Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology
and Natural Resource Management

Doctor Philosophiae (Dr.philos.)
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Effects of Brush Cutting on Hardwood Browse Production and Moose Winter Foraging

Elgens vinterbeite og beitemønster etter manuell fjerning av lauvoppslag

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Figure 1. An upland willow near New Hazelton, British Columbia, Canada following a single growing season of regrowth after roadside brush cutting. Note the large compensatory resprouts and delayed autumn leaf senescence characteristic of plants recovering from severe mechanical damage. October 28, 2012.

Control the food supply and you control the population

– Henry Kissinger, 1970

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Ås, April 2014
Roy V. Rea

Within British Columbia, paved and unpaved road (and associated roadside verge) length increased by 82% between 1988 and 2005. Estimates of unpaved roads in 2005 varied from 400,000 to 550,000 km across the province (BC Forest Practices Board, 2005). Many more backcountry roads have been built since

– *Columbia Mountains Institute, 2012*

CONTENTS

ABSTRACT

The impacts that cutting and removal of above-ground hardwood shrub and tree biomass have on browse resource availability for herbivores such as moose are obvious. Less obvious are the impacts that cutting and specifically - the season of cutting - can have on browse plant response and how moose perceive and utilize the shoots of plants recovering (compensating) from cutting treatments. Several experiments were conducted over a 15-year period in northern British Columbia, Canada to specifically determine the influence of brush cutting and twig clipping on the response of browse plants such as willow, aspen and birch. Plant response was assessed by examining changes to shoot production, morphometry, and chemistry and to leafing phenology. Changes to the value of winter browse for moose were of primary interest. The influence of cutting time on the use of resprouts and compensatory shoots by moose in winter relative to the use of shoots of uncut plants was assessed through spring browse surveys in the field and cafeteria-style feeding trials with human-habituated moose in mid-winter at a wildlife shelter. Findings suggest that the season of cutting and clipping as well as clipping intensity and a combination of cutting and clipping influenced plant compensatory responses and such responses varied by plant species and growing site. Generally, cutting stimulated the growth of large compensatory shoots in the years after cutting and plants cut early in the growing season produced the largest shoots in the year of cutting. Plants cut during plant quiescence and dormancy produced the largest shoots in the years following brush-cutting. Plants cut later in the growing season also delayed leaf senescence longer into the autumn while cutting time had variable effects on spring leaf flush. In winter, larger shoots had higher fiber content and, therefore, reduced digestible energy and protein, but were also generally lower in phenolic compounds such as lignin and tannins. Moose selected for smaller shoots in cafeteria trials when winter shoots were offered *ad libitum*, but such selection varied by species and the availability of shoot sizes when whole plants were offered in trials. The biomass and cumulative length of shoot materials removed by moose was directly related to how much biomass was available. Relative to cutting, winter browsing and clipping on plants had less of an effect on subsequent shoot growth, but did influence shoot biomass production, digestibility and tannin content in the years after cutting when clipping intensity was considered. When clipping was conducted during the growing season, clipping increased compensatory leaf and shoot biomass production as well as stem dieback (necrosis) relative to controls with clipping earlier in the growing season resulting in more stem dieback. Moose diet selection and foraging decisions involve tradeoffs between plant quality and quantity; plant management impacts both. I conclude that managers should seriously consider how brush-cutting impacts hardwood browse production and quality and how plant response may influence moose (or other herbivore) activity patterns and habitat use in areas targeted for vegetation management.

PROLOGUE

The relationship between herbivores and their forage base is highly evolved and intricately tuned. Some herbivore-plant interactions appear to be so refined that authors have described some herbivores as possible “managers” of their own forage supply (Pyke et al. 1977; Jachmann and Bell 1985; see review by Gordon and Lindsay 1990). Such attributions have been applied to some plant-herbivore systems because of the ways in which herbivores: a) select plants upon which to forage; b) select the type and amount of plant parts to consume; and c) perceive and respond to previously browsed vs. unbrowsed plants.

Whether or not plants are repeatedly browsed depends in large part on how plants respond to the initial damage imposed by the herbivore or other damage agents (Danell and Bergström 1989, Haukioja and Koricheva 2000). These interactions have intrigued ecologists for decades with some of the first published clipping (deer *Odocoileus* spp. Raf. browsing) experiments being launched in the 1930s (Aldous 1952) and hundreds of related studies being conducted since.

How browse plants respond to cutting and specifically to cutting time has been given much less attention, and is, together with moose (*Alces alces* L.) browse selection, the main subject of the following thesis and is considered in detail in the pages that follow.

INTRODUCTION

Early seral forests and their management

Early successional winter ranges are considered critical foraging habitats for moose (Dodds 1960, Peek 1998). Plants growing within these rangelands are used by moose and other fauna for food and cover, but are also impacted by factors such as disease outbreaks, fire, logging, land development, and vegetation management. How natural and anthropogenic forces impact vegetation resources for wildlife is of considerable interest to managers trying to manage (and in some cases protect) plant resources because the production of poor winter ranges can lead to poor overwintering survival of the animals that inhabit them.

The effects of forest renewal following forest fires and harvesting on habitat and forage quality for moose are well known (Peek 1998). Removal of mature overstory trees as a result of fire or during logging operations opens up the forest canopy and allows pioneering hardwood species such as willows (*Salix* spp. L.), birch (*Betula* spp. L.) and aspen (*Populus tremuloides* Michx.) to gain the competitive edge and flourish.

Pioneering species growing in post-disturbance habitats comprise a major portion of the moose diet and act to attract moose, which use these areas as long as forage abounds (generally 5-20 years post-disturbance; Dodds 1960, Peek 1998). Also, where young forests are managed for conifer production or rights-of-way maintenance, forest cleaning operations (brushing and weeding of hardwood species) will impact the distribution and abundance of forage for moose. Forage quality is also likely to be impacted by brush management (Bergström and Hjeljord 1987), but why and how is largely unstudied.

Nearly all early seral forests in British Columbia, Norway and throughout many parts of the range of moose are managed to reduce competition from woody broadleaved deciduous species and increase conifer yields or to reduce forest encroachment into linear corridors. The percentage of landbase occupied by young forest plantations (< 20 years old) in BC is ~2.1% (Hectares BC 2012[1]) and in Norway is ~17.1% (Granhus et al. 2012) while rights-of-ways (powerlines and public roads through forested areas but not including seismic lines, railroads, gas lines and other rights-of-ways) span over 560,000,000 kms in BC (Hectares BC 2012) and 330,000 kms in Norway (O. Hjeljord, Norwegian University of Life Sciences). The impacts to browse quantity and quality due to brush management in these areas are, therefore, substantial and may influence the activity patterns and distribution of moose (Scotter 1980, Thompson and Stewart 1998).

Systemic herbicides are often used to reduce hardwood growth in forest plantations and along rights-of-ways. Their use, however, comes with unintended side effects such as impacting small mammal population dynamics (Sullivan et al. 1998) and reducing browse availability for herbivores for several years following their application (Hjeljord and Grønvold 1988, Lautenschlager 1992). An increase in public outcry against the use of herbicides (Wagner et al. 1998) has, therefore, led some agencies to depend more on mechanical means (e.g., brush-cutting) of controlling brush. Increases in the use of mechanical brush control methods has, in turn, lead to an increased need to study the impacts of cutting on plant response as well as forage production, accessibility and quality.

Browse production and use

According to the Optimal Foraging Theory (MacArthur and Pianka 1966), animals such as moose will select feeding sites in relation to patch size and plant quality and quantity in an effort to maximize energy intake with minimal energy expended on seeking and obtaining food items. Use of winter range by moose, however, is complex because moose must deal with patchy distributions of forage items and thermal cover, as well as battle deep snows that bury and reduce the availability of browse and impede mobility. The presence of predators such as wolves can also influence how and when moose feed on wintering grounds (Ripple and Beschta 2004). In these respects, ideally each bite of winter browse taken by a moose should be directed at maximizing biomass and nutrient intake per cropping effort.

Well-established is the relationship between browse shoot morphometry and shoot digestibility (Hjeljord et al. 1982, Danell and Bergström 1989, Palo et al. 1992). The bark to woody cortex ratio is higher for smaller shoots and lower for larger shoots (Hjeljord et al. 1982). In general, both major nutrients and secondary defensive compounds are stored in the bark (Pehrson 1984, Tahvanainen et al. 1985) while the woody cortex contains more structural components such as cellulose and lignin –

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[1] Hectares BC is a multi-agency geospatial analysis tool that allows scientists, researchers, government and others to access and work with geographic information in the natural resource area and can be found at: http://www.hectaresbc.org/app/habc/HaBC.html

increasing structural, but minimizing nutritious (and defensive) components in larger shoots. Despite this relationship, large shoots comprise an important component of the moose diet (Penner 1978; Machida 1979; Danell et al. 1985*b*; Risenhoover 1987).

Large shoots are regularly produced in plant crowns and are reportedly preferred by moose over smaller lateral shoots (Bryant and Kuropat 1980, Heikkilä and Härkönen 2000). However, moose also select large compensatory shoots produced by plants following severe browsing, breakage, cutting, and other forms of damage (Bryant and Kuropat 1980, Danell et al. 1985*a*, Nellemann 1990, Stephenson 1995). The size, chemical composition and, therefore, attractiveness of compensatory shoots to moose, however, appear to relate specifically to the amount of crown tissue removed during the damage event which caused the production of such shoots. Compared to light browsing, severe browsing and cutting lead to significant losses of stem and shoot biomass and growing points. Large imbalances in root:shoot ratios lead to more resources being directed to fewer growing points which influence both size and quality of new shoots produced following damage (Bergström and Danell 1987, du Toit et al. 1990, Hester et al. 2004).

The influence of cutting time

Plant compensatory responses from cutting (Hardesty et al. 1988, Douglas et al. 1996, Oppong et al. 2002) and clipping (Guillet and Bergström 2006, den Herder et al. 2009) depend largely on the season of damage. In general, plants damaged during plant dormancy will respond more vigorously than plants damaged during the growing season (Kays and Canham 1991, Del Tredici 2001). For example, willows clipped to simulate deer browsing (Guillet and Bergström 2006) and cut to simulate beaver (*Castor canadensis* L.) browsing (Kindschy 1989) were less able to compensate for damage when treatments were performed in summer than when treated in winter. Reduced resprouting and suckering of immature aspen (*Populus tremuloides* L.) occurred when cutting was performed after leaf flush relative to cutting before leaf flush (Weber 1990). Early summer sheep (*Ovis aries* L.) grazing on shrubs increased, but late summer grazing decreased, the subsequent quality of winter browse produced on grazed plants, but was species dependent (Alpe et al. 1999). These results suggest that cutting influences plant response and quality and that the impact of brush-cutting on these attributes cannot be accurately predicted without accounting for the time of cutting.

Objectives

In this thesis, I examine and synthesize 15 years of research that was conducted in northern British Columbia on hardwood plant response to brush cutting. I investigated and present here how the season of cutting stems (brush cutting) and cutting twigs (clipping and browsing) of deciduous shrubs and trees influenced plant compensatory response. I focused primarily on the impacts that the season of brush cutting had on browse production and quality (chemical, morphological and phenological) for moose in the years after cutting. How moose selected shoots of uncut plants of various species compared to compensatory shoots from plants cut at different times of the year was also investigated and is presented.

I collected and assessed winter shoots because of the importance of browse in the winter diets of moose, but also to control better for rapid changes in plant phenology which occur in spring and summer (Owen-Smith 2008) and because the feeding trials that I conducted with moose were only possible during the winter months (i.e., adult moose were absent from the wildlife shelter with which I collaborated from April through December each year).

The specific goals of this thesis are to:

1) Compare the influence of cutting stems (brush cutting) and twigs (simulated browsing) on plant response and browse production and quality for moose (papers 1 and 2).
2) Describe specifically, the influence of time (season) of cutting and simulated browsing on browse production and quality of winter browse for moose (papers 3, 4, 5, and 6).
3) Determine moose forage preferences for winter shoots of cut and uncut plants of different species (papers 7, 8, 9, and 10).
4) Provide recommendations for how to use brush-cutting as a tool to influence moose browsing in forest plantations and linear corridors (papers 3, 4, 9, 10, and 11).

STUDY AREA

This thesis is based on research conducted in northern British Columbia (Figure 2) through the University of Northern British Columbia between 1995 and 2010.

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Sa Majesté la Reine du chef du Canada, Ressources naturelles Canada.

Figure 2. Map of British Columbia, Canada indicating the area (circled) in which the research described within this thesis was conducted.

LIST OF PAPERS

This thesis consists of the following 11 papers, referred to by their Roman numerals and organized according to the objectives stated in the introduction.

Paper I
Rea, R.V., and M.P. Gillingham. 2007. Initial effects of brush-cutting and shoot removal on willow browse quality. Rangeland Ecology and Management 60: 566–573.

Paper II
Rea, R.V., and M.P. Gillingham. 2008. Effects of plant compensation across sites on regression estimates of shoot biomass and length. Alces 44: 21–30.

Paper III
Rea, R.V., and M.P. Gillingham. 2001. The impact of the timing of brush management on the nutritional value of woody browse for moose *Alces alces*. Journal of Applied Ecology 38: 710–719.

Paper IV
Rea, R.V., K.N. Child, D.P. Spata, and D. MacDonald. 2007. Influence of cutting time on brush response: Implications for herbivory in linear (transportation) corridors. Environmental Management 40: 219–230.

Paper V
Carson, A.W., R.V. Rea, and A.L. Fredeen. 2009. Compensatory shoot growth in trembling aspen (*Populus tremuloides* Michx.) in response to simulated browsing. Alces 45: 101–108.

Paper VI
Carson, A.W., R.V. Rea, and A.L. Fredeen. 2007. Extent of stem dieback in trembling aspen (*Populus tremuloides*) as an indicator of time-since simulated browsing. Rangeland Ecology and Management 60: 543–547.

Paper VII
Rea, R.V. 2010. Impacts of moose (*Alces alces*) browsing on paper birch (*Betula papyrifera*) morphology and potential timber quality. Silva Fennica 45: 227–236.

Paper VIII
Rea, R.V., O.G. Hjeljord, and M.P. Gillingham. Factors influencing willow and birch shoot selection and biomass consumption by moose in winter *(Submitted)*

Paper IX
Rea, R.V., K.N. Child, D.P. Spata, and D. MacDonald. 2010. Road and rail side vegetation management implications of habitat use by moose relative to brush cutting season. Environmental Management 46: 101–109.

Paper X
Rea, R.V., D.P. Hodder, O. Hjeljord, and A. Langen. 2010. Paper birch (*Betula papyrifera*) shoot selection by moose (*Alces alces*) following a forest-cleaning experiment. Scandinavian Journal of Forest Research 25: 157–163.

Paper XI
Rea, R.V. 2003. Modifying roadside vegetation management practices to reduce vehicular collisions with moose. Wildlife Biology 9: 81–91.

SYNOPSIS

Here, I present a summary of results from the eleven papers cited above in order of their listing.

Plant response to damage

Plant attributes altered by clipping and cutting
(Papers 1, 2, and 3)

My research indicates that hardwood plants such as willow and paper birch (*Betula papyrifera* Marshall) responded morphologically and chemically to tissue damage from browsing and clipping. Increasing levels of shoot removal generally led to more plant resources being directed to fewer buds and shoots that subsequently produced larger "compensatory" shoots (papers 1, 2, and 3) with higher fiber content and lower digestibility, but also reduced levels of defensive (tannin and lignin) compounds (papers 2 and 3). However, such plant responses varied by species and were dependent on factors such as growing site and forms and degrees of damage (papers 1, 2, and 3). Although increasing levels of damage tended to stimulate the production of larger, more fibrous shoots in browse plants, repeated intense damage had the opposite effect in the years immediately following damage (paper 1), suggesting cumulative impacts (such as intense browsing preceded by cutting) can inhibit compensation.

More severe forms of above-ground biomass removal such as brush cutting also caused plants to adopt a compensatory growth form, with plants generally taking on a more multi-stemmed, shrubby architecture (papers 1 and 3; Figure 1, inside cover). Damage from cutting also changed the morphometry (length to weight to diameter relationships) of current annual shoots (paper 2). Brush cutting delayed autumn leaf senescence in cut plants longer than in controls and some delays in spring leaf flush were detectable in brush-cut plants (paper 3). Specifically, how leafing phenology and other forage attributes were affected by brush cutting, however, depended on the time of the year that brush cutting was conducted.

Impacts of cutting time on plant architecture, shoot morphology and chemistry, and leafing phenology
(Papers 3, 4, 5, and 6)

Stem and shoot removal reduces above-ground biomass and browse resources for herbivores in the short term. Just how long resources were unavailable depended largely on the severity of damage (cutting vs. clipping and percentage of biomass removal) and the time of the year that tissues were experimentally removed (papers 3, 4, 5, and 6).

Plant architecture

Plants brush cut between the onset of dormancy and spring leaf flush grew and developed over the course of the following growing season, producing vigorous compensatory regrowth and reconstructing crown tissues that were then available as fall and winter browse. Plants cut during the growing season, however, produced relatively little to no fall and winter browse in the year of cutting, albeit varying degrees of compensation continued in the years subsequent to the year of cutting (papers 3 and 4). Effects on plant compensation and subsequent architecture following cutting lasted for several years (papers 1 and 4) and were influenced by cutting time. Plants cut early or late in the growing season were taller on average than those cut during the middle of the growing season (but in both cases much shorter than controls; paper 4) 3 years after cutting, albeit post-cutting crown development appeared to depend largely on species autecology and tissue use by herbivores in the years after cutting.

Shoot morphology

Crown reconstruction and resulting plant height was dictated by the degree of resprouting following cutting, with plant height in the first year after cutting being a product of compensatory shoot length (paper 3). Not surprisingly, Scouler's willows (*Salix scouleriana* Barratt ex Hook.) cut early in the growing season produced longer, heavier and thicker shoots by the fall after cutting relative to willows cut later in the summer (paper 3). In a different experiment, willows, twinberry (*Lonicera involucrata* (Richardson) Banks ex Spreng.) and birch revealed similar patterns of growth following cutting (paper 4). However, patterns of shoot growth became less predictable in years subsequent to the year of cutting, with plants cut later in the season generally producing larger shoots in the second year after cutting (papers 3 and 4). Three years after cutting, plants cut in the middle of the growing season produced the smallest shoots of all cutting treatments (paper 4). Although combined shoot and leaf biomass produced by aspen in spring was greater for plants clipped (not cut) during the previous June and August relative to controls, the relationship of post-treatment biomass production to time of clipping was less clear than in cut plants (paper 5).

Shoot chemistry

The long-term effects of cutting time on winter twig chemistry remain unstudied. However, cutting time did influence lignin, tannin, digestible energy, and digestible protein levels (and several mineral elements; Rea 1999) in willow shoots for the first 2 years after cutting (paper 3). Willows cut later in the year (July) produced shoots that contained less lignin than shoots of earlier- (June-) cut or uncut controls; tannin was also less concentrated in the shoots of these plants in the first winter after cutting. Winter shoots of late-cut willows contained more digestible energy and protein than those cut earlier in the previous growing season, but had less energy and more protein than uncut controls (paper 3). Tannin, lignin and digestible energy and protein levels were lower in the shoots of plants cut later in the growing season than those cut earlier or from controls in the second winter after cutting.

Leafing phenology

Brush cutting altered plant chemistry and phenological development (papers 1 and 3) that altered spring leaf flush and fall leaf senescence (and therefore leafy forage availability) for different plant species in different ways for several years after cutting (papers 3 and 4). Spring leaf flush occurred earlier for willows cut earlier during the previous growing season compared to those cut later (papers 3 and 4), while twinberry plants cut in June and August flushed leaves earlier in the following spring than those cut at other times, but not earlier than controls (paper 4). Changes to the timing of leaf flush following cutting continued for up to three years in some species after cutting, but showed less clear patterns in the timing of leaf flush in response to cutting as time-since-cutting elapsed (paper 4).

An extension of the growing season as measured by delays in leaf senescence revealed that plants cut later in the growing season generally delayed senescence longer into fall than uncut plants or those cut earlier for several years after cutting (papers 3 and 4), albeit delays in senescence and how many years after cutting those delays occurred were species-dependent (paper 4). Brush-cut willows and twinberry plants delayed senescence beyond uncut controls in the first year after cutting (papers 3 and 4) with plants cut later in the growing season generally delaying senescence as long, or longer than plants cut earlier in the year (papers 3 and 4). Twinberry (paper 4) and willow (paper 3) plants cut in the late summer also exhibited some delays in leaf senescence compared to earlier-cut and uncut plants in the second year after cutting, but site and year effects were apparent. Willows cut in August delayed senescence in the third year after cutting (paper 4).

Changes to plant architecture, leafing phenology, and shoot morphology and chemistry influenced the hardwood plants I studied and how they grew, but also influenced how moose used them for food in winter.

Moose (winter) foraging ecology

Browse selection
(Papers 7, 8, 9, and 10)

Moose used fewer twigs (biomass) and appeared to be more selective in their choice of shoots when browsing hand-assembled thickets of willows of higher density, but removed more biomass from less dense thickets (paper 8). This type of selection may help to explain why birch trees growing in the Aleza Lake Research Forest were browsed significantly more when growing farther away from other trees in regenerating forest stands (paper 7). Here, birch trees growing in more open sites were increasingly hedged and stunted in growth (and consequently had lower wood quality) as a result of recurrent browsing and stem breakage. Such repeated use suppressed vertical crown development and kept compensatory shoot production within the reach of moose (papers 7 and 9).

Plants containing more and larger shoots provided more potential browse biomass for moose in the winters after cutting, but only insofar as shoots remained within the reach of moose and above the snow pack. However, even plants recovering from brush cutting that had crowns fully available for moose to browse were not fully depleted, with moose on average consuming anywhere between 0.5 (uncut twinberry) and 82.2 (uncut birch) percent of current annual shoots over the course of a winter (paper 9). Although untested in my thesis, varying levels of consumption of plants resprouting from differently-timed cutting treatments may have been attributable to several factors such as plant height, availability above the snow pack, and previous use of shoots by other animals. Additionally, biomass consumption is also directly linked to the standing biomass of individual plants (paper 8) and presumably the size (papers 9 and 10) and chemistry of shoots.

Determining levels of shoot consumption from plants cut at different times of the year was easiest to document by conducting feeding trials. Results from cafeteria-style trials clearly indicated a preference of moose for individual shoots of smaller size, regardless of when the plants-from which the shoots were harvested-had been cut (paper 10). In trials with whole plants that had not been previously cut or browsed, standing plant biomass (the pre-feeding trial weight of plants) was the major determinant in how much biomass moose consumed. Moose also removed more cumulative shoot length from more massive plants, but the degree to which this happened varied by species and the density of plants presented in the trial (paper 8); factors such as the number of days moose fed on any given species and the position of a plant within the larger thicket also influenced consumption (paper 8). Together, such findings reveal that the selection of browse items (from either previously-cut or uncut plants) by moose is complicated and can only be partially explained by shoot morphometry and chemistry.

Moose and plant compensation
(Papers 9 and 10)

Moose preferentially cropped small shoots and tips of larger compensatory shoots in cafeteria trials, but browsed down to larger shoot diameters as smaller shoots and shoot tips became depleted (papers 8 and 10). The compensatory resprouts and suckers of willows, birch, alder (*Alnus* spp. Mill.) and twinberry were browsed by moose in the year after brush cutting (paper 9) and then repeatedly browsed (but to lesser extents) in subsequent years. My field studies in the Aleza Lake Research Forest, indicate that moose repeatedly hedged pole-sized paper birches year after year in the process of browsing and rebrowsing compensatory shoots (paper 7). My observations indicate that moose generally appeared to be accustomed to browsing compensatory shoots extensively throughout all of my study sites in northern BC– with some shoots being browsed to smaller and some to larger diameters. Similar patterns of rebrowsing particular plants year after year are evident on shrubs and trees in moose winter ranges in the Cape Breton Highlands, Nova Scotia; Terra Nova Park, Newfoundland; Isle Royale, Michigan; Yellowstone National Park, Wyoming; Biebrza Valley, Poland; and Telemark County, Norway (personal observations) and is likely widespread throughout the range of moose.

Browse plant management

Influence of brush cutting practices on browse resources
(Papers 3, 4, 9, and 10)

Brush cutting, like severe browsing and stem breakage by moose (paper 7), drastically altered plant architecture, lowered plant crowns and ultimately increased browse availability (paper 4). Unlike stem breakage, however, twig availability (along with all above-ground biomass) was initially eliminated in these brush-cutting or cleaning operations, as was the intention with such treatments (Härkönen et al. 1998).

My research results suggest that the “release” of coniferous crops from hardwood competition following brush cutting is short-lived. Brush-cut plants generally began to compensate for damage in the first growing season after cutting by producing relatively large root suckers and stump sprouts (papers 1, 2, 3, 4, and 10) with large leaves (Rea and Massicotte 2010), and altered shoot chemistry (papers 1 and 4). The magnitude of response and size of compensatory shoots and leaves produced after cutting, however, was influenced by cutting time (papers 3, 9, and 10), with plants cut at certain times (generally during plant quiescence and dormancy) producing as much as 2 to 4 times the browse biomass as uncut controls (papers 4 and 10).

Plants cut late in the growing season and fall resprouted minimally or not at all before plant dormancy and were unavailable as browse in the winter after cutting, while those cut earlier were available as food in the fall, early winter, and in the spring after cutting (papers 3 and 4). Plants cut later in the year or those cut before the growing season, however, produced relatively more browse in the first full growing season after cutting. Such plants generally continued to produce large shoots and leaves and extend their growing seasons into autumn for several years after cutting (papers 3 and 4), but delayed senescence was heavily influenced by the degree to which animals browsed compensatory shoots in the first and subsequent post-cutting years.

Strategic brush management
(Papers 3, 4, 9, 10, and 11)

Cutting changed the relationship of moose to those plants upon which they foraged for several years after cutting. Cutting lowered plant crowns, altered shoot morphometry (paper 3), reduced shoot digestibility and phenolic content (papers 1 and 3), and delayed leaf senescence (paper 3). However, changes to browse quality varied by growing site (papers 1 and 2) and importantly varied with season of cutting (paper 3).

Brush cutting that was conducted between root reserve exhaustion (leaf flush; mid-May to mid-June in northern BC) and replenishment (June-July; Kramer and Kozlowski 1979) appeared to limit plant compensatory response and browse production, particularly in the first two years after cutting (paper 9). Shoots produced by plants cut in June and July were moderately-sized (papers 3, 4, and 10), produced lower levels of browse biomass than those cut later (paper 4) and contained more tannin, but had similar digestibility levels when compared with plants cut later (paper 3). Cutting at this time also caused less of a delay in leaf senescence than when cutting was done before or after leaf flush.

My research and review of the literature (paper 11) indicates that brush cutting in June and early July should minimize resprouting and the attractiveness of browse to moose. Such cutting should minimize browse use by moose and may be well-suited for managing brush in areas that moose are unwanted (i.e., road and rail corridors). Stimulating the production of increased browse biomass and shoot attractiveness through cutting before or after leaf flush, on the other hand, could increase browse attractiveness and may be appropriate for the management of remote rights-of-ways or even conifer plantations where browsing moose pose little, if any, threat. Cutting at this time may even help to control hardwood growth (assuming moose are not feeding on conifers as well; i.e., European moose eating Scots pine).

DISCUSSION

Plant response to mechanical damage

Browsing, clipping and cutting all lead to the removal of stem and shoot tissues and result in damages to plants. How plants respond morphologically and physiologically to this type of damage depends on several factors examined in my thesis, including severity of damage, how often damage occurs, plant species, growing site, and season/timing of damage (Maschinski and Whitham 1989, Canham et al. 1994, Danell et al. 1994, Houle and Simard 1996, Del Tredici 2001, Lindroth et al. 2007).

Severity of damage

Although light browsing/clipping appeared to have little impact on woody shrubs and trees in my (paper 1) and other studies (Bergström and Danell 1987, Edenius et al. 1994), more severe forms of browsing, stem breakage, and brush cutting altered plant architecture, subsequent growing patterns, and the availability and quality of compensatory growth for moose here (papers 1, 2, 3, 4, 7, and 9) and elsewhere (Telfer and Cairns 1978, Bergström and Danell 1987, Molvar et al. 1993, Stevenson et al. 1998, Persson et al. 2007). Changes to plant architecture and growth form following severe browsing have been documented in many species including willow, birch and acacia in response to feeding by hare (Bryant 1981, 2003), moose (Bergström and Danell 1987), and African savannah browsers (Du Toit et al. 1990), respectively. Generally, heavy browsing stimulates future increases in browse availability for herbivores (Rooke et al. 2004) while stunting vertical plant development through hedging (Danell and Bergström 1989, Romero-Manzanares and García-Moya 1990, Gadd et al. 2001, Best et al. 2003, Guillet and Bergström 2006, Keigley and Frisina 2008).

Loss of shoot materials to severe damage reduces nodal and inter-nodal shoot materials and associated buds, thus reducing the number of available growing points for subsequent shoot development (Danell et al. 1985*b*, Danell and Bergström 1989). This imbalance in root to shoot (and shoot bud) ratios results in a reallocation of root reserves to fewer growing points in subsequent growing seasons, which I (papers 1, 3, 4, 10) and others (Bergström and Danell 1987, Du Toit et al. 1990, Hester et al. 2004) found caused plants to produce fewer, but larger shoots after damage, but also shoots lower in digestibility, and tannin and lignin concentrations (papers 1 and 3).

Increases in shoot size following severe damage are often accompanied by a longer plant growing period/season (McNaughton 1983, Xue et al. 2013) as indexed by green leaf retention (delayed senescence) in fall, but also early leaf flush in spring (Kindschy 1985). Such increases are thought to be a result of the particular phenological stage of the plant at the time of cutting, plant rejuvenation, and the reallocation of existing nutrients to relatively fewer shoots (Millington 1963, Larson 1978, Tuomi et al. 1989, Danell et al. 1997). Extensions in the growth period usually last as long as plants continue to compensate for lost shoot biomass (Willard and

McKell 1978), which according to the delays I detected in leaf senescence and spring leaf flush (papers 3 and 4), may be as little as 3 to 4 years after cutting, but as discussed below, were influenced by cutting season.

Repeated damage

Repeated damage can alter plant compensatory responses (Tsiouvaras et al. 1986, Latt et al. 2000) and result in root reserve exhaustion, further altering browse availability and quality and possibly killing plants (Dodds 1960, Krefting et al. 1966, Wright 1970). I found no evidence that brush cutting or a combination of cutting and subsequent clipping/browsing killed hardwood shrubs and trees with which I experimented in interior BC (albeit this phenomenon does appear to occur locally with red osier dogwood (*Cornus stolonifera* Michx.; *personal observations*). However, I did find evidence that brush cutting followed by severe winter clipping/browsing reduced regrowth vigor (winter shoots were smaller) and altered shoot chemistry (tannin content increased) in willows in the short-term (paper 1). Also severe stress from repeated clipping (simulated moose browsing) impacted birch compensatory responses in Sweden by stimulating the production of larger shoots with lower chemical nutrients, but varied in degree between species (Danell and Bergström 1989).

Species-specific responses

Resprouting and compensatory ability following damage varies widely by species (Sipe and Bazzaz 2001, Hester et al. 2004, Neke et al. 2006, Vesk 2006). Birch, willow, alder and twinberry all responded differently to my cutting treatments and subsequent browsing by moose (papers 4 and 9), suggesting as others have (Canham et al. 1994, Van Hees et al. 1996), that species-specific accounting be considered when quantifying compensatory responses. Such taxa-specific responses appear to be the result of differences in plant apparency, growing site productivity, vascular connections, and life history traits such as longevity (Herms and Mattson 1992, Strauss and Agrawal 1999, Haukioja and Koricheva 2000, Stowe et al. 2000, Pakeman 2004, Persson et al. 2007). Riparian species such as willows that have evolved in disturbed environments, for example (Keoleian and Volk 2005, Kusovkina and Volk 2009), are better adapted to stream bank scouring and beaver cutting than other hardwoods and may be capable of more vigorous resprouting (Kindschy 1985), which is one reason that species such as willows and their close relatives are used as perennial biomass coppice crops (Kusovkina and Volk 2009). Postulated differences in autecology and physiology between hardwoods (such as birch) and conifers contributed to different responses to simulated moose browsing, but were moderated by growing site conditions (Persson et al. 2007).

Site effects

The morphometry of willow winter shoots that I studied in northern BC varied between cut and uncut plants, but also varied significantly by site (paper 2). Sites upon which plants grew proved to be influential in determining various morphometric and chemical attributes of willow shoots produced after the combined effects of cutting and clipping (papers 1 and 2). Growing site has been demonstrated to influence plant growth and response to various forms of damage (Danell and

Bergström 1989, Danell et al. 1991, Sipe and Bazzaz 2001, Pakeman 2004, Vesk 2006, Fryxell 2008), with site attributes such as plant density, soil conditions, moisture, and nutrient regimes being factors most likely to influence plant response (Hjältén et al. 1993, Sipe and Bazzaz 2001, Osem et al. 2004, Persson et al. 2007). Soil fertility (total nitrogen) and moisture gradients were used to explain resprouting in woody plants after fire in Australia (Clarke et al. 2005). Persson et al. (2007) suggested that soil nutrients and/or water on different sites also helped explain plant responses to clipping treatments, but further underscored the need to consider how different species responses vary with site productivity and the times of the year that plants are browsed.

How season of damage influences plant response

Findings presented herein agree with Marquis (1996) and Maschinski and Whitham (1989) that the timing of damage and the phenological stage of the plant at the time of damage are critical to determining plant response. In my experiments, significant changes to the morphological, chemical, and phenological attributes of browse plants resulted from tissue removals in different seasons, but varied depending on the type/degree of damage. Timing had a significant influence on patterns of shoot dieback in lightly-clipped aspen stems (paper 6), but very little influence on morphological and phenological aspects of plant compensation, even though clipped stems produced more biomass after clipping than controls (paper 5). Meanwhile, season of brush cutting substantially determined compensatory (winter) shoot morphology and leafing phenology in willow (paper 3), birch (papers 4 and 10) and several other hardwoods (paper 4) and altered (winter) shoot chemistry in willow (paper 3).

Effects of season of cutting and clipping

Season of cutting is known to alter plant suckering and resprouting ability with plants cut during plant dormancy producing significantly larger shoots than those cut in the growing season (DeBell and Alford 1972, Kays and Canham 1991, Xue et al. 2013). Such effects are due to the heavy reliance of hardwoods such as willow and birch on stored root reserves to subsidize resprouting after cutting (Kays and Canham 1991); which I found influenced winter browse quality in the years after cutting (papers 3, 4, and 10). Birches cut in May and June produced shoots 4 and 2 times larger respectively, when measured in the winter after cutting than shoots measured on controls (paper 10), but such responses were species-specific (paper 4). Similar results have been reported for a variety of other plants by several other authors (Hardesty et al. 1988, Oppong et al. 2002, Guillet and Bergström 2006).

Kays and Canham (1991) examined species-specific responses to cutting and attributed such responses to differences in life history growth patterns (determinant vs. indeterminant growth) with seasonal effects attributed to the ability of plants to sprout in late summer (indeterminant species), root reserve quantities, and plant phenological stage at the time of cutting. They suggested that plants cut before or after the growing season (when root starch reserves were elevated) were more capable of a vigorous compensatory response than when resources were directed to photosynthesis and reproduction and noted, as I did (papers 3 and 4), that cutting season influenced the timing of leaf senescence.

Generally, I noted longer delays in leaf senescence, but also delays in leaf flush, when plants were cut later in the growing season, albeit plants cut during plant dormancy delayed senescence (and thereby provided green leafy forage) longest (paper 4). Kindschy (1989) similarly noted an extension of the growing season for willows cut to simulate beaver cutting in June and July. Changes to leafing phenology in my experiments were most prominent in the year after cutting and varied by year-since-cutting and species. As reported by Marquis (1996), such changes likely depended on whether different species used stored resources or current assimilates for reproduction–which may also help to explain differences in shoot size to nutrient content ratios.

Although less studied than cutting, plant response to season of clipping/browsing is equally likely to be governed by plant phenological stage and carbohydrate reserve levels in roots, but also reserves in stems (Hester et al. 2004) which are removed during cutting, but not clipping. Wright (1970) studied the influence of intense (80%) clipping on sagebrush and discovered that clipping reduced subsequent yields least when done in fall and most when done in mid-summer; he contended that carbohydrate reserve levels and differences in plant phenology could be used to explain differences.

Plants clipped or browsed later in the growing season are more likely to suffer from lower nutrient availability, delayed phenological status, and a truncated growing season than those damaged earlier or during dormancy (Maschinski and Whitham 1989). Tissue removal from clipping or browsing is least costly for plants when done during plant dormancy when nutrient and carbon capital are housed in stems and root tissues, and most costly in spring and summer when newly expanding leaves and shoots are acting first as resource sinks–but then once developed–as carbon sources (Skarpe and van der Wal 2002).

Although tissue and nutrient losses stress plants regardless of site conditions, plants growing on nutrient-poor sites may allocate more nutrients to defense over growth following damage (Bryant et al. 1983). Therefore, effects of season of cutting (or severe clipping) and site appear to interact to influence browse production and quality (papers 1 and 3), albeit my current works were not designed to test such interactions. Nevertheless, compensatory shoot biomass was larger, and lignin and tannin concentrations lower, in brush-cut relative to uncut willows (papers 1 and 3) with clipping intensity influencing the magnitude of plant response (paper 1). Here, I found defensive compounds to be lower in plants cut from early- to mid-summer in the first, and mid- to late-summer in the second, winter after cutting, which underscored the influence of cutting time and time-since cutting on plant response.

The relationship of shoot size to shoot nutrient content that I report above, and has been reported by others (Hjeljord et al. 1982, Risenhoover 1987), was altered in the compensatory shoots of plants cut previously at different times in the growing season. Although we did not measure changes to shoot chemistry following seasonal clipping trials, willows cut in July were significantly more digestible (had less fiber, but more gross energy and crude protein) than shoots growing from plants cut at other times of the growing season that had similar-sized shoots (paper 3). Furthermore, lignin and tannin concentrations in willow shoots varied by cutting season with lignin concentrations being lower in the shoots of plants cut later in the growing season, for up to two years after cutting. Such changes, due to cutting season, may be related to how stored resources or current assimilates are being translocated and used at the time of cutting (Bryant et al. 1991, Marquis 1996, Lindroth et al. 2007), but are unknown and require further research (Danell and Bergström 1989).

Clearly, cutting and severe clipping both damage plants and stimulate compensatory growth. If such damage occurs sometime during plant dormancy, plants can use remaining tissue reserves to mount vigorous compensatory responses (Kays and Canham 1991, Kozlowski and Pallardy 1997), producing large shoots which flush leaves earlier in spring and delay leaf senescence in fall. Plants cut late in the growing season have lower tannin and lignin concentrations, but also lower digestibility in winter, while plants cut during the growing season mount similar, but less exaggerated responses; presumably, intense clipping in these seasons would reveal similar responses. However, such responses are also likely to be moderated by myriad factors present during the growing season (e.g., hot, dry days, insects, and certain pathogens), which are absent during plant quiescence and dormancy. Consequently, how moose perceive and use such growth will depend on how plants, at a particular stage of phenological development, allocate resources to compensatory shoots.

Moose winter feeding and shoot selection

Leaves comprise an important component of the moose diet. Leaves are especially important to moose in late fall and early spring (Renecker and Hudson 1985, 1986, Schwartz et al. 1988, Danell et al. 1994, Renecker and Schwartz 1998) because they provide a readily accessible pool of nutrients (Blair et al. 1980, Chapin 1980) to moose at a time of the year when nutritious foods are otherwise difficult to locate (Hardesty et al. 1988). When foraging on leaves, moose and many other herbivores will select the greenest leaves available (Bergerud and Manuel 1968, Hobbs et al. 1981, Renecker and Hudson 1985, Regelin et al. 1987, Owen-Smith 2008), suggesting that moose are likely to be attracted to the early flushing and late senescing leaves of brush cut plants, albeit only twig- and not leaf-eating behaviors of moose were tested in this thesis.

I (papers 1, 3, and 11) and others (Penner 1978, Risenhoover 1987, Schwartz 1992, Bowyer and Bowyer 1997, Stolter 2008) have maintained that moose choose large shoots when browsing in winter and often select shoots of previously-damaged plants (Danell et al. 1985*b*, Singer et al. 1994). This selection is presumably due to changes in the morphology and chemistry of compensatory growth that make these large shoots more palatable and easy to browse (Danell et al. 1985*b*), and also enables moose to increase bite size and intake rates per cropping effort (Vivås et al. 1991, Shipley and Spalinger 1992, 1994; Gross et al. 1993, Shipley et al. 1999). However, larger shoots are more fibrous, less digestible and more difficult to fracture and may increase energy expenditures required for processing (Shipley et al. 1999). If moose are cropping at large bite diameters from plants without compensatory shoots, bites are more likely to include older, more fibrous stem materials that will further reduce digestibility and nutritional value (Hjeljord et al. 1982, Wolfe et al. 1983, Vivås and Sæther 1987).

Experiments that I conducted with human-habituated moose using both previously-cut and uncut plants (see papers 8 and 10), suggest that moose do crop winter shoots at large diameters, but mix those bites with small diameter shoots if available, regardless of whether or when plants had been previously damaged. Although not specifically measured, my observations indicate that initial (first pass) smaller diameter bites were likely to be as filling as bites taken in the second or third pass when moose recropped shoots at larger diameters. When allowed to take no more than two bites from stems, moose cropped winter shoots of willows at an average diameter of 3.7mm (Rea 2012), compared with an average of 4.5mm when moose had more time to browse (papers 8 and 10). By virtue of crown architecture, smaller shoots were connected to other smaller shoots above the point at which moose cropped their initial bites. Fewer shoots were connected to thicker portions of the stem, leaving moose retaking larger bites with thicker, but fewer shoots per mouthful. In general, both moose and deer are known to crop larger dormant shoots as shoot density declines (Vivås and Sæther 1987, Shipley and Spalinger 1995), but paradoxically will also select smaller bites as time available for foraging increases (Shipley et al. 1999) assuming an abundance of small shoots is available and competitive influences from conspecific browsers absent.

The diameters to which moose cropped shoots also depended on species-specific shoot morphology. Moose were incapable of browsing thicker-stemmed willows to the smaller diameters found on the shoots of species such as twinberry. Moose browsing large diameter pine shoots were similarly unable to take smaller bite diameters that characterized their browsing of species such as Douglas fir with smaller current annual shoots (Rea et al. 2013). Belovsky (1981) reported similar differences in how moose on Isle Royale, Michigan browsed smaller diameters of the more “plate-like” branch and needle architecture of cedars when compared to thicker-stemmed pines from which they took large bite diameters. Larger mean diameters of shoot tips of *Sorbus aucuparia* also constrained moose and deer browsing to much larger bites of that species when compared to species with smaller shoots (Shipley et al. 1999). Why moose browse at large diameters on species such as pine and *Sorbus* sp. with large shoots is partially explained by shoot morphology. Why moose browse only at small and not large diameters on species such as Douglas fir or birch (paper 8) appears to be more complex.

Browsing smaller shoots that have larger surface area to volume ratios enables moose to increase the intake of bark to wood and therefore the ratio of nutrient to fiber content (Eastman 1984, Danell and Huss-Danell 1985, Radwan and DeBell 1988, Schwartz 1992). Smaller shoots are higher in digestible protein and energy (Bryant et al. 1985, papers 1 and 3)–both of which are important in diet selection by moose (Regelin et al. 1987, Robbins et al. 1987*a*, Schwartz et al. 1987). Consumption of smaller shoots also requires less masticating and processing (Gross et al. 1993, Shipley et al. 1994, 1999) and may have been important to moose in our short-term experiments. Like nutrients, however, anti-herbivore chemicals such as tannins are also stored in and under bark tissues (Bryant et al. 1991, Palo 1984, Millard et al. 2001) endowing smaller shoots with relatively more tannin, and potentially making smaller shoots less palatable (Palo et al. 1992, Shipley et al. 1999), thus possibly influencing longer-term diet choices in moose (Stolter et al. 2005).

Tannin levels are relatively low in winter shoots (Hagerman and Robbins 1993), but nevertheless can reduce protein and dry matter digestibility (Robbins et al. 1987*a*; Robbins et al. 1987*b*; Hagerman et al. 1992) or may act as toxins (Mehansho et al. 1987). These chemicals may concentrate in the winter tissues of some species (Palo 1984). Tannins and other phenolics such as lignins are known to play a role in diet selection (Bryant et al. 1983; Coley et al. 1985; Robbins et al. 1987*b)* and as revealed by some authors, are directly correlated with decreases in winter browse consumption (Stolter et al. 2005). Clearly, moose are faced with trade-offs between consuming fiber, nutrients and chemical deterrents with every bite taken from large or small shoots or portions thereof.

My results combined with those of Vivås and Sæther (1987), suggest as previously discussed, that moose initially select smaller, more digestible shoots when browsing, but then in the process of re-cropping the same plant, shift to the consumption of larger materials as resources become depleted. Additionally, moose are likely to eat small twigs under some circumstances and large twigs under others, even within the same feeding spell (Owen-Smith 2008) in an effort to balance fiber and nutrient intake. Clearly, the diameter to which moose browse and the shoot biomass they remove from each plant will depend on the time spent browsing each plant, but also myriad other factors.

Winter browse abundance is a product of plant density and architecture (plant height, shoot density and shoot size; Persson et al. 2005). Nutrient and toxin levels (as well other biotic and abiotic factors) being equal, moose should select areas with higher browse abundance. These factors will influence the number of visits that moose make to plants, what parts of the plants moose will browse, and how often (Edenius 1991). Of the many scales at which moose select food–predominantly one (individual tree level) –was studied here. Some attention was given herein to patch (thicket)-level browsing (paper 8), but only as it related to pressure exerted by moose in timed trials on small tree patches made up of hand-assembled densities of individual birches and willows. These experiments revealed that individual plant- and thicket-level biomass consistently influenced the way in which moose browsed on plants. The position of plants within thickets, thicket density, and other factors also helped to partially explain moose winter browsing, but less consistently than plant biomass. All else being equal, moose simply ate more from more massive plants.

CONCLUSIONS AND RECOMMENDATIONS

Moose will select patches and feeding sites and spend more time in habitats where forage is more abundant, nutrients are more concentrated, and toxin levels are lower (Bailey and Provenza 2008). Forage availability and quality will dictate feeding patterns, habitat selection, and animal distributions (Bailey and Provenza 2008), with the amount of time spent by animals in feeding patches being proportional or “matched” to forage quantity and quality (Senft et al. 1987). The brush cutting, clipping, and browsing treatments presented here influenced the morphological, chemical, and phenological attributes of plants which altered this moose-plant “matchability”.

As discussed throughout the above pages, tissue removal generally caused plants to extend their growing season and produce large shoots high in fiber (reduced digestibility) and low in phenolic compounds. Plant response was altered by brush cutting far more significantly than clipping or browsing, but depended on species- and site-specific factors and was moderated by time or season of cutting. Determining the value of browse produced by plants following differently-timed cuttings was neither possible from lab analysis alone, nor was it possible using spring browse surveys or even winter feeding trials where each bite could be examined first hand. In fact, some findings determined with different methods revealed varying and sometimes conflicting results. Only after re-evaluating earlier assumptions, scrutinizing and then building on previous findings and amalgamating results from the different experiments published herein, did patterns emerge.

Overall, my findings suggest that cutting hardwoods early in the growing season in the weeks following leaf flush and expansion (typically early to late June in northern BC) generally resulted in a less vigorous response from plants and the production of compensatory shoots that were larger in the first, but moderately-sized in the second and each successive year after cutting (paper 3). The shoots from these early-cut plants also had low digestible energy (but not necessarily protein) and elevated lignin and tannin content in the years immediately after cutting (paper 3).

If small rather than large shoots are of higher quality and more preferred by moose (paper 10), then shoots produced in the years following pre-growing season or late-growing season cutting will be preferred (paper 10) relative to plants cut immediately after leaf flush. Generally, plants cut in early spring and late summer produced more resprout materials (with more buds) in the first full growing season after cutting (papers 4 and 10) from which more small shoots could arise in subsequent growing seasons (paper 4). Plants cut late in the growing season also delayed leaf senescence into late fall, relative to earlier-cut plants.

If small shoots (and patches thereof) that contain less tannin and lignin and delay leaf senescence are perceived and used differentially by moose, then plant cutting time matters. Although the specific details of how various plant species growing on different sites will respond to cutting remains to be studied in more detail, a common pattern of plant response to cutting time has emerged from results presented here. Plants cut outside the early growing season produce shoots with traits more attractive to moose in the years after cutting while plants cut in the weeks following leaf flush do not. Compensatory ability and subsequent shoot attributes appear to be linked to levels of root reserves which are exhausted in plants whose leaves have recently flushed and expanded.

Throughout many parts of their range, moose have grown accustomed to depending on browse resources in clear cuts and rights-of-ways for their growth and survival (Child, 1998, Thompson and Stewart 1998). Control of the quantity and quality of browse in these areas can influence herbivore occupancy and health (Thompson and Stewart 1998). Vegetation management can, therefore, be a powerful tool of wildlife management that must be considered, designed and executed deliberately. As reasoned throughout the works herein–timing brush cutting operations to produce abundant, high quality browse is appropriate for winter ranges, clear cuts (where crop trees are not threatened), and remote stretches of linear corridors, but not road or rail corridors or other places where attracting animals into such habitats can bring them into conflict with humans.

I acknowledge that a continuum of plant responses will result from cutting and will vary by species, time of cutting, site and regional conditions, as well as other factors. Much research into factors directly responsible for plant response has yet to be conducted. Considerations for extraneous factors that influence how moose forage on the shoots of cut and uncut plants (e.g., snow depth, use of shoots by other animals, proximity to human habitations) also remain to be tested. I contend that all such factors should be seriously considered before vegetation management begins. In the meantime, experiments designed to help us better understand plant response to cutting and how moose in winter utilize cut and uncut plants will help us determine how to manage plants, all of which–according to the findings presented here–is likely to be of considerable consequence to moose.

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PAPER I

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Initial Effects of Brush Cutting and Shoot Removal on Willow Browse Quality

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Abstract

We examined the initial effects of brush cutting (removal of all aboveground biomass), as well as clipping (removal of current annual shoots) and ungulate browsing (collectively referred to as shoot removal) on the morphology and nutrient quality of Scouler's willow (*Salix scouleriana* J. Barratt ex Hook.) for ungulates on sites 2 and 4 years after brush cutting. We specifically assessed changes in the biomass, tannin content, digestible energy, and digestible protein of shoots from brush-cut willows relative to shoots of uncut willows to determine how browse plants respond to this form of vegetation management. In winter, the resprouted current annual shoots of willows that had been brush cut were larger in mass and lower in digestible protein than shoots of uncut willows for at least 4 years after brush cutting. Shoots of brush-cut willows were also lower in tannin and digestible energy than the shoots of uncut plants for two winters after brush cutting. In the second winter after brush cutting, shoot biomass decreased and tannin content increased with increasing shoot removal during the previous winter. In the fourth winter after brush cutting, shoot mass increased and digestible energy decreased in shoots with greater shoot removal. Nutrient quality was otherwise unaffected by the amount of shoot removal during the previous winter. Because of the occasional importance of site effects in this study, we recommend that long-term studies maximize the number of sampled sites. Because brush cutting alters the quality of regenerating browse and can affect how ungulates utilize such browse for several years after brush cutting, we further recommend that forest vegetation managers consider potential impacts of brush cutting on ungulate winter range.

Resumen

Examinamos los efectos iniciales del corte de arbustos (remoción de toda la biomasa aérea), corte (remoción del crecimiento del año en curso), y el ramoneo por ungulados (referidos colectivamente como remoción de ramas) sobre la morfología y calidad de nutrientes del Scouler's willow (*Salix scouleriana* J. Barratt ex Hook.) para los ungulados en sitios con 2 y 4 años posteriores al corte de arbustos. Específicamente evaluamos los cambios de la biomasa, contenido de taninos, energía y proteína digestibles de las ramas de "Scouler's willow" con corte de arbustos en relación a ramas de "Scouler's willow" sin corte de arbustos (sin corte) para determinar como las plantas responden a esta forma de manejo de la vegetación. En invierno, las ramas rebrotadas en el año en curso de plantas de "Scouler's willow" que habían recibido corte de arbusto fueron superiores en biomasa y más bajas en proteína digestible que las ramas sin corte, al menos cuatro años después del corte de arbustos. Durante los dos inviernos posteriores al corte de arbustos, las ramas de "Scouler's willow" con corte de arbusto también presentaron contenidos más bajos de taninos y energía digestible que las ramas de plantas sin corte. En el segundo invierno después del corte, la biomasa de las ramas disminuyó y el contenido de taninos incrementó con el aumento de la remoción de ramas durante el invierno previo. En el cuarto invierno después del corte de arbustos, con una mayor remoción de ramas, la biomasa de las ramas aumentó y la energía digestible disminuyó. La calidad de nutrientes no fue afectada por la cantidad de remoción de ramas en el invierno previo. Debido a la importancia ocasional de los efectos del sitio en este estudio, recomendamos que estudios de largo plazo maximicen el número de sitio de muestro. Dado que el corte de arbustos altera la calidad del forraje ramoneadle en regeneración y puede afectar como los ungulados utilizan tal forraje por varios años después del corte de los arbustos, nosotros además recomendamos que los manejadores de la vegetación del bosque consideren los impactos potenciales del corte de arbustos sobre el pastizal invernal de los ungulados.

Key Words: forage, moose, plant response, *Salix scouleriana*, silviculture, ungulate, vegetation management

INTRODUCTION

Management of forest vegetation influences wildlife food and cover. In particular, herbicide and mechanical brush cutting operations that reduce competition of woody deciduous plants (e.g., willows *Salix* spp.) with planted conifers also reduce browse for ungulates (Hjeljord and Grønvold 1988; Posner and Jordan 2002). How herbicides and some mechanical treatments such as roller chopping affect deciduous browse availability and quality has been studied (Hjeljord 1994; Raymond et al. 1996; Schindler et al. 2004).

Brush cutting differs from roller chopping and other forms of mechanical control in that plants are sawn cleanly at the point of top removal with brush saws rather than shattered or crushed (Bell et al. 1997); the angle of cut, stump height, and surface exposure of the stump at the point of top removal significantly influences how plants respond to damage (Har-

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rington 1984; Bell et al. 1997). Brush cutting is known to alter plant quality and availability in the short term (1–2 years; Bryant et al. 1985; Rea and Gillingham 2001). However, the influence that brush cutting has on somewhat longer-term initial effects of brush cutting and subsequent removal of shoots by browsing and clipping on the chemistry and morphology of browse shoots is less understood.

Brush cutting is replacing herbicide applications in many Canadian jurisdictions (Lautenschlager 1993; Rea 1999; Posner and Jordan 2002) and can occur wherever forests are being managed, including ungulate winter and cattle summer ranges. Because this form of vegetation management is expanding, and our understanding of how such treatments specifically influence browse quality and availability is limited, we examined the initial effects of brush cutting and subsequent shoot removal on plant quality. We selected an important browse (Scouler's willow; *Salix scouleriana* Barratt ex Hook.) for ungulates (Alldredge et al. 2002) to examine the effects of brush cutting and shoot removal from clipping and browsing on shoot morphology and nutrient (chemical) quality in the second and fourth winter following brush cutting.

METHODS

The Study Area

We studied six sites that were clear-cut logged (ranging from 15 to 40 ha in size) and then planted in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) near Vanderhoof, British Columbia, Canada (lat 54°05′N, long 123°55′W). All sites are characterized by open stands of lodgepole pine with poorly developed shrub and herb layers, and a well-developed moss layer dominated by lichens; soils on all sites are clay and/or sandy loam (Rea 1999).

To determine the effects of brush cutting (i.e., the mechanical removal of all aboveground biomass) on willows, we selected six sites where brush cutting had been conducted either 2 or 4 years previously. Three of the sites (i.e., Layton, Buck and Sackner) were clear-cut logged 12 to 15 years prior to our study (early 1980s); these three sites were then brush cut during the 1993 growing season (June to September) and we sampled them 4 years after brush cutting (winter of 1996–1997). The other three sites (i.e., Sawmill, Huckleberry, and Waterlily) were clear-cut logged 9 to 11 years prior to the beginning of the study (mid 1980s) and were brush cut during the 1995 growing season (sampled 2 years after brush cutting; winter of 1996–1997).

During brush cutting operations in 1993 and 1995, all aboveground biomass, except approximately 10 cm of stump tissue, was removed from willows and all other deciduous shrubs and trees on each site. The tops of the plants were left scattered on the site to decompose. Wildlife strips (sensu Santillo 1994; areas established for wildlife food and cover after clear-cut logging but prior to brush cutting treatments) were not brush cut on each of the six sites and contained willows about 4 to 5 m tall at the beginning of this study; willows that had been brush cut had regrown to approximately 1 to 2 m in height at the time of the study. All sites (except Waterlily) had a long history of browse utilization by moose (*Alces alces* L.) and deer (*Odocoileus* spp.). Additionally, free-range cattle (*Bos taurus* L.) utilized Buck and Sackner sites in summer.

Experimental Design

During the winter of 1995–1996, we randomly selected six Scouler's willow plants from brush-cut areas and six willows from the wildlife strips (controls) on each of the three plantation sites that had been brush cut in 1993 (i.e., Layton, Buck, and Sackner) and each of the three sites brush cut in 1995 (i.e., Sawmill, Huckleberry, and Waterlily). We removed current annual shoots accessible above the snowpack from the sampled plants by clipping at specific intensities in order to simulate the removal of current shoots by moose (Danell et al. 1997). We collected no shoots, every third shoot, two of every three shoots, or all shoots for 33%, 66%, and 100% shoot removals, respectively.

Because of unanticipated browsing by moose (increase in intended treatment of shoots) and snow burial of stems at the time of our clipping (decrease in intended treatment of shoots), we were forced to reassess the actual shoot removal on each plant. In the spring of 1996, therefore, we determined the percentage of shoots removed by clipping and subsequent overwinter ungulate browsing by counting all overwintering shoots and classifying them as browsed/clipped or undamaged and then dividing the number of browsed/clipped shoots by the total number of shoots on the plant. We quantified the range of clipping in combination with natural browsing (0% to 98% shoots removed) and treated shoot removal (clipping plus browsing) as a covariate in our ANCOVA analyses described below.

In December of 1996, we visited each of our six sites and harvested shoot samples (between 20 and 300 shoots from brush cut and between 200 and 800 shoots from uncut willows based on the percentage removals in our original treatments) in subzero weather while plants were dormant to inhibit postsampling metabolic activities within the shoot tissues. Sampled shoots were clipped at the current annual growth scar. Shoots were collected early in winter so as to avoid damage from winter browsing, but in some cases shoots showed signs of summer browsing by cattle or deer. Shoots were used to assess morphological and chemical attributes of our study plants as described below.

Collections from each willow were placed in separate plastic freezer bags in the field 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 to determine mass. If more than 30 shoots were collected from a willow, we randomly subsampled 30 shoots for morphometric measurements. Following morphometric measurements, all shoot material for each plant was combined, sectioned to approximately 10-cm lengths and dried to a constant mass (± 0.1 g) at 39°C in a forced-draft drying oven (Despatch LAD series 2-24-3; Despatch Industries, Minneapolis, MN). We then milled the dried material with a Thomas-Wiley mill (Swedesboro, NJ) using a 0.5-mm sieve screen, and hand mixed the samples to homogenize them. Gross energy was determined with a bomb calorimeter (Parr model 1341; Parr Instrument Company, 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 $CaSO_4$ (W. A. Hammond Drierite Co., Xenia, OH) for 24 hours.

We determined elemental nitrogen using an elemental CHN analyser (Na Series 2; Carlo Erba Instruments, Milano, Italy) following procedures outlined by the manufacturer and Pella and Colombo (1973). The elemental analyser was calibrated using atropine (4.84% N) and the National Institute of Standards and Technology standard number 1573a (3.03% N). Because elemental nitrogen approximates the nitrogen content of a sample with the same accuracy and precision as total Kjeldahl nitrogen (TKN; Hellinga et al. 1998), we substituted elemental nitrogen for TKN in equations outlined in Hanley et al. (1992) for estimating digestible protein. Digestible dry matter was used to compute in vitro digestible energy (gross energy × digestible dry matter). We computed digestible dry matter using equations developed for deer (*Odocoileus* spp.) and other cervids that secrete salivary tannin-binding proteins, as described in Hanley et al. (1992).

We used a fiber-refluxing/distillation apparatus (Labconco model 30006; Labconco Corporation, Kansas City, MO) and procedures outlined in Goering and Van Soest (1970) to estimate the fiber fractions in our samples for use in determining digestible dry matter. We omitted sodium sulphite from the Neutral Detergent Fiber (NDF) procedure as recommended by Hanley et al. (1992) for the determination of NDF from browse stems. We also omitted the optional wash with hexane from the Acid Detergent Fiber (ADF) procedure (Goering and Van Soest 1970). We did not use asbestos 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).

We followed the recommendation of Hanley et al. (1992) and did not apply the tannin correction factor in calculations for either digestible protein or digestible dry matter because dormant twigs contain relatively small amounts of tannin (Palo 1984). Although crude tannin content was not quantified for use in digestibility determinations, we did determine the relative differences in tannin content between samples from the different brush cutting treatments in order to help understand changes to one of the chemical characteristics known to influence winter browse selection by moose. We assessed tannin content using a radial diffusion protein precipitation assay that we modified from Hagerman (1987; Rea 1999).

Statistical Analyses

To test the effect of brush cutting on the morphology and chemistry of willow shoots, we used a nested analysis of covariance (ANCOVA; Zar 1999) with the percentage of shoots that were clipped or browsed during the previous year used as a covariate. Treated willows (brush cut vs. uncut) were considered to be nested within sites. In the nested ANCOVA model, we treated site as a random effect and treatment (brush cut or uncut) as a fixed effect. We used PROC GLM for the mixed model in SAS (SAS 2005) specifying the appropriate test terms for the random and fixed effects. Least-square means (LSMEANS statement) were calculated for all model effects. We report back-transformed, adjusted means (and standard errors), which represent the marginal means for each effect adjusted for all other factors in the ANCOVA model (e.g., covariate effects set to their mean value). Significant differences in adjusted site effects were tested with Tukey's range test. Homogeneity of variances was tested using a Levene's test (Milliken and Johnson 1984). A Kolmogorov–Smirnov test was used to test assumptions of normality (Zar 1999). Where appropriate, square root, inverse, inverse square root, or log transformations (Tabachnick and Fidell 1996) were applied to normalize data and/or homogenize the variance of the shoot attribute being tested between treatments. Where an effect of the covariate was significant, we further explored the significance with linear regression analysis and report the direction of the slope of the response variable regressed on the covariate. Because the sites were initially treated in different years (i.e., 1993 and 1995), times of post-brush cutting are 2 years for Huckleberry, Waterlily, and Sawmill (1995) sites, and 4 years for Buck, Layton, and Sackner (1993) sites. The α for all analyses was 0.05.

Table 1. Results (*P* values) of comparisons between brush cut and uncut willows for morphological and chemical attributes in the second (1995 brush-cut sites) and fourth (1993 brush-cut sites) years after brush cutting treatments. Data were analyzed with a nested ANCOVA (see text). The shoot removal column indicates the significance of the effect of the percentage of shoots that were clipped or browsed during the previous winter. Where the effect of the shoot removal covariate was significant, a + or − sign indicates the slope of the covariate (see text). DM indicates dry matter.

Years since brush cutting	Shoot attribute	Treatment (brush cut/uncut)	Shoot removal	Site
2	Biomass (g)	< 0.001	0.001 (−)	0.898
	Tannin content[1]	0.013	0.022 (+)	0.542
	Digestible energy ($kcal \cdot g^{-1}$)	< 0.001	0.203	0.456
	Digestible protein (% DM)	0.011	0.389	0.587
4	Biomass (g)	0.007	0.014 (+)	0.080
	Tannin content[1]	0.545	0.304	0.027
	Digestible energy ($kcal \cdot g^{-1}$)	0.095	0.046 (−)	0.164
	Digestible protein (% DM)	0.035	0.744	0.483

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

RESULTS

Shoot Morphology

Willows responded to brush cutting by producing shoots that were significantly heavier than the shoots of uncut willows (as much as four to five times heavier on Sawmill and Huckleberry sites) for 2 (Table 1; Figure 1) and 4 (Table 1; Figure 2) years after brush cutting. Biomass of shoots, however, was also affected by shoot removal during the previous winter from clipping and browsing, but the effect of shoot removal was different 2 and 4 years after brush cutting (Table 1). In the second winter after brush cutting, shoot mass decreased with increasing shoot removal (Table 1; negative slope of shoot removal in year 2). In contrast, sites that were measured 4 years after brush cutting had shoots whose biomass generally increased with increasing shoot removal during the winter before measurement (Table 1 and Figure 3A; positive slope of covariate in year 4). For the 4-year, post–brush cutting replicates, site was not significant (Table 1), but the Layton

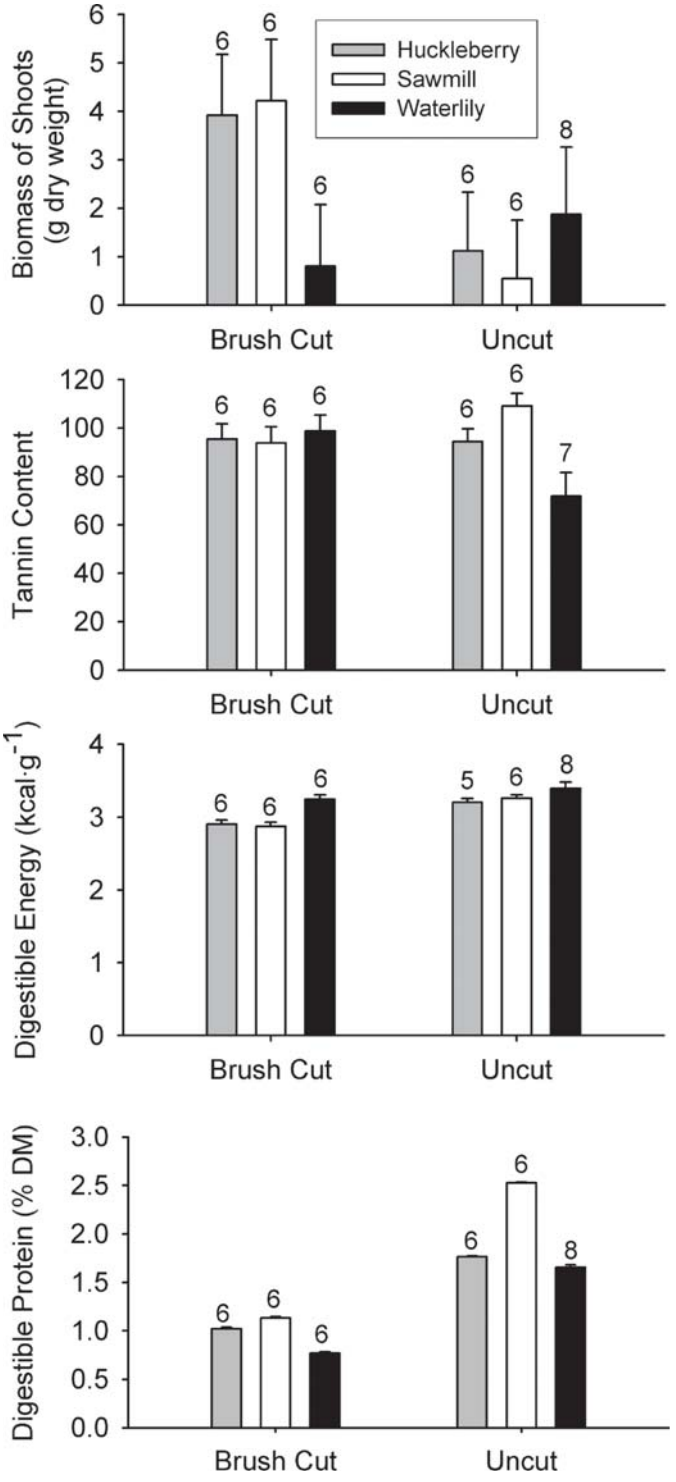

Figure 1. Comparisons of mean (and SE) morphological and chemical attributes of shoots from brush-cut and uncut willows collected in the second year after brush cutting (1995 brush-cut sites). DM indicates dry matter. Sample sizes are shown above each error bar. Means (and SE) are the back-transformed means adjusted for all other factors in the ANCOVA model (SAS: LSMEANS) including the covariate of the amount of current annual shoots removed by clipping and browsing.

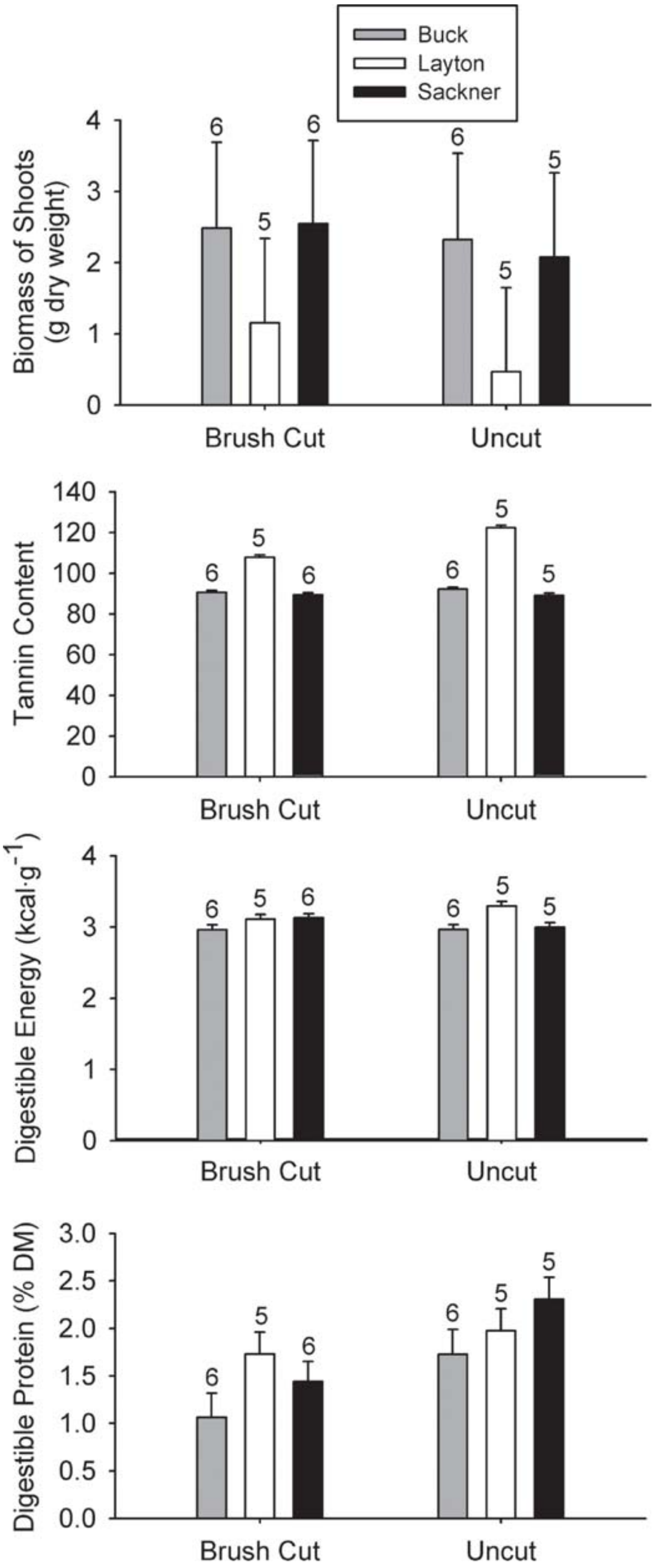

Figure 2. Comparisons of mean (and SE) morphological and chemical attributes of shoots from brush-cut and uncut willows collected in the fourth year after brush cutting (1993 brush-cut sites). DM indicates dry matter. Sample sizes are shown above each error bar. Means (and SE) are the back-transformed means adjusted for all other factors in the ANCOVA model (SAS: LSMEANS) including the covariate of the amount of current annual shoots removed by clipping and browsing.

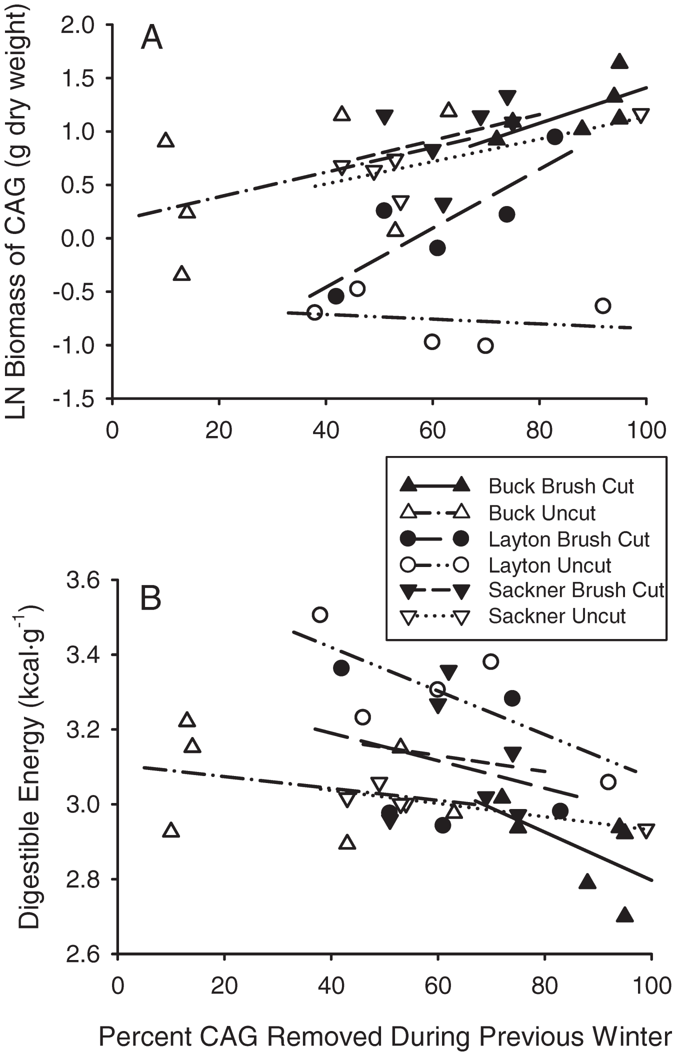

Figure 3. Scatter plots illustrating two examples of the effect of the covariate on the natural logarithm of biomass **(A)** and on digestible energy **(B)** in the fourth year after brush cutting for three sites brush cut in 1993. Each regression line represents the influence of the covariate (percent removal) on the dependent variable. The significance of the covariates are presented in Table 1.

uncut samples showed a different response than the other site treatments to increasing shoot removal (Figure 3A).

Shoot Chemistry

The response of tannin content was different between the 2-year and 4-year postcutting treatments. Tannin content was lower in the brush-cut shoots in the second year after brush cutting (Table 1; Figure 1), but not in sites measured 4 years after cutting (Table 1; Figure 2). On sites measured 2 years after brush cutting, shoot tannin content increased with increasing shoot removal (Table 1; positive slope of shoot removal in year 2). Tannin content was unaffected by shoot removal at the sites measured 4 years after brush cutting. There was, however, a significant effect of site on tannin content of shoots (Table 1) at the 4-year postcutting sites: the shoots of both brush-cut and uncut willows growing on our Layton site had significantly higher tannin content than sampled willows growing on Sackner and Buck sites.

The response of digestible energy content of shoots differed between sites measured 2 and 4 years after brush cutting. Brush cutting reduced the digestible energy content of willow shoots 2 years after cutting (Table 1; Figure 1), but there was no response in digestible energy content of shoots to brush cutting on sites measured 4 years after cutting (Table 1; Figure 2). Conversely, there was no response in digestible energy content to shoot removal 2 years after brush cutting, but on the 4-year sites, digestible energy decreased with increasing intensity of shoot removal (Table 1 and Figure 3B; negative slope of shoot removal in year 4). Site by itself did not explain significant variation in digestible energy (Table 1).

Digestible protein was lower in the shoots of brush-cut plants on both 2- and 4-year, postcutting sites (Table 1; Figures 1 and 2). Digestible protein was unaffected by the intensity of the previous year's shoot removal, or by site alone (Table 1).

DISCUSSION

Plant Response

We observed that the effects of brush cutting on Scouler's willow included increases in shoot mass (but also shoot length and basal diameter; Rea 1999) and decreases in digestible protein for at least 4 years post–brush cutting, and reductions in digestible energy and tannin content in the short term. Others have reported related effects on desert shrubs following roller chopping (Schindler et al. 2004), but the longer-term effects of brush management on woody browse availability and quality are largely unknown (Allegretti et al. 1997).

Plants generally respond to increased clipping intensities by producing large shoots (Bergström and Danell 1987), but decreases in shoot sizes with increased clipping intensities during the previous year might also occur when plants are severely stressed (Danell and Bergström 1989). This type of response could help to explain why Scouler's willows in our study produced larger compensatory shoots with increased shoot-removal intensity 4 years after brush cutting, but not when intense shoot removal was measured 2 years after brush cutting (clipped during the previous winter). Vigorous vegetative regeneration and the production of large compensatory shoots following mechanical damage (i.e., cutting, browsing) is a growth strategy employed by several species of willows (Sennerby-Forsse and Zsuffa 1995). This type of growth response to damage is particularly adaptive for plants such as Scouler's willow growing in young boreal forests where plant competition for canopy occupancy is intense (Aarssen and Irwin 1991) and where the highest herbivore pressures are exerted closest to the ground (Danell et al. 1987).

Although ungulates, such as moose, are known to break down and browse the smaller top shoots of taller (6 to 9 m) birches (Danell and Bergström 1985), large shoots and sprouts produced in the years after intense tissue removal are particularly attractive to large ungulates (Danell et al. 1985; Singer et al. 1994; Bergström and Guillet 2002; Hessl and Graumlich 2002). Selecting more massive shoots enables large ungulates to increase bite size and intake rates per cropping effort (Gross et al. 1993;

Shipley et al. 1994), which can facilitate maximizing energy intake while minimizing the amount of time spent foraging.

Except for digestible protein, changes in the chemical attributes of willow shoots following brush cutting appear to be less persistent than corresponding increases in shoot mass. Shoots from brush-cut plants were lower in tannin content and digestible energy for 2, but not 4, winters after brush cutting. Additionally, the lignin content of these shoots was reduced for 2, but not 4, years after brush cutting (Rea 1999). Our chemical analyses indicate that reductions in digestibility 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 compensatory shoots.

The tannin content of willow shoots produced in the year after shoot removal increased with an increase in the previous year's intensity of shoot removal when analyzed in the second winter after brush cutting. Although plants stressed by repeated hare browsing following cutting have been shown to produce shoots that are higher in phenolic compounds such as tannins (Bryant et al. 1985), reductions in the tannin and lignin content of browse shoots following various forms of plant damage are also reported (Nellemann 1990, crushing; Singer et al. 1994, clipping; Schindler et al. 2004, roller chopping).

Shoots lower in phenolics, such as tannins and lignins, are selected by browsers, regardless of digestibility (Bryant et al. 1983; Risenhoover 1987; Singer et al. 1994). These chemicals interfere with rumen microbial activity (Blair et al. 1980), reducing shoot nutrient quality (Spalinger et al. 1986; Shipley and Spalinger 1992), and are specifically avoided by ungulates (Risenhoover 1987; Nellemann 1990). Cervids appear to avoid tannin-containing browses even though such animals produce salivary-tannin-binding proteins to help neutralize the effects of dietary tannins (Hagerman and Robbins 1993; Juntheikki 1996). Such avoidance might be related to the inability of animals to completely bind all tannins in deciduous browse (including some willows; Juntheikki 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 (Juntheikki 1996). The production of shoots with even slight reductions in tannin content, such as those produced in the second year after brush cutting, therefore, might well increase browse quality—at least in the short term. The smaller shoots of uncut plants in this study might be due to the growth-inhibiting effects of tannins, rather than declines in tannin content being due to the allocation of resources towards growth and away from chemical defence; resource availability is known to drive the production and accumulation of tannins (Coley et al. 1985). Reductions in tannin content are likely due to the allocation of plant resources into shoot elongation or physical defences (Schindler et al. 2004) rather than the production of chemical defences.

Site Effects

An important result of this study is the lack of consistency among sites in the measured plant response (Table 1) both in terms of shoot biomass and chemistry. For example, variations in resource availability between sites might help to explain the differences in tannin content that we detected between willows growing on the Layton vs. Sackner and Buck sites. Although sites were chosen to maximize similarity among sites, site differences in the amount of precipitation, browsing history, soil type, and leeching likely exist. Site effects have been detected in other studies of plant response to clipping/browsing, but have been suggested by other authors to be less important and more flexible than the morphological and chemical responses of plants to damage, which tend to be of a more generalized nature across the landscape (Danell et al. 1997).

At the beginning of the study, we applied specific clipping treatments (0%, 33%, 66%, and 100%) to trees in midwinter. Because of the absence of exclosures, however, moose browsed the experimental trees after our clipping. Further, burial of lower branches by snow resulted in an under-clipping of lower branches. Consequently, total shoot removal (clipping and browsing) had to be reassessed in the spring and subsequently treated as a covariate rather than as distinct treatment levels in our analyses. The complexity of the design makes it difficult to interpret specific site effects. The inability to exclude natural browsing from our study meant that the level of the covariate could change from year to year. This change meant that we only assessed one year of data from the 2- and 4-year sites without following within-site effects for longer periods of time. Our results, therefore, should be treated as a possible indication of a longer-term response that needs further study.

IMPLICATIONS

Regardless of any site effect detected, Scouler's willow appears to compensate for brush cutting by producing large compensatory shoots, low in digestibility in the long term and lower in tannin content in the short term relative to shoots of uncut willows. Although the measured responses of Scouler's willow shoots for 2 and 4 years after brush cutting suggest an initial response of willow to brush cutting and clipping, our data cannot portray the full range of morphological and chemical changes that likely occur throughout the succession of the shrub field. We also do not know how moose responded behaviorally to these changes in willow chemistry and morphology. Although the study area is extensively used by moose (e.g., the confounding of our clipping experiment discussed above), we do not know how the habitat use and selection of shoots by moose change after brush cutting operations. The relative importance of changes in available biomass and shoot chemistry could be either amplified or minimized, depending on how moose respond spatially to these management activities.

Brush cutting likely will continue to replace herbicide treatment of broad-leaved plants in many jurisdictions. As such, understanding the influence of brush cutting on plant response and quality in both the short and long term is integral to understanding the influence of this form of vegetation management on range quality. To better understand the effects of brush cutting, we recommend that long-term studies, ideally that make use of exclosures to better control for clipping and browsing effects, be undertaken. Given the unexpected importance of site in our study, we further recommend that such work should maximize the number of sites examined so that stronger inference can be made to the effects of brush cutting on browse for moose and other ungulates.

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PAPER II

EFFECTS OF PLANT COMPENSATION ACROSS SITES ON REGRESSION ESTIMATES OF SHOOT BIOMASS AND LENGTH

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ABSTRACT: Regression estimates for determining browse shoot biomass from bite diameters and shoot basal diameters are commonly used to estimate biomass consumption and the impacts that herbivores have on range resources. Such estimates tend to be based on equations built from data taken across the continuum of shoot morphometries present on plants within a given study area. How these morphometric relationships differ between the shoots of undamaged and damaged (e.g., following browsing, shoot breakage, or brush-cutting) plants is unclear. To assess the effects of plant compensation and the importance of site on shoot morphometrics for Scouler's Willow (*Salix scouleriana)*, we clipped and measured current annual shoots at 5 sites in central British Columbia. Each site had been previously brush-cut and current annual shoots were collected from both brush-cut and control willows. For each treatment and site, we developed separate regressions to predict shoot weight from length, weight from basal diameter, and length from basal diameter. Comparisons of individual regressions indicated that different regressions, or even different forms of regressions (i.e., power function versus linear), are needed to accurately predict shoot weight and length depending on whether or not plants are producing compensatory or non-compensatory shoots. For some willows in the same treatment category (brush-cut versus uncut), the appropriate regressions differed among some sites. These results suggest that the effects of plant compensation following mechanical damage have important implications to the extrapolation and interpretation of shoot morphometric relationships, and thus, biomass estimates across different study areas.

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Key words: Biomass estimation, browse, compensatory growth, mechanical brushing, plant response, regression analysis, *Salix scouleriana*

In the absence of direct observations and measurements, determining biomass consumption of browse shoots by ungulates is difficult and time consuming (Provenza and Urness 1981). One method of estimating biomass removal is to develop regression equations for shoot biomass based on the diameter and other morphometric parameters of the current annual shoot (Telfer 1969a, Lyon 1970, Provenza and Urness 1981). In this way, shoot biomass beyond the point of browsing (consumption) can be estimated (Ferguson and Marsden 1977, Provenza and Urness 1981, MacCracken and Van Ballenberghe 1993) in a non-destructive manner (Thilenius 1990). Likewise, availability of browse, carrying capacity of ranges (Telfer 1969a), and animal stocking rates (Ruyle et al. 1983) can be estimated using similar equations that predict biomass from measurements taken at the basal diameter of shrub and tree shoots.

Regression equations for estimating shoot biomass and length from other shoot attributes have been developed for several browse plants commonly consumed by moose (*Alces alces* L.; e.g., Telfer 1969b, Thilenius 1990, MacCracken and Van Ballenberghe 1993). These equations, however, have not accounted for variations in shoot architecture resulting from exaggerated vegetative shoot growth on plants compensating for various forms of mechanical damage such as browsing, breakage, and cutting. In this paper, we investigated whether equations predicting biomass and shoot length for Scouler's willow (*Salix scouleriana* Barr.) varied among plants that were compensating for mechanical damage from brush-cutting between 2 and 3 years after cutting and undamaged plants at 5 sites in central British Columbia.

STUDY AREA

Our study area consisted of 5 sites that were clear-cut logged (15-40 ha in size) and then planted with lodgepole pine (*Pinus contorta* Dougl. *ex* Loud. var. *latifolia* Engelm.) near Vanderhoof, British Columbia, Canada (lat 54°01'N, long 124°00'W). All sites were characterized by open stands of lodgepole pine with poorly developed shrub and herb layers, and a well-developed moss layer dominated by lichens; soils on all sites were clay and/or sandy loam (Rea 1999).

METHODS

Site Histories

We selected 5 sites where brush-cutting had been conducted to determine the effects of mechanical damage on willow shoot morphometry 2 and 3 years after brush-cutting. Three of the sites (Layton, Buck, and Sackner) were clear-cut logged 12-15 years prior to our study; these sites were then brush-cut during the 1993 growing season (June-September) and sampled 3 years later (winter 1995-96). The other 2 sites (Sawmill and Huckleberry) were clear-cut logged 9-11 years prior to the beginning of the study, were brush-cut during the 1995 growing season, and sampled 2 years later in winter 1996-97.

During brush-cutting operations in 1993 and 1995, all above-ground biomass, except ~10 cm of stump tissue, was removed from willows and all other deciduous shrubs and trees at each site. Wildlife strips (*sensu* Santillo 1994; areas established for wildlife food and cover after clear-cut logging but prior to brush-cutting treatments) at each site were not brush-cut and contained willows about 4-5 m tall at the beginning of this study; willows that had been brush-cut on these sites were about 1-2 m tall. All sites had a long history of browse utilization by moose and deer (*Odocoileus* spp.). Additionally, free-range cattle (*Bos taurus* L.) utilized the Buck and Sackner sites in summer.

Current Annual Shoots

During the winter of 1995-1996, we randomly selected 6 Scouler's willow plants from brush-cut areas and 6 from the wildlife strips (controls) on each of the 3 plantation sites that had been brush-cut in 1993. We similarly selected willows at each of the 2 sites brush-cut in 1995 in the winter of 1996-1997. Once willows were selected, we clipped shoots accessible above the snowpack. Shoots were systematically collected at different clipping intensities (as part of a larger study, Rea 1999, Rea and Gillingham 2001) from willows in the Layton, Buck, and Sackner sites at the time we selected the plants during the winter of 1995-1996, and from the Sawmill and Huckleberry sites during the winter of 1996-1997.

We collected all shoot samples while plants were dormant in mid-winter by clipping shoots at the current annual growth scar. We sealed all collected shoots in plastic freezer bags in the field to inhibit water loss during transportation back to our laboratory at the University of Northern British Columbia. All shoots were weighed to the nearest mg and measured for length (cm) and basal diameter (mm). When >30 shoots were collected from a particular willow, we randomly sub-sampled 30 shoots for morphometric measures.

Regression Analyses

We began by examining the fit of 4 linear and non-linear regressions for each treatment (Brush-cut versus Uncut) at each of the 5 sites; we considered linear ($Y = a + bX$), power ($Y = a + bX^c$), and exponential ($Y = ae^{bX}$ and $Y = a + be^{cX}$) regression models. Following the recommendation of Verwijst (1991) for biomass estimation, we did not use any log-transformed variables in any regression model. For each site and treatment, we developed separate regressions for: 1) shoot weight (Y) based on shoot length (X), 2) shoot weight (Y) based on shoot basal diameter (X, at the point of the growth scar), and 3) shoot length (Y) based on shoot basal diameter (X). In choosing the best regression for each set of data, we considered R^2 values (r^2 for linear regression) and the fit of residuals. Linear models were selected if the residuals did not justify a non-linear relationship. In all but 1 of the non-linear relationships, the power function was the best fit; because the power function was a very close second to the exponential model in the single other case, we chose to use the power function to simplify the comparison with other non-linear predictions.

We fit all nonlinear models with PROC NLIN (version 9.1, SAS Institute 2003); linear regressions were fit with the regression procedure (REG) in STATA (version 9.2, STATACorp. 2007). Confidence intervals around individual regression parameters were estimated by asymptotic approximations in the respective packages. We considered morphometric relationships to be different between treatments and/or among sites if the form of the regression was different (i.e., linear versus power), or if the confidence intervals around individual parameters of regressions of the same form did not overlap. We did not apply Bonferroni corrections to the confidence intervals because individual regressions with non-overlapping simple confidence intervals would yield different biomass estimates. We considered an α of 0.05 throughout our analyses.

RESULTS

Shoot Weight from Shoot Length

All regression estimates of shoot weight from shoot length were best fit with power functions. In addition, there were no differences among regressions in shoot weight (Y) predicted by shoot length (X) for brush-cut willows across all sites (Table 1). There were, however, differences in regression equations for uncut plants among sites (i.e., one or more parameters in the power functions were significantly different from each other, Table 1). These differences included regressions for uncut willows at the 2-year post-cutting sites (i.e., Huckleberry uncut versus Sawmill uncut) and at the 4-year sites (e.g., Buck uncut versus Sackner uncut).

There were also numerous differences among regression equations developed for shoot weight versus shoot length when shoots from brush-cut and uncut plants were compared (Table 1, Fig. 1). Although the parameter that varied was not consistent among comparisons, any equation that varied significantly in any parameter would yield a significantly different prediction.

Shoot Weight from Shoot Basal Diameter

All regression estimates of shoot weight from shoot basal diameter were also best fit with a power function. With the exception of 1 case (Huckleberry versus Buck) that represented a difference in year-since-brush-cutting, we detected no difference in the form or parameters of the regression equations that explained the relationship of shoot weight (Y) to basal diameter (X) for shoots of brush-cut plants.

There was less consistency in the regression parameters of the power functions among uncut treatments (Table 2). Although the 2, 2-year sites (i.e., Huckleberry and Sawmill) were not different, there were differences in equations between 4-year sites (e.g., Table 2: Buck versus Sackner and Sackner versus Sawmill). Relationships for uncut plants also differed significantly between 4-year, post-cutting sites (Table 2: Layton and Sackner). There were no differences in equations for shoots of brush-cut and uncut plants growing on sites that were sampled 2 years after

Table 1. Comparison of coefficients for shoot weight (Y) versus shoot length (X) regressions. All regressions were best fit with a power function ($Y = A + BX^c$). Brush-cut (BR) and uncut (UN) treatments were compared for each of 5 sites in central British Columbia. Letter entries in the table represent significant differences in the parameters (A, B, and C)[a] in the power function between treatments and among sites. Because the table is symmetrical, only the cells above the diagonal (—) are completed. Cells with no entries above the diagonal indicate that the corresponding regressions were not different from each other.

		Site									
		Buck		Huckleberry		Layton		Sackner		Sawmill	
Site	Treatment	BR	UN	BR	UN	BR	UN	BR	UN	BR	UN
Buck	BR	—					B				
	UN		—	B C	C			C	C	C	
Huckleberry	BR			—	B C		A B C		B C		A B C
	UN				—		A C				B C
Layton	BR					—	A B				
	UN						—	A B C	B C	B C	
Sackner	BR							—			A B C
	UN								—		B C
Sawmill	BR									—	B C
	UN										—

[a] A = The intercept of the power function equation.

B = The slope of the power function equation.

C = The exponent of the power function equation.

Note: The appearance of a letter in the table indicates a significant difference in either the intercept (A), slope (B), or exponent (C) between the two equations being compared.

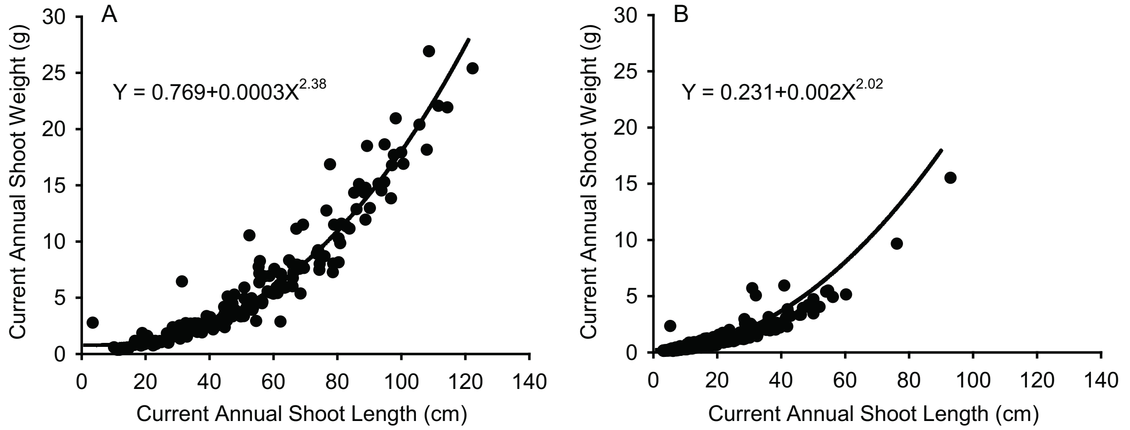

Fig. 1. Observed and predicted values for current annual shoot weight versus shoot length for brush-cut (A; $n = 191$) and uncut (B; $n = 240$) willows on the Huckleberry site.

cutting (Table 2). Similarly, the relationship between shoot weight and basal diameter did not vary between cut and uncut plants within the same site.

Shoot Length from Shoot Basal Diameter

Unlike the relationships between shoot weight versus shoot length and shoot weight versus basal diameter, shoot length could not be predicted from basal diameter by a single equation form (Table 3, Fig. 2). Again, the effect of brush-cutting appeared more important than site effects in that all brush-cut treatments did not differ in equation form (Table 3: linear). There were, however, differences in the slope (E) for brush-cut treatments within and among treatments 2 and 3 years post-cutting. In those instances in which power functions were better fits than linear regressions, it was always for uncut treatments, although there was no consistency within and among 2- and 3-year sites. Finally, there were many differences within sites between cut and uncut treatments regardless of the number of years since cutting (Table 3, Fig. 2).

DISCUSSION

A fundamental difference appears to exist between the shoot morphometrics of brush-cut plants and those of uncut plants in which the growth form of compensatory shoots appears more consistently predictable than that of shoots from undamaged plants. This phenomenon appears to be true both within and between sites regardless of the time since brush-cutting. Our results further suggest

Table 2. Comparison of coefficients for shoot weight (Y) versus shoot basal diameter (X) regressions. All regressions were best fit with a power function ($Y = A + BX^c$). Brush-cut (BR) and uncut (UN) treatments were compared for each of 5 sites in central British Columbia. Letter entries in the table represent significant differences in the parameters (A, B, and C)[a] in the power function between treatments and among sites. Because the table is symmetrical, only the cells above the diagonal (—) are completed. Cells with no entries above the diagonal indicate that the corresponding regressions were not different from each other.

		Site									
		Buck		Huckleberry		Layton		Sackner		Sawmill	
Site	Treatment	BR	UN	BR	UN	BR	UN	BR	UN	BR	UN
Buck	BR	—		C	C		C				
	UN		—								
Huckleberry	BR			—			B C				
	UN				—	C	B C	C			
Layton	BR					—					C
	UN						—	B C	B C	C	C
Sackner	BR							—			B C
	UN								—		C
Sawmill	BR									—	
	UN										—

[a] A = The intercept of the power function equation.

B = The slope of the power function equation.

C = The exponent of the power function equation.

Note: The appearance of a letter in the table indicates a significant difference in either the intercept (A), slope (B), or exponent (C) between the two equations being compared.

Table 3. Comparison of coefficients for shoot length (Y) versus shoot basal diameter (X) regressions. Some regressions were best fit with a power function ($Y = A + BX^c$) while other regressions were linear ($Y = D + EX$). Brush-cut (BR) and uncut (UN) treatments were compared for each of 5 sites in central British Columbia. Letter entries in the table represent significant differences in the parameters (power: A, B, C; linear: D, E)[a] in the regressions between treatments and among sites (Note: no A or B parameters were significantly different from each other). An * indicates that differences existed because the same form of regression could not be fit to the corresponding entries in the table. Because the table is symmetrical, only the cells above the diagonal (—) are completed. Cells with no entries above the diagonal indicate that the corresponding regressions were not different from each other in form or parameters.

		Site									
		Buck		Huckleberry		Layton		Sackner		Sawmill	
		BR	UN	BR	UN	BR	UN	BR	UN	BR	UN
Site	Treatment	(Linear)	(Linear)	(Linear)	(Power)	(Linear)	(Linear)	(Linear)	(Power)	(Linear)	(Power)
Buck	BR	—	E		*	E	D E		*		*
	UN		—	D E	*		E	E	*	E	*
Huckleberry	BR			—	*	E	D E		*	E	*
	UN				—	*	*	*		*	
Layton	BR					—	D E	E	*	E	*
	UN						—	D E	*	E	*
Sackner	BR							—	*		*
	UN								—	*	C
Sawmill	BR									—	*
	UN										—

[a] A = The intercept of the power function.

B = The slope of the power function.

C = The exponent of the power function.

D = The intercept of the linear equation.

E = The slope of the linear equation.

Note: The appearance of a letter in the table indicates a significant difference in the parameter between the two equations being compared.

that when considering undamaged plants, the relationship between shoot weight and length may be more influenced by site than other morphometric relationships.

Although all regressions for predicting shoot weight from shoot length and weight from basal diameter were best fit to a power function, linear equations were better suited to predict shoot length from basal diameter for all brush-cut plants. The regressions used to predict weight from length of shoots taken from uncut willows on the Buck and Layton sites were also better described with linear equations, whereas the shoots of uncut plants on the remaining 3 sites were better characterized by a power function.

Our results are based on a relatively small sample size of twigs and plants. If larger samples resulted in more within-site variability, then the confidence intervals around the parameters would be wider and perhaps fewer significant differences would be detected between treatments and among sites. We would expect that a small sample size,

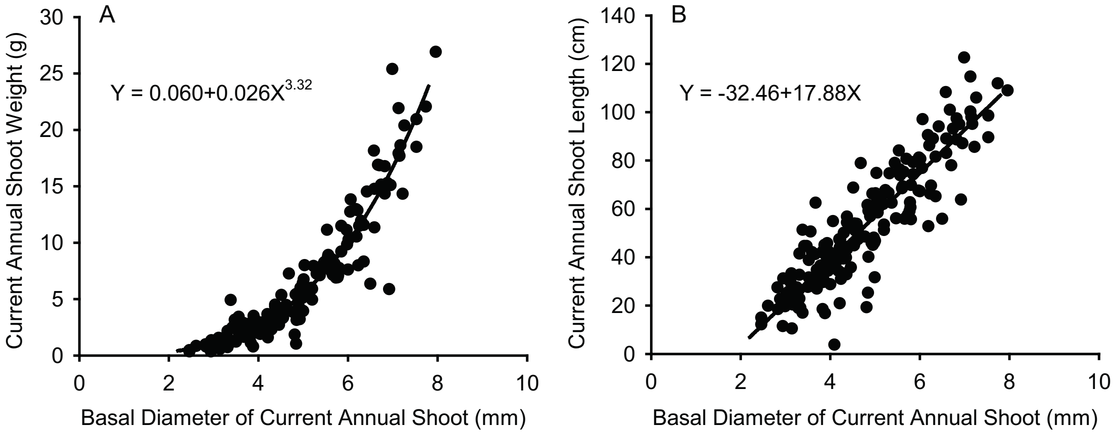

Fig. 2. Observed and predicted values for current annual shoot weight versus current annual shoot basal diameter (A; *n* = 191), and length of current annual shoot versus current annual shoot basal diameter (B; *n* = 191) for brush-cut willows at the Huckleberry site.

however, would increase and not decrease the variation in the regressions.

Our results do not suggest a distinct pattern between the way in which equations differed from one another relative to site or time since brush-cutting (2 versus 3 years post-cutting). There were differences in the equations between plants growing on sites that had been brush-cut 2 years versus 3 years earlier. But this was also true when comparing within year since cutting and across sites. Therefore, we make no generalizations regarding site and year effects.

The fact that predictive equations for predicting shoot biomass of brush-cut plants did not differ between sites and year since cutting, and all other comparisons demonstrated significant differences, suggests a consistency in the relationship of shoot mass to length and basal diameter of compensatory shoots not found in the shoots of undamaged plants (Ferguson and Marsden 1977) and is, to our knowledge, previously unreported. However, it is unclear why predictive equations of biomass from the length and diameter of larger shoots would be more consistent across sites and year-since-treatment than predictive equations generated from the same parameters on non-compensatory shoots. Perhaps apical and lateral buds of winter shoots exhibit consistency in size and mass and influence morphometric relationships disproportionately more for smaller and moderately sized shoots arising from undamaged plants than for heavier shoots. Such relationships are not necessarily true outside of the winter dormant period (Schewe and Stewart 1986).

Season and year of shoot collection (Telfer 1969a, Schewe and Stewart 1986, Thilenius 1990), plant species differences (Telfer 1969b, Potvin 1981, MacCracken and Van Ballenberghe 1993), site/microsite and aspect (Lyon 1970, Peek et al. 1971, Ruyle et al. 1983, Schewe and Stewart 1986), plant size/age (Lyon 1970, Peek et al. 1971), and shoot age and position on the plant (Telfer 1969a, Lyon 1970, Ferguson and Marsden 1977) are known to influence predictive equations of 1 shoot attribute from another. However, no such claims have been made for the influence of compensatory growth on such equations.

Ruyle et al. (1983) found that the form of quadratic equations used to predict oven-dried shoot weight from other shoot attributes varied by the total number of kg of snowberry plants utilized in pastures by sheep. MacCracken and Van Ballenberghe (1993) speculated that shoot size and age could significantly influence the character, and thereby, the utility of the regression equation. Peek et al. (1971) speculated more specifically that browsing pressure was likely to account for variation in equations developed for mountain ash. Our results seem to support such speculation and suggest that attempting to predict 1 attribute from another without accounting for shoot response to damage, could result in less accurate predictions than if separate regressions were developed for sites containing different treatment histories.

Our findings also indicate that using regression models to predict 1 shoot attribute from another should include some attention to site (Lyon 1970, Peek et al. 1971, Ruyle et al. 1983), and more importantly, to shoot-specific details. Both the intercept and form of predictive equations for 1 shoot attribute based on another varied depending on whether or not shoots were compensatory and on the site at which the parent plant was growing. Because plant compensation appears to be at least partially responsible for variation in shoot morphometric relationships, we suggest that the development of separate equations for shoots of compensatory and non-compensatory plants from different sites is likely to increase efficiencies in the field and increase predictive power more so than simply increasing sample sizes in an attempt to reduce variability (Peek et al. 1971).

Estimates of shoot weight from basal diameter are often used by rangeland managers to approximate available and/or browsed biomass (e.g., Ferguson and Marsden 1977, Provenza and Urness 1981, MacCracken and Van Ballenberghe 1993). Equations we developed to predict shoot weight from basal diameter were consistent in form and parameters for brush-cut, but not uncut willows. Estimating shoot biomass from shoot basal diameter with the use of our predictive equation for the shoots of brush-cut plants from the Buck site reveals that a typical shoot with a basal diameter of 5 mm would weigh 4.79 g, whereas a shoot from an uncut plant on the same site with a basal diameter of 5 mm would weigh 3.50 g. Estimating 100 such shoots per plant and 100 such plants per hectare, reveals that a difference of nearly 13 kg of browse per ha could go unaccounted for if prediction equations ignored differences between plants producing compensatory or non-compensatory shoots. Increases in the number of shoots per plant or plants per hectare exaggerate such discrepancies.

The degree to which predictive equations tested here varied between brush-cut and uncut plants underscores the need for managers to begin to account for whether or not plants used in building such equations are compensating from damage. Although brush-cutting appears to represent an extreme form of damage not likely to occur in nature, willows scoured by ice flows and broken by snow press (Danell et al. 1987) and browsers (Telfer and Cairns 1978) can incur similar magnitudes of damage. In fact, browse surveys are often conducted in areas influenced by anthropogenic activities such as brush-cutting and logging where interest in browse availability and the utility of such areas for rangeland use is commonly expressed (Shafer 1963, Rea and Gillingham 2001). Even so, moderate forms of damage in more remote areas can cause plants to respond with vigorous vegetative regeneration (Danell et al. 1985) that is likely to influence attributes used in regression equations (Telfer 1969a). Regardless of the damage agent involved or to what degree compensation proceeds, implementing sampling designs that examine plant compensation as well as site effects will allow researchers and managers to better account for the range of variation in shoots growing on differently treated plants on different sites and, as a result, increase the accuracy of their predictions.

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PAPER III

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

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Summary

1. We examined how the removal of above-ground biomass (mechanical brushing) at different times of the year affected the nutritional value of regenerating shoots of Scouler's willow *Salix scouleriana* for moose for two winters after brushing.
2. Brushing trials were conducted throughout the 1996 and 1997 growing seasons in central British Columbia on a 10-year-old regenerating clear-cut replanted in lodgepole pine *Pinus contorta* var. *latifolia*.
3. We assessed the nutritional value of the browse in relation to length, diameter, mass, digestible energy, digestible protein, tannin and lignin content of current annual growth shoots in winter, as well as the phenology of plant leafing.
4. One winter after brushing, willows brushed in early July had shoots that were lower in lignin, higher in digestible protein and lower or not different in tannin content compared with shoots from earlier brushed or unbrushed willows. Willows brushed in early July also had long, heavy, shoots that were high in digestible energy and delayed leaf senescence.
5. In the second winter after brushing, willows that were brushed in July had larger shoots that were lower in digestible energy, digestible protein, tannin and lignin content and delayed leaf senescence compared with several other treatments. Willows brushed after July regenerated negligible shoot material in the first year after brushing. Willows brushed in September delayed leaf flush in the first post-brushing spring.
6. To increase the nutritional value of woody browse for cervids, we suggest that brushing should be performed in early to mid-July (mid-summer).
7. Reductions in browse quality and quantity may negatively affect many mammalian species. Therefore, we recommend that the needs of other fauna potentially affected by changes in shrub architecture, shoot morphology and shoot chemistry be considered when planning the timing of brush management activities.

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

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Introduction

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

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

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

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

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

Materials and methods

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

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

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

SHOOT COLLECTIONS AND ANALYSIS

During the first 2 weeks of December 1996, we collected shoots from 15 of the 30 willows (randomly chosen) from the 14 June 1996 treatment and from the unbrushed 1996 controls. During the first 2 weeks of December 1997, we collected shoots from all 30 of the 1 June 1997, 1 July 1997 and unbrushed 1997 control willows. Shoots from the 30 July 1996, 15 September 1996, 1 August 1997 and 1 September 1997 treatments were considered to have grown insufficiently to be available as winter browse for moose and were therefore not collected in the first winter after brushing. In the second winter after brushing, we collected shoots from the 15 previously unanalysed 14 June and 1996 controls and shoots from all 30 of the 30 July and 15 September 1996-brushed willows.

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

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

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

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

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

MEASURING LEAFING PHENOLOGY

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

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

STATISTICAL ANALYSES

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

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

Results

Overall, mechanical brushing altered the nutritional value of willows. The specific plant attributes affected and the degree to which the value of browse was altered, however, depended on when willows were brushed. Plant age had no effect on morphological or chemical changes in nutritional value after treatment (all $P \geq 0{\cdot}135$).

SHOOT MORPHOLOGY

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

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

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

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

Table 2. Comparison of morphological and chemical attributes of shoots of Scouler's willow brushed on 1 June or 1 July 1997 as well as unbrushed controls measured in the first winter after brushing ($n = 30$ for all morphological attributes and $n = 15$ for all chemical attributes). $P < 0{\cdot}001$ for overall comparisons among brushed and unbrushed willows for all attributes. Means sharing a common superscript are not significantly different from each other, as determined by Tukey's HSD post-hoc comparisons

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

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

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

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

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

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

SHOOT CHEMISTRY

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

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

LEAFING PHENOLOGY

A higher proportion of willows brushed in 1996 and 1997 retained green leaves in the first autumn after brushing relative to unbrushed controls. This trend was apparent when measured once (1996 treatments; see statistics below) or when measured on a weekly basis (19 September to 10 October for 1997 treatments; Table 4). Additionally, a higher proportion of willows brushed on 30 July 1996 ($n = 28$) had green leaves relative to willows brushed on 14 June 1996 ($n = 28$; $\hat{p} = 0{\cdot}857$, $z = -3{\cdot}055$, $P = 0{\cdot}001$), while a higher proportion of those brushed on 14 June retained green leaves relative to unbrushed 1996 controls ($n = 30$; $\hat{p} = 0{\cdot}466$, $z = -3{\cdot}669$, $P < 0{\cdot}001$). Delays in senescence with later brushing times were also apparent when measured weekly in the first autumn for plants brushed in 1997 (Table 4). Although willows brushed later in the year had more green leaves on 17 October 1997, plants brushed in July and August of the same year showed no significant differences in patterns of leaf senescence from 5 September to 10 October (Table 4). Plants brushed in July and August 1997, however, delayed leaf senescence compared with June brushing treatments, from 3 October to 17 October (Table 4).

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

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

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

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

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

Discussion

SHOOT MORPHOLOGY

The morphology of regenerating browse shoots varied with treatment time for at least 2 years after brushing. Shoots produced by plants cut early in the growing season were the largest in the first winter, but smallest in the second winter, after brushing relative to plants cut later in the year. Generally, plants respond to mechanical damage by allocating resources away from reproduction and into vegetative growth; resources are directed to proportionately fewer growing points and cause the plant to reassume a more juvenile form of growth (Bryant *et al.* 1991). More specifically, the differences in plant response due to the timing of brushing were probably related to root to shoot ratios (Willard & McKell 1978) and concentrations of root reserves at the time of cutting (Kays & Canham 1991).

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

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

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

SHOOT CHEMISTRY

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

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

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

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

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

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

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

LEAFING PHENOLOGY

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

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

Premature leaf flush could likewise increase the availability of leaves for ungulates foraging in the early spring. Our results suggest that brushing plants in the early to mid-summer has no effect on leaf emergence in the first post-treatment spring. Autumn brushing, however, did cause delays in leaf emergence in the spring following brushing, thereby reducing leaf availability and the overall value of browse for moose.

IMPLICATIONS FOR MOOSE AND OTHER HERBIVORES

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

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

Because reductions in browse quantity and/or quality negatively affect cervids (Oldemeyer *et al.* 1977; Schwartz, Hubert & Franzmann 1988), the timing of brushing should be considered where ungulate management is an objective. In such areas, retaining unbrushed leave-strips within stands and maintaining unbrushed stands across the landscape should be considered (Rea 1999). Such management strategies are important because brushing can alter plant architecture and aspects of shoot quality for at least 5 years (Rea 1999). Browse plants produce shoots that are more nutritious, succulent and accessible to ungulates for up to 3 years after fire (Stein *et al.* 1992) and can restore reserves lost to cutting within 2 years (Kays & Canham 1991). Presumably, then, brushing could be performed on 3–4-year rotations where concerns for ungulates exist and allowances in the silvicultural prescriptions can be made. Determining how long the effects of brushing persist beyond this amount of time and, furthermore, how plants (both brushed and residual; Härkönen 1998) are affected by multiple brushings needs to be addressed before we can understand how frequently brushing treatments should be applied with respect to ungulate management.

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

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PAPER IV

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RESEARCH

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

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

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

Introduction

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

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

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

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

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

Methods

Study Area

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

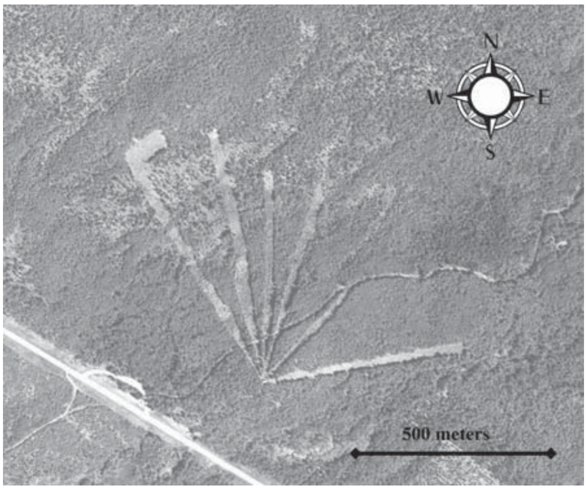

Fig. 1 The Tabor Mountain Wildlife Viewing Area established in 1979 provided a unique study area for the project. Strips of vegetation radiating away from the viewing tower were randomized and cut at different times of the year in 2001. Moose and other animals browsing in any of the strips could be monitored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

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

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

Field Surveys

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

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

Morphometric Measurements

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

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

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

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

Leaf Senescence Surveys

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

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

Statistical Analyses

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

Results

Shoot Length

Year 1

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

Year 2

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

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

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

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

Year 3

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

Biomass

Year 1

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

Year 2

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

Year 3

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

Total Plant Height

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

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

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

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

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

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

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

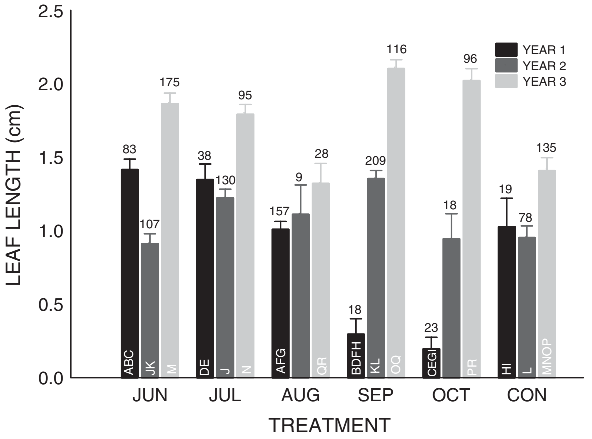

Fig. 2 Differences (± 1 SE) in onset of leaf flush between willows cut at different times during 2001 (treatment) as measured by average leaf length during the springs of 2002, 2003, and 2004. Note: Treatments sharing a common letter assignment within a survey year are the only treatments significantly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

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

Leaf Flush

Year 1

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

Year 2

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

Year 3

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

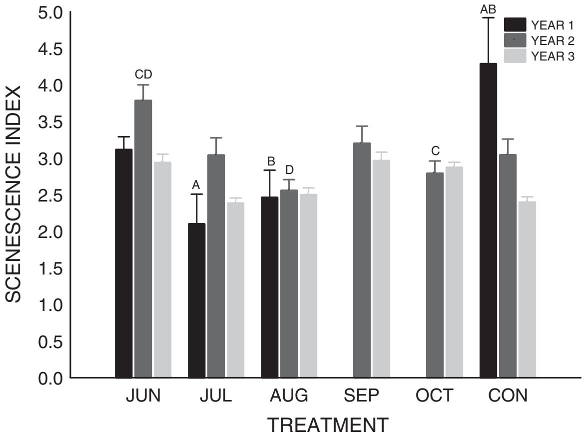

Fig. 3 Differences (± 1 SE) in progression to senescence of twinberry plants brush-cut at different times during 2001 (treatment) as measured by a senescence index (0 = least senescent; 5 = most senescent; see text) during the autumns of 2001, 2002, and 2003. Note: Treatments sharing a common letter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

ing more advanced leaf flush than uncut controls or plants cut at other times of the year.

Leaf Senescence

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

Year 1

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

Year 2

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

Year 3

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

Discussion

Brush Response

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

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

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

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

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

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

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

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

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

Brush Attributes and Herbivore Preferences

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

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

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

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

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

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

Conclusions and Recommendations

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

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

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

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

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

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

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

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

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

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

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

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PAPER V

COMPENSATORY SHOOT GROWTH IN TREMBLING ASPEN (*POPULUS TREMULOIDES* MICHX.) IN RESPONSE TO SIMULATED BROWSING

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ABSTRACT: Moose (*Alces alces*) browsing influences plant growth and architecture. We sought to determine the impact of the timing of moose browsing on bud development and growth in aspen shoots in the subsequent spring through simulation by clipping aspen (*Populus tremuloides*) stems in the field in June, July, and August 2005 at the University of Northern British Columbia, Prince George, BC. To observe new leaf+shoot development in aspen over a 60-day period, the top meristems of both simulated browse treatments and unbrowsed controls were harvested in January 2006, and incubated in a growth chamber that simulated local springtime conditions. Total leaf+shoot biomass produced from stems was higher for June- and August-'browsed' stems relative to unbrowsed controls. Mean stem diameter was significantly higher and number of total buds significantly lower on clipped relative to unclipped stems. The number of buds that broke winter dormancy and became active in the growth chamber remained relatively constant for both clipped and unclipped aspen, but with fewer dormant buds on clipped stems than controls. Overall, our findings suggest that the mechanical effects of moose browsing on aspen stimulate the production of compensatory leaf+shoot biomass, and therefore potential browse.

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Key words: *Alces alces, Populus tremuloides,* browsing, herbivory, plant-animal interaction.

The nature and level of plant response to browsing by moose can vary (Bergström and Danell 1995). Response may be species dependent or may vary individually within a species as a result of differences in time of year or the amount of tissue removed (Rea and Gillingham 2001). The compensatory growth response of many plants browsed in winter (Danell et al. 1985) and the growing season (Bergström and Danell 1995, Gadd et al. 2001) is equal to the level of annual growth in unbrowsed plants of the same species. However, the degree of compensatory growth (e.g., location of meristems, number of dormant buds activated, shoot size, and length) varies in response to the degree of browsing damage; such variance can affect both plant productivity and quality of forage. For example, birch (*Betula pendula* and *B. pubescens*) produced larger shoots with larger and more chlorophyll-rich leaves following browsing (Danell et al. 1985).

Almost all studies of plant response to herbivory have documented the overall effects of browsing damage to individual plant health and morphology, but few have investigated specifically how individual "plant units" respond. Honkanen and Haukioja (1994) speculated that individual plant units, such as branches or ramets, can act as semiautonomous units in that response to damage as an isolated unit would be similar to its response when attached to the parent tree.

In order to examine the compensatory response of aspen meristem units, we observed isolated meristems under incubation that were clipped in simulated browsing treatments during the previous growing season. We believed that the response to clipping damage would result in greater allocation of new biomass to stems as compared to undamaged branches, as found in a similar study by Stevens et al. (2008). Prior to the simulated browsing treatments, we experimented by incubating different stem cuttings of different woody shrubs and trees at different times of the year to observe their growth response. We determined that branches of aspen that were clipped at different times during the previous growing season altered their tissue repair physiology in response to clipping (Carson et al. 2007). Here, we sought to determine whether the timing of simulated browsing would influence the compensatory growth response of aspen in the next growing season.

STUDY AREA

We conducted our study on an approximately 20 ha area located adjacent to the University of Northern British Columbia (UNBC) endowment lands near Prince George, B.C., Canada (lat 53° 53' N, long 122° 40' W). The topography was rolling at an elevation of 780 m above sea level. The climate is continental and characterized by seasonal extremes with cold winters and warm, moist summers. Mean annual precipitation is approximately 460 mm; snow fall averages approximately 200 cm and the mean annual temperature ranges 1.7-5 °C (Atmospheric Environment Service 1993). The study area was clear-cut approximately 15 years prior to the study. Young trembling aspen was the dominant tree species on site, while pioneering species such as shrub willows (*Salix* spp.), paper birch (*Betula papyrifera*), and alder (*Alnus* spp.) were also present. Moose and deer (*Odocoileus* spp.) are both native and foraged within the study area. Our observations indicated that most browsing of aspen was by moose (~1.5 moose/km^2; Walker et al. 2006) at the time of this study.

METHODS

The simulated browsing (clipping) treatments imposed on aspen saplings (approximately 1-5m height) within the aspen-dominated stand (14,240 ± 5696 S. D. stems/ha) were described in Carson et al. (2007). Four simulated browsing treatments (no-browse control and three growing-season clipping dates: 1 June, 16 July, and 30 August 2005) were imposed on 200 naturally growing aspen saplings. To approximate the mechanical effects of browsing, apical stems were clipped at 4.0 mm stem diameter proximal to the apical meristem, which is the average bite diameter of shoots browsed by moose in the study area (Carson et al. 2007).

The top 50 cm of winter-dormant stems from the aspen sapling crowns of control and simulated browsing aspens were harvested 7-14 January 2006. Approximately 5 aspen stems from within each treatment and control were collected on each of the 7 harvest dates for a total of 160 stems from the original 200. Forty of the individuals were damaged or killed by moose between the time of treatment and harvest (Carson et al. 2007). Immediately after removal, stems were placed in water buckets with their cut stem ends immersed in water to a depth of approximately 10 cm to reduce the effects of cavitation (Williamson and Millburn 1995). Harvested stems were then transported to the Enhanced Forestry Laboratory (EFL) at UNBC to record the extent of stem dieback resulting from the simulated browsing treatments imposed during the previous summer (Carson et al. 2007), and prepared for sprouting in an Environmental Growth Chamber (EGC; Model GCW 30, Chagrin Falls, Ohio, USA).

The necrotic (dieback) region below the point of summer clipping of each harvested stem segment was cut off at the terminus to eliminate unproductive and potentially phytopathogenic stem tissue. Harvested stems were reduced to a set mass of 12.0 ± 3.0 g by cutting from the stem bottom (harvest point) and were defined as "set weight stems." Set weight stems were incubated in water baths within the controlled growth chamber for 45 days at a light and temperature regime that approximated the mean local climate in May, followed by 15 days at the mean climate conditions in

June (Meteonorm 4.0; Fig. 1). During the first 4 weeks, the daytime photosynthetically active radiation (PAR), air temperature, and relative humidity (RH) were set at 600 Watts m^{-2}, 15 °C, and 44% RH, respectively, over a 16-h photoperiod; a 17-h photoperiod at 650 Watts m^{-2}, 19 °C, and 48% RH was used in the last 2 weeks. Conditions at night were held constant during the full incubation period (0 Watts m^{-2}, 6 °C, and 87% RH). Water baths only contained plants from the same treatment to avoid possible effects due to water-mediated hormone transport between stems of different treatments. Baths were covered with white plastic and trays were painted white to prevent any light-induced temperature change to the medium (Fig. 1a). Stems were incubated in the growth chamber for 60 days (Fig. 1b). During incubation, stems were monitored for the time of bud burst and maximum growth time prior to leaf desiccation as a result of stem embolism and/or cavitation (Williamson and Millburn 1995). A data logger (HOBO Temp/External Channel Data Logger, Onset Computer Corporation, H08-002-02, Massachusetts, USA) was used to monitor light intensity, temperature, and RH throughout the incubation period.

After the 60-day growing period, set weight stems were harvested and separated into new growth (new leaf+shoot) and pre-existing stem. The number of active and dormant buds was recorded for each stem. Fresh weights for new growth and pre-existing stem were recorded, and then dried at 60 °C for 2 (leaf+shoot) or 6 (old stem) days to measure oven-dry weight.

Statistical Analyses

We used one-way analysis of variance for unequal sample sizes (ANOVA; Zar 1999) to compare differences between clipping treatments and controls; new growth and pre-existing stem mass, mean stem diameter normalized to set weight stem mass, and dormant and active buds normalized to set weight stem mass were compared. Tukey's honestly significant difference (HSD) test for unequal sample sizes (Zar 1999) was used for post-hoc comparisons among treatments. All ANOVAs were performed using Statistica (Version 6.0, Statsoft 2005, Tulsa, OK). We used linear regressions to determine the relationship between the number of active buds and dry leaf mass per stem unit. Regression equations were computed using Excel (Microsoft Office 2003).

Fig. 1. Harvested stem tops of aspen (12 ± 3.0 g) within an Environmental Growth Chamber at; a) initial and b) final stages of a 60-day incubation period to assess regrowth potential.

RESULTS

Overall, significant differences in the ratio of leaf+shoot mass:total branch mass (new growth + pre-existing stem) were observed between the treatments and controls when examining the fresh weight of incubated stems (Table 1). Specifically, June and August

Table 1. Mean ratio of new growth (leaf+shoot) mass:total branch mass in clipped aspen stems and unclipped control stems after simulated browsing (clipping) at 3 different times during summer. Means in a row not sharing a common superscript indicate significant differences as determined by Tukey's HSD post-hoc tests.

	Month of simulated browsing									
	June		July		August		Control			
	n = 31		n = 38		n = 34		n = 39			
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	F	P
New growth:total branch ratio										
Fresh weight	0.088^{ab}	0.004	0.077^{cb}	0.004	0.090^{a}	0.002	0.075^{cd}	0.004	4.385	0.006
Dry weight	0.058	0.003	0.053	0.003	0.060	0.002	0.051	0.003	2.192	0.092

clipping trials had higher leaf+shoot mass to total branch mass when compared to controls. Also, the ratio of leaf+shoot mass to total branch mass for August-clipped stems was higher than that of July-clipped stems. No differences were found relative to dry weight of incubated stems, although June and August clipped stems were about 10% heavier than controls and approached statistical significance (*P* = 0.092).

The ratio of mean diameter normalized to the set weight stem mass was higher for treatments (~0.44 mm/g for all treatments) than controls (0.33 mm/g; *F*(1,3) = 24.5, *P* = < 0.001). However, Tukey's HSD indicated that only controls were different from treatments (*P* = < 0.001). The ratio of dormant buds (*F* (1,3) = 9.599, *P* < 0.001) and total buds (*F* (1,3) = 5.5015, *P* = 0.001) normalized to set weight stem mass was not different among clipping treatments, but was higher for controls than for any clipping treatment (Fig. 2). We found no differences (*F* (1,3) = 0.4436, *P* = 0.722) in the ratio of active buds normalized to set weight stem mass between any clipping treatment or the control (Fig. 2). Weak relationships were detected between the number of active buds and dry leaf mass (Fig. 3); as the number of active buds increased, the dry leaf mass increased for all treatments

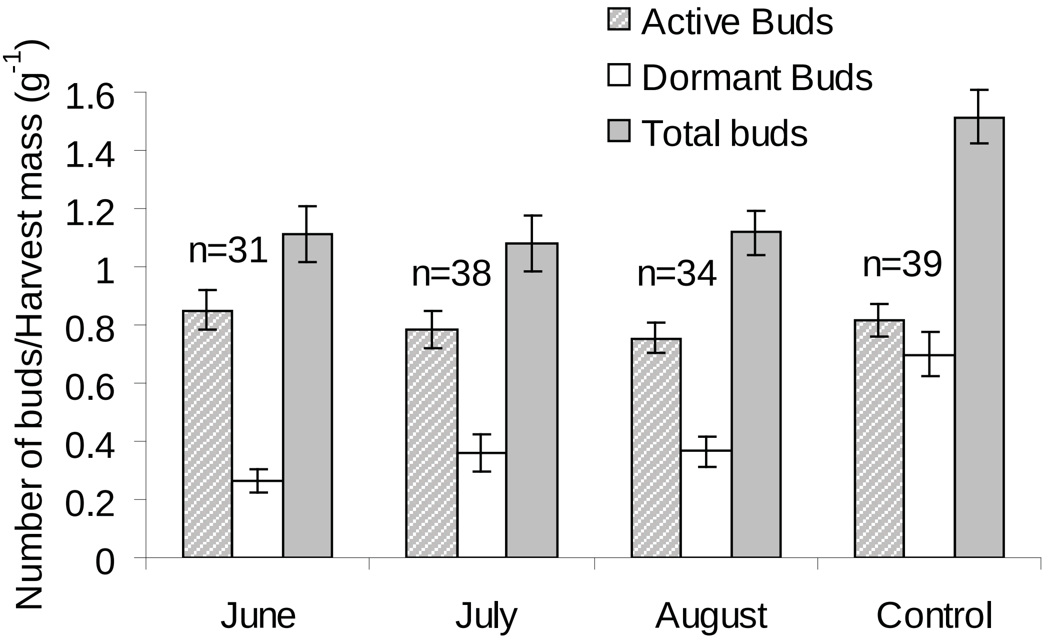

Fig. 2. The number of active buds and dormant buds normalized by the set weight stem mass (12 ± 3.0 g) prior to incubation for treatments after 60 days of incubation in a growth chamber. The numbers of total and dormant buds for all treatments were significantly different from the control (P < 0.001).

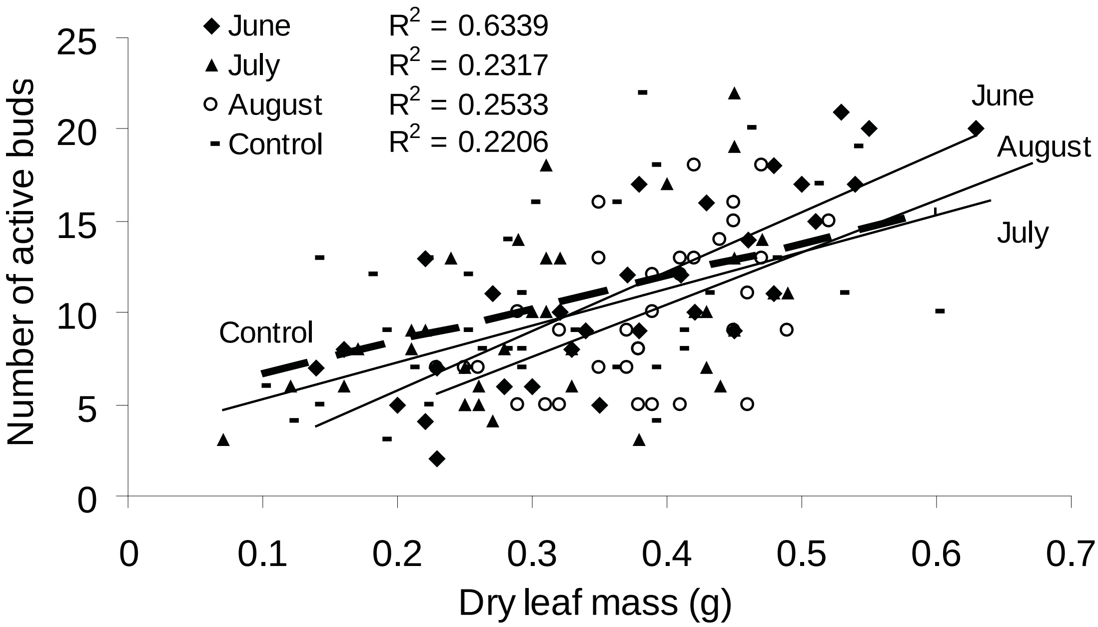

Fig. 3. Relationship between the number of active buds and the dry leaf mass per set weight stems (12 ± 3.0 g) for treatments and controls.

and the control (June: $Y = 32.349x - 0.6691$, $R^2 = 0.6339$; July: $Y = 20x + 3.2593$, $R^2 = 0.2317$; August: $Y = 28.507x - 0.9541$, $R^2 = 0.2533$; and Control: $Y = 17.704x + 4.8627$, $R^2 = 0.2206$).

DISCUSSION

Clipping stems to simulate browsing generally produces the same responses as natural browsing (Haukioja and Huss-Danell 1997), but the effects of clipping and natural browsing on plant morphology and productivity have not been adequately examined in aspen. Indeed, the question of whether browsing animals such as moose positively 'cultivate' their browse species is an open one. We found no evidence that season of simulated browsing on meristems affected the overall production of leaf and stem mass or influenced the proportion of active vs. dormant buds in the spring following clipping. However, we were able to demonstrate a significant effect of simulated browsing on these quantitative aspects of regrowth in aspen stem units when compared with unclipped controls. Given that young aspen is important browse for moose, and that aspen can rapidly grow beyond browsing height of moose, a positive feedback from aspen browsing on forage availability is of more than academic interest.

Overall, our findings suggest that moose browsing can stimulate the production of more compensatory leaf+shoot biomass (potential browse) than is produced by unbrowsed stems. Although aspen is not a preferred browse species in our area, it is consumed frequently by moose in areas of northern BC and elsewhere (Renecker and Schwartz 1998), especially in the absence or low abundance of other preferred browse. Aspen has a high juvenile growth rate and productivity that combined with its ability to tolerate stress better than other tree species (Lieffers et al. 2001), may explain the compensatory response we observed in response to clipping. Stevens et al. (2008) examined herbivory tolerance in aspen and found a positive correlation between tolerance and increased allocation of new biomass to stems under high nutrient conditions.

Because we clipped aspens on the main stem, a loss of apical meristem dominance may help explain the compensatory response we observed. According to the sink-source hypothesis, a change in the ability of meristems to compete with other plants and even other branches of the same plant for resources is the primary way in which damage affects plants (Honkanen and Haukioja 1994). In this way, plant tissues (such as our aspen meristems) that have been damaged or removed by browsing (or clipping) are no longer available to photosynthesize and "sink" resources. This results in a reallocation of plant root resources to shoot production and plant compensation derived from axillary bud development (Pratt et al. 2005).

Simulated browsing treatments also had an effect on the mean diameter of winter-dormant stems (normalized to set weight stem mass), increasing mean diameter of such stems over unclipped controls. Clipping was conducted at a diameter pre-determined from bite marks of moose within the study area, so it was not surprising that unclipped stems with their intact leaders would have a lower mean diameter than stems damaged from browsing or clipping. Although this difference between the mean stem diameter was an artifact of the clipping treatment, the change in architecture (either by clipping or browsing) can have a direct effect on a tree's ability to compensate for tissue loss from browsing over time. Plants with larger mean diameters had a lower number of total buds, presumably affecting the plants capability for shoot production relative to smaller diameter shoots. Like our aspens, the mean shoot diameter of birch (*Betula* spp.) was shown to be higher on stems previously browsed by moose than on unbrowsed trees of the same age (Danell 1983).

While the number of active buds per gram of stem tissue was similar between treatment and control stems, the number of dormant buds was significantly less on clipped stems (Fig. 2). The reduction of dormant buds is likely related to the availability of total buds on clipped stems and their capacity to activate in response to tissue loss. For example, active buds represented 76.8% of total buds on stems clipped in June and only 53.6% of total buds on controls. Thus, stems clipped in June had approximately the same number of active buds as controls despite a reduction in the total number of buds available. Therefore, it appears that aspen can compensate from a single summer browsing event during the following spring through the activation of dormant buds.

If we relate the number of active buds to the production of new leaf+shoot mass for both treatment and control individuals - we find some correlation (Fig. 3; we did not test differences between clippings, but illustrate individual trends for the sake of interest). Our results indicated a somewhat positive relationship between the number of active buds and production of leaf mass. For single browsing events, a stem's ability to maintain the required number of active buds to maximize growth does not seem to reduce plant productivity. It is possible that repeated browsing events on the same stems could eventually hamper the tree's ability to compensate for tissue losses and decrease new shoot production by reducing the availability of meristems. While not evaluated, this negative feedback on vertical growth could have other beneficial effects for the browser (e.g., shoots and leaves produced in the following year might remain within reach of moose).

When we compared the response of plant units and individual plants to damage from simulated browsing, we found similar responses. Clipped stems had significantly fewer mean buds per stem than the controls; similarly, Bergstrom and Danell (1987) found an overall reduction in the mean number of buds per tree on clipped individuals. As well, clipped individual stems in our experiment produced the same leaf+shoot biomass as unclipped stems. Defoliation of long shoots on individual birch (*Betula pendula*) during the summer resulted in lower leaf biomass on defoliated trees; however, total leaf biomass produced during the season was about the same on both treated and untreated individuals (Bergstrom and Danell 1995). Although we did not see a difference in the production of new leaf+shoot biomass between clipping treatments, clipping at different times of the growing season can produce variable levels of biomass production as compared to unclipped stems. Thorne et al. (2005) found that the frequency of clipping alone had no significant effect on biomass, rather, it was specific combinations of seasonal clipping that produced the highest variation.

We suggest further investigation into the relationships among meristem availability, height-specific browse production, and aspen's ability to compensate for tissue loss, specifically with respect to the influence of varying intensity and frequency of browsing events. Related research has identified activation from bud dormancy as a basic component of compensatory response within plants (Tuomi et al. 1994), but as with our study, has been tested only within the scope of a single browsing event. Stevens et al. (2008) found that the response of aspen to herbivory was dependent on soil nutrient conditions; we presumed that soil conditions were reasonably consistent within our relatively small study site. A more detailed approach may be required to observe aspen response to repeated and variable levels of browsing intensity. Furthermore, the relationship between stem volume and number of buds should be studied over a variety of branch sizes to better understand the general characteristics governing morphometric responses and browse production in aspen stems, as well as stems of other browse species. Palatability and nutritional differences between compensatory growth of clipped aspen stems versus unclipped stems is also of interest. Moose are known to select for compensatory shoots that grow from plants that have been browsed or cut (Danell et al.1985), and appear to select for shoots based on the season of cutting (Alpe et al. 1999). Presumably, nutritive quality varies depending upon the season of browsing (Rea and Gillingham 2001), however, such responses are unmeasured in aspen.

We did not find distinct differences in shoot/leaf production between clipping treatments as we did between controls and clipped stems. However, we did not assess whether our clipped samples included only new (current year) or a combination of new and old growth. In retrospect, accounting for whether we clipped new or old growth might have helped us discern any effects associated with new and older growth, and possible interactions with time of clipping. We recommend that similar research account for the age of clipped growth as opposed to clipping indiscriminately at the diameter of an average bite.

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PAPER VI

Rangeland Ecol Manage 60:543–547 | September 2007

Research Note

Extent of Stem Dieback in Trembling Aspen (*Populus tremuloides*) as an Indicator of Time-Since Simulated Browsing

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Abstract

Simulated browsing treatments were imposed on an important browse species of the North American moose (*Alces alces* L.) to see if the development and extent of subsequent stem dieback in trembling aspen (*Populus tremuloides* Michx.) could be used to determine the time of browsing during the growing season. Two hundred naturally growing aspen saplings of similar size and form were randomly selected in a 20-ha area near the endowment lands of the University of Northern British Columbia, Prince George, British Columbia, Canada. Plants were randomly assigned to treatment categories so that the apical meristems of 50 plants each were assigned to a control or were clipped on one of the following dates 6 weeks apart: 1 June, 16 July, and 30 August 2005. The leader of each aspen was clipped and dieback was left to progress until the onset of winter dormancy. Our results showed that the earlier the simulated browsing occurs in the growing season, the greater the length of stem dieback, up to the maximum of the subapical axillary node below the point of clipping. The average rate at which dieback progressed varied between treatments and decreased throughout the growing season. Our results suggest that the ratio of the actual length of stem dieback to the overall length of stem between the clip point and the subapical axillary node serves as a good indicator for estimating the time at which aspen meristems have been browsed during the growing season.

Resumen

Se aplicaron tratamientos de ramoneo simulado a una importante especie arbustiva para el alce de Norte América (*Alces alces* L.), para ver si el desarrollo y la cantidad de muerte descendente de los tallos del "Trembling aspen" (*Populus tremuloides* Michx.) pudieran ser usados para determinar el periodo de ramoneo durante la estación de crecimiento. En un área de 20 ha, cercana a los terrenos de la Universidad del Norte de Columbia Británica en Prince George, British Columbia, Canadá, se seleccionaron, en forma aleatoria, 200 plántulas de "Aspen" de una población natural, todas de tamaño y forma similar. Las plantas se asignaron aleatoriamente a los tratamientos, de tal forma que los meristemos ápicales de 50 plantas fueron asignados a un control o fueron cortadas en una de las siguientes fechas con seis semanas de separación entre ellas: 1 de junio, 16 de julio, y 30 de agosto del 2005. El tallo principal de cada plántula fue cortado y se dejo que ocurriera la muerte descendente hasta el inicio de la dormancia invernal. Nuestros resultados mostraron que entre más temprano ocurra la simulación del ramoneo en la estación de crecimiento mayor es la longitud de la muerte descendente de los tallos, hasta el máximo del nudo subápical axilar abajo del punto de corte. La tasa promedio a la cual progresó la muerte descendente varió entre tratamientos y disminuyó a través de la estación de crecimiento. Nuestros resultados sugieren que la relación de la longitud actual de la muerte descendente con la longitud del tallo entre el punto de corte y el nudo subápical axilar sirve como un buen indicador para estimar la época en la que los meristemos del "Aspen" han sido ramoneados durante la estación de crecimiento.

Key Words: cattle, clipping, meristem, moose, plant response, stem necrosis

INTRODUCTION

Deciduous shrubs and trees are an important source of food for wild ungulates such as moose (*Alces alces* L.; Danell 1982). Although browsing ungulates tend to concentrate foraging efforts less on twigs in summer when aquatics, forbs, and other forage items are plentiful, browsing on stem materials does occur throughout the year (Danell et al. 1994). Free-range cattle are also known to browse twigs during the summer months (Visscher et al. 2006).

Understanding the seasonal use of rangeland plants is integral to assessing how important particular plant species are in the seasonal diet choices of ungulates. Such data can help in determining rangeland quality and carrying capacity, as well as identifying preferred forage items of wild and domestic animals sharing rangelands at specific times of the growing season.

Currently, no method appears to be available for use in approximating the time at which stems are browsed. Consequently, we investigated the utility of using patterns of aspen stem dieback (also referred to as apical dieback or necrosis; Chaar et al. 1997) in response to clipping as a means to estimate when stems are browsed. Our hypothesis was that the total amount of stem dieback observed on dormant stems that had been previously browsed was dependent on the amount of time dieback had to occur during the previous growing season,

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and therefore could serve as an indicator of when stems were browsed. We assumed that dieback progression along a stem was time-dependent and was unrelated to the amount of stem tissue removed by biting or clipping.

STUDY AREA

The study took place on an approximately 20-ha area located adjacent to the University of Northern British Columbia endowment lands near Prince George, British Columbia, Canada (lat 53°53′N, long 122°40′W). The topography is rolling and the site elevation is 780 m above sea level. The climate is continental and characterized by seasonal extremes with cold winters and warm, moist summers. Mean annual precipitation is approximately 460 mm; snow fall averages approximately 200 cm and mean annual temperatures range from 1.7°C to 5°C (Atmospheric Environment Service 1993). The study area was clear cut approximately 15 years prior to the study. Trembling aspen (*Populus tremuloides* Michx.) is the dominant species on the site. Pioneering species such as willow (*Salix* spp.), paper birch (*Betula papyrifera* Marsh.), and alder (*Alnus* spp.) are also present. Moose and deer (*Odocoileus* spp.) are both native to the area and use browse species within the study site. Our observations, however, indicate that most of the browsing on aspen in our study area is done by moose (approximately 1.35 moose · km^{-2}; Walker et al. 2006).

METHODS

In the spring of 2005, the bite diameters of 50 stems, previously browsed by moose, were measured to obtain a reference for clipping. Subsequently, two hundred unbrowsed aspen saplings of similar size and form within the site were then selected and 50 each were randomly assigned to one of three clipping treatments and a control group. Clipping treatments were applied 6 weeks apart on 1 June, 16 July, and 31 August 2005.

For each clipping treatment, the leader of each individual aspen was clipped at a diameter of 4.0 mm (following a determination of the average bite point diameter) to simulate browsing by moose. Between 7 and 14 January 2006, the top 50 cm of all aspens that had been clipped in 2005 was harvested from each plant. A total of 160 stems were recovered from the original 200 individuals; forty individuals were damaged or killed by moose between treatment time and top harvest.

The amount of dieback on each stem was determined by peeling the bark away from the edge of the simulated browse point to the base of the stem to reveal the extent of the necrosis within the underlying tissue. The entire length of stem that could have experienced dieback (typically to the subapical axillary node; sensu Chaar et al. 1997) was considered the dieback potential (DP; Fig. 1). The dieback length (DL) was measured from the simulated browse line to the dieback terminus (the point to which the dieback had actually progressed down the stem; Fig. 1) at 4 locations around the stem circumference and then averaged. The difference between DP and DL was termed the residual length (RL), and was the part of the stem that was healthy, but had the potential for dieback to occur if time allowed. The ratio DL/DP, termed the normalized dieback ratio (NDR; Fig. 1) was used to describe the portion of the DP that experienced dieback. Average rate of dieback (mm · d^{-1}) is the amount of dieback (DL) that occurred over the time between clipping and the onset of winter dormancy.

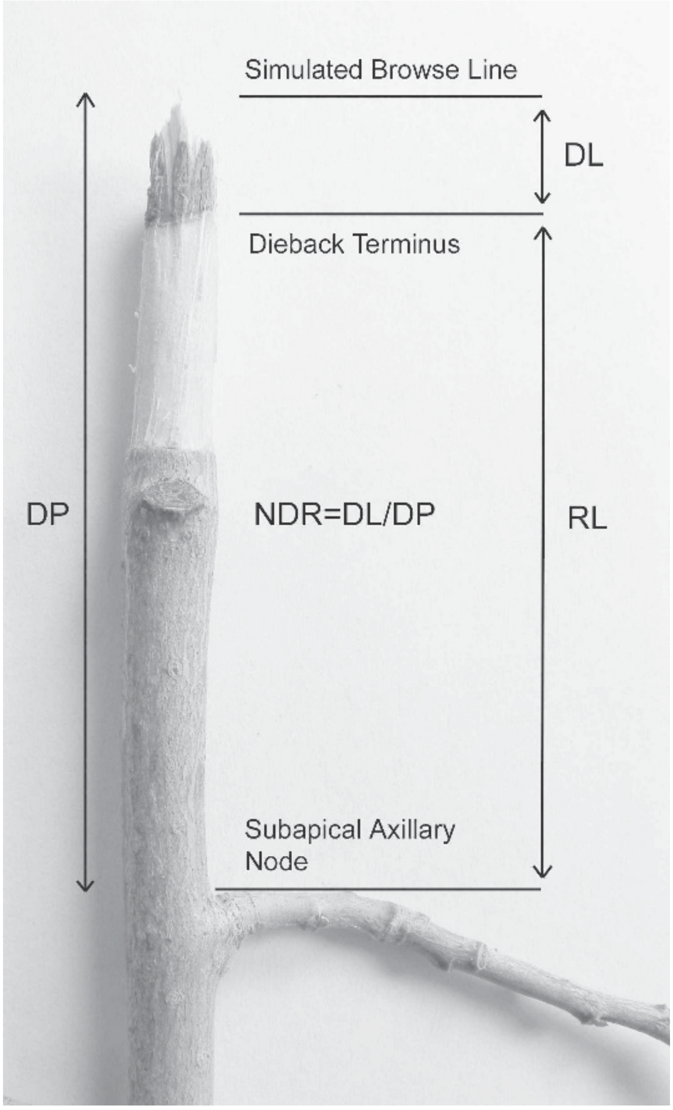

Figure 1. Picture of an aspen stem illustrating the anatomy of stem dieback after browsing depicting: dieback length (DL) measured between the edge of the simulated browse line and the dieback terminus; residual length (RL) measured as the distance between the dieback terminus and the subapical axillary node; and dieback potential (DP) measured between the simulated browse line and the subapical axillary node. The normalized dieback ratio (NDR) is DL/DP.

Statistical Analyses

We used one-way analysis of variance for unequal sample sizes (ANOVA; Zar 1999) to compare differences in stem dieback, potential dieback, and the normalized dieback ratio between clipping 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 1999). Square root transformations (Tabach-

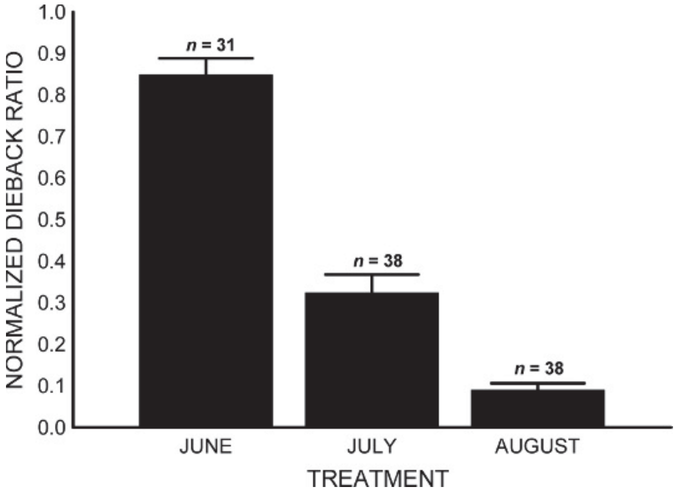

Figure 2. Comparison of the average (+1 SE) normalized dieback ratio for aspen stems subjected to simulated browsing at three different times (1 June, 16 July, and 31 August) during the 2005 growing season. All treatments are significantly different from one another ($P < 0.05$).

nick and Fidell 1996) were applied to normalize our rate and normalized dieback ratio data. Tukey's honestly significant difference (HSD) test for unequal sample sizes (Zar 1999) was used for posthoc comparisons among treatments when a significant effect was detected. All ANOVAs were performed using Statistica (StatSoft 2005). We used linear regression to determine the relationship between the average rate of dieback and the dieback potential. Regression equations were computed using graphics software (DeltaGraph v.5.0.1; SPSS Inc, and Red Rock Software, Salt Lake City, UT).

RESULTS

The absolute length of stem dieback (DL) after simulated browsing was significantly affected by time of simulated browsing and was largest for plants clipped earliest in the growing season $F_{2,104} = 42.858$, $P < 0.001$ between all three clipping trials. Because dieback could potentially extend all of the way back to the subapical axillary node (see Fig. 1), but was not consistent among stems, we normalized the dieback length (NDR). The NDR was different among all three clipping trials and was smallest for those plants clipped later in the year $F_{2,104} = 105.494$, $P < 0.001$ (Fig. 2).

The average rate of dieback ($\mathrm{mm} \cdot \mathrm{d}^{-1}$) was greatest for plants clipped in June $F_{2,104} = 13.772$, $P < 0.001$, but was not significantly different among plants clipped in July and August. Similarly, there was an increase in the average rate of dieback with an increase in potential length for dieback (DP; Fig. 3). Stems with long dieback potentials ($Y = 0.0087x - 0.0171$, $R^2 = 0.995$) had higher average dieback rates than those with short dieback potentials ($Y = 5E^{-05}x + 0.0959$, $R^2 = 0.0028$; Fig. 3).

DISCUSSION

Our findings indicate that several differences in stem dieback occur and are measurable among stems clipped at different times of the growing season. The attributes that show the most significant differences are the length of dieback and residual length. The dieback potential and length of dieback are significant in calculating the "normalized dieback ratio" (NDR). This ratio appears to be a reasonable method for approximating the time during the growing season in which shoots are browsed. Because studies have shown that clipping stems to simulate browsing can produce the same response as natural browsing (Haukioja and Huss-Danell 1997), it is reasonable to assume that both clipping and natural browsing affect leaf and shoot characteristics in similar ways.

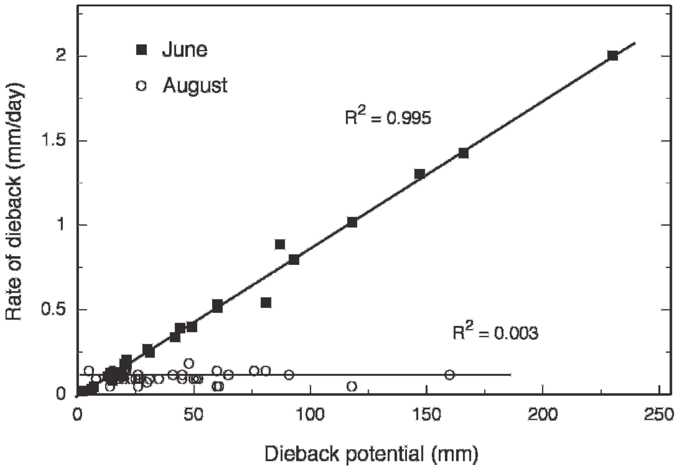

Figure 3. The relationship between the average rate of dieback and the dieback potential (length between the simulated browse line and the subapical axillary node). Note: Days to dormancy is the number of days from the time of clipping treatment until 23 September 2005 (estimated dormancy initiation; see text).

The length of dieback was dependent on the timing of the clipping event during the growing season and the length between the point of clipping and the subapical axillary node (DP). It appears that the time at which the clipping event occurred determined the amount of time available for dieback to progress down the stem until the onset of winter dormancy (about 23 September; personal communication, Jos V. Hage, Art Knapp Plant Land, Prince George, BC, 21 September 2006). Although more severe tissue removal occurs during treatment, brush-cutting appears to have a similar influence on cambium dieback in young aspen (Bell et al. 1999); cambium dieback is more pronounced in the stumps of summer- vs. fall-cut aspens.

Stems clipped in June had the greatest amount of time for the dieback to progress down the stem, followed by July, and then August where the amount of time for dieback to occur was 92 days less than plants clipped in the June trial. Although stems clipped earlier generally revealed the greatest amount of dieback when compared with late-clipped stems, dieback was clearly moderated by the amount of tissue between the clip point and the subapical axillary node. This suggests that the greater the distance that dieback must travel to reach the subapical axillary node (DP), the more quickly it progresses (Fig. 3). Regardless of the dieback potential, stem dieback progressed towards the subapical axillary node within a given period of time. The average rate of dieback progression, therefore, differs between stems with different dieback potentials. Therefore, it seems that the length of dieback is not a good indicator for determining when stems are browsed. This is simply because the length of dieback is dependent on the dieback potential. Stems with different dieback potentials browsed at the same time during the growing season show different average rates of dieback progression and therefore different lengths of dieback. For the same reason, residual length is not a good predictor for determining the time at which browsing occurred—it shares an inverse relationship with the dieback length.

The most accurate predictor for determining when aspen stems are browsed appears to come from calculating the normalized dieback ratio, which is the ratio of the length of dieback to the potential dieback on a given stem. Regardless of how quickly dieback progresses down the stem, or how far it has to travel from the clip point to reach the subapical axillary node, the normalized dieback ratio represents how much stem has died back relative to the total amount of tissue wherein dieback is able to occur.

The "normalized dieback ratio" measurements appear to roughly correspond with the percentage of the growing season that dieback has to progress and appears to be useful for approximating the time during which the browsing event occurs. For example, on average, stems clipped on 1 June reached a normalized dieback ratio of approximately 85%. The interval between 1 June and 23 September also comprises approximately 85% (114/135) of the growing season (1 May to 23 September) in northern British Columbia. Shoots clipped at the end of August, on the other hand, reached an average normalized dieback ratio of 10%, and 30 August to 23 September represents 16% (22/135) of the growing season. Stems characterized by reaching 100% of their dieback potential are most likely to have been browsed at the very beginning of the growing season or sometime prior to the initiation of stem metabolic activities in spring. Conversely, stems showing no signs of stem dieback when analyzed in winter are stems likely damaged during the current dormant period; dormant stems appear incapable of initiating dieback until stem dormancy is broken in spring (personal observations).

Although the phenomenon of dieback appears to be present in other species (e.g., *Amelanchier alnifolia* Nutt., *Acer douglasii* Hook., *Betula papyrifera* Marshal; personal observations) at the study site, factors such as the average rate of dieback and the variation in dieback potential are likely to vary between species and could affect the utility of this technique for estimating the time of browsing for various species. Because aspen carbon allocation strategy involves a relatively early switch from carbon production to carbon storage (Lieffers et al. 2001), the reduction in the average rate of dieback might occur earlier in the growing season for aspen compared to other shrubs and trees used by ungulates. If the carbon allocation strategy of another plant involved a reduction in the average rate of dieback later in the growing season, higher rates of dieback progression are likely to occur for longer periods and the estimated time to complete dieback could be reduced. Further experimentation might reveal some differences in patterns of dieback between various species. Furthermore, conducting clipping trials over the entire growing season at smaller intervals (e.g., every 2 weeks) could also reveal some finer detail in patterns of dieback progression within and between species.

MANAGEMENT IMPLICATIONS

Our results indicate that the normalized dieback ratio, when assessed during plant dormancy, can serve as an indicator of when in the previous growing season aspen stems were browsed. This ratio can be easily obtained from individual stems in the field by removing the bark just below a bite point on a stem and dividing the dieback length by the overall dieback potential of the stem. The quotient obtained corresponds closely with, and therefore approximates, the amount of growing season that transpired between the occurrence of browsing and the onset of plant dormancy.

Although we only investigated the dynamics of stem dieback on aspen in one study area, the technique we developed likely has some application for assessing the timing of browse on aspen and other plant species in other regions. We suggest that this technique could be useful for naturalists and rangeland managers as a tool to help evaluate patterns of animal behavior and nutrition or the impacts of browsing on the physiology and seasonal nutrient dynamics of plants used as food by both wild and domestic ungulates.

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The authors would like to thank Adam Kantakis and Dorianna Hoekstra for their assistance with the clipping trials. We thank Aaron Skoblenick for volunteering his time during the harvest of aspen stems and John Orlowsky and Steve Storch of the Enhanced Forest Lab at UNBC for providing supplies and general assistance. We also thank Dr Phil Burton and two anonymous reviewers for the valuable suggestions on earlier drafts of this manuscript.

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PAPER VII

SILVA FENNICA
Silva Fennica 45(2) research articles
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The Finnish Society of Forest Science · The Finnish Forest Research Institute

Impacts of Moose (*Alces alces*) Browsing on Paper Birch (*Betula papyrifera*) Morphology and Potential Timber Quality

Roy V. Rea

Rea, R.V. 2011. Impacts of Moose (*Alces alces*) browsing on paper birch (*Betula papyrifera*) morphology and potential timber quality. Silva Fennica 45(2): 227–236.

Although moose browsing effects on the growth and morphology of birch are well studied, effects of moose browsing on potential timber quality of birch have received little attention. Here, an assessment was made of the impacts of moose (*Alces alces* L.) damage to Paper Birch (*Betula papyrifera* Marsh.) trees from a 20-year old clear cut area in a sub-boreal spruce forest within the Aleza Lake Research Forest, near Prince George, British Columbia, Canada. Specifically, differences in overall tree architecture and in the internal characteristics of trees that had been severely damaged and suppressed by moose winter browsing were compared to birch trees that had not been damaged by moose in this way and were considered free-to-grow. The average stem diameter, number of annular growth rings, and height of stem breaks made by moose on suppressed birches at the point of breakage was 17.9 ± 6.6 mm, 4.6 ± 1.2, and 141.8 ± 32.0 cm, respectively. Stem diameters and the heights above-the-ground of stem breaks made by moose during sequential breakage events were not significantly different (all $p \geq 0.05$) from one another. Decay was significantly (all $p \leq 0.001$) more extensive in trees where branches had been broken off by moose than in trees with no breaks or where breaks were from unknown agents. Suppressed birches were significantly ($p = 0.048$) more exposed (farther from their nearest tree neighbor) when compared to birches that were free-to-grow. The distance from birch trees to species-specific neighbors (of any species) did not differ (all $p \geq 0.05$) between suppressed and free-to-grow birches. Suppressed birches damaged from intense browsing and stem breakage were significantly ($p \leq 0.001$) farther away from other birches showing signs of slight to moderate browsing than free-to-grow birches were from similar conspecifics. Because moose appear to impact the potential wood quality of birch, forest managers should consider the impacts that browsing and stem breakage can have on birch timber where these trees co-occur with and are eaten by moose.

Keywords browse damage, deciduous, forestry, hardwood, silviculture, ungulate, wood quality
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1 Introduction

Moose are recognized as an agent of severe damage to forest stands throughout many parts of their circumpolar range (Bergerud and Manuel 1968, Jalkanen 2001, De Jager and Pastor 2008). Which trees in a forest stand are sought out and browsed by moose varies according to regional differences in moose preferences and tree species availability (Peek 1998, Persson et al. 2000). Although moose damage to conifer stands throughout Scandinavia is commonly reported (Danell et al. 1991, Heikkilä and Härkönen 1996), similar levels of damage to conifers are rarely reported from western North America (Rea and Child 2007). Here, hardwoods such as willow and birch – not pine or other softwoods – tend to comprise the majority of the moose winter diet (Renecker and Schwartz 1998).

Interactions between moose and broadleaved deciduous tree species such as birch have been well studied (Renecker and Schwartz 1998), particularly in Scandinavia (Bergström and Danell 1987, Danell and Bergström 1989, Danell et al. 1997, Persson et al. 2005, Persson et al. 2007, DeJager and Pastor 2008). However, the direct impacts of moose on the ability of birch to become part of the merchantable segment of a forest stand and the impact of moose damage on birch growth and wood quality per se has received little attention (Härkönen et al. 2009).

The impacts of moose on birch tree autecology in the Aleza Lake Research Forest (ALRF) of British Columbia, Canada was examined to determine the ability of moose to impact directly the ability of paper birches to mature naturally. Determining whether or not moose suppress birch recruitment into later seral stages and how such suppression affects the growth and potential lumber quality of birch was the primary objective of the research.

2 Methods

2.1 Study Area

The study site was located within the Aleza Lake Research Forest (approximate latitude of 54°07´ North, and longitude of 122°04´ West at an elevation of 600–750 m asl) in north central British Columbia. The research forest is a 9000 ha university-based outdoor research facility and working forest ~60 km east of Prince George, BC, Canada. The research forest is located in the Upper Fraser River basin, on the eastern edge of the Central Interior Plateau, near the foothills of the northern Cariboo and Rocky Mountain ranges and is described by Jull and Karjala (2005).

Situated in the Wet Cool (SBSwk1) subzone of the Sub-boreal Spruce biogeoclimatic zone (Pojar et al. 1987), the research forest typifies a montane transitional zone between a climate of drier plateau forests to the west, and the wet, snowy mountain forests in the nearby Interior Cedar Hemlock (ICH) and Engelmann spruce-subalpine fir (ESSF) forests to the east (Jull and Karjala 2005). About 85% of the ALRF is composed of gently rolling to gullied terrain that is covered by upland spruce-fir forests and wetlands with some hardwoods. The remaining 15% is composed of the Bowron River floodplain which is a complex mosaic of alluvial sites, ranging from old river channels, alluvial wetlands and freshly-deposited gravel bars and higher terraces (Jull and Karjala 2005). Moose densities in the surrounding area in the years preceding our assessments and when moose would have been browsing on birches that we evaluated were 0.45–0.60 moose/km^2 (Heard et al. 1999, Heard et al. 2001).

2.2 Field Work

Data from birches were collected from an ~30 ha area of a hybrid white spruce (*Picea glauca* [Moench] Voss. × *englemannii* [Parry ex Engelm.] T.M.C. Taylor)/subalpine fir (*Abies lasiocarpa* Hook.[Nutt.]) forest area that had been clear-cut and planted with spruce approximately 20 years prior to the present study. Early successional, mid-sized shrubs and trees growing in the study area included alder (*Alnus* spp.), birch (*Betula papyrifera*), willow (*Salix* spp.) and aspen (*Populus tremuloides* Michx.). The study area was selected based on whether or not a mix of birches could be found that were: 1) suppressed as a result of repeated heavy browsing and multiple stem breakage events by moose and 2) growing freely above the reach of moose.

Fifty eight birch saplings were selected from within the study area for evaluation. Old roads and log decking landings were used to gain access to different parts of the study area. Birches were selected from across the stand type and were located within the stand between 50 and 400 meters from haul roads. Selection procedures were based on damage to birches. Birches that showed signs of heavy and repeated browse use by moose, had multiple stem breaks and were obviously suppressed in growth (n = 24) were selected for evaluation and characterization. Birches that were characterized by a distant history of no or slight to moderate browse use by moose, but at survey time appeared free-to-grow (n = 35), with robust main stems and mature leaders well beyond the reach of browsing moose were selected for comparative purposes.

The majority of birches that were selected were assessed exclusively in the field. However, 24 trees were also selected for removal from the stand and transport back to the Enhanced Forestry Laboratory at the University of Northern British Columbia for closer inspections of the impact of browsing and breakage on internal tree attributes. For those trees assessed exclusively in the field, measurements recorded included: tree height, base diameter at ~30 cm above the ground, diameter at breast height (~1.3 m above the ground), distance to the nearest tree species that was as tall or taller and as thick or thicker in diameter at the trunk than the birch being assessed and, distance to the nearest birch that had a canopy within the reach of moose and not classified as either suppressed or free-to-grow, but that showed signs of slight to moderate (in some cases no) browsing. Trees that were not taken back to the lab were cored in the field (at ~30 cm above the ground) for age determinations. Twenty birches were aged using cores and disks to cross-validate the two techniques. Each birch selected for assessment was photographed in the field.

2.3 Lab Work

Twenty-four of the trees that we transported back to our lab had been repeatedly and extensively browsed by moose over their life time as evidenced by their hedged form and stunted vertical growth. We photographed each tree brought to the lab against a light-colored backdrop to enhance contrast (Fig. 1).

Fig. 1. A typical suppressed birch damaged by moose in the Aleza Lake Research Forest and taken from the study area for assessment at the Enhanced Forestry Lab.

A 2–3-cm thick disk was cut from the bottom of the main stem of each birch and sanded on one side so that the annular rings could be counted to determine the tree age at ~30 cm above the ground. An ~1-cm thick disk was also cut and sanded from the three most recent breakage points on each tree so that a determination of the mean stem age at breaks created by moose during winter browsing events could be made (see Telfer and Cairns 1978). The chronological order of breaks was assessed by evaluating their position on the tree and the amount and age (using the number of current annual growth scars) of shoots arising from below the breakage. Also recorded were the height and stem diameter at each break. The morphometry or "hedgedness" of each tree was also assessed by measuring and averaging the length of branches from trunk center out to the branch tips along two sides of each birch from the base of the tree to the top in 5-cm increments.

Finally, the degree of internal decay within the main stem of trees that came from branch breakage events caused by moose and other agents on trees brought into the lab was evaluated. Decay was assessed by bandsawing birches through portions of the stems from which both broken and healthy branches originated. Bandsawing exposed the origins of branches and revealed portions of the tree affected by decay that had invaded stems from break points on branches. The width of the branch collar where each branch was attached to the main stem was recorded, as was the average width and length of the decay core and the average width of the main stem in which the decay was detected. From these measurements, indices of decay were developed using:

DECAY INDEX 1 = ADCD * ADCL
DECAY INDEX 2 = ADCD * ADCL / SW
DECAY INDEX 3 = (ADCD * ADCL / SW) / BCD

where
ADCD = average decay core diameter (width),
ADCL = average decay core length, SW = stem width,
and BCD = branch collar diameter (width).

2.4 Statistical Analyses

To test differences in the diameter, age, age/diameter relationship and breakage height above the ground of the last 3 breaks made by moose on birch stems and the distance from suppressed and free-to-grow birch trees to the nearest neighbor (any tree species) and specifically to the nearest birch that was slightly to moderately browsed, analysis of variance (ANOVA; Tabachnick and Fidell 2007) was used. ANOVAs were also used to test for differences in the amount of internal decay caused by branch breakage from moose browsing and other factors. Homogeneity of variances for all ANOVA comparisons were tested using a Levene's test (Milliken and Johnson 1984). A Kolmogorov-Smirnov test was used to test assumptions of normality (Gotelli and Ellison 2004). Linear regression analysis (Gould and Gould 2002) was used to test the relationship of tree height to age and height to base diameter between suppressed and free-to-grow birches. All analyses were conducted in Statistica 9 (Statsoft 2009).

3 Results

Varying significantly from unbrowsed, free-to-grow birches (which were effectively branch-free up to and beyond the reach of browsing moose), suppressed birches were, multi-stemmed, branched and more hedged in appearance (Fig. 1).

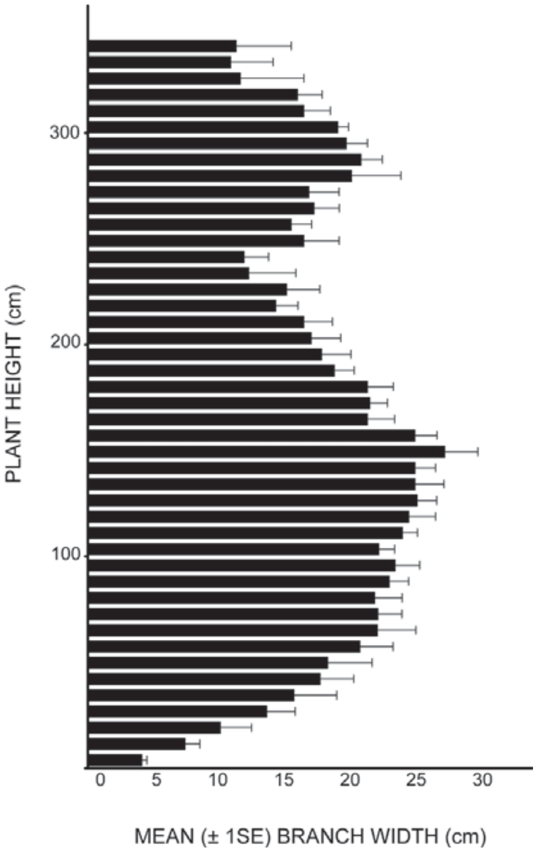

Fig. 2. The relationship of the mean (± 1SE) branch width (from the main stem center line to the tip of the longest branch) to plant height of birch trees (n=23) browsed by moose at the Aleza Lake Research Forest. Imagining the Y-axis as the midline of the main stem of the tree allows for a visualization of how wide the widest branches of trees were on average at 5-cm intervals up and along one side of the tree from bottom to top (~3.5 m high).

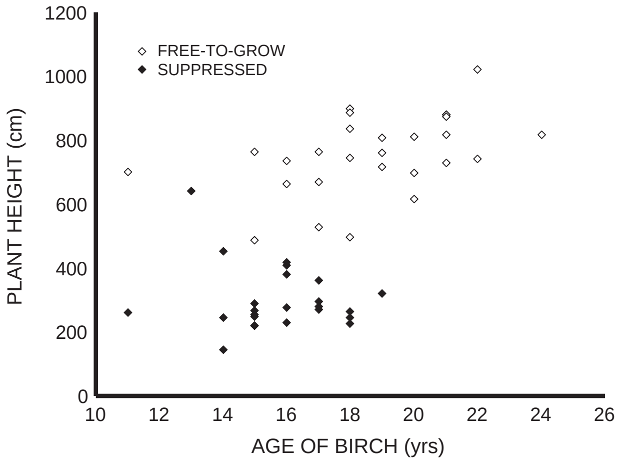

Fig. 3. Relationship between the age and height of birches that have been suppressed (n = 24) through repeated moose browsing and those that were free-to-grow (n = 27).

On average, birches were just under 3.5 m tall and had a morphology or silhouette which could be described as hour glass-shaped with the longest lateral branches occurring at 1.5 and 2.8 m above the ground (Fig. 2).

The average base diameter and age of trees assessed in lab was 59.5 ± 10.9 mm and 12.5 ± 1.8 years, respectively. Suppressed birches were shorter at a given tree age (TREE HEIGHT = 440.23 – 8.91AGE) than free-to-grow birches (TREE HEIGHT = 166.47 + 32.25AGE; Fig. 3). Similarly, suppressed birches were shorter at a given base diameter (TREE HEIGHT = 129.27 + 25.44BASEDIAMETER) than free-to-grow birches (TREE HEIGHT = 452.13 + 34.69BASEDIAMETER). No differences (P = 0.560) existed between suppressed and free-to-grow birches in the density of annuli per given basal stem diameter (age to diameter relationship).

The average number of breaks (not bites) on trees assessed in lab was 6.54 ± 3.59 breaks. The average diameter, number of annuli and height of breaks made by moose on birches assessed in lab (n = 24) was 17.9 ± 6.6 mm, 4.6 ± 1.2 annuli (range of 3 to 8 annuli), and 141.8 ± 32.0 cm, respectively. There was no significant difference in the diameter (F(1,2) = 0.330, p = 0.720), age (F(1,2) = 1.28, p = 0.285) or break height above the ground (F(1,2) = 0.359, p = 0.700) of the last 3 breaks made by moose on the main/collateral stems of birches.

Fig. 4. A sagittal section of a young birch tree showing evidence of the original apical meristem having been browsed by moose (white arrow). Topping of the birch by moose created a response in the plant which allowed the birch to continuing growing – apparently facilitated by a lateral meristem assuming apical control. Dieback of the mainstem, however, appeared to create an entry point for the formation of decay which can be seen in the center of the birch and which continued down the length of the birch (but which is not seen in the image due to how the plant was sectioned).

All indices of decay assessed indicated that decay (Fig. 4) was significantly (all $p \leq 0.001$) more extensive in sections of trees where branches had been broken off by moose than in tree sections where breaks were from unknown agents (Fig. 5), or where branches were healthy and unbroken (causing no decay at all).

Birch trees suppressed by moose were significantly (F(1,1) = 4.083, p = 0.048) more exposed

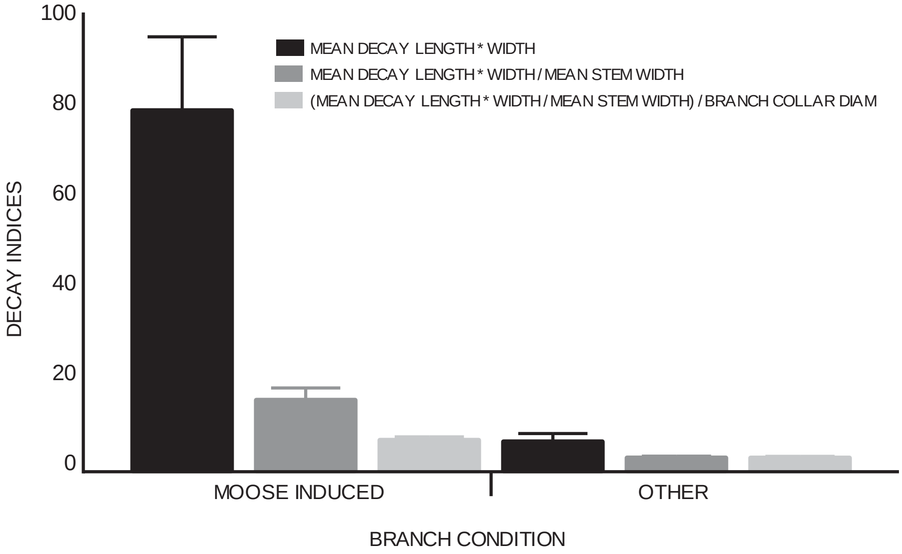

Fig. 5. Mean (± 1SE) decay index scores for three different indices of decay caused by branch breakage from moose (n = 39 intrusions) or other unknown agents (n = 14 intrusions). Black is the mean length of wood decay cores found in the inner stem of suppressed trees and originating from the breakage point multiplied by the mean width of the decay core. Dark grey is the index in black divided by the mean width of the stem through which the core of decay is contained. Light grey is the dark grey index divided by the diameter of the branch collar in the branch in which the break occurred. Note: Most unbroken branches showed no signs of decay where the branches originated from the main stem. Therefore, only those branches that were not broken by moose (but by other agents or had cracks at their base) but showed some signs of decay at their origins were assessed for any contribution of decay to individual birches brought into the lab and sectioned.

(farther from their nearest tree neighbor) when compared to birches that were free-to-grow. There were no significant differences (all $p \geq 0.05$) in the distance to specific tree species neighbors (conifers or hardwoods) from birches (either suppressed or free-to-grow). Suppressed birches, however, were significantly farther away from other birches showing signs of slight to moderate browse history than free-to-grow birches were from similar conspecifics ($F(1,1) = 12.573$, $p \leq 0.001$).

4 Discussion

Many of the young birch trees growing in the study area were repeatedly damaged by moose from winter browsing and breakage events and were hedged and stunted in growth. Such multi-stemmed, twisted and bushy birches with low branching looked very different than other single-stemmed, free-to-grow birches of the same age that contained branches high in the crown of the tree, well above the reach of moose.

Although we selected suppressed and free-to-grow birches for comparison, a full range of damage levels to birches could be found in the study area. Some birches appeared to have never been browsed by moose while others with light, moderate and severe levels of damage existed in a heterogeneous mix among the conifers and other hardwoods in the stand.

Not surprisingly, suppressed birches were shorter at a given age and given base diameter than free-to-grow birches. Tree forming birches were similarly affected in Sweden in response to intense simulated winter browsing by moose (Bergstrom and Danell 1987) with trees being 40% (*Betula pendula)* and 57% (*B. pubescens)* shorter on average than controls. Additionally, the number of annuli per given stem diameter did not vary between suppressed and free-to-grow birches, suggesting that moose damage had no effect on tree girth or the way in which annular rings were laid down in the tree trunk. That the stem diameter to annuli ratio in this study was not affected by browsing appears counterintuitive given the extensive remodeling and gross morphological alterations to the upper portions of the tree. Bergstrom and Danell (1987) reported smaller annual increases in stem diameters when comparing 5–8 years old browsed to unbrowsed birches over a 3 year period, but diameter to annuli ratios were not specifically assessed and most trees increased in diameter significantly during the study period, regardless of clipping intensity. Danell and Huss-Danell (1985), however, reported no differences in the age or stem diameters of birches that showed a history of moderate when compared to slight browsing and Schatz et al. (2008) reported no changes to the stem diameters of *Betula pendula* following pruning. Together, such findings suggest that birch is extremely tolerant to mechanical damage and that cambial growth in the trunk is neither suppressed nor is it accelerated in response to heavy browsing and/or stem breakage.

Of the birches selected for assessment, suppressed birches generally showed signs of heavy and repeated use. These birches were not only thoroughly browsed, but on average had main and collateral stems that had been broken by moose to access shoots above their reach (Telfer and Cairns 1978) a total of 6 or 7 times over the life of the birch, or about once every two years. Repeated use of shrubs and trees by moose from year to year has been reported by others and may suggest a preference by moose for individual trees (Löyttyniemi 1985, Bergqvist et al. 2003).

Stem breaks occurred at predictable places on birches at about 1.5 meters above the ground where stems were 15–20 mm in diameter. Although some breaks occurred on older, thicker stem sections and above this height, moose appeared to limit breakage to stems that, at breast height (~ 1.3 meters), contained 4 to 5 years of growth. Once leaders were above the browse line – enough that mainstems at breast height contained 8 to 9 annular rings – they appeared to be free-to-grow and presumably too thick for moose to snap. Branches growing from the lower portions of the trees, if present, were rebrowsed extensively regardless of whether the tree was suppressed or free-to-grow.

Breakage events by moose not only affected the morphology of the tree and its ability to grow into the tree layer, but subjected each birch to large and upward facing wounds that provided entry points for moisture and pathogens, presumably similar to those described by Lilja and Heikkilä (1995). Sectioning of birches revealed that all breaks on trees, aside only from the most recent, resulted in decay. Decay and the associated discoloration of heartwood was typically extensive (on average was 40% of the tree interior for the length of the section in which decay occurred) in those trees inspected and, therefore, of substantial consequence where timber quality is valued. These findings appear to correspond with those of Härkönen et al. (2009), where they recorded flaws in stem form as well as pith and wood discoloration/decay in European white birch (*B. pubescens*) and silver birch (*B. pendula*) as a result of moose damage. Similar color defects were also reported by Schatz et al. 2008 in silver birch following pruning.

Birches suppressed by moose damage tended to be farther away from other trees (birches as well as other tree species) than those that were undamaged by moose. Proximity to other trees has been found to be related to the degree of damage incurred by trees from herbivores (Milchunas and Noy-Meir 2002) since trees in the open are less concealed by neighboring vegetation and easier to feed upon. Because tree neighbors (of any species other than birch neighbors studied) shorter and presumably younger than study birches were not considered to have had an influence on levels of moose damage to birch, only trees that were as tall as or taller than each study tree were assessed for nearest neighbor measurements.

Theoretically, it should have been easier to find trees taller than suppressed trees (i.e., these neighbors should be more abundant than trees taller than free-to-grow birches) for taking nearest neighbor measurements. Despite this potential bias, nearest neighbor trees were always significantly farther from suppressed than free-to-grow trees – suggesting free-to-grow trees grew in denser patches while suppressed trees were more exposed. This relationship held true for all non-birch nearest neighbors, regardless of tree species.

The distance between suppressed birches and the nearest birch neighbor that was neither suppressed nor free-to-grow, but within the reach of moose and possibly showing signs of use was also greater when compared to the distance between these birches and those classified as free-to-grow. Together, these data appear to support the Associational Avoidance Hypothesis (Milchunas and Noy-Meir 2002) which suggests that plants growing in the open (such as suppressed birches) are less likely to be protected from herbivores in search of food than those adjacent to and mixed within neighboring plant complexes.

5 Management Implications

Overall, these findings suggest that moose impact birch by altering its ability to compete with surrounding vegetation and to be successfully recruited into the tree layer. Suppression was not characteristic of all birch within the stand. Instead, some birches growing farther from other trees – in more open parts of the stand – appeared to be targeted by moose repeatedly and caught in some type of feeding loop as described by De Jager and Pastor (2010), from which they appeared unable to escape. This does not imply that all birches growing within the open were as subjected to repeated browsing as those measured, rather an open habitat was more characteristic of where suppressed birches could be found when compared to free-to-grow birches. In short, suppressed and malformed birches were rarely seen growing in more densely forested parts of the study area.

A measurement specifically of distance to the nearest birch neighbor currently growing amongst suppressed and free-to-grow birches and within the reach of moose may be an irrelevant metric given current browse pressures on younger trees would have had no past influence on older birches acquiring free-to-grow status. Nevertheless, surrounding birch densities (as with other tree species) may continue to influence the rebrowsing of suppressed trees and such documentation may be of value to managers interested in how moose may perceive and use neighboring birches in relation to suppressed and free-to-grow trees. Interestingly, data from nearest neighbor birch assessments indicated that some level of browsing continues on birches within the reach of moose in both open and less open portions of the study area, albeit to what degree such birches were browsed was not specifically measured.

The damage to birch incurred by moose has two important implications to forest managers interested in cultivating birch. First, birches repeatedly targeted as a food resource by moose tended to be hedged, multi-stemmed, extensively branched and stunted in vertical growth. Such browsing may help to reduce birch densities and/or vigor and the competitive effects of birch on coniferous crop trees (Mielikäinen 1980, 1985), but also leads to the growth of birches that are crooked, twisted-grained, discolored and knotty – resulting in lower wood quality. Second, browse and breakage events imposed by moose on birches predisposed plants to internal decay formation. This decay weakens the tree (birches with rotten boles that appeared to have been snapped by wind or snow loading events were found in the study area) and reduces the potential lumber quality of the tree and, therefore, its merchantability.

Although birch trees do not currently comprise a significant component of industrialized forestry throughout western Canada, this is not true in places such as Fennoscandia where moose and birch also co-occur (Härkönen et al. 2009). Additionally, local changes to forest stand dynamics (e.g., mountain pine beetle epidemics) and changes in world economics may lead to the opening and expansion of markets where birch is in higher demand. To meet any such demands, forest managers tending stands for future merchantability must begin now, while young birches are within the reach of moose and while cleaning and thinning operations are being planned, to consider the impacts that moose may have on the quality of birch timber realized at harvest time.

Given that birches growing farther from their nearest neighbors at Aleza Lake were more heavily browsed than those less exposed, minimizing such exposure through innovative silvicultural and stand tending techniques may help to reduce damage. Such treatments may only be considered, however, within a regionally-specific context where considerations are made not only for tree species composition, the larger-scale distribution of food resources and moose densities, but for trade-offs between current browse abundance and range quality and hypothetical future gains from high quality birch.

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PAPER VIII

FACTORS INFLUENCING WILLOW AND BIRCH SHOOT SELECTION AND BIOMASS CONSUMPTION BY MOOSE IN WINTER

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ABSTRACT

Patterns of browsing on plants by moose (*Alces americanus*) in winter reflect, among other things, plant accessibility and quality as well as choices made by moose to maximize protein and energy intake, but are complex and difficult to characterize. Here, we examined which factors were important in explaining shoot selection and biomass removal of birch (*Betula papyrifera*) and willow (*Salix scouleriana*) twigs by human-habituated moose in winter. We evaluated browsing patterns through the use of 37 timed feeding trials over a three-day period in which hand-assembled, species-specific trials containing various densities of either willow or birch saplings were presented to moose one at a time. For both species, the pre-trial weight of saplings (whole sapling biomass) was the most important factor in explaining the amount of biomass eaten, the cumulative length of all shoot materials removed from saplings by moose, and the amount of edible biomass left uneaten. For willow, but not for birch, the number of days moose were fed willows partially explained the average bite diameters and the amount of edible biomass left uneaten following trials. The location of the sapling within the trial that moose browsed helped to explain the cumulative shoot length removed by moose, while sapling density influenced the amount of edible willow biomass left uneaten. At the individual sapling level, the pre-trial weight of saplings was important in helping to explain the amount of biomass eaten and the amount of edible biomass left behind in both willow and birch trials. In addition, sapling density influenced the amount of willow biomass eaten and both sapling density and the trial day helped to explain the amount of edible willow biomass left behind. Overall, sapling weight – a metric that does not appear to have been previously measured or reported in this context – was the most important factor for explaining differences in shoot selection and biomass consumption by moose at both the trial and individual sapling level.

KEY WORDS: *Alces*; *Betula*; Birch; Browse; Feeding Trial; Forage; Moose; *Salix*; Willow; Winter

INTRODUCTION

Winter browse selection by moose (*Alces americanus*) is a complex mix of opportunity, nutritional need, and forage availability. In winter, moose feed extensively on the twigs of early-seral deciduous woody plants such as willow (*Salix* spp.) and birch (*Betula* spp; Renecker and Schwartz 1998). These two species are a major winter staple of moose throughout much of their range and are considered both preferred and principal food items, depending on availability (Renecker and Schwartz 1998). Willow is generally of higher nutritional value to moose than birch (Oldemeyer 1974, Hjeljord et al. 1982, Regelin et al. 1987) and is generally more preferred (Schwartz et al. 1988, Renecker and Schwartz 1998, Shipley et al. 1998). These differences may be related to the relative ease of processing willow versus birch (Nordengren and Ball 2005) and/or the relative inability of (and higher physiological costs required for) moose to detoxify and excrete the secondary metabolites of birch relative to willow (Palo 1984). Birch, however, can also be important to moose (Vivås and Sæther 1987) and is preferred over some species of willow by moose in some regions (Hörnberg 2001), suggesting that further studies are required to delineate plant preference rankings and the importance of various species to moose (Danell et al. 1985, Schwartz et al. 1988, Bryant et al. 1989).

Moose generally browse in the upper and outer portions of willow plants, birch, and other shrub and tree species and will often break plant stems down to access upper twigs where possible (Telfer and Cairns 1978, Bryant and Kuropat 1980, Bergström and Danell 1987, Vivås and Sæther 1987). Moose are known to select smaller, less fibrous shoots when available, but will also select basal shoots from previously browsed and otherwise damaged trees (Bergström and Hjeljord 1987, Risenhoover 1987) and crop twigs to large bite diameters in order to increase intake rates on individual trees with fewer shoots or when tree density per patch is limited (Shipley et al. 1999, Vivås and Sæther 1987).

To establish how browsers use plants during winter, rangeland ecologists conduct browse-use surveys in spring (Hamilton et al. 1980, Cumming 1987, Keilland and Osborne 1998). Such surveys can help ecologists assess browse biomass removal from winter ranges and, specifically, which shoots from plants and which plants from patches are used by browsers (Vivås et al. 1991, Milchunas and Noy-Meir 2002). Although informative from a range-use perspective, such surveys convey little about how much and what kinds of twigs were eaten from various plants and convey even less about animal foraging ecology, per se. Foraging dynamics, the mechanics of browsing, and the use of plant biomass to determine preference rankings, rather, is best understood through direct observations and measurements in nature (Renecker and Hudson 1986, Gillingham et al. 1997) and/or through the use of feeding trials (Schwartz et al. 1988, Shipley and Spalinger 1992, 1995).

Feeding trials with captive moose have been used by ecologists to distinguish principal (most eaten) from preferred food items (Renecker and Schwartz 1998) and to examine cropping and intake rates of moose eating fresh alfalfa (Gross et al. 1993*b*) and unbranched current annual shoots of red maple in winter (Shipley and Spalinger 1992) – the latter in relation to size and distribution of patches (Shipley and Spalinger 1995). These kinds of trials could also be used to determine changes in feeding patterns relative to the time of day and the number of days animals are exposed to a particular forage item, because even short-term foraging patterns are known to change over time (Parsons et al. 1994, Bernays et al. 1997). Changes in forage consumption throughout the day or from one day to the next, however, do not appear to have been previously studied with moose, but should be pursued (Nordengren and Ball 2005). Although plant size and/or stage of maturity (Renecker and Schwartz 1998), plant density per patch (Shipley et al. 1999, Vivås and Sæther 1987), and spatial distribution (Shipley and Spalinger 1995) are separately known to influence foraging decisions by moose, how these factors together specifically influence the use of willow compared to birch in winter is unclear and remains to be tested.

We used a series of timed feeding trials with human-habituated moose during winter to determine if species, sapling biomass, density of saplings and the position of saplings within trials influenced feeding strategies used by moose for winter browsing. Delineating how the density of plants within trials and the pre-trial weight of individual saplings (both a measure of biomass) influenced browse consumption was of particular interest. How moose differentially browsed on willow and- birch throughout the day and from one day to the next, both at the trial level as well as the level of saplings nested within trials, was examined. Specifically, we compared our results to our hypotheses that: a) moose will consume more biomass per sapling and per trial – removing relatively more shoot length and cropping shoots to larger diameters while leaving less edible shoot material behind – when browsing on less massive saplings and trials with fewer saplings; b) moose will decrease their intake with increased exposure to saplings (number of hours and days into the trials); and c) moose will take larger bites and consume more biomass from willows than from birch.

METHODS AND MATERIALS

Sapling Collections and Pre-Browse Measurements

We collected 215 whole saplings (~2-2.5 m tall) of willow (*Salix scouleriana* Barratt ex Hook.) and birch (*Betula papyrifera* Marsh.) near the Endowment Lands of the University of Northern British Columbia (UNBC), Prince George, Canada on 20 February, 2009. Once collected, all saplings were transported to the Enhanced Forestry Laboratory (EFL) on campus and weighed (to the nearest gram). We tagged each sapling at its base using a unique aluminum tag. We removed a thin linear strip of bark from along the bottom of each sapling near its base and oriented saplings in a prostrate position with the bark stripped portion facing upwards on a table containing a measurement grid divided into 5-cm increments. A 2-m long ruler with 5-cm increments was held along the length of the sapling suspended at ~50 cm above the table. Saplings were then photographed with high-resolution photography. Once weighed and photographed, we separated saplings by species and wrapped saplings into two separate tarps and stored them outside in the cold (0 to -17°C). On 25 February 2009, we transported all saplings to the Northern Lights Wildlife Shelter in Smithers, BC in the back of a pick-up truck so that saplings were kept at ambient outdoor winter temperatures enroute (-24 to -30°C).

Feeding Trials

We conducted cafeteria-style feeding trials over a 3-day period from February 25-27, 2009 (-9 to -28°C) with 3 unfasted human-habituated moose (1 adult female and 2, 9-month-old calves), which had been raised at the Northern Lights Wildlife Shelter in Smithers, BC, Canada (54° 50’ 59.24” N; 127° 06’ 01.65” W). To conduct whole-sapling trials in a fashion that closely resembled feeding in nature, we designed a feeding station device out of two 6” x 6” x 16’ (15.2 cm x 15.2 cm x 4.9 m) long pine beams and two ratchet straps. These beams were used to clamp saplings at their base so that they stood erect and could not be dislodged by moose during feeding. Previously cut, unbrowsed saplings were inserted and pinched between these beams and held in place with ratchet straps for bouts of feeding (Figure 1). Trials consisted purely of willows (day 1 and 2) then birch (day 2 and 3).

To test the influence of sapling density on biomass removal and shoot selection, we varied the spacing and number of saplings per trial (4 saplings - 48” (122 cm) spacing; 5 saplings - 36” (91 cm) spacing; 8 saplings - 24” (61 cm) spacing; Figure 2) using single-species trials of willows (n = 19 trials) then birch (n = 18 trials). In this way, we were able to examine and test differences in moose feeding patterns on those saplings nested within trials of varying densities. Feeding bouts (hereafter referred to as trials) varied in length (9-60 min) so we corrected for this in our analysis (see below), but were normally 15 min long regardless of the number of saplings presented or number of moose participating throughout the trial. The same three moose fed during each trial but for different amounts of time, so the number of moose feeding and number of minutes per trial were recorded for each trial so that average browse consumption per minute per average moose could be calculated. Fresh saplings not previously fed upon were mixed and haphazardly selected for each trial. Saplings were kept wrapped in tarps both before and after trials and were stored in an enclosure at outdoor ambient temperatures. All three moose paid close attention to all of our movements during the experiment, and participated fully in the trials each day. Following the completion of all trials, saplings were re-wrapped in tarps and transported back to the Enhanced Forestry Laboratory at UNBC for the post-trial assessments.

Post-Browse Measurements

At the EFL, saplings were re-weighed with the difference between the pre- and post-browse mass (wet weight) constituting biomass removal from browsing. Saplings were then reoriented on our photographic backdrop according to the bark stripped marking we had made on each trunk before the pre-browse photographs were taken and re-photographed. Because saplings were continuously kept wrapped in tarps except for trials and measurements, and weight losses due to dehydration were negligible in birch during an earlier experiment conducted under similar conditions (Rea et al. 2010), we did not measure or correct for weight loss due to dehydration.

Along with re-weighing and re-photographing each sapling after the feeding trials, we moved from the bottom to the top of each sapling and recorded the stem diameter (bite mark) and height above the ground for each bite taken from each stem by moose.

Carson et al. (2007) concluded that several browse species eaten by moose in our area were cropped in winter to a 4-mm diameter on average. Using this average, we classified all materials remaining on saplings after trials as edible (≤4 mm; even though moose did take larger bites) or inedible (>4 mm) and clipped away all “edible” shoot materials less than 4 mm in diameter before saplings began to dry. We weighed the amount clipped from each sapling to the nearest gram and termed this edible biomass left uneaten. The main structural portion of the sapling that we left unclipped and was uneaten by moose was what we termed inedible biomass.

Photographic analysis

Pre-browse and post-browse photographs were imported into ArcGIS (VERSION 9.3.1, ESRI 2010, Redlands, California) and assessed side-by-side so that we were able to determine which shoots were removed by moose during the trials. Following calibrations using photographs of saplings on the measurement grid, we used ArcView's measurement tool to determine the length of each shoot(s) removed by moose from each branch on each photograph. This GIS technique has been tested with Scouler's willow against hand measuring (GIS measurement = 0.991•(Hand measured technique) + 2.1455; $F_{1,48} = 3853.9$, $P < 0.0001$; $r^2 = 0.988$; J. Svendsen, *unpublished data*) and allowed us to determine if shoot materials removed from saplings above each bite mark were comprised of a single or branched shoot as well as the cumulative length of all shoot materials removed.

Statistical Analyses

Measurements collected during our trials were analyzed in two different ways. We examined some metrics at the experimental unit level (trials) while others were examined within saplings – our nested approach (saplings within trials). We adjusted all trial data for the average number of moose feeding over the time period in which each trial was conducted. For example, if one moose fed for a 15 minute trial, but was joined by another moose for the last 7.5 minutes of the trial, we calculated 1.5 moose feeding for the 15 minute trial period (i.e., 0.1 moose/min). To evaluate browsing patterns and the efficiency of feeding by moose in trials and on individual saplings within trials, we examined the amount of biomass removed, cumulative length of shoots removed and the amount of edible biomass left behind per moose per min of trial. These are later termed total biomass, cumulative length of shoots and edible material left uneaten.

Trials

Twig biomass removed, the average diameter of bites taken on shoots, the total cumulative length of shoots removed, and the amount of edible material left over and uneaten by moose from the saplings nested within trials were examined at the trial (containing 4, 5, or 8 saplings) level. We ran separate analyses for birch and willow and for each of our dependent variables (e.g., % biomass eaten, average bite diameter; STATA:reg) with sapling density, the time of day the trial was conducted, which day within the experiment (day 1, 2, or 3) the trial was conducted, original sapling biomass (pre-trial weight), and where within the trial browsing occurred (in the middle [inner] or on the ends [outer]) as independent variables. Sapling position was a categorical variable while all other independent variables were continuous. Metrics were summed (biomass eaten, shoot length removed, biomass left uneaten) or averaged (average bite diameter) as appropriate across all saplings in each trial. The pre-trial weight of saplings was summed for all saplings within a trial (and therefore depends on the weight of the individual sapling and the number of saplings within the trial) so that, on average, biomass for trials of 8 saplings would be double that for trials of 4.

Saplings within Trials

In these analyses, individual saplings were considered to be nested (as random effects) within trials and we used a mixed-effects linear regression (Stata xtmixed) to nest sapling (the replicate) within the trial (experimental unit). Again, density of saplings within the trial, the trial time, trial day, as well as the position of the sapling in the trial were all used as independent variables with density of saplings, trial time and trial day being continuous variables while position was a categorical variable. For all models, continuous independent variables were examined for collinearity (STATA: collin; Ender 2010); variables with a variance inflation factor <10 were considered to be independent. Residuals from all models were examined for model fit and homogeneity of residual variances. All intercepts were included in all models. All analyses were conducted in STATA 12 (StataCorp, College Station, TX).

RESULTS

Trials

Willow: The amount of biomass removed by moose increased with increasing available biomass as did cumulative shoot length removed from trials (Table 1). More shoot length was removed from the middle portions of the trial when compared with the ends (Table 1). Average bite diameters taken by moose decreased as trial days progressed (Table 1). The amount of edible biomass left on saplings after the trials increased with increasing trial biomass and the number of days into the trial and decreased with increasing sapling density within the trial (Table 1).

Birch: The amount of biomass eaten, the cumulative shoot length removed, and edible biomass left uneaten increased with an increase in available trial biomass (Table 1). Average bite diameters taken by moose was not influenced by any of those factors that we measured during the trials.

Saplings within Trials

As the pre-trial weight of both willow and birch saplings increased, so did the amount of biomass eaten and the amount of edible biomass leftover on individual saplings by moose after the trials. The amount of biomass eaten decreased with increasing sapling density for willow, but not with increasing density of birch saplings. The amount of edible biomass left behind on willows also increased as trial days progressed, but decreased with increasing density of saplings (Table 2).

DISCUSSION

Biomass Consumption

Biomass removal for both birch and willow increased with increasing sapling pre-weight under every circumstance (both at the trial and sapling level) we evaluated. Although the specific relationship of total sapling weight to biomass removal does not appear to have been previously evaluated, the amount of available forage is known to explain absolute consumption by moose at several spatial scales (Månsson et al. 2007). Contrary to what was indicated by our study the total number of browsed saplings per plot has been found to increase with increasing sapling density in some studies (Heikkilä and Mikkonen 1992, Heikkilä 1993). Within a foraging bout, however, Vivås and Sæther (1987) and Shipley and Spalinger (1995) reported – as our data indicate for willows (but not for birch) in denser trials – that moose used fewer twigs (biomass) per sapling with an increase in sapling density. This suggests that moose consistently use biomass in relation to availability, but simply become more selective while increasing use as willow density per trial increases. Why this particular relationship appears to have held true in our study for willows, but not for birch, may be related to the larger and more fibrous bites taken on willow requiring more processing time with an increase in bite size (Shipley and Spalinger 1992) – a relationship that is much less predictable when smaller bites (e.g., birch) are taken (Shipley and Spalinger 1992).

A reduction of biomass removal with pre-trial sapling weight was only detectable at the willow sapling level and not when willow consumption was assessed at the trial level, revealing that saplings may be perceived and browsed individually by moose regardless of, or supplementary to, their connection with the larger trial. While testing winter browsing patterns between species, Danell et al. (1991*a*) found that selection occurred primarily at the tree rather than the thicket (trial) level. An alternative explanation could be that individual moose browsing side-by-side focused individually on saplings within trials so that something different was happening to individual forage items by different animals (see discussion by Gross et al. 1993*a*) than to the trial at large.

Cumulative Shoot Length Removal

The cumulative shoot length removed by moose from both willow and birch trials increased with increasing sapling pre-weight, suggesting increased consumption with increased availability, but varied by position of the plant within the trial for willow. More shoot length was removed from willows within the trial (towards the center of the feeding station) than those positioned on either end. Measuring both shoot length removal and biomass removal may at first appear redundant given the direct relationship of biomass to length (Provenza and Urness 1981, MacCracken and Van Ballenberghe 1993). However, our metric was cumulative shoot length removal (a sum of all current and past year's growth removed by moose and summed across all saplings within a trial) and has not, to our knowledge, been measured in this context. Shoot biomass-to-length relationships vary between and within species (Rea and Gillingham 2008) and will influence how moose browse plants. For example, Shipley et al. (1999) described a particular difference in how moose browsed more "branchy birches" in relation to willows and other hardwoods, noting that moose regularly broke off more than one twig when browsing birch. Here, the cumulative length of two thinner birch shoots cropped in a single bite would be longer than one thicker, but equally massive willow shoot – a difference detectable using cumulative shoot length, but not biomass consumption.

Why willows (but not birch) that were in the center of the feeding station appeared to lose more cumulative shoot length (but not biomass) to browsing than station ends is puzzling, but may be related to which animals fed where in trials. Dominant cattle will preferentially take middle positions in feeding stalls and spend more time eating than those with lower social rank (Friend and Polan 1974). Although we did not take systematic measures of individual animal's feeding positions at the station, photographs taken occasionally throughout the feeding trials indicates that the adult cow often occupied the middle positions to the exclusion of the calves (see Figure 1). If the cow spent more time selecting thinner and more numerous shoots, shoot length, but not biomass, may show an increased take from saplings in mid, but not end positions. Again, why such patterns were not evident in birch is unknown, but may be related to a lower intensity browsing that seemed to characterize the use of birch by moose throughout our trials.

Bite Diameter

During winter, moose select bites from twigs that maximize energy and nutrient gains, but limit fiber intake (Vivås et al. 1991). Because shoot quality decreases with an increase in shoot diameter (Hjeljord et al. 1982, Vivås and Sæther 1987), browsers such as moose carefully select bites to ensure physiologically appropriate intake rates are in balance with the amount of time required to process forage items (Robins 1983). Such choices are influenced by factors such as clipping rates and twig characteristics, which can vary by species (Vivås et al. 1991). We found that bite diameters taken on willows (but not birch) were negatively influenced by trial day, but by no other independent variables. Illius et al. (2002) reported that roe deer showed similar declines in bite mass removal as patch exploitation progressed by demonstrating that animals depleted larger bites first. Edenius (1991) described decreases in bite mass removal (as indexed by bite diameters) by moose when feeding on Scots pine, but also reported constant bite diameters for aspen as browse was depleted. Vivås and Sæther (1987) and Shipley and Spalinger (1995) noted that bite sizes taken by moose increased and quality decreased as stem availability declined, yet Shipley et al. (1998) indicated that, contrary to their expectations, the average diameters of twigs selected by moose was not influenced by browse density. Edenius (1991) also pointed out – as our results seem to indicate – that parameters other than bite size, such as the number of bites per sapling (or cumulative shoot length removed), may be better predictors of browse use by moose in winter.

Minimal variability in bite diameters and associated shoot quality taken by moose between saplings and trials within a species may be partly accounted for by the fact that moose were not fasted prior to or during our 3-day experimental period. Moose at the shelter have continuous access to forest lands in and around the shelter and are also supplementally fed vegetative materials twice daily by shelter staff. As a result, moose were able to feed selectively among available shoots, cropping them to diameters that likely reflected a selection for shoot quality rather than a need for gut-filling.

Edible Biomass Uneaten

Edible biomass left uneaten was our best estimate of the amount of potential edible biomass left uneaten by moose at both the trial and individual sapling level. Moose obviously browse plant shoots beyond 4 mm and did so within our study. However, we settled on a 4-mm cut-off diameter as an index of edibility even before we had measured bite diameters taken by moose in this experiment because it was a locally documented average (Carson et al. 2007) and has been used as a cut off diameter by others simulating moose browsing and in assessing browse quality (Danell et al. 1985, Danell et al. 1991*b*, Shipley et al. 1999).

More massive plants had more biomass for moose to consume, but also contained more twig materials (≤4 mm) for moose to leave uneaten – which our result show happened at both the sapling and trial level for both willows and birch. The Satiety Hypothesis (Bailey and Provenza 2008) suggests that animals may build up an aversion to foods just eaten, which may help explain differences in willow use by moose in the first two days of our trials. Explaining why this didn’t happen for birch is difficult, but may simply be due to moose eating less total birch (7.8 kg) than willow (10.2 kg) over a similar time frame; it is also likely related to differences in twig types cropped, secondary chemistry, and other species-specific factors. Satiety increases with increased fiber intake (Slavin and Green 2007), leaving moose that are browsing smaller-stemmed birches less likely to become satiated with time. Whether such mechanisms are likely to operate from one day to the next or only describe shorter-term foraging dynamics requires further testing.

Why there were fluctuations in willow biomass left uneaten (but not biomass removal) with trial may be due to differences in the types of twigs consumed vs. those left behind over time and an artifact of how we classified "edible" biomass left over using the 4-mm threshold. If moose took fewer, larger diameter bites from bigger saplings, but also left an increased number of smaller (≤4 mm) diameter shoots on those saplings as trials progressed, biomass removal and edible biomass left over (as we classified, cut, and weighed it) could remain static and increase, respectively. A strategy of selecting fewer, larger bites by moose may also help to explain how more edible biomass remained on willows from trials of lower sapling density (see Vivås and Sæther 1987) and, if such a strategy were used, may reconcile how more (>4 mm in diameter) and less or equal to (≤4 mm) willow biomass could have been consumed simultaneously by one or multiple moose at both the trial and sapling level. Unfortunately, intricate details of the foraging strategies of individuals or combinations of animals feeding were not recorded during the trial, leaving us unable to quantify forage selection and feeding intensity, per se.

Why moose browsed willows and birch differentially is difficult to judge from our study, but is likely related to browse selection. Willow, in general, is more preferred (Oldemeyer 1974, Hjeljord et al. 1982, Palo 1984, Regelin et al. 1987) and important to moose (Renecker and Schwartz 1998) than other browse species, suggesting moose may be more familiar (and specialized in their interactions) with willow. Additionally, willow is easier to process and of higher quality than birch (Nordengren and Ball 2005). Previous experience as well as species and biomass availability of various browses naturally occurring in the forest surrounding the shelter also likely predisposed moose in this trial to browse sapling species differentially.

Because our birches on average had smaller twigs from which smaller bites were taken (2.69 mm bite diameter on average for birch [n = 4189] vs. 4.48 mm for willows [n = 2609]) and because smaller shoots are better defended against herbivores (at least within species; Stolter 2008), simple differences in shoot size may have limited browsing on birch. Nordengren and Ball (2005) also observed that moose obtained more food when feeding on willows (taking larger bites that were chewed less) than on birch.

In conclusion, the pre-trial weight of saplings consistently influenced patterns of browse removal by moose at both the trial and sapling level, with moose consuming more biomass from more massive saplings – especially from willow. This finding clearly suggests that moose eat more from more massive plants (e.g., more vigorous plants growing under good light and soil conditions), but also in relation to both availability and preference. Sapling position within the trial, the density of trials, and the day in which feeding occurred within the trial also influenced some aspects of how moose fed on willows, but not birch. Moose browsed shoots to larger diameters and removed more biomass from willows than birch, all of which suggests moose more intricately prehended and were more selective when browsing willow over birch. If we had offered both willow and birch together, a conclusion about preference may have also been possible.

Our study shows a complicated picture of moose browse selection. We feel that cafeteria trials like ours using pre-weighed, mixed species assemblages of different densities and spatial arrangements could help to establish more conclusively moose browsing behavior for willow versus birch as well as for other browse found in the heterogeneous and complex environments that often characterize moose winter ranges.

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Table 1. The relative importance of independent variables in explaining total biomass and cumulative shoot lengths removed and average bite diameters taken from trials as well as the amount of edible biomass left uneaten within the trial by moose following trials with willow and birch. Note: For the categorical variable of position, the coefficient is inner relative to outer. Although intercepts were included in all regressions, their coefficents are not reported here.

Dependent Variable	Independent Variable	Sapling Species					
		Willow			Birch		
		Coefficient	S.E.	P	Coefficient	S.E.	P
Biomass Eaten	Density	-0.474	0.383	0.216	-0.357	0.319	0.262
	Start Time	-0.000	0.005	0.984	-0.002	0.003	0.501
	Trial Day	-0.107	1.965	0.956	0.222	0.303	0.464
	Pre-weight	0.007	0.001	<0.001	0.004	0.001	<0.001
	Sapling Position	1.779	1.028	0.084	0.055	0.761	0.943
Shoot Length Removed	Density	-2.3882	3.983	0.549	1.147	6.717	0.864
	Start Time	-0.031	0.048	0.520	-0.064	0.050	0.199
	Trial Day	-10.828	20.536	0.598	-6.915	8.157	8.157
	Pre-weight	0.057	0.008	<0.001	0.045	0.016	0.005
	Sapling Position	27.463	10.793	0.011	12.784	22.771	0.575
Average Bite Diameter	Density	0.010	0.077	0.896	0.030	0.037	0.421
	Start Time	-0.001	0.001	0.122	0.001	0.001	0.560
	Trial Day	-1.076	0.367	0.003	-0.033	0.041	0.425
	Pre-weight	-0.001	.0002	0.205	0.001	0.001	0.510
	Sapling Position	0.154	0.196	0.432	-0.097	0.093	0.297
Edible Biomass Left Uneaten	Density	-0.765	0.363	0.035	-0.156	0.127	0.219
	Start Time	0.006	0.004	0.094	0.001	0.001	0.702
	Trial Day	5.812	1.666	<0.001	0.019	0.086	0.822
	Pre-weight	0.005	0.001	<0.001	0.001	0.000	<0.001
	Sapling Position	-0.143	0.844	0.866	0.559	0.306	0.067

Table 2. The relative importance of independent variables in explaining total biomass removed and edible biomass left uneaten on individual saplings by moose following trials with willow and birch.

Dependent Variable	Independent Variable	Sapling Species					
		Willow			Birch		
		Coefficient	S.E.	P	Coefficient	S.E.	P
Biomass Eaten	Density	-0.404	0.150	0.007	-0.199	0.109	0.067
	Start Time	-0.001	0.002	0.584	-0.001	0.001	0.231
	Trial Day	-0.995	0.770	0.197	0.065	0.073	0.372
	Pre-weight	0.009	0.001	<0.001	0.004	0.001	<0.001
	Sapling Position	0.308	0.250	0.218	-0.309	0.180	0.086
Edible Biomass Left Uneaten	Density	-0.335	0.140	0.017	-0.060	0.043	0.165
	Start Time	0.003	0.002	0.076	0.001	0.000	0.473
	Trial Day	2.197	0.718	0.002	0.033	0.026	0.194
	Pre-weight	0.008	0.001	<0.001	0.001	0.001	<0.001
	Sapling Position	-0.010	0.247	0.965	0.100	0.063	0.112

Figure 1. The feeding station used during the feeding trials was constructed of heavy wooden beams that were used to pinch and anchor the saplings to the ground to simulate natural feeding conditions. 25 February, 2009.

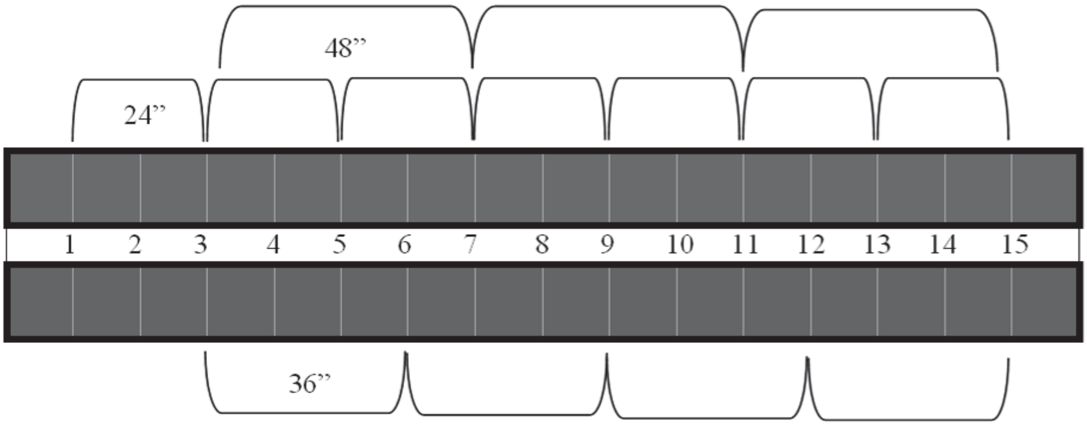

Figure 2. Depiction of the feeding station foundation that was constructed out of two 16’ (4.87 m) long wooden beams (grey bars). Positions were 12” (30.5 cm) apart. In high density trials, those 8 saplings spaced at 24” apart were in positions 1, 3, 5, 7, 9, 11, 13, 15 while low-density trials that contained 4 saplings spaced at 48” (122 cm) apart were anchored in positions 3, 7, 11 and 15 during the trials. Positions 3, 6, 9, 12, and 15 were used for trials where saplings were spaced at 36” (91.4 cm).

PAPER IX

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Road and Rail Side Vegetation Management Implications of Habitat Use by Moose Relative to Brush Cutting Season

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Abstract Plants cut at different times produce resprouts that vary in their nutritional value relative to when they are cut. To determine how vegetation management in transportation (road and rail) corridors at different times of the year could influence browse quality in the years following cutting, and how this could potentially influence encounters between herbivores and vehicles, we undertook a 3-year study. In 2001, at a wildlife viewing area near Prince George, British Columbia, Canada, we established a control area and treatment areas where shrubs and trees that are used as food by moose (*Alces alces*) were cut at the beginning of June, July, August, September, and October. In the fall, moose were most often observed browsing the resprouts of plants cut in August (years 1 and 2 post-treatment) and September (year 3). Cumulative winter track counts were highest in the uncut control area in the years following cutting. Spring pellet counts revealed that most pellets were deposited in the uncut (years 1 and 2) and August-cut (year 3) areas during winter. With the exception of the first year after cutting, browse removal by moose was highest for plants cut later in the growing season. Overall, our findings suggest that following cutting, plants cut later in the year are selected more often by moose relative to those cut earlier. To reduce browse use of corridor vegetation in areas where concerns for moose-vehicle collisions exist, we recommend that vegetation maintenance activities be conducted in the early summer months of June and July.

Keywords Brush-cutting · Forage · Moose · Plant quality · Selection · Vegetation management

Introduction

Feeding is the predominant activity of moose (*Alces alces*) and other ungulates in transportation corridors (Peek and Bellis 1969; Puglisi and others 1974; Groot Bruinderink and Hazebroek 1996). Since plant quality and attractiveness in transportation corridors are known to influence the amount of time moose spend near roads and rails (Jaren and others 1991), eliminating plants or decreasing plant quality have been suggested as countermeasures that could be used to mitigate ungulate-related vehicle collisions (Jaren and others 1991; Lavsund and Sandegren 1991; Gundersen and others 1998).

Plant–based mitigation strategies previously employed include removal of the forage base, spraying chemical deterrents, planting non-browse species or installing alternative food sources and feeding stations (Jaren and others 1991; Lavsund and Sandegren 1991; Gundersen and others 1998). Unfortunately, these strategies tend to be too expensive to implement across the landscape (Jaren and others 1991; Sielecki 2000), are not environmentally

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appropriate, or permanently destroy habitat for other wildlife (Oetting and Cassel 1970).

Roadside brush-cutting is practiced regularly in many parts of the world to increase sight lines for motorists and reduce vegetation growth under adjacent utility lines. Because the nutritive quality of plants can be altered as a result of tissue removal at different times of the year (Gutteridge 1997; Alpe and others 1999; Rea and Gillingham 2001), one potential method of reducing the attractiveness of road and rail side plants to herbivores could be to cut at more strategic times (Rea 2003). Elucidating a cutting time that stimulates plants to produce lower quality and less attractive resprouts could allow for the employment of conventional cutting methods that are more cost-effective and at the same time discourage corridor use by browsers.

Moose and several other large herbivores prefer browse shoots that are large, low in tannin, cellulose and lignin, and high in digestible energy and digestible protein (Bryant and Kuropat 1980; Danell and others 1985; Regelin and others 1987; Risenhoover 1987). Although such attributes are known to change in the resprouts of plants following brush-cutting at different times of the year (Hardesty and others 1988; Rea and Gillingham 2001), how moose or other herbivores perceive and alter foraging strategies relative to such changes (i.e., their consumption of shoots from plants cut at different times) is unclear.

As part of a 3-year study in which we measured use of resprouts from brush-cut plants, we recorded variations in the way moose utilized habitat and browsed woody shrubs and trees in areas that were cut at different times of the year in a wildlife viewing area. Our objectives were to: (1) determine the influence of brush-cutting time on plant quality and attractiveness to moose and (2) recommend cutting times based on our results outside of the transportation corridor for vegetation maintenance activities within transportation corridors that resulted in the production of browse that was least attractive to moose.

Study Area

Research was conducted in the Tabor Mountain Wildlife Viewing Area (53° 54’ 35.98”N, 122° 19’ 39.36”W) in the Grove Burn, approximately 30 km east of Prince George, British Columbia, Canada. The site is located in the sub-boreal spruce forest ecotype (Meidinger and Pojar 1991). The climate is generally wet and cool, with precipitation evenly distributed throughout the year. Mean annual temperature at Prince George is 4.0°C, and ranges from a monthly mean daily average of -9.6°C in January, to a monthly mean daily average of 15.5°C in July. The mean annual precipitation is 600.8 mm, with 216 cm of it falling as snow (Environment Canada 2010). 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 (*Salix* spp.) (Porter 1990).

In 1961, a wildfire burned the area in which we subsequently located our research site. In the years following the fire, the site was pioneered by early seral vegetation (e.g., willows and alder *Alnus* spp.) and served as prime winter range for moose and deer for several decades.

To take advantage of the wildlife viewing opportunities in the area, a local wildlife club (Spruce City Wildlife Association, Prince George, BC) collaborated with the BC Ministry of Environment, Hudta Lake Correctional Institute, and the Habitat Conservation Trust Fund to create a wildlife viewing area in the Grove Burn in 1979. The wildlife association built a wildlife-viewing platform approximately 4 m above the ground, approximately 250 m to the north of the Yellowhead Highway 16 East to Jasper, AB. With the platform as the focal point, 6 linear strips approximately 1-2 ha in size were cut away from the platform using a Hydroaxe. The strips ranged in orientation away from the platform from 80°NE to 330°NW (Fig. 1).

The terrain at the site is predominantly flat, but slopes down and away from the viewing platform in all directions at approximately a 5% grade. The site has served as a

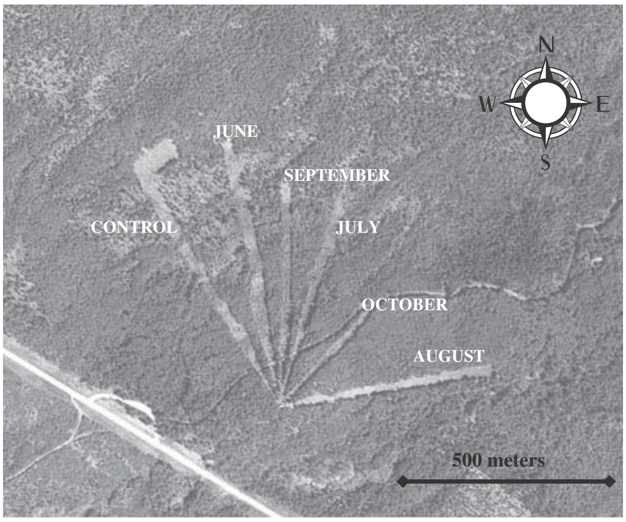

Fig. 1 The Tabor Mountain Wildlife Viewing Area established by clear cutting strips in 1979, provided a unique study area for the project. Strips were randomized and all second growth vegetation was cut at different times of the year in 2001 (indicated by month cut). Moose browsing in any of the strips radiating away from the platform could be monitored simultaneously by one observer

wildlife viewing area since the area was developed for that purpose in 1979. In 1990, larger maturing shrubs and trees that began pioneering the site in 1979 were again cut back on each strip with chainsaws by Spruce City Wildlife Association members, while smaller plants were left uncut. This cutting was performed to increase sight lines and promote browse production to enhance moose viewing opportunities. We could detect no visible difference in the composition or seral stage of the vegetation growing in these strips when we selected the site for the current experiment.

Methods

In May 2001, we randomized these managed strips and assigned each one to a cutting date. Strips were not selected as a means or intended to imitate road or rail corridors. Although the viewing area was close enough to the highway ($\sim$250 m) for highway noises to be heard, road effects such as car exhaust, vehicle movements, headlights and corridor infrastructure were all absent. This removed important factors present within transportation corridors, but allowed us to specifically test the effects of brush cutting on browsing and habitat use without the confounding influences of traffic and corridor maintenance activities. We also selected the viewing area because it provided a space for us to clearly separate treatment areas using mature forest buffers (see Fig. 1) growing between the strips and provided us with the ability to clearly view moose browsing in treatment areas following timed cuttings.

Strips were brush-cut at the beginning of June, July, August, September, and October of 2001. One strip remained uncut to serve as a control. All plants were cut at approximately 10 cm above the ground. Within these strips, we monitored plant response to cutting time (these findings can be found in a companion paper—Rea and others 2007) and then assessed utilization of plant resprouts and movement patterns of moose. We assessed overall utilization by using direct observations, track counts, pellet counts and browse utilization surveys during each year of the study (Fig. 2).

Fall and Winter Surveys

Moose Observations

To determine which resprouts from which cutting treatments were being used preferentially by moose, we monitored moose browsing activity from the observation tower. We recorded observations between mid-October and mid-December of 2001, 2002 and 2003.

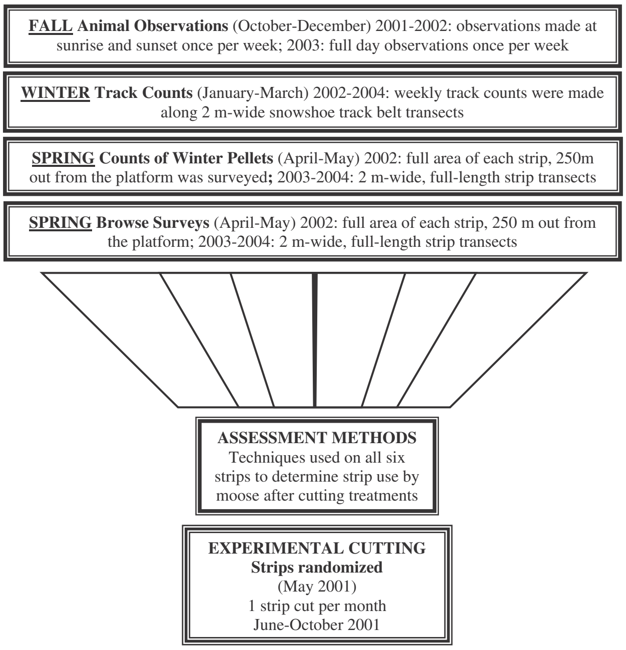

Fig. 2 A diagrammatic representation of the seasonal methods used during our study to collect data from the wildlife viewing area

In the autumn of 2001 and 2002, an observer was stationed at the viewing platform once per week for approximately 2 hours just prior to and 3 hours following sunrise and for approximately 3 hours prior to and 2 hours just following sunset. In an effort to ascertain whether or not we were missing important feeding activities over the course of the day by restricting our observations to morning and evening hours, observations were made once per week all day from just 1 hour prior to sunrise to just 1 hour after sunset in the autumn of 2003.

Following strict training procedures in which all observers were trained on site by the principal investigator to ensure consistency in our counting technique, moose behaviour was observed and recorded by slowly and methodically scanning each strip with the naked eye and binoculars at 2 to 3 minute intervals. If we observed an animal in a strip, we used a 15-60 x 60 mm zoom spotting scope and recorded as much as we could about the animal and its behaviour while simultaneously scanning the other strips for any other animal activity. For the purpose of this study, we specifically recorded the amount of time each moose spent browsing within each strip.

Track Counts

We performed weekly track counts in all 6 strips from January through March 2002, 2003, and 2004 to determine moose activity in each strip. We laid out transects using snowshoes down the length of each strip and we counted the number of moose tracks bisecting these transects on a weekly basis in each strip. To reduce the occurrence of accidentally counting a set of moose tracks more than once from moose that were using the snowshoe trail, we considered tracks distinct if the track set deviated more than 1 m beyond the transect. Once tracks were counted, we marked the set of tracks where they left the snowshoe trail with a snowshoe imprint to reduce the chances of double counting.

Spring Surveys

Pellet Counts

We counted all moose pellets after snow melt that fell within areas assessed for browse use. Because more than half of the pellets we found were scattered down trails and throughout the strips (apparently due to moose walking while defecating) and were not contained in "groups" per se, we elected to report total pellet numbers. We included areas in each of the strips within 250 m of the observation tower in the spring of 2002 and then along 2-m wide belt transects that ran diagonally down the length of each strip in the springs of 2003 and 2004 (see Rea and others 2007). We included only newly deposited pellets, not the previous year's (which we smashed underfoot during survey periods), in these counts and then normalized the counts to account for variation in differences within individual strip dimensions. New pellets were those that would have been deposited by moose and remained frozen during the cold season between the fall (September/October) and when we performed spring surveys (April/May).

Browse Use

We assessed percentage of browse used for each plant in the survey areas described above by counting the total number of shoots browsed on each plant and dividing that by the entire number of shoots on each plant. In rare cases (usually in the uncut control strip), we calculated browse use on large, multi-stemmed plants by performing the same calculation on one third or one half of the plant and then multiplying that number by 3 or 2, respectively. We report predominantly on differences in browse use between the 4 most abundant browse species at the site (willow, alder, birch and twinberry), but also report on the combined use of all browse species within each treatment.

Statistical Analyses

We tested differences in percent browsing (number of shoots removed) between plants in various treatment areas using analysis of variance (ANOVA; Sokal and Rohlf 1995). We tested homogeneity of variances using a Levene's test (Milliken and Johnson 1984). We used a Kolmogorov-Smirnov test to test assumptions of normality (Zar 1984). When sample sizes were approximately equal, we used a Tukey's HSD test for post hoc comparisons; otherwise we used a Spjotvoll/Stoline for unequal sample sizes test for post hocs (Zar 1984). Additionally, we report basic statistics for differences between moose observations, track counts and pellet counts between treatment strips (areas cut at different times of the year). Track and pellet count data were normalized to account for variation in strip lengths. We did not calculate percent differences in our results from controls because leaving plants uncut is one of several management options for which we wanted to report treatment effects.

Results

Moose Observations

Most moose were observed using browse in the August-cut strip during the autumns of 2001 and 2002 (Fig. 3). In 2003, moose were seen in the morning and evening hours as in 2001 and 2002, (and only once in mid-day) and most often in the September-cut strip. Moose were never observed in the October-cut strip and only one moose was observed in the July-cut strip (autumn 2001; Fig. 3).

Track Counts

The uncut control strip had the highest cumulative count and 3-year average of moose tracks during each year of the study (Table 1). The October-cut strip had the lowest number of tracks each year, with July having the second to

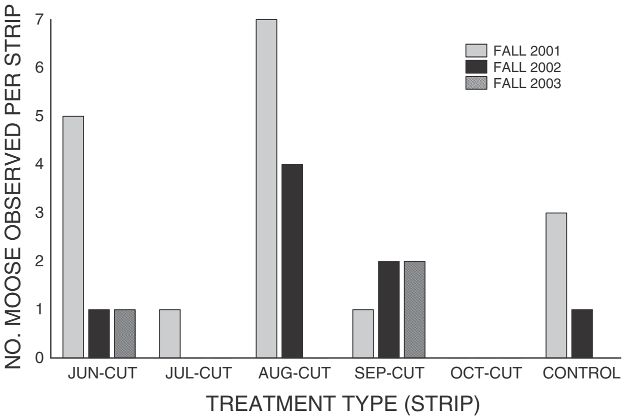

Fig. 3 Total number of moose observed browsing treated plants between early October and mid-December 2001, 2002 and 2003 in strips (treatment areas) that had been brush-cut at different times during 2001

Table 1 Normalized track counts (corrected to the number of track sets counted on a weekly basis and totaled each winter then averaged across 250 m sections of transect—the length of the October strip). Counts were taken from transects that ran diagonally down the entire length of each treatment strip. Counts were made between January and March of each year of the study

Treatment strip	Track counts				
	2002	2003	2004	Totals	3 Yr normalized Ave ± SD
June	18	21	16	55	18.3 ± 2.5
July	14	14	9	37	12.3 ± 2.9
August	19	24	8	52	17 ± 8.2
September	15	22	16	44	17.7 ± 3.8
October	6	8	9	23	7.7 ± 1.5
Control	25	28	18	71	23.7 ± 5.1

lowest numbers of tracks and June, August and September showing moderate levels of activity (Table 1).

Pellet Counts

Of 101 groupings of pellets that we found along our transects, we determined that moose deposited an average of 99.97 ± 25.82 pellets per group. Because of the large variation in pellets per group and the fact that most of the pellets were loosely grouped, or not grouped at all and often merged between groups, we decided to compare total pellets, rather than groups, between treatments. We found that along the width of our sampling areas, most moose pellets were deposited in 2002 and 2003 in the control strip – the strip with the highest 3 year average for pellet deposition (Fig. 4). In 2004, the August-cut strip contained the highest density of moose pellets. With the exception of 2002, the July-cut strip consistently contained the least number of moose pellets (and had the lowest 3 year average) and in 2002 showed the second lowest number of moose pellets following the September-cut strip (Fig. 4).

Browse Use Year 1

In the first spring after brush-cutting, willows cut in June and July had been browsed more than those cut in August and uncut controls (Table 2, Year 1). No shoots were produced or available for browse use in the first winter after cutting for plants cut in September or October 2001. There was no difference in browsing on June- and July-cut or August-cut and uncut control willows (Table 2). Twinberry (*Lonicera involucrata*) plants were browsed significantly more in the uncut control strip than in any of the brush-cut strips. August-cut alders were browsed significantly more than July-cut and control alders which were browsed less than those cut in June. Control birches were browsed more than July and August-cut birches (Table 2). Analysis of the average percentage of shoots removed from all browse species (All Brush) present on the site indicates that plants in the control strip were used less than those that had been cut – which all had similar average levels of removal (Table 2).

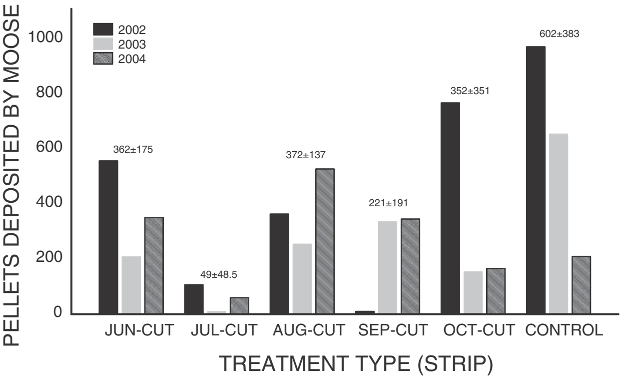

Fig. 4 Number of new over wintering pellets deposited by moose and counted in surveyed areas of each strip during each spring (2002–2004) of the study. Note: Numbers above bars indicate the mean ± 1SD pellets collected in each treatment strips over the 3 year period. In 2002, the areas surveyed included the entire width of each strip for the first 250 m from the viewing platform. In 2003 and 2004, areas surveyed were 2-m wide belt transects that ran the diagonal length of each transect. The 2003 and 2004, total pellet numbers have been normalized to account for differences in strip dimensions (see Methods)

Browse Use Year 2

In the second year after brush-cutting, October-cut willows were browsed more than June-cut and control willows. June-cut willows were browsed less than October- and September-cut willows (Table 2, Year 2). Twinberry controls were browsed less than June-, July- and September-cut plants, while June-cut twinberry was browsed more than control and October-cut plants (Table 2). September-cut alders were browsed more than control alders (Table 2, Year 2) and control birches were browsed more than birches cut in June (Table 2). In year 2, average brush removals were lowest for plants in the June- and July-cut strips, but similar for all other treatment strips and were highest for the fall-cut strips.

Browse Use Year 3

Three years after cutting, willows cut in October had the highest and June-cut willows had the lowest levels of browsing (Table 2, Year 3) October-cut alders were browsed more than control and August-cut alders which were browsed less than all other treatments (Table 2). Control birches were browsed more than all but October-

Table 2 Mean (±1SE) percentage of plant shoots browsed by herbivores in the first (2001–2002), second (2002–2003) and third (2003–2004) year after cutting and measured in spring after cutting, from different species cut at different times during 2001

Year	Species	Cutting time										Control		*F*	*P*
		June		July		August		September		October					
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
1	Willow	$^{271}71.2.0^{ab}$	1.9	$^{174}69.2^{\ cd}$	2.4	$^{615}58.8^{ac}$	1.3	–	–	–	–	$^{134}55.4^{bd}$	2.7	15.09	<0.001
	Twinberry	$^{110}27.5^{a}$	2.3	$^{70}22.3^{b}$	2.9	$^{21}24.6^{c}$	5.3	–	–	–	–	$^{156}47.5^{abc}$	2.0	24.63	<0.001
	Alder	$^{41}15.6^{a}$	2.4	$^{14}9.6^{b}$	4.0	$^{14}29.4^{bc}$	4.0	–	–	–	–	$^{155}3.8^{ac}$	1.2	18.47	<0.001
	Birch	$^{13}43.0$	8.3	$^{13}29.7^{a}$	8.3	$^{51}28.4^{b}$	4.2	–	–	–	–	$^{13}64.5^{ab}$	8.3	5.49	0.001
	All Brush	$^{443}53.7^{a}$	1.6	$^{279}52.2^{b}$	2.0	$^{716}54.3^{c}$	1.3	–	–	–	–	$^{494}35.5^{abc}$	1.5	22.22	<0.001
2	Willow	$^{479}26.0^{bc}$	1.4	$^{350}30.5$	1.7	$^{442}31.6$	1.5	$^{424}32.7^{c}$	1.5	$^{428}35.6^{ab}$	1.5	$^{443}29.5^{a}$	1.5	4.74	<0.001
	Twinberry	$^{326}3.8^{ad}$	0.4	$^{351}2.6^{b}$	0.4	$^{289}2.2$	0.5	$^{325}2.5^{c}$	0.4	$^{463}1.6^{d}$	0.4	$^{336}0.5^{abc}$	0.4	6.95	<0.001
	Alder	$^{63}5.6$	2.0	$^{78}6.1$	1.9	$^{59}6.4$	2.1	$^{84}13.3^{a}$	1.8	$^{57}9.4$	2.2	$^{83}1.7^{a}$	1.7	4.61	<0.001
	Birch	$^{9}38.2^{a}$	11.6	$^{12}63.1$	10.0	$^{37}62.1$	5.7	$^{11}71.7$	4.8	$^{24}69.8$	7.1	$^{54}82.2^{a}$	4.7	3.31	0.007
	All Brush	$^{921}16.3^{ad}$	1.0	$^{837}16.1^{bc}$	1.0	$^{945}20.5^{ab}$	0.8	$^{1112}17.6^{e}$	0.9	$^{888}21.5^{cde}$	1.9	$^{1020}19.4$	0.9	5.36	<0.001
3	Willow	$^{434}14.3$	1.4	$^{412}26.2^{bde}$	1.4	$^{395}28.9^{ce}$	1.5	$^{424}20.8^{ad}$	1.4	$^{421}39.1$	1.4	$^{393}25.5^{abc}$	1.5	34.98	<0.001
	Twinberry	$^{333}0.7$	0.2	$^{320}0.9$	0.2	$^{328}0.8$	0.2	$^{325}0.6$	0.2	$^{318}1.2$	0.2	$^{331}0.5$	0.2	1.00	0.416
	Alder	$^{72}9.6^{acdef}$	2.3	$^{76}14.6^{dgi}$	2.2	$^{54}5.1^{bf}$	2.7	$^{85}16.6^{cgh}$	2.1	$^{102}17.8^{ehi}$	1.9	$^{83}4.4^{ab}$	2.1	7.08	<0.001
	Birch	$^{21}17.9^{bcd}$	5.5	$^{9}25.1^{cegh}$	8.4	$^{121}6.5^{dh}$	2.3	$^{28}23.4^{bef}$	4.8	$^{34}38.1^{afg}$	4.3	$^{64}49.9^{a}$	3.2	27.35	<0.001
	All Brush	$^{932}9.1$	0.8	$^{856}15.1^{ab}$	0.8	$^{1160}14.5^{acd}$	0.7	$^{967}13.3^{bce}$	0.8	$^{964}21.9$	0.9	$^{1014}16.1^{ed}$	0.8	25.05	<0.001

All Brush refers to combined mean browse removals for all brush species assessed in each strip. Superscripted prefixes indicate sample sizes. Means sharing a common superscripted suffix across a species/group within a year for years 1 and 2 *are* the only treatments significantly different from one another. Means sharing a common superscripted suffix within year 3 across a species/group are *not* significantly different from one another. Tukey's HSD or a Spjotvoll/Stoline for unequal sample sizes tests were used for post hocs. "–" indicates insufficient regrowth for sampling in year 1

SE standard error of the estimate

cut birches and August-cut birches were browsed less than all other treatment categories besides those cut in June and July. (Table 2) Average brush removals in year 3 were highest for the October-cut and lowest for the June-cut plants.

Discussion

Our findings indicate that moose in the Grove Burn used hydro-axed strips that were cut with brush saws at different times during the summer to different intensities in the years after cutting. How much the variation in browsing between strips was related to the effects of brush-cutting treatments or other factors is clear in some respects, but less apparent in others.

In the first 2 years after brush-cutting, moose track and pellet density data show similar patterns of animal activity in treatment strips—both counts were highest in the uncut control strip relative to any of the brush-cut strips. This suggests that, at least after snowfall, moose moved into the control strip and spent most of their time in that area where shoots were available above snow (Schwab and Pitt 1987; Jenkins and others 1990) and did so independent of whether such shoots were more or less attractive or nutritious than those covered by snow in brush-cut strips. In year 3, pellet data show that moose moved into brush-cut strips, likely in response to shoots being longer and more available above winter snows.

Although movement to the control strip was the predominant shift in habitat use in winter, such patterns were not evident in the fall when moose observations were recorded. In fall, more moose were observed using the August-cut strip (at the opposite end of the viewing area relative to the control strip) in 2001 and 2002 and used browse in the September-cut strip predominantly during 2003. In fact, only 4 moose were ever observed using the control strip during the study. Despite these observations, moose may have been using the control or other strips more in the autumn despite the fact that we were unable to observe such use. It was apparent that most moose visitations to the viewing area were under the cover of darkness; most of our observations of moose were recorded just prior to sunrise or just after sunset when moose are known to be most active (Klassen and Rea 2008). Here, the use of infrared monitoring equipment would have helped us to delineate better which strips were being more heavily used, but the type of equipment required to see down the entire length of each strip was too costly for us to acquire.

Because one of our main objectives was to directly observe moose utilization of shoots arising from plants cut at different times, we selected to use the wildlife viewing area (described in the methods section) for our experiment. This made determining which treatment areas that moose were using unequivocal, but did not allow us to use the more technically sound approach of a randomized block design for our cutting and plant response trials (an approach less amenable to unambiguously observing differential selection of treated shoots by moose). Nevertheless, our findings suggest that plant response to cutting followed an intuitive and predictable outcome—namely that plants cut earlier in the growing season produced longer shoots and more biomass than those cut later (Rea and others 2007). Such findings agree with those of others (Kays and Canham 1991) and suggest that plant responses in our trials were based largely on cutting time (the effect we were testing), albeit other potential differences (e.g., edaphic, solar insolation) between strips within the site may have still imposed confounding and unknown influences on plant response.

Although moose viewing was an important part of our study, the most convincing evidence for moose using various strips is pellet deposition and browse use. Pellet deposition has been used by others as an index of habitat use in some areas (Bozzo and others 1992; Härkönen and Heikkilä 1999). Both pellet deposition and browse use allowed us to track evidence of use during those hours that we were not on site to view animals.

Total pellet deposition over the duration of the study was clearly lowest in the July- and September-cut strips. Track data show a very similar trend to pellet data (albeit pellets were also likely deposited in the fall and early spring before and after track counts were made) suggesting reduced use in July- and October-cut strips by moose. Observational data do indicate that fewer animals visited the October-cut strip, but this may have been an artefact of strip length. Of all strips, October-cut was the shortest (~250 m), at about half the length of the other strips. This made the occurrence of a moose being on the shorter strip less likely. Since most moose observed in the viewing area were generally observed at more than 250 m from the viewing tower, moose uncomfortable with using habitat closer than 250 m from the observer would not likely have used the October-cut strip while the observer was present. Given that pellet deposition and other such surveys overall may be poor indicators of habitat/browse quality unless patch size and distribution at multiple scales are carefully considered (Van Horne 1983), we used direct browse use as another index of plant attractiveness after cutting.

Tracks and pellets at the site suggested that in addition to moose, strips were visited occasionally by deer and hare, but that moose were the predominant visitors to the site. Furthermore, bite marks (type of bite and bite diameter) suggested that the majority of bites on individual plant shoots were from moose. This does not preclude the fact that each bite mark observed may have been taken by moose on shoots that had been previously browsed by moose or other animals and we, therefore, acknowledge the potential error inherent in spring browse surveys.

Except in the first post-cutting year, twinberry and alder plants appeared to be seldom browsed and were likely of little importance for moose when other browses such as willows and birch were available. Altogether dismissing such data, however, would be negligent given that the resprouts from newly cut twinberry and alder formed a large portion of plant shoots at our site consumed by moose in the first post-cutting year relative to how much those plants were used in the second and third year after brush-cutting. That such differences in consumption existed between the first and subsequent years following cutting suggests a uniqueness of quality in first year resprouts relative to older shoots. A general reduction in the percentage of biomass removed by moose with year-since-cutting may also be partially explained by increases in plant biomass with time-since-cutting (Rea and others 2007), if moose removed relatively constant amounts of shoot biomass from each plant browsed. Assessing plant biomass removal from the control site (those plants not compensating for cutting) in the years after brush-cutting suggests that moose drawn to resprouts in cut strips also browsed twice as much in the year after cutting as in the second and third post-cutting years.

With the exception of the first post-cutting year when only the shoots of June- and July-cut plants were available as browse above snow, the shoots of willows (which tend to form an important component of browse plant biomass for moose; Renecker and Schwartz 1998) from plants cut in October were browsed more than those cut in June; July were browsed least. When differences were significant, browse use of birch appeared to follow similar patterns.

Use fluctuated between species and years after cutting, and availability of resprouts with year-since-cutting appeared to influence use of the control strip. Although there was some variation in species composition (e.g., willows ranged from between 12-24% of available individuals in strips), use varied from year to year regardless of species mix. Variation in plant height, architecture, shoot length, biomass, diameters, chemical composition as well as inter- and intra-specific plant juxtapositions and clumping (most of which we did not quantify in this study) in addition to species mixing will, along with other factors, influence foraging by moose (Renecker and Schwartz

1998). Acknowledging our inability to account for each factor and recognizing differences in species preferences by moose, but recognizing from our findings that such preferences may change with time-since-cutting, we also calculated and report an average percent removal of shoots from all species combined (All Brush). Some loss of details in species-specific selection occurs by averaging percent removals, but evaluating broad patterns of percent use also provides an intuitive and generalized index of browse use along road and rail sides where species mixing and plant preferences will vary across the landscape.

Evaluating the overall percent usage of browse (All Brush) indicates the selection of previously cut brush over uncut controls in the first year after cutting and a reduction of use in uncut plants and plants cut in the early, relative to later parts (i.e., August and October) of the growing season in year 2. In year 3, moose appeared to focus their foraging efforts on the shoots of plants cut late in fall and less on those from plants cut early in the growing season.

Reduced consumption of shoots from plants cut earlier rather than later appears logical considering that plants damaged earlier in the year tend to suffer a loss of nutrient input back to roots which consequently have less available resources to allocate to shoot growth in subsequent years (Bryant and others 1991). Additionally, plants damaged earlier in the year produce shoots in the years after the first post-cutting growing season that are smaller, which are less preferred by moose (Penner 1978; Machida 1979; Danell and others 1985; Risenhoover 1987; Shipley and others 1994) and which contain anti-herbivore chemicals that are not found in plants damaged later (i.e., fall and winter) in the year (Bryant and others 1991).

Management Implications

Our findings suggest that important browse species such as willow and birch are used more by moose when cut later in fall than when cut in June and July and that differences in animal use and movements between areas brush-cut at different times of the year could be important from a vegetation management point of view. Our study only provides implications of cutting time within the transportation corridor and would need to be replicated on road and rail sides to test the application of our results in areas where traffic and maintenance activities (such as road deicing) may moderate animal response to plant cutting season. Nevertheless, it would be prudent for corridor managers to consider the influence that cutting season appears to have on moose and other herbivores that may be attracted to vegetation cut at one time of the year versus the other and the implications these interactions may have on the probability of road and rail traffic encountering animals.

These recommendations are not intended for all rights-of-way or even for all stretches of a transportation corridor where healthy populations of herbivores such as moose exist. Obviously, not all road and rail-side areas foster the growth of browse species sought out by herbivores and only some areas of corridor contain the combination of site attributes that make road and rail side browsing attractive. In areas where herbivores are known to use corridor vegetation, however, particularly in collision hotspots, cutting in early summer is recommended. Since the effects of cutting time do not appear to last much longer than 3 years (Rea 1999), cutting in these areas should be undertaken at 3 to 4 year intervals. Where brush-cutting intervals can, however, be performed on a more regular basis (i.e., once per year) recommendations for cutting in early summer should be closely evaluated against fall cutting which removes winter shoot availability altogether.

A reduction in browse quality and or availability through the use of more deliberate brush management planning will not reduce all collisions. However, the integration of these findings into road and rail side vegetation management planning in areas frequently used by herbivores can allow managers to take more proactive measures towards mitigating collisions in a relatively inexpensive and familiar way—simply altering the timing of vegetation management should in no way over complicate the planning process. Furthermore, in areas where managers are willing to apply these recommendations to larger areas of the corridor, cost savings in the form of a longer vegetation control cycle (due to reduced resprouting following mid-summer cuttings) appear to be simultaneously achievable (Rea 2005).

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PAPER X

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ORIGINAL ARTICLE

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

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Abstract

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

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

Introduction

Large herbivores such as moose are often reported to preferentially select resprouts of plants that have been previously cut or browsed (broken) rather than the shoots of undamaged plants (Danell et al., 1985; Hessl & Graumlich, 2002). Resprouts are generally larger than the shoots of undamaged plants and when eaten allow larger intake rates per cropping effort (Danell et al., 1985; Renecker & Schwartz, 1998; Gross et al., 1993). Resprouts are also widely reported to have fewer phenolic anti-herbivore chemicals (tannins/lignins). However, large shoots may also contain fewer minerals and more fiber than smaller shoots (Danell & Bergström, 1989; Rea & Gillingham, 2001), making them less attractive to moose throughout various parts of their range (Hagen, 1983; Vivås & Sæther, 1987; Histøl & Hjeljord, 1993).

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

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

Materials and methods

Field studies

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

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

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

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

Moose followed the researchers, carefully and systematically inspecting each pile as the materials were distributed on the feeding grounds. Once the materials were in place, moose were allowed to feed on the piles of shoots for approximately 24 h, moving between feeding piles and in and out of the surrounding woodlands at will. After 24 h, all shoots and shoot portions left in and around the piles were meticulously collected and bagged, then the bags were weighed (to nearest 100 g) and transported to the laboratory at the University of Northern British Columbia, Prince George, BC (53°53′ N, 122°40′W, 780 m a.s.l.). On the shoots that were not presented to moose, the length of shoots was measured to the nearest centimeter and the basal diameter of each shoot was measured to the nearest millimeter. Because after the first year of the study there was reason to believe that supplementary or sylleptic branches arising from the main current annual shoots (and growing from the lateral buds that were formed in the current growing season; *sensu* Cline & Dong-Il, 2002) played a role in forage selection, the number of sylleptic branches arising from second year shoots from all treatments was also measured. On shoots that were recovered from the feeding trial, shoot diameter at the point of browsing and the length of shoots from the basal diameter to point of browsing or shoot tip were measured.

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

Statistical analyses

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

Results

Year 1

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

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

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

Year 2

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

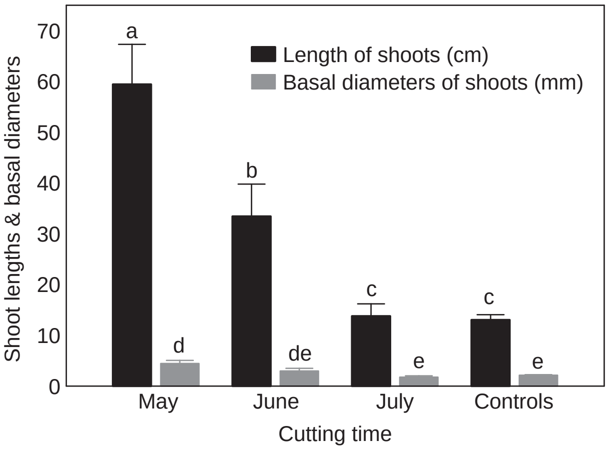

Figure 1. Average (± 1 SE) length and basal diameter of winter shoots from controls and plants cut at various times during the previous (2003) growing season. Measurements were taken in the first winter (2004) after cutting and resprouting. $n = 15$ shoots per treatment category. Bars with common letter designations are not significantly different from one another as determined by Tukey's *post hoc* comparisons.

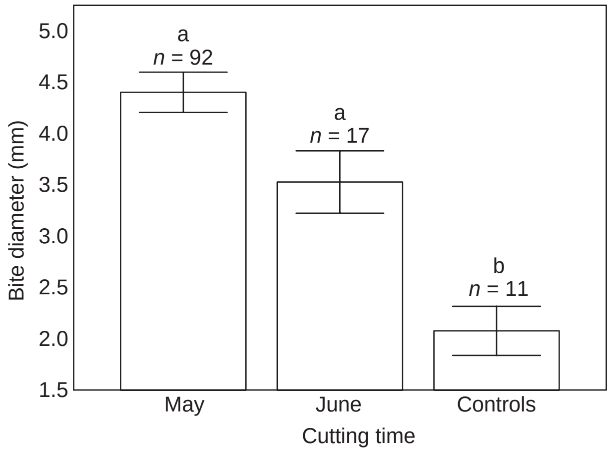

Figure 2. Average (± 1 SE) bite diameters measured on shoots collected from birches cut at different times of the 2003 growing season and left over by moose following feeding trials in February 2004. July shoots that were eaten by moose were fully consumed so those that were left over had no bite marks on them available to measure. Bars with common letter designations are not significantly different from one another as determined by Spjotvoll/Stoline *post hoc* comparisons.

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

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

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

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

Discussion

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

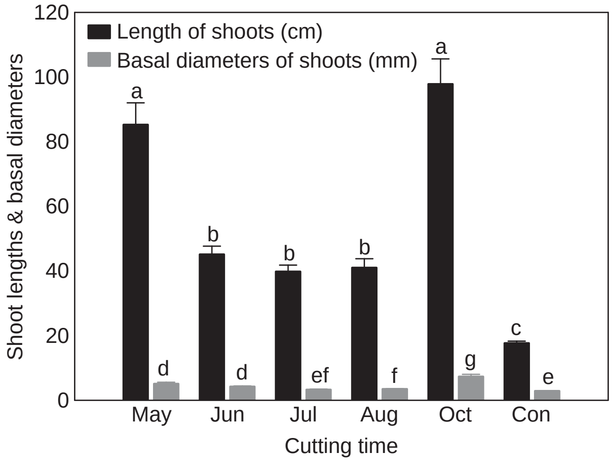

Figure 3. Average (± 1 SE) length and basal diameter of shoots produced by birches during the second (2004) postcutting growing season. Measurements were taken in February 2005; $n = 15$ birches per treatment category. Bars with common letter designations are not significantly different from one another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

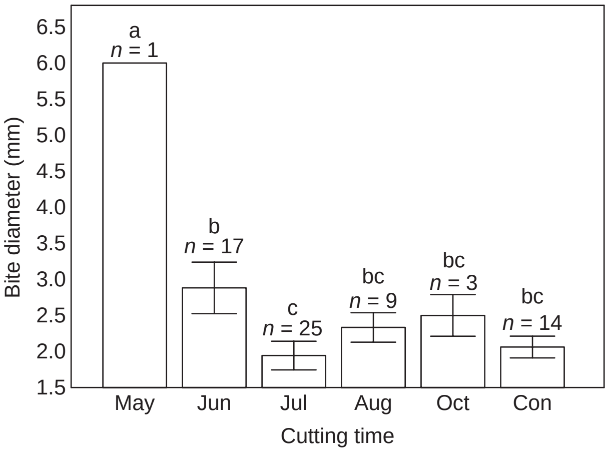

Figure 4. Average (± 1 SE) bite diameters taken by moose in February 2005 on shoots produced by birches during the 2004 growing season following cutting at different times in 2003. n = number of shoots left over from trials from which bite diameters were measured. Bars with common letter designations are not significantly different from one another as determined by Spjotvoll/Stoline *post hoc* comparisons.

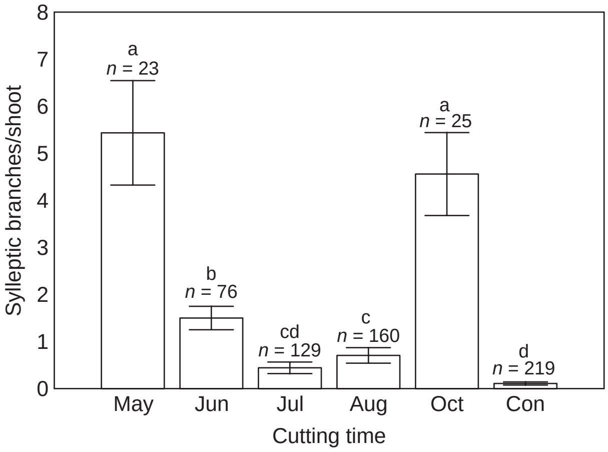

Figure 5. Average (± 1 SE) number of sylleptic branches found on second year current annual shoots of birches from different treatment categories. n = number of shoots of the 15 plants per treatment category upon which sylleptic branches were detected. Bars with common letter designations are not significantly different from one another as determined by Tukey's *post hoc* comparisons.

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

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

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

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

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

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

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

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

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

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

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

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

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

In conclusion, these findings suggest that (1) the timing of forest cleaning affects the size of shoots produced by birches after cutting, and (2) moose select shoots in winter from treatments that promote the growth of smaller shoots, rejecting larger shoots that contain sylleptic branches. Although shoot selection in more natural settings will be moderated by environmental factors that drive foraging behavior, this study found moose showing a clear preference for smaller shoots when such factors were artificially controlled.

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

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PAPER XI

REVIEW

Because of its applied character, wildlife science needs opportunities to summarise existing knowledge by reviewing, either by presenting leading ideas and results of study teams, or summarising advanced knowledge of selected scientific or management problems.

Modifying roadside vegetation management practices to reduce vehicular collisions with moose *Alces alces*

Roy V. Rea

Rea, R.V. 2003: Modifying roadside vegetation management practices to reduce vehicular collisions with moose *Alces alces*. - Wildl. Biol. 9: 81-91.

Vegetation management practices currently used within transportation corridors are primarily aimed at minimising encroaching shrub and tree growth in order to increase driver visibility and road safety. Such practices create prime foraging habitat for ungulates such as moose *Alces alces* by inhibiting forest succession and maintaining early seral shrub communities. Increased foraging activity within the corridor increases the likelihood of encounters between moose and motorists. Moose-related vehicular collisions are costly in terms of material damage claims and have significant negative impacts on public safety and moose populations in many parts of their range. Although several countermeasures have been developed in an attempt to reduce the frequency of these collisions, few have proven effective and even fewer have taken into consideration possible links between roadside vegetation management, the quality of browse regenerating from cut vegetation, and how moose use browse within the transportation corridor. To better understand these relationships, I reviewed the literature on ungulate-related vehicular collisions in combination with literature on plant response to mechanical damage. Many authors recognise the need to reduce the attractiveness of vegetation growing within transportation corridors. To date, diversionary feeding, forage repellents, establishment of unpalatable species and elimination of roadside brush have been used. Unfortunately, such techniques are only semi-effective or are not cost-efficient when applied across the landscape. It has long been recognised that the ability of plants to regenerate following mechanical damage is influenced by the timing of damage. Current research suggests that the quality of regenerating plant tissues for herbivores also depends on when plants are cut. Plants cut in the middle of the growing season produce regrowth that is high in nutritional value for at least two winters following brush-cutting as compared to plants cut at other times of the year, and uncut controls. Because roadside brush is generally cut during mid-summer, possible links between the quality of regenerated browse and increases in ungulate-related vehicular collisions during the autumn and winter should be elucidated. Based on this review, I recommend cutting brush early in the growing season and emphasize the need for collaborative long-term research to properly address this issue.

Key words: browse quality, brush-cutting, plant response, roadkill, road safety, ungulate, wildlife collision

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Vehicular collisions with moose *Alces alces* are currently a serious problem throughout much of the range of moose (Oosenbrug, Mercer & Ferguson 1991, Rattey & Turner 1991, Gundersen & Andreassen 1998). Collisions with moose and other ungulates appear to be on the rise worldwide (Groot Bruinderink & Hazebroek 1996) and have increased by more than 200% in some regions in less than a decade (Cook & Daggett 1995).

It is estimated that 29,000 humans are injured and 211 die annually in the US due to vehicular collisions with deer (the term deer in this work refers to members of the genus *Odocoileus*) alone (Conover, Pitt, Kessler, DuBow & Sanborn 1995). In France, approximately 50 people die and 2,500 are injured in ungulate-related vehicular collisions each year (Groot Bruinderink & Hazebroek 1996). In Sweden, 5-20 deaths and 500 injuries are reported each year as a direct result of moose-related vehicular collisions (MRVCs; Lavsund & Sandegren 1991). In northern New England, one in every 50 MRVCs results in a human fatality (Forman & Deblinger 1998).

Material damage claims following ungulate collisions cost billions of dollars each year; more than USD 50 million were spent on deer collision repairs in a single year in the state of New York alone (Decker, Loconti-Lee & Connelly 1990). The average cost for repairing vehicles can run from USD 4,000 per vehicle following a collision with a deer (Del Frate & Spraker 1991) to USD 15,150 per vehicle following a collision with a moose (Thomas 1995).

Wildlife-related vehicular collisions negatively impact animal numbers (Harrison, Hooper & Jacobson 1980, Cook & Daggett 1995, Thomas 1995) and are considered a long-term threat to populations of ungulates in certain areas (Jackson & Griffin 1998). In Newfoundland, Canada, approximately 4,800 moose roadkills were reported between 1988 and 1994 (Joyce & Mahoney 2001). These numbers are generally considered conservative because up to half of the ungulates killed by vehicles are never reported (Allen & McCullough 1976, Lavsund & Sandegren 1991); animals involved in collisions may wander from the corridor before dying (Moen 1979, Del Frate & Spraker 1991), are salvaged or scavenged (Child, Barry & Aitken 1991) or simply go undetected (Sielecki 2000). In some areas, collisions kill more ungulates than do hunters (Cook & Daggett 1995). In some parts of North America, roadkills are often reported as the chief cause of moose mortality second only to legal hunting (Del Frate & Spraker 1991) and may exceed 10% of the total annual harvest (Belant 1995). On a yearly basis, collisions with moose (automobiles and trains combined) claim approximately 6% of the annual allowable harvest nationwide in Canada (Child 1998).

Animal losses to road traffic can in part be attributed to the placement of human transportation corridors. These corridors tend to be routed through lowlands that follow the natural contours of the land (Thomas 1995) and often bisect or parallel prime habitat and natural routes traditionally used by ungulates and other wildlife for travel and migration (Andersen, Wiseth, Pedersen & Jaren 1991). Because of this overlap, road corridors are an integral part of many species' home range (Case 1978).

Roadsides often comprise remnants of natural vegetation in areas that tend to otherwise be heavily developed. Corridors provide islands and conduits of habitat for a variety of species and are used for feeding, breeding, nesting, dispersal and recolonisation (Bennett 1991). Some species rely exclusively on roadside habitat (Oetting & Cassell 1970, Way 1977). Roadside areas can also harbour feral animals and noxious weeds (Saunders & Hobbs 1991), creating a paradox for managers faced with the task of managing corridors with multiple objectives in mind (Bennett 1991).

Although reindeer *Rangifer tarandus fennicus* and caribou *R. t. tarandus* tend to avoid transportation corridors (Curatolo & Murphy 1986, Klein 1971), many ungulates, including moose (Kelsall & Simpson 1987, Thomas 1995), are known to use corridors for a variety of purposes (Table 1). For example, corridors may be used by ungulates for travel during periods of deep snow, but appear to be used predominantly for feeding (Peek & Bellis 1969, Puglisi, Lindzey & Bellis 1974, Groot Bruinderink & Hazebroek 1996).

Table 1. Various corridor activities engaged in by ungulates.

Corridor activity	Reference
Use of roadside watering holes	Groot Bruinderink & Hazebroek 1996
Use of natural mineral licks, highway de-icing compounds, sodium-rich pools	Grenier 1973, Damas & Smith 1983, Hardy 1984, Jolicoeur & Crête 1994
Use of aquatic feeding areas	Hardy 1984
Insect avoidance	Kelsall & Simpson 1987
Pavement warming	Kelsall & Simpson 1987
Use of roadside cover	Thompson & Stewart 1998
Use for migration and travel (especially in winter when snow is deep)	Andersen et al. 1991, Child et al. 1991, Del Frate & Spraker 1991, Schwartz & Bartley 1991
Loafing	Pils & Martin 1979
Use of edge	Bashore et al. 1985, Finder et al. 1999
Avoidance of hunters	Pils & Martin 1979
Use of roadside vegetation and slash	Pils & Martin 1979, Schwartz & Bartley 1991, see text

Roadside forage

Ungulate activity in utility and transportation corridors increases in spring and autumn and appears to be linked to the utilisation of early greening and late senescing forages that are found in these areas (Harrison et al. 1980, Bashore, Tzilkowski & Bellis 1985, Kelsall & Simpson 1987, Lavsund & Sandegren 1991). These peaks in foraging activity correspond with those times of year when most collisions with moose and other ungulates occur (McDonald 1991, Gleason & Jenks 1993, Sutton 1996, Sielecki 2000). In general, clearings and corridors provide an abundant source of preferred foods for ungulates (Bédard, Crête & Audy 1978, Thompson & Stewart 1998, Finder, Roseberry & Woolf 1999) that are superior in nutritional quality (Hughes & Fahey 1991, Ricard & Doucet 1999) and more spatially concentrated than those found in adjacent woodlands (Carbaugh, Vaughan, Bellis & Graves 1975, Groot Bruinderink & Hazebroek 1996).

The quality and availability of browse along managed roadsides tend to remain relatively constant. This is largely due to roadside brush-cutting that is aimed at increasing sight lines and driver visibility by suppressing plant maturation and forest succession. Although this is done to increase road safety, this practice perpetuates the growth of early successional vegetation that is attractive to herbivores like moose. For this reason, highway transportation corridors have been described as long pastures bisected by highspeed lanes (Bellis & Graves 1971) and serve as foraging grounds for elk *Cervus elaphus* (H. Flygare, unpubl. data), mountain goats *Oreamnos americanus* (Leedy & Adams 1982), bighorn sheep *Ovis canadensis* (Harrison et al. 1980, Leedy & Adams 1982), wild boar *Sus scrofa* (Groot Bruinderink & Hazebroek 1996), bison *Bison bison* (Damas & Smith 1983), deer (Puglisi et al. 1974, Carbaugh et al. 1975, Waring, Griffis & Vaughn 1991), moose (Kelsall & Simpson 1987, Child et al. 1991, Thomas 1995) and other herbivores (Arnold, Weeldenburg & Steven 1991, Bennett 1991).

Ungulates increase their foraging activities between dusk and dawn when they can move about under the protective cover of darkness (Peek & Bellis 1969, Carbaugh et al. 1975). Given that dark coloured animals such as moose are more difficult for motorists to see at night (Moen 1979, Thomas 1995, Sutton 1996), increased foraging activity and ungulate mobility between dusk and dawn are, not surprisingly, intimately tied to peaks in ungulate-related collisions (Carbaugh et al. 1975, Jaren, Andersen, Ulleberg, Pedersen & Wiseth 1991). Ungulate collisions appear to occur consistently between dusk and dawn regardless of the time of year or the ungulate population in question (Grenier 1973, Oosenbrug, McNeily, Mercer & Folinsbee 1986, Rattey & Turner 1991, Waring et al. 1991, Garrett & Conway 1999).

I reviewed the literature on patterns of ungulate-related collisions, plant response to tissue removal and vegetation management in transportation corridors as well as ungulate foraging behaviour. My objective was to elucidate new ways to manage roadside vegetation to reduce corridor attractiveness and moose utilisation of roadsides with an aim to reduce collisions with moose.

Countermeasures

A variety of countermeasures have been used in an attempt to reduce collisions with ungulates (Damas & Smith 1983). Many of these countermeasures, however, have proven ineffective. Deer reflectors, for example, are commonly installed on roadsides in an attempt to scare ungulates but have proven to be ineffective (see Groot Bruinderink & Hazebroek 1996) and cost USD 7,500 per km to install (Sielecki 2000). Exclusionary fencing is extremely effective at keeping ungulates out of transportation corridors but costs USD 45,000 per km to install. Furthermore, fencing is unsightly, requires frequent repair, and often prevents animals that make it into the corridor from escaping (Kent 1994, Sielecki 2000). In addition, the widespread use of fencing can greatly increase the fragmentation effect of transportation corridors on the movements of various species. On the other hand, managing corridor vegetation in a way that makes the corridor less attractive to species such as moose appears to be a more practical and promising tool for mitigation (Jaren et al. 1991, Lavsund & Sandegren 1991, Gundersen, Andreassen & Storaas 1998).

Planting unpalatable species within the corridor and luring animals away to strategically located feeding areas far from the road is an effective means of reducing wildlife collisions (Harrison et al. 1980, Cook & Daggett 1995, Romin & Bissonette 1996), as is completely eliminating palatable corridor brush such as birch *Betula* spp., poplar *Populus* spp. and willow *Salix* spp. (Jaren et al. 1991, Lavsund & Sandegren 1991). Unfortunately, these strategies are generally cost-prohibitive (Jaren et al. 1991, Sielecki 2000) and, in some cases, destroy habitat for other wildlife on a long-term basis (Oetting & Cassell 1970).

Manipulating the existing forage base within the corridor to produce low-quality browse may be a more cost-effective alternative for deterring feeding within the corridor (Sielecki 2000). Reducing the quality of roadside vegetation can be accomplished through applying noxious chemicals such as lithium chloride directly to the browse (Harrison et al. 1980). However, such strategies tend to be expensive and environmentally unsound. Although previously unreported, stimulating the growth of less palatable roadside browse through more carefully designed brush-cutting may prove less costly and equally, or more, effective.

Plant response to damage

It has long been established that mechanical damage to plants alters plant morphology, chemistry, the overall growth patterns and subsequently, the palatability of plant tissues for herbivores (Bryant, Danell, Provenza, Reichardt, Clausen & Werner 1991, Singer, Mark & Cates 1994). This type of response appears to have evolved as part of a generalised adaptive response against tissue removal by herbivores (Rhoades 1985, Bryant et al. 1991, Whitham, Maschinski, Larson & Paige 1991) but also occurs following other forms of stem breakage or tissue removal, including pruning, wind-breakage, snow press, ice scouring (Danell, Elmqvist, Ericson & Salomonson 1987), and brush-cutting (Oldemeyer & Regelin 1987, Nellemann 1990, Rea 1999). The morphology of current annual shoots (hereafter referred to as shoots) of broadleaf trees and shrubs often changes in response to damage. Plants generally respond to damage by producing large shoots (Willard & McKell 1978, Hjeljord & Grønvold 1988, Rea 1999) or by producing shoots that are more heavily armed (Gowda 1997). Depending on the intensity of damage, the overall architecture of the plant (tree-like vs hedge or shrub-like) may also be altered (Rea 1999).

Plants regenerating from mechanical damage also tend to produce shoots that are chemically different from the shoots of undamaged plants. Some woody browse plants, for example, produce shoots that contain higher concentrations of plant defensive compounds such as tannins, and are less digestible and contain lower concentrations of mineral elements following damage (Scotter 1980, Rhoades 1985), albeit plant chemical responses to damage vary significantly (Bryant, Wieland, Clausen & Kuropat 1985, Rhoades 1985, Singer et al. 1994).

Changes in the leafing phenology of plants also occur in response to mechanical damage. Plants can delay leaf senescence in the autumn and flush leaves earlier in the spring following damage relative to undamaged plants (Danell & Bergström 1985, Rea & Gillingham 2001). These changes alter the availability of leafy vegetation for herbivores at times of the year when nutritious plants are generally scarce (Renecker & Schwartz 1998).

Extensive research on plant response to damage (see Rhoades 1985, Bryant et al. 1991, Whitham et al. 1991) has shown that plant response varies with, among other things, the intensity, timing and frequency of damage (Danell & Bergström 1985, Whitham et al. 1991). For example, the timing of cutting (DeBell & Alford 1972, Harrington 1984, Kays & Canham 1991, Lepage, Pollack & Coates 1991) and clipping (Willard & McKell 1978, Bergström & Danell 1987a) stimulates plants to alter the morphology of browse shoots produced following damage. It has recently been concluded that the timing of browsing affects the chemistry of regenerating shoots and thus their palatability to ungulates (Alpe, Kingery & Mosley 1999), as does the timing of brush-cutting (Rea & Gillingham 2001).

Ungulate forage preferences and the corridor

Ungulates such as moose select browse based predominantly on quality (Thompson & Stewart 1998). Ungulates prefer browse plants that delay leaf senescence in the autumn and possess large shoots high in digestible energy and protein but low in plant defensive compounds (Bergström & Danell 1987b, Singer et al. 1994). Because late autumn and winter are times of nutritional deprivation for ungulates (Hobbs, Baker, Ellis & Swift 1981), roadside brush-cutting operations that inadvertently stimulate nutritious regrowth may act to increase the attractiveness of roadsides to moose. If corridors become more attractive to moose, roadside utilisation would tend to increase, as would the likelihood of collision.

Inarguably, other landscape features and animal behaviours influence ungulate use of areas such as roadsides (Treweek, Watt & Hambler 1997, Finder et al. 1999) and subsequently the frequency of collision. For example, collisions with moose often occur at distinct locations such as drainages (Thomas 1995) and the outlets of side valleys (Gundersen et al. 1998). The risk of ungulate collisions may also be greater near wooded, rather than open areas such as fields (Damas & Smith 1983). However, some authors report that deer collisions are randomly scattered within transportation corridors, with little concentration according to landscape features (Allen & McCullough 1976, Gleason & Jenks 1993). This suggests that other small-scale attributes such as browse diversity (R.V. Rea, unpubl. data) or other forage-based features of the corridor might influence animal activity.

Design features such as ditch depth and cut slope as well as corridor width may also influence how animals use the corridor (Kelsall & Simpson 1987, McGuire & Morrall 2000). Moose are particularly influenced by corridor width, for example, given that they predominantly use forest edges (Child 1998), and narrower corridors contain relatively more edge per cleared area (Bashore et al. 1985, Finder et al. 1999).

Driver visibility as well as the proximity of animals using the forest edge to the roadbed also varies with corridor width. Edge location in the corridor is generally considered fixed following corridor construction. Because it is not practical to relocate corridor edges, reducing browse attractiveness at the forest edge-corridor interface through post-construction vegetation management practices may be the only practical way to reduce the use of corridor edge by herbivores (Harrison et al. 1980, Damas & Smith 1983, Kelsall & Simpson 1987). Reducing the quality of forages growing near the corridor edge has been recommended by several authors studying the problem of ungulate-related vehicular collisions (Jaren et al. 1991, Cook & Daggett 1995, Ricard & Doucet 1999).

To date, studies on reducing the appeal of roadside forage for reducing ungulate collisions have primarily focused on the removal of browse from corridors. Cutting (Jaren et al. 1991, Lavsund & Sandegren 1991) and steam killing (Schwartz & Bartley 1991) vegetation within transportation corridors, for example, have proven effective (as much as a 56% reduction in train collisions; Jaren et al. 1991), but costly when practised repeatedly (Jaren et al. 1991, Sielecki 2000).

Cutting time as a countermeasure

Although several studies report the effects of the timing of cutting on shrub and tree regeneration, most have focused on how the physical and not the chemical characteristics of shoots and sprouts change following coppicing or silvicultural treatments (Belanger 1979, Kays & Canham 1991, Lepage et al. 1991, Babeux & Mauffette 1994). And while the nutritional quality of browse shoots is generally correlated with shoot morphology (Danell & Bergström 1985), this is not invariably true, particularly in the first two years after cutting when the effects of cutting time are considered (Rea & Gillingham 2001).

It is known that the quality of regenerating shoots of willow *Salix scouleriana* increases in the first two years after cutting when willows are cut during the middle of the growing season. Willows cut in mid-July produce shoots that, when collected in winter, are low in plant defensive compounds (tannin/lignin) and high in digestible energy and protein and delay leaf senescence into late autumn relative to plants cut at other times of the year and uncut controls (Rea & Gillingham 2001). These findings suggest that summer roadside brush-cutting operations could, inadvertently, be stimulating plants to produce nutritious regrowth that is attractive to moose.

Delays in leaf senescence due to roadside brush-cutting could alone be problematic where concerns for collisions with ungulates exist. Moose prefer greener vegetation (Bergerud & Manuel 1968, Hobbs et al. 1981) and, like other ungulates, will concentrate foraging efforts on leaves rather than shoots in autumn as long as leaves are available (Hobbs et al. 1981, Renecker & Schwartz 1998). Delayed leaf senescence in corridor plants could potentially extend the period of increased foraging activity and mobility that moose demonstrate when switching from decomposing summer forages to nutrient-rich browse shoots (Kelsall & Simpson 1987), thereby increasing their exposure to vehicular traffic. Similar problems are likely to occur in the spring given that ungulates are attracted to early-greening roadside forages (Kelsall & Simpson 1987, Anderson 1991, Renecker & Schwartz 1998) and the timing of brush-cutting alters the timing of leaf flush in spring (Rea 1999).

Altering the timing of brush-cutting can stimulate the production of less nutritious browse by willow (Rea & Gillingham 2001). Cutting plants at a time that reduces plant quality could potentially discourage moose from foraging in the corridor and decrease the probability of collision. Brush-cutting in early June for example, results in the production of browse that is significantly less nutritious for the first two years after brush-cutting than browse produced by plants cut later in the growing season or by uncut controls (Rea & Gillingham 2001). Although it has yet to be tested, cutting immediately following leaf flush could result in the production of even lower quality regrowth. Plant resources flushed into newly expanding leaves would be lost to early cutting before photosynthesis could restore root reserves (Bryant et al. 1991, Kays & Canham 1991). Reduced nutrient stores weaken the plant's capacity for vegetative regrowth and the building of nutrient-rich shoots (Kays & Canham 1991). Plants cut earlier in the year are also less likely to delay leaf senescence when compared to later cutting dates that tend to promote delayed senescence for at least two years after brush-cutting (Rea & Gillingham 2001).

Recommendations

I recommend cutting brush in early spring shortly after woody plants have flushed their leaves. For reasons previously discussed, regrowth from this treatment regime should be lower in nutritional value and palatability for moose relative to plants cut in the middle of the growing season, when most roadside brush-cutting operations are currently carried out. The later in the season that plants are cut, the more likely it is that they will produce nutritious regrowth in the years following brush-cutting. Although regrowth from plants cut later (e.g. autumn) will not be available to moose in the first winter after brush-cutting and is not as nutritious as regrowth from plants cut in July in the second winter after cutting, such regrowth, when available, is more nutritious than regrowth from plants cut early in the year (Rea & Gillingham 2001). Based on my review of the literature, cutting from July to March is not recommended in areas where concerns for collisions with ungulates exist.

Cutting roadside brush in the early spring means that conventional, tractor brush-cutting practices may not be feasible to use. If the corridor is too wet and the ground too soft for tractors to be used, other techniques such as manual brush-cutting may be required. Using manual brush-cutting would not only allow brush management regardless of season but would also allow further experimentation with the height and angle of the stump cut, which is also known to alter plant response (Belanger 1979, Harrington 1984, Babeux & Mauffette 1994). Techniques such as girdling and torching permanently kill woody browse species (Olson, Macrigeanis & Davis 1981, Danell et al. 1987) and could also prove effective means, either alone or in combination with specific cutting times, for reducing the appeal of the roadsides to ungulates. Although 'ecological side-effects' should be considered prior to use, silvicultural herbicides may also prove useful in some situations where other techniques fail to reduce collisions with moose. The use of any or all of these alternatives as countermeasures should be applied across the entire width of the corridor section being treated (including highway medians) and should be closely monitored. This strategy will ensure that the efficacy of the treatment and its implications for road safety can be tested in isolation.

Practices such as cutting only tall-growing plants under corridor utility lines (pers. obs.) should be discouraged. Such practices may promote the growth of low-growing, palatable species in the corridor that must no longer compete with taller plants and can utilise nutrients from the decomposing slash (plant cuttings) of taller cut plants (Payne & Bryant 1998). Furthermore, because slash is attractive to ungulates (Alkon 1961, Renecker & Schwartz 1998), all slash should be mulched or removed from the corridor. Incidentally, similar measures should be considered when more mature vegetation is felled during corridor construction and widening given that the crowns of many tree species are attractive forage for moose (pers. obs.).

Although cutting brush in corridors more than once per season can be expensive, inhibiting regrowth through repeated brush-cutting may also prove feasible (Jaren et al. 1991) if limited to areas where ungulate collisions are recurrent, assuming such management does not simply displace moose to the next section of the corridor. It should be kept in mind, however, that the consequence of multiple cuttings can lead to carbon exhaustion of the plants being cut (DeBell & Alford 1972), killing shrubs and altering roadside plant composition and seral trajectories (Parr & Way 1988, Anderson & Katz 1993). Understanding the effects of repeated cuttings on corridor vegetation is relevant considering that browse diversity appears to influence the number of collisions per site (R.V. Rea, unpubl. data).

Currently, no information exists on changes in plant quality or moose foraging behaviour relative to the length of the vegetation control cycle (Ricard & Doucet 1999). Although the effects of brush-cutting on plant quality can last for at least five years (Rea 1999), precisely how long the effects of the timing of cutting on quality persist are unknown. Preliminarily, control cycles should be scheduled on a three-year rotation to test the effect of treatments because plants can reassume some characteristics of their pre-treatment growth form in as little as two to three growing seasons following brush-cutting (Rea 1999). Assessing plant response on a yearly basis could help to determine the long-term effects of brush-cutting on plant quality and help to determine how often roadside plants should be cut.

Regardless of the brush management strategy employed, corridor vegetation must be managed in a way that considers both the forage and non-forage values of the corridor for other organisms as well as moose. Even closely-related species of ungulates may respond to similar management strategies in different ways (Kent 1994), emphasizing the need to understand and manage for multiple values (Anderson 1991, Lautenschlager, Bell, Wagner & Reynolds 1998). This may mean concentrating brush management activities in certain sections of the corridor or within a specified distance from the road surface while employing current or alternative practices aimed at conserving other habitat values elsewhere in the corridor.

It must be remembered that these recommendations are based largely on mechanical brush-cutting operations that were tested in a conifer plantation setting. Plantation brush-cutting differs from roadside brush-cutting in two important ways. Firstly, during roadside cutting all plants are removed. In the plantation setting, however, conifers (and deciduous plants that are not in direct competition with conifers; Härkönen 1998) are left uncut and continue to grow, consuming surrounding resources. This makes nutrient acquisition easier for plants cut in plantations versus transportation corridors (Blair 1971) and may, therefore, in part determine the plants ability to compensate for damage. Secondly, although brush in plantations may be cut more than once before the conifers reach a free-to-grow stage, it is rarely cut more than two or three times. Roadside plants, alternatively, tend to be cut back on a regular basis for the life of the corridor. For these reasons, spring cuttings can be implemented but their effects should be tested using long-term monitoring programs to assess the quality of various browse species regenerating from cutting. Because ungulate food preferences and plant responses vary by both species and geographic area (Kelsall & Simpson 1987), indiscriminate implementation of these and future research findings to all possible management areas is not recommended and should be approached with caution.

Conclusions

Current vegetation management practices in transportation corridors are often based on operational and logistical constraints; roadsides are cut when the ground is dry and brush-cutting tractors can be used. Although these maintenance practices are aimed at increasing road safety, they may also inadvertently, create ideal foraging habitat for animals such as moose (Damas & Smith 1983) depending on the time of the year that vegetation management is performed (Fig. 1). Understanding the effects of these management activities in relation to plant response and ungulate behaviour should therefore be considered by agencies responsible for managing vegetation in and near transportation corridors (Cook & Daggett 1995, Romin & Bissonette 1996, Jackson & Griffin 1998). Several authors have suggested that highway authorities, state/provincial and federal agencies, insurance companies, conservation groups and industry must collaborate more closely on research that aims to reduce such collisions (Scotter 1980, Kent 1994, Cook & Daggett 1995, Child 1998) before impacts to animal populations, the danger to motorists and pub-

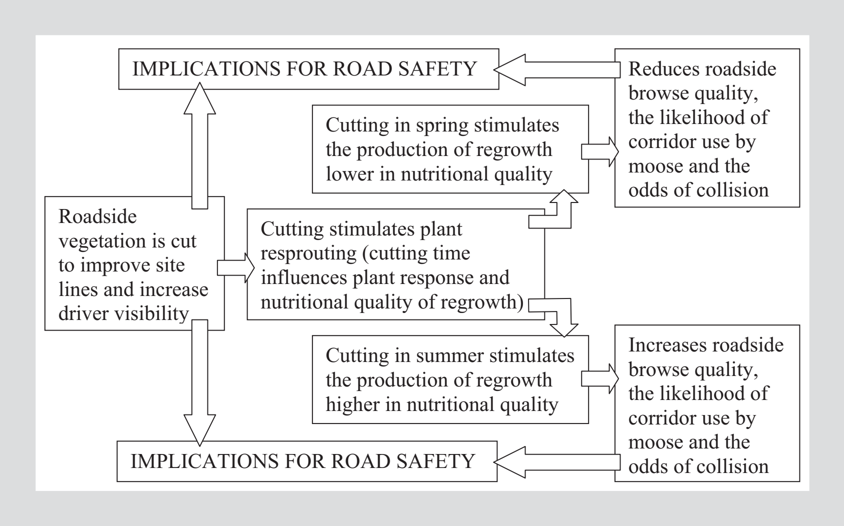

Figure 1. Theoretical relationships developed for application to roadside vegetation management as a result of a review and synthesis of currently published works on ungulate-related vehicular collisions and plant response to the timing of cutting.

lic costs escalate further (Child et al. 1991, Groot Bruinderink & Hazebroek 1996, Thompson & Stewart 1998).

Finally, there will always be a risk of collision where moose and vehicles co-exist (Jaren et al. 1991) and no countermeasure, forage-based or otherwise, will ever completely eliminate MRVCs. However, even a small reduction in collision frequency substantially reduces societal costs and the deleterious effects on animal populations (Gleason & Jenks 1993). In this respect, management strategies aimed at reducing MRVCs can only provide positive returns and should, therefore, be viewed in terms of an investment for current and future generations of both humans and moose.

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