EFFECTS OF PLANT COMPENSATION ACROSS SITES ON REGRESSION ESTIMATES OF SHOOT BIOMASS AND LENGTH

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ABSTRACT: Regression estimates for determining browse shoot biomass from bite diameters and shoot basal diameters are commonly used to estimate biomass consumption and the impacts that herbivores have on range resources. Such estimates tend to be based on equations built from data taken across the continuum of shoot morphometries present on plants within a given study area. How these morphometric relationships differ between the shoots of undamaged and damaged (e.g., following browsing, shoot breakage, or brush-cutting) plants is unclear. To assess the effects of plant compensation and the importance of site on shoot morphometrics for Scouler's Willow (*Salix scouleriana)*, we clipped and measured current annual shoots at 5 sites in central British Columbia. Each site had been previously brush-cut and current annual shoots were collected from both brush-cut and control willows. For each treatment and site, we developed separate regressions to predict shoot weight from length, weight from basal diameter, and length from basal diameter. Comparisons of individual regressions indicated that different regressions, or even different forms of regressions (i.e., power function versus linear), are needed to accurately predict shoot weight and length depending on whether or not plants are producing compensatory or non-compensatory shoots. For some willows in the same treatment category (brush-cut versus uncut), the appropriate regressions differed among some sites. These results suggest that the effects of plant compensation following mechanical damage have important implications to the extrapolation and interpretation of shoot morphometric relationships, and thus, biomass estimates across different study areas.

In the absence of direct observations and measurements, determining biomass consumption of browse shoots by ungulates is difficult and time consuming (Provenza and Urness 1981). One method of estimating biomass removal is to develop regression equations for shoot biomass based on the diameter and other morphometric parameters of the current annual shoot (Telfer 1969a, Lyon 1970, Provenza and Urness 1981). In this way, shoot biomass beyond the point of browsing (consumption) can be estimated (Ferguson and Marsden 1977, Provenza and Urness 1981, MacCracken and Van Ballenberghe 1993) in a non-destructive manner (Thilenius 1990). Likewise, availability of browse, carrying capacity of ranges (Telfer 1969a), and animal stocking rates (Ruyle et al. 1983) can be estimated using similar equations that predict biomass from measurements taken at the basal diameter of shrub and tree shoots.

Regression equations for estimating shoot biomass and length from other shoot attributes have been developed for several browse plants commonly consumed by moose (*Alces alces* L.; e.g., Telfer 1969b, Thilenius 1990, MacCracken and Van Ballenberghe 1993). These equations, however, have not accounted for variations in shoot architecture resulting from exaggerated vegetative shoot growth on plants compensating for various forms of mechanical damage such as brows-

ing, breakage, and cutting. In this paper, we investigated whether equations predicting biomass and shoot length for Scouler's willow (*Salix scouleriana* Barr.) varied among plants that were compensating for mechanical damage from brush-cutting between 2 and 3 years after cutting and undamaged plants at 5 sites in central British Columbia.

STUDY AREA

Our study area consisted of 5 sites that were clear-cut logged (15-40 ha in size) and then planted with lodgepole pine (*Pinus contorta* Dougl. *ex* Loud. var. *latifolia* Engelm.) near Vanderhoof, British Columbia, Canada (lat 54°01'N, long 124°00'W). All sites were characterized by open stands of lodgepole pine with poorly developed shrub and herb layers, and a well-developed moss layer dominated by lichens; soils on all sites were clay and/or sandy loam (Rea 1999).

METHODS
Site Histories

We selected 5 sites where brush-cutting had been conducted to determine the effects of mechanical damage on willow shoot morphometry 2 and 3 years after brush-cutting. Three of the sites (Layton, Buck, and Sackner) were clear-cut logged 12-15 years prior to our study; these sites were then brush-cut during the 1993 growing season (June-September) and sampled 3 years later (winter 1995-96). The other 2 sites (Sawmill and Huckleberry) were clear-cut logged 9-11 years prior to the beginning of the study, were brush-cut during the 1995 growing season, and sampled 2 years later in winter 1996-97.

During brush-cutting operations in 1993 and 1995, all above-ground biomass, except ~10 cm of stump tissue, was removed from willows and all other deciduous shrubs and trees at each site. Wildlife strips (*sensu* Santillo 1994; areas established for wildlife food and cover after clear-cut logging but prior to brush-cutting treatments) at each site were not brush-cut and contained willows about 4-5 m tall at the beginning of this study; willows that had been brush-cut on these sites were about 1-2 m tall. All sites had a long history of browse utilization by moose and deer (*Odocoileus* spp.). Additionally, free-range cattle (*Bos taurus* L.) utilized the Buck and Sackner sites in summer.

Current Annual Shoots

During the winter of 1995-1996, we randomly selected 6 Scouler's willow plants from brush-cut areas and 6 from the wildlife strips (controls) on each of the 3 plantation sites that had been brush-cut in 1993. We similarly selected willows at each of the 2 sites brush-cut in 1995 in the winter of 1996-1997. Once willows were selected, we clipped shoots accessible above the snowpack. Shoots were systematically collected at different clipping intensities (as part of a larger study, Rea 1999, Rea and Gillingham 2001) from willows in the Layton, Buck, and Sackner sites at the time we selected the plants during the winter of 1995-1996, and from the Sawmill and Huckleberry sites during the winter of 1996-1997.

We collected all shoot samples while plants were dormant in mid-winter by clipping shoots at the current annual growth scar. We sealed all collected shoots in plastic freezer bags in the field to inhibit water loss during transportation back to our laboratory at the University of Northern British Columbia. All shoots were weighed to the nearest mg and measured for length (cm) and basal diameter (mm). When >30 shoots were collected from a particular willow, we randomly sub-sampled 30 shoots for morphometric measures.

Regression Analyses

We began by examining the fit of 4 linear and non-linear regressions for each treatment (Brush-cut versus Uncut) at each of the 5 sites; we considered linear ($Y = a + bX$), power ($Y = a + bX^c$), and exponential ($Y = ae^{bX}$ and $Y = a + be^{cX}$) regression models. Following

the recommendation of Verwijst (1991) for biomass estimation, we did not use any log-transformed variables in any regression model. For each site and treatment, we developed separate regressions for: 1) shoot weight (Y) based on shoot length (X), 2) shoot weight (Y) based on shoot basal diameter (X, at the point of the growth scar), and 3) shoot length (Y) based on shoot basal diameter (X). In choosing the best regression for each set of data, we considered R^2 values (r^2 for linear regression) and the fit of residuals. Linear models were selected if the residuals did not justify a non-linear relationship. In all but 1 of the non-linear relationships, the power function was the best fit; because the power function was a very close second to the exponential model in the single other case, we chose to use the power function to simplify the comparison with other non-linear predictions.

We fit all nonlinear models with PROC NLIN (version 9.1, SAS Institute 2003); linear regressions were fit with the regression procedure (REG) in STATA (version 9.2, STATACorp. 2007). Confidence intervals around individual regression parameters were estimated by asymptotic approximations in the respective packages. We considered morphometric relationships to be different between treatments and/or among sites if the form of the regression was different (i.e., linear versus power), or if the confidence intervals around individual parameters of regressions of the same form did not overlap. We did not apply Bonferroni corrections to the confidence intervals because individual regressions with non-overlapping simple confidence intervals would yield different biomass estimates. We considered an α of 0.05 throughout our analyses.

RESULTS
Shoot Weight from Shoot Length
All regression estimates of shoot weight from shoot length were best fit with power functions. In addition, there were no differ-ences among regressions in shoot weight (Y) predicted by shoot length (X) for brush-cut willows across all sites (Table 1). There were, however, differences in regression equations for uncut plants among sites (i.e., one or more parameters in the power functions were significantly different from each other, Table 1). These differences included regressions for uncut willows at the 2-year post-cutting sites (i.e., Huckleberry uncut versus Sawmill uncut) and at the 4-year sites (e.g., Buck uncut versus Sackner uncut).

There were also numerous differences among regression equations developed for shoot weight versus shoot length when shoots from brush-cut and uncut plants were compared (Table 1, Fig. 1). Although the parameter that varied was not consistent among comparisons, any equation that varied significantly in any parameter would yield a significantly different prediction.

Shoot Weight from Shoot Basal Diameter
All regression estimates of shoot weight from shoot basal diameter were also best fit with a power function. With the exception of 1 case (Huckleberry versus Buck) that represented a difference in year-since-brush-cutting, we detected no difference in the form or parameters of the regression equations that explained the relationship of shoot weight (Y) to basal diameter (X) for shoots of brush-cut plants.

There was less consistency in the regression parameters of the power functions among uncut treatments (Table 2). Although the 2, 2-year sites (i.e., Huckleberry and Sawmill) were not different, there were differences in equations between 4-year sites (e.g., Table 2: Buck versus Sackner and Sackner versus Sawmill). Relationships for uncut plants also differed significantly between 4-year, post-cutting sites (Table 2: Layton and Sackner). There were no differences in equations for shoots of brush-cut and uncut plants growing on sites that were sampled 2 years after

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Table 1. Comparison of coefficients for shoot weight (Y) versus shoot length (X) regressions. All regressions were best fit with a power function (Y = A + BX^c). Brush-cut (BR) and uncut (UN) treatments were compared for each of 5 sites in central British Columbia. Letter entries in the table represent significant differences in the parameters (A, B, and C)[a] in the power function between treatments and among sites. Because the table is symmetrical, only the cells above the diagonal (—) are completed. Cells with no entries above the diagonal indicate that the corresponding regressions were not different from each other.

		Site									
		Buck		Huckleberry		Layton		Sackner		Sawmill	
Site	Treatment	BR	UN	BR	UN	BR	UN	BR	UN	BR	UN
Buck	BR	—					B				
	UN		—	B C	C			C	C	C	
Huckleberry	BR			—	B C		A B C		B C		A B C
	UN				—		A C				B C
Layton	BR					—	A B				
	UN						—	A B C	B C	B C	
Sackner	BR							—			A B C
	UN								—		B C
Sawmill	BR									—	B C
	UN										—

[a]A = The intercept of the power function equation.

B = The slope of the power function equation.

C = The exponent of the power function equation.

Note: The appearance of a letter in the table indicates a significant difference in either the intercept (A), slope (B), or exponent (C) between the two equations being compared.
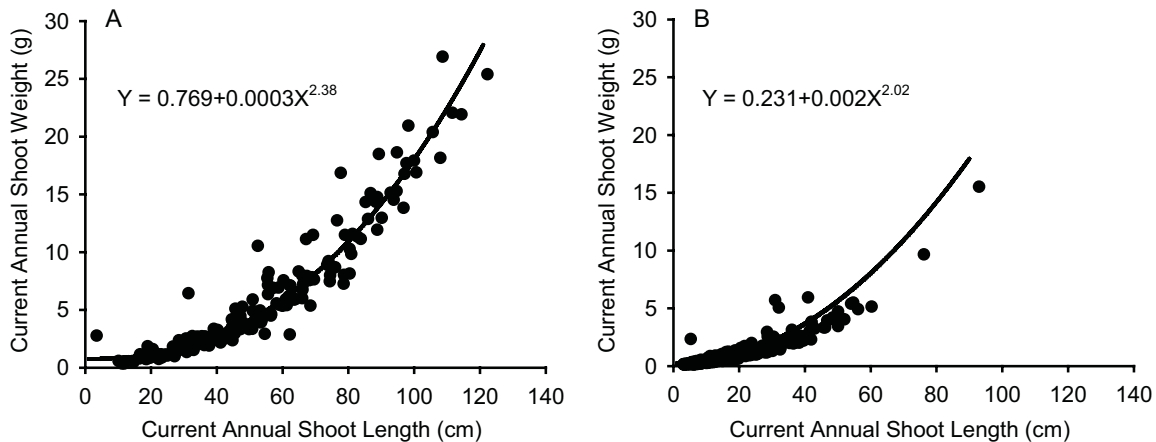

Fig. 1. Observed and predicted values for current annual shoot weight versus shoot length for brush-cut (A; $n = 191$) and uncut (B; $n = 240$) willows on the Huckleberry site.

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cutting (Table 2). Similarly, the relationship between shoot weight and basal diameter did not vary between cut and uncut plants within the same site.

Shoot Length from Shoot Basal Diameter

Unlike the relationships between shoot weight versus shoot length and shoot weight versus basal diameter, shoot length could not be predicted from basal diameter by a single equation form (Table 3, Fig. 2). Again, the effect of brush-cutting appeared more important than site effects in that all brush-cut treatments did not differ in equation form (Table 3: linear). There were, however, differences in the slope (E) for brush-cut treatments within and among treatments 2 and 3 years post-cutting. In those instances in which power functions were better fits than linear regressions, it was always for uncut treatments, although there was no consistency within and among 2- and 3-year sites. Finally, there were many differences within sites between cut and uncut treatments regardless of the number of years since cutting (Table 3, Fig. 2).

DISCUSSION

A fundamental difference appears to exist between the shoot morphometrics of brush-cut plants and those of uncut plants in which the growth form of compensatory shoots appears more consistently predictable than that of shoots from undamaged plants. This phenomenon appears to be true both within and between sites regardless of the time since brush-cutting. Our results further suggest

Table 2. Comparison of coefficients for shoot weight (Y) versus shoot basal diameter (X) regressions. All regressions were best fit with a power function ($Y = A + BX^c$). Brush-cut (BR) and uncut (UN) treatments were compared for each of 5 sites in central British Columbia. Letter entries in the table represent significant differences in the parameters (A, B, and C)[a] in the power function between treatments and among sites. Because the table is symmetrical, only the cells above the diagonal (—) are completed. Cells with no entries above the diagonal indicate that the corresponding regressions were not different from each other.

		Site									
		Buck		Huckleberry		Layton		Sackner		Sawmill	
Site	Treatment	BR	UN	BR	UN	BR	UN	BR	UN	BR	UN
Buck	BR	—		C	C		C				
	UN		—								
Huckleberry	BR			—			B C				
	UN				—	C	B C	C			
Layton	BR					—					C
	UN						—	B C	B C	C	C
Sackner	BR							—			B C
	UN								—		C
Sawmill	BR									—	
	UN										—

[a]A = The intercept of the power function equation.

B = The slope of the power function equation.

C = The exponent of the power function equation.

Note: The appearance of a letter in the table indicates a significant difference in either the intercept (A), slope (B), or exponent (C) between the two equations being compared.

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Table 3. Comparison of coefficients for shoot length (Y) versus shoot basal diameter (X) regressions. Some regressions were best fit with a power function ($Y = A + BX^c$) while other regressions were linear ($Y = D + EX$). Brush-cut (BR) and uncut (UN) treatments were compared for each of 5 sites in central British Columbia. Letter entries in the table represent significant differences in the parameters (power: A, B, C; linear: D, E)[a] in the regressions between treatments and among sites (Note: no A or B parameters were significantly different from each other). An * indicates that differences existed because the same form of regression could not be fit to the corresponding entries in the table. Because the table is symmetrical, only the cells above the diagonal (—) are completed. Cells with no entries above the diagonal indicate that the corresponding regressions were not different from each other in form or parameters.

		Site									
		Buck		Huckleberry		Layton		Sackner		Sawmill	
		BR	UN	BR	UN	BR	UN	BR	UN	BR	UN
Site	Treatment	(Linear)	(Linear)	(Linear)	(Power)	(Linear)	(Linear)	(Linear)	(Power)	(Linear)	(Power)
Buck	BR	—	E		*	E	D E		*		*
	UN		—	D E	*		E	E	*	E	*
Huckleberry	BR			—	*	E	D E		*	E	*
	UN				—	*	*	*		*	
Layton	BR					—	D E	E	*	E	*
	UN						—	D E	*	E	*
Sackner	BR							—	*		*
	UN								—	*	C
Sawmill	BR									—	*
	UN										—

[a]A = The intercept of the power function.

B = The slope of the power function.

C = The exponent of the power function.

D = The intercept of the linear equation.

E = The slope of the linear equation.

Note: The appearance of a letter in the table indicates a significant difference in the parameter between the two equations being compared.

that when considering undamaged plants, the relationship between shoot weight and length may be more influenced by site than other morphometric relationships.

Although all regressions for predicting shoot weight from shoot length and weight from basal diameter were best fit to a power function, linear equations were better suited to predict shoot length from basal diameter for all brush-cut plants. The regressions used to predict weight from length of shoots taken from uncut willows on the Buck and Layton sites were also better described with linear equations, whereas the shoots of uncut plants on the remaining 3 sites were better characterized by a power function.

Our results are based on a relatively small sample size of twigs and plants. If larger samples resulted in more within-site variability, then the confidence intervals around the parameters would be wider and perhaps fewer significant differences would be detected between treatments and among sites. We would expect that a small sample size,
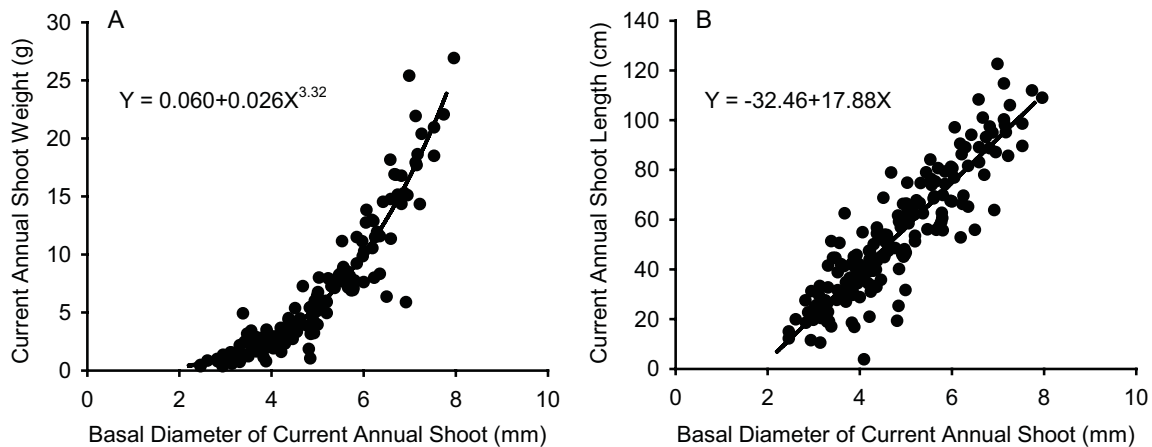
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Fig. 2. Observed and predicted values for current annual shoot weight versus current annual shoot basal diameter (A; $n = 191$), and length of current annual shoot versus current annual shoot basal diameter (B; $n = 191$) for brush-cut willows at the Huckleberry site.

however, would increase and not decrease the variation in the regressions.

Our results do not suggest a distinct pattern between the way in which equations differed from one another relative to site or time since brush-cutting (2 versus 3 years post-cutting). There were differences in the equations between plants growing on sites that had been brush-cut 2 years versus 3 years earlier. But this was also true when comparing within year since cutting and across sites. Therefore, we make no generalizations regarding site and year effects.

The fact that predictive equations for predicting shoot biomass of brush-cut plants did not differ between sites and year since cutting, and all other comparisons demonstrated significant differences, suggests a consistency in the relationship of shoot mass to length and basal diameter of compensatory shoots not found in the shoots of undamaged plants (Ferguson and Marsden 1977) and is, to our knowledge, previously unreported. However, it is unclear why predictive equations of biomass from the length and diameter of larger shoots would be more consistent across sites and year-since-treatment than predictive equations generated from the same parameters on non-compensatory shoots. Perhaps apical and lateral buds of winter shoots exhibit consistency in size and mass and influence

morphometric relationships disproportionately more for smaller and moderately sized shoots arising from undamaged plants than for heavier shoots. Such relationships are not necessarily true outside of the winter dormant period (Schewe and Stewart 1986).

Season and year of shoot collection (Telfer 1969a, Schewe and Stewart 1986, Thilenius 1990), plant species differences (Telfer 1969b, Potvin 1981, MacCracken and Van Ballenberghe 1993), site/microsite and aspect (Lyon 1970, Peek et al. 1971, Ruyle et al. 1983, Schewe and Stewart 1986), plant size/age (Lyon 1970, Peek et al. 1971), and shoot age and position on the plant (Telfer 1969a, Lyon 1970, Ferguson and Marsden 1977) are known to influence predictive equations of 1 shoot attribute from another. However, no such claims have been made for the influence of compensatory growth on such equations.

Ruyle et al. (1983) found that the form of quadratic equations used to predict oven-dried shoot weight from other shoot attributes varied by the total number of kg of snowberry plants utilized in pastures by sheep. MacCracken and Van Ballenberghe (1993) speculated that shoot size and age could significantly influence the character, and thereby, the utility of the regression equation. Peek et al. (1971) speculated more specifically that browsing pressure was likely to account for variation in

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equations developed for mountain ash. Our results seem to support such speculation and suggest that attempting to predict 1 attribute from another without accounting for shoot response to damage, could result in less accurate predictions than if separate regressions were developed for sites containing different treatment histories.

Our findings also indicate that using regression models to predict 1 shoot attribute from another should include some attention to site (Lyon 1970, Peek et al. 1971, Ruyle et al. 1983), and more importantly, to shoot-specific details. Both the intercept and form of predictive equations for 1 shoot attribute based on another varied depending on whether or not shoots were compensatory and on the site at which the parent plant was growing. Because plant compensation appears to be at least partially responsible for variation in shoot morphometric relationships, we suggest that the development of separate equations for shoots of compensatory and non-compensatory plants from different sites is likely to increase efficiencies in the field and increase predictive power more so than simply increasing sample sizes in an attempt to reduce variability (Peek et al. 1971).

Estimates of shoot weight from basal diameter are often used by rangeland managers to approximate available and/or browsed biomass (e.g., Ferguson and Marsden 1977, Provenza and Urness 1981, MacCracken and Van Ballenberghe 1993). Equations we developed to predict shoot weight from basal diameter were consistent in form and parameters for brush-cut, but not uncut willows. Estimating shoot biomass from shoot basal diameter with the use of our predictive equation for the shoots of brush-cut plants from the Buck site reveals that a typical shoot with a basal diameter of 5 mm would weigh 4.79 g, whereas a shoot from an uncut plant on the same site with a basal diameter of 5 mm would weigh 3.50 g. Estimating 100 such shoots per plant and 100 such plants per hectare, reveals that a difference of nearly 13 kg of browse per ha could go unaccounted for if prediction equations ignored differences between plants producing compensatory or non-compensatory shoots. Increases in the number of shoots per plant or plants per hectare exaggerate such discrepancies.

The degree to which predictive equations tested here varied between brush-cut and uncut plants underscores the need for managers to begin to account for whether or not plants used in building such equations are compensating from damage. Although brush-cutting appears to represent an extreme form of damage not likely to occur in nature, willows scoured by ice flows and broken by snow press (Danell et al. 1987) and browsers (Telfer and Cairns 1978) can incur similar magnitudes of damage. In fact, browse surveys are often conducted in areas influenced by anthropogenic activities such as brush-cutting and logging where interest in browse availability and the utility of such areas for rangeland use is commonly expressed (Shafer 1963, Rea and Gillingham 2001). Even so, moderate forms of damage in more remote areas can cause plants to respond with vigorous vegetative regeneration (Danell et al. 1985) that is likely to influence attributes used in regression equations (Telfer 1969a). Regardless of the damage agent involved or to what degree compensation proceeds, implementing sampling designs that examine plant compensation as well as site effects will allow researchers and managers to better account for the range of variation in shoots growing on differently treated plants on different sites and, as a result, increase the accuracy of their predictions.

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