METHODOLOGICAL INSIGHTS

Assessing impacts of large herbivores on shrubs: tests of scaling factors for utilization rates from shoot-level measurements

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Summary

1. Accurate methods for estimating the intensity of browsing by herbivores are fundamental to understanding the ecology of shrub communities. Quantifying browse utilization on shrubs at large scales is difficult because shrubs have complex, spatially variable growth forms. Most existing methods estimate browsing rate at the scale of linear current-year shoots or twigs. How such fine-scale estimates relate to the proportion of current-year growth consumed from whole plants or plots is often unknown. The relationship is likely to be complex because herbivores selectively browse more productive plants and plant parts.

2. Using a clipping experiment designed to mimic elk *Cervus elaphus* browsing, we quantified how utilization estimates at the scale of individual current-year shoots of two willow species, *Salix bebbiana* and *Salix geyeriana*, relate to actual mass removed at the scale of rooted stems. Three approaches to scaling were examined: (i) taking an average, (ii) multiplying by the proportion of shoots clipped and (iii) multiplying by a novel scaling factor that weights utilization by productivity. To address how to scale-up from stems to plots, we applied the most accurate stem-level method to elk-browsed willow and compared plot-level estimates by two scaling approaches.

3. In scaling from shoots to stems, the novel scaling factor was most successful and resulted in accurate estimates for up to *c.* 45% of current annual growth clipped. In scaling from the stem to the plot, elk preference for more productive stems caused a simple average of stem-level utilization to differ from a productivity-weighted average by 15%.

4. *Synthesis and applications.* In order to reflect accurately the proportion of biomass consumed at a whole-plant level, fine-scale estimates of utilization should be weighted by an estimate of pre-browse productivity, as this is mathematically equivalent to summing pre-browse and post-browse mass before calculating the proportion consumed. In developing methods to estimate utilization at plot scales, an important consideration is the choice of sampling unit, which should be both amenable to unbiased sampling and tractable in terms of measuring productivity.

Key-words: browse utilization, browsing, estimation methods, foraging patterns, herbivory, plant productivity, Yellowstone, willow, woody plants

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Introduction

Consumption of plants by large herbivores influences the structure and function of ecosystems by shaping competitive relationships among plant species and by altering rates and pathways of nutrient cycling (Hobbs

1996; Augustine & McNaughton 1998; Danell *et al.* 2003). Consequently, methods for estimating accurately the intensity of grazing and browsing by herbivores are fundamental to understanding many processes in ecology and ecosystem science.

Although procedures for estimating the grazing intensity of herbaceous plants are relatively well established (McNaughton, Milchunas & Frank 1996), estimating the browsing intensity of woody plants is far more problematic. Because shrubs have complex growth forms and only a proportion of the plant is available to browsers, researchers often estimate the utilization rate by counting browsed vs. unbrowsed twigs (Maccracken & Viereck 1990; Bergstrom & Guillet 2002; Edenius, Ericsson & Naslund 2002) or quantifying the proportion of mass removed from individual, linear shoots of the current year (Ferguson & Marsden 1977; Jensen & Urness 1981; Mahgoub, Pieper & Ortiz 1988). It is unknown how these estimates relate to units at larger spatial scales that might facilitate comparisons among landscapes or with other ecosystem variables.

In this study we quantified how estimates by two existing methods at the scale of individual current-year shoots relate to actual mass of current-year growth removed at the scale of rooted stems when scaled three different ways. We then compared two ways of scaling stem-level measurements to the plot level. We used two willow species as representative models: *Salix bebbiana* Sarg. and *Salix geyeriana* Anderss. Willow are the preferred browse species for many mammalian herbivores (Bryant & Kuropat 1980) and their productivity is typical of browse species in that it varies both within and between plants (Rutherford 1979). Using a clipping experiment designed to mimic the browsing patterns of an ecologically important browser, elk *Cervus elaphus* L., we addressed how herbivore selectivity affects the process of scaling utilization estimates. We developed a novel scaling factor designed to address this selectivity and tested its performance.

Methods

STUDY AREAS

Salix bebbiana and *S. geyeriana* stems used in the clipping experiment were selected from Sheep Creek in Roosevelt National Forest, Colorado, USA, a 3–4-m wide stream utilized by deer, elk and cattle. Field measurements used to quantify elk browsing patterns were taken from Blacktail Deer Creek, a 4-m wide stream in the northern elk wintering range of Yellowstone National Park, USA, where *S. bebbiana* and *S. geyeriana* are dominant species. Sheep Creek and Blacktail Deer Creek have similar semi-arid climates and the growth form of willows in both areas is short (1–2 m tall), with many browsed shoot stubs that have died back to the bud scar, indicating a history of heavy browsing (Keigley, Micheal & Frisina 1998).

STEM CLIPPING EXPERIMENT

Growth form of willows

Individual *S. bebbiana* and *S. geyeriana* plants may reach 2–3 m in height, and grow from seed or cut branches to form discrete clumps with one to many stems that join together below the ground surface at the root crown. We defined a 'stem' as a portion of the individual that emerges from the ground surface. A 'shoot' is the generally unbranched growth of the current year. A typical stem in our study might contain 100 current-year shoots, with a highly skewed size distribution comprising a few long shoots and numerous smaller shoots growing from side branches. Stems provide an ideal unit for quantifying willow utilization because their morphology is complex enough to incorporate some of the variability affecting herbivore browsing patterns, while being discrete enough to serve as a basis for scaling to the plot level.

Clipping procedure and quantifying actual percentage clipped

Because willows in the Rocky Mountains are browsed primarily in winter, we performed the clipping experiment in September 2005, after completion of the season's growth but before winter browsing. Two observations from field measurements of elk-browsing patterns at Blacktail Deer Creek were notable and were incorporated into our design. First, the average size of shoots that are browsed is larger than those that escape browsing. Secondly, some shoots may be completely consumed. The average basal diameter of browsed shoots was twice as large as that of unbrowsed shoots [browsed vs. unbrowsed means $\pm$ 95% confidence interval (CI) (mm); *S. bebbiana* 2·69 $\pm$ 0·39 vs. 1·56 $\pm$ 0·46; *S. geyeriana* 2·68 $\pm$ 0·27 vs. 1·19 $\pm$ 0·17], and 21% of stems had at least one instance of browsing into second-year wood, indicating complete consumption of some first-year shoots.

We selected 15 *S. geyeriana* and 13 *S. bebbiana* stems for the clipping procedure and clipped them successively to achieve a range of clipping intensities. To simulate light browsing, we clipped portions of the uppermost, easily accessible shoots, which tended to be longer and thicker than less-accessible shoots. To simulate moderate browsing, we clipped more of the easily accessible shoots. To simulate heavy browsing, we clipped off most shoots along with small amounts of second-year wood. The procedure resulted in three mass fractions that were dried and weighed individually. Second-year wood was excluded. The percentage of current annual growth (CAG) removed at a given clip level was calculated by summing masses of the given clip fraction along with prior clipped fractions and comparing the sum with the total mass of CAG. Total CAG was found by drying and weighing all portions of current-year shoots that remained after the clipping procedure and adding this mass to the mass of current-year growth that had been previously removed. To verify the procedure, we calculated
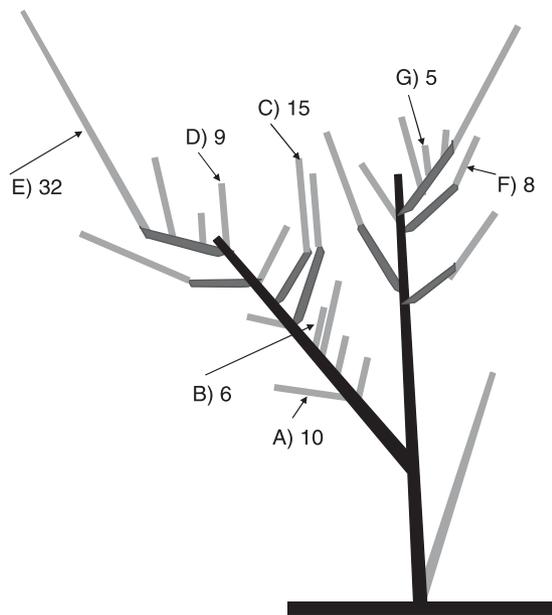
Fig. 1. Diagram illustrating shoot sampling protocol for a stem. Letters indicate the order of measurements; numbers indicate lengths in centimetres. To represent adequately the shoot size distribution in this example, we chose a sampling ratio of 3, which means we recorded measurements on every third shoot encountered as we worked apically from the base of the stem, accommodating side branches by sampling the lowest branches first. Here, seven measurements were made, with two shoots apical of the last shoot sampled. The count of shoots was then calculated as $7 \times 3 + 2 = 23$. If four of the seven measured shoots were browsed, along with the two apical of the last shoot sampled, then the count of browsed shoots is estimated as $4 \times 3 + 2 = 14$, and the count of unbrowsed shoots as $3 \times 3 + 0 = 9$.

the size difference between clipped and unclipped shoots across clip levels, which was similar to the difference we observed for browsed and unbrowsed shoots in the field [clipped vs. unclipped means ± 95% CI (mm); *S. bebbiana* 2·67 ± 0·17 vs. 1·58 ± 0·058; *S. geyeriana* 1·78 ± 0·16 vs. 0·99 ± 0·035].

Estimating percentage clipped

We tested the accuracy of two shoot-level methods when combined with three approaches to scale them to the stem, as well as one method that estimated mass before and after clipping directly at the stem level. All methods required measuring an unbiased sample of shoots on each stem. We developed a systematic sampling protocol for selecting shoots to measure, which simultaneously provided a count of browsed and unbrowsed shoots (Fig. 1).

Shoot-level measurements. One common technique for measuring utilization of shoots, referred to here as the mass–diameter regression (MDR) method, relates diameter at the bud scar of a shoot to mass prior to browsing, and diameter at the browse point to mass removed (Ferguson & Marsden 1977; Mahgoub, Pieper

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& Ortiz 1988; Maccracken & Vanballenberghe 1993) A second method in current use, referred to here as the diameter difference (DD) method, calculates utilization with a formula based on the difference between diameter at the bud scar and the browse point (Jensen & Urness 1981; Pitt & Schwab 1990; Singer, Mark & Cates 1994; Hebblewhite *et al*. 2005).

To apply the MDR method, we estimated the pre-clip mass of each clipped shoot using a regression between base diameter and mass (r^2 values; *S. bebbiana* 0·94; *S. geyeriana* 0·95; see Appendix S1 in the supplementary material) and mass removed using a regression between clip point diameter and shoot mass apical of the clip point (r^2 values; *S. bebbiana* 0·94; *S. geyeriana* 0·93; see Appendix S1 in the supplementary material). The percentage clipped at the shoot level (MDR_{shoot}) was calculated as the ratio of mass removed to total mass.

To find the percentage clipped by the DD method, we applied the following formula to each shoot measurement (Jensen & Urness 1981):

$$DD_{shoot} = \left(\frac{D_p - D_t}{D_b - D_t} \right) \qquad \text{eqn 1}$$

where D_p is the diameter at the browse or clip point, D_t is the average diameter of unbrowsed or unclipped shoot tips, and D_b is the base diameter.

Scaling factors. We tested three scaling factors. First, we took the simplest approach to scaling by averaging MDR_{shoot} and DD_{shoot} over each stem to find $MDR1_{stem}$ and $DD1_{stem}$.

When browsing intensity is low, many shoots will not be browsed. Therefore, the average utilization rate of browsed shoots may overestimate browsing intensity at the whole-plant or community scale. Pitt & Schwab (1990) applied the solution of multiplying the shoot-level rate by the proportion of shoots that are browsed. To test this second approach to scaling, we applied equation 2 below for the MDR method estimate and equation 3 below for the DD method estimate:

$$MDR2_{stem} = \left(\frac{c}{c + u} \right) \times MDR1_{stem} \qquad \text{eqn 2}$$

$$DD2_{stem} = \left(\frac{c}{c + u} \right) \times DD1_{stem} \qquad \text{eqn 3}$$

where *c* is the number of clipped shoots on the stem and *u* is the number of unclipped shoots on the stem.

Herbivores tend to select for larger than average shoots (Armstrong & Macdonald 1992; Danell, Bergstrom & Edenius 1994), hence multiplying the utilization rate of browsed shoots by the proportion of shoots that are browsed may underestimate browsing intensity at the whole-plant or community scale. We tested a third, novel scaling factor to account for this. Instead of using a proportion based on a count of clipped vs. unclipped shoots, we used a proportion based on the mass of clipped vs. unclipped shoots. This is not identical to the

proportion of mass removed by the clipping procedure. It is the proportion of the total pre-clip shoot mass contained in clipped shoots. Obtaining a field estimate of this proportion requires measuring both the proportion of shoots browsed and the average pre-browse mass of browsed vs. unbrowsed shoots, which can be estimated from base diameters after browsing. In our experiment, we measured base diameters on all shoots selected by the sampling ratio, regardless of whether they were clipped or not, then estimated their pre-clip mass using a regression between base diameter and mass (r^2 values; *S. bebbiana* 0·94; *S. geyeriana* 0·95; see Appendix S1 in the supplementary material). We then found the average pre-clip shoot mass for each category (clipped or unclipped) on each stem. We used these estimates in equation 4 to scale the MDR method estimate:

$$MDR3_{stem} = \left(\frac{c \times \bar{C}}{c \times \bar{C} + u \times \bar{U}} \right) \times MDR1_{stem} \qquad \text{eqn 4}$$

where $\bar{C}$ is the estimated average pre-clip mass of clipped shoots, and $\bar{U}$ is the estimated average mass of unclipped shoots (other symbols as above). To scale the DD method estimate, we applied equation 5:

$$DD3_{stem} = \left(\frac{c \times \bar{C}}{c \times \bar{C} + u \times \bar{U}} \right) \times DD1_{stem} \qquad \text{eqn 5}$$

Biomass comparison method. At high browsing intensities some shoots may be completely consumed, and any method relying on only post-browsing measurements becomes unreliable because it is impossible to estimate the mass of current-year growth of the missing shoots (Jensen & Urness 1981; Armstrong & Macdonald 1992). We tested a before-and-after method, called here the biomass comparison (BC) method, to address this problem. It is not based on scaling-up measurements of shoot-level utilization. Instead, the biomass of all CAG on the stem is quantified before browsing, and then compared with an estimate of CAG remaining on the stem after browsing. It is analogous to a long-used method first suggested by Nelson (1930), in which individual shoots are marked in the field and their lengths are measured before and after browsing. However, instead of marking individual shoots, an entire stem is marked, which allows the mass of completely browsed shoots to be quantified.

We estimated CAG prior to clipping by measuring shoot lengths and applying a regression equation relating length to mass (r^2 values; *S. bebbiana* 0·99; *S. geyeriana* 0·99; see Appendix S1 in the supplementary material) to each shoot measurement. We then found the average shoot mass and multiplied by a count of shoots to estimate total CAG. We estimated the portion of CAG remaining after clipping (CAG_{left}) by measuring the lengths of all unclipped shoots and diameters at the base and clip point of all clipped shoots. The mass of unclipped shoots was estimated as before clipping. The mass of clipped shoots was found by applying a multiple regression equation relating base diameter and the difference between base and clip diameter to

mass (r^2 values; *S. bebbiana* 0·87; *S. geyeriana* 0·89; see Appendix S1 in the supplementary material). We summed the estimates of clipped and unclipped shoot mass to find the CAG remaining after clipping. The stem-level percentage clipped was calculated as:

$$BC_{stem} = \left(1 - \frac{CAG_{left}}{CAG} \right) \qquad \text{eqn 6}$$

Statistical analyses

We tested the accuracy of each technique at the stem level by regressing estimates of percentage clipped against measured values. We tested for significant deviations from a 1:1 line using a simultaneous test for an intercept of 0 and a slope of 1 in a test statement in SAS PROC REG (SAS/STAT software, Version 9·1 of the SAS System for Windows, © 2002–03 SAS Institute Inc.). *F*-values indicated the magnitude of deviation from an ideal fit. We also quantified the estimated error of each method at low clipping intensity (25% clipped) and high clipping intensity (75% clipped).

SCALING FROM THE STEM TO THE PLOT

If herbivores prefer more productive stems as well as more productive shoots, then a simple average of stem-level utilization may not reflect biomass removed at the plot level. To address this issue, we estimated CAG and utilization using the BC method for 38 *S. geyeriana* and 39 *S. bebbiana* stems randomly selected from a 20 × 20-m plot on the Blacktail Deer Creek drainage in Yellowstone. We determined if elk preferred stems with higher CAG by comparing utilization rates for the most productive quartile of stems with the lower quartiles. To quantify the effect of herbivore preference for productive stems on the plot-level utilization rate, we compared two methods for scaling-up stem-level measurements. The first method was a simple average of BC_{stem}. The second method was analogous to the third scaling factor described above. Biomass and productivity remaining were summed for all stems before making the utilization calculation, as in equation 7:

$$BC_{plot} = \left(1 - \frac{\sum CAG_{left}}{\sum CAG} \right) \qquad \text{eqn 7}$$

This method is mathematically equivalent to averaging BC_{stem} weighted by CAG.

Results

STEM CLIPPING EXPERIMENT

At low clipping intensity (25% of current-year growth removed), *MDR*1 overestimated utilization by 11% and *DD*1 by 37% for *S. bebbiana* (Fig. 2a,b). For *S. geyeriana* the overestimates were 18% and 35% for these two methods (Fig. 3a,b). Scaling the methods by the proportion of browsed shoots overcorrected the problem. *MDR*2 underestimated utilization by 20% and *DD*2 by

16% for *S. bebbiana* (Fig. 2c,d), while for *S. geyeriana* the underestimates were 20% and 18% for the two methods (Fig. 3c,d). In contrast, both shoot-level methods were relatively accurate when scaled by the proportion of shoot mass browsed. For *S. bebbiana*, the *MDR*3 estimate was within 5% of the actual percentage browsed and the *DD*3 estimate was within 11% (Fig. 2e,f). For *S. geyeriana*, the *MDR*3 estimate was within 3% and the *DD*3 estimate was within 6% (Fig. 3e,f).

At high clipping intensity (75% of current-year growth removed), the trends were different. With the exception of *DD*1, all methods based upon scaling-up shoot-level measurements underestimated the percentage clipped. The underestimation of percentage clipped for *S. bebbiana* was 16% by *MDR*1, 50% by *MDR*2, 27% by *MDR*3, 41% by *DD*2 and 7% by *DD*3 (Fig. 2a,c–f). For *S. geyeriana* the underestimation was 15% by *MDR*1, 61% by *MDR*2, 32% by *MDR*3, 58% by *DD*2 and 25% by *DD*3 (Fig. 3a,c–f). *DD*1 did not underestimate utilization but this method predicted high values of percentage clipped regardless of actual values (Figs 2b and 3b).

The BC method provided accurate estimates for both species at both low and high clip intensities. Estimates were within 10% of actual values throughout the range of actual percentage clipped (Figs 2g and 3g).

SCALING FROM THE STEM TO THE PLOT

The productivity of stems at our study plot in Yellowstone was highly skewed. The most productive quartile of stems accounted for 73% and 67% of total current-year biomass measured for *S. bebbiana* and *S. geyeriana*, respectively. Consumption of the most productive quartile of stems averaged significantly higher than consumption of the lower three quartiles (highly productive vs. less productive means ± 95% CI; *S. bebbiana* 71·3% ± 22% vs. 47·9% ± 13·2%; *S. geyeriana* 80·1% ± 8·1% vs. 59·1% ± 10·6%). As a consequence of these patterns, calculating plot-level utilization as a simple average of stem-level utilization resulted in estimates that were *c.* 15% lower than BC_{plot} (equation 7) (simple average vs. BC_{plot}; *S. bebbiana* 54% vs. 71%; *S. geyeriana* 64% vs. 78%).

Discussion

Shoot-level utilization measurements accurately reflected stem-level utilization rates for browsing intensities of less than *c.* 45%, but only when scaled by a weighting factor that accounts for herbivore preference for large shoots. While applying this weighting factor requires estimating pre-browse shoot mass, these estimates may be obtained from basal diameters, making pre-browse measurements unnecessary. When > 45% of shoot biomass was removed, however, shoot-level estimates failed to predict accurately actual removal at the stem level, because some shoots were removed entirely. In this case pre-browse measurements may be necessary to account for completely consumed shoots, as in the BC method. In scaling from the stem level to the plot level, we again found that herbivore preference for higher productivity influenced the relationship between utilization rates at smaller vs. larger scales. We recommend
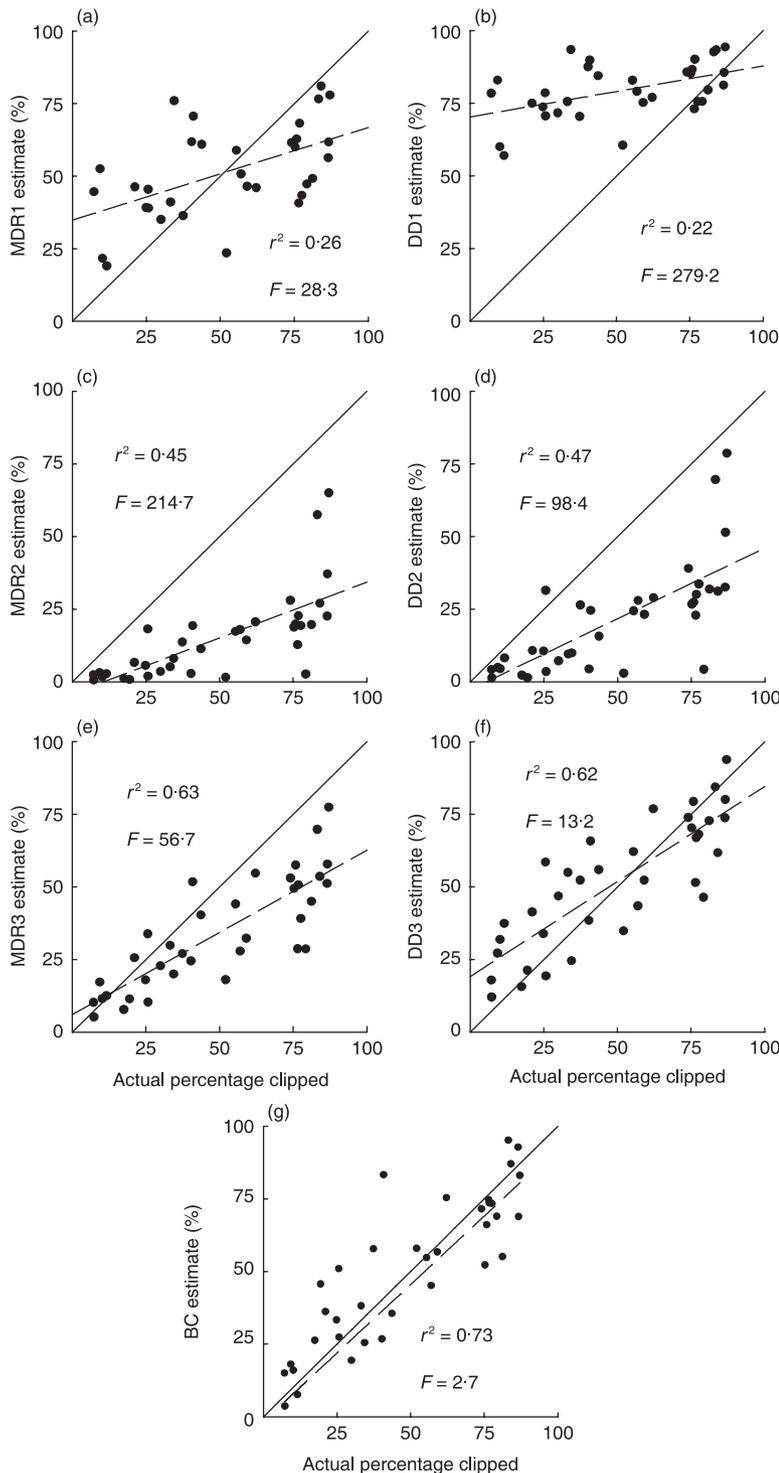

Fig. 2. Results of regressing actual percentage clipped of *S. bebbiana* stem current annual growth against estimates by seven methods: two shoot-level methods, (a) the mass-diameter regression (MDR) method and (b) the diameter difference (DD) method, scaled by taking a simple average; the MDR method (c) and the DD method (d) scaled by multiplying by the proportion of browsed shoots; the MDR method (e) and the DD method (f) scaled by multiplying by the proportion of shoot mass browsed; and (g) the biomass comparison (BC) method. A perfect model would conform to the solid 1:1 line; dashed lines indicate a linear least-squares fit to the data. *F*-values indicate the magnitude of deviation of the dashed line from the 1:1 line.

weighting the smaller scale estimate by an estimate of pre-browse productivity, as this reflects the proportion of biomass removed at the plot level, rather than the average proportion of biomass removed from stems.
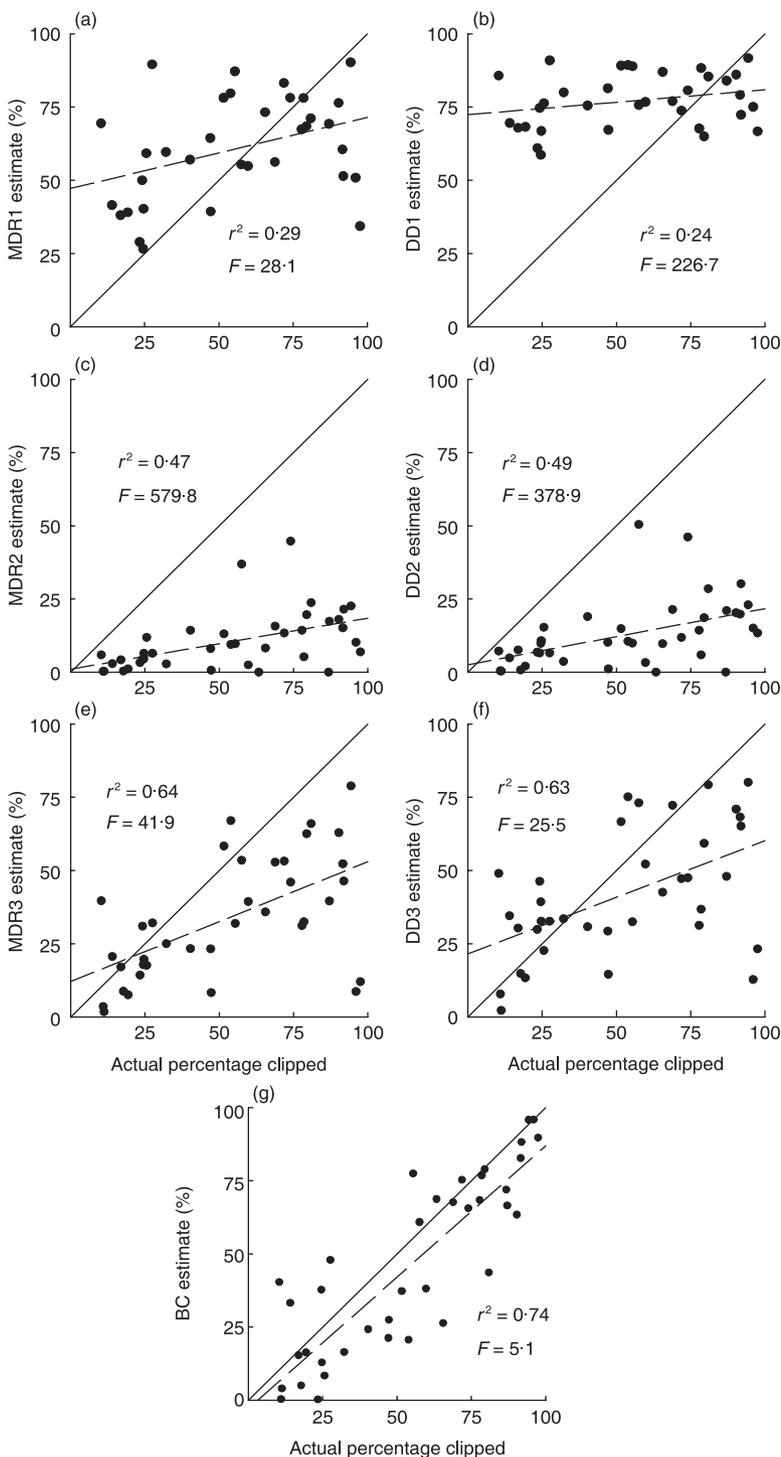

Fig. 3. Results of regressing actual percentage clipped of *S. geyeriana* stem current annual growth against estimates by seven methods: two shoot-level methods, (a) the mass-diameter regression (MDR) method and (b) the diameter difference (DD) method, scaled by taking a simple average; the MDR method (c) and the DD method (d) scaled by multiplying by the proportion of browsed shoots; the MDR method (e) and the DD method (f) scaled by multiplying by the proportion of shoot mass browsed; and (g) the biomass comparison (BC) method. A perfect model would conform to the solid 1:1 line; dashed lines indicate a linear least-squares fit to the data. *F*-values indicate the magnitude of deviation of the dashed line of the 1:1 line.

Alternatively, one could sum estimates of productivity and estimates of biomass removed before calculating the proportion.

The choice of method and scaling technique greatly impacts utilization estimates in the field. In our study plot in the Blacktail drainage of Yellowstone, the BC method estimate of utilization for *S. bebbiana* in 2002–03 was 71%. The *DD*2 method estimate for a nearby plot was 26% lower (F. Singer, unpublished data). Results of our clipping experiment indicated that at high browsing intensity the *DD*2 method underestimated utilization by 41% at the stem level. Therefore the discrepancy between the estimates at the plot level is probably the result of underestimation by the *DD*2 method, which does not account for an elk preference for larger shoots.

The general theme of weighting small-scale utilization estimates by an estimate of pre-browse productivity is broadly applicable in the study of woody plants impacted by large herbivores. Shrubs and saplings that have high potential productivity, and are therefore potentially important browse species, tend to have high spatial variability in productivity (Rutherford 1979). Large herbivores respond to spatial variability in complex ways at the patch scale (Senft *et al*. 1987; Edenius *et al*. 2002; Palmer *et al*. 2004; Searle *et al*. 2005), as well as at the scale of shoots within a plant (Armstrong & Macdonald 1992; Danell, Bergstrom & Edenius 1994). Because both productivity of browse species and consumption by herbivores vary at multiple scales, it is unlikely that a simple average of utilization at any scale will provide an accurate utilization estimate at a higher scale. We propose, none the less, that by making a careful choice of scaling units and weighting their utilization rates by an estimate of their pre-browse productivity, it is possible to make reproducible estimates of browse utilization for most species.

The most important modification needed in extending this work to other species is the choice of sampling units, such as a stem, sapling, branch, or small area, on which to base measurements. A selection of units that is unbiased with respect to factors that might affect herbivore preference, such as topography, size and density, is essential. The unit must therefore be both tractable in terms of measuring biomass and amenable to unbiased sampling. A shoot is very easy to measure, but very difficult to sample in an unbiased way directly from the plot scale. Armstrong & MacDonald (1992) developed a method of using strings placed across the plot to select heather shoots nearest to randomly chosen points in space, but for any species with variable shoot size this method would be biased, as larger shoots cover more space and would therefore be selected preferentially. A stem or branch is easier to select (although perhaps not trivially so), but more difficult to measure. If the stem or branch contains a large number of current-year shoots, it may be necessary, as was the case with willows in our study, to subsample shoots systematically and apply a weighting factor in order to estimate

their utilization. A small plot is easiest to select and may be a good choice for very short, dense shrubs, but estimating biomass and utilization might require more effort. For tree species such as aspen and birch, individual saplings or suckers are a good choice.

A second factor to consider is the choice between before-and-after and post-browsing-only measurements. In making this choice it is ideal to mark and track a few scaling units over at least one season in order to determine if browsing is heavy and complete shoot consumption common. If browsing is heavy, only a before-and-after approach will result in accurate estimates.

Like most methods for measuring shrub utilization, all methods described here consider utilization to be the percentage of current-year growth removed (Rutherford 1979). Recognizing that browsers may consume older wood as well as the current year's growth, some researchers consider utilization to be the proportion of tissue removed that is smaller in diameter than the maximum bite size of the herbivore of interest (Shafer 1963; Telfer 1969). However, the accuracy of estimation methods using this definition depends on mass removed relating in a predictable way to bite diameter regardless of the age of tissue at the browse point. If the plant species of interest branches from one year to the next, these methods are less reliable. Also, these methods are less useful in comparing utilization rates across ecosystem types that have different dominant herbivores. We advocate expressing utilization as the percentage of current-year growth consumed in order to develop utilization estimates that are comparable among ecosystems, a problem that previously has limited inference (Bergstrom 1992).

In conclusion, accurate scaling of shoot-level utilization rates to whole plants and plant communities must account for variability in productivity of the browse species and herbivore preferences in response to this variability. When herbivores browse more productive plants and plant parts preferentially, utilization rates at smaller scales may accurately estimate utilization at higher scales only if the small-scale units are selected randomly and their average utilization is weighted by pre-browse productivity.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Appendix S1. Regression equations relating shoot measurements to mass.