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Weight Distribution in the Current Annual Twigs of Barclay Willow

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Abstract

The current annual twigs of unbrowsed Barclay willow (*Salix barclayi* Anderss.) grow as gently tapering cylinders. Consequently, the distal half of the twig has only 33 to 41 percent of the total weight. Longer twigs have proportionally less weight in the distal end. The total weight of an unbrowsed twig can be estimated by simple regression of weight on an independent variable that approximates the volume of the twig (diameter of the twig immediately above the most recent bud scar times total length of the twig). Simple regression can also be used to estimate the weight of twig removed by browsing. The best estimator of weight of twig removed is an independent variable that approximates the volume of the twig left attached to the plant (diameter of the twig at the point of browsing times length of twig remaining).

Keywords: Barclay willow, current annual twigs, browse, weight estimation, browsing.

Introduction

Tall shrub willows (*Salix* spp.) are important forage in the winter diet of Alaskan moose (*Alces alces gigas*) (Oldemeyer 1983, Oldemeyer and others 1977, Peek 1974, Wolff 1976). The current annual twig (the current season's woody growth distal of the most recent bud scar) is browsed most. Accurate determination of twig weight and the extent to which it is removed by browsing moose is requisite for management of the forage resource.

All techniques used to measure forage use consider three major requirements: (1) a measure of availability, (2) a measure of loss, and (3) the availability-to-loss ratio. Although availability can be determined from regression and ratio with counts of browsed and unbrowsed twigs, determination of loss is not as straightforward.

Direct estimation of twig weight by clipping is inconvenient because shrub willows are large and, consequently, have a substantial amount of twig weight. Even more important, clipping may result in inaccurate estimations and is unavoidably destructive.

The weight of willow twigs has been estimated by regression on basal diameter of the twig (Connolly and Grigal 1983, Grigal and others 1976, Ohmann and others 1976, Peek and others 1971, Telfer 1969, 1972). If twigs are heavily browsed, the estimate of the standing crop of twig weight may be biased without an accurate estimate of the weight lost to browsing.

A commonly used technique to estimate twig weight lost to browsing, developed by Shafer (1963), converts a count of browsed twigs to weight of browse lost by use of average weight of browsed twig. Others (Joyal 1976, Parker and Morton 1978, Wolff 1976, 1981) have modified some operational details of this method, but the essentials are unaltered.

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During a study of the total aboveground productivity of Barclay willow (*Salix barclayi* Anderss.)[1] on the wetlands of the Copper River Delta, in south-central coastal Alaska, doubts arose about the ability of established methods to accurately estimate twig-weight loss caused by wintertime browsing by moose. It seemed a correction factor based on an average weight of browsed twig would be strongly influenced by the initial length of the twig. Not only might longer twigs be preferred by browsing moose, but the linear distribution of long twigs might differ from that in short twigs. If a high correlation was present between the weight of the removed portion of the twig and the easily obtained measurements from the portion of the twig remaining on the plant, the average weight of a browsed twig could be estimated directly.

Study Area

The study was conducted in early October 1981 in the 0.6-hectare Alaganik Moose Exclosure on the Copper River Delta, 29 kilometers south of Cordova, Alaska. This exclosure was established in the fall of 1979. Barclay willow is the predominant willow species in the exclosure. Stem density was 968 $\pm$ 92 stems per are and maximum height rarely exceeded 2.5 meters (m).[2]

Methods

Collection and Preparation

A batch sample of current annual twigs was collected for determining the distribution of willow twig lengths in the exclosure. One to five randomly selected twigs were clipped immediately below the most distal bud scar from randomly selected stems of Barclay willow. Only twigs longer than 50 millimeters (mm) and growing 0.5 meter or more above the ground surface were collected. Total sample size was the number of twigs collected within a 30-minute clipping period.

Clipped twigs were ovendried at 70 °C for 24 hours and sorted into four length-classes: 50 to 150 mm, 151 to 250 mm, 251 to 350 mm, > 350 mm. The number of twigs in each class was determined, and two 10-percent subsamples were selected from each class. One subsample was used to develop the regression model. The other was retained to test the model.

The overall length of each twig was measured to the nearest millimeter, and the twigs were cut into quarter-lengths. Each quarter-length was weighed to the nearest 0.01 gram and its basal diameter measured to the nearest 0.1 mm. The weights of the four quarters for each twig were added to obtain total twig weight.

Statistical Analysis

All possible subsets regression (Frane 1983) was used for analysis. Regression analyses were made for each quarter twig-length and for the total twig-length, both by individual length-class and for the total sample. The significance of the differences between twig quarter-weights was tested with analysis of variance program (Davidson and Toporek 1983). Statistical significance was $p \geq 0.05$ for all statistical tests.

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[1] Scientific and common names of plants are from Hultén (1968).

[2] Are = 100 square meters (a square 10 m by 10 m).

Results

All selected Barclay willow twigs grew as unbranched, tapered cylinders; however, taper was not uniform. The sample batch included 1,064 twigs: 281, 50 to 150 mm; 351, 151 to 250 mm; 274, 251 to 350 mm; and 158, > 350 mm in length. Descriptive statistics for the 10-percent proportional sample used to develop the regression equation and the additional 10-percent sample used to validate the model are given in table 1.

The two subsamples are statistically similar in all respects. The following results are for only the subsample used to develop the regression model. Twigs in the > 350-mm length-class were the least common, but they produced 48 percent of the total weight of the subsample. Only 5 percent of the sample came from twigs in the 50- to 150-mm length-class, although twigs of this length were the second most frequent in the subsample. Twigs in the two longest length-classes had a combined frequency of only 40 percent but produced 78 percent of the total subsample weight; hence, the importance of the longer twigs in the production of weight.

Table 1—Descriptive statistics for the regression and validation samples

Twig length-class	n	Weight: Regression sample $\bar{y}$	$s_{\bar{y}}$	Weight: Validation sample $\bar{y}$	$s_{\bar{y}}$	Basal diameter: Regression sample $\bar{x}$	$s_{\bar{x}}$	Basal diameter: Validation sample $\bar{x}$	$s_{\bar{x}}$	Total length: Regression sample $\bar{x}$	$s_{\bar{x}}$	Total length: Validation sample $\bar{x}$	$s_{\bar{x}}$
Millimeters		*Grams*				*Millimeters*							
50-150	28	0.21	0.02	0.20	0.02	2.1	0.07	2.1	0.07	104.9	5.6	104.4	5.5
151-250	35	.63	.03	.63	.03	2.9	.06	2.8	.05	197.3	4.5	195.0	4.2
251-350	27	1.44	.08	1.31	.06	3.7	.08	3.6	.09	296.8	6.1	294.6	6.2
>350	16	3.86	.49	3.90	.44	5.0	.23	5.1	.24	465.9	24.8	466.6	26.1
All classes	106	1.21	.14	1.18	.14	3.2	.10	3.1	.11	238.8	12.4	237.4	12.4

Distribution of Weight Within the Twig

Mean weight of the quarter-length segments of the four classes of Barclay willow twigs used for regression analysis are given in table 2. For all classes except the shortest, the means for weight of basal and second quarters and second and third quarters were not statistically different; basal quarters were always heavier than third quarters, except in the shortest twig length-class. Distal quarters always weighed the least, except in the 50- to 150-mm twig class where this difference was not statistically significant.

Table 2—Weights of Barclay willow twig quarter-lengths used in regression

Twig length-class	Quarter	Weight $\bar{x}$	Weight $s_{\bar{x}}$	Proportional weight
Millimeters		-----*Grams*----		*Percent*
50-150	Basal	0.064	0.008	30
(n=28)	Second	.061	.007	29
	Third	.051	.006	24
	Distal	.035	.004	17
151-250	Basal	.199	.011	32
(n=35)	Second	.176	.010	28
	Third	.153	.009	24
	Distal	.104	.006	16
251-350	Basal	.520	.029	36
(n=27)	Second	.415	.027	29
	Third	.314	.019	22
	Distal	.191	.011	13
>350	Basal	1.525	.210	39
(n=16)	Second	1.107	.140	29
	Third	.799	.096	21
	Distal	.430	.048	11
All classes	Basal	.445	.057	37
(n=106)	Second	.347	.040	28
	Third	.265	.028	22
	Distal	.157	.015	13

The distal quarter of the willow twig had significantly lower average weight compared with all other quarters (table 2). The proportional distribution of weight is more informative than actual weight. For the total subsample, the distal quarter of the twig supplied 13 percent of the average total weight; the distal half, 35 percent; and the distal three-quarters, 63 percent. This proportional distribution of weight was similar for all four twig length-classes but was less pronounced in the two shorter classes. In all but the shortest class, the distal quarter of the twig had significantly less weight than the adjacent third quarter (table 2). As twig length increased, the proportion of weight in the basal quarter also increased. Browsing the distal end of longer twigs removed proportionally less weight than did browsing of shorter twigs.

Estimation of Whole Twig Weight

Five independent variables were used to estimate total twig weight (W): basal diameter (B), squared basal diameter (B^2), total twig length (L), basal diameter times total twig length (BL), and squared basal diameter times total twig length (B^2L). Strong multicolinearity was present between the five independent variables ($r = 0.983$ to 0.863). Multiple regression was not appropriate, consequently, and only simple regression was used.

For the entire sample and the three longest twig length-classes, the best estimators of total twig weight (as indicated by r^2) were the two variables BL and B^2L. Both were approximations of twig volume (table 3). For twigs in the 50- to 150-mm length-class, B^2 alone was equal to B^2L and slightly superior to BL as an estimator of twig weight. Weight was more evenly distributed throughout twigs in the 50- to 150-mm length-class than in the other classes. Twig length alone was the least suitable estimator of twig weight for both the total sample and individual subsamples.

Table 3—Best simple regression models ($\hat{y}$=bx-a) for estimation of twig weight for individual twig length-classes and the total sample of twigs

Twig length-class	n	r^2	Standard error of the estimate	Regression[a]
Millimeters				
50-150	28	0.696	0.070	W=0.0648(B) -0.0888
151-250	35	0.707	0.103	W=0.0013(BL)-0.1356
251-350	27	0.733	0.223	W=0.0017(BL)-0.3979
>350	16	0.940	0.496	W=0.0020(BL)-0.9063
All classes	106	0.965	0.269	W=0.0018(BL)-0.3562

[a] All regressions are statistically significant. W = ovendry weight of twig; B = basal diameter of twig; and L = total length of twig.

The best estimate of whole twig weight was for the entire 106-twig sample. The individual twig length-classes showed a slight trend toward better estimates of weight as twig length increased.

Test of the Weight Estimation

The test subsamples were not statistically different from the sample used to develop the regression models. The ability of the regression model to estimate actual twig weight was compared at both the mean values of the test sample and the extreme values of the 95-percent confidence limits (table 4). For the total sample, the estimated mean value agreed very closely (less than 1 percent greater) with the actual mean, and the differences at both 95-percent confidence limits were positive above 3 percent. Estimates of weight within individual twig length-classes were less accurate and did not show a consistent bias. For the overall sample, the close agreement between estimated weight and actual weight indicates that a regression with basal diameter times total length can be a useful procedure and can give accurate results.

Table 4—Comparison of actual and regression-estimated twig weight in the test sample at the mean and the 95-percent confidence limit extremes

Twig length-class	Twig weight at: Lower confidence limit	Mean	Upper confidence limit
		Grams	
50-150 millimeters:			
Actual	0.16	0.20	0.24
Estimated	.18	.21	.25
Percentage[a]	+11	+5	+4
151-250 millimeters:			
Actual	.57	.63	.69
Estimated	.52	.58	.61
Percentage[a]	-9	-8	-8
251-250 millimeters:			
Actual	1.19	1.31	1.43
Estimated	1.29	1.18	1.59
Percentage[a]	+8	+9	+10
> 350 millimeters:			
Actual	2.96	3.90	4.84
Estimated	3.46	3.98	4.45
Percentage[a]	+14	+2	-9
All classes:			
Actual	.90	1.18	1.46
Estimated	.93	1.19	1.51
Percentage[a]	+3	<1	+3

[a] [(Actual - estimated) ÷ estimated] x 100.

Estimation of the Weight of a Browsed Twig

The remaining portion of the browsed twig was weighed to estimate the weight that was removed by browsing. This was done with the same 106 twigs used to develop the total twig-weight regression. Three basic measurements were used: the diameter of the twig at the point of browsing (P), the diameter of the twig at the bud scar (B), and the length of the portion of the twig between these two diameters (L). The three measurements can be made precisely and rapidly under field conditions on browsed twigs still attached to the plant.

The relation between twig weight browsed to the remaining twig was tested only at 1/4, 1/2, and 3/4 of the total length of the twig. Although this systematic selection did not simulate actual losses because of browsing herbivores, it did provide a consistent and comparable set of attributes for analysis.

The diameter of the twig at the point of browsing (P) times the length of twig remaining (R) was the best overall estimator of the weight of the browsed portion (table 5). In all three categories for twig-length removed, independent variables that approximated the volume of the twig remaining (that is, diameter times remaining length) had the highest correlation with the weight of the twig removed. As the length of the remaining portion of the twig decreased, r^2 values increased. Consequently, greater use may be more adequately estimated than light use.

Table 5—Best regression models ($\hat{y}$=bx-a) for estimation of the weight of the browsed portion of Barclay willow twigs

Portion of twig removed	r^2	Standard error of estimate	Regression[a]
Distal 1/4	0.936	0.039	W = 0.0004 (PR) - 0.0224
Distal 1/2	0.962	0.087	W = 0.0015 (PR) - 0.0743
Distal 3/4	0.972	0.145	W = 0.1543 (PR) - 0.1543

[a] W = estimated weight of browsed portion; P = twig diameter at point of browsing; and R = length of twig remaining. All regressions are statistically significant.

Discussion

When a moose browses 50 percent of the current unused length of a Barclay willow twig, less than 50 percent of the weight of the twig is removed. A twig 500 mm in length for example, would need to have between 65 and 70 percent of its length browsed to remove 50 percent of its weight. This is a considerable length of woody material to be browsed, even by a moose. For shorter twigs, slightly less of the length needs to be browsed to remove 50 percent of the twig weight because smaller twigs have more weight in the distal section than do long twigs. The shortest twigs (50-150 mm) measured in this study, nevertheless, would have to be browsed 60 percent in length to remove 50 percent of the weight.

Because the concentration of weight is in the basal portion of a twig of current annual growth, the effect of twig weight lost to browsing is minimized. A shrub with half the number of twigs browsed half their length may appear heavily used, but actual weight loss would be less than 20 percent; thus, browsing may often be overestimated visually.

Many intrinsic mensurational factors influence the degree to which an individual twig is browsed. Length of the twig, length of other twigs, and their juxtaposition and location on the plant in relation to twigs of different lengths all may influence how much of an individual twig is removed by a browsing herbivore. Extrinsic factors such as the size of the browsing animal, how hungry it is, competition from other animals, and individual preference can also affect length of twig removed. Unless these factors are known, the amount of a twig that might be browsed in field conditions must be considered a random variable.

The above applies only to twig-weight losses. Browsing of twigs, however, means much more than just a loss of weight. Browsing of leafless twigs in the fall, winter, and spring directly removes some of the next year's leaf and flower buds. The shrub will try to replace the buds in part with stored photosynthates. In addition, browsed twigs on Barclay willow appear to die back from the point of browsing and become nonfunctional dead wood. Just how much of the twig must be removed to cause this conversion from living wood to dead wood and the rate at which the conversion takes place is under study. From the standpoint of the shrub, browsing that removes only a very small amount of weight may be physiologically demanding, and the influence of browsing should be considered in this context.

Application

The high correlations between the volume of twig that remains on a browsed plant and the weight of twig removed indicates the technique discussed in this paper has practical application for the estimation of willow twig utilization. Some restrictions and limitations must be considered before applying the technique elsewhere. First, the work was done in one geographic region with a single species of willow. Second, the twigs used for regression analysis were straight, unbranched, tapered cylinders. Third, the correlation between remaining twig volume and original twig weight was defined for removal of 1/4, 1/2, and 3/4 of twigs between 50 and 700 mm in length.

If the method is used elsewhere, the regression given here must be tested to determine the correspondence between actual and predicted biomass. New regression coefficients may have to be calculated. Use of the technique with another species of willow should not be limiting if the twigs grow as straight, unbranched, tapered cylinders. Where willows have crooked, branched twigs, the proportional distribution of weight in the twig may be unlike that of the twigs used here, and a strong twig-volume-weight correlation may be absent. Actual twig utilization does not occur in quarter-length increments. But because the quarter-length weight values are almost linearly distributed, the weight-lost relation for any given length of twig can be determined by interpolation.

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