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Interrelationship of Forage and Moose in Game Management Unit 13

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SUMMARY

Key activities of this study were to determine diet quality, browse availability, and browsing effects. Feltleaf willow (*Salix alaxensis*) within exclosures in Tyone Creek and Oshetna River drainages were clipped at 30, 60 and 90 percent in winters 1996, 1997, 1998, and 1999 to simulate light, medium and heavy rates of utilization by moose. After 4 years of sustained utilization, catkin production was directly proportional to the number of twigs unbrowsed in the previous winter and, therefore, was not a good indicator of plant vigor. Changes in total phenolics and protein-precipitating capacity (BSA) of tannins were not significant, but appeared to decline at 30% utilization, then rise with higher utilization to levels similar to the unbrowsed plants. Crude protein and percent digestible protein were significantly higher for plants in the 30% utilization treatment. Protein binding by tannins resulted in digestible protein levels of 0.9, 1.1 and 2.5% in feltleaf willow, diamondleaf willow, and dwarf birch browse, respectively. Current annual growth of feltleaf willow was significantly highest when utilized at 60%. Winter utilization of feltleaf willows outside exclosures ranged from a high of 82% in a winter of deep snow accumulation to as low as 12% during a winter of little snow accumulation. Utilization and snow accumulation were positively correlated ($p < 0.01$). Hillside stands of diamondleaf willow (*Salix pulcra*) and dwarf birch (*Betula nana*) were preferentially browsed even when covered by snow, indicating their importance in dietary mixing. Considering that moose in the Nelchina Basin continued to have low reproductive rates during years when winter browse availability was not limited, tannin-protein interactions of Nelchina summer forages, as well as winter forages of more productive moose ranges, should be examined to help explain current findings.

Key words: Browse, digestible protein, habitat, moose, tannins.

CONTENTS

BACKGROUND

The Alaska State Board of Game selected human consumptive use as the priority for wildlife management in Game Management Unit 13 (GMU 13). In accordance with this priority, the Department of Fish and Game (DF&G) must determine what biological potential may exist for increasing the productivity and/or harvest of game species, including moose. Management biologists have questioned whether Unit 13 moose are limited by forage resources, predation, or a combination of both.

Availability of nutrients to moose is one aspect of ecological carrying capacity that must be determined before these questions can be answered. Nutrient availability is affected by forage productivity, by factors that affect forage availability to the animal, including snow depth and previous utilization history, and by chemical characteristics of forages which affect their digestibility. Assessment of these factors will be useful in development or modification of strategies to manage harvest and habitat for the welfare of Unit 13 moose.

According to Bishop and Rausch (1974), range condition has operated as a limiting factor to the moose population in Unit 13 in the past. Ballard et al. (1991) believed the degree of this limitation was unclear, but recognized the significance of severe winters and their influence on forage availability as possible causes of declines in Unit 13 moose productivity. They also recognized the possibility of habitat decline resulting from fire suppression and subsequent vegetation succession.

Prior browse utilization can affect both the quantity and quality of food available to moose (Moen et al. 1990, Wolff and Zasada 1979, Molvar et al. 1993, Danell et. al. 1994, McKendrick et al. 1980), causing decreases in moose reproduction (Franzmann and Schwartz 1985, Boer 1992) and increased mortality. Factors of snow accumulation in winter (Bishop and Rausch 1974, Schwab and Pitt 1991, Coady 1974, Telfer 1970 and 1978) and amount of solar radiation in summer (Bo and Hjeljord 1991) complicate forage-moose relationships. Frequency and intensity of fire also affect ecological carrying capacity for moose (Spencer and Hakala 1964, Wolff and Zasada 1979).

Prior utilization or other plant disturbances may affect production of plant defensive compounds, which in turn affect nutrient availability to the herbivore. One of the most widely distributed groups of plant defensive compounds is tannin. Typically, hydrolyzable tannins have been assumed to accumulate primarily in dycotoledonous forbs, and leaves of shrubs and trees (Hagerman et al. 1992). Winter-dormant browse stems have not been recognized to contain significant amounts of tannins (Hanley et al. 1992). Because tannins are a complex group of chemicals, measurements of their biological effects rather than their quantities in plants are fundamental to understanding their ecological significance (Hanley et al. 1992).

Milke (1969) ranked feltleaf and diamondleaf willows, not only as highly preferred, but as the two willow species being most “important” to moose in interior Alaska. Important willows are not only considered palatable and preferentially browsed, but they should also occur in such abundance or stature as to produce readily available browse. In the study area, feltleaf willow is primarily a riparian species and typically grows 2 to 3 m tall, providing abundant browse above the level of snow accumulation. By contrast, diamondleaf willow primarily occupies hillsides and typically grows to heights of only 1 m or less, becoming covered by snow in years of greater than average accumulation. Both species are dominant in their respective habitats, diamondleaf habitat being much more extensive than that of feltleaf which is restricted to riparian sites.

OBJECTIVES

Key activities were to determine diet quality, browse availability, and browsing effects. To identify relationships of moose browse availability and quality to utilization, I tested the following null hypotheses:

H1. Previous levels of utilization by moose do not limit productivity of principal winter browse species in Unit 13A.

H2. Dry-matter digestibility, tannins, total phenolics, and digestible protein of current annual growth are not affected by browsing history of the shrub.

METHODS

WINTER FORAGES AND UTILIZATION

I determined mid and late winter forages of moose by backtracking them in winters 1995 through 2000, then measuring and counting freshly browsed twigs at feeding sites. This allowed determination of forage species and plant parts (Hobbs and Spowart 1984). I focused utilization surveys on feltleaf willow stands because I assumed they represented the principal forage available to moose during critical periods when snow covers all other forages. Ten permanent transects were established in both the Oshetna River and Tyone Creek drainages. Transects were spaced at one-mile intervals. Each transect was oriented perpendicular to the stream bank. At every 4-m interval, for a total of 30 points, the nearest individual stem of feltleaf willow was selected for determination of percent utilization. On each stem, percent utilization of all twigs above 0.5m, but below 2.5m on stems greater than 4cm dbh, was determined in spring the first year, then only for terminal clusters in subsequent years.

WINTER BROWSE QUALITY

Principal foods (>5% of diet) were collected in late February 2000, kept frozen, then freeze-dried for grinding and weighing. Samples were kept frozen and then freeze-dried to prevent tannin binding with proteins prior to analysis. Determination of tannins from oven- or air-dried samples can result in formation of tannin-protein complexes, which appear as lignin and result in lower calculations of dry matter digestibility and digestible protein.

I measured the biological effect of tannins by determining their protein-precipitating capacity with the bovine serum albumin (BSA) assay (Martin and Martin 1982, Robbins et al. 1987). I used the Van Soest method to isolate cell contents, cell wall, hemicellulose, cellulose, lignin, cutin and cell wall minerals (ash). I did phenolic extractions according to Grahm (1992) and determined nitrogen by combustion using a LECO CHN-5000 analyzer.

BROWSING EFFECTS

Effects of browsing and clipping on feltleaf willow availability were evaluated in terms of shrub survival, total current annual growth (CAG) per stem, and browse quality. Feltleaf willow was evaluated in this manner, because it was expected to be the principal source of browse when deep snow covered diamondleaf willow in upland sites. Based on descriptions of moose-browse interactions elsewhere, I assumed that these plants were most likely to be overbrowsed and would be most indicative of "carrying capacity." I also measured catkin production (Cook 1977) to determine its value as an indicator of willow vigor.

Interpretation of browsing effects requires knowledge of browsing histories of individual shrubs (Shepherd 1971). Within the principal study area, browsing histories were approximated through interpretation of shrub structures (numbers and chronological positions of previous browsing points) and supported by interpretation of historical moose trend-count data. Browsing effects were also determined through clipping treatments, since histories of clipped plants are more certain. Four exclosures (600 m^2) were constructed in 1995 within riparian willow stands to protect clipping treatments from browsing interference by moose.

Each exclosure was divided into 4 equal quadrants, and all willows in each quadrant were clipped to represent 1 of 4 levels of utilization: none (control), light (30%), moderate (60%), and heavy (90%). Measurements of current annual growth, number of twigs, catkin production, and mortality were recorded for each of 30 permanently tagged stems within each quadrant. A "stem" was defined as any above-ground portion of the willow, which at the soil surface was not visibly attached to any other part of the plant. "Heavy" clipping treatments were intended to simulate 90% utilization, or approximately 15% more than what Wolff and Zasada (1979) suggested represents the carrying capacity of feltleaf willow. Clipping treatments were repeated in winters 1996, 1997, 1998, and 1999. Shrub response was analyzed in 2000, following repeated measures, randomized block design, blocking on site (exclosure) in each vegetation type.

RESULTS AND DISCUSSION

WINTER FORAGES AND UTILIZATION

Winter utilization of feltleaf willows by moose ranged from a high of 82% in winter 1994–95, a season of record snow accumulation, to a low of 12% during winter 1995–96. A rank correlation (Kendell's τ) between percent utilization and winter severity (mean snow depths January through March) showed positive correlation ($p < 0\ .01$) (Fig 1). The winter severity index for the 7-year period of this study was 24.6 compared with a 30-year mean of 18.0. In the 30 years of snow depth recordings in or near the study area, winter severity has never exceeded that of winter 1994–95.

Snow seldom prevented moose from browsing extensive hillside stands of diamondleaf willow during most winters. Apparent preferential use of hillsides by moose during all but winter 1994–1995 suggested preference for diamondleaf willow and associated species. Examination of feeding sites and microscopic analysis of fecal samples (Table 1) revealed that moose utilized unexpectedly large quantities of dwarf birch relative to the amount of feltleaf willow utilized. Fragments of feltleaf willow (identified as "*Salix* spp. hair") were completely absent from fecal samples from the Oshetna River drainage, further indicating the relatively limited use of that species. Moose often clipped dwarf birch stems down to 2- or 3-year-old wood, although they seldom took stems older than one year from other species. Dwarf birch is generally considered to be of low palatability, and it typically is covered by snow. Its utilization suggests that it has a significant role in diet mixing to meet the nutritional requirements of moose. Results of fecal analysis should be interpreted with caution, considering that some species such as dwarf birch are less digestible than other species and therefore tend to be over represented. In addition, I believe that portion of the fecal analysis identified as balsam poplar (*Populus balsamifera*) is in error and is probably representative of additional *Salix*, because browsable stems of it do not occur within 12 kilometers of where fecal samples were collected.

Although availability of winter browse appears more than adequate most years, the low reproductive rates of moose in this area suggest a relatively poor overall quality of diet. During this study, no 2-year-old cows and less than 50% of 3-year-old cows produced calves, and approximately 25% of all adult cows produced twins (Ward Testa, personal communication).

Body fat reserves of adult cow moose in the study area are significantly lower than those of moose on several other ranges across the state (Stephenson and Testa, unpubl. Data). If a nutritional problem exists, it may not necessarily be limited to winter diets.

Wolff and Zasada (1979) reported that approximately 75% utilization of feltleaf willow occurred when moose were at carrying capacity. In the Oshetna and Tyone drainages this value was matched or exceeded only once in 7 years, when snow was extremely deep. Otherwise, utilization has been moderate to low, suggesting high browse availability most years. Snow accumulation in 6 of 7 years was not sufficient to prohibit browsing of hillside diamondleaf willow communities. Surprisingly, in most years, moose also intensively browsed hillside patches of dwarf birch (*Betula nana*) in mid and late winter, regardless of readily available feltleaf willow in drainages. The phenomenon of browsing on dwarf birch was preceded by early winter utilization of feltleaf willow twigs growing within 50 cm of the ground, but complete avoidance of higher twigs growing within easier reach.

WINTER BROWSE QUALITY

Feltleaf willow, diamondleaf willow, and dwarf birch all exhibited high levels of protein binding by tannins, but dwarf birch much less so than the other two species (Table 2). Consequently, dwarf birch provided significantly more digestible protein than the other two species, even though its dry matter digestibility was significantly lower. This helps explain the effort made by moose to dig through snow to obtain dwarf birch even when feltleaf willow was much more readily available.

BROWSING EFFECTS

Number and mean length of feltleaf current annual twigs under different levels of utilization were determined in exclosed clipping treatments in late March 2000. Mean length of current annual growth multiplied by mean number of twigs per stem (Figure2) indicated that all 3 levels of utilization produced more current annual growth than the control, but only plants utilized at 60% were significantly more productive (Table 3).

Catkin production under light, moderate and heavy utilization, respectively, averaged 55%, 27% and 3% of the control. However, since catkin production was directly proportional to the number of twigs remaining from the previous year (i.e. in their second season of growth) it was not a useful indicator of plant vigor, as flowering is in some other woody species.

The protein precipitating capacity (BSA) of tannins in feltleaf willow appeared to decline under light utilization but differences were not significant with varying utilization (Fig 3, Table 4). Total phenolics followed a similar pattern (Fig 4, Table 5). The relatively high levels of tannins and phenolics across all treatments for this species suggest that factors other than or in addition to browsing history are responsible for their production. Comparisons with feltleaf willow from other ranges may provide insight into factors affecting production of these compounds.

Light utilization (30%) did result in a significant increase in crude protein (Fig. 5, Table 6), that probably accounted for a similar, significant response in % digestible protein (Fig. 6, Table 7). Percent digestible protein of plants utilized at 60% and 90% was as high as that of unbrowsed plants.

Percent digestible protein by dwarf birch was more than double that of either feltleaf or diamond willow (Table 2) even though crude protein production by dwarf birch was intermediate to the other two species, and % digestible dry matter of dwarf birch was only 65% of the other two species. These differences indicate the significance of tannins in protein digestibility within the principal winter forages of moose in the Nelchina basin and their importance in assessment of carrying capacity for moose.

From the standpoint of browse production, clipping treatments and natural utilization rates over the past 7 years indicate that the current population of moose is not overutilizing feltleaf willow in the Nelchina Basin. Severe winters, which restrict moose to floodplains, are infrequent and probably never occur 4 years in a row, comparable to that produced by the heavy utilization treatment. By subjective comparison, the relatively more abundant species--diamondleaf willow and dwarf birch--likewise do not appear overutilized in winter. However, high levels of tannins and low levels of digestible protein observed in principal winter forages indicate that moose in the Nelchina Basin may be experiencing severe nutritional limitations in winter relative to their nutritional requirements.

RECOMMENDATIONS

An overriding concern in the design of the utilization response treatments in this study was how to purposely affect an individual's growth without that "individual" also being affected by possible below-ground connections to other "individuals" which were treated differently. Competition between true individuals in the root zone was another concern. I was similarly concerned that competitive influences could also occur above ground if canopies adjoining sampled stems were not treated uniformly. Consequently, I decided that treatments must be uniformly applied to all stems within vicinity of stems actually measured for response. Treatment of all stems within a treatment area was time consuming and tedious, but most importantly, it failed to take into account possible variations in substrate, water table, and other below-ground variables which could have contributed to differences in the performance of individuals across any given treatment site. Therefore, I recommend that questions addressed by these clipping treatments be accomplished much more efficiently by clipping and following the responses of willows grown from seeds or cuttings in pots or transplant gardens. This would ensure individuality and uniform substrate and microclimatic conditions, thereby eliminating confounding interactions and variables over which I had no control.

Because moose in the Nelchina Basin continued to have low reproductive rates during years when winter browse availability was not limited, tannin-protein interactions of Nelchina summer forages and winter forages of more productive moose ranges should be examined to help explain current findings and to assess moose nutrition in the study area. I recommend that an investigation of browsing effects on winter browse of diamondleaf willow and dwarf birch be conducted and that their importance in dietary mixing be addressed. The role of nitrogen cycling in moose should also be investigated to determine the significance of low protein digestibility relative to moose nutritional requirements.

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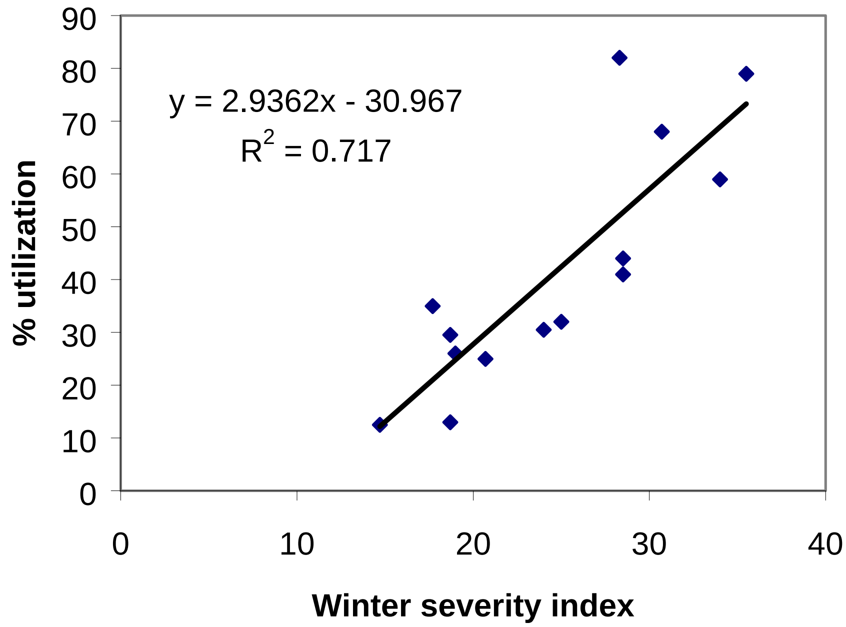

Figure 1. Relationship of feltleaf willow utilization to winter severity.

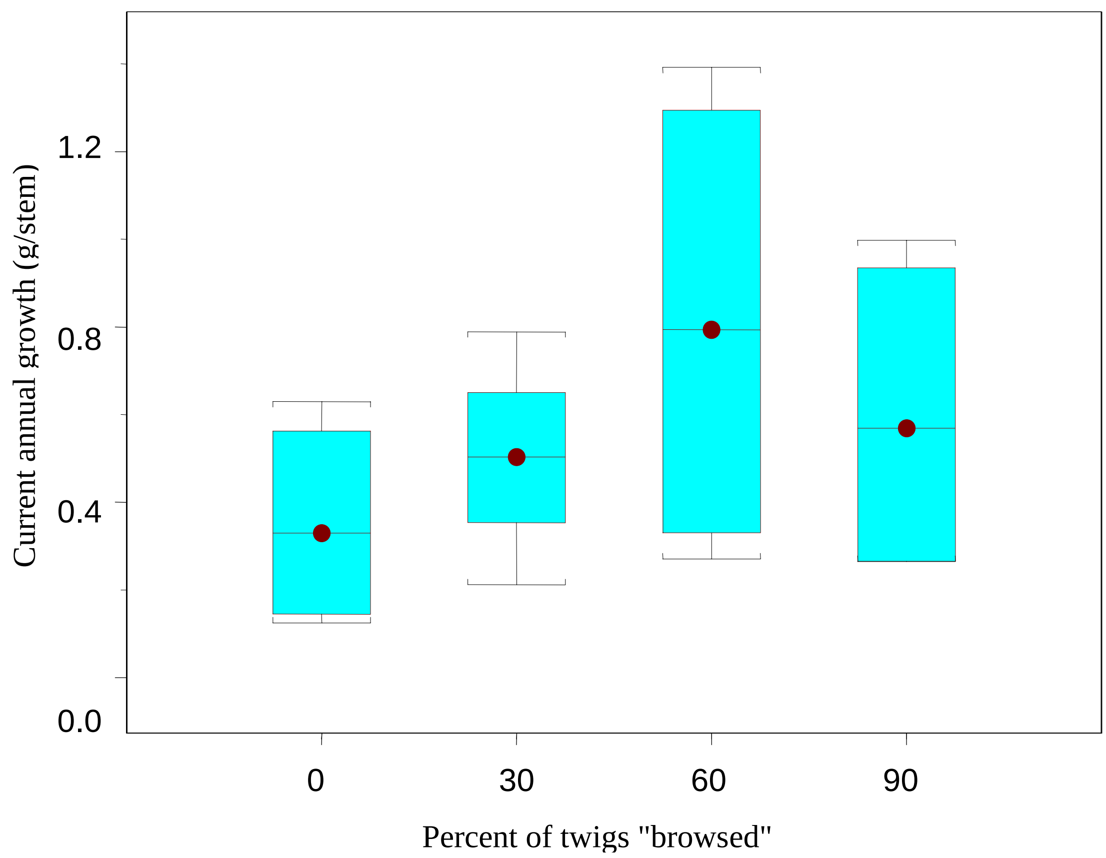

Figure 2. Current annual growth of feltleaf willow following 4 years of clipping to simulate 4 rates of browsing utilization.

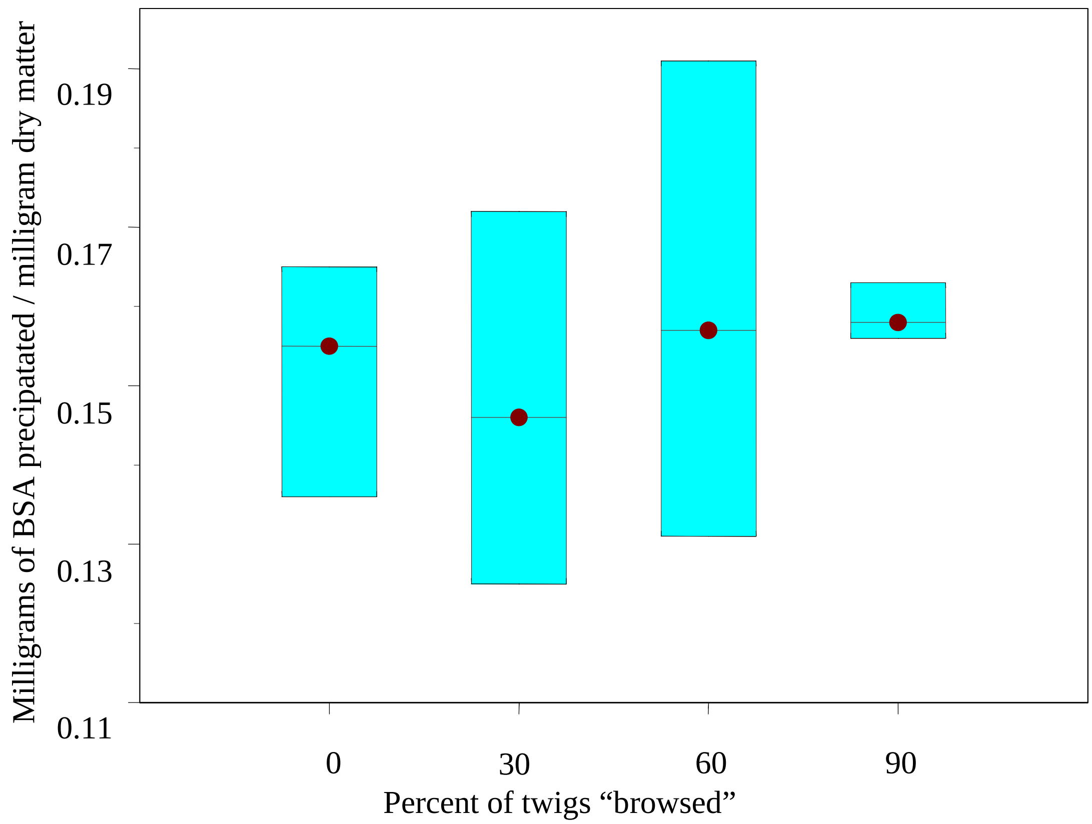

Figure 3. Protein precipitating capacity of feltleaf willow following 4 years of clipping to simulate 4 rates of browsing utilization. Measured in milligrams of bovine serum albumin (BSA) precipitated per milligram of forage dry matter.

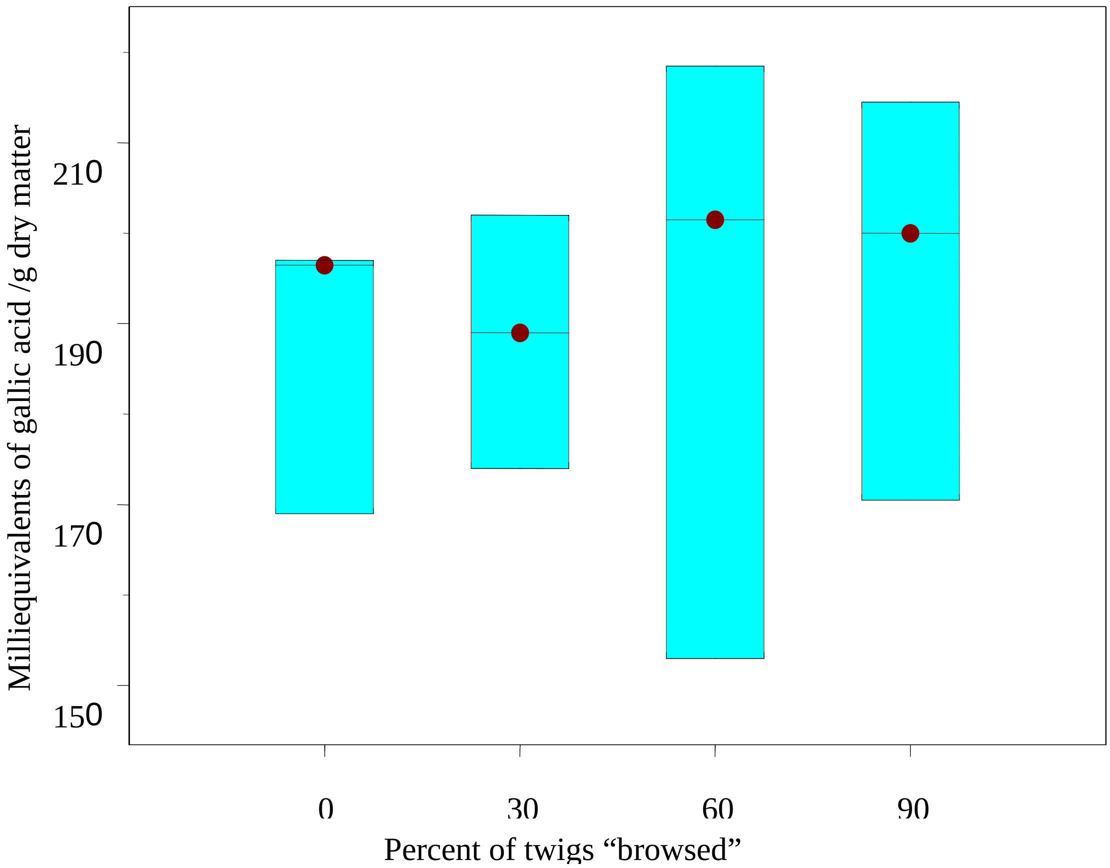

Figure 4. Total phenolics of feltleaf willow following 4 years of clipping to simulate 4 rates of browsing utilization. Measured in milli-equivalents of gallic acid per gram of forage dry matter.

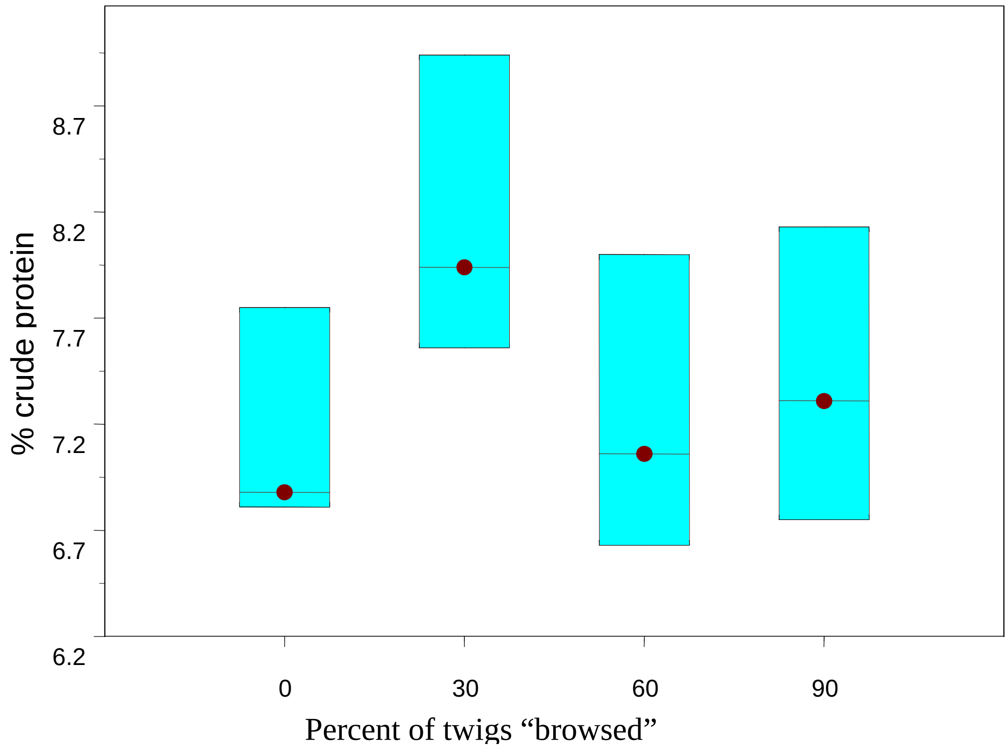

Figure 5. Crude protein of feltleaf willow following 4 years of clipping to simulate 4 rates of browsing utilization.

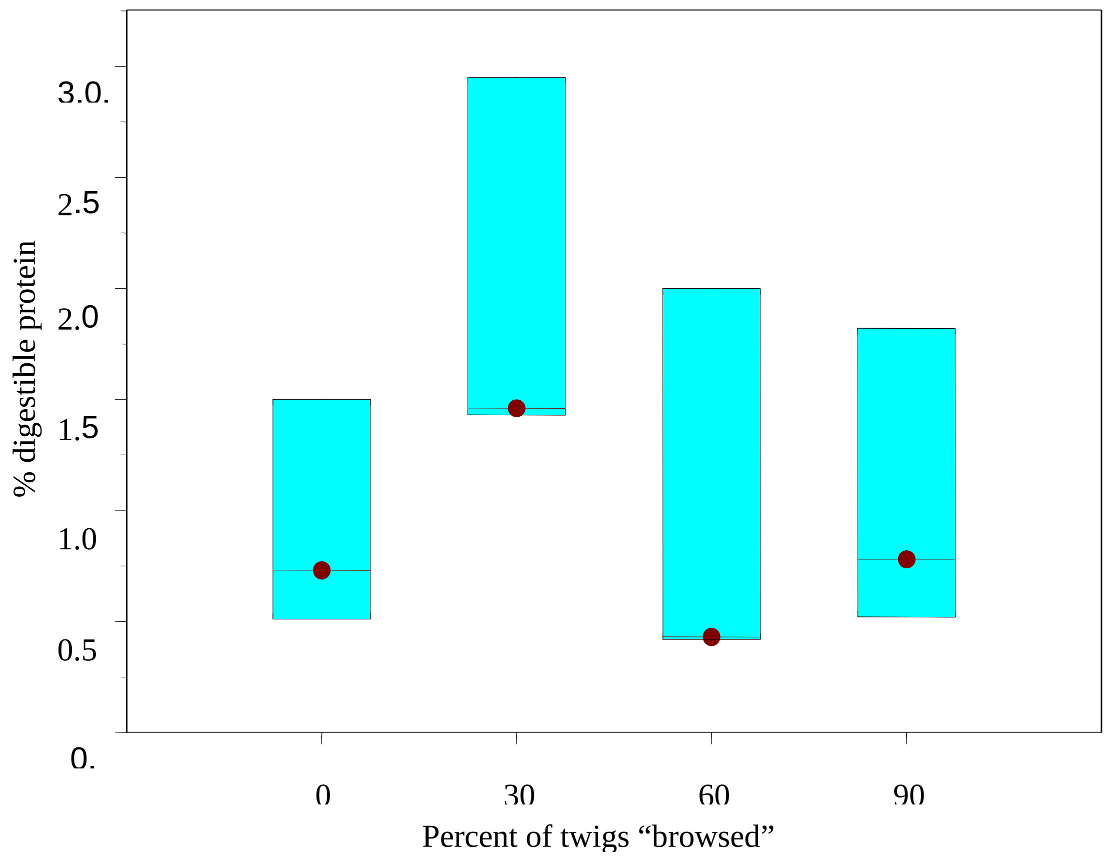

Figure 6. Digestible protein of feltleaf willow following 4 years of clipping to simulate 4 rates of browsing utilization.

Table 1. Late winter diets of moose in Oshetna and Tyone drainages determined by fecal analysis for winter 2000. Values are percent of total.

	Oshetna River (N = 31)	Tyone/Little Nelchina (N = 18)
Alnus stem	4.7	6.5
Betula nana leaf	3.0	0
Betula nana stem	12.9	18.5
Populus balsamifera stem	17.2	3.5
Salix spp. hair	0	5.6
Salix spp. leaf	3.4	5.8
Salix spp. stem	56.0	57.9
shrub leaf	2.0	0
shrub stem	0.5	1.1

Table 2. Crude protein, BSA, digestible protein and dry matter digestibility of principal winter browse used by moose in the Oshetna and Tyone drainages. Forage samples were collected in winter 2000.

	% Crude protein	BSA[a]	% Digestible Protein	% Digestible Dry Matter
Salix alaxensis	7.5	0.186	0.90	45.7
Salix pulchra	6.06	0.237	1.13	44.0
Betula nana	8.28	0.110	2.52	28.8

[a] Milligrams of bovine serum albumin precipitated/milligram of dry matter.

Table 3. Comparison of current annual growth treatment means. Tukey's 95% CI's around differences between means included 0.0 if means were not significantly different. Only the difference between the control and the 60% clipping treatment was significant. Clipping treatments were made in winters 1996, 1997, 1998, and 1999.   Samples for analysis were collected in winter 2000.

Treatment contrasts	Estimate	Std. Error	Lower bound	Upper bound
0–30	-0.1480	0.142	-0.591	0.2940
0–60	-0.4590	0.142	-0.901	-0.0166
0–90	-0.2470	0.142	-0.689	0.1960
30–60	-0.3110	0.142	-0.753	0.1320
30–90	-0.0983	0.142	-0.541	0.3440
60–90	0.2120	0.142	-0.230	0.6550

Table 4. Comparison of protein-precipitating capacity (BSA) treatment means. Tukey's 95% CI's around differences between means included 0.0 if means were not significantly different. No differences were significant. Clipping treatments were made in winters 1996, 1997, 1998, and 1999. Samples for analysis were collected in winter 2000.

Treatment contrasts	Estimate	Std. Error	Lower bound	Upper bound
0–30	0.004330	0.0157	-0.0502	0.0588
0–60	-0.007670	0.0157	-0.0622	0.0468
0–90	-0.007000	0.0157	-0.0615	0.0475
30–60	-0.012000	0.0157	-0.0665	0.0425
30–90	-0.011300	0.0157	-0.0658	0.0432
60–90	0.000667	0.0157	-0.0538	0.0552

Table 5. Comparison of total phenolic treatment means. Tukey's 95% CI's around differences between means included 0.0 if means were not significantly different. No differences were significant. Clipping treatments were made in winters 1996, 1997, 1998, and 1999. Samples for analysis were collected in winter 2000.

Treatment contrasts	Estimate	Std. Error	Lower bound	Upper bound
0–30	-0.833	16.6	-58.3	56.6
0–60	-3.500	16.6	-60.9	53.9
0–90	-7.500	16.6	-64.9	49.9
30–60	-2.670	16.6	-60.1	54.8
30–90	-6.670	16.6	-64.1	50.8
60–90	-4.000	16.6	-61.4	53.4

Table 6. Comparison of crude protein treatment means. Tukey's 95% CI's around differences between means included 0.0 if means were not significantly different. Clipping treatments were made in winters 1996, 1997, 1998, and 1999. Samples for analysis were collected in winter 2000.

Treatment Contrasts	Estimate	Std.Error	Lower Bound	Upper Bound
0–30	-1.0000	0.104	-1.360	-0.640 ****
0–60	-0.0833	0.104	-0.443	0.276
0–90	-0.2500	0.104	-0.610	0.110
30–60	0.9170	0.104	0.557	1.280 ****
30–90	0.7500	0.104	0.390	1.110 ****
60–90	-0.1670	0.104	-0.526	0.193

Table 7. Comparison of % digestible protein treatment means. Tukey's 95% CI's around differences between means included 0.0 if means were not significantly different. Clipping treatments were made in winters 1996, 1997, 1998, and 1999. Samples for analysis were collected in winter 2000.

Treatment contrasts	Estimate	Std. Error	Lower bound	Upper bound
0–30	-1.0300	0.16	-1.590	-0.478 ****
0–60	-0.0367	0.16	-0.595	0.518
0–90	-0.1270	0.16	-0.682	0.428
30–60	0.9970	0.16	0.442	1.550 ****
30–90	0.9070	0.16	0.352	1.460 ****
60–90	-0.0900	0.16	-0.645	0.465

APPENDIX

Additional federal aid-funded work not described above that was completed during this project are listed below.

COLLINS, WILLIAM B. 2001. Heavy grazing of Canadian bluejoint to enhance hardwood and white spruce regeneration. North. J. Appl. For. 18:19–21.

_____, and E. F. Becker. 2001. Estimation of horizontal cover. J. Range Manage. 54:67–70.

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