EFFECTS OF SIMULATED MOOSE BROWSING ON DRUMMOND'S WILLOW

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Abstract: A study was conducted from 1973 to 1983 on the north slope of the Uinta Mountains in Utah and Wyoming to evaluate the effects of varying simulated levels of winter browsing by moose (Alces alces) on Drummond's willow (Salix drummondiana). Plants within a 0.4-ha exclosure were clipped annually with levels of removal of 0%, 30%, 60%, or 90% of the cumulative growth $\le$ 0.5 cm in diameter. Numbers of stems, branches, and suckers per plant were decreased by all clipping intensities, but only the 90% treatment produced declines exceeding those observed among control plants. After 8 years of sustained clipping, browse production in the 30% treatment had declined to an average of 35% of the production in 1973. Comparable levels of browse production in the other two clipping intensities were 27 and 10%, respectively, of original levels. Plants clipped at the 90% rate showed significantly ($P \le 0.05$) higher mean protein and phosphorous values than plants in the other treatment levels. A comparison of 1- to 5-year old willow growth revealed that crude protein and phosphorous content and digestibility decreased with increasing age.

An increasing moose population in northern Utah has been investigated since 1969. Previously, Babcock et al. (1983) described the growth of the principal population segment on the north slope of the Uinta Mountains (Utah and Wyoming), and discussed the management implications of differences in herd productivity produced by manipulation of the adult sex ratio in that herd. In this paper, we present the results of a 10-year clipping study (1973-1983) designed to investigate the effects of various simulated levels of moose browsing on vigor, production, nutrient content, and digestibility of Drummond's willow.

Drummond's willow is the primary winter browse species for moose on the Uinta North Slopes. This species accounted for 93% of all the winter feeding occurrences observed by Wilson (1973) and comprised 59% of the willows on the study area. Based on these figures, estimates of average daily energy requirements for moose, as well as caloric content of the key browse species, Wilson estimated the carrying capacity of the winter range as the equivalent of 445 adult animals for a 6-month period. Results obtained from browse transects during the period 1966-1971 indicated a mean annual utilization of 26% of current annual growth (CAG) of the willow on the study area (Wilson 1971: Table 9). However, since the population appeared to be approaching rapidly the limits of its estimated winter range carrying capacity, it was deemed important to obtain more precise information on the level of browsing pressure the willow could withstand, while continuing to maintain production and adequate nutrient levels for moose.

STUDY AREA AND METHODS

The topography, climate, and vegetation of the Uinta North Slope study area as well as the history of its moose herd have been detailed elsewhere (Wilson 1971, Babcock 1977, Babcock et al. 1983). During the period 1972-1982, annual precipitation on the Uinta North Slope averaged 65 cm, but 1975 and 1977 were characterized by near record extremes in total annual precipitation of 93 cm and 46 cm, respectively. The freeze-free (> 0^{0} C) period on the Uinta North Slope is 0-40 days with an average of 25 days on the Henry's Fork study site described below (E. Arlo Richardson, pers. comm. 1984)

The following arbitrary definitions of various plant parts were used during the study: (1) stem = a major supporting structure (diameter > 0.5 cm) to which branches are attached; (2) branch = a woody extension (≤ 0.5 diameter) growing from a stem and comprising one or more years' growth increments arising from a branch; (3) sucker = a long slender stem of current annual growth arising from the base of a plant; and (4) whip = a dead stem. The ages of growth increments for branches were designated according to the number of growing seasons (each of approximately 3 months duration) they had completed.

In 1972 a 0.4-ha exclosure with a 4.5-m fence was constructed in the Henry's Fork drainage, located in the western portion of the study area at an elevation of approximately 2600 m. Forty Drummond's willow plants within the exclosure were selected as subjects for the clipping study. Plants selected for treatment were subjected to clipping intensities of 0% (control) 30%, 60%, or 90% (by number of branches + suckers) of the cumulative growth≤ 0.5 cm in diameter. Ten replications of each treatment level were located randomly throughout the exclosure to minimize possible biases due to difference in exposure, moisture and microclimate.

Clipping treatments were performed in late December or early January each year on dormant plants. The plants were clipped with pruning shears, starting from snow level (approximately 1 m above ground) and moving upward, systematically removing the prescribed percentage of branches. Clipping treatments for a given plant remained the same throughout the course of the investigation (1973-1983).

Our clipping treatments differed from those employed by several other investigators who clipped only CAG (e.g. Aldous 1952, Garrison 1953, Cook and Stoddart 1960, Krefting et al. 1966, Shepherd 1971). Our decision to include at least 2-year old growth, rather than merely CAG, was based on the fact that natural browsing by moose is not limited to annual growth. Bassett (1951) noted that about 15% of the willows in the Snake River bottoms of Wyoming showed moose utilization of 2-year old wood. On the Uinta North Slope, Wilson (1971) found that Drummond's willow growth browsed by moose averaged 0.5 cm in diameter, with frequent observations of branches nipped to 2.0 cm and occasionally up to 2.5 cm. Babcock's (1977) data indicated that the average size of willow branches browsed by moose included at least 2-year old growth as well as CAG. A clipping scheme that includes older growth increments should simulate more closely natural browsing.

Data collected from each treated plant included a subjective rating (good, fair, poor) of general plant vigor; numbers of live stems, branches, suckers, and dead stems (whips) present; and the number of branches removed. Air dry weights were recorded for all clipped forage. All but the latter two measurements were used as indices of plant vigor, and were collected from control plants also. All whips were removed when the plants were clipped the first time. Accordingly, whips present in subsequent years died during the course of the study. For each of the treated plants, the amount of forage available to moose (1-, and 2-year old branches + suckers) was estimated by dividing the weight of clipped material by the respective clipping intensity.

Clipped forage samples from each treated plant were analyzed at the Soil and Plant Analysis Laboratory (Utah State University, Logan) to estimate the content of dry matter, ash, crude protein (N x 6.25), phosphorous, and calcium. Dry matter digestibility of the browse samples was estimated by the "two-stage" *in vitro* technique as described by Tilley and Terry (1963). Because moose rumen liquor could not be obtained, domestic goats were used as a source of rumen inoculum. These animals were all maintained on a diet of 100% Drummond's willow for a period of 15 days prior to collection of the inoculum so that the rumen microorganisms could adjust to the willow forage. Moen (1973) maintained that rumen fluid obtained from animals on the same diet would probably produce similar *in vitro* digestibility results, despite the fact that the animals may be of two different species. Similarly, Welch et al. (1983) found little difference in the ability of rumen inocula sources from several species to digest a variety of forages.

As part of the present investigation, 10 plants were selected randomly in the winter of 1972-73 and 10 stems cut from each plant and

separated into their respective growth increments. Procedures identical to those described above were employed to determine the nutrient (except calcium) content and digestibility of the various years' growth.

Analysis of variance (ANOVA) was the principal technique employed in statistical treatment of the data collected during the study. One-way ANOVA and standard t-tests were used to test the null hypotheses that willow plants in the various treatment groups did not differ in terms of condition, production, nutrient content, and digestibility at the time of the initial clipping in 1973. Apparent differences in plant production and forage quality in response to treatment were tested by means of two-way ANOVA, with treatment and years as the main effects. Least significant difference tests were used to determine the significance of observed differences in the above parameters between individual treatments. A similar approach was employed in analysis of differences in nutrient composition and digestability of current and past years' willow growth. In this case, however, the ANOVA incorporated a randomized block design in which individual plants (N = 10) constituted the blocks with 10 replications (stems) per block.

RESULTS AND DISCUSSION

Responses of Willow to Clipping

At the time of the initial clipping, the willow plants in the various treatment categories showed no significant ($P \leq 0.05$) differences in height, general vigor, and in numbers of stems, suckers and whips; only branch numbers among the control plants and those in the 90% group were significantly ($P \leq 0.05$) higher than among plants in the 30% category (Table 1). Based on these findings, we concluded that the plants in the four treatment groups were reasonably comparable at the outset of the study.

Interpretation of plant response to treatment is complicated by variability due to differences among individual plants and possibly environmental factors such as precipitation levels, which may have influenced plant production across all treatment levels. ANOVA revealed highly significant ($P < 0.01$) differences in the mean numbers of stems, branches, suckers, and whips per plant among years (Table 2). For this reason, it is useful to examine changes among the control plants during the study before addressing plant response to treatment.

The control plants exhibited short-lived, initial increases in the numbers of branches and suckers, possibly due to the removal of dead whips, which decreased the shading effect on the plants and stimulated new growth. However, comparison of 1974-78 and 1979-83 means for the various plant parts (Table 1) revealed decreases in stem, branch and sucker numbers of 35, 34, and 9%, respectively. This phenomenon is probably due to diminished production and decadence as the results of continuing non-use. Prior to the establishment of the exclosure, the control plants had been subject to moderate moose browsing. Martinson (1960) and Tueller and Tower (1979) reported that average production of bitterbrush (*Purshia tridentata*) plants protected from browsing was approximately 70% less than those that were browsed annually. The latter investigators noted that vegetation stagnation from non-use constitutes a major problem in exclosure-type studies, and that the phenomenon may manifest itself as early as the second year after establishment of an exclosure.

Table 1. Temporal changes in numbers of Drummond's willow stems, branches, suckers, and whips in relation to four levels of clipping intensity, 1973-1983.[a]

		Numbers of plant parts			
Plant part	Treatment (% clipped)	1973	(1974-78)	(1979-83)	% change between means
Stems	Control	104	86	56	-35
	30%	66	56	35	-38
	60%	64	47	31	-34
	90%	86	55	13	-76
Branches	Control	431	544	359	-34
	30%	209	357	238	-33
	60%	242	356	229	-36
	90%	362	544	107	-80
Suckers	Control	27	70	64	-9
	30%	25	48	48	0
	60%	29	58	53	-9
	90%	37	103	63	-39
Whips	Control	48	8	6	-25
	30%	28	9	5	-44
	60%	22	10	4	-60
	90%	37	8	4	-50

[a]for simplicity all entries are given as whole numbers

Table 2. F values obtained from analyses of variance for indices of Drummond's willow plant vigor in relation to clipping intensity, 1974-1983.

Source of Variation	D.f.	Stems	Branches	Suckers	Whips
Treatment	3	43.01**	12.95**	10.77**	1.51
Year	10	18.63**	12.35**	10.45**	41.18**
Interaction (Trt. x Yr.)	30	1.12	2.14**	2.22**	2.15**

* Significant ($\underline{P} \leq 0.05$)

** Significant ($\underline{P} \leq 0.01$)

Variations in annual precipitation levels were examined as a possible factor accounting for some of the temporal changes in the number of plant parts observed among the control plants. This possibility was investigated by means of a series of regression trials involving numbers of various plant parts during the period 1973-1981 as a function of annual precipitation in the preceding year. These tests yielded only one significant ($\underline{P} \leq 0.05$) correlation. Specifically, branch numbers among the control plants were correlated (r = 0.72) with precipitation levels.

The changes in 5-year means for various plant parts in the respective treatment levels are given in Table 2. Examination of these changes reveals that the plants in the 30 and 60% treatments exhibited decreases in the number of stems, branches and suckers that were comparable to those among the control plants. Only the 90% clipping rate lead to decreases in excess to those shown by the control data.

In spite of ephemeral increases in 1976 and 1977, the average forage (available to moose as defined previously) per plant decreased linearly ($\underline{P} \leq 0.01$) in all treatments during the course of the study (Table 3). During the period 1979-1983, forage production among plants in the 30% treatment had declined to an average of 35% of the production observed in 1973. Comparable levels in the other two clipping intensities were 26% and 10%, respectively, of original levels. In 1979, production had fallen below 100 g in 30% of the plants in the highest clipping intensity; by 1983, the incidence of plants producing less than 100 g had doubled.

In summary, sustained clipping by the method employed in this study resulted in decreases in the amount of available forage in all treatment levels. Because forage samples were not collected from the

Table 3. Estimated average available willow forage production (g) per plant in relation to clipping intensity, 1973-1983.[a]

	Level of clipping intensity		
Year	30%	60%	90%
1973	1,589 (1.0)[b]	1,480 (1.0)	1,715 (1.0)
1974	1,178 (0.7)	727 (0.5)	656 (0.4)
1975	876 (0.6)	597 (0.4)	518 (0.3)
1976	1,122 (0.7)	727 (0.5)	564 (0.3)
1977	1,183 (0.7)	800 (0.5)	551 (0.3)
1978	944 (0.6)	582 (0.4)	366 (0.2)
1979	608 (0.4)	458 (0.3)	238 (0.1)
1980	513 (0.3)	355 (0.2)	119 (0.1)
1981	508 (0.3)	438 (0.3)	254 (0.1)
1982	604 (0.4)	356 (0.2)	106 (0.1)
1983	585 (0.4)	292 (0.2)	106 (0.1)

[a]Available forage production comprises the total production of 1- and 2- year old branches.

[b]Figures in parenthesis denote yields relative to levels observed in 1973.

control plants, we have no means to assess directly possible changes in available forage in that category. Aldous (1952) reported that clipping annual growth of willow at rates of 25 and 50% produced numerical declines in stem numbers, but that this response was compensated by substantial increases in the weight of annual production.

Several investigators that have noted that clipping studies are subject to numerous biases. Culley et al. (1933) and Jameson (1962) maintained that clipping does not accurately simulate animal herbivory, because animals feed either selectively or at random rather than utilizing the plant uniformly. In addition, litter accumulation from clipping may differ from that of natural herbivory, and there is no trampling effect. The clipping regime imposed in this study was probably unnaturally severe, because it is unlikely that shrubs would be subject to the same browsing intensity during a 10-year period. However, Penner (1978) and Machida (1979) observed that browsing of willow by moose in a given year predisposes the plant to a greater probability of being utilized the following year. Similar results were reported by Bergstrom (1984) for two species of birch (Betula spp.) in Sweden.

In this study, varying snow depths introduced a confounding effect on the experiment, especially the extremes of 1975 and 1977. However, this variable affected the plants in all treatments, thus allowing relative comparisons. Normal snow cover on the study area protected the lower portions of the plants from treatment in most years to a height of approximately 1 m. This may have buffered the effects of clipping on the plant as a whole, thereby preventing mortality. A similar protective effect of the snow cover probably applies to the outermost stems and branches of some plants which are laid down under the snow and remain free from treatment. We submit, however, that such conditions are not unlike those occurring with natural moose browsing.

Nutrient Content and Digestibility of Willow Forage

Forage quality in relation to age- Levels of ash, crude protein and phosphorous as well as dry matter digestibility all decreased significantly ($P \leq 0.05$) with increasing age of willow growth. Table 4 shows that the mean values for all constituents and the digestibility of current year's growth were significantly higher than those of older growth. In the process of plant maturation, soluble carbohydrates are converted to structural carbohydrates with resultant increases in cellulose, hemicellulose, and lignin. Cell walls thicken and crude protein, phosphorous and ash (mineral) content as well as digestibility decrease.

The nutrient content and digestibility of 1- and 2-year old willow forage observed in this study are generally comparable to values reported in the literature for other willow species during the winter period (November-March) from various locations in North America and Sweden (see reviews by Oldemeyer 1974, Gassaway and Coady 1974 as well as more recent papers by Cederlund and Nystrom 1981, Hjeljord et al. 1982, and Eastman in press). Houston (1968) noted a pronounced decrease in forage quality and digestibility between 6- and 18-month old growth in blueberry willow (Salix pseudocordata) due to significant differences in the chemical composition and increased lignification of older stems. He hypothesized that poor quality diets, comprising greater proportions of older willow twigs, might adversely affect the physical condition and reproductive performance of pregnant cows.

Table 4. Nutrient composition and digestibility of current and past year's growth of Drummond's willow.

Parameter	Age of Growth	Mean[1]	±95% C.I.
% Ash	1	2.2 a	0.3
	2	1.9 a	0.3
	3	1.8 a	0.3
	4	1.4 b	0.4
	5	1.0 c	0.2
% Crude protein	1	7.4 a	0.3
	2	5.1 b	0.3
	3	4.8 c	0.4
	4	3.2 d	0.3
	5	2.9 d	0.4
% Phosphorous	1	0.14 a	0.01
	2	0.10 b	0.01
	3	0.08 b,c	0.01
	4	0.06 c,d	0.00
	5	0.05 d	0.01
% Digestibility	1	36.4 a	5.9
	2	27.4 b	2.8
	3	24.5 b,c	2.6
	4	20.4 c,d	2.7
	5	16.5 d	2.6

[a]Means within a group followed by the same letter are not different at $P \leq 0.05$)

Wilson (1971) used a digestibility factor of 50% in his calculations of the carrying capacity of the key browse species on the winter range of the Uinta North Slope. Our results indicate that this figure is too high, and probably resulted in overestimation of the range's carrying capacity. Moreover, Wilson's estimate was based on the energy content of current annual willow growth only. As noted previously, however, the browse consumed by moose includes 2- and probably some 3-year old growth. Since digestibility of the browse decreases with age, this would result in further overestimation of the carrying capacity.

Forage quality in relation to clipping intensity - The mean values obtained for ash, crude protein, phosphorous and calcium content and digestibililty of willow samples from the various clipping intensities are given in Table 5. Because the 1973 samples could not be expected to reflect the effects of clipping, they were analyzed separately from the results for 1974-1983 and were excluded from the computation of the treatment means given in the table. Nutrient analyses were not performed on the 1980 browse samples, nor were digestibility trials for the 1982 and 1983 samples. Finally, the validity of the calcium values obtained from the 1982 samples was questionable; accordingly, these values were omitted from the table.

Statistical analyses revealed no significant ($P \leq 0.05$) differences for any of the nutrient components or digestibility among plants in the three treatment groups at the time of first clipping. There were, however, highly significant ($P \leq 0.01$) differences among the following years for all of the nutritional parameters (Table 6).

Table 5. Nutrient content and digestibility of Drummond's willow in relation to clipping intensity (values given are percentages)[a].

Treatment level	Ash	Crude protein	Phosphorus	Calcium	Dry matter digestibility
30% clip					
1973	2.0	6.3	0.10	0.47	30.4
1974	2.1	6.3	0.11	0.51	35.4
1975	1.9	6.2	0.11	0.47	33.2
1976	2.0	6.2	0.12	0.53	32.9
1977	3.1	8.2	0.14	0.69	19.9
1978	2.4	6.5	0.12	0.46	36.8
1979	2.7	7.2	0.12	0.51	39.4
1981	2.8	6.6	0.13	0.55	42.2
1982	2.0	6.2	0.11	--	--
1982	1.8	5.3	0.10	0.40	--
$\bar{x}$	2.3	6.5	0.12	0.52	34.3
60% clip					
1973	2.1	6.2	0.10	0.48	30.9
1974	1.9	6.6	0.12	0.45	35.5
1975	1.8	6.4	0.12	0.42	35.1
1976	1.9	6.5	0.13	0.54	33.4
1977	3.1	8.6	0.15	0.60	21.3
1978	2.4	6.7	0.12	0.43	35.1
1979	2.6	7.5	0.13	0.47	40.1
1981	2.7	6.6	0.13	0.50	42.9
1982	1.8	6.1	0.12	--	--
1983	2.0	6.4	0.12	0.40	--
$\bar{x}$	2.2	6.3	0.12	0.48	34.7
90% clip					
1973	2.2	6.4	0.10	0.52	32.2
1974	2.0	7.9	0.14	0.43	36.1
1975	1.8	6.8	0.12	0.39	36.3
1976	2.0	7.0	0.13	0.45	36.3
1977	3.0	8.8	0.15	0.60	22.6
1978	2.4	7.3	0.13	0.43	35.4
1979	2.4	7.4	0.13	0.47	37.4
1981	2.6	6.9	0.13	0.51	40.9
1982	1.8	6.7	0.13	--	--
1983	1.8	6.7	0.12	0.36	--
$\bar{x}$	2.2	7.3	0.13	0.46	35.0

[a]Means do not include 1973 values

Table 6. F values obtained from analyses of variance of nutrient content and digestibility of Drummond's willow browse as a function of clipping intensity.

Source of variation	Ash	Crude protein	Phosphorous	Calcium	Digestibility
Treatment	1.73	18.69**	18.69**	7.92**	1.22
Year	60.19**	24.13**	24.13**	17.04**	93.96**
Interaction (Trt. x Yr.)	0.42	2.16**	0.55	0.46	1.52

* Significant ($\underline{P} \leq 0.05$)

** Significant ($\underline{P} \leq 0.01$)

Specifically, 1977 was characterized by higher ash, protein, phosphorous and calcium values in all treatments, while digestibility was 35-50% lower than the mean for other years. Above average digestibility values also occurred in 1980 and 1981. Significant differences among treatments were limited to protein, phosphorous and calcium content. The mean protein and phosphorous values for plants in the 90% treatment were higher than those in other treatment levels. The observed differences probably reflect the fact that as the study progressed, the annual samples from all clipping treatments contained an increasingly greater fraction of younger growth with higher nutritional value as explained above. Surprisingly, calcium content appeared to be inversely related to clipping intensity.

CONCLUSIONS AND RECOMMENDATIONS

The primary strength of this study lies in its long-term nature. In retrospect, however, we conclude that the treatment regimen employed was more severe than the degree of herbivory that the willow plants would have been exposed to under most natural conditions. Although moose may browse portions of a given plant at the intensities clipped in the study, it is unlikely that identical portions would be subject to the same utilization levels for extended periods of time except in areas of extremely high population densities. A more realistic treatment regimen would be one that incorporates a quasi-stochastic clipping pattern, based on observed natural browsing patterns, such as those reported by Bergstrom (1984). We emphasize, however, that the clipping levels should not be limited to current annual growth.

Given that the present study represents a potential "worst possible case" scenario, we note that the 30% and 60% clipping rates resulted in declines in plant production indices that were comparable to those observed among the control plants. It would be useful to examine the effects of simulated utilization levels in the range of 70-80%. An important shortcoming of this study was the failure to sample the control plants at minimal levels (i.e. 5-10%) for the purpose of estimating potential forage yields, nutrient content and digestibility. The incorporation of such a modification would enhance future investigations.

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