

**VARIABLE FIRE SEVERITY IN ALASKA'S BOREAL FOREST:  
IMPLICATIONS FOR FORAGE PRODUCTION AND  
MOOSE UTILIZATION PATTERNS**

A  
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### **Abstract**

Over 1 million hectares burn annually across interior Alaska's boreal forest, altering the composition and distribution of vegetation communities that provide critical winter habitat for Alaskan moose (*Alces alces gigas*). Within a burn, fire severity (the amount of residual soil organic matter following a fire event) is spatially variable and drives the trajectories of post-fire succession. I examined the response of moose to patterns of regeneration resulting from variable fire severity within two burns in interior Alaska. I found significantly higher production of forage biomass (kg/ha) in high fire severity sites than in low severity sites. Proportional removal of forage biomass by moose was 36% higher on sites with higher fire severity compared with low severity sites. I used multiple regression models to examine the role of forage distribution following fire on proportional removal. The overall explanatory power of any landscape descriptors was moderate at best. Winter forage is a limiting factor for moose reproductive potential, especially in areas with low predation rates. Changes in moose habitat potential is easily measured using remote sensing and GIS techniques and should be assessed to combine field-based knowledge of moose response to variations in regeneration to large-scale patterns of vegetation regeneration following wildfires.

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## INTRODUCTION

Wildfires annually burn 1 to 3 million hectares across Alaska's boreal forest (Dyrness *et al.*, 1986). A mosaic of early successional forest stands results from wildfires and persists over time; this post-fire vegetation legacy is cited as a major influence on improving wildlife habitat across interior and northern Alaska (ADF&G, 2004). Specific post-fire pathways of vegetation regeneration depend on several factors. In this study I focused on site-specific fire severity, defined as the amount of soil organic matter combusted during a fire event (Greene *et al.*, 2004; Johnstone & Chapin, 2006; Schimmel & Granstrom, 1996). Interior Alaska is predicted to experience increased temperatures and decreased precipitation with continued global climate change in the coming decades (Serreze *et al.*, 2000). These changes are predicted to alter the fire regime, specifically leading to larger and more severe fires in an ecosystem that already burns at relatively short intervals (50 to 150 years) (Dyrness *et al.*, 1986).

Across the boreal landscape, within-burn patterns of post-fire regeneration directly impact moose (*Alces alces*) forage composition and spatial distribution. These changes may vary over different spatial scales. Foraging and activity patterns of individuals are influenced by an ecological hierarchy of resource distribution, ranging from individual plant morphology to forage patch distribution across an entire home range (Bowyer & Kie, 2006; Senft *et al.*, 1987). During the winter months, starting sometimes as early as August or September, moose are in a neutral or negative energy balance and begin losing weight on their winter diet (Schwartz *et al.*, 1988). In areas

where predator numbers are low and there is low to moderate calf mortality, access to forage resources during the winter months is a major limiting factor for moose survival .

Numerous studies have looked at the relationships between herbivores and the distribution of forage resources in a heterogeneous landscape (Bowyer *et al.*, 1998; Hobbs *et al.*, 2003; Kie *et al.*, 2002; Saether & Andersen, 1990). The effects of fire on foraging habitat have been studied in several species, including moose, but have mostly focused on patterns of utilization between entire burns and between burned/unburned areas (Gasaway *et al.*, 1988; Kilpatrick & Abendroth, 2001; Loranger *et al.*, 1991; Maier *et al.*, 2005; Peek, 1974; Weixelman *et al.*, 1998). Individual fires can cover 10s to 10000s of hectares in interior Alaska. Each burn represents a dramatic change in vegetation within its perimeter and as such, moose habitat. Further understanding of within-fire vegetation changes and moose response to variable regeneration patterns is critical for making more informed habitat and population management decisions for moose in the boreal forest.

In this study I examined moose winter foraging patterns within two wildfires (> 10 years old) in interior Alaska. The main objectives of my thesis were to 1) Assess the predictability of regeneration of post-fire vegetation given variable fire severity in terms of moose forage production; 2) Examine the relationship between variable fire severity and moose forage utilization in winter; and 3) Explore impacts of post-fire landscape heterogeneity on moose forage consumption. In Chapter 1, I directly address the effects of fire severity on the regeneration of post-fire vegetation and browse utilization by moose. I hypothesized that increased fire severity would lead to increased moose forage

production and that moose would respond to this difference through increased proportional removal of forage biomass in high versus low severity sites. This work was conducted within a fire outside of Delta Junction, AK (burned in 1994). I sampled the foraging habitat and moose utilization during the winter of 2006-07. In Chapter 2, I present results from the Rosie Creek burn (burned in 1983) near Fairbanks, AK where I examined the effects of post-fire regeneration patterns on landscape heterogeneity and the response of moose via proportional forage removal. I hypothesized that fire would lead to increased landscape heterogeneity of vegetation distribution and that landscape metrics, used to quantify heterogeneity, would be able to explain a significant portion of variability in proportional removal of forage by moose. These approaches, one non-spatial and one explicitly addressing the spatial effects of fire severity, allowed me to compare and contrast these two fires and the joint effects of forage production and distribution on moose utilization and overall post-fire moose habitat.

Chapter 1 is formatted for submission to the journal *Wildlife Biology*. Chapter 2 is formatted for submission to the *Journal of Applied Ecology*.

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## Chapter 1

### **Impacts of fire severity on secondary succession and moose winter foraging habitat in the boreal forest**

#### **ABSTRACT**

Given the widespread presence of fire in the boreal forest, understanding the role of post-fire succession and vegetation establishment in changing moose foraging habitat is an important component to the future management of moose in Alaska. This research focused on the current winter forage distribution and moose utilization patterns across three fire severity categories based on post-fire soil organic matter depth (high, medium, and low) within a 4800 hectare burn from 1994 25 kilometers east of Delta Junction, Alaska. Within the burn, we surveyed 20 plots in concordance with the Alaska Department of Fish & Game browse survey protocol to estimate the biomass of current year production and removal by moose throughout the winter of 2006-07. Our primary goal was to examine the effects of fire severity on moose winter browsing. Moose removed 33% of all forage across the study area. We found significantly higher relative removal by moose in high severity sites than in low or medium severity sites ( $p < .05$ ).

Significant differences in bite densities (grams/m<sup>2</sup>) also reduced the estimates of daily intake in low severity sites, with lower severity sites trending towards the minimum possible individual daily requirement.

## INTRODUCTION

Fire is the primary disturbance in Alaska's boreal forest, burning between 1 and 3 million hectares annually (Dyrness *et al.*, 1986). The post-fire landscape may be composed of a higher proportion of early successional stands, where successional pathways have led to deciduous species colonizing locations that were previously dominated by black or white spruce (*Picea mariana*, *P. glauca*). This mosaic of vegetation may directly affect moose winter foraging habitat and utilization patterns. Numerous studies have looked at the effects of fire on herbivore population dynamics, habitat, and foraging (Canon *et al.*, 1987; Kilpatrick & Abendroth, 2001; Riggs & Peek, 1980) including moose (MacCracken & Viereck, 1990; Maier *et al.*, 2005; Peek, 1974; Weixelman *et al.*, 1998). The purpose of this study was to assess the influence of fire severity, or the amount of soil organic matter (SOM) combusted during a fire event, on post-fire successional dynamics within the context of moose habitat. Secondly, we examined these effects on moose winter foraging within a burn.

### *Fire in the boreal forest*

Biotic and abiotic factors influence the spatial distribution of forest regeneration following wildfires (de Groot *et al.*, 2003; Hellberg *et al.*, 2003; Pastor *et al.*, 1999).

Moreover, fire events can increase diversity and density of plant species within the first 50 years after burning (Kashian *et al.*, 2005). Increased diversity in the vegetative community across the landscape is due in part to differences in post-fire successional pathways within burn perimeters. Fire severity is an important factor driving post-fire secondary succession. It is influenced by multiple interacting forces, including the composition of the pre-fire vegetation community, weather patterns, fire behavior, and topographic variables (Epting & Verbyla, 2005; Johnson, 1992; Johnstone & Chapin, 2006; Schimmel & Granstrom, 1996; Viereck *et al.*, 1986). Post-fire vegetation establishment in the boreal forest generally follows one of two pathways: self-replacement or relay floristics (Dyrness *et al.*, 1986; Johnstone & Chapin, 2006; Landhaeusser & Wein, 1993). In self-replacement succession, the same species that made up the pre-fire community re-establishes after the disturbance. In interior Alaskan plant communities, relay floristics succession occurs where the herbaceous understory dominates immediately after fire, followed by shrub and deciduous tree establishment and culminating in a late-seral spruce stand.

In spruce-dominated boreal forests, deep soil organic horizons generally restrict germination of deciduous species. Many studies have shown self-replacement by spruce during post-fire succession where fire severity is low and a deep organic horizon exists (Greene *et al.*, 2004; Johnstone & Chapin, 2006; Johnstone & Kasischke, 2005; LeBarron, 1939). Relay floristics may take place when fire severity is high and the organic layer is combusted to the extent that the mineral layer of the soil is exposed so shrub and deciduous tree species can germinate (Johnson, 1992). Hardwoods, such as

aspen (*Populus tremuloides*) and birch (*Betula neoalaskana*), are able to disperse via wind over long distances; small hardwood stands in surrounding areas provide a sufficient seed source for relay floristics to occur given suitable soil conditions for germination.

#### *Fire and moose habitat*

Throughout the winter, moose are in a neutral to negative energy balance (Schwartz *et al.*, 1988). They have to meet their nutritional requirements through foraging on woody browse and begin losing weight on this diet in the early fall (Franzmann & Schwartz, 1997). The main winter browse species in interior Alaska include twigs of several willow species (*Salix spp.*), paper birch, aspen, balsam poplar (*Populus balsamifera*), and alder (*Alnus viridis*). In addition to predation, obtaining sufficient nutrition to survive through the winter on these low-quality foods is a limiting factor in moose survival (Van Ballenberghe & Ballard, 1998).

Several factors mediate moose utilization of burned areas, including the generation of deciduous vegetation, pre-fire population densities and movement patterns, local predation pressures, snow depths and movement corridors, and patches of unburned or lightly burned cover distributed among forage areas. Peek (1974) found an increase in moose population density, specifically from increased immigration of yearlings, in the first two years following a large fire in northeastern Minnesota. In contrast, Gasaway and others (1988) found no immigration into a 500 km<sup>2</sup> burn in interior Alaska five years after the fact, though moose in close proximity significantly increased their utilization of

the burned areas during summer months and during the pre-rut migration. Immediately following a fire near Fairbanks, Alaska in 1983, abundant regeneration of aspen, willow and birch was present with active moose foraging in the area (MacCracken & Viereck, 1990).

Several studies have suggested that favorable moose habitat in burns persists and peaks between 20 and 30 years following wildfires (Loranger *et al.*, 1991; MacCracken & Viereck, 1990; Maier *et al.*, 2005; Weixelman *et al.*, 1998). During the mid-winter season on the Kenai Peninsula, moose removed more forage in stands that had burned 11 to 30 years prior than from those that had burned either 7 to 10 years or more than 70 years prior (Weixelman *et al.*, 1998). Maier *et al.* (2005) modeled moose cow densities in interior Alaska and found moose positively associating with areas burned 11 to 40 years ago at spatial scales of 15 and 23 km<sup>2</sup>.

Since the 1950s in interior Alaska's boreal forest there has been an increase in the frequency of large fire years; in the last 5 decades 33% of individual fires have burned over 100,000 ha (Kasischke *et al.*, 2006). Within a single burn, moose may respond to finer-scale patterns by increasing their foraging efforts in areas that have higher forage production. Given the breadth of land burned annually and increased forage production following fires, understanding the within-fire vegetation and herbivory dynamics coupled with greater understanding of fire behavior and scope, may gain managers important insight into future habitat for moose in interior Alaska.

This study focused on the forage production and utilization patterns by moose among different fire severities within a 13-year-old burn outside of Delta Junction,

Alaska. To examine the fine-scale patterns of fire severity on moose habitat, we hypothesized: 1) There would be more forage biomass produced in sites that were severely burned than in those which experienced lower severity burning; and 2) Moose would preferentially utilize areas of high fire severity.

## **STUDY AREA**

We utilized study sites from extensive work earlier on vegetation response to fire severity (Johnstone & Kasischke, 2005) located approximately 25 miles east of Delta Junction, Alaska, within the 1994 Hajdukovich Creek fire (referred to here as DJ94) (Fig. 1). The fire began in mid-June of 1994 and burned approximately 4800 hectares. The crown fire was extinguished in August, with ground smoldering lasting until early October (Michalek *et al.*, 2000). The pre-fire vegetation was dominated by stands of black spruce with a few aspen/aspen-spruce mixed stands throughout (Johnstone & Kasischke, 2005; Michalek *et al.*, 2000). Pre-fire soil organic layer depths were estimated to be greater than 25 cm in black spruce stands (Johnstone & Kasischke, 2005). The fire event was variable in its impacts on the black spruce forest with some areas experiencing complete combustion of the organic layer while other areas had only small amounts of organic duff burned off (Michalek *et al.*, 2000). Fire severity classes were determined by Michalek and others (2000) through post-fire satellite imagery and then field-checked for their correspondence with the degree of soil organic matter (SOM) combusted during the fire event. Sixty-one percent of the burn was classified as low severity, with nearly 6% as medium severity and just over 33% as high severity

(Michalek *et al.*, 2000) (Fig. 3). The study area is within the Tanana River valley and the overall topography is flat.

## **METHODS**

We sampled twenty sites among fire severity strata within the DJ94 burn perimeter that were used in a previous study of post-fire successional pathways (Johnstone & Kasischke, 2005). Sites were located using a handheld Garmin eTrex GPS unit (Garmin International, Inc. Olathe, KS, USA) (coordinates in UTM NAD1983 Zone 6). Previous research established the sites as either high ( $n = 11$ ), medium ( $n = 3$ ), or low severity ( $n = 6$ ) based on the amount of soil organic matter consumed in the fire event. The plots were distributed along the trail system within the burn scar and accessed by snow machine and snowshoes in late March 2007.

### *Plot biomass measurements*

A browse assessment protocol was used to estimate the biomass of forage production and removal (Seaton, 2002). This protocol is currently being implemented across interior Alaska for moose habitat assessments by the Alaska Department of Fish & Game (ADF&G, Tom Paragi, *pers. comm.*).

At each site we established 30 m-diameter plots with the site GPS coordinate as the center (5 m – 9 m accuracy). Random number tables of paces and compass azimuth were used to locate three plants within the accepted height range available to moose for browsing (0.5 m – 3.0 m) of each forage species (birch, balsam poplar, aspen, and

willows). Willows were identified to species (*Salix scouleriana*, *S. bebbiana*, *S. glauca*, and *S. arbusculoides*; Collet, 2004; Simpson, 1986):. While *Salix* were identified to species in the field, they were grouped into *Salix spp.* for final analysis. For each plant we recorded: species, height, estimated number of current annual growth (CAG) twigs, percent dead material by volume, and architecture class. Plant architecture classes were defined by the percentage of the current growth by volume of the plant arising from any lateral branching that was due to moose browsing and were as follows: unbrowsed (< 5%), browsed (5 - 50%), and broomed (> 50%). This classification provides a quick index for categorizing the browsing pressure on a plant throughout the course of its life (Seaton, 2002).

CAG diameter was measured on 10 twigs (> 1 cm long) per plant using dial calipers to the nearest 0.1 mm for a total of 30 twigs measured from each forage species within each plot. The diameter at point of browsing (DPB) was measured if the twig was browsed. More than three plants were sampled if more twigs were needed, until 30 twigs or all of the twigs available in the plot were measured. Browsing by snowshoe hares was present in the study site and the smooth-cut stems were differentiated from the rough-edged browse pattern of moose browse.

Stem densities were estimated within each plot using a 2 m wide and 30 m long belt transect from a random starting point on the plot perimeter through the plot center. Within the transect, stems of all forage species and non-forage tree species (*Picea spp.*) above 0.5 m (typical snow depth by late winter) were counted. If a site was obviously divided in species composition then a transect that was visually representative of the site

composition was used for stem density. This sample density was then multiplied by the plot area (706.86 m<sup>2</sup>) to obtain an estimated stem count within each plot.

### *Mass - Diameter Regressions*

Twigs were collected for mass - diameter regression equation development from all forage species except *Salix glauca* (data for this species in the Delta Junction area was provided by the Alaska Department of Fish & Game, Tom Paragi, *pers. comm.*). Twigs were weighed immediately upon returning to the lab or were kept frozen until weighed. They were clipped and weighed at each whole diameter interval, from 2 to 10 mm. Samples of wet weight twigs from all diameter classes were then dried at 80°C for 24 to 48 hours. They were then reweighed to determine the percentage of dry weight by diameter class.

The data were log transformed and a regression equation was fitted to relate dry mass to diameter (MacCracken & van Ballenberghe, 1993; Seaton, 2002) within a program developed specifically for this purpose in program R (R Foundation for Statistical Computing, <http://www.R-project.org>). Dry weight calculations were then back transformed, also in R, in order to obtain the original units of grams of dry mass.

### *Biomass Calculations*

Biomass was calculated using the estimated dry weights from the mass : diameter regression equations. The formula used for estimating biomass production and removal was:

$$\hat{B}_k = \sum_j \frac{M_{jk}}{m_{jk}} \sum_i \frac{N_{ijk}}{n_{ijk}} \sum_h \hat{z}_{hijk} \quad [1]$$

$\hat{B}_k$  is the site estimate of removal or production biomass in grams. Twigs are denoted by  $h$ , plants by  $i$ , species by  $j$ , and the sites by  $k$ .  $M$  and  $m$  are the total and sampled plants in each plot, while  $N$  and  $n$  are the total and sampled twigs. Individual twig biomass is represented by  $\hat{z}$  (Seaton, 2002).

### *Intake Models*

We used a foraging model from Seaton (2002), adapted from Moen, et al.(1998), to estimate individual daily intake in kilograms/day. This estimate was produced by multiplying the bite rate by bite mass by the time spent foraging, and dividing by 1,000. Bite rate estimates were determined for the entire burn and specific fire severity classes using mean bite density (# twigs/m<sup>2</sup>) per class. Following Moen (1998), bite rate is estimated from the rate at which bites can be cropped (*CropRate*), the amount of time spent processing each bite (*Rmax*), and the amount of time spent searching (*SearchTime*) :

$$BiteRate = \frac{\left( \frac{Rmax}{Rmax/CropRate + BiteSize} \right)}{1.0 + SearchTime} \quad [2]$$

$$SearchTime = 20.0 * BiteDensity^{-1.5}$$

Literature estimates were used for foraging time (400 minutes/day; Risenhoover, 1989), and maximum crop rate (40 bites/minute; Moen *et al.*, 1998). SearchTime is an estimate of the amount of time spent in each site searching for forage, and was calculated using bite density estimates (# of twigs/m<sup>2</sup>) from the field data. Rmax is the maximum amount of time spent processing forage ( $0.662BM^{0.76}$ ; Shipley & Spalinger, 1992), given a moose at a constant weight (400 kg; Gasaway & Coady, 1974). Rmax was set at 63 grams/minute. Bite Size is the mean bite mass (grams) estimated from the mean CAG or DPB, respectively, across all sites and within fire severity classes.

### *Statistical Analysis*

All statistical analysis was performed with SAS software, version 8.0 (SAS Institute Inc. 2002). Linear regression was used to examine the influence of soil organic matter depth on vegetation regeneration (PROC REG). Differences between CAG and DPB diameters were tested using t tests (PROC TTEST). One-way ANOVAS were used to test for vegetation and moose response differences between severity classes (PROC GLM). Estimates of biomass production and removal were generalized by area across the burn in two ways. First we took averages of production and removal from all sites and multiplied that by the area of the burn. To compare this estimate to the resulting

estimate when addressing fire severity distribution we used averages from the fire severity classes and weighted them by the proportion of high, medium, and low severity areas and calculated the whole-fire biomass estimates for the DJ94 burn.

Alpha levels were set *a priori* at 0.05. Tukey's adjustment for pairwise comparisons was used to test for differences among severity classes. Values reported are means with one standard deviation in parentheses. All models were checked to ensure that they met basic assumptions of normality and homogeneity of variance.

## RESULTS

The number of stems of forage species declined significantly with increasing soil organic matter depth ( $R^2 = 0.42$ ,  $p = .002$ ) and quickly dropped off when SOM was greater than 5 cm deep. In contrast, the mean number of spruce (non-forage) stems did not change with SOM ( $p = .63$ ) (Fig. 2). The stem density of all forage species (aspen, birch and willows) was 1.80 (0.57) stems/m<sup>2</sup> across all high severity sites, 1.54 (0.71) stems/m<sup>2</sup> in medium severity and 0.67 (0.34) stems/m<sup>2</sup> in low severity sites. Forage stem density was significantly higher in high compared to low severity sites ( $F_{2,17} = 7.44$ ,  $p = .005$ ). Density of spruce ranged between 0.02 and 0.15 stems/m<sup>2</sup>; there was no difference in spruce density between severity classes.

Past browsing has resulted in 84% of plants in the study area exhibiting broomed architecture, whereas 13% were classified as browsed and 3% were unbrowsed. These proportions were similar across all severity classes as well as between forage species.

There were no significant differences in CAG or DPB diameters between fire severity classes or species. Within each forage species the mean CAG and mean produced twig dry masses were significantly smaller than the mean DPB and mean removed dry masses (all t-tests  $p < 0.001$ ) (Table 1). Moose browsed at diameters beyond current annual growth on 9.9% of the twigs sampled across the study area.

An overall average of 189.90 (104.03) kg/ha of forage biomass was produced. However, high severity sites produced a mean of 225.71 (63.62) kg/ha, whereas 214.73 (117.25) kg/ha were produced in medium severity sites and 68.63 (48.52) kg/ha in low severity sites. Production in low severity sites was nearly 70% lower than production in high and medium severity sites ( $F_{2,17} = 4.78, p = .023$ ). This variation was largely due to the differences in aspen production; birch and willow spp. did not vary significantly with fire severity (Fig. 3).

Absolute forage removal was estimated at 68.77 (47.19) kg/ha across all sites. Estimates of removal per hectare were significantly larger in high severity sites, 104.37 (35.30) kg/ha, than in medium severity sites, 59.12 (39.38) kg/ha, and low severity sites, 16.86 (18.87) kg/ha ( $F_{2,17} = 8.92, p = .002$ ). There was no significant difference in removal between medium and low severity sites. Aspen dominated the differences between removal between fire severity classes ( $F_{2,17} = 7.34, p = .005$ ), with significantly more absolute removal in high sites than in both medium and low sites (Fig. 3).

Total proportional removal differed significantly with fire severity ( $F_{2,17} = 7.46, p = .005$ ). Proportional removal in high severity sites was significantly higher, 46% (0.13), than both medium, 26% (0.12), and low, 19% (0.16), severity sites. There was no

significant difference between the low and medium severity sites. Relative removal of willow was significantly higher in high severity sites, 44% (0.21), than in low severity sites, 17% (0.09) ( $F_{2,17} = 5.05, p = .02$ ) (Fig. 4). Across all sites, 33% (0.17) of current annual growth was removed by moose from the study area.

Average twig mass did not vary significantly with fire severity, however across all sites the mean twig mass from the point of browsing, 0.82 (0.40) g, was significantly greater than the mean current annual growth twig mass, 0.66 (0.20) g ( $t(19) = -2.52, p = .02$ ). This affects the results of the intake model, depending on whether the CAG or DPB measurements were used to estimate average bite mass of twigs. DPB has been used to estimate daily moose intake over the winter season prior to sampling, while CAG has been used for an estimate of possible daily intake for the rest of the season (Seaton, 2002). If the DPB twig mass is used, the intake model estimates that 7.83 (3.75) kg/day could be removed by a moose. The CAG bite mass is smaller, and as such brings this estimate of daily intake down to 6.22 (1.72) kg/day. The DPB daily intake estimate is significantly larger than the CAG estimate ( $t(19) = 2.44, p = .025$ ). There were no statistically significant differences in estimated intake between fire severity classes, although low severity sites were much closer to the 4.5 kg/day limit of daily requirements (Gasaway & Coady, 1974) at 4.90 (3.43) kg/day, in contrast to the high severity sites where average estimates of daily intake were 8.03 (1.95) kg/day. Variable bite density is the parameter driving the difference between these estimates. Bite density was nearly three-fold greater in high severity sites (35.2 twigs/m<sup>2</sup>) than in low severity sites (13.27 twigs/m<sup>2</sup>).

Over half of the land burned in the DJ94 fire was classified as low severity, and 33% classified as high severity (Michalek *et al.*, 2000). Using fire severity-specific estimates of production in conjunction with the remote sensing image of burn severity to take into account the area covered by each severity class, the overall estimate of forage production was 127.75 kg/ha. If an overall average of production was used, irrespective of differences in severity, and multiplied across the burn perimeter the production estimate is 189.90 kg/ha. Pooling data and not taking into account significant differences in biomass production given differential fire severity led to an overestimation of production by 62 kg/ha. However, the difference between absolute removal estimates was just 4.89 kg/ha. An estimated 63.87 kg/ha was removed from the study area when taking fire severity distribution into account, whereas an estimated 68.77 kg/ha removed when assuming homogeneity within the burn perimeter.

## **DISCUSSION**

Global climate change is predicted to increase the frequency and severity of large wildfires across the boreal landscape, creating the potential for increased moose habitat in the form of widely distributed deciduous stands. In this study we found that within pre-fire black spruce stands, areas that experienced high severity fire produced more forage biomass per hectare than less-severely burned areas, and moose responded to this heterogeneous environment by removing proportionally more forage from high severity sites.

Post-fire plant communities may follow predictable regeneration patterns. Variable fire behavior across the course of an individual fire event creates a spectrum of fire severities (hence a range of depths in soil organic matter) that may facilitate different successional pathways. In post-fire sites, we found a sharp decrease in aspen stem density where the post-fire soil organic matter had been measured as deeper than 5 cm. A similar relationship between the SOM horizon and deciduous stem densities was also seen in the same sites by Johnstone and Kasischke (2005), who documented increased aspen density with increased fire severity. However, they also observed a decrease in the density of regenerating spruce with increased fire severity. In the current study we found no relationship between spruce density and fire severity (Fig. 2). Whereas the spruce stem density did not change with organic matter depth, the increased presence of aspen in these high severity stands would presumably continue as a deciduous-dominated stand before reaching a later successional stage of spruce.

The DJ94 fire occurred within Game Management Unit (GMU) 20D which encompasses nearly 1.5 million hectares, of largely black spruce dominated boreal forest, as well as part of the Alaska Range alpine ecosystem. Much of the boreal area in GMU 20D has burned since 1979, over two-thirds of which burned between 2001 and 2004 (BLM, 2005). The moose density estimate from 2006 in southwestern 20D is just over 2 moose/km<sup>2</sup> (DuBois, 2004), one of the highest moose densities for an area in this size in North America and well over moose density estimates for other areas in interior Alaska, including those considered to have high moose densities such as the Tanana Flats region in GMU 20A (1.1 moose/km<sup>2</sup> in 2000; Seaton, 2002). In addition predator control

programs in the 1980s and low snow depths in GMU20D (DuBois, 2004), it is possible the fires that have occurred in this area have contributed to the increase in moose density by providing a substantial amount of woody forage through the winter. Future management decisions will need to take into account the distribution of forage resources throughout the GMU, which should include an assessment of how the fire regime and individual fire behavior have shaped, and may shape in the future, winter moose habitat.

Browsing pressure by moose in the study area has been high since the DJ94 burn, as demonstrated by the high percentage of broomed architecture in plants throughout the study area. Monitoring of browsing pressure in a 1987 burn in the southwestern portion of GMU 20D by the Alaska Department of Fish & Game showed that the proportion of broomed plants increased by 80% between 2001 and 2007 (Tom Paragi, *pers. comm.*). Within the DJ94 burn moose browsing has visibly affected the growth patterns of the plants and possibly affected the rate of succession in some of these stands. Over 80% of the plants in this study exhibited broomed architecture, regardless of severity class. Work by Kielland et al. (1997) on river floodplains in interior Alaska showed significant decreases in canopy heights and increased number of twigs on early successional plant exposed to seven years of moose browsing, relative to unbrowsed plants. Over time, excessive browsing may result in the death of plants which has been seen in some of the aspen saplings in this and other areas (*pers. obs.*). However, browsing at an intermediate rate may suppress the rate of sapling growth, possibly extending the period of increased forage availability following high severity fires.

Estimates from the intake model suggest that within the study area, moose are currently able to meet their daily intake requirement of 4.6 kg/day (Gasaway & Coady, 1974), with the average daily intake across all sites estimated to be 7.83 (3.75) kg/day. Although not statistically significant, the intake estimate for high severity sites was almost twice as high as in low severity sites. This was due to considerably larger bite densities in high severity sites. This increase in bite density would decrease the amount of time moose would need to spend searching for forage and increase foraging efficiency within high severity patches.

High burn severity sites had increased absolute biomass production, supporting the hypothesis that areas severely burned can produce more winter forage for moose than areas that were less severely burned. Similar trends were seen in production and removal estimates from burned sites in the Tanana Flats region (GMU 20A) were 243 and 82 kg/ha, respectively, while unburned sites had production and removal estimates of 49 and 15 kg/ha (Seaton, 2002). The major fires in the central Tanana Flats area occurred over 20 years ago and have contributed to high forage production in the Flats, an area of high moose density in interior Alaska.

Mean bite diameters of twigs were larger than mean current growth diameters, irrespective of fire severity class. Nearly 10% of twigs sampled were browsed beyond the current annual growth diameters. Browsing on larger diameters on twigs may indicate poorer quality forage and an overall poorer nutritional environment (Hjeljord *et al.*, 1982; Vivas & Saether, 1987). As the diameter of a twig increases, the bark : wood ratio decreases and more of the ingested forage lacks nutritional value for the moose,

simply taking up space in the rumen and increasing the energetic cost of digestion. There is a trade-off, however, as smaller diameter twigs may not be consistently available across the landscape in high enough density to fill the rumen within the available foraging time per day. It is noteworthy in this study that bite diameters were on average 12% larger than the current growth diameters and when used in estimating daily intake, this larger mean bite mass corresponds to a higher estimate of possible intake by 1.61 kg/day. This may be a possible indicator of increased pressure on the forage resources with an increasing moose population density. Another often used indicator of decreasing moose habitat quality is the percent of cows observed with twin calves during aerial census. This twinning rate decreased in southwest 20D from 25.9% in 2006 to 16.7% in 2007 (Steve DuBois, *pers. comm.*).

Moose removed 33% of the available forage across the entire study area. This level of proportional removal is the second highest compared with other areas in interior Alaska (Boertje *et al.*, 2007; Seaton, 2002). However, a closer look reveals that proportional removal was 36% higher in the high severity sites than in low severity sites. In a study of possible indices to use for indicating density dependent nutritional limitation in moose populations, Boertje *et al.* (2007) suggested that when proportional removal is greater than 35% the moose population may be nearing the capacity of the habitat to support their density; they additionally observed decreased twinning rates with increasing proportional removal. In this study area the overall removal was close to this cutoff. In high severity sites proportional removal was well above this value, with an average of 46% of the forage biomass being removed. Proportional removal in the Alaska Range

foothills of southwestern GMU 20D in 2007 was estimated to be 30%, and 22% in the flats region (Tom Paragi, *pers. comm.*). Given that the current study was conducted in a burn within the flats region of 20D it is evident that there are hotspots of foraging over this large area that differ widely from the overall mean. Efforts for large-scale monitoring of browse resources and foraging pressure should consider further stratifying beyond topography (i.e. flats vs. foothills) based on areas of widely different vegetation patterns, such as burn scars from the past several decades.

Changes in plant species composition can affect the overall habitat quality for moose, with widespread areas of increased preferred forage species (e.g. willow spp. and aspen) densities possibly providing better quality winter foraging habitat. Moose possess physiological, morphological, and behavioral adaptations to surviving on ranges of low forage quality over the subarctic winter. Moose responded to a range of higher forage quality (indexed by digestibility) in Norway with more daily activity and higher net intake of digestible forage than in a range with lower quality forage resources (Saether & Andersen, 1990). A few large fires have occurred near Delta Junction, AK in the last thirty years. In this study we found small-scale (within fire) responses by moose in terms of significantly higher proportional removal in areas of higher burn severity. As previously mentioned, the moose population in southwestern GMU 20D has grown dramatically to about 5.6 moose/mi<sup>2</sup>, influenced in part by increased range quality due to widespread burning. This kind of compounded response may be indicative of a population-level multiplicative effect where even slightly increased forage resources for individual moose leads to population-wide increases in numbers (White, 1983). Due to

predator control efforts in this region this moose population is not considered to be predator-limited (DuBois, 2004). Similar types of compounding effects would probably not be seen where there is a much higher mortality rate of calves and yearlings due to predation irrespective of habitat quality and forage resource distribution.

Currently, black spruce stands make up more than 40% of the landscape in interior Alaska (Chapin III *et al.*, 2006). Just over 38 million hectares are in post-fire secondary succession arising from fires approximately 20-30 years ago, from the mid-1970s through to the mid-1990s (BLM, 2005). Since the mid-1990s (through to 2006), almost 75 million hectares have burned in interior Alaska, 63 million of which burned between 2001 and 2004 (BLM, 2005). These fires will directly impact moose habitat by facilitating an increasingly complex vegetation community across the landscape. Examining the within-fire dynamics of post-fire succession can help us to better understand the impacts of burning on the boreal landscape and its impacts on moose forage, possibly into future decades. Also worthy of further consideration are the possible feedback effects of increased acreage of deciduous stands throughout the boreal forest and the changes this may have on the fire regime.

## **CONCLUSION**

Wildfires in the interior boreal forest often cover tens of thousands of hectares and result in patchy regeneration of both spruce (through self-replacement succession) and deciduous (through relay floristics) stands across the landscape. The vegetative communities that arise from these different pathways during post-fire succession have

direct impacts on moose winter forage resources in these areas. The peak of post-fire succession, from a moose habitat prospective, can last from 12 to 30 years following the fire event. However, by examining immediate post-fire severity dynamics through remote sensing techniques and on the ground sampling, we can estimate the potential regeneration pathways over a burn and thus make projections of future moose habitat. In a changing climate, with forecasted increases in area burned and fire severity across the boreal forest, it is becoming increasingly important to understand how fire impacts the landscape and how these impacts shape the populations of moose in Alaska in order to assess and manage populations over time. In this study we saw that variable fire severity over relatively small spatial scales predictably changes forage production and in turn affects moose response during winter foraging.

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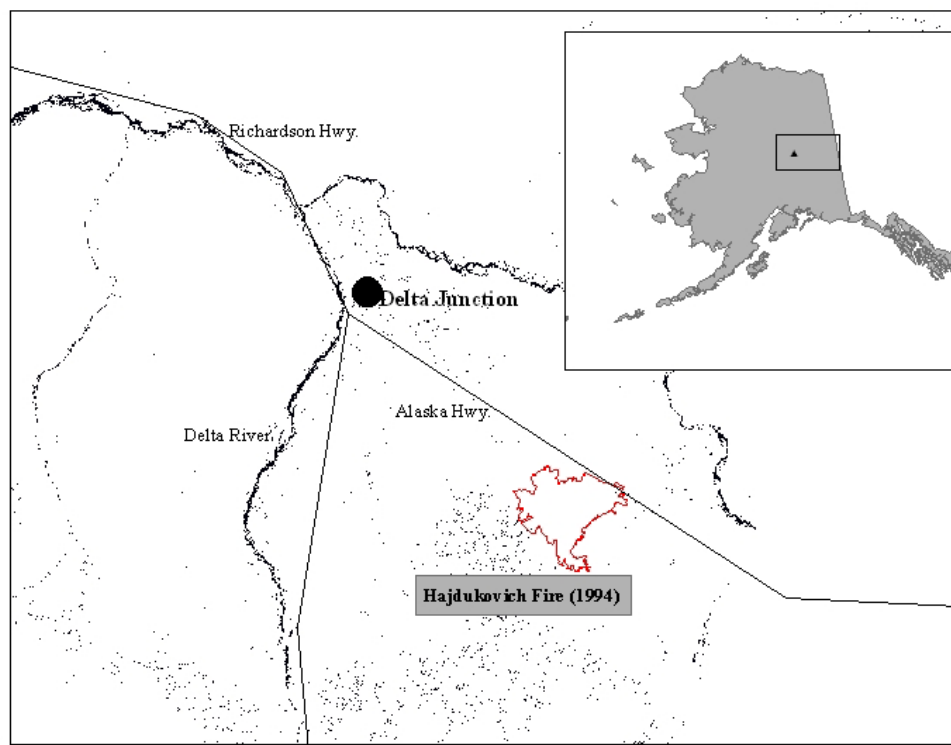


Figure 1.1. The 1994 Hajdukovich fire (DJ94) occurred approximately 25 km east of Delta Junction, Alaska.

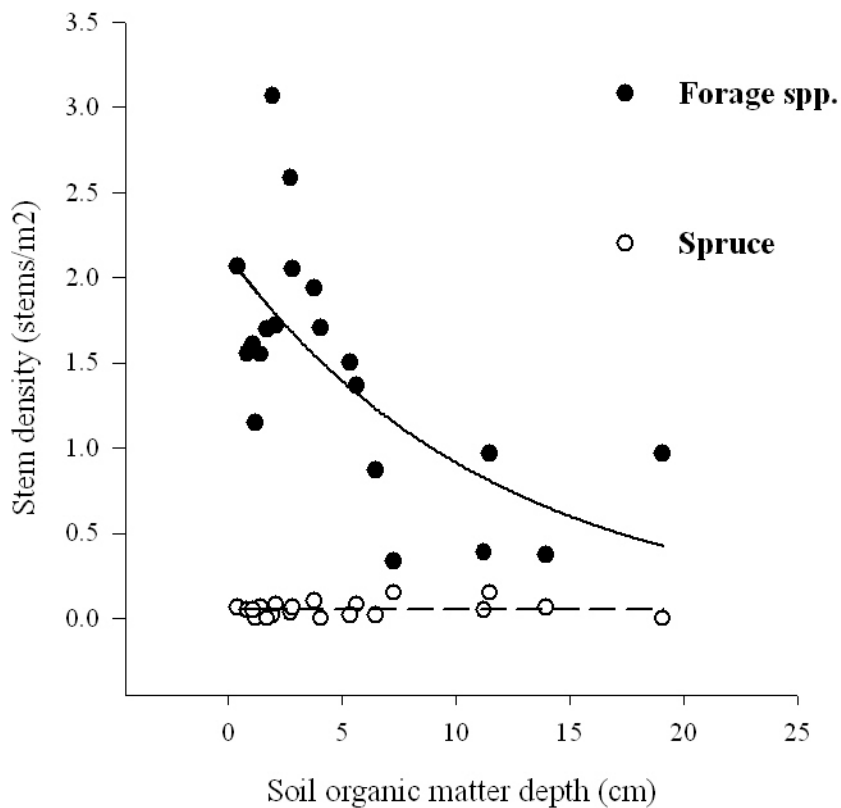


Figure 1.2. Stem density of forage (aspen, birch, willow spp.) and non-forage (black spruce) plants between 0.5 – 3.0 m high, corresponding with soil organic matter depth (cm) (qualitative fire severity categories corresponded to SOM as following: high (0 – 3 cm), medium (3.01 – 10 cm), high (>10.01 cm). The equation for the regression on forage data is:  $y = 2.13 * e^{-0.08x}$ .

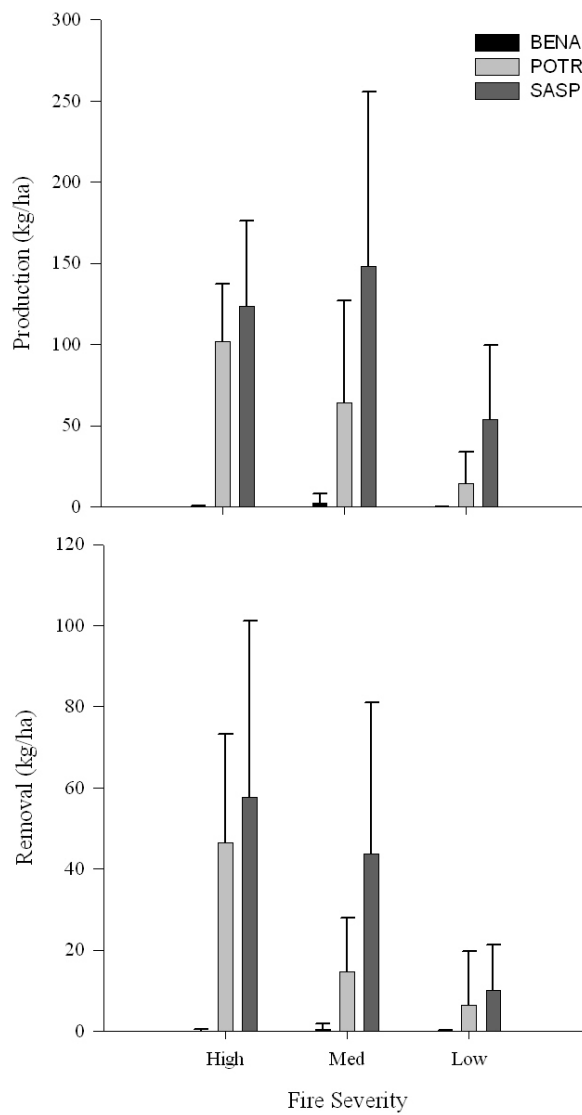


Figure 1.3. Absolute production and removal of forage biomass by fire severity class (kg/ha). Different letters indicate significant differences between severity classes, within the category of production or removal ( $\alpha = .05$ ).

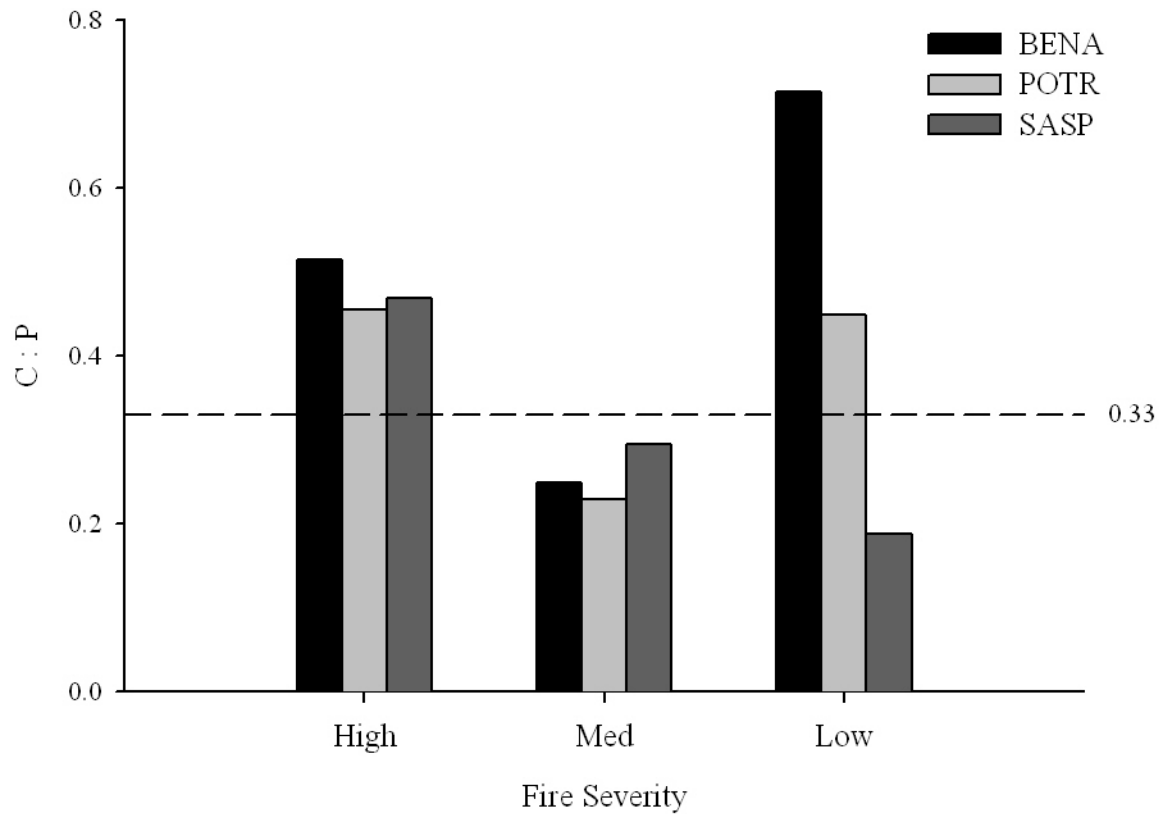


Figure 1.4. C:P (the proportion of removed biomass to produced biomass) by species within fire severity classes. Across all sites an average of 33% of forage biomass was removed relative to what had been produced.

Table 1.1. Twig diameters and dry masses by species. CAG = mean current annual growth diameter (mm), DPB = mean diameter at point of moose browsing (mm),  $\bar{z}$  produced = mean dry mass produced (g),  $\bar{z}$  removed = mean dry mass removed by moose (g). p-values are from t-tests of differences within species between twig diameters and dry masses, respectively.

<b>Species</b>	<b>CAG</b>	<b>DPB</b>	<b>p</b>	<b><math>\bar{z}</math> produced</b>	<b><math>\bar{z}</math> removed</b>	<b>p</b>
BENA	2.14 (0.33)	2.33 (0.57)	<0.0001	0.59 (0.40)	0.74 (0.82)	0.0001
POTR	2.33 (0.31)	2.63 (0.56)	<0.0001	0.64 (0.24)	0.79 (0.37)	<0.0001
SASP	2.33 (0.24)	2.63 (0.42)	<0.0001	0.69 (0.33)	0.80 (0.46)	<0.0001

Chapter 2.

**Fire severity and resulting landscape heterogeneity: Implications on proportional removal by moose in winter at multiple scales of analysis**

**Abstract**

Wildfires in the boreal forest are able to shift the species composition of vegetation and its spatial distribution from 10s to 1000s of square kilometers. While studies have been done in the past on large scale (> 15 km<sup>2</sup>, or whole fire) responses of moose (*Alces alces*) to these changing landscapes, effects within burns on browse utilization by moose have seldom been examined. In this study we focused on the relationships between relative forage removal by moose and vegetation distribution dynamics at five spatial scales (60, 120, 480, 1000, and 2000 m) in a 35 km<sup>2</sup> landscape that burned during spring 1983 in interior Alaska. Using aerial photography and Landsat TM satellite imagery, we found pronounced changes in overall spatial heterogeneity and species composition of vegetation from 1978 to 2004. The burn resulted in a dramatic increase in broadleaf stands and increases in the dispersion and connectivity of vegetation patches. Across the burn proportional removal averaged 24% and ranged from 0 to 54%.

Multivariate regression models were developed at four scales (excluding 2 km), and included quantitative indices of spatial heterogeneity and topographic variables. Based on model assessment using AIC<sub>c</sub>, heterogeneity parameters had considerably more support than topographic variables at all scales except 480 m. In addition to the overall age of a burn, the distribution of fire severity and resulting landscape diversity within a burn perimeter must be addressed to assess the impacts of fire on potential moose winter habitat over time in the boreal forest.

### **Introduction**

Forage resources are usually unevenly distributed over a landscape, especially following disturbances such as wildfire (Boyce *et al.*, 2003; Turner *et al.*, 1994). Herbivores may respond to landscape heterogeneity with changes in foraging patterns over varying spatial scales (Boyce *et al.*, 2003; Kashian *et al.*, 2005; Wallace *et al.*, 1995). For moose in winter, the distribution of these resources directly affects their energy balance; individuals must balance the costs of searching for food across a variable landscape with the benefit of obtaining energy from a landscape that is relatively low in nutrients. Wildfires are a common disturbance vector in the Alaskan boreal forest (Dyrness *et al.*, 1986; Kasischke *et al.*, 2006). They annually alter the landscape at large scales leaving legacies of post-fire vegetation regeneration (Chapin *et al.*, 2006). Moose occur in moderate to high densities throughout interior Alaska, and the matrix within which they are foraging changes with post-fire composition and distribution of early-successional regeneration. These fire-induced landscape changes may be predictable, and as such could provide important information for managing moose habitat and

populations. We examined the effects of forest fire on moose winter habitat within a burn outside of Fairbanks, Alaska in terms of variable fire severity and the resulting landscape heterogeneity. This was done at five spatial scales (60 m, 120 m, 480 m, 1 km, and 2 km) within the fire perimeter to address changes in foraging patterns that may be explained by the landscape at different scales.

Biotic and abiotic factors influence the spatial distribution of forest regeneration following wildfires (de Groot *et al.*, 2003; Hellberg *et al.*, 2003; Pastor *et al.*, 1999). Moreover, fire events can increase diversity and density of plant species within the first 50 years after burning (Kashian *et al.*, 2005). Increased diversity in the vegetative community across the landscape is due in part to differences in post-fire successional pathways within burn perimeters. Fire severity is an important factor driving post-fire secondary succession. It is influenced by multiple interacting forces, including the composition of the pre-fire vegetation community, weather patterns, fire behavior, and topographic variables (Epting & Verbyla, 2005; Johnson, 1992; Johnstone & Chapin, 2006; Schimmel & Granstrom, 1996; Viereck *et al.*, 1986). Post-fire vegetation establishment in the boreal forest generally follows one of two pathways: self-replacement or relay floristics (Dyrness *et al.*, 1986; Johnstone & Chapin, 2006; Landhaeusser & Wein, 1993). In self-replacement succession, the same species that made up the pre-fire community re-establish after the disturbance. In interior Alaskan plant communities, relay floristics succession occurs where the herbaceous understory dominates immediately after fire, followed by shrub and deciduous tree establishment and culminating in a late-seral spruce stand.

In spruce-dominated boreal forests (*Picea spp.*), deep soil organic horizons generally restrict germination of deciduous species. Many studies have shown self-replacement by spruce during post-fire succession where fire severity is low and a deep organic horizon exists (Greene *et al.*, 2004; Johnstone & Chapin, 2006; Johnstone & Kasischke, 2005; LeBarron, 1939). Relay floristics may take place when fire severity is high and the organic layer is combusted to the extent that the mineral layer of the soil is exposed so shrub and deciduous tree species can establish (Johnson, 1992). Hardwoods, such as aspen (*Populus tremuloides*) and birch (*Betula neoalaskana*), are able to disperse via wind over long distances; small hardwood stands in surrounding areas provide a sufficient seed source for relay floristics to occur given suitable soil conditions for establishment.

Since the 1950s in interior Alaska's boreal forest there has been an increase in the frequency of large fire years; in the last 5 decades 33% of individual fires have burned over 100,000 ha (Kasischke *et al.*, 2006). Increases in broadleaf stands following fires may translate into increased forage resources available to moose in interior Alaska. The spatial distribution of vegetation patches following fire may be an important factor in determining the quality of post-fire moose habitat in addition to absolute changes in vegetation.

The spatial structure of post-fire vegetation can vary in its degree of heterogeneity depending on the sizes of similar vegetation patches and their distribution in relation to one another and contrasting vegetation patches over the landscape (Fig. 1). Within-burn vegetation distribution may play an important role in hierarchical resource selection by

moose during the winter, when forage resources are second only to predation as a limiting factor in their survival (Van Ballenberghe & Ballard, 1998).

In 1983 a fire burned 35 km<sup>2</sup> outside of Fairbanks, Alaska. The Rosie Creek burn, as it was called, covered nearly two-thirds of the Bonanza Creek Long Term Ecological Research site within the Tanana Valley State Forest. The Rosie Creek burn is now over 20 years old and as such falls within the age-range of peak post-fire habitat for moose, given vegetation regeneration patterns in interior Alaska.

To explore the impacts of fire on landscape patterns and moose foraging, the main objectives of this study were threefold (1) Assess the changes in absolute vegetation coverage and corresponding metrics of landscape heterogeneity between 1978 and 2004 in the 1983 Rosie Creek Burn, (2) Estimate fire severity from vegetation change where possible and quantify and contrast forage biomass production and removal by moose within severity classes, and (3) Use multivariate regression to examine the effects of heterogeneous landscape structure on moose foraging. We hypothesized that (a) Overall heterogeneity of vegetation distribution over the Rosie Creek burn (RCB) would increase following wildfire, (b) Forage production and proportional removal by browsing would be higher in high severity sites than in low severity or unburned sites, and (c) Metrics of landscape heterogeneity would be able to explain a significant portion of the variation in proportional removal of browse across the RCB and would change at different spatial scales.

## **STUDY AREA**

The Rosie Creek burn occurred 25 km southwest of Fairbanks, AK (Fig. 2). The fire began in May 1983 and its perimeter encompassed approximately 35 km<sup>2</sup>. The fire burned over south facing slopes in three main valleys. Elevation ranged from 120 m to over 300 m. Pre-fire vegetation consisted of 63 – 180 year old stands of white spruce, black spruce, paper birch, and aspen (MacCracken & Viereck, 1990). Fire severity was variable; between 5 and 76% of the forest floor organic layer was lost across the burn (Juday & Dyrness, 1985). Current vegetation consists of large aspen and birch stands at higher elevations within the burned area and scattered black spruce early regeneration at lower elevations. Outside of the burn perimeter are mature (100 + years) spruce and mixed mature birch/spruce stands. The moose population in this area (Game Management Unit 20B) was estimated at 1.1 moose/mi<sup>2</sup> in 2003 (Young, 2004b).

## **METHODS**

### *Plot biomass measurements*

We used a browse assessment protocol to estimate the biomass of forage production and removal (Seaton 2002). This protocol is currently being implemented across interior Alaska for moose habitat assessments by the Alaska Department of Fish & Game (Tom Paragi, *pers. comm.*).

Using the sampling tool in Hawth's Tools (<http://www.spatial ecology.com/htools/>) in ESRI® ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, Calif., USA), we established a grid of 84 circular plots (30 m-diameter) with a random start point within the RCB perimeter (GIS shapefile;(BLM, 2005). Site GPS coordinates were used as the center of each plot and were located using

a Garmin eTrex handheld GPS unit (Garmin International, Inc. Olathe, KS, USA) (5 m – 9 m accuracy). In the field we used random number tables of paces and compass azimuth to locate three plants within the height range available to moose for browsing (0.5 m – 3.0 m) of each forage species (Seaton, 2002): alder (*Alnus viridis*), birch, balsam poplar (*Populus balsamifera*), aspen, and willows (*Salix spp.*). Willows were identified to species (*Salix scouleriana*, *S. bebbiana*, *S. alaxensis*, *S. pulchra* and *S. arbusculoides*; (Collet, 2004; Simpson, 1986). Although *Salix* were identified to species in the field, they were grouped into *Salix spp.* for the final analysis. For each plant species we recorded: height, estimated number of current annual growth (CAG) twigs, percent dead material by volume, and architecture class. Plant architecture classes were defined by the percentage of the current growth by volume of the plant arising from any lateral branching that was due to moose browsing and were as follows: unbrowsed (< 5%), browsed (5 - 50%), and broomed (> 50%). This classification provides a quick index for categorizing the browsing pressure on a plant throughout the course of its life (Seaton, 2002).

CAG diameter was measured on 10 twigs (> 1 cm long) per plant using dial calipers to the nearest 0.1 mm for a total of 30 twigs measured from each forage species within each plot. The diameter at point of browsing (DPB) was measured if the twig was browsed. More than three plants were sampled if more twigs were needed, until 30 twigs or all of the twigs available in the plot were measured. Browsing by snowshoe hares was present in the study site and the smooth-cut stems were differentiated from the rough-edged browse pattern of moose.

Stem densities were estimated within each plot using a 2 m wide and 30 m long belt transect from a random starting point on the plot perimeter through the plot center. Within the transect, stems of all forage species and non-forage tree species (*Picea spp.* and *Larix laricina*) above 0.5 m (typical snow depth by late winter) were counted. If a site was obviously divided in species composition then a representative, not random, transect was used for stem density. This sample density was then multiplied by the plot area (706.86 m<sup>2</sup>) to obtain an estimated stem count within each plot.

#### *Mass - Diameter Regressions*

Twigs were collected for mass - diameter regression equation development from all forage species. Twigs were weighed immediately upon returning to the lab or were kept frozen until weighed. Twigs were clipped and weighed at each whole diameter interval, from 2 to 10 mm. Samples of wet weight twigs from all diameter classes were then dried at 80°C for 24 to 48 hours. They were then reweighed to determine the percentage of dry weight by diameter class.

The data were log transformed and a regression equation was fitted to relate dry mass to diameter (MacCracken & van Ballenberghe, 1993; Seaton, 2002) by using a program developed specifically for this purpose in program R (R Foundation for Statistical Computing, <http://www.R-project.org>). Dry weight calculations were then back transformed, also in R, in order to obtain the original units of grams of dry mass. We used diameter and mass data from the Tanana Flats (in close proximity to the study area) from the Alaska Department of Fish & Game where more diameter classes were needed (Tom Paragi, *pers. comm.*).

### *Biomass Calculations*

Biomass was calculated using the estimated dry weights from the mass : diameter regression equations. The formula used for estimating biomass production and removal was:

$$\hat{B}_k = \sum_j \frac{M_{jk}}{m_{jk}} \sum_i \frac{N_{ijk}}{n_{ijk}} \sum_h \hat{z}_{hijk} \quad [1]$$

$\hat{B}_k$  is the plot estimate of removal or production biomass in grams. Twigs are denoted by  $h$ , plants by  $i$ , species by  $j$ , and the sites by  $k$ .  $M$  and  $m$  are the number of total and sampled plants in each plot, while  $N$  and  $n$  are the number of total and sampled twigs. Individual twig biomass is represented by  $\hat{z}$  (Seaton 2002).

The consumption to production ratio (C:P, also referred to as proportional removal) was calculated by dividing the estimated consumed by moose biomass by the biomass produced at each site. Standard deviations were calculated for production and removal values across the study area.

### *Remote Sensing*

Orthorectified aerial photographs of the Bonanza Creek Experimental Forest (including the entire RCB area) in 1978 and Landsat TM satellite imagery from 2004 for the same area were provided by Dave Verbyla (UAF, NRM). The study area was clipped from these images in ArcGIS. A burn scar raster layer (courtesy of D.Verbyla) from 1985 Landsat imagery was used to clip burned from unburned pixels. This layer was created to estimate of the Normalized Burn Ratio (NBR) using Landsat imagery from

1983 (pre-fire) and 1985 (post-fire). Although this layer was only of burned pixels, field validation revealed little to no correlation between the NBR values and soil organic matter depths (Verbyla & Lord, 2007); thus fire severity could not be estimated using remote sensing for this study. The four layers, burned and unburned pixels from 1978 and 2004, were then imported into the remote sensing program ERDAS IMAGINE® (Leica Geosystems LLC, 2007). Unsupervised classification, where the computer uses an algorithm to delineate unique classes based on spectral values, was performed to create two vegetation types in each of two fire classes (burned broadleaf, burned conifer, unburned broadleaf, and unburned conifer). The “burned” area in 1978 refers to the area that proceeded to burn five years later. Classification accuracy assessment using an error matrix could only be done on the 2004 image with field data from 2006; overall accuracy was 55%. Visual checks were done for accuracy assessment with the 1978 classification against the original aerial photographs. Pixel size for all final images was 25-m.

### *GIS Analysis*

Classified vegetation rasters from ERDAS IMAGINE were imported into ArcGIS for analysis. All data were projected in UTM Zone 6, NAD 83. The burned pixels were clipped out of the 1978 and 2004 vegetation rasters and were exported as ASCII text files for analysis of vegetation distribution change in FRAGSTATS (McGarigal *et al.*, 2002). Fire severity was inferred post-facto by assessing pixel changes in vegetation classification from 1978 to 2004. Conifer stands that changed to broadleaf were classified as high severity, whereas conifer stands remaining as conifer in 2004 were classified as low severity. Pixels that were classified as broadleaf stands in 1978 and

subsequently burned were attributed an unknown severity. Pixels that were within the burn perimeter but did not experience burning were classified as unburned.

Topographic variables were calculated from a 60 m digital elevation model (DEM) raster downloaded from the USGS National Elevation Dataset website (data available from U.S. Geological Survey, EROS Data Center, Sioux Falls, SD, <http://seamless.usgs.gov/>). The DEM was used in ArcGIS to calculate percent slope across the study area. At each spatial scale the mean elevation and mean slope were calculated, and at scales sampled larger than the original DEM (> 60 m) the standard deviations of elevation and slope were also calculated.

#### *FRAGSTATS Metrics*

To assess the impacts of landscape heterogeneity on moose browse utilization, landscape metrics were calculated from the 2004 vegetation raster at five scales (60 m, 120 m, 480 m, 1 km, and 2 km) as well as for the entire RCB area. At all scales, the landscape under study was centered on the sampled browse plots.

Metrics from the landscape ecology program FRAGSTATS describe the shape, isolation, contrast, interspersion, connectivity and diversity of patches across a landscape. A subset of 18 metrics from these categories was calculated to describe the vegetation patterns within the sampling blocks at each of the five spatial scales using the 2004 classified vegetation map of the Rosie Creek burn. Of these 18 landscape metrics, only ones that were either significantly correlated with proportional removal or used to describe landscape change were reported, resulting in 11 landscape metrics being reported in this analysis, 7 of which were correlated with proportional removal and 4

more were used in landscape change analysis. All topographic parameters and heterogeneity metrics are described in Table 1.

One landscape metric, TECI, quantifies both the amount of edge between different vegetation and burn types (broadleaf and conifer, burned and unburned) and the contrast between these categories. We assigned arbitrary weights to reflect the varying contrasts between the possible adjacencies where 0 indicated no contrast and 1 indicated the most contrast. Burned conifer and unburned broadleaf pixel adjacencies were assigned the highest contrast values (1) along with burned broadleaf and unburned conifer pixel adjacencies. The next highest contrast was between burned and unburned broadleaf and between burned and unburned conifer pixel adjacencies. Lower contrasts were assigned to unburned pixels of different vegetation types and burned pixels of different vegetation types. Zero contrast was assigned when the pixel classifications were the same for both burn class and vegetation type.

In order to derive non-overlapping samples of landscape parameters, sample sizes decreased at the two largest scales. Sample size was 84 for each of the blocks at 60 m, 120 m, and 480 m scales. As the individual study plots were just over 500 m apart from one another, at larger scales the sample blocks began to overlap. At the larger scales, the plot values of proportional removal were averaged to obtain a single estimate for a sample block. The 1 km scale consisted of 25 sample blocks, and 9 sample blocks composed the 2 km scale.

For the 1 km and 2 km spatial scales the sampling squares were clipped out of the classified vegetation raster and a full landscape analysis was performed on these blocks

in FRAGSTATS. Metrics were calculated for the 60 m, 120 m, and 480 m scales using the moving window option in FRAGSTATS at each of these scales. Moving window analysis computes values of each metric for each pixel from the surrounding pixels within a user-specified radius. The output text files were then converted into rasters in ArcGIS and the point data was extracted using Hawth's Tools.

### *Statistical Analysis*

One-way ANOVAs were used to test for differences in browse production, removal, and proportional removal among estimated fire severity classes. Spearman's correlation coefficients between landscape variables and proportional removal, as well as the correlation coefficients between the landscape variables themselves were calculated in the program SAS, version 8.0 (SAS Institute Inc. 2002). Program R was used to examine scatterplot matrices at all scales between variables to check for possible non-linear relationships.

As found in similar studies, many of the FRAGSTATS landscape metrics were highly correlated with one another (Hargis *et al.*, 1998). To minimize multicollinearity when modeling the influence of these variables on proportional removal, metrics were removed from highly correlated pairs with Spearman's correlation coefficients  $> 0.70$ . The 7 landscape metrics were reduced to four metrics in subsequent modeling: AI, COHES, FRAC, and TECI (Table 1).

Six *a priori* multiple regression models were run at the 60 m scale and 9 models at all other scales (120 m, 480 m, and 1 km) were run with proportional removal as the response variable (standard deviations of topographic variables could be calculated at the

60 m scale). These models were chosen to explore the potential of heterogeneity and topography in explaining variation in proportional removal of forage by moose. The global model included all of the heterogeneity parameters (FRAC, TECI, COHES, AI) as well as the topography parameters (Topo: ELEV, SLOPE, E\*S). In the models at scales greater than 60 m parameters of topographic variability were also included (TopoVar: ELEVSD, SLOPESD, ESD\*SSD). The Topo models included the topographic parameters, while the TopoVar models included the parameters of topographic variability. Four models dealt exclusively with heterogeneity and included Edge (TECI), Complexity (FRAC), Distribution (AI and COHES), and Het (TECI, FRAC, AI, and COHES). The HetTopo and HetTopoVar models combined the Het model with either the Topo model or the TopoVar model. Models were assessed using Akaike's information criterion, adjusted for small sample size,  $AIC_c$  (Burnham & Anderson, 2002). As no models had overwhelming support ( $w_i$ , or the strength of evidence for one model given the set of models analyzed,  $> 0.90$ ), model averaging was used for parameter estimates at each spatial scale to look at direction and magnitude of effects (Burnham & Anderson, 2002). Global models were checked for adherence to assumptions of normality and homogeneity of variance.

## **RESULTS**

### *Landscape change, 1978 to 2004*

Results from the vegetation classifications from 1978 aerial photography and 2004 Landsat satellite imagery show visually distinct patterns of vegetation change across the burned landscape (Fig. 3). Quantitative analysis of this distribution shows

considerable changes in vegetation composition and distribution between 1978 and 2004 in the RCB. Hectares of broadleaf stands increased by over 400%, whereas conifer stands decreased by 50% in 2004 compared with 1978 (Table 2). Landscape metrics generally indicated an increase in the patchiness and dispersion of vegetation patches across the RCB between 1978 and 2004. While patch density increased from 28 to 42 vegetation patches per hectare, the overall area of these patches decreased by an average of 1 hectare and the mean distance between similar patches (ENN) decreased to just under 30 m (Table 2). Contagion, an index of patch dispersion or ‘clumping’, decreased markedly between 1978 and 2004, indicating a more dispersed and heterogeneous composition of vegetation across the burn (Table 2).

Within the area that eventually burned in 1983, there were almost 2400 hectares of conifer stands in 1978. From these conifer stands, 1370 hectares were classified as broadleaf in 2004. Stands that changed from conifer to broadleaf between 1978 and 2004 were presumed to have undergone high enough severity burning to expose mineral soil beds suitable for broadleaf species germination. Of the burned pixels, just under 1000 ha remained as conifer stands in 2004, and were thus estimated to have experienced low severity burning (Fig. 4). No fire severity estimates based on successional pathways could be made for the stands that were broadleaf in 1978. However, these broadleaf stands represented only 12% of the vegetation across what would become the RCB.

#### *Overall browse results*

Within the perimeter of the RCB an estimated 267.3 (305.5) kg/ha of forage biomass was produced, and 79.0 (116.5) kg/ha of forage was removed by moose over the

course of the 2005-06 winter. Over 80% of the produced and removed forage biomass was composed of willow species or birch. Mean C:P ratio was 24% (0.14) and ranged from no removal in two sites to a maximum C:P ratio in one site of 54%. Proportional removal by species ranged from just over 10% of alder to nearly 35% of willow. Aspen and balsam poplar had mean C:P ratios between 20 and 25%, while on average just over 15% of the produced birch biomass was removed across all sites (Fig. 5). Nearly one-third of the 84 sites in this study had estimated C:P ratios that were equal to or greater than 33%.

Across the RCB, as well as within the estimated fire severity classes, there was a large amount of variation in both production and removal, however less in proportional removal (Table 3). Comparisons of the coefficients of variations for these estimates show that there was twice or three times as much variation in production (CV = 114%) and removal (CV = 147%) than in proportional removal (CV = 58%).

Field estimates of neither biomass production (kg/ha) nor removal (kg/ha) differed significantly between estimated severity classes, nor between burned and unburned areas. There was a tendency however, towards higher production in burned sites (all estimates of severity combined) than in unburned sites (Table 3). The C:P ratio was 31% (0.09) in the low severity sites, which was significantly higher than 21% (0.14) C:P in high severity sites (ANOVA,  $F_{3,78} = 4.26$ ,  $p = 0.01$ ). There were no significant differences in conifer or deciduous stem densities among severity classes.

*Landscape heterogeneity and browsing*

The mean values associated with the various landscape metrics and topographic variables tended to change with increasing spatial scales (Fig. 7). Most metrics indicated increasing heterogeneity with increasing scale, with a jump in values occurring between the 240 m and 1000 m scales. Contagion and AI decreased as the scale increased. Average fractal dimension (FRAC) indicated a slight increase in complexity with an increasing scale (data not shown).

Of the 18 landscape metrics calculated, 7 were significantly correlated with proportional removal at one or more spatial scales (Table 4). If a metric was significantly correlated with proportional removal at a smaller scale it was generally insignificant at larger scales and vice versa. At the two smallest scales, FRAC was positively correlated with proportional removal. Cohesion was positively correlated with proportional removal at the 1 km scale. All of the other significant landscape variables were negatively correlated with proportional removal, including slope at the three smallest scales, and had correlation coefficients ranging from -0.23 (CONTAG at 60 m) to -0.54 (III at 1 km) (Table 4). The largest number of significant relationships between landscape parameters and proportional removal were found at the 480 m and 1 km scales. There were no significant correlations at 2 km, possibly due to small sample size ( $n=9$ ). No further analysis was done at this scale.

At each scale Akaike weights indicating support for a given model were generally distributed between three top models, making the selection of a single best model inappropriate (Burnham & Anderson, 2002) (Table 5). Heterogeneity parameters had relatively stronger support than the topographic parameters at all scales except at 480 m

(Table 6). At 1 km, topographic parameters added nearly no additional support; models including heterogeneity parameters had a collective weight of 0.9. The top three models at 1 km were Edge, Complexity, and Distribution (Table 5). Model averaged parameter estimates at this scale suggest that proportional removal decreases with increasing edge and increasing fractal dimension, or complexity, of vegetation patches. However, parameter estimates across all scales were all quite small,  $< 0.01$ , except those for fractal dimension (-2.88 to 1.07) (Table 7). Parameter estimates for AI and COHES contrasted one another, with one being negative and the other positive at all scales (Table 7). These two metrics comprised the Distribution model, and were important parameters in the 120 m models ( $w_i = 0.3$ ) and 1 km ( $w_i = 0.1$ ). FRAC, mean fractal dimension, was included at all scales in the models with the most support, and its weight indicating its importance as a parameter across all models ranged from 0.2 to 0.4.

TECI was present and had negative parameter estimates in the top three models at all scales (Tables 5 and 7). At the 60 m scale the Topo model was as probable as the Edge model, and both had weights only slightly below the Complexity model (Table 5). Elevation and slope both had negative parameter estimates, though their interaction term was positive (Table 7). All models at this scale including topographic parameters had a collective weight of 0.25, compared to the 0.75 weight of all heterogeneity models (Table 6). Variation in topography had support at the 480 m scale (Table 5). In contrast to the other spatial scales, topographic parameters had a higher collective weight than heterogeneity parameters (Table 6).

## **DISCUSSION**

Using remote sensing and post-facto inferences of fire severity from vegetation change coupled with field estimates of moose browse biomass, this study found distinct changes in overall vegetation distribution and increases in landscape heterogeneity 22 years following a wildfire in interior Alaska. We found considerably more support for parameters of heterogeneity than topographic parameters in explaining variations in moose winter browsing pressure in terms of proportional removal of produced forage biomass.

Increasing fire severity can lead to increased broadleaf seedling germination (Cater & Chapin, 2000; Johnson, 1992; Johnstone & Chapin, 2006), and the production of more forage habitat for moose across a landscape. Two years immediately following the Rosie Creek fire total biomass of forage species ranged from 21 kg/ha to 1,668 kg/ha and was correlated with pre-fire stand type and age (MacCracken & Viereck, 1990). Between 1978 and 2004 there was a 400% increase in area of broadleaf stands within the RCB. These broadleaf stands largely arose from the 1983 fire, as only 12% of the landscape was classified as pre-fire broadleaf.

Proportional removal (C:P) can vary widely across a relatively small area; within the 35 km<sup>2</sup> of the RCB, we documented that from 0 to over 50% of produced vegetation was cumulatively removed over the course of the 2005-06 winter. C:P has been suggested as a possible metric of moose range quality across Game Management Units in Alaska (Boertje *et al.*, 2007); however, little work has been done to examine the effects of scale and study area extent on C:P estimates. Although this metric was variable across the study area, there was considerably less variation in the C:P ratio than absolute

production or removal estimates. On average, 24% of the produced forage biomass was removed across all sites. Mean C:P ratios across other large areas of interior Alaska range from 9% (on the range of a low-density population in Yukon Flats NWR) to >40% in the Tanana Flats/Foothills region, an area of generally high moose density (Boertje *et al.*, 2007; Young, 2004a). Though not statistically significant, unburned sites in the RCB tended to have considerably lower proportional removal than areas that had been burned. The average C:P ratio in unburned sites was 18%, compared with 28% in burned areas (Table 2). Unburned sites sampled in this study all fell within the overall perimeter of the RCB and were sampled by chance due to the random grid sampling. The lack of significant difference between these two averages may be a result of a small unburned sample size ( $n = 8$ ). Lower proportional removal in unburned sites may be an indication of less time being spent by moose in these mature stands within the burn perimeter, possibly resulting from a tendency toward less forage production in these areas. In a comparison between burned and unburned aspen stands in Colorado, elk (*Cervus canadensis*) were found to spend significantly less time traveling while in burned stands and have more bites per minute than in unburned stands (Canon *et al.*, 1987).

Production across the RCB averaged 267 (306) kg/ha, compared to two years immediately following the Rosie Creek fire when production estimates of available forage biomass ranged from 13 kg/ha to 178 kg/ha (MacCracken & Viereck, 1990). Production of browse biomass was similarly high, 243 kg/ha, in burns > 20 years old the Tanana Flats region of interior Alaska (Seaton, 2002) and in high severity burn sites from a 1994 burn near Delta Junction, Alaska, 226 kg/ha (Lord, M.S. Thesis).

In contrast to our initial hypothesis, low fire severity sites had significantly higher C:P ratios than did high severity sites. Within the first two years following the Rosie Creek fire, all forage species were present in both high and low severity sites, though in higher densities where mineral soil had been exposed (MacCracken & Viereck, 1990). Survival of these initial colonizing seedlings in low severity sites may have increased the quality of these stands over time, as posited by MacCracken and Viereck (1990). This finding of increased C:P in low severity stands is in direct contrast to a similar study done where the opposite was found in a 12 year old burn from 1994, southeast of Delta Junction, Alaska (Lord, M.S. Thesis). Although it is generally stated that burns that are 11 – 30 years old may provide more forage than older or younger stands (Maier *et al.*, 2005; Weixelman *et al.*, 1998), this and the Delta Junction studies demonstrate that within-burn vegetation patterns can change over this time span, nor is the amount of biomass or moose utilization constant over space within a fire perimeter.

Habitat use by animals has been described as hierarchical, with decisions of use being made based on different parameters at different scales (Johnson, 1980). For example, within a home range moose may make nested foraging decisions based on differences in individual plant morphology (Jia *et al.*, 1997; Kielland & Osborne, 1998; Stolter *et al.*, 2005), within-patch plant spacing (Danell *et al.*, 1991; Edenius *et al.*, 2002; Shipley *et al.*, 1998), and various levels of patch composition and distribution across a landscape (Cassing *et al.*, 2006; Dussault *et al.*, 2005; Gasaway *et al.*, 1988; Histol & Hjeljord, 1993; Jandt, 1992; Loranger *et al.*, 1991; Maier *et al.*, 2005; Månsson *et al.*, 2007; Weixelman *et al.*, 1998). In this study we used multiple spatial scales within a

burn perimeter for the purpose of exploring possible changes in foraging patterns given landscape parameters at a coarse patch-scale, 60 m, up to 1 km. The relationships between moose utilization patterns and landscape variation changed in the RCB at different spatial scales. Previous studies have demonstrated the importance of spatial arrangement of resources on herbivore movement patterns and foraging behavior (Boyce *et al.*, 2003; Johnson *et al.*, 2001; Kie *et al.*, 2002; Searle *et al.*, 2006; Turner *et al.*, 1994). Spatial distribution of resources may contribute to the sexual segregation of moose in Alaska during the winter (Bowyer *et al.*, 2001; Oehlers, 2007). The results from this study continue to substantiate the need to examine spatial structure of resource distribution when attempting to understand moose foraging patterns.

Differences in fire severity can lead to dramatic differences in post-fire successional pathways, resulting in a patchy mosaic of broadleaf and conifer stands across the burned area. Twenty-three years following the RCB, we found increasing edge area and decreasing patch size as well as substantial decrease in the contagion index, or clumping pattern, of contiguous vegetation patches. Most metrics of increasing heterogeneity across scales were negatively correlated with proportional removal in a bivariate analysis (Table 3). Two metrics, fractal dimension and cohesion, showed a positive relationship with relative removal at different scales (< 240 m and > 120 m, respectively). Though not statistically significant, contagion and the aggregation index (AI) were both positively related to relative removal at 1 km and 2 km. Other metrics such as total contrasting edge and patch richness density were negatively correlated with relative removal, as was fractal dimension at scales > 120 m and cohesion at scales > 120

m. Increased cohesion, aggregation, and grouping (contagion) of similar vegetation patches at larger scales may facilitate increased patch residence time for moose and lead to increased proportional removal of forage biomass (Edenius *et al.*, 2002; Johnson *et al.*, 2001; Wallace *et al.*, 1995). Increases in complexity (fractal dimension) at larger scales and metrics such as contrasting edge (TECI) would lead to a more dispersed and variable environment in terms of vegetation patches and may lead to increased movement and decreased foraging time, thus decreasing proportional removal.

Quantitative metrics of landscape heterogeneity were of higher relative importance than topographic parameters in explaining variations in proportional removal of browse biomass by moose across the RCB. Even so, models with substantial support incorporated different individual landscape metrics and changed with scale; this demonstrate that relevant ecological relationships may change with changing spatial scale. Moose may select habitats within their home ranges which provided abundant food resources but are also boarded by mature stands that provided cover from snow and minimize predation by wolves (Allen *et al.*, 1987; Dussault *et al.*, 2006). Snow depth was between 45 and 55 centimeters across the entire study area, not considered deep enough to be restricting moose movement (Gasaway & Coady, 1974). At the three smallest scales, distance to cover was not significantly related to proportional removal (data not shown).

Variable topography can affect a fire event, with increased severity a possibility when fire moves up slopes (as long as fire residence time does not decrease dramatically) and can add to the patchy landscape resulting from variable fire behavior. The study area

is comprised of three main valleys, two of which have relatively steep slopes (5 – 20%) and rise from flat elevations of 130 m to over 300 m. Topographic variables elevation and slope, as well as their respective standard deviations at scales greater than 60 m, were all negatively correlated with proportional removal at the first three spatial scales (except for mean elevation, which was not significant at any scale) (Table 3). Moose use of winter browse resources in British Columbia also decreased significantly with increasing slope and with increasing elevation (Serrouya and D'Eon 2002), though this was likely due to high snow depths at higher elevations. Increased proportional browse removal in flat areas may be a result of decreased energy expenditure needed to reach the shrubs in these areas. In several studies, elk have been seen to increase their utilization of open habitats and be more likely to forage in areas of low elevation (Boyce *et al.*, 2003; Wallace *et al.*, 1995). However in this area wolf predation may be limiting and influencing moose movements away from open areas (Van Ballenberghe & Ballard, 1998). Additionally, snow depths ranged from 0.45 to 0.5 m across the RCB and restricted movements due to high snow depths at higher elevations was not an issue.

Within the RCB perimeter, the 1983 fire increased the number of broadleaf stands and contributed to large changes in the spatial patterns of vegetation distribution between 1978 and 2004. Aspatial analysis of fire severity (Lord, M.S. Thesis) combined with spatial analysis on the effects of landscape patterns on moose browse utilization (this study) leads to the conclusion that not only fire severity but also the spatial patterns of post-fire succession may be critical in determining post-fire moose habitat potential. Global climate change predictions include increased fire frequency and increased fire

severity across the boreal forest. This widespread and changing disturbance regime needs to be recognized as a complex driver of moose habitat quality and quantity across the boreal forest. Managers should incorporate the increasing understanding of multi-scale moose habitat interactions with the fire regime in interior Alaska when assessing current and future habitat and moose population goals.

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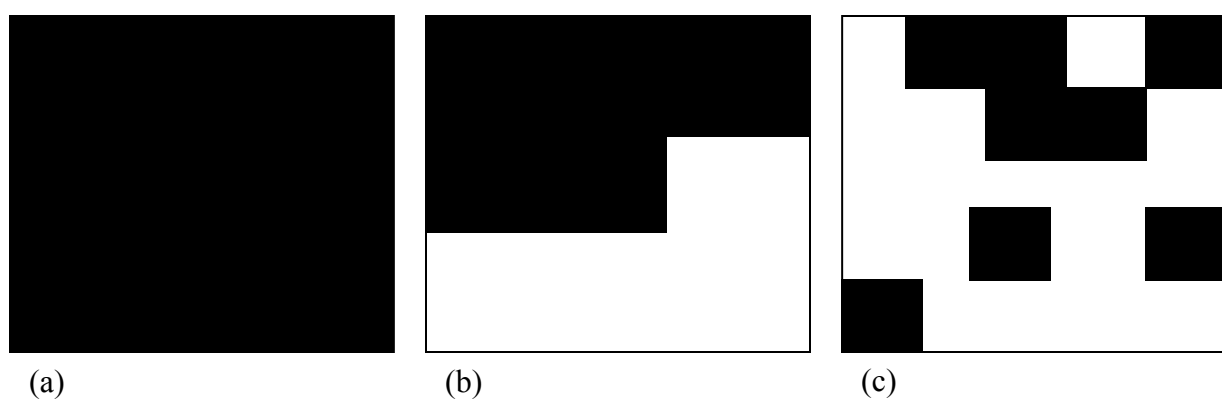


Figure 2.1. Examples of possible spatial arrangements of vegetation patches over a landscape. (a) contiguous and homogenous, (b) large uninterrupted patches of similar types, and (c) highly heterogeneous. Landscapes (b) and (c) have more edge than (a), and (b) has higher connectivity and aggregation than (c).

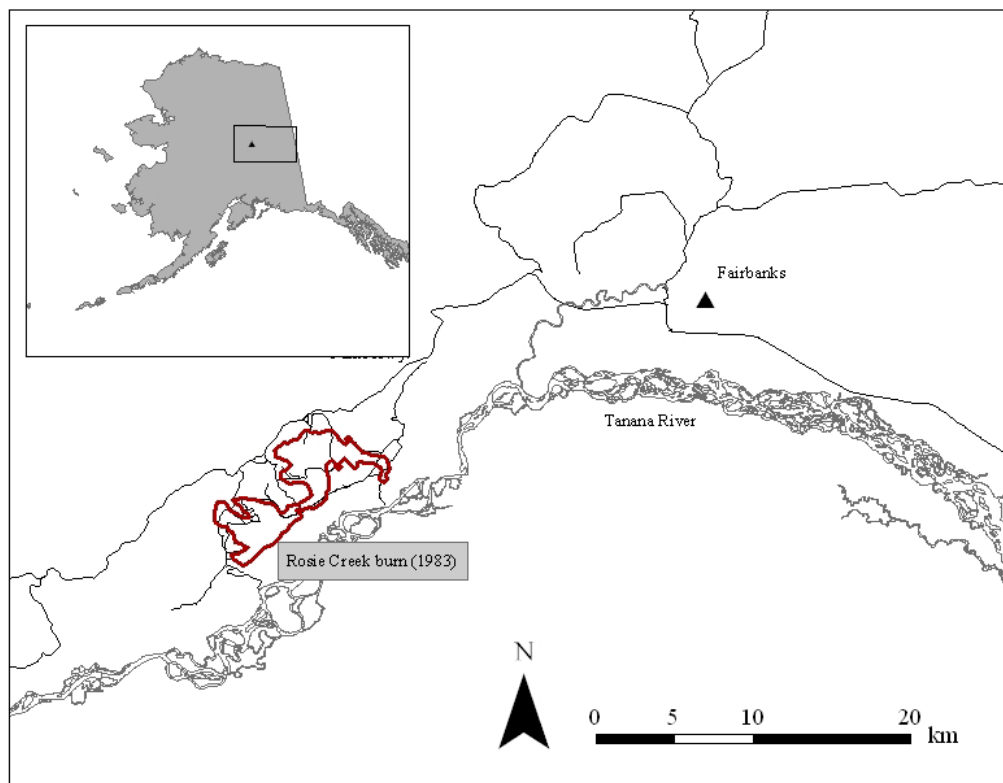


Figure 2.2. The Rosie Creek burn occurred in 1983, approximately 25 miles southeast of Fairbanks, AK.

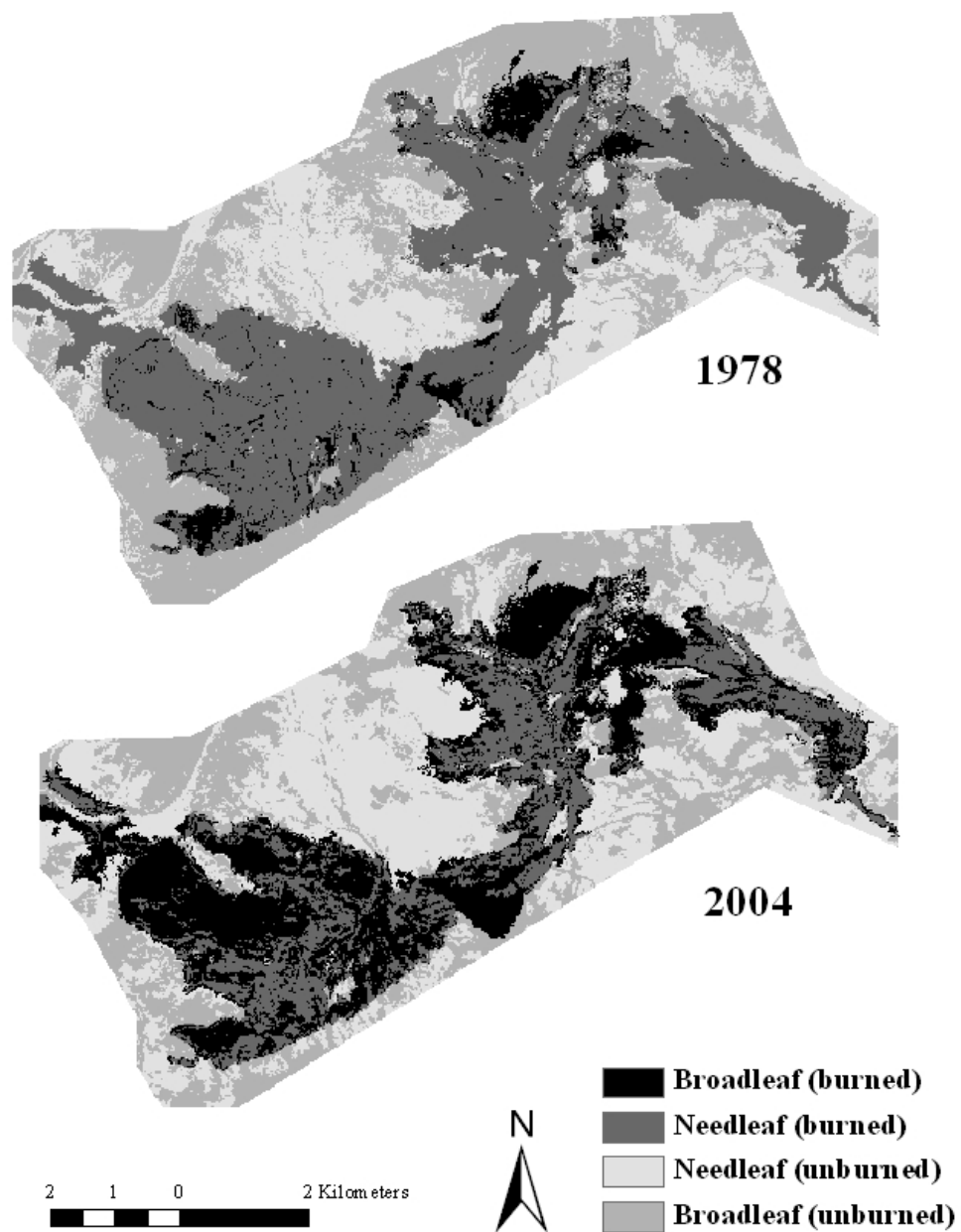


Figure 2.3. Vegetation distribution change in the Rosie Creek burn from 1978 to 2004, classified from aerial photography (1978) and Landsat TM imagery (2004).

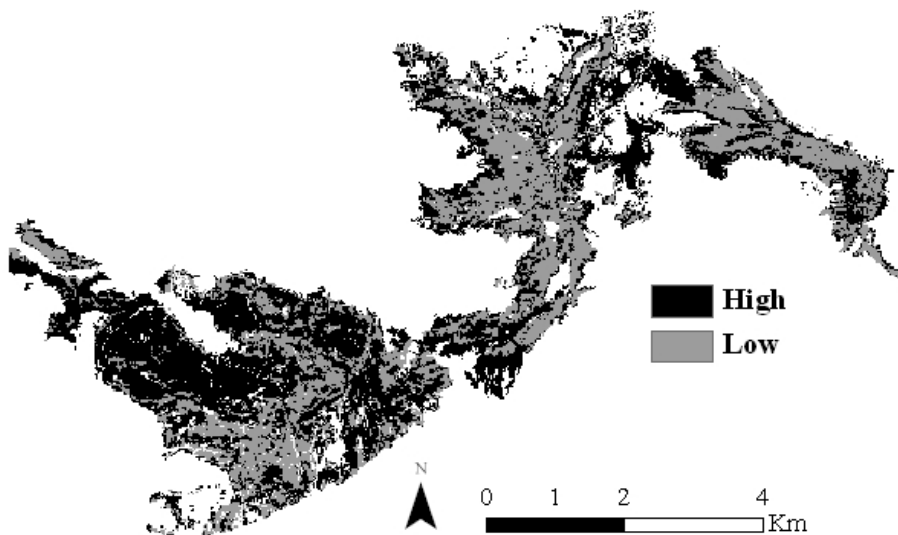


Figure 2.4. Estimates of fire severity within the Rosie Creek burn based on vegetation change from pre-fire conifer stands. Conifer stands in 1978 that are currently classified as broadleaf are considered high severity, whereas conifer stands from 1978 that are still classified as conifer stands are considered here to be low severity areas.

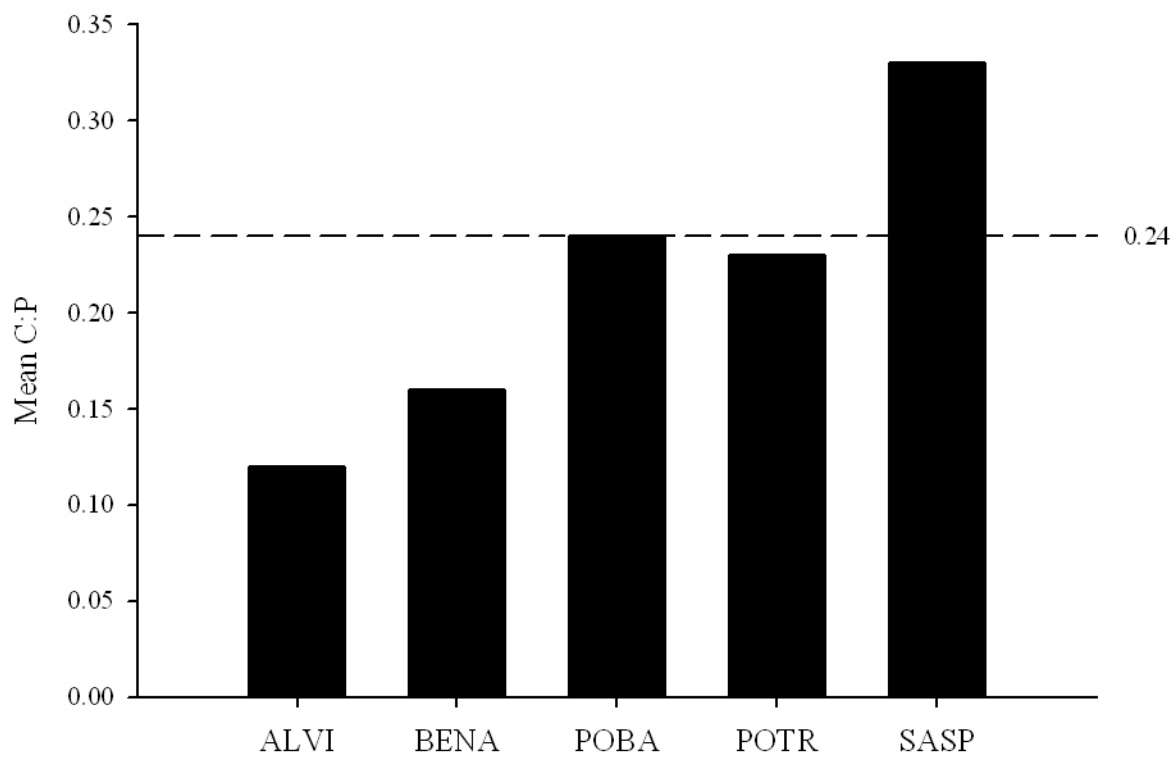


Figure 2.5. Mean C:P (consumption to production ratio) across the Rosie Creek burn of the five forage species (ALVI = green alder, BENA = paper birch, POBA = balsam poplar, POTR = trembling aspen, SASP = willow spp.). The dashed line represents the overall average, 0.24.

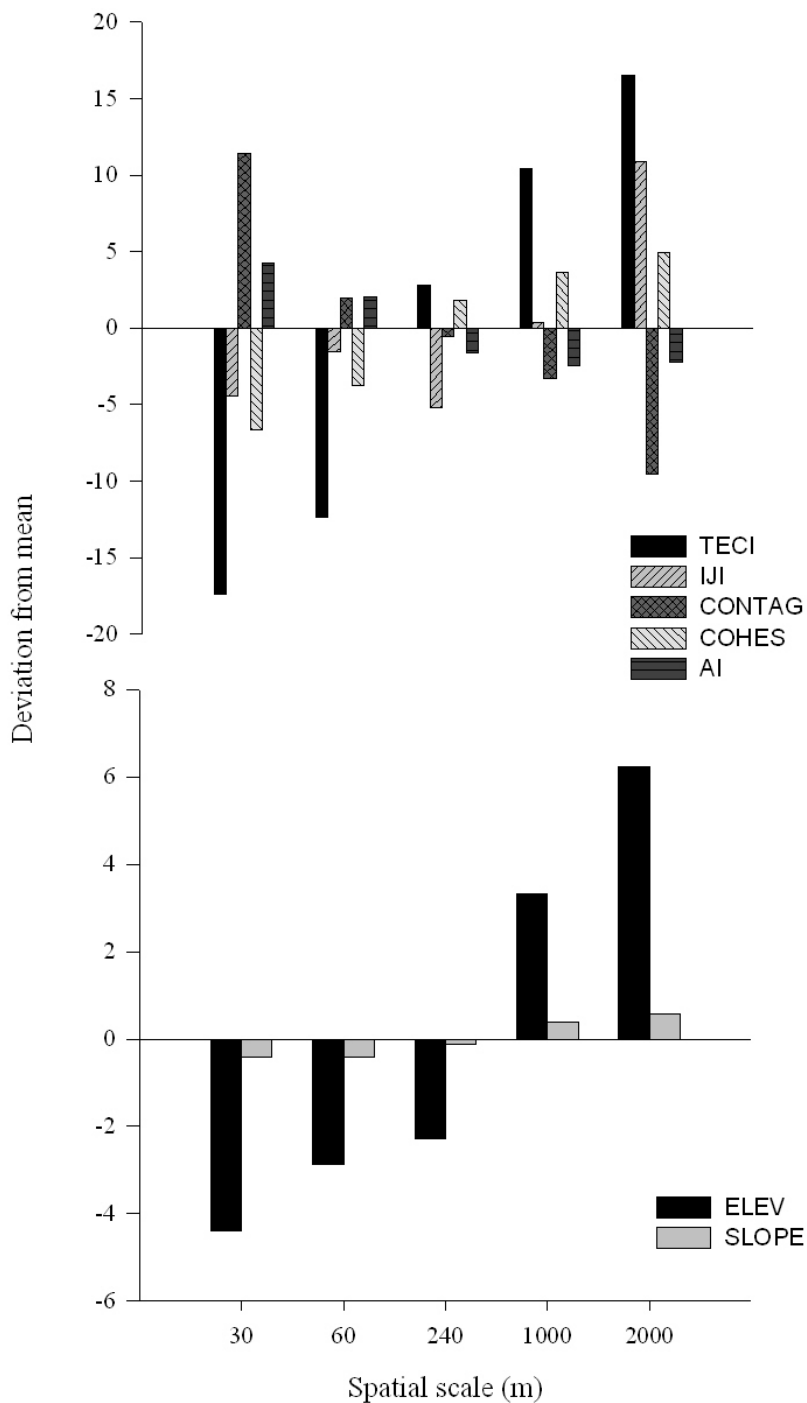


Figure 2.6. Changes in landscape metrics and topographic variables with increasing spatial scale across the study area in 2004. Landscape metrics and topographic variables are explained in Table 1.

Table 2.1. Parameters of heterogeneity and topography used in examining vegetation change and moose utilization response in the Rosie Creek burn.

<b>Parameter</b>	<b>Abbreviation</b>	<b>Definition</b>
<i>Topography</i>		
Elevation	ELEV	average elevation (m) derived from DEM
Slope	SLOPE	average percent slope from DEM
Elevation*Slope	E*S	interaction between slope and elevation
<i>Topographic Variability</i>		
Elevation standard deviation	ELEVSD	standard deviation of elevation values within the study area, beginning at 60 m
Slope standard deviation	SLOPESD	standard deviation of slope values within the study area, beginning at 60 m
ElevSD * SlopeSD	ESD*SSD	interaction between the standard deviations of slope and elevation
<i>Heterogeneity Metrics</i>		
Aggregation index	AI	percent of similar patches adjacent to one another
Cohesion	COHES	unitless measure of overall connectivity between similar patches
Fractal dimension	FRAC	unitless measure of shape complexity
Interspersion and juxtaposition index	IJI	percent of similar-patch adjacencies that nears 1 when all patches are equally adjacent to all other patches
Diversity index	SHDI	>0 and increases with increasing patch richness and/or evenness
Contagion	CONTAG	percent nears 1 when pixels of similar classification are maximally clumped
Nearest neighbor	ENN	average distance (m) to the nearest similar patch
Patch density	PD	number of patches per unit area
Patch richness density	PRD	number of vegetation types per unit area
Area	AREA	average area (m) of vegetation patches
Total edge contrast	TECI	percent that nears one when there is more edge between patches of increasing contrast

Table 2.2. Changes in landscape metrics between 1978 and 2004 within the Rosie Creek burn. (BL = hectares of broadleaf stands, NL = hectares of conifer stands, NP = # patches, PD = patch density, TECI = total edge contrast index, AREA = mean patch area, ENN = mean nearest neighbor distance, CONT = Contagion, SHDI = Shannon's diversity index). Difference values in bold highlight the parameters that decreased in value between 1978 and 2004.

Year	Landscape Value								
	BL	NL	NP	PD	TECI	AREA	ENN	CONT	SHDI
1978	312	2378	755	28.1	17.08	3.6	73.7	57.7	0.21
2004	1636	1046	1136	42.3	26.67	2.4	27.7	16.0	0.48
<i>Change</i>	<i>1325</i>	<b><i>-1332</i></b>	<i>381</i>	<i>14.4</i>	<i>9.58</i>	<b><i>-1.2</i></b>	<b><i>-55.4</i></b>	<b><i>-41.7</i></b>	<i>0.27</i>

Table 2.3. Mean values for browse biomass produced (kg/ha), removed (kg/ha), and the consumption : production (C:P) ratio. Values are reported by estimated severity class (Unk = Unknown severity class, Unb = unburned) as well as the overall average for each parameter. One standard deviation is reported in the parentheses. Within each column significant differences are denoted by different letters.

Fire Severity	Mean Production (kg/ha)	Mean Removal (kg/ha)	C:P
<b>High</b> (n = 43)	292.9 (307.3)	76.4 (99.5)	0.26 ac
<b>Low</b> (n = 24)	258.6 (326.2)	88.2 (132.6)	0.34 b
<b>Unk</b> (n = 7)	289.1 (385.0)	121.3 (196.2)	0.42 abc
<b>Unb</b> (n = 8)	137.2 (110.7)	28.2 (41.0)	0.21 ac
<b>Total</b>	267.3 (305.5)	79.0 (116.5)	0.30

Table 2.4. Spearman correlation coefficients at different scales for either landscape metrics or topographic parameters and the associated C:P ratio. Only metrics that had significant correlations with the C:P ratio within at least one scale are reported here. Abbreviations stand for: TECI = total edge contrast index, PRD = patch richness density, IJI = interspersions and juxtaposition index, FRAC = mean fractal dimension, CONTAG = contagion index, COHES = patch cohesion index, AI = aggregation index, ELEVSD = standard deviation of elevation, SLOPE = percent slope, SLOPESD = standard deviation of percent slope. Full descriptions of metrics can be found in the text. Asterisks denote significance level, \* =  $p < 0.05$ , \*\* =  $p < 0.001$ .

<b>Parameter</b>	<b>Spearman's Correlation Coefficient</b>				
	<i>60 m</i>	<i>120 m</i>	<i>480 m</i>	<i>1 km</i>	<i>2 km</i>
TECI	0.10	-0.02	-0.25 *	-0.43 *	-0.57
PRD	0.14	-0.10	-0.26 *	-0.11	0.08
IJI	0.29	-0.38	-0.13	-0.54 **	-0.58
FRAC	0.22 *	0.22 *	0.06	-0.24	-0.43
CONTAG	-0.23 *	-0.18	-0.17	0.36	0.17
COHES	-0.14	0.03	0.08	0.49 **	0.27
AI	-0.07	-0.22 *	-0.13	0.25	0.20
ELEVSD	-	-0.21 *	-0.29 **	-0.27	-0.55
SLOPE	-0.25 *	-0.26 **	-0.29 **	-0.31	-0.63
SLOPESD	-	-0.24 *	-0.43 **	-0.37	-0.55

Table 2.5. Model results for four spatial scales examining landscape parameters effects on proportional removal by moose. Models are described in the text and include topographic variables elevation, slope (Topo), their standard deviations (TopoVar) and interactions, and heterogeneity metrics (Het) AI and COHES (Distribution), FRAC (Complexity), and TECI (Edge).  $K$  = # of parameters,  $AIC_c$  values are shown as well as the difference between the  $AIC_c$  and the  $AIC_{cmin}$  values,  $\Delta_i$ .  $w_i$  is the model weight within the set of models in a given spatial scale. Rank is based on the weight, and is only reported for those models where  $\Delta_i < 10$ .

<b>Model</b>	<b>K</b>	<b><math>AIC_c</math></b>	<b><math>\Delta_i</math></b>	<b><math>w_i</math></b>	<b>rank</b>
<i>60 m</i>					
Global	9	-132.922	7.559	0.008	6
Topo	5	-139.776	0.705	0.240	3
Edge	3	-140.148	0.333	0.289	2
Complexity	3	-140.481	0	0.342	1
Distribution	4	-137.047	3.433	0.061	4
Het	6	-136.952	3.528	0.059	5
<i>120 m</i>					
Global	12	-122.894	18.531	0.000	-
Topo	5	-137.443	3.982	0.056	4
TopoVar	5	-137.406	4.019	0.055	5
Edge	3	-139.378	2.047	0.148	3
Complexity	3	-141.426	0	0.413	1
Distribution	4	-140.792	0.633	0.301	2
Het	6	-135.482	5.94	0.021	6
HetTopo	9	-130.243	11.183	0.002	-
HetTopoVar	9	-131.423	10.003	0.003	-
<i>480 m</i>					
Global	12	-130.444	13.260	0.000	-
Topo	5	-137.501	6.203	0.027	6
TopoVar	5	-143.704	0	0.592	1
Edge	3	-140.833	2.871	0.141	3
Complexity	3	-140.874	2.831	0.144	2
Distribution	4	-137.059	6.646	0.021	7
Het	6	-138.083	5.622	0.036	5
HetTopo	9	-131.816	11.888	0.002	-
HetTopoVar	9	-138.215	5.489	0.038	4
<i>1 km</i>					
Global	12	-2.843	41.993	0.000	-
Topo	5	-37.072	7.764	0.010	5

TopoVar	5	-38.096	6.739	0.017	4
Edge	3	-44.836	0	0.506	1
Complex	3	-43.964	0.871	0.328	2
Distribution	4	-42.129	2.707	0.131	3
Het	6	-36.413	8.422	0.008	6
HetTopo	9	-22.037	22.799	0.000	-
HetTopoVar	9	-23.891	20.944	0.000	-

Table 2.6. Relative importance of heterogeneity (AI, COHES, FRAC, and TECI) and topographic (ELEV, SLOPE, E\*S, ELEVSD, SLOPESD, ESD\*SSD) parameters at each spatial scale to proportional browse removal by moose, derived from summing Akaike weights ( $w_i(j)$ ) across models including these parameters. Full descriptions of parameters are found in Table 1.

Parameter Group	$w_+(j)$			
	60 m	120 m	480 m	1 km
Heterogeneity	0.75	0.88	0.38	0.97
Topography	0.25	0.12	0.66	0.03

Table 2.7. Model averaged parameter estimates,  $\hat{\beta}_j$ , for predicting the proportional browse removal by moose at each spatial scale. AI and COHES are heterogeneity metrics from the Distribution model. FRAC is the metric used in the Complexity model and TECI is the metric for the Edge model. ELEV, SLOPE, and their interaction term are from the Topo model. The standard deviations of these parameters and the corresponding interaction term are from the TopoVar model. Parameters are fully described in Table 1. Values in bold are the parameters that are in the top three models at each scale.

Parameter	$\hat{\beta}_j$			
	60 m	120 m	480 m	1 km
AI	0.0019	<b>-0.0046</b>	-0.0081	<b>-0.0035</b>
COHES	-0.0028	<b>0.0055</b>	0.0032	<b>0.0352</b>
FRAC	<b>1.0680</b>	<b>0.8499</b>	<b>-0.1050</b>	<b>-2.8848</b>
TECI	<b>-0.0002</b>	<b>-0.0006</b>	<b>-0.0041</b>	<b>-0.0058</b>
ELEV	<b>-0.0011</b>	-0.0009	0.0002	0.0002
ELEVSD	-	-0.0146	<b>0.0072</b>	0.0051
SLOPE	<b>-0.0559</b>	-0.0473	-0.0009	-0.0162
SLOPESD	-	-0.0755	<b>-0.0104</b>	-0.0206
ELEV*SLOPE	0.0002	0.0002	0.0001	0.0000

ELEVSD*SLOPESD	-	0.0060	<b>-0.0046</b>	-0.0012
Intercept	-0.1348	-0.1614	0.0514	0.9701

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## CONCLUSION

In this study I examined the effects of variable post-fire regeneration and spatial distribution of vegetation on moose utilization of forage resources during winter. A single wildfire in the boreal forest changes not only the composition but also the distribution of vegetation stands within its perimeter. I focused on fire severity, the amount of soil organic matter combusted during a fire event, in determining the regeneration trajectory of post-fire vegetation. Areas that experienced high severity burning were correlated with increased broadleaf regeneration and high broadleaf stem densities in two fires in interior Alaska. Moose foraging patterns were correlated with vegetation types within these burns and were also influenced by the distribution of vegetation patches (25 m resolution) at multiple spatial scales (60 m, 120 m, 480 m, and 1 km).

In Chapter 1, I found that high fire severity sites were used disproportionately more than low severity sites by moose during winter foraging. Increased fire severity led to significantly more broadleaf (specifically aspen) regeneration and proportional removal of forage biomass by moose was 36% higher in high versus low severity areas. Sampling within the fire perimeter and assuming a homogenous distribution of post-fire

regeneration (without accounting for variable fire severity) in the Delta Junction fire would lead to a 33% overestimation of forage production, as over 60% of the area burned was classified as low severity.

I focused on the spatial changes in moose habitat as a result of fire and variable fire severity in Chapter 2. I found that broadleaf stands increased by 400% following the Rosie Creek fire (1983) outside of Fairbanks, AK. These stands were variably distributed within the fire perimeter, and the spatial variability of vegetation stands also increased following the fire as well. Proportional biomass removal by moose ranged from 0 to over 50%. Quantitative metrics of heterogeneity were relatively more important than topography in explaining the variability in proportional removal.

Comprehensive habitat management in the boreal forest should include mapping of wildfires using remote sensing to assess the amount and degree of spatial variability of fire severity classes. In Chapter 2, fire severity estimates for the Rosie Creek burn (1983) were derived from vegetation change detected between 1978 aerial photography and 2004 Landsat TM satellite imagery. Due to the age of the fire (23 years old), commonly used remote sensing techniques to assess fire severity were not possible. For burns that occurred later than this date, pre- and post-fire Landsat TM data is readily accessible. This type of post-fire analysis could be of great utility in projecting possible moose habitat distribution within management areas. Fires that occurred from the mid-1980s through the mid-1990s are currently in the stage of regeneration generally accepted to be preferred moose habitat. In another ten years the large fires from the early 2000s will also be in this range. Assessing now the distribution of fire severity in these burn

perimeters will reveal important information regarding the future habitat matrix for moose in interior Alaska. In areas where predation is low and habitat availability is a limiting factor in population growth this could be of utmost importance in determining future management actions.

There are numerous studies on the responses of moose to natural disturbances such as fire, as well as on the impacts of artificial habitat enhancement on moose populations. Habitat manipulation is done in interior Alaska to help improve moose habitat, especially near human development centers where wildfires have been suppressed (Paragi & Haggstrom, 2005). Some studies have looked at the effects on habitat of various manipulations, including mechanical brush cutting and prescribed fire (Bowyer *et al.*, 2001; Collins & Schwartz, 1998; Stephenson *et al.*, 1998). Individual wildfires in Alaska's boreal forest can burn over 100,000 hectares annually and as part of the natural fire regime create potentially similar end results as artificial habitat manipulation. As seen in this and many other studies, fire directly impacts vegetation composition and spatial distribution over the landscape, and as such exerts an enormous impact on moose habitat in interior Alaska.

Within a 13 year old burn, described in Chapter 1 (DJ94), moose removed significantly more forage biomass from high severity sites than low severity sites. However this pattern was opposite in an older burn, the Rosie Creek burn in Chapter 2. This burn occurred in 1983 and moose removed proportionally more biomass from low severity sites within its perimeter. These results were unexpected; in both cases I hypothesized that with increasing fire severity moose forage utilization would also

increase. It is possible that as a burn ages, high severity sites where forage stem densities were high may become less desirable to moose when foraging due to increased height and browsing pressure over time. On the other hand, low severity sites often still have forage species present; over time these plants may develop such that low severity sites are composed of increased forage stems at readily available height ranges (0.5 m – 3.0 m). The post-fire vegetation in low severity sites in Delta Junction had a significantly lower mean Shannon's diversity index (incorporating forage species richness and evenness) than low severity sites in the Rosie Creek burn (1.0 vs. 1.7, ANOVA  $F_{1,26} = 4.26$ ,  $p = .049$ ). This may be due in part to the later successional stage of the Rosie Creek burn, which is 11 years older than the Delta Junction burn. This suggests temporal variation in moose utilization of post-fire habitat even within the 11 – 30 year old age range of peak post-fire regeneration of forage vegetation.

While both chapters addressed fire severity, in the Rosie Creek burn I assessed the impacts of post-fire heterogeneity on moose foraging patterns. However, considerable differences in vegetation and moose utilization were seen in sites representing variable fire severity the Delta Junction burn. A further step, and one that may be of great utility to managers of moose populations, is addressing not only the aspatial affects of fire severity (i.e. solely accounting for the proportion of high and low severity areas within a burn perimeter), but to incorporate their spatial distribution as I did in the Rosie Creek burn. Numerous previous studies have examined the scales at which herbivores use their forage resources both spatially and aspatially (Bowyer *et al.*, 1996; Cassing *et al.*, 2006; Edenius, 1993; Månsson *et al.*, 2007; Senft *et al.*, 1987; Vivas & Saether, 1987).

Wildfires are a complex driver of changing wildlife habitat. Managers should incorporate knowledge of large-scale population patterns over a dynamic landscape with that of foraging decisions made at multiple scales. This requires balancing the need for data and decision making over large areas with efficiency needs that come with budget and time constraints.

Setting population objectives in Game Management Units (GMUs) across the state should be done within the context of a complex and changing habitat matrix, driven in part by the fire regime. Throughout the GMUs of northern and interior Alaska, wildfire is commonly referred to as a primary means of improving moose habitat (ADF&G, 2004). During the 1960s through the 1980s, widespread suppression of wildfires occurred in and around populated areas of the state. Public attitudes have shifted in recent decades to include increased recognition of the prevalence and importance of fire (Clark & Hardy, 1997). However, there is a need for increased understanding concerning the importance of the natural fire regime in maintaining wildlife habitat (Dombeck *et al.*, 2004). Public outreach should be combined with fire and wildlife research for making responsible fire and game management decisions, especially within the urban-wildfire interface (Cortner *et al.*, 2006).

Areas of high fire severity can comprise anywhere from less than 10% to over 60% of a single burn. In this study I found that increased fire severity lead to both increased production and variable fire severity significantly affected proportional removal of forage biomass by moose. Additionally, the spatial distribution of post-fire vegetation was of relative importance in explaining variation in proportional forage

removal. Ignoring these combined effects of fire leads to the possibility of grossly under or overestimating moose habitat in the boreal forest, where wildfires are a constant driver of a changing landscape and can cover significant portions of Game Management Units in interior Alaska. As demonstrated in this and other studies, remote sensing techniques allow for large-scale assessments of ecological processes, including fire severity patterns within burns. This relatively easy analysis can provide biologists and managers with an opportunity to combine field-based knowledge of post-fire moose response to variable fire severity with landscape-level analysis of the current and possible future habitat matrix for moose in interior Alaska.

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**APPENDIX A. FIRE SEVERITY EFFECTS AND ADDITIONAL BROWSE DATA FOR THE ROSIE CREEK BURN AND THE DELTA JUNCTION BURN**

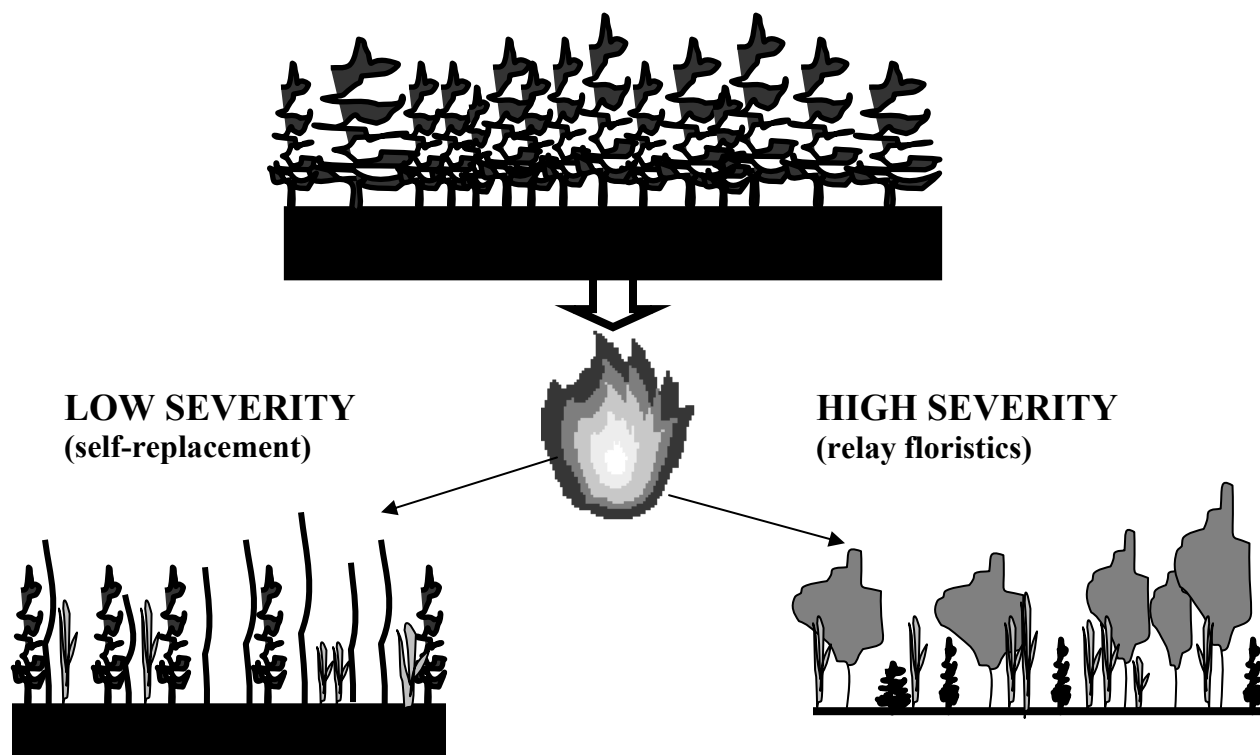


Figure A1. Pathways of post-fire succession forced in part through variations in fire severity leading to different soil organic matter depths.

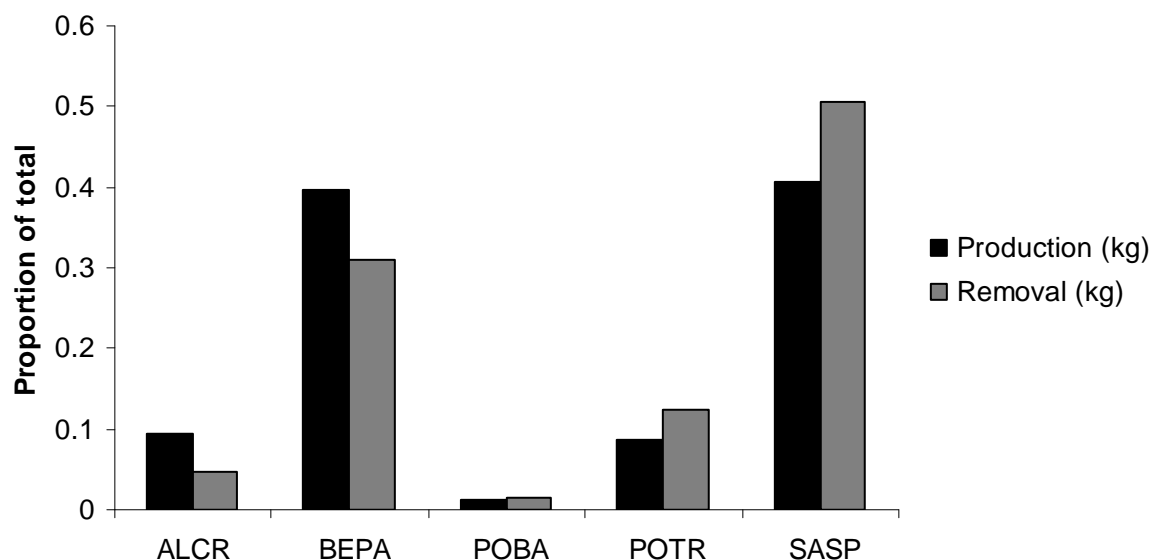


Figure A2. Rosie Creek Burn. Species composition of the produced and removed biomass of the five forage species in the study area (ALCR = green alder, BEPA = paper birch, POBA = balsam poplar, POTR = trembling aspen, SASP = willow spp.).

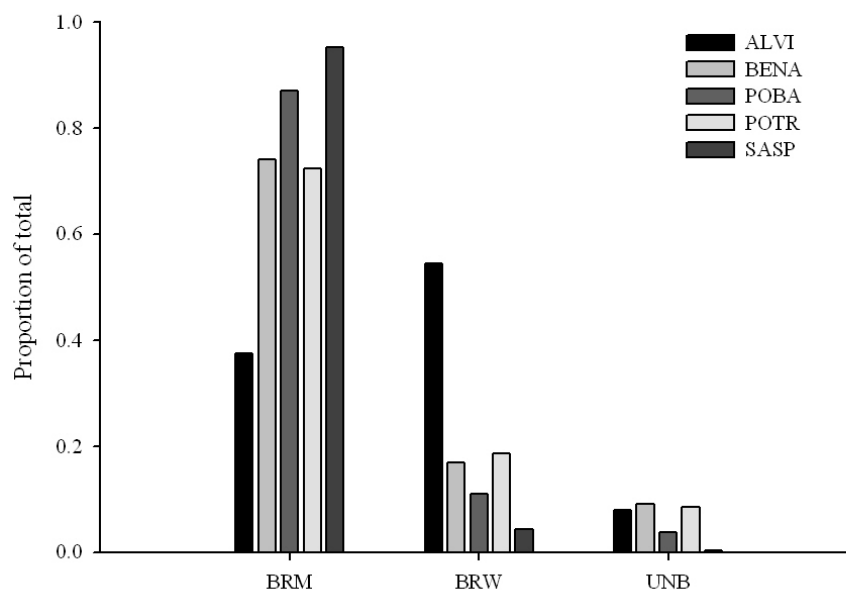
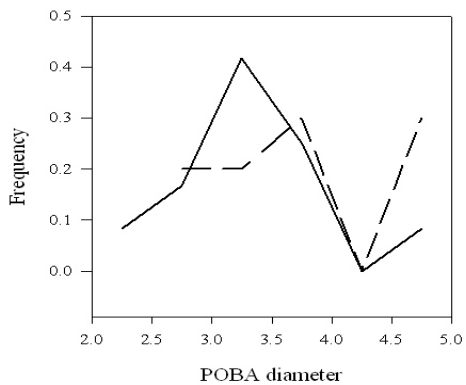
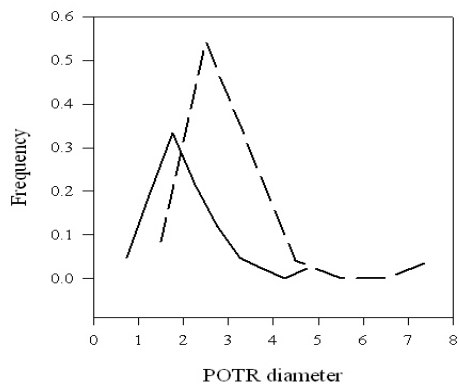
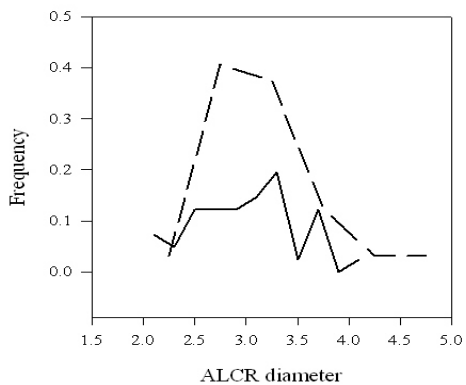
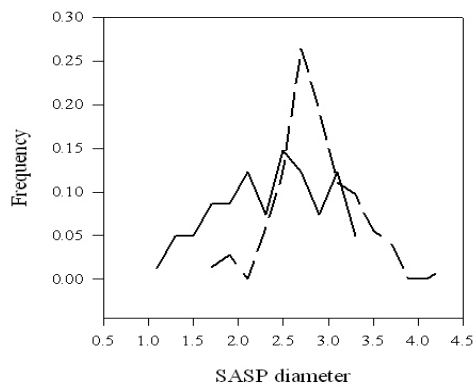
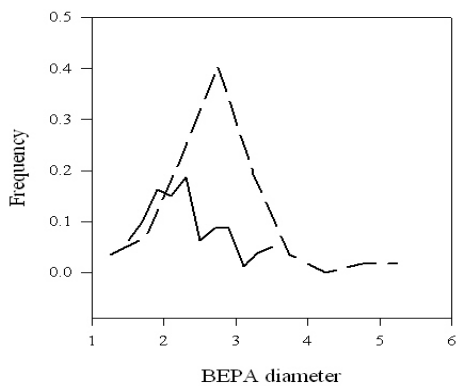


Figure A3. Rosie Creek Burn. Plant architecture distribution. BRM = broomed (>50% lateral branching due to browsing by moose), BRW = browsed (5 – 49 % lateral branching), UNB = unbrowsed (< 5% lateral branching). ALVI = green alder, BENA = birch, POBA = poplar, POTR = aspen, SASP = willow spp.



— CAG  
 - - DPB

Figure A4. Rosie Creek Burn. Frequency distributions of mean CAG and DPB. ALVI = green alder, BENA = birch, POBA = poplar, POTR = aspen, SASP = willow spp.

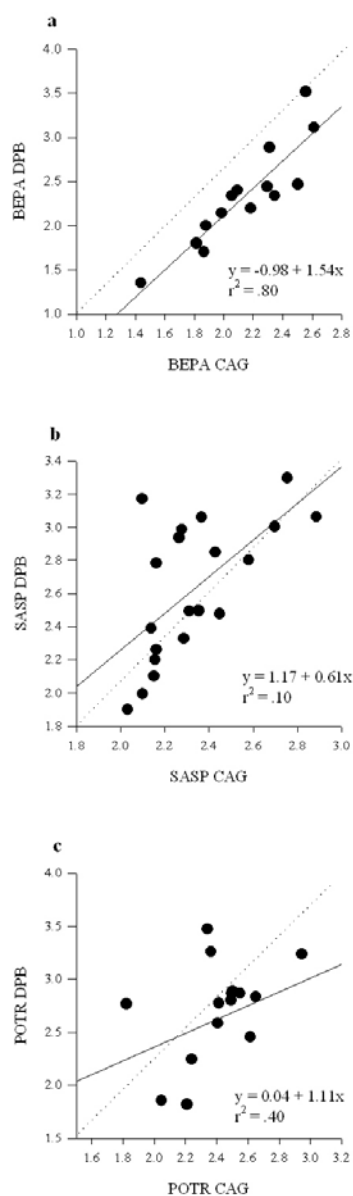


Figure A5. Delta Junction. Mean point of browsing diameter (DPB) relationship to current growth diameters (CAG) for each forage species: birch, willow spp., and aspen. Each point represents the average diameters at each plot ( $n \leq 21$ ). Dotted lines are a straight line equation, where  $X = Y$  and are given for comparison to what proportional

removal would look like. Solid lines are the regression equations through the data. Coefficients and  $r^2$  values are shown for each relationship. Axis are diameters in millimeters. ANCOVA results indicate that only in birch do we see slopes significantly different from a 1:1 relationship ( $F_{3, 24} = 49.15$ ,  $p = 0.02$ ). Both willow spp. and aspen have significantly different intercepts from that expected with a 1:1 relationship between CAG and DPB.

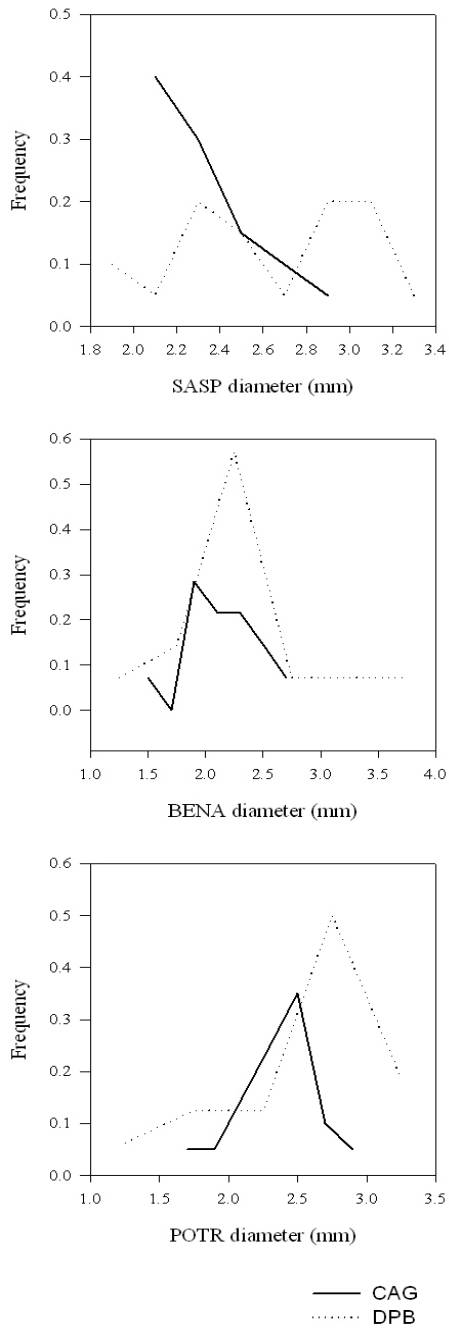


Figure A6. Delta Junction. Species CAG (current annual growth) and DPB (diameter at point of browsing) diameter frequency distributions. SASP = willow spp., BENA = birch, POTR = aspen.

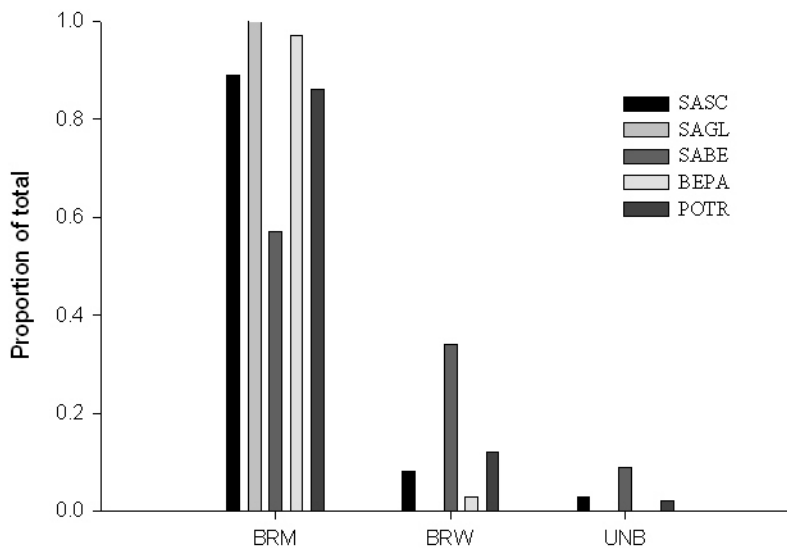


Figure A7. Delta Junction. Proportion of plant architecture classes represented by species. BRM = broomed (>50% lateral branching due to browsing by moose), BRW = browsed (5 – 49 % lateral branching), UNB = unbrowsed (< 5% lateral branching). SASC = Scouler willow, SAGL = *Salix glauca*, SABE = Bebb’s willow, BEPA = birch, POTR = aspen.

**APPENDIX B. DRY MASS – DIAMETER REGRESSIONS CALCULATED FOR  
BIOMASS ESTIMATION IN THE ROSIE CREEK BURN AND DELTA  
JUNCTION BURN**

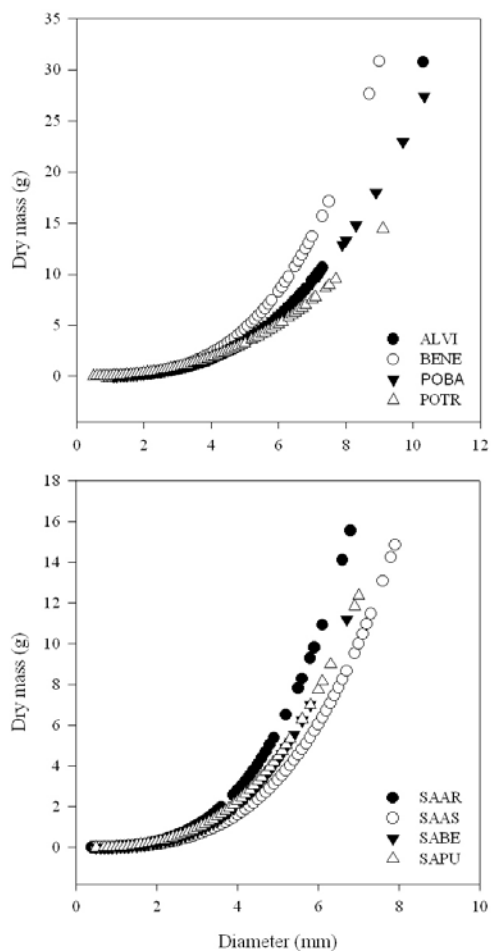


Figure B1. Rosie Creek burn. Dry mass : diameter regressions. ALVI = green alder, BENA = birch, POBA = poplar, POTR = aspen, SAAR = *Salix arbusculoides*, SAAS = *S. alaxensis* and *S. scouleriana*, SABLE = *S. bebbiana*, SAPU = *S. pulchra*.

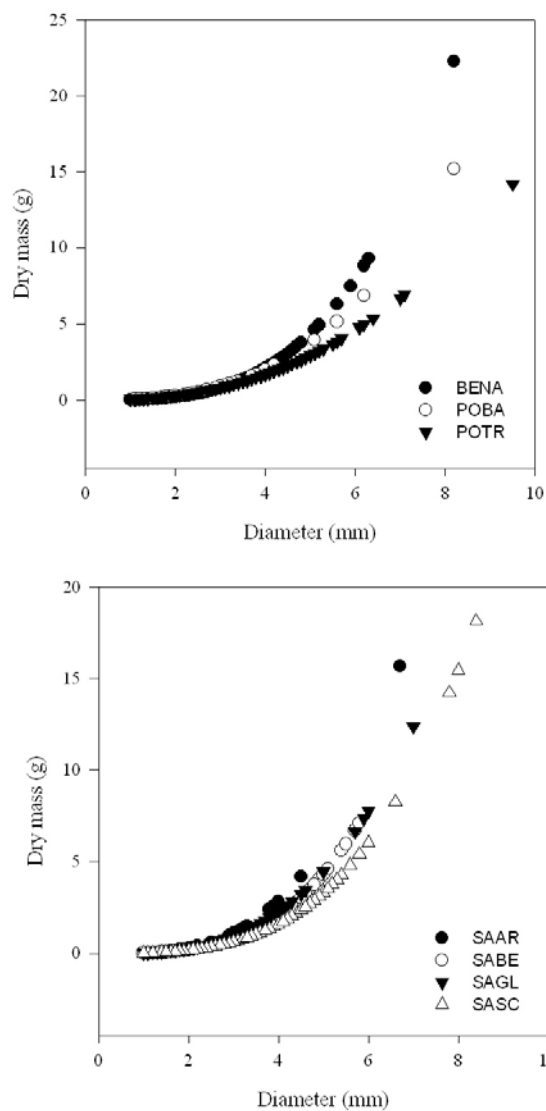


Figure B2. Delta Junction. Dry mass : diameter regressions. BENA = birch, POBA = poplar, POTR = aspen, SAAR = *Salix arbusculoides*, SABE = *Salix bebbiana*, SAGL = *Salix glauca*, SASC = *Salix scouleriana*.