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Author(s): Erik M. Molvar, R. Terry Bowyer, Victor Van Ballenberghe, V. Van Braunenberone

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Original papers

Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community

Erik M. Molvar¹, R. Terry Bowyer², Victor Van Ballenberghe²

¹ Institute of Arctic Biology, and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

² Pacific Northwest Research Station, U.S. Forest Service, 201 East 9th Avenue, Suite 206, Anchorage, AK 99501, USA

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Abstract. Moose (*Alces alces*) browsing on diamondleaf willow (*Salix planifolia pulchra*) caused significant increases in subsequent growth of stems and leaves in tree-line plant communities in central Alaska, USA. Willows growing in the shade were significantly more palatable for moose than those growing in the sun. Moose density had strong effects on rates of nutrient cycling, ostensibly through effects of browsing and inputs from fecal and urinary nitrogen. Moose are a keystone herbivore that likely mediate rates of nutrient cycling in northern ecosystems.

Key words: *Alces alces* – Moose – Nutrient cycling – *Salix* – Willow

Browsing by herbivores has numerous effects on boreal plant communities. Changes in composition of plant communities occur as palatable plants are eaten by herbivores and thereby reduced in frequency (Snyder and Janke 1976; Pastor et al. 1988). Cropping by herbivores also results in plants of shorter growth form (Grimes 1977; Hytteborn et al. 1987; Brandner et al. 1990). Additionally, browsing may alter plant carbon-nutrient balance. Moderate levels of browsing result in increased growth (Bergstrom and Danell 1987), and leaf nutrient content (Garrison 1972), as well as decreased levels of secondary defense compounds when plants are stressed by herbivory (Bryant et al. 1983). Nonetheless, extreme levels of herbivory may cause boreal shrubs to revert to an unpalatable juvenile form (Bryant 1981; Bryant et al. 1983).

Finally, herbivores may facilitate nutrient transfer into the soil. Urinary nitrogen enriches soil and can stimulate plant growth (Day and Detling 1990; Jaramillo and Detling 1992). Fecal inputs of nitrogen may significantly boost soil nitrogen mineralization (Ruess and McNaughton 1987) leading to increased rates of plant

growth (Bazely and Jefferies 1985; Hik and Jefferies 1990). Further, decaying carcasses increase soil productivity on a microsite basis, which can cause local shifts in plant distribution (McKendrick et al. 1980). These effects are known to draw herbivores back to fertilized areas (Day and Detling 1990), initiating positive feedback loops and increasing rates of nutrient cycling (Bryant and Chapin 1986). Only at high population density do large herbivores exceed the ability of their food resources to support them, and thereby initiate strong negative feedbacks (McCullough 1979). Because nutrients are major factors limiting primary productivity in boreal environments (Haag 1974; Moore 1980), herbivores could have a strong influence on plant productivity and species composition.

At the community level, herbivores may maintain patches of high-quality vegetation, resulting in a long-term increase in rates of nutrient cycling, as modeled by Pastor and Naiman (1992). This phenomenon has been termed “herbivore optimization” (Hik and Jefferies 1990). Moose (*Alces alces*) are known to make extensive use of browse in boreal ecosystems (Ludewig and Bowyer 1985; Joyal 1986; Van Ballenberghe et al. 1989). Experimental clipping and defoliation studies, however, do not accurately mimic the foraging patterns of herbivores (Archer and Tieszen 1980, Baldwin 1990), and thus have limited applications. Consequently, we examined effects of the browsing of free-ranging moose on an undisturbed ecosystem to test the effects of herbivores upon morphological characteristics of willows, their quality as forage, and rates of nitrogen mineralization.

Hypotheses

We investigated the following hypotheses concerning the factors that affect plant growth and nutrient cycling in treeline communities. C is more limiting, relative to other nutrients, in woody plants growing in the shade compared to plants in full sunlight (Bryant and Chapin 1986). Thereby, overall plant growth, the C:N ratio,

and C-based plant defenses are lower in the shade than in full sunlight (Bryant et al. 1983, 1991). Thus, we postulate that shaded plants should be of higher forage quality than those growing in the sun.

We also hypothesized that willow productivity per growing point should be higher in an area of high moose density due to fertilization by urine and feces from moose. Furthermore, because of release from apical dominance, annual productivity per stem and per leaf should increase with browsing intensity until the plant is killed or reverts to juvenility (Bryant et al. 1991, 1992). Carbon-balance theory suggests that the lateral stems from a browsed twig should have greater rates of growth than unbrowsed twigs on the same plant. Thus, we hypothesize that individual stems that are browsed by moose will show greater regrowth than unbrowsed stems on the same plant.

Finally, we hypothesize that differences in the chemistry of plant litter and nutrients affected by moose density should lead to increased rates of decomposition as the intensity of moose utilization of an area increases. These increases in decomposition rates should be reflected in higher rates of soil respiration and nitrogen mineralization. Answers to these questions should provide insights into whether moose herbivory optimizes future forage quality of woody plants at moderate levels of browsing, and results in increased nutrient cycling on a local level.

Study area

Our study area is comprised of treeline areas in the Jenny Creek and Savage River drainages of Denali National Park and Preserve, in central Alaska, USA (63°45' N, 150° W). This area is dominated by open shrub tundra with a large component of resin birch (*Betula glandulosa*), which is of little forage value to moose (Van Ballenberghe et al. 1989). Interspersed along the sides of the valley are open-canopy patches of spruce (*Picea* spp.) that have large components of willow (*Salix* spp.) in the understory. Van Ballenberghe (in press), who described the study area in detail, noted that fire is uncommon in these treeline habitats.

In our study area, moose exerted the greatest browsing pressure on the system, whereas caribou (*Rangifer tarandus*), snowshoe hare (*Lepus americanus*), willow ptarmigan (*Lagopus lagopus*), and insects were less important components of the herbivore assemblage. We chose diamondleaf willow, *Salix planifolia pulchra*, as the basis for our study because it is the largest component of the summer diet for the moose in the Park (Van Ballenberghe et al. 1989).

Methods

Our study matched two plots approximately 2 km apart, each encompassing approximately 1 ha. These plots consisted of a spruce stand and surrounding open areas used by moose. The moose density of each stand was estimated by helicopter surveys of moose conducted during late September and early October in 1988, 1989,

and 1991. One stand had comparatively high moose density (\bar{X} = 1.8 moose/km², SD = 0.09), and the other low moose density (\bar{X} = 0.7 moose/km², SD = 0.25). The high-density site had a northern exposure, whereas the aspect of the low-density site was southward. In addition, soils on the high-density site were originally derived from Middle Tertiary continental sandstones, while low-density soils evolved from alluvial material derived from Birch Creek schist.

Each site was further divided into adjacent areas of sun and shade. A plant was "shaded" if a spruce or other large tree existed within 10 m of the plant in an 180° arc to the south. Similarly, a plant was designated as "sun" only if it did not have a large tree within 50 m to the south in the same arc. A discrete clump of willow was treated as an individual plant if it was >3 m from a previously sampled plant. Within each treatment, 30 diamondleaf willows were sampled along randomly located transects during autumn 1990, yielding data on 120 individual plants. Of these, 111 entries were sufficiently complete to warrant inclusion in a multivariate analysis of variance (MANOVA). Within each plant, current annual growth of leaders browsed and unbrowsed the previous season were measured for stem length, and mature leaves were collected so that leaf area could be measured using a Li-Cor electronic area meter. Both of these measures index plant growth per growing point. The proportion of stems browsed during the previous year of growth for the whole plant was measured to investigate the effect of tissue removal by moose on plant growth. Additionally, several stems were removed at random from each plant for later chemical analyses.

Samples of stems were analyzed for chemical composition and *in vitro* dry matter digestibility (Tilley and Terry 1963). Samples were divided by treatments (sun and shade) and further divided into three categories of overall previous browsing: high (≥50%), moderate (25–49%) and low (<25%). Individual stems were then composited to obtain adequate material such that three distinct samples for each of six treatment cells were generated. Analysis of stems for chemical composition was performed using the Van Soest detergent process, yielding percentage measurements of crude fiber, acid detergent fiber, lignin, and ash (Van Soest 1982). Percent crude protein was measured using macro-Kjeldahl titration (Robbins 1983). *In vitro* digestibility trials were performed using rumen inocula from domestic cattle (Tilley and Terry 1963). For each sample, results from the composition analysis were used to calculate predicted values of digestibility first developed by Van Soest (1965). The difference between predicted digestibility and observed digestibility was termed "digestibility depression." Person et al. (1980) argued that this measure is an index to the effects of plant secondary compounds, which are known to be present in willows (Bryant et al. 1989). Measures of chemical composition were analyzed using MANOVA by browsing intensity and shading regime (Johnson and Wichern 1988).

Soil samples were collected during late summer 1991 using a 7-cm diameter soil corer. Five random locations beneath *S. p. pulchra* plants were sampled on both sites with high and low moose density (total sample size = 10). At each of these random locations, three 15 cm-deep cores were collected, which were later composited by locations for soil analyses that included soil exchangeable nitrogen (Bremner and Mulvaney 1982), nitrogen mineralization rates, and soil respiration rates. One additional core was taken at each location to measure water content of the soil and percent organic matter. The water content of each core was compared with measures of soil decomposition, in addition to reflecting the availability of water in the rooting zone of willows.

Two soil samples were excluded from further analysis because they were diagnosed as statistical outliers. The first outlying sample, from the low-density site, displayed a nitrogen mineralization rate of 45 μg N × g OM⁻¹ × d⁻¹, which was 11 times greater than the mean respiration rate for remaining soils on the low-density site. This unusual sample also showed an overall soil respiration rate of 65.3 μg CO₂-C × g soil⁻¹ × d⁻¹, some 3.5 times greater than the mean rate for remaining samples. The second outlier that was deleted from statistical analyses came from the high-density site.

It had an unusually high initial NH_4 content of 17.7 ppm from the extracted sample. This soil sample immobilized N during the course of the experiment, resulting in a net loss of available N of $1.92 \mu\text{g N} \times \text{g soil}^{-1} \times \text{d}^{-1}$, while maintaining a soil respiration rate of $96.1 \mu\text{g CO}_2\text{-c} \times \text{g soil}^{-1} \times \text{d}^{-1}$, well within the range of the other samples. The high initial levels of NH_4 lead us to suspect that this soil sample was the site of recent urine deposition by moose.

Water holding capacity (WHC) was measured, from a sample composited across all locations in a site, for sites with both high and low moose density. Water in the soil as a percentage of water holding capacity was used as an index to water tension. Rates of nitrogen mineralization were calculated based on performance of soil held in aerobic microcosms at 60% WHC and 15°C over a 20-day period (Jenkinson 1968). Mineralized nitrogen was defined as the difference in combined totals of KCl extractable NO_2 , NO_3 , and NO_4 , which were obtained at the beginning and end of the incubation period (Bremner 1965). Rates of soil respiration were measured by CO_2 produced by same samples between day 9 and day 16 of the experiment (Anderson 1982). Percent organic matter was measured by combusting dry soil samples in a muffle furnace for 24 h at 550°C and examining the change in mass. These indices of soil decomposition rate were analyzed according to site and water tension using MANOVA.

Results

Browsing intensity

In the field, we examined the patterns of browsing intensity between sites with high and low moose density to determine how well estimates of moose density from aerial surveys reflected patterns of moose foraging. Browsing intensity was significantly ($t = -7.67$, $P = 0.0001$) higher on the site with higher moose density ($\bar{X} = 42.9\%$ of twigs browsed per plant, $SD = 23.8\%$) compared to the low-density site ($\bar{X} = 18.3\%$, $SD = 17.1\%$) (Table 1).

Growth per growing point

The same trend observed for leaves was reflected in the stems; current annual growth was longer on the high-density site (Table 1). With percent browsing held as a covariate, there were still significant differences in growth rates between the high and low density sites (ANCOVA, $F = 42.03$, $P = 0.0001$). For stem length, moose density again showed an overall positive relationship with growth per growing point. Shading within site was also a significant correlate of stem growth ($F = 7.46$, $P = 0.0001$). Shading did not show a consistent trend within sites; with percent browsing held as a covariate, adjusted

means showed that current annual growth of stems increased from shade ($\bar{X}_{\text{adj}} = 235.7$ mm) to sun ($\bar{X}_{\text{adj}} = 265.8$ mm) on the high density site, but declined from shade ($\bar{X}_{\text{adj}} = 230.8$ mm) to sun ($\bar{X}_{\text{adj}} = 194.7$ mm) on the low-density site. Percent browsing on the whole plant significantly affected plant growth ($F = 9.35$, $P = 0.0001$), while the browsing history of individual stems did not affect future stem growth ($F = 2.12$, $P > 0.90$).

The growth response of willows was linked to moose density. Leaf area was much greater in the high-density site than on the low-density site (Table 1). There also was a small difference in growth response as indicated by leaf area between shaded and unshaded plants. Percent browsing accounted for a significant proportion of the variation in leaf area ($F = 7.41$, $P = 0.0001$). Shade class within site and browsing history of the individual stem were not related to leaf area ($P > 0.70$). With percent browsing as the covariate, moose density was the strongest factor influencing leaf growth (ANCOVA, $F = 84.08$, $P = 0.0001$).

A nested MANOVA, using both leaf area and stem length as dependent variables, tested effects of environmental variables on growth of diamondleaf willow per stem. Plant growth per growing point was associated with site (high vs. low moose density; $F = 18.46$, $P < 0.001$) light availability ($F = 4.84$, $P = 0.02$) within each site (sun vs. shade) and percent of whole-plant browsing ($F = 6.98$, $P < 0.01$). Browsing history of individual stems was not related to future rate of stem growth ($F = 1.06$, $P > 0.65$). A positive relationship existed between browsing intensity and whole-plant productivity when both leaf area and stem length were considered. For current annual growth of stems, simple regression indicated a positive relationship with browsing intensity ($r^2 = 0.27$, $\hat{y} = 197 + 132x$, $F = 40.27$, $P < 0.0001$); a similar relationship existed for leaf area ($r^2 = 0.19$, $\hat{y} = 4.58 + 3.15x$, $F = 25.29$, $P < 0.0001$).

Chemical composition

Chemical assays on current annual growth of stems also were evaluated using MANOVA. Chemical properties (Table 2) of stems were significantly related to both shade class ($F = 23.08$, $P = 0.0001$) and browsing intensity ($F = 5.04$, $P = 0.0022$). Univariate ANOVAs were performed to elucidate the relationships between dependent variables and shading regime and browsing intensity (Table 2). Percent crude protein responded to shading re-

Table 1. Mean (\pm standard error) for willow characteristics from areas of high ($n = 60$) and low ($n = 51$) moose density, Denali National Park, Alaska, autumn 1990

Willow Characteristics	Moose density		Low	
	High		Sun	Shade
	Sun	Shade	Sun	Shade
Leaf Area cm^2	6.22 \pm 0.217	6.50 \pm 0.248	4.35 \pm 0.187	4.58 \pm 0.187
Current Annual Growth (mm)	278 \pm 9.8	238 \pm 6.4	182 \pm 9.2	228 \pm 7.5
%Stems Browsed	51.2 \pm 4.8	35.2 \pm 3.6	11.5 \pm 2.7	23.5 \pm 3.4

Table 2. Comparison of mean \pm standard error for chemical composition of willow stems in shaded ($n=9$) and sunny ($n=9$) microsites, Denali National Park, Alaska, late summer 1990

Variable	Shade	Sun	P-Values ^b
% Crude Protein	6.14 \pm 0.11	5.49 \pm 0.83	0.0179
% Cell Solubles	43.9 \pm 3.4	38.6 \pm 1.9	0.0001
% Neutral Detergent Fiber	56.1 \pm 3.4	61.4 \pm 1.9	0.0001
% Acid Detergent Fiber	44.4 \pm 0.8	46.6 \pm 1.6	–
% Lignin	16.2 \pm 0.5	14.7 \pm 0.3	–
% Ash	0.028 \pm 0.01	0.009 \pm 0.09	–
% <i>In vitro</i> dry matter digestibility	36.0 \pm 2.9	32.6 \pm 0.9	0.0209
% digestibility depression ^a	–7.7 \pm 1.5	–10.1 \pm 1.3	0.0749 NS
Lignin:nitrogen ratio	16.44 \pm 1.75	16.81 \pm 0.56	0.1611 NS

^a IVDMD minus predicted digestibility (Van Soest 1965)

^b Dashes indicate that variables were not included in the MANOVA because of model over parameterization

Table 3. Mean \pm SE of soil characteristics and indices of potential soil decomposition rate for sites with high ($n=5$) and low ($n=5$) moose density, Denali National Park, Alaska, autumn 1991. P-values indicate significant ($P<0.05$) outcomes from sequential Bonferroni pair-wise comparisons

Parameter	High-Density Site	Low-Density Site	P
Overall Soil Respiration ($\mu\text{g CO}_2\text{-C/g soil} \times \text{day}^{-1}$)	88.8 \pm 22.0	18.8 \pm 3.4	NS ^a
Soil Respiration per g OM ($\mu\text{g CO}_2\text{-C/g OM} \times \text{day}^{-1}$)	129.9 \pm 22.7	183.1 \pm 16.8	NS ^a
Overall N Mineralization ($\mu\text{g N/g soil} \times \text{day}^{-1}$)	5.60 \pm 0.71	0.48 \pm 0.27	*
N Mineralization per g OM ($\mu\text{g N/g OM} \times \text{day}^{-1}$)	8.59 \pm 1.29	3.93 \pm 1.67	NS ^a
% Organic Matter	63.3 \pm 0.45	10.0 \pm 1.48	*
Water Holding Capacity (gH ₂ O/g soil dwt.)	3.02	0.97	–
% Water Content	63.5 \pm 2.10	23.5 \pm 3.18	*
% Water Holding Capacity	58.5 \pm 4.61	40.0 \pm 7.20	*

^a NS = Not significant

* = Significant ($P \leq 0.05$); water holding capacity was not tested because it was used in calculating % water holding capacity

game, but not to browsing intensity ($F=0.38$, $P>0.65$). Crude protein was higher in shaded areas than in unshaded ones (Table 2). Percent neutral detergent fiber (NDF) responded to both shade class (Table 2) and browsing intensity ($F=12.19$, $P=0.001$). NDF was higher for plants in full sunlight than for those in shaded microsites (Table 2). Levels of NDF were higher for plants browsed at moderate intensity ($\bar{X}=61.6\%$, $SD=2.1$), than for plants browsed at low ($\bar{X}=56.7\%$, $SD=3.9$) or high ($\bar{X}=58.1$, $SD=3.8$) intensities.

In vitro digestibility responded significantly to shading regime; shaded plants were more digestible than plants in open areas (Table 2). Plants subjected to high browsing intensity showed slightly lower digestibility ($\bar{X}=32.6\%$, $SD=2.6$) than plants browsed at low or moderate intensity ($\bar{X} \pm SD = 35.2 \pm 13\%$, and $35.1 \pm 3\%$, respectively), but this difference was marginally nonsignificant ($F=3.42$, $P=0.064$). Overall, plant chemistry showed a stronger response to shading regime than to browsing intensity.

Lignin:nitrogen ratio and digestibility depression for willows at the three levels of browsing intensity were compared using 90% T^2 simultaneous confidence intervals (Johnson and Wichern 1988). Willows subjected to low and moderate browsing intensities during the pre-

vious year had slightly higher lignin: Nitrogen ratios ($\bar{X}=16.9 \pm 2.3$ and $\bar{X}=17.35 \pm 2.4$, respectively) than willows subjected to intense browsing ($\bar{X}=15.32 \pm 0.6$), but this pattern was not significant. Nonetheless, digestibility depression was significantly more severe for heavily browsed plants ($\bar{X} = -11.59 \pm 2.47\%$) compared to willows browsed at low ($\bar{X} = -8.42 \pm 1.49\%$) or moderate intensities ($\bar{X} = -6.69 \pm 4.72\%$).

Soils

Soil samples differed greatly between sites of low and high moose density. Soils on the high-density site had a much deeper organic horizon than soils on the low-density site, which is expressed in the significantly higher organic matter (OM) content on the high-density site compared to the low-density site (Table 3). This greater content of organic matter led to a higher water holding capacity on the high-density site than on the low-density site. As a result, the gross water content of the soil was significantly greater on the high than on the low-density site (Table 3). The difference in water tension between sites as indexed by percent of WHC, however, was smaller although still significant (Table 3).

We performed a MANOVA using site (high or low moose density) and water tension (% of WHC) as independent variables to determine their effect on overall respiration rate (per g soil), respiration per g organic matter, overall N mineralization rate (per g soil), and N mineralization rate per g OM. Wilks' lambda indicated site had a significant overall effect ($F=69.31$, $P=0.0143$) while water tension did not ($F=7.75$, $P>0.10$).

Overall soil respiration was greater on the high-density site, but not significantly so (Table 3). Likewise, respiration per gram OM mineralization of nitrogen per gram OM did not differ between sites with high and low moose density. In contrast, overall N mineralization on the high-density site significantly exceeded that of the low-density site (Table 3).

Discussion

Resource availability and willow response to herbivory

The release from apical dominance resulted in larger stems and leaves for willow following autumn and winter browsing by moose. These plant characteristics responded positively to increased browsing intensity on the plant as a whole. Although quality of stems did not improve as a result of browsing, moose feeding on larger stems and leaves would be able to maximize nutrient intake in a shorter period of time (Vivas et al. 1991), thereby improving the value of such forage to moose.

Annual biomass productivity per growing point increased with increasing browsing intensity on the plant as a whole. Stafford (1990) demonstrated through experimental clipping that browsing history of the individual leader was not a significant factor affecting growth of individual stems and leaves within plants for *S. alaxensis*. Our results suggest the same for *S.p. pulchra* browsed by free-ranging moose.

Our study does not address possible changes in the number of buds or overall biomass of the browsed shrub. Any browsing will reduce the total nutrient stores of the plant and perhaps result in decreased fitness. Nonetheless, 70% of the biomass of *S.p. pulchra* may be below ground (Chapin 1980), operating as a store for nutrients. Archer and Tieszen (1980) indicated that diamondleaf willow initiated growth annually from only 20% of available buds. Thus, only in the case of severe browsing would an individual plant face severe constraints in the availability of nutrient reserves or growing points. In addition, while herbivory decreases catkin production in woody plants (Bergstron and Danell 1989; Stafford 1990), vegetative reproduction via adventitious shoots may be stimulated by browsing (Grimes 1977; Stafford 1990). As a result of these adaptations to herbivory, the response of overall forage biomass to herbivory in diamondleaf willow remains unclear.

There was a significant effect of shade on the quality of willow stems per unit mass. Willows in sunny areas tended to have higher cell wall contents and lower percentage of cell solubles than willows that received more shade (Table 2), thereby reducing their forage value to

moose. Indeed, percent protein and *in vitro* digestibility were significantly higher for shaded plants than plants in the open. These findings agree with those of Machida (1979), who reported that protein content in *S.p. pulchra* was significantly higher in shaded plants than in plants exposed to full sunshine. Supportative data also are provided by Hjeljord et al. (1990). These factors contributed to higher overall forage quality inside the forest compared to open tundra, despite the effects of potential competition with overstory plants for soil nutrients (Moore 1980). This has been explained by Bryant and Chapin (1986) as a result of plant growth in sunny areas outstripping the availability of soil nutrients as a result of their higher rate of carbon fixation. Consequently, shaded plants are of higher forage quality for moose, and should produce litter that is of higher quality for soil decomposers.

Defense compounds in diamondleaf willow were probably responsible for the 6 to 11% depression in digestibility shown in this study. Diamondleaf willow does not contain toxic phenyl glycosides (Matsuki 1992), and thus only tannins are known to be available for defense. The role of tannins as defense compounds is controversial (Robbins et al. 1987; Provenza et al. 1990; but see Clausen et al. 1990). Because we used rumen liquor from cattle that were accustomed to a diet of monocots in our assays for digestibility, the depression that we report is probably greater than that which a moose would experience. Diamondleaf willow is poorly defended by toxins that inhibit digestibility compared to other browse species in Alaska (e.g., Weixelman 1992). Digestibility depression was greatest in plants that had the lowest proportion of lignin with respect to nitrogen content, indicating that defense compounds were likely factors contributing to depression of digestibility. We did not find a clear pattern in digestibility depression across varying browsing intensities, although plants that were browsed most heavily had higher levels of toxins. Overall, the influence of secondary compounds on digestibility does not appear to be a critical factor influencing forage quality for diamondleaf willow at browsing intensities we measured.

Our results demonstrated that site had the strongest effect of any variable measured on growth per growing point and indices of soil decomposition rate. Moose density, however, was potentially confounded with aspect, overall percent soil moisture, and soil parent materials. Because plants on the high-density site showed higher overall rates of growth despite its northern aspect, we infer that aspect did not contribute directly to the increased growth occurring on the high-density area. Although our index of water tension, which reflects the availability of water to plant roots and microflora, was higher on the high-density site, water tension did not significantly affect soil respiration and rates of N mineralization. It is therefore unlikely that differences in soil water content on our study sites influenced plant growth or soil decomposition rates appreciably during the period in which we measured this variable. Soil moisture maybe more important at other times of year. Differences in parent materials are initially important to devel-

oping soils (Jenny 1941), but are much less so for plant growth than dynamics occurring in the organic layer of the soil (Flanagan and Van Cleve 1983). Moreover, similar vegetative types (tundra, brush, spruce, riparian) occurred within both types of parent materials in the eastern end of Denali National Park. Likewise, moose density outside our study plots varied markedly within both the sandstone and schist soils (Van Ballenberghe, unpubl. data). Moreover, the schist parent materials on the low-density site would be expected to yield higher-quality soils than sandstone parent materials on the high-density site (K. Van Cleve, Pers. Commun.). Although we cannot entirely rule out edaphic factors, it is likely that moose are strongly affecting the growth of willows in our study sites.

Site also interacted with shading regime in influencing the growth of stems. Plants on the low-density site showed higher stem growth in shaded areas. Because soils were thinner and more N limited on the low-density site, we suggest that this trend is a result of greater nutrient stress for plants in open areas, where carbon fixation outstrips nitrogen uptake from the soil (Bryant and Chapin 1986). Plants on the high-density site showed greater stem growth in sunny areas. Increased rates of nutrient cycling on this site, mediated by the presence of moose, may have boosted N levels sufficiently to alleviate the nutrient stress of plants exposed to full sunlight, allowing them to achieve greater growth. Thus, it appears that moose herbivory and nutrient inputs are indeed a powerful influence on the growth and nutrient status of browse plants in treeline ecosystems.

Effects of moose herbivory on ecosystem nutrient dynamics

We cannot discern whether moose initially caused one site to be of higher quality than another, or were simply attracted to the better site. Nonetheless, once moose began using the high-density site to a greater extent than the low-density one, their presence likely began a positive feedback loop that increased current annual growth through fertilization and browsing. Indeed, fecal nitrogen for cervids is known to increase with increasing forage quality (Leslie and Starkey 1985; Hodgman and Bowyer 1986), and feces tend to be deposited in areas of greater utilization (Etchberger et al. 1988). This positive feedback creates an even stronger difference between sites, which should be manifested in greater moose selection of the high-density site as a feeding area.

Ultimately, herbivory would be expected to select for plants that have high levels of secondary defense compounds (Bryant and Chapin 1986), which may result in a long-term shift in the composition of plant communities (Pastor et al. 1988), and thus lower forage quality for herbivores. Nevertheless, moose populations in interior Alaska are in many cases limited to low population densities by predation (Gasaway et al. 1992), which may prevent heavy browsing and thereby weaken selection for the development of plant secondary compounds.

Van Ballenberghe (unpubl. data) noted that annual

fecal inputs of moose in Denali National Park approached the level of a commercial fertilizer treatment. Our results lead us to hypothesize that moose inputs of N and other minerals through urine and feces result in higher rates of soil nutrient turnover, and this in turn increases the growth rates of plants at a rate commensurate with the density of moose at a particular site. Indeed, the rate of Nitrogen mineralization was significantly higher on the site with a high-density of moose. Organic content of soil also was positively related to moose density. Flanagan and Van Cleve (1983) noted that fungal biomass in soil was highly correlated with organic matter content, and pointed out that fungi were the most important decomposers in boreal-forest soils. We further hypothesize that moose exert a positive influence on soil microbiota through their inputs of nutrients.

In addition to priming the soil with direct nutrient inputs, moose mediate rates of nutrient cycling indirectly by affecting the type of litter that enters the soil. Plants browsed by moose had larger leaves, and stems showed significantly higher annual growth. Our results demonstrated that lignin:N ratio, which is a negative correlate of decomposition rate (Flanagan and Van Cleve 1983), was lower for plants that were browsed heavily. Although digestibility depression, an index of tannin content, was significantly higher in heavily browsed plants, tannins leach from leaf litter at faster rates for browsed stems (Irons et al. 1991), thus making litter more rapidly available to decomposers. Indeed, microcosm experiments by M. Wagener (unpubl. data) have shown that *Salix alaxensis* leaves from browsed plants decompose in soil much more rapidly than leaves from unbrowsed plants. Thus, both nutrient inputs and increases in litter quality mediated by moose increase decomposition and N mineralization rates in soil systems.

Similarly, stream systems that are dependent on leaf litter may be beneficiaries of the short-term positive feedback loop created by moose herbivory. Browsing by moose increases decomposition rates of leaf litter in streams (Irons et al. 1991). At the same time, an increase in growth and decrease in C:N ratio results in plant matter that is a higher quality substrate for microbial activity (Melillo et al. 1984). This results in greater nutrient inputs into streams per unit time.

Moose may function as a keystone herbivore in Alaskan ecosystems, exerting a critical influence on plant productivity and nutrient dynamics. We believe additional research to separate the effects of moose browsing, nutrient inputs from their feces and urine, and the confounding effects of edaphic factors on nutrient dynamics and plant growth is especially important. Likewise, it is essential that we gain further insights into the effect of ungulate population dynamics on such ecosystem processes.

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