co. St. Louis, Mo.) can kill deciduous plants and reduce browse availability for as many as 9 years following treatment (Hjeljord 1994), the retention of wildlife strips is particularly important for ensuring a continued browse supply for animals such as moose wintering in regenerating forest stands (Santillo 1994).

Although mechanical brushing does not affect the production of browse as long as herbicides (Hjeljord and Grønvold 1988), it does reduce available biomass in the years immediately after brushing (Härkönen 1998) and can alter the nutritional value of regenerating browse for moose (see Chapter 1). Consequently, the retention of wildlife strips also provides forage in areas where brush is being reduced mechanically, as well as chemically. These wildlife strips, however, also contain commercially important crop trees and are, therefore, eventually brushed once other deciduous shrubs and trees within

the site begin to recover from brushing. The amount of time required for plants to recover from brushing and provide suitable post-brushing habitat, at least in terms of browse quality for moose, however, is largely unknown.

Brushing is known to alter the nutritional value of current-annual-growth shoots (measured from the previous year's growth scar to the shoot tip and hereafter termed "shoots") of willows in the first and often second year after brushing. For example, brushing late in the growing season generally caused willow saplings to produce shoots that were larger and lower in tannin content, lignin and digestibility than the shoots of unbrushed willows in the first 2 winters post brushing (see Chapter 1). Willows brushed in June, however, had shoots that were not significantly different in basal diameter, lignin and digestible protein content than the shoots of unbrushed willows in the second winter following brushing, even though such differences existed during the previous winter.

Feltleaf willows (*Salix alexensis*) cut or browsed in winter are able to compensate for damage, re-establish their root-to-shoot ratios and reassume a pre-damage form of growth in as little as 3 years post-cutting (Bryant et al. 1985). Although the shoots of willows may even begin to reassume attributes similar to those of uncut plants in as little as 2 years following damage, (see Chapter 1), the length of time required by plants brushed during the growing season to fully compensate for damage remains unclear. Because the amount of time required for plants to fully compensate for damage is highly dependent on the intensity of damage (Danell and Bergström 1989; Whitham et al. 1991), compensating for the complete removal of above-ground biomass following summer brushing is likely to require several years of post-damage compensatory growth (Chapin 1980).

Cutting and browsing willows in winter leads to increases in the concentration of tannins as well as increases in proteins, carbohydrates, lipids, lignin and mineral elements such as phosphorus for several years following damage (Bryant et al., 1985). Increases in nitrogen, magnesium, potassium and phosphorus occur following summer clipping of the sedge *Eriophorium vaginutum* (Ouellet et al. 1994). Heavy browsing and/or pruning also stimulates browse plants such as willow and birch (*Betula* spp.) to produce larger shoots that are higher in fibre content (Wolff 1978; Borkowska and Konopko 1994; Danell et al. 1994), which are often lower in chemical deterrents to browsing, such as tannins (Danell and Bergström 1989; Dutoit et al. 1990; Singer et al. 1994). Other forms of severe mechanical damage can likewise alter plant morphology and chemistry (Danell et al. 1987; Nellemann 1990; Stephenson 1995) as well as the phenology of plant leafing in the years following injury (see Chapter 1; Danell et al. 1985*b*; Kindschy 1989).

Changes in plant physiochemistry following mechanical damage are a result of changes brought about in the plant due to the loss of apical dominance and plant rejuvenation (Bryant et al. 1985). Such changes lead to a reallocation of plant resources from flower and fruit production to compensatory (*sensu* Belsky 1986) vegetative growth. This reallocation leads to changes in the nutritive quality of plant tissues for herbivores (Danell et al. 1985*a*), but only persists until the effects of juvenile reversion subside following compensatory growth and the root-to-shoot ratio rebalances (Millington 1963; Danell et al. 1997).

Moose select browse based on the morphological, chemical and phenological characteristics of plants (Schwartz 1992; Danell et al. 1994), many of which are altered by mechanical brushing (see Chapter 1). The quality of browse for moose is, therefore, likely to be affected by such damage-induced changes until plants have fully

compensated for brushing. Determining how long brushing affects the morphological, chemical and phenological attributes of browse plants may help resource managers determine how long to retain wildlife strips before brushing them and when to schedule management strategies for adjacent forest stands where concerns for the quality of browse for moose exist. Understanding these changes and how long they persist may also help to contrast some of the effects of mechanical brushing with those of herbicide applications.

To evaluate the effects of brushing on the nutritional value of browse and to determine how long such effects last, we selected a plant that is often brushed and is important as browse for moose in winter, Scouler's willow (Roberts 1986; Porter 1990; Weixelman et al. 1998). We determined the effects of brushing on 1) shoot morphology, 2) shoot chemistry, and 3) patterns of leaf senescence in the first 5 years following treatment. Additionally, we determined how moose used the shoots of brushed and unbrushed willows in the third winter following brushing and determined if clipping and/or browsing affected the nutritional value of willows in the year after shoot removal by clipping and/or browsing.

#### Methods

#### The study area

The study area comprised 6 similarly-classified (DeLong et al. 1993) regenerating pine clearcuts ~ 15 to 40 ha, near Vanderhoof, British Columbia, Canada ( $54^{\circ}05$ 'N,  $123^{\circ}55$ 'W; Fig. 2.1). All sites were in the sub-boreal spruce dw3 biogeoclimatic zone characterized by open stands of lodgepole pine with poorly developed shrub and herb layers, and a well-developed moss layer dominated by lichens (Meidinger and Pojar



Fig. 2.1. Location of study sites within the Vanderhoof Forest District. Sites are as follows: • Sackner Pit (B.C. Geographical Map Classification System-Forest district cutblock number: 93J002-001), • Triple Buck (93J002-002), • North Layton (93K019-007), • Sawmill Pit (93K019-030), • Huckleberry Cut (93K019-027), and • Waterlily Lake (93J001-007).

1991). Soils on all sites are clay and/or sandy loam (D. Sommerville, Vanderhoof Forest District, Vanderhoof, B.C., Canada, personal communication). The terrain is flat to rolling and all sites are between 750 and 800 m.

Three of the sites (North Layton, Three Buck; Sackner Pit) were clear cut 12 to 15 years prior to the initiation of the study and were mechanically brushed throughout the 1993 growing season (June to September). The other 3 sites (Sawmill Pit; Huckleberry Cut; Waterlily Lake) were clear cut 9 to 11 years prior to the beginning of the study and were mechanically brushed throughout the 1995 growing season. Wildlife strips left on the sites brushed in 1993 contained willows ~ 5 m tall at the beginning of this study (winter 1995) while brushed willows on these sites were ~ 2 m tall. Unbrushed plants on the 1995 sites were ~ 4 m tall while brushed plants within these sites were ~ 1 m tall at the beginning of the study. Moose densities in the surrounding area were ~ 0.5 animals per km<sup>2</sup> at the time of the study (D. Heard, Ministry of Environment Lands and Parks, Prince George, B.C., Canada, personal communication).

#### Experimental Design

During the winter of 1995-96, we randomly selected 6 Scouler's willow plants from mechanically-brushed areas within the plantations and 6 willows from the wildlife strips on each of the 3 sites brushed in 1993. We could not select willows from sites brushed in 1995 until the following spring, as brushed plants had not grown sufficiently following treatment to be visible above the snow. We randomly selected willows that were of similar size and form that we had identified to species according to leaf characteristics, shoot morphology and catkin anatomy following Argus (1992).

During the winter of 1995-96 we randomly collected shoots from each of the 6 brushed and unbrushed willows on the 1993 sites. During the winter of 1996-97, we

collected shoots from the 6 brushed and 6 unbrushed willows from each of the 6 (1993 and 1995) sites. To increase our ability to detect differences between brushed and unbrushed plants within and among sites, we increased the sample size of willows from each site to 13 brushed and 13 unbrushed in the spring of 1997. We did this by randomly selecting an additional 7 willows from both brushed areas and wildlife strips. During the winter of 1997-98 we collected shoot samples from all 13 brushed and unbrushed willows from each site.

Each of the original 6 willows within the brushed and unbrushed areas from each site was randomly selected for a clipping treatment. Two of the 6 brushed and unbrushed willows were clipped to remove 33% of current annual shoots; 2 were clipped at 66% and 2 at 100%. Clipping intensities were imposed by clipping every third shoot, leaving every third shoot, and clipping all shoots, for 33, 66, and 100% removal of shoots, respectively.

Following winter clippings, we determined that some of the winter shoots were unavailable for collections due to burial by snow; in addition moose had browsed other shoots after clipping treatments were imposed. Because these factors altered the targeted amount of tissue removal intended for each specific plant, each willow plant was revisited again in the spring of each year and the exact percentage of shoot removal was determined. We determined percent shoot removal by counting all overwintering shoots and classifying them as clipped/browsed or undamaged and then dividing the number of clipped/browsed shoots by the total number of shoots on the plant. Consequently, the level of clipping and browsing was subsequently considered to be a covariate in our analyses.

We collected all shoot samples while plants were dormant, in February of 1996, and December of 1997 and 1998 in sub-zero weather to inhibit post-sampling metabolic activities within the shoot tissues. Collections from each willow were separated in the field into separate plastic freezer bags for (1) tannin analysis and (2) all other analyses. Following collections, bags were sealed and then stored at -20 °C until analyzed. All shoots were weighed and measured for length, basal diameter and tip (apical bud) diameter. When more than 30 shoots were collected from a particular willow, however, we randomly sub-sampled 30 shoots for morphometric measures. Following morphometric measurements, all shoot material from each plant was combined, cut to  $\sim$ 10-cm lengths and dried to a constant mass (±0.1g) at 39 °C in a forced-draft drying oven (Despatch LAD series 2-24-3; Minneapolis, MN.). Dried material was then milled with a Thomas-Wiley mill (Swedesboro, N.J.) and a 0.5-mm sieve screen, then homogenized by hand-mixing. We determined elemental nitrogen (EN), neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL) content, gross energy, digestible protein and digestible energy content using procedures outlined in Chapter 1. The amount of tannins (hereafter referred to as "tannin content") in willow shoots was estimated from an index of tannin that was derived from the use of a radial diffusion technique that we modified from Hagerman (1987; see Chapter 1).

#### Measuring Leaf Senescence

We assessed differences in leaf senescence in fall by estimating the predominant leaf colour of each willow in the brushed and unbrushed areas of each site on given dates, in both the falls of 1996 and 1997. We classified plants according to procedures outlined in Chapter 1. Stage of leaf senescence in the fall of 1996 was determined for 12 brushed and 12 unbrushed willows randomly selected from each site by estimating the

predominant leaf colour of each willow on a single day in mid-fall (8 October 1996) when most deciduous plants were in full fall colours. Stage of senescence in the fall of 1997 was assessed for 13 brushed and 13 unbrushed willows that were randomly selected from each site by estimating the predominant leaf colour of each willow on a weekly basis from 5 September 1997 through 17 October 1997. Frost damage to leaves following the week of 17 October 1997 precluded further classification of stages of leaf senescence on the basis of predominant colour of foliage.

### Browse Survey

To determine how moose utilized the shoots of brushed and unbrushed willows in winter we established a line transect ~ 600 m long in the spring of 1998 through an unbrushed wildlife strip and brushed areas of a block (Huckleberry Cut site) that had been brushed in 1995. We sampled the first 50 brushed and 50 unbrushed willows that we encountered as we moved down the transect that were within 5 m of either side of the transect. For each willow sampled we selected 5 browsed shoots by randomly selecting (using a random number table) a primary, secondary, tertiary, etc., branch until a current years shoot was selected. We then measured the diameter of the shoot at the point of browsing and the basal diameter. According to bark characteristics we then determined whether or not each browsed shoot had been browsed beyond the current annual shoot and into older stem tissues. Measurements taken from shoots were subsequently averaged for each willow.

# Statistical Analyses

To test the effect of brushing on the morphology and chemistry of willow shoots in the third winter post-brushing (the first winter of the study) for the 3 sites brushed in 1993, we used a nested analysis of variance (ANOVA; Zar 1984) with treatment (brushed

or unbrushed) nested within site. Following the first winter of the study, all other morphological and chemical comparisons made between brushed and unbrushed plants, across the 6 sites, were made using a nested analysis of covariance ANCOVA (Zar 1984) with the previous year's percentage of clipping and browsing used as a covariate. ANCOVA analysis was not used during the analysis of the first winter's data, as we did not collect information on the percentage of shoots removed by moose in the year prior to collections. In the nested ANOVA/ANCOVA models we treated site as a random and treatment (brushed or unbrushed) as a fixed effect. When appropriate, square root, inverse or log transforms (Tabachnick and Fidell 1996) were applied to normalize data and/or homogenize the variance of the shoot attribute being tested between treatments. Homogeneity of variances were tested using a Levene's test (Milliken and Johnson 1984). A Kolmogorov-Smirnov test was used to test assumptions of normality (Zar 1984). Tukey's HSD test (Zar 1984) was used for post-hoc comparisons.

A z test (Zar 1984) was used to analyze the differences in the proportions of willows bearing predominantly green leaves on various dates in the fall of 1996 and 1997. We used ANOVA to compare shoot diameters at the point of browsing between shoots from brushed and unbrushed willows. We used a Kruskal-Wallis ANOVA by Ranks test (Kruskal and Wallis 1952) to determine differences in the number of shoots from brushed and unbrushed willows that had been browsed past current annual growth and into older stem materials. All analyses were conducted using Statistica (StatSoft Inc. 1997).

### Shoot Morphology

Mechanical brushing affected the shoot morphology of willows for several years following treatment (Fig. 2.2). Although the length and mass of willow (brushed and unbrushed) shoots varied among sites (Table 2.1), willows responded to mechanical brushing by producing shoots that were longer and heavier than the shoots of unbrushed willows for at least 5 years post-brushing (Fig. 2.2, Table 2.1). The basal diameters of willow shoots also varied among sites (Table 2.1); brushed plants had shoots with thicker basal diameters in the second, third and fifth year following brushing (Fig. 2.2, Table 2.1). Shoot length, mass and basal diameter increased in the shoots of brushed plants, but the tip diameter of these shoots decreased in the second and third year following brushing. In the fifth year following brushing, shoot tips of willows were significantly different among sites (Table 2.1).

With an increase in the percentage of shoots removed during the previous winter, both experimentally (clipping) and by moose (browsing), shoot mass, basal diameter and tip diameter decreased during the following year when analyzed in the second postbrushing winter. An increase in clipping/browsing during the previous winter, however, also led to an increase in shoot length and mass during the following year when analyzed in the third to fifth winters post-brushing (Table 2.1). The previous year's clipping/browsing also caused an increase in basal diameter of the following year's shoots with increased clipping/browsing when analyzed in the third and fifth year postbrushing but had no effect on these attributes in other post-brushing years (Table 2.1).



Fig. 2.2. Comparisons of mean morphological attributes of shoots from brushed and unbrushed willows collected for 2 to 3 winters post-brushing for 1995-brushed sites (Huckleberry Cut, Waterlily Lake, Sawmill Pit) and for 3 to 5 winters post-brushing for 1993-brushed sites.
\* indicates a significant effect of brushing when site effects are considered. Error bars = 1 SE, n is shown above each bar.

**Table 2.1.** *P* values for comparisons between brushed and unbrushed plants for morphological attributes of shoots across all sites by year since brushing. The clipping column indicates the effect of the percentage of shoot removal by clipping/browsing during the previous winter when treated as a covariate in the analyses. Values in parentheses represent slopes for significant effects of the covariate.

Shoot Attribute	Year 2		Year 3 (1995 Sites)		Year 3 (1993 Sites) <sup>†</sup>		Year 4 (1993 Sites)			Year 5 (1993 Sites)				
	(1995 Sites)													
	Treatment	Site	Clipping	Treatment	Site	Clipping	Treatment	Site	Treatment	Site	Clipping	Treatment	Site	Clipping
Length (cm)	<0.001	<0.001	0.110	<0.001	<0.001	<0.001 (+0.105)	<0.001	<0.001	0.050	<0.001	0.022 (+0.016)	<0.001	<0.001	0.029 (+0.004)
Mass (g)	<0.001	0.042	0.001 (-0.024)	<0.001	<0.001	<0.001 (+0.012)	<0.001	<0.001	0.007	<0.001	0.014 (+0.011)	0.001	0.001	0.036 (+0.006)
Basal Diam. (mm)	<0.001	0.013	0.012 (-0.005)	<0.001	<0.001	<0.001 (+0.008)	<0.001	<0.001	0.092	<0.001	0.223	0.025	0.014	0.011 (+0.007)
Tip Diam. (mm)	0.020	0.071	0.023 (-0.007)	0.041	0.254	0.268	0.099	0.502	0.858	0.914	0.832	0.211	0,006	0.519

<sup>+</sup> For the first winter's sampling, we did not measure the previous winter's browsing by moose. Consequently, the effect of the covariate could not be assessed for these data.

#### Shoot Chemistry

Mechanical brushing affected the chemistry of Scouler's willow shoots for winters following brushing (Fig. 2.3). Although tannin content in the shoots of willow varied among sites from 3 to 5 years post-brushing (Fig 2.3), tannin content was lower in the shoots of brushed when compared to unbrushed plants in the second year after brushing (Fig. 2.3, Table 2.2). The lignin content of willow shoots also varied among sites for 2 to 5 years post-brushing, but was lower in the shoots of brushed plants for as many as 3 years post-brushing (Table 2.2). The digestible energy content of willow shoots was different between sites for at least 5 years post-brushing and was lower in the shoots of brushed plants for 2, 3 and 5 years after brushing (Fig. 2.3, Table 2.2). Digestible protein also varied among sites for 2 to 3 years post-treatment and was lower in the shoots of brushed when compared to unbrushed plants for at least 5 years postbrushing (Fig. 2.3, Table 2.2).

As the previous year's clipping and browsing intensity on willows increased, the tannin and lignin content of shoots produced in the following year increased when plants were analyzed in the second year after brushing (Table 2.2). Increased clipping/browsing intensity, however, caused a decrease in digestible energy and digestible protein of the following year's shoots when analyzed in the third to fifth and fifth post-brushing years, respectively (Table 2.2). The previous year's clipping/browsing had no effect on these attributes in other post-brushing years.

# Leaf Senescence

A higher proportion of brushed plants had predominantly green leaves when



**Fig. 2.3.** Comparisons of mean chemical attributes of shoots from brushed and unbrushed willows collected for 2 to 3 winters post-brushing for 1995-brushed sites (Huckleberry Cut, Waterlily Lake and Sawmill Pit) and for 3 to 5 winters post-brushing for 1993-brushed sites. \* indicates a significant effect of brushing when site effects are considered. DM = dry matter. Error bars = 1 SE. *n* is shown above each bar.
**Table 2.2.** *P* values for comparisons between brushed and unbrushed plants for chemical attributes of shoots across all sites by year since brushing. The clipping column indicates the effect of the percentage of shoot removal by clipping/browsing during the previous winter when treated as a covariate in the analyses. Values in parentheses represent slopes for significant effects of the covariate.

Shoot Attribute	Year 2 (1995 Sites)			Year 3		Year 3 (1993 Sites) <sup>†</sup>		Year 4 (1993 Sites)			Year 5 (1993 Sites)			
				(1995 Sites)										
	Treatment	Site	Clipping	Treatment	Site	Clipping	Treatment	Site	Treatment	Site	Clipping	Treatment	Site	Clipping
Tannin Content <sup>‡</sup>	0.013	0.053	0.022 (+0.453)	0.192	0.021	0.065	0.255	0.003	0.476	<0.001	0.201	0.625	0.003	0.255
Lignin (% DM)	0.005	0.002	<0.001 (+0.001)	0.244	0.191	0.072	0.031	0,003	0.333	0.014	0.056	0.519	0.036	0.177
Dig. Energy (kcal/g DM)	<0.001	<0,00}	0.203	0.018	0.004	0.010 (-2.859)	0.913	<0.001	0.095	0.002	0.034 (-3.122)	0.003	<0.001	<0.001 (-3.700)
Dig. Protein (% DM)	0.006	0.037	0.389	0.256	0.594	0.083	0.018	0.008	0.035	0.061	0.744	0.045	0.078	0.022 (-0.010)

<sup>+</sup> For the first year's sampling, we did not measure the previous year's browsing by moose. Consequently, the effect of the covariate could not be assessed for these data.

**‡** Tannin content is the square of the diameter (mm) of the precipitation ring (see text).

compared to unbrushed plants on 8 October 1996, in the second fall after brushing, on 2 of the 3 sites brushed in 1995 (Sawmill Pit:  $\hat{p} = 0.33$ , z = -1.68, P = 0.048; Huckleberry Cut:  $\hat{p} = 0.67, z = -1.87, P = 0.031$ ). Brushed plants from only 1 of the 3 sites brushed in 1993, however, showed signs of delayed leaf senescence in the fourth fall after brushing (Three Buck:  $\hat{p} = 0.35$ , z = -1.74, P = 0.041). When we measured differences in the proportion of brushed and unbrushed plants retaining green leaves on a weekly basis in the fall of 1997, we found that brushed plants from 2 of the 1995 sites (Huckleberry Cut and Waterlily Lake) showed a delay in leaf senescence in the third fall after brushing (Table 2.3). The third site (Sawmill Pit), however, showed no differences (all P > 0.061) in leaf senescence between brushed and unbrushed willows on any of the sampling dates. Patterns of leaf senescence in the fifth fall (1997) after brushing for plants brushed in 1993 were not guite as clear. Of the 3 sites brushed in 1993, only brushed plants in North Layton showed a delay in leaf senescence towards the end of the observation period; unbrushed plants at Sackner Pit showed a delay in leaf senescence for the majority of the observation period (Table 2.3). At the Three Buck site, however, no differences (all P > 0.342) in senescence between brushed and unbrushed plants were observed throughout the observation period.

## Browse Survey Results

The average shoot diameter at the point of browsing was not significantly different between the shoots of brushed (3.95  $\pm$  0.58 mm) and unbrushed willows (3.83  $\pm$  0.56 mm;  $F_{1.98}$  = 1.144; P = 0.287) when analyzed in the third spring after brushing. The shoots of unbrushed willows were, however, browsed past current annual shoots and into older stem materials significantly more often (82.0%) when compared to the shoots

**Table 2.3.** Proportion of willows in each brushing treatment (n = 13) bearing predominantly green leaves as calculated at weekly intervals in the fall of 1997 for 2 sites brushed in 1993 and 2 sites brushed in 1995. Proportions sharing a common superscript within a site are not significantly different from each other as determined by separate *z* tests.

Sampling Date:		1993 \$	Sites		1995 Sites					
	Sackner Pit		North Layton		Huckleb	erry Cut	Waterlily Lake			
	Brushed	Control	Brushed	Control	Brushed	Control	Brushed	Control		
19 Sep 1997	1.00"	1.00"	1.00	0.93 <sup>b</sup>	1.00	1.00	1.00	1.00		
28 Sep 1997	0.75	1.00	0.80 <sup>c</sup>	0.80 <sup>c</sup>	0.94°	0.87 <sup>e</sup>	1.00	0.77		
3 Oct 1997	0,69	0.93	0.53	0.20	0.94	0.47	1.00	0.77		
10 Oct 1997	0.69	0.93	<b>0.46</b> <sup>d</sup>	0.20 <sup>d</sup>	0.88	0.33	0.92 <sup>f</sup>	0.77 <sup>r</sup>		
17 Oct 1997	0.56	0.87	0.40	0.13	0.75	0.33	0.58 <sup>g</sup>	0.46 <sup>g</sup>		

**Note:** No differences existed in leaf senescence between brushed and unbrushed willows on any of the above days for the 1995 Sawmill Pit site or the 1993 Three Buck site.

of brushed willows (15.6%;  $\chi_1^2 = 66.67, P = <0.001$ ).

# Discussion

## Shoot Morphology

Although shoot morphology of both brushed and unbrushed willows varied among sites, mechanical brushing caused willows to produce shoots each year that were larger than the shoots of unbrushed plants for 4 to 5 winters post-brushing. Willows responded to brushing by producing compensatory shoots in the first and second year following damage that had smaller tip diameters, but were 4 to 5 times the length and mass of shoots of unbrushed willows growing in wildlife strips. In successive years, willows continued to produce current annual shoots that, on average, were larger than the shoots of unbrushed willows, although the magnitude of difference between shoots of brushed and unbrushed willows appeared to decline with time since brushing. By the fourth and fifth year post-brushing, the shoots of brushed willows, although still significantly larger, were on average, less than twice the size of shoots from willows growing in wildlife strips (Fig. 2.2).

Mechanical damage from clipping and browsing often affected the morphology of shoots produced in the year following clipping/browsing (effects of the covariate in comparisons among treatments). Generally, in the post-brushing years in which the effect of clipping/browsing was significant (years 3 to 5; Table 2.1), an increase in the intensity (4-98% of current annual shoots) of clipping/browsing during the previous winter caused an increase in the size of shoots produced during the succeeding year. In the second winter after brushing, however, increased clipping intensity during the previous winter seemed to have the opposite effect: an increase in the previous winter's clipping led to decreases in the size of shoots produced in the following year.

Plants often respond to increased clipping intensities by producing larger shoots (Danell and Huss-Danell 1985; Bergström and Danell 1987*a*; Danell et al. 1994), but decreases in shoot sizes with increased clipping intensities may also occur when plants are severely stressed (Danell and Bergström 1989). This type of response may help to explain why willows normally produced larger compensatory shoots with increased clipping intensity except when clipping was imposed in the first winter (following a single truncated growing season) after severe damage from brushing.

Vigorous vegetative regeneration and the production of large compensatory shoots following mechanical damage (i.e., cutting, browsing) is a common growth strategy for deciduous shrubs and trees that pioneer early-seral sites (Coates and Haeussler 1986; Sennerby-Forsse and Zsuffa 1995). Black cottonwood (Populus trichocarpa) saplings, for example, produce sprouts over 3 m tall and over 3 cm in diameter in the first 2 years following coppicing (DeBell and Alford 1972). This type of growth response to damage is particularly adaptive for plants such as willows growing in young boreal forests where plant competition for canopy occupancy is intense (Aarssen and Irwin 1991; Hjalten et al. 1993) and where the highest herbivore pressures are exerted closest to the ground (Danell et al. 1987). The capacity to respond in this fashion appears to be particularly developed in plants that must frequently compensate for herbivory (Ouellet et al. 1994). Physiochemically, such responses have been attributed to an attempt by the plant to re-establish its disrupted root-to-shoot ratio (Kramer and Kozlowski 1979; Tschaplinski and Blake, 1994), and involve the allocation of plant resources into shoot growth and crown formation in the years immediately following tissue removal.

Total biomass and the absolute number of growing points on a plant decreases following removal of stem tissues. This loss results in a disproportionate allocation of plant resources to relatively fewer growing points which leads to the production of fewer, but larger shoots (Bergström and Danell 1987*a*). As plants regenerate, branch and produce new meristematic tissues in the years after damage, however, the number of above-ground growing points increases and the amount of plant resources distributed to each new shoot becomes proportionately reduced (Danell et al. 1985*b*). An increase in meristem numbers with time coupled with a decrease in resource allocation per meristem causes willows compensating from damage to produce more, but smaller shoots, eventually leading plants to reassume a form of growth and overall biomass production similar to that of pre-damaged plants.

Our data suggest that the shoots of willow generally become smaller with time since brushing (Fig. 2.2). These data indicate that following the first 2 post-treatment years of vigorous compensatory growth, plants produce shoots similar in morphology to those produced by more mature or unbrushed willows. Although the shoots of brushed willows were still significantly larger than the shoots of unbrushed willows in the fifth winter after brushing, decreases in the shoot size of brushed willows with time since brushing suggest a trend in which both brushed (following several years of compensatory growth) and unbrushed plants eventually produce shoots of similar size. As plants begin to regenerate and reassume a more mature, predamaged form of growth in the years following brushing, previous differences in the chemistry and leaf phenology also begin to disappear in as little as 2 to 3 years post-brushing.

## Shoot Chemistry

Brushing promoted the growth of large compensatory shoots that were lower in tannin, lignin, digestible energy and digestible protein for at least 2 winters after brushing (Fig. 2.3). Although in most cases the previous winter's clipping and browsing did not affect the chemistry of shoots produced in the succeeding year, clipping/browsing did affect shoot chemistry in some years. The tannin and lignin content of willow shoots produced in the year after clipping, for example, increased with an increase in the previous year's clipping/browsing intensity when analyzed in the second winter after brushing. As the previous year's clipping/browsing intensity increased the content of digestible energy and digestible protein found in the shoots produced in the year after clipping/browsing intensity increased the content of digestible energy and digestible protein found in the shoots produced in the year after clipping/browsing decreased when analyzed from 3 to 5 years after brushing, respectively (Table 2.2).

In those cases in which increased clipping/browsing intensity affected shoot chemistry, plant response was generally similar to brushing (except for the positive effect on tannin and lignin content in the second post-brushing year). The added stress of clipping/browsing on recently-brushed willows may have promoted the production of shoots that responded differently (in terms of tannin and lignin content as well as morphology) to increased clipping intensity in the second post-brushing year. Plants stressed by repeated hare browsing following cutting, for example, may produce shoots that are higher in phenolic compounds such as tannins and lignin during winter (Bryant et al. 1985). Overall, however, we found that the tannin and lignin content remained lower in the shoots of brushed Scouler's willow for 2 and 3 years following treatment, respectively, when these plants were compared to unbrushed willows growing in the wildlife strips. Reductions in the tannin and lignin content of browse have also been shown to occur following other forms of mechanical damage (Dutoit et al. 1990; Nellemann 1990; Suter 1993; Singer et al. 1994).

Reductions in the tannin and lignin content of shoots following brushing are likely due to the allocation of plant resources into shoot elongation over the production of chemical defences, as the production of tannins and lignin often compete with growth for common metabolic substrates such as phenylalinine (Herms and Mattson 1992). Alternatively, the inverse relationship between shoot size and phenolic content may be driven largely by tannin production rather than resource competition, because tannins are important antagonists and regulators of giberellin hormones that promote stem growth and elongation (Kramer and Kozlowski 1979). The smaller shoots of unbrushed plants may be due to the growth-inhibiting effects of tannins, rather than tannin content being reduced due to the allocation of resources towards growth and away from chemical defence. In either case, Scouler's willow appears to compensate for mechanical damage by producing large compensatory shoots low in phenolic metabolites. This strategy, although not shared by all boreal plants (Bryant et al. 1983), allows for vigorous growth following damage and leads to increases in plant nutritional value with respect to chemical anti-herbivore defence (Herms and Mattson 1992).

In addition to reductions in tannin and lignin content, brushing likewise resulted in reductions in the dry matter digestibility of shoots produced following brushing. Such reductions were due to increases in structural materials such as cellulose and hemicellulose (as determined by detergent analysis) apparently synthesized to support the growth of large vegetative shoots. Reductions in dry matter digestibility resulted in decreases in digestible protein and digestible energy in the shoots of post-brushed growth when compared to unbrushed willows and were significant for at least 4 to 5 years following brushing.

Decreases in digestibility often occur in association with increases in shoot size and are likely a result of the increasing proportion of structural cortex to bark materials found in relatively large shoots (see Chapter 1). Because homogenizing and analyzing extremely large shoots can reduce the bark to cortex ratio as well as the digestibility of plant tissues, some authors have recommended that the more distal portions of shoots (i.e. those that are utilized by moose), as well as whole shoots, be analyzed (Eastman 1984; Danell and Bergström 1985). Following such a recommendation may have revealed smaller differences between the digestible protein and energy (and possibly tannin) of shoots from brushed and unbrushed willows in our study.

# Site Effects

The shoots of willows collected from different sites in the same post-brushing winter often varied in morphology and/or chemistry within and between brushing treatments (brushed and unbrushed). The differences between the shoots of brushed and unbrushed willows, however, were similar among sites. Analysis of these site effects revealed that 1 of the 3 sites from each of the 2 brushing years appeared to be largely responsible for the effects of site detected in the analyses. Brushed and unbrushed willows from both the 1993-brushed North Layton and 1995-brushed Waterlily Lake sites produced shoots that were generally smaller with higher chemical contents than either of the other 2 sites brushed in 1993 or 1995, respectively. Although differences in site elevation (~ 50 m; North Layton and Waterlily Lake) do not explain the differences detected in the shoots of willows among sites, differences in yearly meteorological conditions between sites (i.e., localized frost pockets, amount of precipitation, etc.) could

affect patterns of plant growth and the nutritional value of plant tissue for herbivores (Kramer and Kozlowski 1979; Bø and Hjeljord 1991).

Variation in the distance between brushed and unbrushed willows across sites may have also contributed to site effects if variation in distances between such plants altered the ability of both brushed and unbrushed willows to send and receive airborne chemical signals from nearby plants. Willows and other plants alter the emission of certain volatile organic compounds into the air following mechanical injury (e.g., herbivore attack; Rhoades 1985). Some evidence suggests that nearby, unattacked plants can detect and respond defensively to such airborne substances by increasing phenolic concentrations and decreasing the nutritive quality of plant tissues (Rhoades 1985). An increase in phenolic concentrations could, in turn, inhibit shoot elongation and the production of large shoots (Kramer and Kozlowski 1979).

Plant proximity and/or root connectivity, site-to-site variation in soil nutrients, moisture and leaching as well as plant population genetics (Eastman 1984) may have also contributed to site effects. Because the nutritive quality of shoots from male and female willows can differ significantly (Danell et al. 1985*a*), differences in the sex ratios of plants between sites may have also contributed to site effects. Whatever the cause, brushed and unbrushed willows growing on the Waterlily Lake and North Layton sites had relatively small shoots with increased chemical concentrations when compared to willows growing on the other 4 sites. Treatment effects, however, revealed the predictability of plant response to brushing across all sites. These results agree with those of Danell et al. (1997), who suggest that the morphological and chemical response of plants to damage are of a more generalized nature across the landscape and more important and less flexible than the external differences among various sites.

Replacing and increasing sampling units (willows) from year to year in an effort to reduce the loss of inferential power prevented us from taking repeated measurements from all plants in consecutive years. Despite replacements and increases in samples, however, some plants were sampled consecutively across each year of the study so that the effects of clipping/browsing (as a covariate) could be assessed. These repeated measurements of some willows throughout the study raised issues of sampling independence. Clipping/browsing levels could not be maintained at a constant level across years for a given plant (as plants were not contained within enclosures and were therefore exposed to browsing by moose after clipping treatments). Consequently, we were unable to track individual willows (repeated measures analysis) across years and simultaneously include the changing effects of clipping/browsing. Therefore, in order to assess the effects of clipping/browsing on plant response to brushing, we did incur some loss of independence among years.

## Leaf Senescence

We detected yearly delays in fall leaf senescence in brushed willows for up to 4 years post-treatment on some sites. Differences in biotic, abiotic and/or meteorological factors among sites likely contributed to differences in senescence among brushing treatments between sites. Although we did not directly measure how much longer brushed plants retained green leaves over unbrushed plants, our results revealed significant differences in the proportion of willows bearing green leaves between brushed and unbrushed willows for up to 3 weeks following the onset of leaf colouring.

Delays in leaf senescence, as indicated by the retention of green leaves in the fall, were significant in brushed willows and obvious on the landscape for up to 4 years after brushing. Similar delays in leaf senescence occurred in red willows (*Salix lasiandra*) in

response to beaver cutting (Kindschy 1989) and in little rabbitbrush (*Chrysothamnus viscidiflorus*) and snowberry (*Symphoricarpos vaccinioides*) in response to clipping (Willard and McKell, 1978). Delays in fall leaf senescence are thought to be a result of plant rejuvenation and the reallocation of existing nutrients to relatively fewer extant shoots (Millington 1963; Danell et al. 1997). Such delays generally only last as long as plants continue to compensate for lost shoot biomass (Willard and McKell, 1978), which according to the delays we detected in the leaf senescence of Scouler's willow, may be as little as 3 to 4 years post-brushing.

#### Implications for Moose

Generalist herbivores preferentially attack plants in which defences have been reduced by physical stress such as mechanical damage (Rhoades 1985). The African elephant (Loxodonta africana), for instance, prefers to browse on large compensatory stump shoots, and is even thought to manage the production and availability of such shoots by selectively felling preferred browse trees (Jachmann and Bell 1985). Moose may or may not consciously farm compensatory growth (Danell et al. 1994), but nonetheless select the shoots of plants that have been previously browsed or broken (Danell et al. 1985b; Suter 1993; Singer et al. 1994) and select the largest shoots available (Penner 1978; Risenhoover 1987a; Schwartz 1992; Bowyer and Bowyer 1997). Moose will even select large stump shoots (such as those produced following brushing) when available (Wolff 1978; Bergström and Hjeljord 1987; Bevins 1989; Suter 1993), presumably due to changes in the morphology and chemistry of compensatory growth that make them more palatable and easy to browse (Danell et al. 1985b). Selecting large shoots also enables moose to increase bite size and intake rates per cropping effort (Shipley et al. 1994; Gross et al. 1993), which can facilitate maximizing energy intake

while minimizing the amount of time spent foraging in the open, away from mature forest cover (Weixelman et al. 1998).

Our data indicated that the moose browsed shoots at similar diameters, on average, when browsing the shoots of brushed (3.95 mm) and unbrushed willows (3.83 mm). Others have described low variability in moose bite diameters on willows over wide geographic areas (Kielland and Osborne 1998). Close examination of bark characteristics of browsed shoots from unbrushed willows, however, revealed that the majority (82%) of these shoots had been browsed well past current annual growth and into older 2 and 3 year old stem tissues. Moose browsed beyond the smaller current annual shoots and into older stems of unbrushed willows presumably in an effort to maintain larger bite sizes (Shipley et al. 1994).

A significantly smaller percentage (15.6%) of shoots from brushed willows were browsed past current annual growth. Compensatory shoots produced following cutting are generally too large for moose to consume in a single bite (Huseby 1982). Consequently, moose generally do not browse past the current annual growth scar and into older stem tissues when feeding on larger stems.

Although browsing the smaller shoots of unbrushed willows alone would increase digestible energy and digestible protein intake, the incorporation of older stem materials into each bite significantly reduces plant digestibility and nutritional value (Hjeljord et al. 1982; Wolfe et al. 1983; Vivås and Sæther 1987). For this reason moose typically avoid browsing older stems (Danell 1983). Reasons other than overall quality per bite, however, may help to explain moose browsing beyond the current annual shoots of unbrushed willows. Browsing in wildlife strips, for example, may afford more cover and protection from predators when compared to browsing in recently brushed and more

exposed areas of the forest stand; such factors can significantly influence foraging strategies (Weixelman et al. 1998).

Although moose typically select browse based on shoot size when other variables are controlled for, moose are also known to select browses that are lower in phenolic compounds such as lignin (Risenhoover 1987b) and tannins (Bryant and Kuropat 1980; Bryant et al. 1983; Singer et al. 1994). Lignin and tannin content are often more important in determining browse selection by herbivores than the digestible energy (Bryant et al. 1983; Coley et al. 1985; Robbins et al. 1987b). Lignin is virtually nondigestible and interferes with the microbial digestion of cellulose (Blair et al. 1980) and tannins can reduce protein and dry matter digestibility (Robbins 1987a; Robbins 1987b; Hagerman et al. 1992) or may act as toxins (Mehansho et al. 1987).

Lignin content determines plant fibrosity and toughness (Spalinger et al. 1986) and may be the reason moose specifically avoid this component of fibre (Risenhoover 1987*b*; Nellemann 1990). Concentrations of lignin have a large influence on the nutritive quality of shoots (Shipley and Spalinger 1992) because increases in lignin concentrations increase the handling time of winter food items (Spalinger et al. 1986). Increases in handling time reduce the rate of forage intake and are costly in terms of the energy budget of the animal, because energy and nutrient intake are highly dependent on forage intake as well as nutritive quality (Spalinger et al. 1986). Although increased handling times and reductions in forage intake are, therefore, likely to occur when moose browse the more lignified, smaller shoots and older stems of unbrushed willows, these problems are not likely to occur when moose browse the shoots of brushed willows in the first 3 years post-brushing.

In addition to lignin, moose specifically avoid tannins (Bryant and Kuropat 1980; Bryant et al. 1983; Suter 1993; Singer et al. 1994) and may avoid other phenolic compounds such as salicylates (salicylic acid; Raskin 1992) when browsing willows, although the role of such compounds in the winter foraging ecology of the moose remain unclear. Moose appear to avoid tannin-containing browses even though they produce salivary-tannin-binding proteins to help neutralize the effects of dietary tannins (Hagerman and Robbins 1993; Juntheikki 1996). Such avoidance may be related to the inability of moose to bind all tannins from all deciduous browses (including some willows; Junetheikki 1996).

Although dormant browse stems contain relatively little tannin when compared to other forage items (Hagerman and Robbins 1993), these small amounts of tannin are sufficient to bind all of the tannin-binding protein from moose saliva (Junetheikki 1996). The production of shoots with even slight reductions in tannin content, such as those produced in the second year after brushing (4-24 % on average; Fig. 2.3) might appear, therefore, to potentially increase the nutritional value of willows for moose. Although we cannot estimate absolute tannin levels in winter browse, these 4-24% decreases likely represent very small absolute differences in tannin content between brushed and unbrushed willows. In addition ungulates appear to be able to compensate for even relatively high levels of tannins with increased digestible energy intake (Merril 1994). Consequently, increased energy intake rates achieved by simultaneously cropping several smaller shoots from unbrushed willows could outweigh apparent increases in the nutritional value of shoots due to reduced tannin and lignin content. Estimating intake rates of moose browsing brushed and unbrushed willows would be necessary to completely understand trade offs in absolute nutritional value.

Although shoots of deciduous trees and shrubs constitute the majority of the moose winter diet (Pierce 1983; Risenhoover 1989), moose select leaves rather than shoot materials in the fall and early winter as long as leaves are available (Regelin et al. 1987). Moose will even forage on fallen leaves in the fall (Renecker and Hudson 1986) even though they typically select the greenest foliage available (Bergerud and Manuel 1968). Because the availability of green leaves in the fall landscape are considered important to moose and other herbivores (Chapin 1980; Schwartz et al. 1988*a*), delays in fall leaf senescence in the years following brushing act to increase the nutritional value of willows for moose.

## Conclusions

Brushing altered the overall nutritional value of browse for moose for several years after brushing. Brushed willows may not have been available in the first winter after brushing (depending on the timing of brushing; see Chapter 1), but these plants retained green leaves in the second fall (and likely the first; see Chapter 1) and had large shoots with reduced tannin and lignin content in the second winter following brushing. In the third winter following treatment, brushed willows had shoots with less lignin that were larger, but contained more structural compounds (i.e., cellulose), that reduced digestible energy and digestible protein compared to shoots of unbrushed plants. Brushed willows continued to show signs of delayed leaf senescence in the third fall after brushing. In the fourth and fifth years following brushing, reductions in lignin content and delays in leaf senescence were no longer apparent and browse shoots continued to remain lower in digestible protein and digestible energy but larger in size.

The previous winter's clipping/browsing intensity often had a significant effect on the nutritional value of shoots produced by willows in the year following

clipping/browsing. Because the intensity and effect of browsing on each plant varied by year, however, we were unable to assess the effects of brushing on individual plants from year to year. The confounding effects of browsing, therefore, reduced our ability to track individual plants and reduced our sampling independence from year to year. Although this likely had little bearing on our findings within years, limiting browsing variability from year to year through the use of exclosures would allow for repeated measurements and the tracking of individual plants across years. In turn, such an approach would allow for closer tracking of the effects of brushing from one post-brushing year to the next.

Irrespective of site, willows responded to brushing by producing shoots that were thicker, longer and heavier than the shoots of unbrushed willows for several years after brushing. Willows also showed consistent reductions in the chemical contents of large shoots produced after brushing, although the number of post-brushing years that these reductions were apparent differed depending on the particular chemical attribute in question.

Aside from reductions in overall available biomass, the most obvious effect of brushing is an increase in the size of shoots produced by willows in the years following brushing. Although large shoots are typically lower in digestible energy and protein, moose are particularly adapted for prehending large bites (e.g., willow shoots; Shipley et al. 1994) and select larger rather than smaller shoots regardless of overall nutritional quality (Jia et al. 1997). Weixelmann et al. (1998) found no correlation's between the use of Scouler's willow and protein content or dry matter digestibility by moose and speculated on the potential role of plant secondary compounds in their diet selection. Despite these findings potential reductions in overall nutritional value due to decreased protein and energy digestibility following brushing could outweigh gains in overall value

due to increased shoot size, decreased tannin and lignin content and delayed leaf senescence.

Cafeteria-style feeding trials are likely the most accurate way to predict moose preferences and intake rates and to understand trade offs faced by moose when selecting for the shoots of brushed versus unbrushed willows. Furthermore, extensive browse surveys within experimentally controlled stands would help to delineate the use of brushed and unbrushed areas without removing natural influences known to drive moose foraging strategies (i.e., snowdepth, predator threats, etc.). Combining such information with our present findings may help resource managers compare the effects of brushing with herbicide applications and determine the overall impacts of brushing on browse quality for moose. This, in turn, may aid managers in the development of vegetation management strategies for wildlife strips and adjacent stands.

Not all woody deciduous plants respond to mechanical damages (i.e., brushing) in the same manner as Scouler's willow (Ouellet et al. 1994; Alpe et al. 1999). Other woody plants such as aspen (*Populus* spp.), birch (*Betula* spp.) and ash (*Sorbus* spp.), however, appear to respond to mechanical damage (at least morphologically) in a fashion similar to that of willow (Coates and Haeussler 1986). For resource managers interested in the specific effects of brushing on particular browse plants, further experimentation on browse species of interest should be conducted because a combination of species, site characteristics, and previous browse history, will likely influence plant response. Furthermore, the timing of brushing (see Chapter 1) influences plant response and the resulting quality of browse for moose.

Obviously each factor associated with a particular influence on plant response to brushing must be investigated to fully understand the overall implications of brushing on

the production and quality of browse. Many questions regarding species-specific plant responses to mechanical brushing and the implications that brushing may have for animals other than moose remain unanswered. Despite this, resource managers can begin to use these results in combination with future findings to manage brush, not only for conifer production, but for wildlife such as moose that are often found wintering in young managed stands.

## **CHAPTER 3. CONCLUSIONS AND RECOMMENDATIONS**

Stand-tending activities such as mechanical brushing affect the availability and quality of browse for moose in winter. The degree to which plants are affected by brushing, however, depends on several factors including plant species, the timing of damage and site characteristics. These factors influence the ability of plants to compensate for such damages. Mechanical brushing must, therefore, be considered in relation to moose ecology as well as conifer production.

This research examined the effects of mechanical brushing on the nutritional value of an important browse for moose in winter: Scouler's willow. We examined the effects of the timing of brushing on the nutritional value of regenerating browse shoots for the first 2 winters after brushing and determined how the nutritional value of shoots was affected in the first 5 years following brushing at the field level (without a timing component). Specifically, data were collected to help to identify: 1) the most appropriate time to brush to increase the nutritional value of browse for moose and; 2) how brushing affected the nutritional value of willows in the first 5 years immediately following brushing.

To assess the effects of the timing of brushing on the nutritional value of Scouler's willow, we brushed willows at 6- and 4-week intervals during the growing seasons of 1996 and 1997, respectively. We then recorded plant response in terms of compensatory shoot growth, leaf senescence and leaf flush and collected samples from willows in the first and second winters following brushing to determine the effects of different brushing treatments on the morphology and chemistry of shoots. To determine the long-term effects of mechanical brushing and the effects of clipping and browsing on the nutritional value of willow following brushing, we compared the quality of browse

produced by brushed and unbrushed willows on 6 sites from 2 to 5 years post-brushing. We also conducted a browse survey to assess the utilization of brushed and unbrushed willows. We considered the nutritional value of willows for moose to increase if willows retained leaves longer and produced shoots that were large and low in tannin and lignin content. We also considered the absolute nutritive value of shoots to increase with an increase in digestible energy and digestible protein content.

Our research indicated that mechanical brushing altered morphological, chemical and phenological attributes of Scouler's willow that are known to influence forage selection by moose for a number of years following brushing. In general, willows responded to brushing by showing signs of delayed leaf senescence and by producing large compensatory shoots lower in tannin, lignin, digestible protein and digestible energy than the shoots of unbrushed plants in the years following brushing.

The specific response of willows to brushing depended on the timing of brushing. Willows brushed in July compensated for brushing by producing new growth that, overall, was more nutritious for moose in the first 2 post-brushing years when compared to plants brushed at other times during the growing season or unbrushed controls. Plants brushed earlier than July did not delay leaf senescence as long and had shoots that were less nutritious than July-brushed willows in the first and second post-treatment year. Although the shoots of willows from plants brushed after July were comparable in quality to the shoots of July-brushed willows in the second post-treatment year, these willows had shoots that were unavailable in the first winter after brushing and showed delayed leaf flush in the first spring following brushing. July-brushed plants also had shoots larger and more nutritious for moose in terms of digestible energy and protein, tannin and

lignin content and showed delayed leaf senescence longer than unbrushed willows in the first 2 winters post-brushing

Although chemical, and to some extent morphological, attributes of willows in both brushed areas and unbrushed wildlife strips varied among sites, the trends in plant response to brushing were similar among sites. Digestible protein and digestible energy were lower in the shoots of brushed when compared to unbrushed willows for 4 to 5 years following brushing. The shoots of brushed willow were, however, lower in tannin and lignin content for 2 and 3 winters following brushing, respectively. Additionally, brushed plants produced shoots that were larger than the shoots of unbrushed willows for at least 4 to 5 years following brushing and showed delayed leaf senescence longer than unbrushed plants for up to 3 consecutive falls post-brushing.

The intensity of the previous winter's clipping and browsing sometimes affected the nutritional value of shoots produced during the following year. When the effect of clipping/browsing was significant, the effects were generally similar (except in the second post-brushing year) to the effect of brushing: shoot size increased and shoot chemistry decreased with an increase in the previous year's clipping intensity. Because moose select browse in late fall and winter based predominantly on shoot size, as well as tannin and lignin content and the presence of leaves, the changes occurring in willows following brushing appear to increase the amount of food normally selected by moose.

Of the suite of shoot attributes altered by mechanical brushing, increases to the size of willow shoots in the years following mechanical brushing may be the most important to moose. Reductions in the lignin and tannin content of these shoots may help to increase their digestibility and palatability and delays in leaf senescence may provide moose with leafy, nutritious forage later into the fall; larger shoots allow moose to take

larger bites and reduce the occurrence of browsing past current annual growth. In this way, large shoots facilitate an increase in the intake of current annual growth and a reduction of older, less nutritious 2- and 3-year-old materials into each bite that often occurs when moose browsed the smaller shoots of unbrushed willows.

Willows brushed in July produced large compensatory shoots, which were low in tannin and lignin and high in digestible protein relative to willows brushed at other times or unbrushed willows. Willows brushed in July also delayed leaf senescence and retained green leaves late in the fall. Although brushing (regardless of timing) reduces overall available browse biomass, changes due to brushing in July led to increases in the overall nutritional value of browse for moose in the first 2 years post-brushing. We, therefore, recommend brushing in July in areas where concerns for an uninterrupted supply of browse for moose exist.

The long term nutritional value of post-brushing growth remains questionable due to reductions in the energy and protein digestibility of compensatory growth. These reductions were associated with increases in the amount of structural materials (i.e., cellulose) which we found in the large compensatory shoots produced following brushing. Although larger shoots aid moose in taking larger bites, understanding the trade offs between increases in shoot (bite) size and reductions in digestibility must be more closely investigated to completely understand the biological significance of changes in browse quality for moose following brushing. Only after conducting cafeteria-style feeding trials and, determining *in situ* intake rates, will the actual value of shoots from brushed and unbrushed plants for moose become evident. Understanding these factors, in combination with the present findings, will help to provide resource managers with information necessary to manage wildlife strips and adjacent forest stands not only for

conifers but for the production of browse for moose. Such information may also be useful to managers considering supplanting chemical methods of brush control with mechanical methods.

Our findings regarding the effects of mechanical brushing on the nutritional value of browse for moose is based solely on the response of Scouler's willow to brushing. Other research into plant morphological responses to cutting, however, suggests that willows respond to damage in a manner typical of other early-successional woody plants. The findings of this study and the implications to the nutritional value of browse for moose are, therefore, likely to be applicable to plants other than willows growing in regions other than the SBS dw3 sub-zone.

The application of our findings to other areas is particularly pertinent when considering changes in shoot morphology following brushing; shoot size increased following brushing regardless of site. Although changes in shoot chemistry often depended on site, the importance of brushing to moose is likely more closely related to the production of larger shoots for several years by brushed plants than changes in shoot chemistry in the years immediately following brushing. For this reason, the implications of brushing on the browse quality of shoots for moose in winter are likely to be similar across several different areas.

Further research into plant response to mechanical brushing will continue to strengthen our understanding of the effects that brushing can have on the production of browse for animals such as moose in the years following brushing. For example, because the intensity of browsing on plants changed from year to year, tracking the effects of brushing on individual plants from one year to the next was impossible. The construction of exclosures, in this case, could help to limit the variability of tissue removal of

individual plants between years and allow for repeated measures and an assessment of brushing on individual plants from one post-brushing year to the next.

Using such measures will help to increase our understanding of how plants respond to such practices imposed at different times, across different plant species and geographical boundaries. This in turn, will aid in the formulation of appropriate management strategies for brush control in areas where concerns for the quantity and quality of browse for moose exist. Implementing such strategies will then allow for a more integrated approach to controlling vegetation in which considerations are made not only for conifer production, but for animals such as moose wintering and foraging in recently brushed stands.

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## APPENDICES



Appendix A. The percentages of 3 forms of fibre in the distal portions of Scouler's willow shoots collected in the winter of 1997 as measured from the shoot tip. To obtain these data 4 to 6 shoots were randomly sub-sampled from shoots collected from 75 brushed and unbrushed willows. These shoots were sectioned, separated by section, combined and homogenized for determinations. Means are determined from analyzing the materials twice. ADF is acid detergent fibre. Error bars represent 1 SE.

Appendix B. Comparison of biomass and mineral content in the shoots of willow brushed in June 1996 (n = 15) in the first winter after brushing and unbrushed (n = 11) controls. Degrees of freedom for all comparisons were 1, 24. ppm indicates parts per million.

Shoot Attribute	Brushed	SE	Unbrushed	SE	F	Р
Mass (g)	4.93	0.54	0.75	0.12	137.3	<0.001
Boron (ppm)	48.4	2.7	39.1	2.5	5.76	0.024
Calcium (%)	0.511	0.014	0.822	0.054	37.10	<0.001
Carbon (%)	48.75	0.20	51.04	0.15	74.19	<0.001
Copper (ppm)	4.34	0.40	3.20	0.22	4.38	0.047
Iron (ppm)	29.09	1.53	41.00	4.35	0.86	0.363
Magnesium (%)	0.117	0.007	0.116	0.009	0.01	0.938
Manganese (ppm)	79.92	5.75	108.35	7.31	9.60	0.005
Nitrogen (%)	0.758	0.018	0.970	0.057	16.04	<0.001
Phosphorus (%)	0.143	0.004	0.138	0.008	0.37	0.551
Potassium (%)	0.422	0.014	0.370	0.020	4.74	0.040
Sulphur (%)	0.056	0.002	0.70	0.005	8.33	0.008
Zinc (ppm)	76.91	2.89	102.51	6.74	14.76	<0.001



Appendix C. Proportion of willows in each brushing treatment that were brushed in 1997 showing signs of fall deer browsing in the same year following mechanical brushing. z tests indicated that June-brushed willows were browsed more than Julybrushed ( $\hat{p} = 0.231$ , z = -3.306, P < 0.001) or unbrushed willows ( $\hat{p} = 0.219$ , z =-3.628, P < 0.001). The amount of browsing was not significantly different ( $\hat{p} =$ 0.046, z = -0.564, P < 0.286), however, among July-brushed and unbrushed willow. Error bars represent 1 SE.