ASPEN COPPICE WITH COARSE WOODY DEBRIS:
A SILVICULTURAL SYSTEM FOR INTERIOR ALASKA MOOSE
BROWSE PRODUCTION

By

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ASPEN COPPICE WITH COARSE WOODY DEBRIS: A SILVICULTURAL SYSTEM FOR INTERIOR ALASKA MOOSE BROWSE PRODUCTION

A

THESIS

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By

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ABSTRACT

Browse production and use by moose (*Alces alces gigas*) in interior Alaska was investigated in 4 and 2-year-old quaking aspen (*Populus tremuloides*) coppice stands following clear-felling without removal of the mature aspen stems. Moose winter browse utilization, as related to distance from cover, coarse woody debris (CWD), and browse species composition, was quantified. Aspen terminal leaders were sampled to relate current annual growth (CAG) dry biomass (g) to leader diameter (mm). Stem density, current annual browse production, and browse use were estimated. Browse use was determined as 1) proportion of aspen stems browsed (stand scale), 2) proportion of browsed leaders per stem (stem scale), and 3) diameter-at-point-of-browsing (leader scale). Aspen sucker density ranged from 23,000-43,000 stems/ha. Terminal leader diameter was found to be a good estimator of individual stem CAG biomass. CWD did not impede moose utilization of stems. Browse use declined from mature stand edge to center (100 m). Beyond 15 m from mature stand edge browse use was low compared to that within 15 m of the stand edge. Clear-felling without removal of stems is a viable silvicultural method to reinitiate seral aspen in lieu of prescribed fire or mechanical treatments on south-facing hillsides.
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In loving memory of Jezibelle
INTRODUCTION

Moose (*Alces alces gigas* Miller) in the boreal forest of interior Alaska use a variety of habitat types at all successional stages (Peek 1997). Early successional stages are created by either natural or human disturbances and often provide abundant hardwood browse. Late successional stages are usually dominated by conifers that provide cover from weather and predation. Moose benefit the most when both of these habitat components are adjacent to one another and well distributed across the landscape (Hundertmark and Schwartz 1996).

Without disturbance, such as wildfire or logging, the increasing conversion of habitat to late successional stages affects the individual and population productivity of boreal forest wildlife species that rely on early successional habitat (Haggstrom and Kellyhouse 1996). Aspen (*Populus tremuloides* Michx), a common cover type in interior Alaska, loses habitat components beneficial to wildlife with stand maturation. In early and mid stand development stages, aspen is an important browse and cover component of habitat for a variety of wildlife (DeByle 1985a,b). Mature aspen stands are commonly too open for effective cover and produce relatively low densities of browse.

Aspen is attractive to wildlife and natural resource managers because it is an aggressive pioneer species that can readily dominate a site after a stand-replacing disturbance. Aspen stands are commonly pure but can be mixed. Because aspen is a seral species, it is however, ultimately excluded by conifers (e.g., commonly white spruce (*Picea glauca* (Moench) Voss) in interior Alaska and loses its reproductive vigor (DeByle and Zasada 1980).
At the stand scale, silvicultural treatments can be a surrogate for natural disturbances to reinitiate succession and allow important habitat species such as aspen to regenerate. A common habitat management objective for many wildlife species that benefit from stands of different age classes is to promote and maintain early seral hardwood stands of different age classes (Gullion 1984) that are adjacent to mature conifer stands such as white or black spruce (*Picea mariana* (Mill.) B.S.P.) (Eastman and Ritchey 1987). Managing for a mosaic of successional stages at the landscape scale benefits many species (Telfer 1974; Hunter et al. 1988) and, thus, increases the effectiveness of the management effort.

Different silvicultural treatments are required for specific circumstances and stand conditions to achieve desired stand development (Smith et al. 1997). Practices commonly applied south of interior Alaska, however, require further study to determine their applicability for the more northern boreal forest environment (Zasada and Packee 1995). The Alaska Department of Fish & Game (ADF&G), in cooperation with other natural resource agencies and land managers in interior Alaska, is trying various clearcut and prescribed fire treatments in mature aspen stands to determine the most cost-effective treatments that encourage aspen regeneration for ruffed grouse (*Bonasa umbellus* L.) habitat (Paragi and Haggstrom 2004).

One type of clearcut treatment is to fell mature aspen and leave the entire tree on site. This approach may be the only alternative for stands on steep terrain or where prescribed fire is inappropriate. However, this method creates a jackstraw of slash that may impact wildlife, including ruffed grouse. Aspen regeneration can be adequate for grouse habitat
objectives, but how such large volumes of coarse woody debris (CWD) influence movement of moose into aspen regenerated clearcuts is unknown.

**Objectives**

The goal of this study was to determine if non-harvest clearcuts are a viable silvicultural treatment for producing aspen browse available to moose. The general objectives were to determine available biomass of winter aspen browse for moose within recently felled stands of mature aspen and determine the pattern of use of aspen browse by moose during winter.

Specific objectives were:

1) Estimate available aspen browse from 2 and 4-year-old coppice growing up through felled, mature aspen trees by:
   a) quantifying current annual growth aspen biomass; and
   b) determining stand density of aspen suckers.

2) Quantify browse use of aspen across clearcuts with large volumes of coarse woody debris by:
   a) determining the effect of distance from stand edge (cover) on browsing intensity;
   b) determining the effect of coarse woody debris on browsing pattern through felled stands;
   c) quantifying browse consumption; and
   d) comparing use of aspen with other browse species.
LITERATURE REVIEW

Regional Physiography

Interior Alaska is part of the Intermontane Plateaus physiographic division, lying between the Brooks Range to the north and the Alaska Range to the south, and occupied by a variety of terrain features from low elevation mountains and rolling uplands to wide valleys and extensive floodplains (Wahrhaftig 1965). Located in the southeast quarter of interior Alaska, along the north side of the Alaska Range, is the Tanana River Valley (120,000 km²). The northern extent of the valley is within the Yukon-Tanana Uplands with the southern edge of the uplands ending abruptly along the Tanana River. To the south of the uplands are the Tanana-Kuskokwim Lowlands, an extensive fluvial plain sprawling northward from the northern slopes of the Alaska Range (Wahrhaftig 1965). The study site is situated along an upland ridge that extends southward into this floodplain.

Climate

Interior Alaska is characterized by a strong continental climate with an extreme annual temperature range. Summer temperatures can range from below freezing to more than 35°C. A greater range, from less than -55°C up to 7°C, occurs in winter. Temperature inversions are common in winter and result in warmer temperatures above valley floors (NCDC 1997).

Mean annual precipitation is 28 cm with the least amount, commonly only a trace, occurring in April, and the highest monthly mean, 5 cm, occurring in August. Snow
cover usually persists from October into April, but both intra and interannual precipitation and snowfall is highly variable (NCDC 1997).

Unpublished climatic data specific to the study area are not available, however, subtle variations in weather are irrelevant to this study; thus, climatic data from Fairbanks, Alaska, 56 km northeast of the study area, is provided in Table 1. Personal observation suggest that data from Fairbanks approximates that of the study area; and, given the objectives of this study only data from September 2000 through April 2001 are pertinent. During this particular winter, mean monthly snowfall was approximately 15 cm with the greatest monthly amount, 39 cm, occurring in April. An observed maximum of only 30 cm of snow was on the ground at any one time. This results from snow settling and solar radiation; the latter increases dramatically in late winter and causes early snowmelt on south-facing slopes (Slaughter and Viereck 1986). The mean temperature for the period was -11°C, 1.5°C above the 30-year mean normal (NCDC 1997).

<table>
<thead>
<tr>
<th>Snowfall cm</th>
<th>SE</th>
<th>Temperature °C</th>
<th>SE</th>
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<tr>
<td>30-year Normal</td>
<td>178</td>
<td>15</td>
<td>-9.5</td>
</tr>
<tr>
<td>2001/02</td>
<td>120</td>
<td>4.5</td>
<td>-11</td>
</tr>
<tr>
<td>Departure</td>
<td>-58</td>
<td></td>
<td>-1.5</td>
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The departure is the deviation of the winter mean (above or below) the 30 yr normal.
Soils

Well-drained upland soils on south-facing slopes are commonly classified as Alfic Cryochrepts that develop from wind deposited micaceous loess. The soil profile is typically a silt loam to silty clay loam (up to 1 m in depth) overlying a deep loess substrate that is underlain by schist bedrock. Loess materials are shallow on ridge tops and increase in depth further down slope where colluvial silt may accumulate up to 30 m in depth at the base of hills and along tributaries feeding the Tanana River (Rieger et al. 1963). Permafrost is discontinuous or absent on southerly slopes (Viereck et al. 1986).

The study site, with its southeast aspect and moderate slope, has some of the thickest loess deposits in Alaska (Pévé 1975). The Fairbanks soil series is a deep, well-drained silt-loam that dominates the felling units (Furbush and Schoephorster 1977; verified by current unpublished data for the Greater Nenana Soil Survey from the Natural Resources Conservation Service in Fairbanks, Alaska (Mulligan forthcoming).

Vegetation

Interior Alaska is covered by the northwestern extension of the boreal forest, a contiguous band of conifer-dominated forest that extends from the Atlantic coast of Canada to the Bering Sea coast of Alaska (Lutz 1960) in which black spruce is the dominant tree species in Alaska (Crimp et al. 1997). Other interior boreal forest cover types include pure or mixed stands of white spruce, aspen, paper birch (*Betula neoalaskana* Sarg.), and balsam poplar (*P. balsamifera* L.) (Eyre 1980). A common
cover type on southerly, upland slopes is mesic white spruce that commonly succeeds aspen and paper birch (Viereck et al. 1986).

Aspen, described by DeByle and Zasada (1980), is the dominant cover type of the study site. Mature aspen stands are nearly pure with white spruce and paper birch mixed in the overstory and white spruce scattered in the understory. Within the mature aspen stands high bush cranberry (*Viburnum edule* (Michx.) Raf.) and rose (*Rosa acicularis* Lindl.) are dominant shrub species. Within felled stands willow (*Salix* spp.), predominately feltleaf willow (*S. alexensis* (Anderss.) Cov.), alder (*Alnus* spp. Mill.), birch, and balsam poplar are scattered at much lower densities than aspen suckers. Balsam poplar becomes more abundant further down the slopes toward the floodplain of the Tanana River and buffaloberry (*Shepherdia canadensis* L.) is the dominant shrub (Appendix 1).

**Disturbance Regimes**

Wildfire is the predominant natural, stand replacing disturbance in Alaskan boreal forests and perpetuates the mosaic of distinguishable stands that vary in species, size, shape, structure, and successional stage (Lutz 1960; Rowe and Scotter 1973; Viereck 1973; Van Cleve et al. 1983; Zasada and Packee 1995; Dale et al. 2001). Fire commonly creates an environment that stimulates abundant regeneration of high-quality hardwood browse beneficial to moose (Cowan et al. 1950; Wolff and Zasada 1979; Dyrness et al. 1986; MacCracken and Viereck 1990; Lautenschlager et al. 1997). However, the browse component of early successional stages is relatively short-lived with browse abundance
and availability diminishing after about 20 years (LeResche et al. 1974; Wolff and Zasada 1979; Regelin et al. 1987; Collins and Schwartz 1998).

Species composition of a stand before disturbance, species with adequate seed crops in adjacent undisturbed stands, and site conditions after a disturbance govern what species regenerate (Spencer and Hakala 1964; Viereck 1973; Zasada 1986; Oldemeyer and Regelin 1987; Oliver and Larsen 1996). For example, common stand initiation on dry uplands of interior Alaska following a major disturbance begins with light-seeded forbs and shrubs (e.g., fireweed and willow) concurrent with immediate vegetative regeneration of aspen and birch, if the parent root system survived the disturbance. This stage is followed by white spruce if an available seed source exists (Viereck 1973).

Aspen stands may be mixed with white or black spruce throughout stand development; however, because of aspen’s shade intolerance aspen is seral to spruce (DeByle and Zasada 1980; Lieffers et al. 1996). Therefore, frequent disturbance is important in maintaining early successional habitat of seral browse species before they are excluded by late successional, non-browse species (Spencer and Hakala 1964). For aspen to benefit from vigorous suckering or maximum seed production and avoid potential decay, a stand replacing disturbance should occur between 75 and 125 years (Perala 1990).

In interior Alaska wildfire suppression (Hardy and Franks 1963; Viereck 1973; Kelleyhouse 1979a) and the lack of extensive commercial harvest in the boreal forest (Sampson et al. 1988; Haggstrom and Kurth 2001) are management concerns because they extend the period between disturbances. This scenario has allowed succession to
proceed and many forest stands to age or convert to spruce. This results in a loss of habitat components important to many wildlife species dependent on early and mid-successional boreal forest stand development stages (Haggstrom and Kelleyhouse 1996) because diversity of habitat types declines with age (Rees and Juday 2002). Therefore, with limited timber harvest based mostly on local demand (Sampson 1996), managing for wildlife habitat diversity with commercially non-consumptive silvicultural treatments is a forest management objective.

Fire suppression policies are evolving into different management strategies at the landscape scale (Kelleyhouse 1979b). Interior Alaska has extensive remote areas where man-made structures, such as trapping cabins, are sparse and often of minimal monetary value. The Alaska Department of Natural Resources (ADNR) determines when and where wildfire suppression effort is appropriate by assigning value to such structures and natural resources (ADNR 2001) and specific use value (e.g., subsistence activities) for the given area (Kellyhouse 1979b).

The trend of early seral stands, declining in proportion to older forest stands (Johnson 1992), can be countered in remote areas with the use of prescribed fire or acceptance of wildfire. Increasing knowledge of fire behavior and how to control it allows suppression efforts to be relaxed where and when ecological benefits from fire can be realized (Pyne et al. 1996). For instance, at the stand scale, fire improves soil conditions (e.g., temperature and pH) that enhances microbial activity (Dymess et al. 1986). The enhancement of site condition promotes the establishment of early seral species, thereby, facilitating stand diversity at the landscape scale (Rowe and Scotter 1973; Viereck 1973).
In the Tanana Valley State Forest (TVSF) (Figure 1) of interior Alaska, limited suppression policies are restricted to 20% of remote areas. Limited suppression is prescribed where habitat, fuel management, or reduced suppression costs are of greater benefit than the timber resource that would be lost by wildfire (ADNR 2001). This policy allows wildfire to run its course in remote areas and applies to other state, native corporation, and federal government lands; and is important for landscape scale management (personal communication with Tom Paragi, ADF&G, Fairbanks).

![TANANA VALLEY STATE FOREST](Image)

Figure 1. Tanana Valley State Forest in interior Alaska.
This 'let burn' policy, however, is not an option near communities. Therefore, silvicultural alternatives must be used as substitutes for wildfire disturbance regimes. The Division of Wildlife Conservation (ADF&G) and the Division of Forestry (ADNR), in cooperation with some native corporations and conservation organizations (e.g., Ruffed Grouse Society), are expanding a proactive approach to habitat management. In areas near settled communities silvicultural treatments such as small prescribed burns and mechanical clearing are effective disturbance agents (Paragi and Haggstrom 2004). This effort in habitat enhancement is pursued as an objective under multiple-use, the general goal of the Tanana Valley State Forest management plan, where timber is not the dominant priority (ADNR 2001).

Following prescribed fire, aspen regeneration can be abundant; however, because exacting conditions (i.e., adequate and dry fuel) are required to carry fire through the aspen stand and effectively scorch stems prior to leaf flush, sucker density varies (Foote and Viereck 1985; Brown and DeByle 1987; Paragi and Haggstrom 2001). Thus, mechanical treatments for regenerating hardwood species in interior Alaska are being evaluated as silvicultural alternatives, especially for areas where prescribed fire is impractical because of human health and safety concerns (Pyne et al. 1996; Paragi and Haggstrom 2004).

Silvicultural practices applied at lower latitudes may require modification in Alaska's boreal forest; especially on sites with permafrost (Zasada and Packee 1995). Effort to manage habitat should be concentrated on uplands that are unaffected by relatively frequent fluvial disturbances that affect floodplain stands (Van Cleve and Viereck 1981;
Collins and Helm 1997). Site preparation treatments should be applied within the first year post disturbance to ensure desired stand initiation objectives are achieved (Collins and Schwartz 1998).

Aspen Production

Aspen, with the greatest distribution of any North American tree (Little 1981), is a common cover type and an associate species in many other cover types throughout its range (Eyre 1980). In Alaska, it is a dominant hardwood species of interior upland forests (Viereck et al. 1983; Crimp et al. 1997) and is receiving concentrated management efforts for wildlife habitat (Paragi and Haggstrom 2004). Regeneration characteristics (Doucet 1989; Schier 1985b), habitat qualities for many wildlife species (Gullion 1984; DeByle 1985b), and ecosystem attributes (DeByle 1985c) make aspen attractive to wildlife and natural resource managers.

Aspen regenerates by seed and suckers and is a competitive pioneering species (Schier et al. 1985a). Seedling-origin stands are found on sites where the severity of disturbance, commonly wildfire, offers an adequate seedbed (Barnes 1966; Quinn and Wu 2001; personal communication with E.C. Packee, University Alaska Fairbanks, School of Natural Resources and Agricultural Sciences). Potential for establishment by seed can be quite good with aspen’s commonly profuse production of seed and its relatively long distance dispersal by wind (Perala 1990). However, the narrow window of time of seed viability and requisite seedbed conditions (e.g., saturated mineral soil surface) often inhibits seedling establishment (Maini 1968; Schier et al. 1985b; Zasada 1986; Perala...
1990; Kay 1993). In some cases stands initiated by seedlings may be recognized by a relatively mixed species composition and a stand profile structure where larger seed-origin stems are surrounded by progressively smaller stems from adventitious roots (Gullion 1984).

Vegetative regeneration provides aspen a competitive advantage to reoccupy a site after a stand-replacing disturbance (Schier et al. 1985a; Perala 1990). Aspen have strong epinastic and apical control and apical dominance, whereby, growth is allocated to terminal leaders and shoot elongation that facilitates rapid canopy dominance in dense stands (Oliver and Larsen 1996). Clearcut coppice to stimulate sucker production is usually the most common method for aspen regeneration (Bartos and Mueggler 1982; Schier et al. 1985a; Doucet 1989; Youngblood and Titus 1996).

Aspen suckers are produced when trees, or the entire clone above ground, are killed and the flow of auxin, a shoot promoting hormone produced in the canopy, is severed from the root system that remains alive. Apical dominance is suppressed when auxin no longer inhibits bud growth in the root system; sucker development is initiated by a hormone (cytokinin) produced in the root tips (Farmer 1962; Brown et al. 1967; Schier 1973; Stenecker 1974; Perala 1990). Sucker production is also influenced by condition (i.e., depth and diameter) of parental roots, stocking and vigor of the parent stand, and clonal genetics (Schier et al. 1985a). Optimal site conditions for suckering include warm, well-drained loamy soils (Perala 1990). Such conditions occur on many severely disturbed sites in Alaska (personal communication with E.C. Packee, University Alaska Fairbanks, School of Natural Resources and Agricultural Sciences).
Sucker production is often prolific and is typically greater in Alaska and the Great Lakes region than in the Rocky Mountain region (Perala 1990). Stands on good quality sites, outside of Alaska, may produce up to 75,000 suckers per hectare during the first two growing seasons (Schier et al. 1985a). In interior Alaska, up to 300,000 stems per hectare can regenerate after fire (MacCracken and Viereck 1990). However, because aspen is very shade-intolerant the density of stands readily declines with rapid canopy closure (Jones and Schier 1985). Competition for canopy dominance, after the expeditious transition from stand initiation to the competitive exclusion stage of stand development, results in mortality of suppressed stems and regular distribution of dominant stems (Oliver and Larson 1996). Thus, aspen stem densities in stands with profuse suckering decline rapidly within five years and stem density becomes relatively equalized among stands (Pollard 1971; Steneke 1972; Bartos and Mueggler 1982; Bella 1986; Doucet 1989). This process results in stands that commonly develop a distinct pure, even-age composition during the early stages of development (Jones and DeByle 1985).

Aspen in Alaska (Sampson et al. 1988; Wurtz and Gasbarro 1996) and many western states (Wengert et al. 1985; Morley 1986) is underutilized as a timber resource. Commercial use, historically concentrated in the Lake States, has expanded into western Canada (Morley 1986; Beck et al. 1989). In Canada, a hurdle for aspen management was the economic incentive to maintain aspen stands by changing management focus from predominately conifers to hardwoods (Corns 1989; Beck et al. 1989; Lieffers and Beck 1994).
Currently, the potential for a timber industry with value-added products in interior Alaska is good (Wallingford and Packee 1988; personal observation with the Alaska Northern Forest Cooperative, Fairbanks, Alaska). The TVSF has 88% of its 0.72 million hectares in forest; stands are predominantly hardwood-white spruce (45%), followed by 31% black spruce, 20% hardwood, and 4% white spruce (Crimp et al. 1997). However, until commercial demands increase, increased management effort for wildlife habitat, if consistent with other management objectives, should be considered. Managing for mixed stands of aspen and white spruce (commercially valuable) may improve site conditions for spruce production (Lieffers et al. 1999) concurrent with providing wildlife habitat.

**Coarse Woody Debris**

The structure of a forest stand is not just the living canopy; it includes dead woody material in both vertical and horizontal arrangements (McComb and Lindenmayer 1999). Coarse wood debris is downed woody material or standing snags and is a critical, dynamic component of the forest ecosystem (Hunter 1990; Crites and Dale 1998; Hagan and Grove 1999; McComb and Lindenmayer 1999; McComb 2003). Over time, as decay proceeds, a variety of microhabitats are created from the same piece of debris. An array of species from fungi to small mammals uses coarse woody debris at different stages of decay and stand development (Crites and Dale 1998; McComb and Lindenmayer 1999; Moses and Boutin 2001; McComb 2003). Through all stages of stand development coarse woody debris provides continued nutrient inputs and soil stabilization (Harmon et al. 1986).
Characteristics and densities of coarse woody debris at the stand scale are influenced by disturbance type, severity and frequency of both initial and subsequent disturbances, and stage of stand development (Spies et al. 1988; McComb et al. 1993; Lee et al. 1997). The greatest diversity of coarse woody debris is found in late successional stages where most stand components prior to initial disturbance are still present and input from ongoing disturbances contribute to the variety of material (Spies et al. 1988; Lee et al. 1997). Therefore, retention of not just coarse woody debris, but also features of mature stands benefit biodiversity (Crites and Dale 1998; McComb and Lindenmayer 1999; Nilsson et al. 2001).

The type and amount of coarse woody debris to retain in a given stand to meet biodiversity objectives for sustainable forestry is unknown (Hunter 1990; Hagan and Grove 1999; Ehnstrom 2001). Hunter (1993) suggests residual material should be modeled from natural disturbance regimes (e.g., fire). However, there are too many dynamic variables that contribute to observed conditions at different scales (Armstrong 1999; Granstrom 2001; Simberloff 2001). Silvicultural treatments can only emulate to some degree conditions created from natural disturbances (Spence 2001).

For instance, felled trees do not completely replicate windthrow because the root system is not exposed for a mineral soil seedbed (Collins and Schwartz 1998). Conditions created from felled trees in this study, however, may mimic conditions from extreme weather events that result in stem-breakage which is different than windthrow. Coarse woody debris can limit suckering (Schier et al. 1985b; Lieffers and Van Rees 2002) but, regeneration objectives can be achieved with large amounts of debris (Paragi
and Haggstrom 2004). Because aspen regeneration is affected by soil temperature (Zasada and Schier 1973) it is unknown whether coarse woody debris negatively affects site conditions, e.g., shading the soil rather than allowing it to warm as observed after a burn.

**Moose Browsing Behavior**

Moose habitat in the boreal forest of interior Alaska consists of different successional stages distributed in an irregular pattern across the landscape (Viereck 1973; Miquelle et al. 1992). This environmental heterogeneity is produced by both natural disturbances including wildfire, wind, fluvial processes, and insect infestations and anthropogenic manipulations involving prescribed fire, logging, and agriculture (Rowe and Scotter 1973; Brassard et al. 1974; LeResche et al. 1974; Peek et al. 1976; Wolff and Zasada 1979; MacCracken and Viereck 1990; Huntly 1991; Thompson and Stewart 1997).

Early seral habitats created by disturbance are selected by moose for high quality forage in spring and summer and abundant browse in winter (Cowan et al. 1950; Peek 1997; Renecker and Schwartz 1997). However, moose, per se, are a continuing disturbance mechanism that may influence the trajectory of succession and stand composition (Miquelle and Van Ballenberghe 1989; Helm and Collins 1997; Andrews 1998; Augustine and McNaughton 1998). Intense browsing pressure suppresses height growth of early seral hardwood browse species and may accelerate succession to conifers (Risenhoover and Maass 1987; Abaturov and Smirnov 1992; Andrews 1998; Connor et al. 2000). Likewise, consumption of browse species diminishes the input of quality litter
(e.g., mineralizable nitrogen) and can allow successional alder or conifer species to rapidly dominate the site (Bryant and Chapin 1986; Bergstrom and Hjeljord 1987; Pastor et al. 1988; McInnes et al. 1992; Kielland and Bryant 1998).

Habitat selection by moose is influenced by the abundance and quality of both forage and cover components that vary seasonally among stands (Spencer and Hakala 1964; Bergstrom and Hjeljord 1987; Saether and Andersen 1990; Miquelle et al. 1992; Peek 1997; Schwartz and Renecker 1997). In a patchy environment, moose contend with energetic constraints from their large body size by occupying areas with abundant browse (Renecker and Schwartz 1997). This differential habitat selection by moose is prevalent in winter and manifested in segregation of sex and age class (Miquelle et al. 1992; Barboza and Bowyer 2000). As a strategy based on physiological constraints and predator avoidance, large post-rut bulls compromise cover in order to select patches of abundant browse to maximize energy intake; conversely, cows, calves, and yearling’s select for cover as a priority over browse resources (Main and Coblentz 1990; Miquelle et al. 1992; Bowyer et al. 1999).

Moose are generalist browsers adept at exploiting a host of habitats; but, within a particular habitat or stand they are selective for rapidly digestible browse components (i.e., bark and buds) (Peek 1997; Renecker and Schwartz 1997). According to optimal foraging theory, herbivores select forage that provides an optimal diet when resources are abundant (i.e., prefer species and plant parts with greater digestibility) and generalize by selecting forage in proportion to its availability when resource levels are low (Westoby 1974; Pyke et al. 1977; Stephens and Krebs 1986). However, as large generalist
herbivores, moose do not operate strictly according to this prediction (Belovsky 1978, 1984; Hanley 1997; Weixelman et al. 1998). In general, winter diet is influenced by not only abundance, but forage composition, availability, and plant morphology within and among stands rather than forage quality (e.g., crude protein content) (Oldemeyer 1974; Oldemeyer et al. 1977; Nudds 1980; Belovsky 1981; Vivas et al. 1991; Kielland and Osborne 1998; Shipley et al. 1998; Weixelman et al. 1998).

Winter foraging strategy is a matter of energy conservation (Oldemeyer 1974; Nudds 1980; Peek et al. 1992; Schwartz 1992; Robbins 1993; Van Soest 1994). Moose have metabolic adaptations to confront declining forage abundance and quality observed in the boreal forest winter environment (Schwartz et al. 1984; Regelin et al. 1985; Schwartz et al. 1987; Hofmann and Nygren 1992; Peek et al. 1992; Schwartz 1992). Low crude protein levels of winter forage (Schwartz 1992) without available water required for protein metabolism (Cameron and Luick 1972; Syrjala et al. 1980) implies digestible energy intake may be the currency that governs diet (Mautz 1978; Swift et al. 1979; Schwartz and Renecker 1997). At maximum daily intake, moose select browse that, at best, only minimize the rate of weight loss during winter (Mautz 1978; Schwartz et al. 1987; Schwartz 1992; Barboza and Bowyer 2001). In other words, if moose consumed their maximum fill of the highest quality diet possible from natural browse components, they would still lose weight through the winter. Thus, it is critical for moose to make choices at the habitat, stand, and stem scales to satisfy energy maintenance requirements through winter (White 1983; Peek 1997; Renecker and Schwartz 1997; Schwartz and Renecker 1997).
Moose utilize many available forage species but show preference for only a few by consuming those species in greater proportion than their relative availability (Renecker and Schwartz 1997). This preference varies in time and among regions, ranges, and stands (Peek 1974, 1997; Andersen and Saether 1992; Shipley et al. 1998).

Generally, at the regional scale, some willow species are commonly a dominant and preferred component of winter diet for Alaskan moose (Cushwa and Coady 1976; Wolff 1976; Risenhoover 1989; Van Ballenberghe et al. 1989; MacCracken and Viereck 1990; Van Ballenberghe 1992; Renecker and Schwartz 1997) and in Fennoscandia (Bergstrom and Danell 1987b; Bergstrom and Hjeljord 1987; Shipley et al. 1998). Aspen and birch are important winter browse and often preferred in early successional stands, such as the case with European aspen (*P. tremula* L.) in Fennoscandia (Peek 1974; Peek et al. 1976; Bergstrom and Danell 1987b; Bergstrom and Hjeljord 1987; Edénius 1992). Other hardwood browse species may be important, but are seldom preferred (Peek et al. 1976; McNicol and Gilbert 1980; Bergstrom and Danell 1987b; Renecker and Schwartz 1997; Shipley et al. 1998). The same selectivity and relative lower preference is observed regionally with the few conifer species browsed (e.g., subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), balsam fir (*Abies balsamea* (L.) Mill.), and Scots pine (*Pinus sylvestris* L.) (Peek 1974; Danell et al. 1991; Bergstrom and Vikberg 1992). Regardless of preference a mixed diet is common (Peek et al. 1976; Bryant and Kuropat 1980; Risenhoover 1989; Weixelman et al. 1998).

At the forest (habitat) scale, availability and abundance of browse species across a given winter range influences species preference and may vary among moose
populations. For instance, the preference for birch (*Betula kenaica* (W.H. Evans) Henry) on the Kenai Peninsula (south-central coast of Alaska) (Oldemeyer et al. 1977; Weixelman et al. 1998) may be due to its dominance; whereas, willow is more common and preferred in the interior (Risenhoover 1989; MacCracken and Viereck 1990; Seaton 2002). Availability of browse, however, may decline through the winter as preferred species are consumed or short stems become covered with snow (Cushwa and Coady 1976; Peek et al. 1976; Weixelman et al. 1998).

Browse selection at the stand scale is influenced by both species composition and relative densities (Vivas and Saether 1987; Saether and Andersen 1990). In Fennoscandia consumption rates of preferred browse, such as aspen, may remain constant among stands regardless of its density within a stand; whereas, consumption of moderately preferred species, such as Scots pine, may vary relative to its density and that of other less preferred species, such as alder. In other words, consumption of aspen is consistently high among all stands, but use of Scots pine is greater than that of alder in stands with higher densities of pine (Danell et al. 1991; Edenius 1991, 1992). Also, stem density influences selectivity between preferred species (Vivas and Saether 1987; Heikkila 1991; Vivas et al. 1991). For example, the consumption of silver birch (*Betula pendula* Roth), preferred in Fennoscandia, declined as its proportional density increased, but remained preferred over the less preferred (*B. pubescens* Ehrh.) (Danell and Ericson 1986).

At the stem scale, moose select leaders on individual stems (saplings) as a function of intake efficiency based on stem density (Lundberg and Danell 1990). Increased intake
can be achieved by taking more bites from fewer stems in dense stands (Danell and Ericson 1986) or with larger bites in low-density stands (Shipley and Spalinger 1995).

Selection of stem leaders is also influenced by leader size, density, and architecture of the stem (Bergstrom and Danell 1987a; Astrom et al. 1990; Vivas and Saether 1987; Vivas et al. 1991). Moose tend to select browse species, such as willow and aspen, with large annual terminal leaders (Bergstrom and Danell 1987b; Bowyer and Bowyer 1997; Shipley et al. 1998). Moreover, moose tend to select stems that produce larger leaders with more branching from compensatory growth in response to previous browsing (Wolff 1978; Bergstrom and Danell 1987a; Molvar et al. 1993; Bowyer and Bowyer 1997; Shipley et al. 1998; Bowyer et al. 2001). Leaders from browsed stems provide greater biomass per bite and, thus, affect foraging efficiency (Danell et al. 1985; Bowyer et al. 2001). However, the broomed architecture resulting from intense browsing may function as a defense mechanism by having small diameter leaders concentrated in close proximity to older growth leaders (Vivas et al. 1991; Seaton 2002). Heavy browsing may also affect palatability (Bryant et al. 1983; Bryant and Chapin 1986).

At the leader scale, bite diameter is governed by plant morphology and physiological constraints of the moose and relates to foraging efficiency. Efficiency, in terms of energy gain per time of unit, is achieved by “selecting” a bite size that optimizes the rate of browse intake (Vivas et al. 1991; Shipley and Spalinger 1995). The problem moose face is that energy gain declines with bites smaller or larger than the “optimal” size for a given browse species (Vivas et al. 1991; Kielland and Osborne 1998). For instance, the digestibility of a given leader is inversely proportional to bite diameter, in that smaller
bites have higher digestibility based on a higher bark to wood ratio (Hjeljord et al. 1982; Spaeth et al. 2002). However, intake rate declines with small bites (Renecker and Hudson 1986b). Thus, moose maximize digestible energy intake by taking bites within a range of diameters that balances dry matter intake with digestibility (Vivas et al. 1991; Shipley and Spalinger 1992).

Foraging efficiency is also affected by intraspecific competition and a predator avoidance strategy. The large body size that generates physiological constraints for the requirement of abundant browse, also allows moose to inhabit relatively open and patchy habitat (Van Ballenberghe 1992). Molvar and Bowyer (1994) suggest that Alaskan moose live in more open terrain than their counterparts in more forested regions because a degree of social behavior facilitates foraging in open terrain. Larger groups may encourage use of forage at greater distances from cover, but foraging efficiency declines because less time is spent foraging and more time in alert posture or aggressive behavior among some individuals (Molvar and Bowyer 1994). In addition, selection of bite size may increase with distance from cover, thus, adding to the decline in foraging efficiency (Molvar and Bowyer 1994; Weixelman et al. 1998).

In terms of cover, studies commonly relate foraging behavior of moose to distance from stand-edge cover rather than percent cover within a stand. Browsing occurs predominantly within 100 m of stand edge considered complete concealment (Hamilton and Drysdale 1975; Hamilton et al. 1980; Bangs et al. 1985; Eastman and Ritchey 1987; Mastenbrook and Cumming 1989; Kufeld and Bowden 1996). Microtopography may also be important in how moose perceive cover (Welsh et al. 1980; Molvar and Bowyer
1994). Therefore, the juxtaposition of mature stands that provide cover with early seral stands that provide browse is advantageous to moose (Eastman and Ritchey 1987; Hundertmark and Schwartz 1996; Kufeld and Bowden 1996; Regelin and Franzmann 1998; Kunkel and Pletscher 2000).
METHODS

Study Site

The Nenana Ridge habitat enhancement area (Figure 2) is within the Fairbanks Management Area of the Tanana Valley State Forest and within Game Management Unit 20B. The area is approximately 56 km southwest of Fairbanks and 24 km northeast of Nenana (64°38'N, 148°48'W). The area is 2,430 hectares in size and roughly 8 km long. The area consists of a relatively even mix of conifer and deciduous upland boreal forest along the southeast side of a ridge that faces southeast toward the Tanana River. This ridge extends from Fairbanks to Nenana and separates the Minto Flats and Tanana Flats.

![Figure 2. Nenana Ridge ruffed-grouse habitat enhancement area.](image-url)
The habitat enhancement area includes a mix of mature forest, clearcuts, prescribed burns, and timber sales that consist of different proportions of spruce, birch, aspen, and balsam poplar. The study site is on a portion of the ridge that consists of a single cohort stand of predominately mature aspen greater than 75 years old. The aspen clearcut stands have a south-southeast aspect and moderate slope (5 to 30 percent) extending from an elevation of 150 m, adjacent to the Tanana River floodplain, to the top of the ridge at 300 m. Microtopography within and among the stands is variable.

Stand Selection

Sampled stands include three felled units that were clearcut in autumn of 1997 (i.e., 4-year-old stands) and three cut in 1999 (i.e., 2-year-old stands). One of the 4-year-old stands appears as two stands, but a narrow cut connects the two. Since each portion is similar in size to the other stands, only one portion was sampled. The clearcut stands range in size from 3 to 7 ha and have irregular perimeters. Distance from stand edge to stand center varies from 70 to 100 m. The stands are basically adjacent to one another but are separated by approximately 100 to 200 m retention of mature standing aspen. The group of three stands from each age class is separated by at least 1 km (Figure 2).

Aspen stands were selected based on similarity in size, proximity to one another, and position along the upper slope of the ridge. The 4-year-old stands were selected because all current annual growth biomass of leaders was considered to be within reach of adult moose. Leaders are usually considered available to moose if the base of the terminal leader is <2.5 m in height (Weixelman et al. 1998). The 2-year-old stands were selected
to compare the use to the 4-year-old stands relative to differences in potential cover (concealment) and available current annual growth.

Stem Selection

For this study the "stem" refers to the entire sapling or individual sucker. A "leader" of current annual growth refers to the common generic term twig (Figure 3). The

Figure 3. Aspen stem and current annual growth leader.
terminal leader, commonly the largest and longest, extends in-line with the main trunk of the stem. There is only one terminal per stem and all others are referred to as lateral leaders.

Only 4-year-old stems in stands cut in 1997 and 2-year-old stems in stands cut in 1999 were sampled. Aspen stems of these two specific age classes were distinctly dominant in stature over younger stems. These stems were predisposed to be browsed because leaders in the upper canopy, between 1.5 and 2.5 m, are commonly selected by moose (Bergstrom and Danell 1987b).

Sampling Organization

The project involved 2 phases: 1) collection of unbrowsed stems, in March of 2002, to develop biomass regressions for current annual growth leaders and 2) measurement of browse use, before bud-break in May 2002, relative to distance from edge of cover (standing timber) and crude measures of coarse woody debris around the sample points. Both browse production and utilization were measured based on the twig-count method of Shafer (1963) that uses twig diameter, length, and weight relationships (Basile and Hutchings 1966; Telfer 1969; Peek et al. 1971). The point-quarter method (Cottam and Curtis 1956; Smith 1996), illustrated in Figure 4a, was used to select stems to be sampled for browse use and measure stand density (stems/ha).

Following the protocol of Paragi and Haggstrom (2004) two sampling zones were established: 1) stand edge buffer zone, from stand edge inward to 15 m, and 2) within the
Figure 4a. Point-quarter method used for determining stem density

stand, from 15 m (edge of buffer zone) inward to stand center. The 15-m buffer zone was not sampled for aspen production because of the possible effects on suckering potential from the adjacent mature timber. For purposes of browsing the 15-m buffer zone is considered an area where moose access into the stand and browse availability is unhindered by coarse woody debris and distance from cover may not be significant influencing factors. Within this buffer zone the distance of 3 m from stand edge was randomly selected to sample browse use to compare with browse use within the stand.
Current Annual Growth (CAG) Biomass of Aspen Leaders

Forty-five aspen stems for each age class were collected using stratified random sampling across the upper, middle, and lower slope to account for possible variability in site condition associated with slope.

To obtain current annual growth, terminal and all lateral leaders of the past growing season were clipped at the bud-scale scar (Figure 3). Beginning at the scar leaders were sub-sampled into leader base diameter classes by clipping the leaders into incremental lengths determined by 1 mm diameter intervals to account for variability in length and biomass for a given diameter class. For example, if the diameter at the scar was 5 mm the leader was clipped again where it tapered down to 4 mm and so forth. Due to the large minimal diameter of young aspen leaders, 2 mm was the smallest diameter class clipped. All pieces of the same leader were kept together to calculate means of both terminal and lateral leader biomass and total stem biomass. Samples were dried for 48 hr at 60°C and weighed to the nearest 0.01 g for dry matter (DM) biomass (Telfer 1969).

Sample Points for Browse Use

To ensure a representative sample at all distances, stands were stratified into two concentric distance strata, one from 15 to 50 m, and one from 50 m to stand center (Figure 4b). Stands were further divided into upper and lower halves relative to their
Figure 4b. Representative clearcut aspen stand with distributed sample points in relation to slope and distance strata.

slope, and the entire stand sectioned into a 5 m x 5 m grid. From this grid 20 sample points per stand were randomly selected using a random number table; one-half of the sample points were selected for each distance strata. From the same grid 20 sample points were randomly selected at 3 m along the stand edge within the buffer zone.

With the point-quarter method four lines protrude at right angles from one reference point (sample point); this creates four adjacent quadrats within one larger imaginary quadrat. Within each quadrat the aspen stem (of the given age class) nearest to the sample point is selected for sampling. Because the four stems are not independent of the
one sampling point all browse use data and distance measures for stem density are averaged; thus, each sample point has a single value.

For browse selection at the stand scale, hence forth referred to as percent of stems browsed, each of the four stems from a sample point was simply counted as either browsed or not. Thus, a proportion of either 0, 25, 50, 75, or 100% for stems browsed was derived for each sample point.

For selection at the stem scale browsing intensity on aspen stems is the proportion of current annual growth leaders browsed per stem, expressed as a percent, and obtained by dividing the number of browsed leaders by the total number of available current annual growth leaders. Diameter (mm) at point-of-browsing and length (cm) of current annual growth, if remaining, from point of browsing to bud-scale scar were measured. Height range of browsed leaders and whether they were terminal or lateral leaders was recorded.

The density of aspen, and the volume and “jackstrawed” conditions of the coarse woody debris made it impractical to sample, using the point-quarter method, the other sparsely distributed browse species (willow, balsam poplar, paper birch). Therefore, a coarse measure of browse use was estimated using 4-m$^2$ quadrats randomly selected from the original grid. A coarse measure of browsing intensity (i.e., 0, 25, 50, 75, 100%) for only willow, poplar, and birch was estimated. Sample size for these other browse species was too small to produce regressions of biomass or browsing intensity values on distance.
Coarse Woody Debris and Cover

A volume index for coarse woody debris does not provide an informative, three-dimensional depiction suitable for addressing obstruction to moose foraging patterns. Therefore, three descriptive measures for coarse woody debris were obtained within a 2-m horizontal radius from each sampled stem. These measures were 1) percent ground cover class (0-25, 25-50, 50-75, and 75-100%) of the coarse woody debris as if viewed from above the sample point, 2) diameter (cm) of the largest piece of debris, and 3) height (cm) above ground of the uppermost downed log ≥10 cm in diameter and suspended by the jackstraw pattern. The 10-cm diameter is an arbitrary minimum, based on personal observation and thought to provide enough resistance to inhibit movement of a slow moving, browsing moose.

Horizontal cover density was measured in the 4-year-old stands using the cover-pole method of Griffith and Youtie (1988). A 2-m pole, marked at 20-cm intervals, was placed upright at 10 m in the 4 cardinal directions from the sampling point. The percent of the pole visually obstructed by stems was observed. Stem height in the 2-year-old stands was insufficient to be considered cover for browsing (standing) moose.

Browse Quality

For nutritional analysis, leaders from 20 stems of each of the four browse species (aspen, willow, birch, poplar) were cut at 4 mm (the approximate mean bite diameter for terminal leaders of aspen), dried at 60°C for 48 hrs, and ground in a Wiley mill using a 20 mesh screen. Analyses for in vitro dry matter digestibility (IVDMD) was estimated
using the Tilley and Terry (1963) method at the University of Alaska Fairbanks (UAF) Institute of Arctic Biology laboratory. Rumen inoculum from a captive reindeer at the UAF Large Animal Research Station was conditioned for two weeks with a mixture of extra browse samples. It is common to use reindeer rumen liquor in lieu of moose when the analyses is for plant quality and not for describing specifics about moose metabolism (Kielland and Osborne 1998; Spaeth et al. 2002).

Analyses for plant cell composition were conducted at the UAF Agricultural and Forestry Experiment Station Plant and Soil Test Laboratory in Palmer, Alaska. Procedures were provided by Rudy Chandler, the laboratory director: crude protein was obtained from a modified Dumas procedure and structural components hemicellulose, cellulose, and lignin were determined by Van Soest detergent analysis.

**Statistical Analyses**

All biomass and browsing analyses were conducted using SAS (2003). All confidence intervals are at 95% using the t-distribution (Fowler et al. 1998).

Simple linear regression was used to determine the relationship between biomass (g) and base diameter (mm) of current annual growth aspen leaders. Based on the pattern of residuals from normal probability and studentized residual plots, logarithmic transformations were used to stabilize error variance and adjust for normality (Neter et al. 1996).

Regressions for biomass on leader length (cm) are not produced for this study because they may be misleading for browse use and consumption estimates when moose browse
beyond current annual growth. Use of these functions would require additional arbitrary measurements for growth from previous years (Oldemeyer 1982).

T-test's were used to compare the means of aspen current annual growth variables leader base diameter (mm), total leader length (cm), and dry matter (g) between terminal and lateral leaders and to compare coefficients of browse use between terminal and lateral leaders. T-tests were also used to compare all differences between age classes. I used Satterthwaite's approximation to account for possible unequal variance (Zar 1999).

Correlations of current annual growth height, diameter, and cover with browsing intensity were examined using the Pearson correlation procedure (multiple regression) to determine the measure of association between the variables (Zar 1999).

Linear regression was used to determine the relationship between browsing intensity of aspen and distance (m) from stand edge (cover) separately for both within the stand, exclusive of the 15-m buffer zone, and including the edge. Regressions were also used for the proportion of stems browsed with distance from cover. An F-test was used to determine the difference in regression slopes (i.e., rate of change) of browsing intensity with distance from cover between age classes. Univariate analysis of variance (1-way ANOVA) was used to determine differences in browsing intensity between the distance strata, 3-15 m, 15-50 m, and 50 m to stand center. Tukey's multiple comparison test, which maintains alpha at five percent when conducting multiple comparisons, was used to determine if there was significant differences between any two strata (Fowler et al. 1998).
Linear regression was used to determine the relationship between diameter-at-point-of-browsing and distance from cover. T-test's were used to compare means of diameter-at-point-of-browsing between terminal and lateral leaders and between years.

Because browse species other than aspen were at low density, only a simple use ratio between aspen and other species was obtained from the counts within plots. No test for browsing intensity between aspen and other species was conducted because data was obtained using different sampling techniques and from different sampling points.

ANOVA was used to determine differences in IVDMD, crude protein, hemicellulose, cellulose, and lignin between browse species.

The objectives of this study do not require tests for differences between 4 and 2-year-old stands, but results from both years are presented separately to provide a general comparison for purposes of deriving questions suited for future studies more narrow in scope.
RESULTS

Regression functions and significance values are provided in Appendix 2. Significance (P) values < 0.05 are significant, and < 0.01 are highly significant. Except for biomass regressions graphical presentations are only for years 2 and 4 combined.

Current Annual Growth (CAG) Biomass of Aspen Leaders

The positive relationships between log transformed biomass (g) and leader diameter (mm) were highly significant for both 4 and 2-year-old stands (Figures 5a and 5b).

![Figure 5a](image)

Figure 5a. Relation of dry matter biomass of current annual growth to leader base diameter for 4-year-old aspen stems on Nenana Ridge west of Fairbanks, AK.
A highly significant relationship was found between terminal leader base diameter (age classes pooled) and total current annual growth (Figure 5c). This may provide a model to efficiently approximate current annual growth of aspen within these age classes.

Differences in morphological characteristics (diameter, length, and dry biomass) are presented in Table 2. Mean current annual growth was significantly greater for terminal leaders compared to lateral leaders for both age classes. Only terminal leader, not primary lateral leader, characteristics were significantly greater for 2-year-old leaders compared to 4-year-old leaders. There were significantly more leaders on 4-year-old stems.
Table 2. Current annual growth (CAG) of leaders for 4 and 2-year-old aspen stems: Mean diameter at the bud-scale scar, total leader length, and total dry mass.

<table>
<thead>
<tr>
<th>CAG Biomass Means with 95% C.I.</th>
</tr>
</thead>
<tbody>
<tr>
<td># leaders/stem</td>
</tr>
<tr>
<td>diameter (mm)</td>
</tr>
<tr>
<td>4-yr 17±1.7</td>
</tr>
<tr>
<td>2-yr 5±0.4</td>
</tr>
</tbody>
</table>

Figure 5c. Relationship between terminal leader base diameter and total current annual growth of aspen, for both age classes on Nenana Ridge west of Fairbanks, AK.
Mean current annual growth biomass (Table 3) for entire aspen suckers (terminal + primary lateral + all non-terminal leaders) was 26±4 g/stem for 4-year-old stands and 32±10 g/stem for 2-year-old stands. No significant difference was found between age classes.

Aspen sucker density of 4 and 2-year-old stands combined ranged from 23,000 to 43,000 stems/ha with a mean of 25,000±1,200. No difference found between age classes.

Based on the above biomass data, the 4-year-old stands produced an average of 783.7±115.9 kg/ha of available current annual growth aspen biomass, compared to 808.2±253.8 kg/ha for 2-year-old stands (Table 3). Again, no difference was found between age classes.

Table 3. Stem densities and total current annual growth (CAG) biomass of aspen.

<table>
<thead>
<tr>
<th>Stem Density (#/ ha)</th>
<th>CAG (g/ stem)</th>
<th>C.V.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>C.I.</td>
</tr>
<tr>
<td>4-yr</td>
<td>29,800</td>
<td>±13,300</td>
</tr>
<tr>
<td>2-yr</td>
<td>25,100</td>
<td>±1,700</td>
</tr>
</tbody>
</table>

Stem selection (stand scale)

Other browse species (willow, birch, poplar) comprised a very low percentage, 3 ±1%, of the total stem density in both 4 and 2-year-old stands (Table 4), exclusive of the 15-m
stand edge buffer zone. However, these other species were preferred over aspen with approximately 90% of their stems browsed compared to a maximum of 55% of aspen stems browsed.

Table 4. Percent of aspen stems browsed compared to other browse species (willow species, paper birch, balsam poplar) within stands, exclusive of the 15-m buffer zone.

<table>
<thead>
<tr>
<th>% Relative Availability</th>
<th>% Stems Browsed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Aspen</td>
</tr>
<tr>
<td>4-yr</td>
<td>96±1</td>
</tr>
<tr>
<td>2-yr</td>
<td>98±1</td>
</tr>
</tbody>
</table>

For aspen, a highly significant relationship was found between the percent of stems browsed and distance from cover when including the stand edge for both 4 and 2-year-old stands and both years pooled (Figure 6a). There were significantly more stems browsed along the stand edge in 2-year-old stands (85±9%) than in 4-year-old stands (65±11%).

No significant relationship was found between the percent of stems browsed and distance from cover within the stands, from edge of 15-m buffer zone to stand center, within either 4 or 2-year-old stands nor when both years were pooled (Figure 6b). Within stands, exclusive of the 15-m buffer zone, there were significantly more stems browsed within 2-year-old stands (55±9%) than within 4-year-old stands (21±8%).
Figure 6a. Percent of aspen stems browsed related to distance from cover, from stand edge (3 m), for both age classes on Nenana Ridge west of Fairbanks, AK.

Figure 6b. Percent of aspen stems browsed related to distance from cover, exclusive of 15-m buffer zone, for both age classes on Nenana Ridge west of Fairbanks, AK.
Browsing Intensity – Selection at the stem scale

Browsing intensity of other browse species (willow, birch, poplar) was 40±8% for 4-year-old stands and 50±9% for 2-year-old stands, exclusive of the 15-m buffer zone, with no significant difference found between age classes.

For aspen, highly significant declines in browsing intensity were found with increasing distance from cover (mature stand edge) to stand center for both 4 and 2-year-old stands and for both age classes combined (Figures 7a). The mean browsing intensity along the stand edge (3 m) was 59±9% in 2-year-old stands which was significantly greater than 23±5% found in 4-year-old stands (Table 5).

![Figure 7a. Browsing intensity, the proportion of browsed aspen leaders per stem, as a function of distance from cover including stand edge (3 m), for both age classes on Nenana Ridge west of Fairbanks, AK.](image-url)
Table 5. Browsing intensity (% of current annual growth leaders browsed per aspen stem) and % of stems browsed within the stand (i.e., from 15 m to stand center) and along stand edge.

<table>
<thead>
<tr>
<th>Stems Browsed</th>
<th>Browsing Intensity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Within Stand</td>
</tr>
<tr>
<td></td>
<td>%</td>
</tr>
<tr>
<td>4-yr</td>
<td>21</td>
</tr>
<tr>
<td>2-yr</td>
<td>55</td>
</tr>
</tbody>
</table>

With both 4 and 2-year-old age classes combined, exclusive of the 15-m buffer, decline in browsing intensity with distance from cover was not significant (Figure 7b).

Figure 7b. Browsing intensity, the proportion of browsed aspen leaders per stem, as a function of distance from cover, exclusive of 15-m buffer zone, for both age classes on Nenana Ridge west of Fairbanks, AK.
However, a browsing intensity of 22±5% in 2-year-old stands was significantly greater than 8.3±3% found in 4-year-old stands (Table 5). No significant difference in browsing intensity within stands was found between distance strata, 15-50 m versus >50 m, for either 4 or 2-year-old stands.

The rate of decline for browsing intensity in 2-year-old stands was significantly faster than in 4-year-old stands. Figure 8 shows that the two regression lines approach a browsing intensity of zero at approximately 75 m; this suggests clearcuts extending beyond this distance for moose browse may be questionable.

![Graph showing the rate of decline in browsing intensity](image)

Figure 8. Difference in rate of decline in browsing intensity, the proportion of browsed aspen leaders per stem, as a function of distance from cover including stand edge (3 m), for both age classes on Nenana Ridge west of Fairbanks, AK.
Leader Selection

No significant relationship for diameter-at-point-of-browsing with distance from cover was found for either 4 or 2-year-old stands nor for years combined. This pattern was found both within the stand and with the edge included; thus, selectivity did not decrease with distance from cover. Because no significant relationship was found at any scale only one graph (Figure 9a) is presented for the relationship and one showing the frequency distribution of diameter-at-point-of-browsing (Figure 9b).

Figure 9a. Relationship of diameter-at-point-of-browsing with distance from cover, including stand edge (3 m), for both age classes on Nenana Ridge west of Fairbanks, AK.
Terminal leader diameter-at-point-of-browsing was significantly greater than that of lateral leaders for both age classes. However, no significant difference for diameter-at-point-of-browsing between age classes was found for either terminal or lateral leaders. The mean diameter-at-point-of-browsing of 4-year-old terminal leaders is $4 \pm 0.4$ mm and $4.4 \pm 0.2$ mm for 2-year-old leaders. Correspondingly, the mean diameter-at-point-of-browsing of 4-year-old lateral leaders is $3.1 \pm 0.1$ mm and $3.3 \pm 0.2$ mm for 2-year-old leaders (Table 6). All browsed terminal leaders sampled in the 4-year-old stands were browsed past the bud-scale scar down in to the previous year’s growth, whereas, $77 \pm 3.9\%$ of the 2-year-old terminal leaders were consumed. Although the diameter-at-point-of-
browsing means are smaller than the mean base diameters of available current annual growth, the larger bite size for terminal leaders corresponds with the larger morphology of terminals (Table 2).

Table 6. Diameter-at-point-of-browsing (dpb) and base diameter (i.e., at bud-scale scar) for terminal and lateral leaders. The dpb along stand edge was combined for both leader types.

<table>
<thead>
<tr>
<th></th>
<th>Terminal Leaders</th>
<th>Lateral Leaders</th>
<th>Terminal Leaders</th>
<th>Lateral Leaders</th>
</tr>
</thead>
<tbody>
<tr>
<td>dpb</td>
<td>Mean C.I.</td>
<td>dpb</td>
<td>Mean C.I.</td>
<td>dpb</td>
</tr>
<tr>
<td>Base</td>
<td>Mean C.I.</td>
<td>Base</td>
<td>Mean C.I.</td>
<td>Base</td>
</tr>
<tr>
<td>4-yr</td>
<td>4.0±0.4</td>
<td>3.1±0.1</td>
<td>3.4±0.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>7.5±0.7</td>
<td>6.4±0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-yr</td>
<td>4.4±0.2</td>
<td>3.3±0.2</td>
<td>3.6±0.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9.5±0.8</td>
<td>6.5±0.8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

No test was performed to determine if previously browsed stems were preferred because complete sampling of previous browsing was not possible. However, a cursory survey of the data collected provided no evidence to suggest that stems with more leaders, possibly a result of previous browsing, were preferred. Also, approximately 55% of stems in 4-year-old stands were previously browsed; this is equivalent to current browsing within 2-year-old stands. All data indicate moose were selective within these aspen stands.
Coarse Woody Debris and Cover

No relationship was observed in browsing intensity among the three coarse woody debris variables (height, diameter, cover) within either the 4 or 2-year-old stands (Table 7). This was expected, based on visual observation, from where large jackstrawed logs were suspended over 1 m high and had created a "corral" effect, but stems beyond the physical reach of moose were browsed; thus, moose were not inhibited in jumping over the logs.

Table 7. Coarse woody debris (CWD) dimensions of mature aspen: Height of the highest suspended log, diameter of the largest log, and percent ground cover.

<table>
<thead>
<tr>
<th>CWD means with 95% C.I.</th>
<th>Height (cm)</th>
<th>Diameter (cm)</th>
<th>% Cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>4-yr</td>
<td>62 ±5</td>
<td>21 ±2</td>
<td>42 ±3</td>
</tr>
<tr>
<td>2-yr</td>
<td>57 ±5</td>
<td>16 ±1</td>
<td>47 ±3</td>
</tr>
</tbody>
</table>

There was no significant difference in height between age classes, but diameter was significantly greater in 4-year-old stands. The 2-year-old stands had significantly more percent ground cover (Table 7). Thus, it is inconclusive if CWD affected browse use between years.
Horizontal cover in 4-year-old stands was consistently only 25% and assumed insufficient to conceal a moose within clearcut stands during winter (Courtois et al. 1998). To address the importance of cover requires sampling from stands with higher cover values.

Snow depth of < 25 cm was observed on the study site in March 2002 and at other locations along Nenana Ridge throughout the winter. Thus, snow depth was not considered a factor in movement (Coady 1974) nor was browse availability to moose (LeResche and Davis 1973). Temperatures during winter 2002 were above normal; it is unknown if foraging behavior was significantly affected due to heat stress (Renecker and Hudson 1986a).

**Browse Quality**

Consistent with Schwartz et al. (1988) *In vitro* dry matter digestibility (IVDMD) and hemicellulose were significantly higher in aspen than in the other browse species; no significant differences occurred among other forage quality measures (crude protein, cellulose and lignin) (Table 8). No significant difference for aspen quality components were found between age classes. Sample size for other species was too small to test.

A specific use of aspen by moose, not well studied, is consumption of bark of mature aspen. From personal observation, bark-stripping on standing and downed mature aspen trees occurred from autumn through spring, primarily along stand edges.
Table 8. Forage quality of hardwood browse in aspen clearcuts from late winter 2002. Other browse represents a mixture of paper birch, balsam poplar, and willow species.

<table>
<thead>
<tr>
<th>Dry Matter (%)</th>
<th>Aspen</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>C.I.</td>
</tr>
<tr>
<td>IVDMD</td>
<td>54.45</td>
<td>±2.42</td>
</tr>
<tr>
<td>CP</td>
<td>7.57</td>
<td>±0.33</td>
</tr>
<tr>
<td>NDF</td>
<td>57.5</td>
<td>±2.03</td>
</tr>
<tr>
<td>ADF</td>
<td>37.13</td>
<td>±1.44</td>
</tr>
<tr>
<td>Hemicellulose</td>
<td>20.37</td>
<td>±0.99</td>
</tr>
<tr>
<td>Cellulose</td>
<td>26.39</td>
<td>±1.62</td>
</tr>
<tr>
<td>Lignin</td>
<td>10.74</td>
<td>±0.84</td>
</tr>
</tbody>
</table>
DISCUSSION

Current Annual Growth (CAG) Biomass of Aspen Leaders

The use of terminal leader diameter at the base of current annual growth (CAG), immediately above the bud-scale scar, for estimating total stem CAG biomass production was shown in this study. This relationship \( Y = -23.031 + 6.107X \) has potential for efficiently estimating browse production of an individual aspen stem. Only as a single measurement is required, the base diameter of the terminal leader. This provides a non-destructive sampling technique that is less expensive and time consuming and will not interfere with future measurements.

Before accepting this model as standard for Alaska, additional sampling is required to address possible regional and site quality differences in Alaska. Within Alaska, potential growth differences may exist between regions (e.g., eastern interior Alaska versus western interior Alaska vs. Copper River Basin vs. southcentral Alaska vs. the Kenai Peninsula) (Zasada and Packee 1995). Because site quality, based on site index, can be highly variable (Gregory and Haack 1965) additional sampling among and within regions is needed to test the validity of the reported relationship.

Aspen in Alaska, at least during early stages of development in terms of stems per hectare, is comparable to production found across the southerly extent of its range and especially in the Rocky Mountain region (Peralta 1990; Telfer 1993). For site conditions similar to those described for this study site, regeneration of aspen from coppice without removal of cut stems is a viable silvicultural system and an alternative to prescribed burning for reinitiating aspen stands.
After two growing seasons, regeneration of all hardwood browse species of all ages within the clear-felled aspen stands, irrespective of abundant coarse woody debris, equaled or surpassed a conservative total stem density management objective of 30,000 stems/ha (Paragi and Haggstrom 2004). Although the stand initiation objective for this study site was for ruffed grouse habitat, canopy and understory conditions for brood rearing do not develop for at least 5 years after clearcutting, at which time adequate stem density for habitat is 22,000 stems/ha (Gullion 1984). During the first few years of stand initiation, before use by grouse begins, the hardwood component is attractive to moose when the most CAG is available for browse.

Site condition, pre-disturbance stand composition, and disturbance characteristics influence stand development (Oliver and Larson 1996). Because clear-felling was the major disturbance of the mature aspen of this study, variability in aspen sucker density among stands in this study may have been influenced by general site attributes such as microtopography and slope. The stand with the greatest stem density, estimated at 43,500 stems/ha, had the least topographic variability (i.e., fewer gullies) and relatively steep slope, thus, received more sun per unit area. In contrast, the stand with the most gentle slope had lower solar incidence and had a stem density estimate of less than 23,300 stems/ha. This demonstrates the importance of site specific silvicultural prescriptions for achieving management goals, particularly in interior Alaska, as suggested by Zasada and Packee (1995) and Collins and Schwartz (1998).

Management objectives must be viewed at the habitat and forest scale because differences in aspen stem densities among stands begin to equalize from stand initiation
through the competitive exclusion stage of stand development (Bella 1986; Oliver and Larson 1996). Stem densities below an initial objective threshold during early stand development may be sufficient for grouse habitat later in stand development (Gullion 1984). There is no established production objective for moose in terms of stems per unit area.

Objectives may be based on optimal habitat conditions for a particular wildlife species; if stem density is less than the objective’s threshold the habitat may be considered adequate because the habitat components will still be used. For example, ruffed grouse can be found where aspen and birch are sparse (personal observation). The goal for grouse and moose may be a large number of stems per hectare (>25,000) but fewer stems will provide supplemental habitat components for grouse and provide cover habitat for moose given the stand will likely be a mixed with spruce early in the stands development. Also, a mixed stand that results from low stem densities typically provides habitat diversity for other species (Paragi and Haggstrom 2001).

Diversity within stands, however, does not always provide desirable habitat. Competitive species during stand initiation should be a concern (Collins and Schwartz 1998). Aggressive herbaceous species such as bluejoint reedgrass (Calamagrostis canadensis (Michx.)) may impact growth of aspen by lowering soil temperature and competing for light and nutrients during stand initiation (Landhausser and Lieffers 1998).

Post-logging treatments can control bluejoint and provide good site conditions for regeneration of hardwood species (Collins and Schwartz 1998). The benefit from felling and extraction operations when the ground is frozen is that aspen regeneration from
suckering is good on non-scarified sites; scarification that exposes mineral soil can increase the regeneration potential of birch, willow, and white spruce (Collins and Schwartz 1998). Rapid and prolific suckering of aspen within these unscarified felled stands subdues bluejoint establishment. Extensive establishment of bluejoint, however, did occur in adjacent timber sales of the study area where scarification by skidding during summer may have damaged the root system of aspen. Thus, without a demand for aspen fiber, felling alone to produce browse is a legitimate alternative for regenerating a hardwood stand.

**Coarse Woody Debris (CWD)**

The CWD conditions in this study are an example of heavy slash conditions that could inhibit suckering of aspen. Because stem densities met grouse management objectives the silvicultural question is to identify stand characteristics where felling without fiber extraction will be an effective method for regenerating and maintaining aspen stands. For example, variation in stem densities is influenced by site preparation, such as windrowing and skidding (Paragi and Haggstrom 2004). Thus, the need for CWD management (i.e., removal or reduction) must be considered. This study suggests that CWD is acceptable for moose habitat.

For long-term stand development the issue of CWD retention for maintaining good site conditions and biodiversity (Hunter 1990; McComb and Lindenmayer 1999) is more than satisfied for these stands. The effects on site condition that will accrue from the input of large volumes of CWD it is unknown. Positive inputs to stand dynamics (e.g.,
exposed mineral soil) normally created by windthrow (Oliver and Larson 1996) and site preparation techniques (Smith et al. 1997) are not produced from felling alone, but are not required for aspen regeneration (Collins and Schwartz 1998). This study further suggests that removal of CWD, at least on southerly facing hillsides, is also not required for adequate aspen regeneration.

To accurately relate CWD with stem densities requires correlations with CWD volume, stem attributes (i.e., tree crowns relative to smooth boles), and ground coverage values (i.e., proportion of logs in contact with the ground) with different felling patterns and stem densities. This study did not address these concerns because the differences in conditions were not provided in the study area.

The question concerning CWD was not whether moose used these stands, but rather how their browsing behavior is affected by these stand conditions. Moose move slowly when browsing, but their modified cursorial gate (Geist 1998) allows them to move effectively through such stand conditions and is akin to deep snow (personal observation). Moose may avoid negotiating over suspended jackstrawed logs at a normal browsing pace likely causing their pattern of travel to be non-linear and incremental – backtracking in order to proceed in a given direction.

CWD may influence the travel pattern of moose through young stands, but it did not restrict browse availability, nor influence selection of individual stems. Thus, the distribution and characteristics of CWD may best be viewed at the stand scale where it may influence foraging efficiency and risk of predation.
Stand composition can also affect the achievement of objectives. If the objective is to produce available browse for moose one concern is the amount of mature white spruce CWD that may render some browse unavailable. The stout, perpendicular stem structure along the bole of mature white spruce, in contrast to the limbless boles of aspen, is an effective barrier to deer and elk (Grisez 1960; Ripple and Larsen 2001) and possibly moose.

If any aspect of browsing is governed by CWD, stem density, or both could not be determined. Contrary to the observations of Vivas and Saether (1987) where more stems were browsed in stands of higher stem density, the number of aspen stems browsed in the Nenana Ridge stands decreased significantly within a short distance from the stand edge. However, browsing intensity within the stands, beyond the 15-m buffer zone, did not decrease significantly with distance from stand edge. This suggests CWD did not inhibit browsing per se. Figures 6a and 6b suggest CWD simply interrupts the browsing path of moose.

Impacts from CWD on other wildlife should be considered. For example, dense stands may provide cover for grouse from avian predators and browse for moose. But, CWD may increase predation rate on grouse from mammalian predators and remains to be investigated for interior Alaska.

**Browse selection at the stand scale**

Selection of browse at the stand scale is influenced by stand composition (Danell et al. 1991), stem density (Lundberg and Danell 1990), and abundance of available browse...
(Andersen and Saether 1992). However, preference for different browse species and partial consumption of plant parts suggests stems can also be considered the scale browsers select from within a stand (Astrom et al. 1990).

Moose, in this study, demonstrated selectivity at the stand scale by showing a distinct preference for other browse species over aspen within the clear-felled stands (Table 4). Preference for browse species found at low densities is common and thought to be influenced by either relative availability (Danell and Ericson 1986) or to satisfy nutrient requirements provided through a mixed diet (Belovsky 1981). Based on visual observations, however, selection of aspen stems appeared equitable with other browse species outside of the clear-felled stands; browse use appeared proportional to availability along stand edges, within mature timber, along the road, and within cutover timber sales.

Stem density has been shown to affect browse selection (Vivas and Saether 1987; Lundberg and Danell 1990 Andersen and Saether 1992; Shipley and Spalinger 1995). Although the young aspen stands in this study are considered simply “dense,” when compared to patches of aspen distributed throughout the larger study area they provide an opportunity for moose to be selective.

Figure 6a shows how aspen use declines significantly once moose enter dense aspen stands. The insignificant decline and weak correlation in the proportion of stems browsed with distance from cover “within” the stands suggests browse use by moose may be influenced more by stem density and stand composition than from distance from cover at least within 100 m from stand edge cover.
Although these inferences of browse use are derived from regressions on distance from cover are limited within a distance of 100 m, browse utilization is consistent with Hamilton et al. (1980) and Mastenbrook and Cumming (1989) who found that browse use within young regenerating clearcuts does not change significantly within 100 m from cover.

**Browse selection at the stem scale**

The pattern of browsing intensity of aspen (Figures 7a and 7b) is similar to that observed with the proportion of stems browsed and selected for other species. The greater browsing intensity along stand edges (Table 5) only confirms, however, that moose have an affinity for stand edges, most likely related to the proximity of cover. The lack of a relationship between browsing intensity and distance from cover suggests that moose are not affected solely by distance from the edge of cover. Consistent with Vivas and Saether (1987) the browsing intensity was lower within the dense stands, thus, I believe stem density may influence the browse selectivity of moose within these high-density aspen stands.

A possible confounding factor affecting browsing intensity is how moose perceive their environment. As an herbivore, moose have a wide visual range when looking forward and behavior can be influenced by environmental cues (Bubenik 1997) including, possibly, stem density. Thus, one could speculate that high browsing intensity along stand edges may be influenced by moose perceiving browse abundance differently than within stands.
Differences in browsing intensity between age classes may be the result of confounding factors associated with stem architecture (Vivas and Saether 1987). Greater browsing intensity and proportion of stems browsed in 2-year-old stands is expected given that there are fewer leaders per stem and the that all leaders are available to both adults and calves. Also, leaders of willow and 2-year-old aspen are commonly parallel to one another, thus, predisposed to heavier browsing. Leaders of 4-year-old aspen, on the other hand, tend to protrude at perpendicular angles relative to the main stem.

It is unknown if the faster rate in decline in BI with distance from cover (Figure 8) within 2-year-old stands is related to biomass availability or possibly a complete lack of cover within the stand. Molvar and Bowyer (1994) found that cows with calves fed less efficiently farther from cover. It is possible that the cover 4-year-old stands provide tempered the rate of decline in browsing intensity through the stands. Thus, evaluating differences between age classes at such a fine scale in order to relate browse use with stem structure may be misleading.

Increasing cover within a stand corresponds with increased patchiness of stem distribution and lower stem density and, thus, available browse. Because moose do forage in the open, it may be more practical to consider distance to the edge of cover and attributes of cover within large stands such as remnant patches of mature timber rather than percent horizontal cover through a stand.
Leader selection

The significantly higher biomass of terminal aspen leaders corresponds to the larger diameter-at-point-of-browsing compared to lateral leaders. Terminal leaders selected were much smaller than those available (Tables 2 and 5). The diameter-at-point-of-browsing for both leader types was smaller than the mean bud-scale scar diameter of the current year’s leader. Although the general pattern of selection is for stems with large leaders, the tendency for taking smaller diameter bites when selecting leaders in dense stands is consistent with Vivas and Saether (1987). This pattern illustrates that moose take bites within a range around some “optimal” bite size (Vivas et al. 1991; Kielland and Osborne 1998) that is smaller than what is available and what the moose can physically handle.

Preference for other browse species is not consistent with quality in terms of digestibility (Weixelman 1998; Vivas et al. 1991). The shortcoming in attempting to directly relate browse selection with quality characteristics is that we do not know the range of nutritional mixtures within which moose operate (Belovsky 1981, 1984). Also, the factor of secondary metabolites used for chemical defense by plants (Bryant and Kuropat 1980; Bryant et al. 1983) must be addressed concurrently with browse quality measures.

Because browse quality at the leader scale changes with leader size (Hjeljord et al. 1982) it may be more informative to relate browse selection based on quality related to diameter-at-point-of-browsing. Diameter-at-point-of-browsing found to be smaller or larger than predicted “optimal” diameters may indicate range conditions where quality
browse is limited (Kielland and Osborne 1998). Also, when evaluating range carrying capacity, plant morphology (degree of brooming) and available bite diameters should be considered rather than simply twig counts (Kielland and Osborne 1998; Seaton 2002).

The lack of significant relationships between diameter-at-point-of-browsing and distance from cover, again, suggests the idea that 100 m from the stand edge is reasonable for moose browse habitat.

A preference for stems with more leaders, indicative of moose selecting previously browsed stems (Bowyer and Bowyer 1997) was not observed. Over half of the aspen stems were previously browsed, but apparently previous browsing intensity within these dense aspen stands was not high enough to elicit compensatory growth of leaders to influence browse use in such dense stands.
Habitat requirements for many wildlife species commonly include a variety of different age classes, species, and structural characteristics. The spatial and temporal scales at which moose function encompass many habitat types (Crichton 1998). Thus, for management purposes, both large (forest) and small (stand) scale strategies and prescriptions must be developed and tailored to ownership goals. Nyland (2002) states that before applying management strategies or practices at the large scale, silvicultural questions at the stand scale must be addressed. Furthermore, because habitat manipulation impacts ecosystems (Spies and Turner 1999), in terms of ecological conditions and species' requirements, it is imperative for the resource manager to understand what actions affect the species and systems beyond the scope of their primary objective.

The specific objective at the large scale must be well-defined: Is it to maximize available moose browse, ruffed-grouse habitat, or habitat that benefits both moose and grouse? In all three cases, the silvicultural prescription to produce moose browse and grouse habitat from mature aspen stands involves stand-replacement methods which could be clear-felling or prescribed fire. Planning is required to produce the desired mix of forage and adjacent cover and this includes developing, across the landscape, a mosaic of stands having different structural characteristics, sizes, and shapes (Hunter 1990). For example, the amount of edge, once considered a benefit for game species, in general (Leopold 1933), must be limited for certain species such as ruffed grouse that benefit more from stands with more extensive interior stand habitat (Hunter 1990). Conversely,
minimizing distance from cover by maximizing stand edge will maximize browse use by moose.

Results from this study suggest a distance from stand edge of 75 to 100 m. This should provide an adequate stand size to meet the habitat needs of ruffed grouse (Gullion 1984) and not predispose stands to overbrowsing by moose.

To address the potential habitat needs and impacts by moose and the overall benefits of the prescription to all species concerned, it is imperative to know population characteristics of the wildlife species of interest are across the landscape. In the Tanana Valley State Forest, there are extensive areas where ruffed grouse are of limited occurrence. Moose are relatively ubiquitous, but population densities vary by landscape conditions (Bowyer et al. 1997). In terms of moose, the population in terms of carrying capacity of the habitat and the factors controlling the density of the moose population must be known (Gasaway et al. 1992; Hundertmark and Schwartz 1996; Rempel et al. 1997; Kie et al. 2003). Poor stands in terms of forage production or small stands with abundant forage production can receive heavy browsing pressure by a moose population at or near the carrying capacity of the range. Such heavy browsing can impact survival of the browse species, impact stand composition, eliminate a seral stage completely, or increase the rate of succession from hardwoods to conifers and change the desired management path of stand development (Bergerud and Manuel 1968; Risenhoover and Maass 1987; Pastor et al. 1988; Andrews 1998; Connor et al. 2000).

At the smaller stand scale, the silvicultural prescription must address the clear-felling effort in terms of size (width and length), edge creation, and species composition
(overstory and understory). The options to burn or clear-fell are related to location and topography. Understory considerations include presence of advance conifer regeneration or evidence that bluejoint grass might take over the site. At the small stand scale some private owners may wish to intensively manage the aspen coppice. For example they may wish to slow down development of the overstory by cutting the dominant trees and encourage greater browse production. Alternatively, they may want to encourage aspen stem development but, concurrently, maintain the amount of browse available to moose by pruning the non-crop trees to create smaller aspen stems with more leader growth. Pruning can induce multi-leader development and, although smaller, the many branched plant will have a greater amount of available browse biomass per stem (Maini 1966; Bergstrom and Danell 1987a; Bowyer and Bowyer 19771).

Managing for specific habitat components for moose and grouse, at both the large and small scale, will benefit biodiversity in general (Hunter 1999; Thompson and Angelstam 1999). The mixture of structural components will provide habitat for numerous wildlife species (Hunter 1990). Aspen supports a broad diversity of wildlife throughout stand development; this is particularly true for avian species (DeByle 1981, 1985b; Gullion 1984). If both wildlife managers and foresters understand the silvicultural techniques and the habitat requirements of the biota, management for both wildlife and wood fiber can be effective (Thompson and Stewart 1997).
CONCLUSIONS AND RECOMMENDATIONS

Clear-felling of aspen without the removal of the mature stems is suitable for the creation of moose browse habitat. Coarse woody debris jackstrawed on hillsides with southerly aspects does not impede the aspen root suckering; sufficient if not prolific suckering occurs. Additional research is needed to confirm the results of this study on similar sites throughout Alaska and on other types of aspen-producing sites.

The potential use of diameter at the bud-scale scar at the base of the terminal leader for estimating total individual current annual growth biomass was demonstrated. This approach has the potential of avoiding destructive sampling and reducing the amount of time required to sample by eliminating clipping, transporting of samples to the laboratory, oven-drying, and weighing as called for in the present protocol. Additional research is needed to test the validity of this approach and to refine the model. The model must be tested within the region as well as elsewhere throughout Alaska on a variety of site-types and for a range of aspen site indices (site quality). A single model may not be sufficient to adequately predict biomass; site specific models by region or site index may be required.

The use of a similar model to estimate available or useable browse based on the diameter of the terminal leader should be investigated. This will require determination of either an optimal browse diameter or a mean bite diameter and then the correlation between leader diameter and finally the correlation with potential browse biomass.
Based on this study, coarse woody debris resulting from clear-felling without stem removal does not impede moose browsing; all current annual browse is accessible to moose.

Moose browsing decreases from the edge of cover (mature stand) into the center of clear-felled stands. Moose browsing intensity within the first 15 m from the edge of cover is greater than farther from the edge of cover. This edge effect is an important consideration in determining clear-felling stand dimensions. Based on this study, moose browsing activity is greatly reduced 75 to 100 m of the stand edge; thus maximum width of clear-felled units should be between 150 and 200 m to maximize browse utilization by moose.
Appendix 1. Scientific and common names of native Alaskan species on the Nenana Ridge study site.

<table>
<thead>
<tr>
<th>Genus-species</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Animals</strong></td>
<td></td>
</tr>
<tr>
<td><em>Alces alces gigas</em> Miller</td>
<td>Alaskan moose</td>
</tr>
<tr>
<td><em>Bonasa umbellus</em></td>
<td>Ruffed grouse</td>
</tr>
<tr>
<td><strong>Trees</strong></td>
<td></td>
</tr>
<tr>
<td><em>Populus tremuloides</em> Michx.</td>
<td>Quaking aspen</td>
</tr>
<tr>
<td><em>P. balsamifera</em> L.</td>
<td>Balsam poplar</td>
</tr>
<tr>
<td><em>Betula nealaskana</em> Sarg.</td>
<td>Paper birch</td>
</tr>
<tr>
<td><em>Picea glauca</em> (Moench) Voss</td>
<td>White spruce</td>
</tr>
<tr>
<td><em>Picea mariana</em> (Mill.) B.S.P.</td>
<td>Black spruce</td>
</tr>
<tr>
<td><em>Salix</em> spp.</td>
<td>Willow</td>
</tr>
<tr>
<td><em>S. alexensis</em> (Anderss.) Cov.</td>
<td>Feltleaf willow</td>
</tr>
<tr>
<td><em>Alnus</em> spp. Mill.</td>
<td>Alder</td>
</tr>
<tr>
<td><em>A. crispa</em> (Ait.) Pursh</td>
<td>American green alder</td>
</tr>
<tr>
<td><strong>Shrubs</strong></td>
<td></td>
</tr>
<tr>
<td><em>Shepherdia canadensis</em> L.</td>
<td>Buffaloberry (soapberry)</td>
</tr>
<tr>
<td><em>Rosa acicularis</em> Lindl.</td>
<td>Wild (prickly) rose</td>
</tr>
<tr>
<td><em>Linnaea borealis</em> L.</td>
<td>Twin flower</td>
</tr>
<tr>
<td><em>Viburnum edule</em> (Michx.) Raf.</td>
<td>High-bush cranberry</td>
</tr>
<tr>
<td><em>Rubus idaeus</em> L.</td>
<td>Raspberry</td>
</tr>
<tr>
<td><em>Arctostaphylos uva-ursi</em> L.</td>
<td>Bearberry (Kinnikinnick)</td>
</tr>
<tr>
<td><strong>Herbaceous plants</strong></td>
<td></td>
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<tr>
<td><em>Galium boreale</em> L.</td>
<td>Northern bedstraw</td>
</tr>
<tr>
<td><em>Geocaulon lividum</em> (Richards.) Fern.</td>
<td>Bastard toadflax</td>
</tr>
<tr>
<td><em>Pyrola</em> spp. L.</td>
<td>Wintergreen</td>
</tr>
<tr>
<td><em>Calamagrostis canadensis</em> (Michx.) Beauv.</td>
<td>Blue-joint reedgrass</td>
</tr>
</tbody>
</table>
Appendix 2. Regression functions and significance values for aspen current annual growth dry biomass and browse use.

**Current Annual Growth biomass (g) related to leader diameter (mm):**

4-year (Fig. 5a): \[\log(g) = -1.183 + 0.305\text{mm}; \quad F = 3.84; \quad 1, 493 \text{ df}; \quad R^2 = 0.84; \quad P < 0.0001\]

2-year (Fig. 5b): \[\log(g) = -1.267 + 0.326\text{mm}; \quad F = 3.86; \quad 1, 462 \text{ df}; \quad R^2 = 0.87; \quad P < 0.0001\]

CAG related to terminal leader (age classes pooled) (Fig. 5c):
\[g = -23.031 + 6.107\text{mm}; \quad F = 4.0; \quad 1, 58 \text{ df}; \quad R^2 = 0.53; \quad P < 0.0001\]

4-year: t-test between terminal and primary lateral leader diameter, length, and dry biomass (P-values = 0.03, 0.035, and 0.01 for, respectively)

2-year: t-test between terminal and primary lateral leader diameter, length, and dry biomass (P-values < 0.0001, 0.0003, and 0.001 for, respectively)

T-test between age classes for terminal leader diameter, length, and dry biomass (P-values = 0.005, 0.005, 0.02, respectively)

T-test between age classes for primary lateral leader diameter, length, and dry biomass (P-values = 0.8, 0.15, 0.36, respectively)

T-test between age classes for number of leaders per stem (P < 0.0001)

T-test between age classes for mean current annual growth (P = 0.27)

T-test between age classes for sucker density (P = 0.36)

**Proportion of stems browsed:**

Entire stand, from edge to center

4-year: Percent stems browsed = 0.692 - 0.008m; \(F = 3.9; \quad 1, 118 \text{ df}; \quad R^2 = 0.26; \quad P < 0.0001\)

2-year: Percent stems browsed = 0.843 - 0.006m; \(F = 3.9; \quad 1, 118 \text{ df}; \quad R^2 = 0.15; \quad P < 0.0001\)
Years pooled (Fig. 6a): Percent stems browsed = 0.771 – 0.007m; F = 3.8; 1, 238 df; 
$R^2 = 0.2$; $P < 0.0001$

Within stand, exclusive of the 15 m buffer zone, inward to stand center

4-year: Percent stems browsed = 0.337 – 0.003m; F = 4.0; 1, 58 df; $R^2 = 0.04$; 
$P = 0.12$

2-year: Percent stems browsed = 0.698 – 0.003m; F = 4.0; 1, 58 df; $R^2 = 0.03$; 
$P = 0.16$

Years pooled (Fig. 6b): Percent stems browsed = 0.523 – 0.003m; F = 3.9; 1, 118 df; 
$R^2 = 0.03$; $P = 0.05$

T-test between age classes for percent of stems browsed along edge stand ($P < 0.0001$)

T-test between age classes for percent of stems browsed within stand ($P < 0.0001$)

**Browsing Intensity (BI):**

Entire stand, from edge to center

4-year: $BI = 0.289 – 0.004m$; F = 4.0; 1, 66 df; $R^2 = 0.24$; $P < 0.0001$

2-year: $BI = 0.666 – 0.009m$; F = 3.95; 1, 98 df; $R^2 = 0.44$; $P < 0.0001$

Years pooled (Fig. 7a): LogBI = -0.409 – 0.01m; F = 4; 1, 168 df; $R^2 = 0.33$; 
$P < 0.0001$

Within stand, exclusive of the 15 m buffer zone, inward to stand center

4-year: $BI = 0.131 – 0.001m$; F = 4.3; 1, 22 df; $R^2 = 0.13$; $P = 0.08$

2-year: $BI = 0.327 – 0.002m$; F = 4.1; 1, 48 df; $R^2 = 0.06$; $P = 0.09$

Years pooled (Fig. 7b): $BI = 0.255 – 0.002m$; F = 4.0; 1, 74 df; $R^2 = 0.05$; $P = 0.06$

T-test between age classes for browsing intensity of other species ($P = 0.13$)

T-test between age classes for browsing intensity of aspen along stand edge 
($P < 0.0001$)

T-test between age classes for browsing intensity of aspen within stand ($P < 0.0001$)
ANOVA between distance strata within stands for 4 and 2-year-old stands (P = 0.29 and 0.23, respectively)

F-test between age classes for slopes of browsing intensity (P = 0.0005)

**Diameter-at-point-of-browsing (dpb):**

Whole stand, from edge to center

4-year: \( \text{dpb} = 3.388 - 0.002m; F = 3.8; 1, 311 \text{ df}; R^2 = 0.004; P = 0.26 \)

2-year: \( \text{dpb} = 3.686 + 0.004m; F = 3.8; 1, 316 \text{ df}; R^2 = 0.007; P = 0.15 \)

Years pooled (Fig. 9): \( \text{dpb} = 3.505 + 0.003m; F = 3.8; 1, 629 \text{ df}; R^2 = 0.004; P = 0.1 \)

Within stand, exclusive of the 15 m buffer zone, inward to stand center

4-year: \( \text{dpb} = 3.236 + 0.0007m; F = 3.8; 1, 143 \text{ df}; R^2 = 0.003; P = 0.8 \)

2-year: \( \text{dpb} = 4.062 - 0.004m; F = 3.8; 1, 207 \text{ df}; R^2 = 0.004; P = 0.4 \)

Years pooled: \( \text{dpb} = 3.639 + 0.0001m; F = 3.8; 1, 352 \text{ df}; R^2 = 0.001; P = 0.97 \)

T-test between terminal and primary lateral leader dbp for both age classes (P < 0.0001)

T-test between age classes for dbp of both terminal and primary lateral leader (P = 0.06 and 0.2, respectively)

**Coarse Woody Debris (CWD):**

Multiple regression of browsing intensity related to cwd height, diameter, and percent ground cover for both 4 and 2-year-old stands (P = 0.56 and 0.55, respectively)

T-test between age classes for cwd height, diameter, and percent ground cover (P = 0.2, 0.001, and 0.02, respectively)
Browse Quality:

T-test between aspen and other browse species for IVDMD and hemicellulose (P = 0.006 and 0.03, respectively – all other components P > 0.15)

ANOVA for aspen quality components between age classes (P = 0.3)
Appendix 3. List of acronyms.

<table>
<thead>
<tr>
<th>Acronym</th>
<th>Definition</th>
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<tbody>
<tr>
<td>ADF&amp;G</td>
<td>Alaska Department of Fish &amp; Game</td>
</tr>
<tr>
<td>ADNR</td>
<td>Alaska Department of Natural Resources</td>
</tr>
<tr>
<td>ANOVA</td>
<td>analysis of variance</td>
</tr>
<tr>
<td>BI</td>
<td>browsing intensity</td>
</tr>
<tr>
<td>C</td>
<td>Celsius</td>
</tr>
<tr>
<td>CAG</td>
<td>current annual growth</td>
</tr>
<tr>
<td>cm</td>
<td>centimeter</td>
</tr>
<tr>
<td>CWD</td>
<td>coarse woody debris</td>
</tr>
<tr>
<td>dpb</td>
<td>diameter at point of browsing</td>
</tr>
<tr>
<td>DM</td>
<td>dry matter</td>
</tr>
<tr>
<td>ha</td>
<td>hectare</td>
</tr>
<tr>
<td>IVDMD</td>
<td><em>in vitro</em> dry matter digestibility</td>
</tr>
<tr>
<td>K</td>
<td>carrying capacity</td>
</tr>
<tr>
<td>Km</td>
<td>kilometer</td>
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<tr>
<td>m</td>
<td>meter</td>
</tr>
<tr>
<td>mm</td>
<td>millimeter</td>
</tr>
<tr>
<td>SE</td>
<td>standard error</td>
</tr>
<tr>
<td>TVSF</td>
<td>Tanana Valley State Forest</td>
</tr>
<tr>
<td>UAF</td>
<td>University of Alaska Fairbanks</td>
</tr>
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</table>
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