DISSERTATION

EFFECTS OF ELK BROWSING AND WATER TABLE ON WILLOW GROWTH AND PHYSIOLOGY: IMPLICATIONS FOR WILLOW RESTORATION IN YELLOWSTONE NATIONAL PARK

Submitted by

Danielle Bilyeu

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY DANIELLE BILYEU ENTITLED EFFECTS OF ELK BROWSING AND WATER TABLE ON WILLOW GROWTH AND PHYSIOLOGY: IMPLICATIONS FOR WILLOW RESTORATION IN YELLOWSTONE NATIONAL PARK BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

David J. Cooper

James K. Detling

Alan K. Knapp

Advisor N. Thompson Hobbs

Director Dan Binkley

ABSTRACT OF DISSERTATION

EFFECTS OF ELK BROWSING AND WATER TABLE ON WILLOW GROWTH AND PHYSIOLOGY: IMPLICATIONS FOR WILLOW RESTORATION IN YELLOWSTONE NATIONAL PARK

Restoration of degraded ecosystems often requires addressing both the direct and indirect effects of stressors. The removal of wolves from the northern range of Yellowstone National Park, USA, has allowed abundant elk populations to heavily browse riparian woody plant communities, resulting in reduced willow stature, extent, and reproduction. Following the reintroduction of wolves, elk browsing on riparian willow has lessened, but willow recovery may be limited due to indirect effects. During wolf absence, elk use of riparian willows competitively excluded beaver, and although beaver are present and active in adjacent areas, they have not reestablished dams on many formerly occupied streams in the northern range. Decades of beaver absence has resulted in stream channel incision and lower water tables near these streams. Because water availability limits willow growth, I hypothesize that a feedback between low water table, low willow productivity, and beaver absence may limit willow recovery even in the absence of elk browsing. I conducted a factorial experiment to examine the response of willow to the cessation of browsing under hydrologic conditions representing the presence vs. absence of beaver. Factors in the experiment included exclosures and dams.

Productivity and rapid height gain in browse-protected plants depended on water table treatment. After four years of protection from elk browsing, *Salix geyeriana* with ambient water table gained only 60 cm in height, and had lower productivity, photosynthetic rate, stomatal conductance, and water potential than plants in control plots. In contrast, browse-protected willows with elevated water table gained 110 cm in height, and had similar productivity to control plants.

Elevated water table also increased height gain and productivity in browsed plots. Using a new technique to detect small changes in browsing pressure, I observed that water table elevation doubled the height gain of willows in response to a slight decrease in ambient browsing pressure occurring over the course of the experiment.

Because lower water availability limits willow height and productivity, and browsing appears to improve water relations, removing browsing under conditions of low water availability is unlikely to result in tall, productive willow stands. In areas where beaver absence has altered historic hydrologic conditions, reducing elk browsing may not be sufficient for willow recovery. This research underscores the need for assessing indirect effects of ecosystem stressors to inform restoration efforts.

Danielle M. Bilyeu

Graduate Degree Program in Ecology

Colorado State University

Fort Collins, Colorado 80523

Summer 2006

DEDICATION

This dissertation is dedicated to Francis J. Singer (1950-2005) who was a member of my graduate committee as well as a valued friend and colleague. Francis served as a wildlife biologist for Federal agencies for 30 years and was instrumental in initiating the research project the results of which are presented here. Francis was encouraging, thoughtful, and generous in his approach to advising, and he is greatly missed.

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CHAPTER 1

INTRODUCTION

The idea that ecosystems can occur in multiple, alternative stable states, originally proposed in the 1960s (Lewontin, 1969), has found recent application in restoration ecology (Beisner et al., 2003; D'Antonio & Meyerson, 2002). The concept of alternative stable states explains why some disturbances to ecosystems are directly reversible, while others are not. Sometimes, perturbations that are sufficiently large in magnitude or duration cause secondary effects that stabilize the alternative state. For example, long-term dominance of an exotic species, *Mesembryanthemum crytallinum* (crystalline ice plant) in South Africa increased soil salinity. Increased salinity remained long after removal of the exotic, complicating restoration efforts (D'Antonio & Meyerson, 2002; Vivrette & Muller, 1977). In the Sahel region of Africa, cattle grazing caused a shift in vegetative cover from perennial grasses to unpalatable forbs and shrubs, which resulted in soil compaction and reduced water infiltration. These changes in soil properties depressed plant productivity and maintained community composition for decades after grazing was moderated (Suding et al., 2004; vandeKoppel et al., 1997). In these examples and others, the trajectory of change following removal of the original stressor is not a simple reversal of the original trajectory (Beisner et al., 2003). Successful restoration in such situations requires recognizing the feedbacks stabilizing the degraded system, and, if possible, mitigating them (Suding et al., 2004).

Several recent studies have suggested that the degradation of riparian vegetation brought about by the long-term absence of wolves from Yellowstone National Park is directly reversible (Beschta, 2003; Ripple & Beschta, 2003, 2004a; Ripple et al., 2001). Evidence suggests that the extirpation of wolves from Yellowstone National Park caused demographic and behavioral changes in the elk population that led to excessive browsing of riparian woody plant communities and widespread degradation of these systems on the northern elk wintering range (Houston, 1982; Ripple, 2001a). Following wolf reintroduction in 1994, browsing pressure in some areas lessened (Ripple & Beschta, 2004b), leading some authors to suggest that wolf reintroduction will allow a broad recovery of historically abundant willow, cottonwood, and aspen stands (Ripple & Beschta, 2004a). However, others contend that the extent to which this trophic cascade will restore degraded riparian communities is unclear (Smith et al., 2003).

At issue are potential secondary effects of wolf absence that may have stabilized the alternative state of degraded willow communities in some areas of Yellowstone's northern range. Recent work has shown that in the absence of wolves, elk may competitively exclude beaver (*Castor canadensis*) (Hebblewhite et al., 2005) by reducing willow standing crop (Baker et al., 2005). Beaver and willow are known to be mutualists, as beaver rely on willow for food and dam building material, but also improve willow habitat by building dams (Baker et al., 2005). Prior to wolf extirpation in Yellowstone, beavers dammed small streams in the northern range such as Lost Creek and Elk Creek (Warren, 1926), which would have improved willow productivity by increasing water availability (Lindroth & Bath, 1999). Because beavers browse areas intermittently, it is likely that short breaks in beaver activity provided opportunities for willows to regain tall stature and produce seed (Baker et al., 2005) and establishment opportunities for willow seedlings as ponds gradually drained (Wolf, 2004). The subsequent regrowth of tall, vigorous willow stands would have provided incentive for beaver to return, creating a positive feedback between intermittent beaver presence, high water table, and high willow productivity that supported historic riparian communities in the northern range.

Following the extirpation of wolves, beaver damming activity in the northern range declined dramatically (Jonas, 1955), disappearing entirely by the late 1980s (Consolo Murphy & Hanson, 1990). Decades of beaver absence led to an unusual hydrologic regime in some parts of the park, as stream channels eroded and water tables on adjacent terraces declined (Wolf, 2004). Presently, although beaver are active in the adjacent Gallatin National Forest and occupy bank dens along larger streams in the northern range such as Lava Creek and Slough Creek (Roy Renkin, personal communication), they have not reestablished dams on the small streams where they historically influenced floodplain hydrology. Degraded willow communities may currently preclude beaver reestablishment. Beaver have been shown to prefer large willow stems (> 4.5 cm in diameter) as food sources (Barnes & Mallik, 1996), likely because the energy gained by harvesting larger stems better justifies the energy expenditure and predation risk associated with cutting the stem and dragging it back to the pond (Baker & Hill, 2003; Barnes & Mallik, 1996; Gallant et al., 2004). In Yellowstone, beaver distribution closely correlates with that of willow stands (Smith et al., 1996). It appears likely that following stream channel incision, the dominant feedbacks in the system have been altered: beaver absence, low water table, and low willow productivity now determine riparian community structure. Because of these altered feedbacks, I hypothesize that willow recovery in the absence of elk browsing will be limited.

The goal of this research is to determine if willow decline in areas historically hydrologically influenced by beaver is reversible through a reduction in elk browsing pressure alone, or if restoration of these areas will also require mitigating the effect of stream channel incision on local water table. I define tall willow communities (greater than 200 cm in height) as the restoration goal, because tall willows are more useful to beaver and therefore more likely to catalyze the return of willow/beaver mutualisms.

I sought to determine the effect of reduced elk browsing on willow height under conditions representing the presence vs. absence of beaver. I implemented an experiment crossing the effects of reduced herbivory and elevated water table and tracked willow height for four years post-treatment. Because tracking ambient browsing pressure was important to understanding treatment effects, I developed an unbiased and reproducible way to quantify browsing pressure, which is described in Chapter 2. The height results are presented in Chapter 3. To provide a deeper level of understanding of height responses, I examined how willow productivity, morphology, and physiology are altered by treatments in Chapter 4, and elucidated a mechanism explaining the observed limited productivity and height of unbrowsed plants. To facilitate application of experimental results to management, I synthesize height, productivity, and morphology results in Chapter 5, and describe implications of these results for willow restoration.

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CHAPTER 2

ASSESSING IMPACTS OF LARGE HERBIVORES ON SHRUBS: TESTS OF SCALING FACTORS FOR UTILIZATION RATES FROM SHOOT-LEVEL MEASUREMENTS

Abstract

Methods for accurately estimating intensity of browsing by herbivores are fundamental to understanding the ecology of shrub communities. Quantifying browsing intensity of 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 of whole plants or plots is often unknown. Because herbivores selectively browse more productive plants and plant parts, the relationship is likely complex. Using a clipping experiment designed to mimic elk (*Cervus elaphus* L.) browsing, I quantified how utilization estimates at the scale of individual, current year shoots of two willow species, *Salix bebbiana* and *S. geyeriana,* relate to actual mass removed at the scale of rooted stems when scaled three alternative ways: by taking an average, by multiplying by the proportion of shoots clipped, and by multiplying by a novel scaling factor that weights utilization by productivity. To address how to scale up from stems to plots, I applied the most accurate stem-level method to elk-browsed willow and compared plot-level estimates by two scaling alternatives. In scaling from shoots to stems, the novel scaling factor was most successful and resulted in

accurate estimates for up to 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%. I conclude that in order to accurately reflect the proportion of biomass consumed at a higher 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 for estimating 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.

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

Although procedures for estimating grazing intensity of herbaceous plants are relatively well established (McNaughton, Milchunas, & Frank 1996), estimating browsing intensity of woody plants is far more problematic. Because shrubs have complex growth forms and only a portion of the plant is consumable, researchers often estimate utilization rate by counting browsed vs. unbrowsed twigs (Bergstrom & Guillet

2002; Edenius, Ericsson, & Naslund 2002; Maccracken & Viereck 1990), or by 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 higher scales that might facilitate comparisons among landscapes or with other ecosystem variables.

In this paper I quantify 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. I then compare two ways to scale stem-level measurements to the plot level. I use two willow species, *Salix bebbiana* Sarg. and *S. geyeriana* Anderss., as model species. 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.), I address how herbivore selectivity affects the process of scaling utilization estimates. I propose a novel scaling factor designed to address this selectivity, and test its performance.

Methods

Study areas

S. 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, semiarid 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 & Frisina 1998).

Stem clipping experiment

GROWTH FORM OF WILLOWS

Individual *S. bebbiana* and *S. geyeriana* may reach 2-3 meters 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. I 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 my study might contain 100 current-year shoots with a highly skewed size distribution of three 60-cm shoots growing from the highest older wood, ten 20-cm 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 PERCENT CLIPPED

Because willows in the Rocky Mountains are browsed primarily in winter, I performed the clipping experiment in September of 2005, after completion of the season's growth, but before winter browsing. Two observations from field measurements of elk browsing patterns in Yellowstone were notable and were incorporated into my design. First, the average size of shoots that are browsed is larger than those that escape browsing, and second, some shoots may be completely consumed. Average basal diameter of browsed shoots were twice as large those of unbrowsed shoots [browsed vs. unbrowsed means ± 95% C. I. (mm): *S. bebbiana* 2.69 ± 0.39 vs. 1.56 ± 0.46; *S. geyeriana* 2.68 ± 0.27 vs. 1.19 ± 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.

I 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, I clipped portions of the uppermost, easily accessible shoots, which tended to be longer and thicker than shoots originating from lower on the stem. To simulate moderate browsing, I clipped more of the easily accessible shoots. To simulate heavy browsing, I 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. Percent 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, I calculated the size difference between clipped and unclipped shoots across clip levels, which was similar to the difference I observed for browsed and unbrowsed shoots in the field [clipped vs. unclipped means ± 95% C. I. (mm): *S. bebbiana* 2.67 ± 0.17 vs. 1.58 ± 0.058; *S. geyeriana* 1.78 ± 0.16 vs. 0.99 ± 0.035].

ESTIMATING PERCENT CLIPPED

I 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. I 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 just above the bud scar (i.e. base diameter) of a shoot to mass prior to browsing, and diameter at the browse point to mass removed (Ferguson & Marsden 1977; Maccracken & Vanballenberghe 1993; Mahgoub *et al.* 1988) A second method in current use, referred to here as the diameter difference method (DD), calculates utilization with a formula based on the difference between diameter at the base and the browse point (Hebblewhite *et al.* 2005; Jensen & Urness 1981; Pitt & Schwab 1990; Singer, Mark, & Cates 1994).

To apply the MDR method I estimated 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, Appendix 1) 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,

Appendix 1). Percent clipped at the shoot level (MDR_{shoot}) was calculated as the ratio of mass removed to total mass.

To find percent clipped by the DD method I 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, Dt is the average diameter of unbrowsed or unclipped shoot tips, and D_b is the base diameter.

SCALING FACTORS

I tested three scaling factors. First, I 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 rates of browsed shoots may overestimate browsing intensity at the whole plant or community scale. Pitt and Schwab (1990) applied the solution of multiplying the shoot-level rate by the proportion of shoots that are browsed. To test this approach to scaling, I applied eqn 2 for the MDR method estimate and eqn 3 for the DD method estimate.

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

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

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

Because herbivores tend to select for larger-than-average shoots (Armstrong & Macdonald 1992; Danell, Bergstrom, & Edenius 1994), 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. I tested a novel scaling factor to account for this. Instead of using a proportion based on a count of clipped vs. unclipped shoots, I 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 my experiment, I 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, Appendix 1). I then found the average pre-clip shoot mass for each category (clipped or unclipped) on each stem. I used these estimates in eqn 4 to scale the MDR method estimate,

$$MDR3_{stem} = \left(\frac{c * \overline{C}}{c * \overline{C} + u * \overline{U}} \right) * MDR1_{stem} \quad \text{eqn 4}$$

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

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

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 (Armstrong & Macdonald 1992; Jensen & Urness 1981). I 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, 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.

I 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, Appendix 1) to each shoot measurement. I then found the average shoot mass and multiplied by a count of shoots to estimate total CAG. I estimated the portion of CAG remaining after clipping (CAG_{left}) by measuring lengths of all unclipped shoots and diameters at the base and clip point of all clipped shoots. Mass of unclipped shoots was estimated as before clipping. 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, Appendix 1). I summed the estimates of clipped and unclipped shoot mass to find CAG remaining after clipping.

Stem-level percent clipped was calculated as:

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

STATISTICAL ANALYSIS

I tested the accuracy of each technique at the stem level by regressing estimates of percent clipped against measured values. A perfect model would produce a 1:1 line with an r^2 of 1.0. I 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. F-values indicate the magnitude of deviation from an ideal fit. I also quantified the estimation 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, I estimated CAG and utilization using the BC method for 38 *S. geyeriana* and 39 *S. bebbiana* stems randomly selected from a 20 X 20 m plot on the Blacktail Creek drainage in Yellowstone. I 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 plot-level utilization rate, I compared two methods for scaling up stem-level measurements. The first is a simple average of BC_{stem}. The second is analogous to the third scaling factor described above. Biomass and productivity remaining are summed for all stems before making the utilization calculation, as in eqn 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), MDR1 overestimated utilization by 11% and DD1 by 37% for *S. bebbiana* (Figs 2a-b). For *S. geyeriana* the overestimates were 18% and 35% for these two methods (Figs 3a-b). Scaling the methods by the proportion of browsed shoots overcorrected the problem. MDR2 underestimated utilization by 20% and DD2 by 16% for *S. bebbiana* (Figs 2c-d), while for *S. geyeriana* the underestimates were 20% and 18% for the two methods (Figs

3c-d). In contrast, both shoot-level methods were relatively accurate when scaled by the proportion of shoot mass browsed. For *S. bebbiana* the MDR3 estimate was within 5% of actual percent browsed and the DD3 estimate was within 11% (Figs 2e-f). For *S. geyeriana* the MDR3 estimate was within 3% and the DD3 estimate was within 6% (Figs 3e-f).

At high clipping intensity (75% of current-year growth removed), the trends were different. With the exception of DD1, all methods based upon scaling up shoot-level measurements underestimated percent clipped. The underestimation of percent clipped for *S. bebbiana* was 16% by MDR1, 50% by MDR2, 27% by MDR3, 41% by DD2, and 7% by DD3 (Figs 2a & 2c-f). For *S. geyeriana* the underestimation was 15% by MDR1, 61% by MDR2, 32% by MDR3, 58% by DD2, and 25% by DD3 (Figs 3a & 3c-f). DD1 did not underestimate utilization, but this method predicted high values of percent clipped regardless of actual values (Figs 2b & 3b).

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

Scaling from the stem to the plot

Productivity of stems at my study plot in Yellowstone was highly skewed. The most productive 25% 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 25% of stems averaged significantly higher than consumption of the less productive 75% of stems [highly productive vs. less productive mean percent CAG consumed ± 95% C. I.: *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 ~15 percent lower than BC_{plot} (eqn 7) [simple average vs. BC_{plot}: *S. bebbiana* 54% vs. 71%; *S. geyeriana* 64% vs. 78%].

Discussion

I found that accounting for herbivore preference for larger shoots is necessary for making accurate stem-level utilization rates from shoot-level measurements. Weighting shoot-level utilization rates by an estimate of pre-browse shoot mass resulted in accurate estimates of stem-level utilization rates for clip intensities of less than roughly 45%. When greater proportions of shoot biomass were removed, however, shoot-level estimates failed to accurately predict actual removal at the stem level because some shoots were entirely removed. At high rates of browsing intensity, 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, I again found that herbivore preference for higher productivity shoots influenced the relationship between utilization rates at smaller vs. larger scales. I recommend 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. Alternatively, one may sum estimates of productivity and estimates of biomass removed before calculating the proportion.

Choice of method and scaling technique greatly impact utilization estimates in the field. In my study plot in the Blacktail drainage of Yellowstone, the BC method estimate of utilization for *S. bebbiana* in 2003-2004 was 71%. The DD2 method estimate for a nearby plot was 26% lower (F. Singer, unpublished data). Results of my clipping experiment indicate that at high browsing intensity the DD2 method underestimated utilization by 41% at the stem level. Therefore the discrepancy between the estimates at the plot level is likely due to underestimation by the DD2 method, which does not account for 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 (Edenius *et al.* 2002; Palmer *et al.* 2004; Searle *et al.* 2005; Senft *et al.* 1987), as well as at the scale of shoots within a plant (Danell *et al.* 1994; Armstrong & Macdonald 1992). Due to the fact that 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. I propose nonetheless 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 the work here 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 and MacDonald (1992) developed a way to use 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 my study, to systematically subsample shoots 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 small, dense shrubs, but estimating biomass and utilization might require more effort. For tree species such as aspen and birch, individual saplings or suckers are likely a good choice.

A second factor to consider is the choice between before-and-after measurements or 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 in 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 percent 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 an 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 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. I advocate expressing utilization as the percent 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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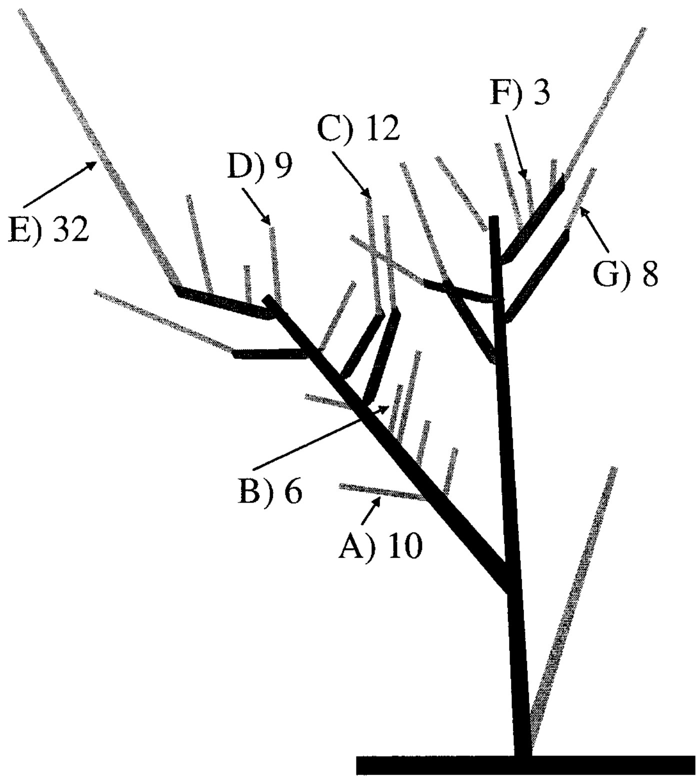

Figure 1. Diagram illustrating shoot sampling protocol for a stem. Letters indicate the order of measurements; numbers indicate lengths in cm. To adequately represent the shoot size distribution in this example, I chose a sampling ratio of 3, which means I recorded measurements on every third shoot encountered as I worked apically from the base of the stem, accommodating side branches by sampling lowest branches first. Here, 7 measurements were made, with 2 shoots apical of the last shoot sampled. The count of shoots was then calculated as 7*3+2 = 23. If 4 of the 7 measured shoots were browsed, along with the two apical of the last shoot sampled, then the count of browsed shoots is estimated as 4*3+2 = 14, and the count of unbrowsed shoots as 3*3+0 = 9.

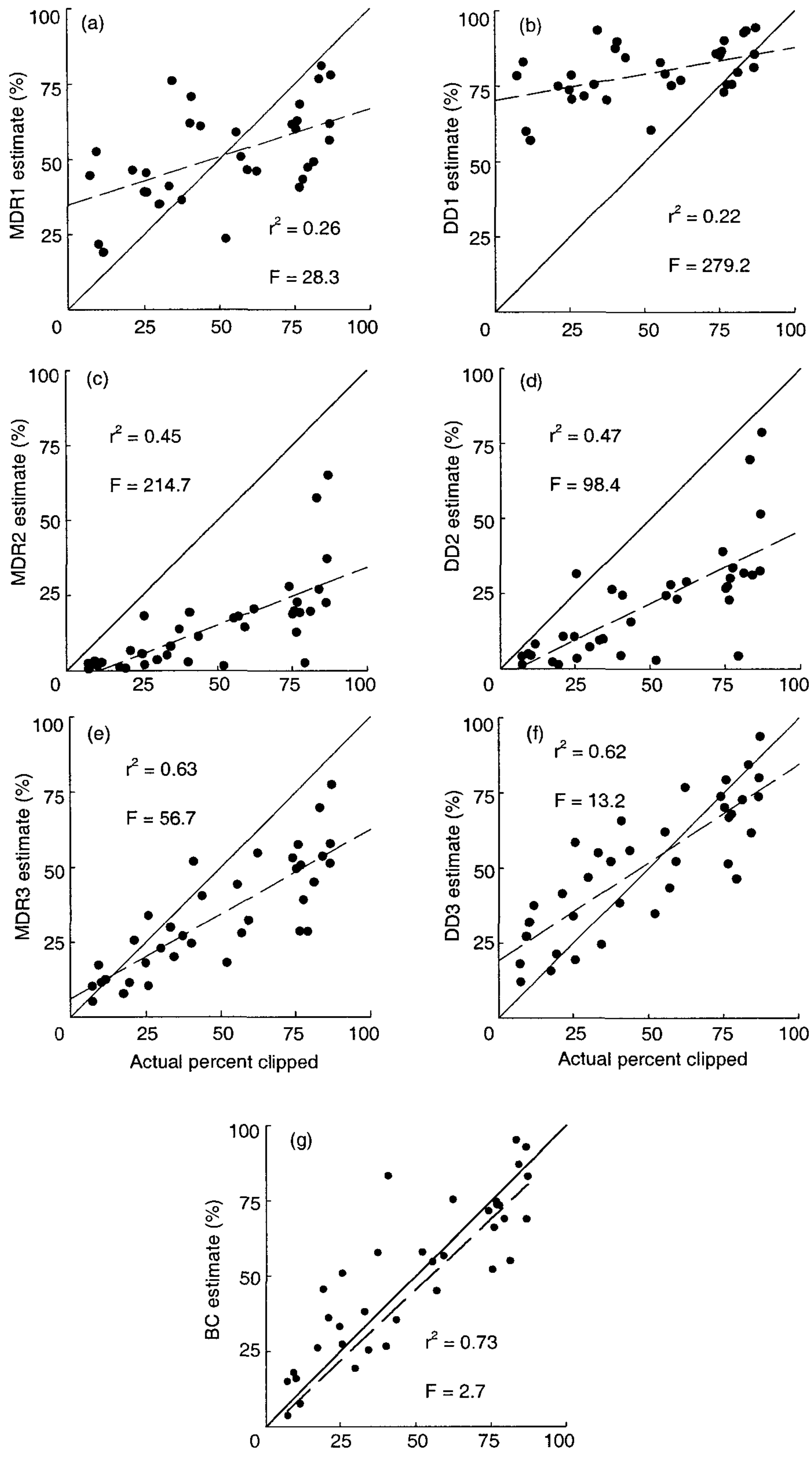
(a)
MDR1 estimate (%)
$r^2 = 0.26$
F = 28.3
(b)
DD1 estimate (%)
$r^2 = 0.22$
F = 279.2
(c)
MDR2 estimate (%)
$r^2 = 0.45$
F = 214.7
(d)
DD2 estimate (%)
$r^2 = 0.47$
F = 98.4
(e)
MDR3 estimate (%)
$r^2 = 0.63$
F = 56.7
(f)
DD3 estimate (%)
$r^2 = 0.62$
F = 13.2
(g)
BC estimate (%)
$r^2 = 0.73$
F = 2.7
0
25
50
75
100
Actual percent clipped

Figure 2. (a-g). Results of regressing actual percent 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; F-values indicate the magnitude of deviation from the ideal fit.

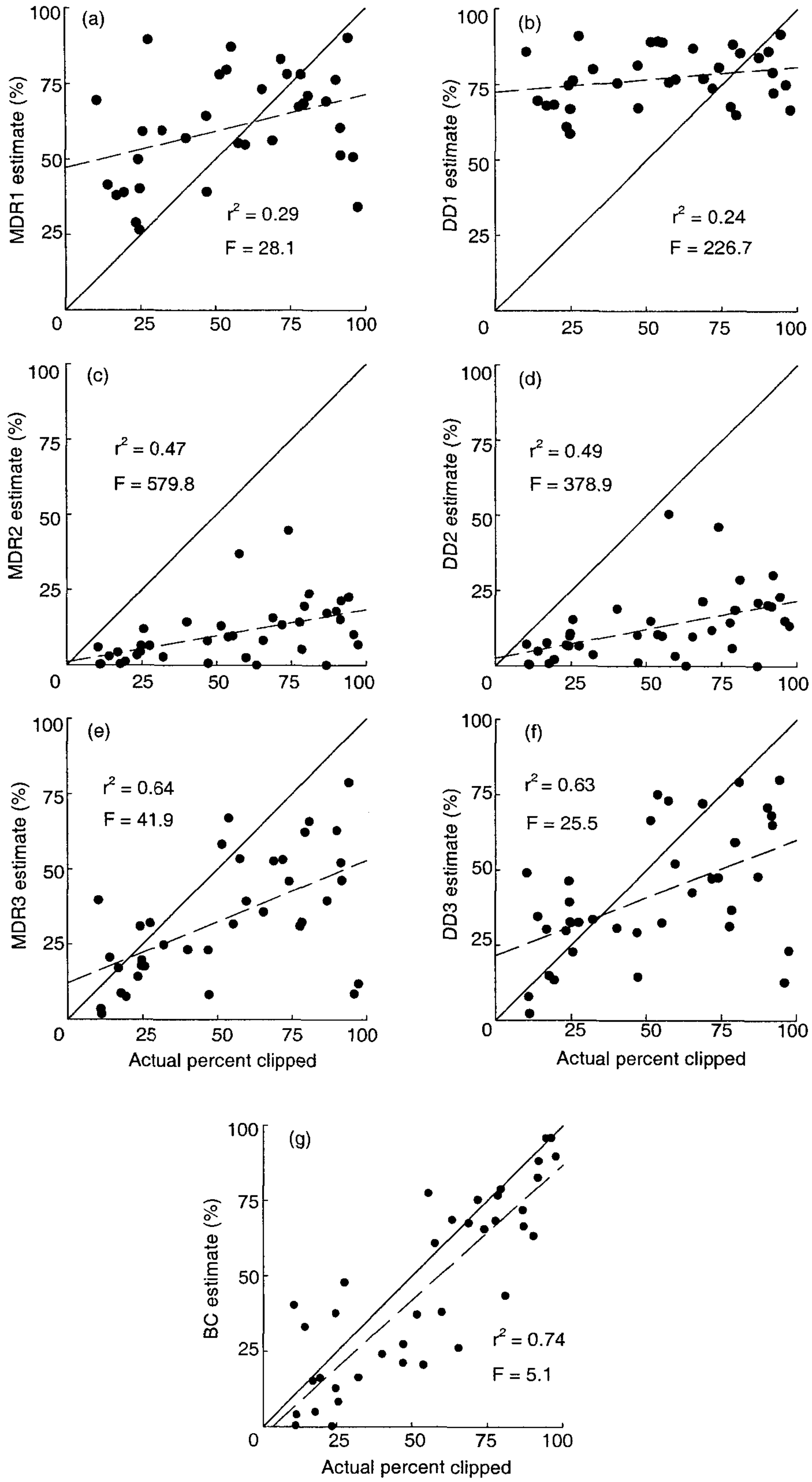
(a)
MDR1 estimate (%)
r² = 0.29
F = 28.1
(b)
DD1 estimate (%)
r² = 0.24
F = 226.7
(c)
MDR2 estimate (%)
r² = 0.47
F = 579.8
(d)
DD2 estimate (%)
r² = 0.49
F = 378.9
(e)
MDR3 estimate (%)
r² = 0.64
F = 41.9
Actual percent clipped
(f)
DD3 estimate (%)
r² = 0.63
F = 25.5
Actual percent clipped
(g)
BC estimate (%)
r² = 0.74
F = 5.1
Actual percent clipped

Figure 3. (a-g). Results of regressing actual percent 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; F-values indicate the magnitude of deviation from the ideal fit.

Appendix 1: Development of regression equations relating shoot measurements to mass for willows at Sheep Creek, Colorado, USA.

I sampled 40 shoots per species, measured length, base diameter, and clip diameter in the field, then dried each shoot to a constant mass and found the end mass and clip mass of each shoot without leaves (Fig. A1). I computed four regressions for each species, each of which required transforming mass to linearize the data and achieve homogeneity of variance (Table A1). In applying the equations to measurements in my experiment, negative intercepts infrequently resulted in negative estimates of mass for extremely small shoots; these were assigned a mass of 0.01 grams.

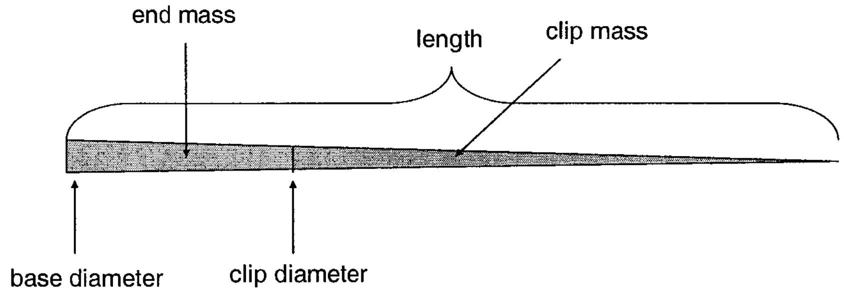

Fig. A1. Shoot-level measurements and mass fractions

Species	Mass fraction predicted (g)	Predictor variable(s): Length (cm) Diameter (mm)	Transformation	Intercept	Parameter(s)	r^2
S. bebbiana	Total mass	Length	$\log(total\_mass + 0.65)$	-0.50	0.03	0.99
	Total mass	Base diameter	$\sqrt[4]{(total\_mass + 0.5)}$	-0.60	0.19	0.94
	End mass	Base diameter, Diameter increment	$\sqrt[4]{(end\_mass)}$	0.13	0.16* base diameter, 0.18* diameter increment	0.87
	Clip mass	Clip diameter	$\sqrt[4]{(clip\_mass + 0.5)}$	0.61	0.18	0.94
S. geyeriana	Total mass	Length	$\log(total\_mass + 0.35)$	-1.1	0.03	0.99
	Total mass	Base diameter	$\sqrt[4]{(total\_mass + 1)}$	0.91	0.17	0.95
	End mass	Base diameter, Diameter increment	$\sqrt[2]{(end\_mass)}$	-0.20	0.20* base diameter, 0.34* diameter increment	0.89
	Clip mass	Clip diameter	$\sqrt[4]{(clip\_mass + 1)}$	0.93	0.17	0.93

Table A1. Regression transformations and parameter estimates. Diameter increment is the difference between base diameter and clip diameter. End mass is mass apical of the clip point. Clip mass is mass basal of the clip point.

CHAPTER 3

WATER TABLE CONSTRAINS HEIGHT RECOVERY OF WILLOW IN RESPONSE TO LESSENED BROWSING PRESSURE IN YELLOWSTONE'S NORTHERN RANGE

Abstract

Large herbivores may introduce changes in ecosystem function that persist even when herbivory is removed, complicating efforts to restore overgrazed and overbrowsed systems. In the northern elk wintering range of Yellowstone National Park, elk browsing on riparian willow has lessened following the reintroduction of wolves, but willow recovery in some areas is uncertain. During wolf absence, elk use of riparian willows competitively excluded beaver, resulting in stream channel incision, erosion of fine sediments, and lower water tables near streams historically occupied by beaver. In such areas, lowered water tables may suppress willow growth even in the absence of elk browsing. I assessed willow height in response to reduced elk browsing pressure under conditions representing the presence vs. absence of beaver using a factorial experiment with two treatments: exclosures and water table elevation. After four years of protection from elk browsing, willows with ambient water table averaged only 106 cm, with negligible height gain in 2 of 3 study species in the last year of the experiment. Browse-protected willows with elevated water table averaged 147 cm and gained 19 cm in the last year of the experiment. I observed a slight decrease in browsing pressure in 2004 and

2005 in browsed plots, resulting in height increases of 22 cm in plants with ambient water table and 46 cm in plants with elevated water table. I conclude that water availability places an upper limit on willow height in the absence of browsing, and also determines the rate of height gain in response to small decreases in browsing pressure. In areas where long-term beaver absence has resulted in incised stream channels, a reduction in elk browsing alone may not be sufficient for recovery of tall willow stands. However, in areas with unaltered hydrology, a small reduction in browsing pressure may be sufficient for willow recovery.

Introduction

Large herbivores can cause enduring changes in the structure and function of ecosystems (Frank & Evans, 1997; Hobbs, 1996; McInnes et al., 1992). The impacts of herbivores often extend beyond the direct effects of defoliation to include indirect influences on the physical environment, nutrient cycling, and the disturbance regime (Hobbs, 2006). These indirect effects can cause herbivore-induced changes in ecosystems to persist even when herbivores are removed. For example, in the Sahel region of Africa, cattle grazing causes shifts in vegetative cover from perennial grasses to unpalatable forbs and shrubs. A concomitant change in soil properties reduces water infiltration, which depresses plant productivity for decades after grazing is moderated (Suding et al., 2004; vandeKoppel et al., 1997). In the boreal forest, moose selectively browse hardwoods, resulting in increased litter input from conifers. Increased conifer litter depresses nitrogen mineralization, creating less fertile soils that can not support fast-growing hardwoods (McInnes et al., 1992; Pastor et al., 1993). In African savannas, grazing by large herbivores interrupts the accumulation of fine fuels needed to carry ground fires. The absence of ground fire allows trees to grow tall enough to escape the ground fires that resume when grazers are removed (McNaughton, 1992; McNaughton et al., 1988; vandeKoppel et al., 1997). In all of these examples, secondary effects of grazing or browsing create alternative states that resist change even when the direct effects of herbivores are moderated.

It has been suggested that browsing by abundant elk populations in the northern range in Yellowstone National Park, USA, has caused a fundamental change in the state of the ecosystem (Beschta, 2003; Kay & Wagner, 1994; Larsen & Ripple, 2005). Winter browsing by elk (*Cervus elaphus* L.) in the northern range has been implicated in the disappearance of historically abundant stands of woody deciduous plants such as willow, aspen, and cottonwood during the past 80 years (Kay & Chadde, 1991; Larsen & Ripple, 2005; Ripple & Larsen, 2000). Evidence suggests that elk browsing of woody riparian vegetation was historically much lower when wolves (*Canis lupus*) were abundant, increased dramatically after wolves were extirpated from the northern range (Beschta, 2005, Beschta, 2003; Larsen & Ripple, 2003), and decreased again following wolf reintroduction in 1994 (Ripple & Beschta, 2004). However, it remains an open question whether woody deciduous plant communities will be restored across the entire range by moderation of elk browsing (Smith et al., 2003).

Willow recovery after release from browsing may be limited in magnitude and spatial extent by indirect effects of elk herbivory that have stabilized the system in an alternative state. In the absence of wolves, interspecific competition between elk and beaver may have resulted in beaver decline, as intensive elk browsing of aspen, cottonwood, and willow saplings and suckers in riparian areas prevented deciduous woody vegetation from reaching the tall heights and large trunk diameters needed by beavers (Baker et al., 2005; Hebblewhite et al., 2005). Damming by beavers was common in the northern range in the early 1900s (Warren, 1926), but declined dramatically during the following 50 years (Jonas, 1955), and disappeared entirely by the late 1980s (Consolo Murphy & Hanson, 1990). Radiocarbon dating of wood buried in sediments collected from incised banks indicates that beaver dams and floodplain accretion have dominated these systems for thousands of years (Wolf, 2004). Without beaver dams, small order streams in the northern range have experienced local water table declines, evidenced by stream incision up to 2 meters in depth through previously ponded, gleyed soils (Wolf, 2004). Because willow distribution is closely correlated with availability of water (Lindroth & Bath, 1999; Peinetti et al., 2002; Pezeshki et al., 1998), stream channel incision and water table decline may limit willow growth. Because willow and beaver are mutualists, and beaver in Yellowstone are particularly dependant on willow (Smith et al., 1996), it appears that a feedback between low water table, low willow productivity, and beaver absence may have locked the system in an alternative, stable state where willow cannot recover even if browsing is moderated.

The recovery of willow height in response to reduced browsing is a key process determining whether moderated browsing can allow return of the system to its historic state. This is because willows taller than 2 meters are not vulnerable to browsing by elk and thereby become a resource exclusively available to beaver, reducing elk/beaver interspecific competition. Moreover, beaver have been shown to prefer willow stems larger than 4.5 cm in diameter as food sources (Barnes & Mallik, 1996), likely because the energy gained by harvesting larger stems better justifies the energy expenditure and predation risk associated with cutting the stem and dragging it back to the pond (Baker & Hill, 2003; Barnes & Mallik, 1996; Gallant et al., 2004). In Yellowstone, stems of sufficiently large diameter are found only in tall, vigorously growing willow stands. I argue that if beavers have access to tall, vigorous willows, they are more likely to build dams and raise water tables, thereby stimulating willow productivity and restoring the positive feedback between beaver activity and willow growth. However, if willows are so constrained by lowered water tables that they cannot grow tall even in the absence of elk herbivory, then the degraded state is stable and more dramatic intervention may be necessary to restore the system to its original state.

It follows that understanding the potential for restoration of willow communities in the northern range depends on the height response of willows to reduced browsing under conditions of water availability representing the presence and absence of beaver. Here, I report results of a manipulative experiment designed to understand the effects of hydrology and herbivory on height dynamics of willow in the northern range in Yellowstone National Park.

Methods

Study area

My study sites were located in the northern range of Yellowstone National Park, USA, a 100,000-hectare (ha) area used intensively by Yellowstone's largest elk herd during winter (Houston, 1982). Elevation spans 1925 to 2000 m. Climate is semiarid; the area receives 260 mm of precipitation annually, 45-65% of which falls during the growing season (Despain, 1987). The landscape consists of large areas of rolling hills of glacial till dominated by *Artemisia tridentata* Nutt. with an understory of *Elymus smithii* (Rydb.) and several other species of cool season grasses, interspersed with small wetlands and wet meadows dominated by *Carex aquatilis* and the willows *S. planifolia* and *S. wolfii*. Higher elevations, particularly north facing exposures, support stands of conifers [*Pseudotsuga menziesii* Mirb., *Picea engelmanni* Parry ex Engelm., *Abies lasiocarpa* (Hook.) Nutt., and *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex Wats.] as well as *Populus tremuloides* Michx. in a patchy distribution (Houston, 1982).

Riparian floodplains form networks that cover 4% of Yellowstone's area. Riparian vegetation is dominated by the willow species *Salix geyeriana, S. bebbiana, S. pseudomonticola* Ball, *S. boothii* Dorn, *S. wolfii* Bebb, and *S. exigua* Nutt. (Houston, 1982), with an understory of herbaceous plants. My study sites were located on terraces adjacent to 3^{rd} or 4^{th} order streams that experienced recent declines in local water table, as evidenced by stream downcutting through previously inundated, gleyed soils, and/or historical record of previous beaver ponding (Jonas, 1955; Warren, 1926). Ambient water tables in my study plots were less than 0.5 m below the surface in the spring, dropping to 1-2 m in late summer. The growth form of all willows in my study plots at the start of the experiment was short (30 to 60 cm tall in spring) with many browsed shoot stubs that had died back to the bud scar, indicating a history of heavy browsing (Keigley & Frisina, 1998).

Experimental Design

I conducted a factorial experiment with a randomized complete block design (Figure 1). Treatments included two levels of browsing by large herbivores (ambient and absent) crossed with two levels of water table (ambient and elevated). Browsing treatments were manipulated by exclosures and water table depth by simulated beaver dams. There were four blocks located on three drainages in the northern range (Appendix 1). Treatments were randomly assigned to plots with in a block. Plots averaged 10 X 20 m in size.

During summer of 2001, I constructed 2.4 m high exclosures from steel field fencing strung between wooden posts and reinforced with steel t-posts. Dams were constructed in fall of 2001 directly downstream of plots that had been selected to receive elevated water. Dams consisted of pine logs and square timbers that completely filled the stream channel. Pond-liner covered the structure and was secured to the streambed upstream of the dams to prevent water flow under or around the sides of the dam.

Browsing Intensity

I quantified browsing intensity outside exclosures as the percentage of current annual growth (CAG) consumed using the biomass comparison method (Bilyeu et al., 2006) on marked, rooted stems each year from 2003 to 2005. This method compares estimates of stem-level CAG in the fall, prior to browsing, with estimates of CAG remaining on the stem in the spring, after browsing. In the fall, CAG is estimated by measuring lengths of current-year shoots, calculating their weight via a length/ dry mass regression ($R^2 > 0.96$, Appendix 2), and summing shoot mass for all tagged stems in each plot. In the spring, similar calculations allow estimation of mass of intact shoots, and mass of partially consumed shoots is estimated via a multiple regression using base diameter and the difference between browse point and base diameter ($R^2 > 0.85$, Appendix 2). Mass of intact shoots and browsed shoot stubs are summed for each plot and provide an estimate of the fraction of prior season's CAG remaining in the plot. Browsing intensity is reported as 1 minus this fraction.

Water Table Depth

To monitor the effect of the dams, I installed two to six groundwater monitoring wells in all plots in July and August of 2001. Wells were constructed of slotted 1.25-inch PVC pipe and were installed with hand augers to a depth approximately 30 cm below the water table, 120 to 280 cm deep. Following installation, wells were pumped dry several times to ensure proper flow between the well and adjacent soil. I recorded water levels approximately every two weeks during the growing season using an electric tape.

Willow Height

In my study area nearly all browsing occurs during winter and all growth occurs during summer. Even when protected from browsing, plants may lose height over winter, because willows often shed living shoots as well as leaves during dormancy (Raven, 1992). Therefore, plants are typically taller in fall than spring, regardless of treatment. I measured fall height of all tagged plants, perpendicular to the ground, in August of each year. Spring height (*H*) was also identified in the fall by finding the maximum height of current year bud scars on the plant (Keigley & Frisina, 1998). I calculated winter height lost due to either browsing outside exclosures or twig shedding inside exclosures (*L*) by subtracting spring height in a given year from fall height the prior year (Figure 2). I calculated the summer height increment (*I*) as the fall height in a given year minus the spring height that year (Figure 2).

The canopies of willows attaining heights of 200 cm to 250 cm are predominantly beyond the reach of browsing by elk (Keigley & Frisina, 1998). Previous studies have tracked height changes through time using height measured in late summer or fall, so that each season *I* as well as *H* was included in the height measurement (Singer et al., 1994). However, I found that because current year shoots are thin enough to be cropped by elk, some or all of *I* outside exclosures may be lost to browsing even when fall height exceeds 200 cm. Inside exclosures, some or all of *I* may be lost to winter twig shedding, which means that fall height may overestimate plant stature. Furthermore, *I* ranges from 5 cm to over 100 cm, thus including it introduces considerable noise in analysis of height changes through time. For these reasons I chose to track changes using *H* rather than fall height (Figure 2). I treated individual plants as sub-samples of the plot and averaged *H* over each plot for each species before analysis.

Statistical Analysis

Treatment effects on *H* were analyzed using repeated measures ANCOVA in SAS PROC MIXED (version 9.1) for a randomized complete block design with a repeated measures structure. An autoregressive (lag = 1) covariance parameter was significant and therefore retained in the model. Pre-treatment (2001) data for each response was included as a covariate. The two treatments, their interaction, treatment by year interactions, and a three way interaction between both treatments and year were included as potential fixed effects. Interactions and year effects were dropped from the model when non-significant at the $\alpha = 0.05$ level. Species were analyzed separately. I report treatment effects with 95% confidence intervals on effect sizes (hereafter CI). Confidence intervals that fail to overlap zero indicate significant effects of treatment.

Treatment effects on *I* are of interest because annual increases in spring height are constrained by the prior season's *I*. Analysis of treatment effects on *I* are complicated by the fact that willows are known to compensate for tissue loss by growing thicker, longer shoots (Peinetti et al., 2001). I expect treatments, particularly exclosures, to affect tissue loss, and I am interested in treatment effects on *I* at both the high values of height loss outside exclosures and the low values found inside exclosures. A simple approach would be to use *L* as a covariate in an ANCOVA analysis of treatment effects on *I*, but this approach is inappropriate for two reasons. First, because *L* is influenced by treatments, it does not fit the definition of a covariate. Second, I do not expect a linear relationship between *I* and *L*. Because resource availability constrains plant growth, an asymptotic relationship is a more biologically realistic model and offers interpretable parameters: the y-intercept (*int*) describes the height increment I predict in the absence of browsing or twig shedding, and the asymptote (h_{max}) represents the plant's maximum capacity to compensate for tissue loss. Therefore, I used an information theoretics approach (Burnham & Anderson, 2002) to compare candidate models based on a Michalis-Menton asymptotic function (Table 1). I allowed each of the two treatments to alter the curve three ways: by influencing the intercept, the asymptote, or both, producing six alternative models (Table 1). I also tested a null model with no treatment effects for a total of seven models.

I compared the strength of evidence in the data for these models using Akiake's Information Criterion, adjusted for small sample size (AIC_c) (Burnham & Anderson, 2002). The lowest AIC_c indicates the "best" model out of the tested set. However, because the scores are based on a given data set, there is some uncertainty that the same model would emerge as best if the models were tested with different data. I quantified this uncertainty by calculating a w_r value for each model, which may be thought of as the "probability" that a given model would have the lowest AIC_c score if tested with many datasets (Burnham & Anderson, 2002). AIC_c, maximum likelihood estimates of model parameters, and confidence intervals on model parameters were obtained by nonlinear fitting in PROC NLMIXED (SAS/STAT software, Version 9.1 of the SAS System for Windows. Copyright © 2002-2003 SAS Institute Inc.). I assumed a normal error distribution and verified this assumption by examining histograms of residuals. For the best approximating model, I report parameter estimates with 95% confidence intervals.

Results

Browsing Intensity and Water Table Depth

Browsing intensity outside of exclosures was heavy, averaging 66% of current year's growth, but diminished slightly during 2004 and 2005 relative to 2003 ($p = 0.02$, Table 2). Dams elevated water table depth by an average of 0.37 meters during the growing season (Table 2), but the effect size in August was as large as 90 cm at some sites in some years (Appendix 3). The observed pattern of attenuated water table decline late in the growing season in dammed plots is similar to that observed for natural beaver dams in the Rocky Mountains of Colorado (Westbrook et al., 2006).

Willow Height

Dams and exclosures caused significant increases in spring height (*H*) of all species (Figure 3). Dam and exclosure effects were additive; there were no significant interactions between dam and exclosure for any species ($p > 0.19$). Therefore, I dropped the interaction term from my model when calculating effect sizes of treatments. After 4 years of treatment, exclosures caused increases in *H* of 46.8 cm (CI = 34.3, 59.4) for *S. bebbiana,* 54.1 cm (32.7, 75.4) for *S. boothi,* and 63.2 cm (53.0, 73.3) for *S. geyeriana.* Dams increased spring height by 42.9 cm (CI = 30.4, 55.3) for *S. bebbiana,* 27.8 cm (6.5, 49.0) for *S. boothi* and 31.5 cm (20.2, 42.9) for *S. geyeriana.*

I observed significant main effects of year on *H* for all species ($p < 0.0001$) due to height gains not attributable to treatments in years 2003- 2005 (Figure 3). Plants in control plots did not gain height between 2001 and 2003 ($p > 0.37$) but gained an across-species average of 20 cm between 2003 and 2005 ($p < 0.02$, Figure 3).

The effect of exclosures depended on year (year x exclosure interaction $p < 0.0001$, Figure 3). Exclosures caused increases in *H* every year in all species until 2004 (year x exclosure interaction for consecutive pairs of years 2001- 2004: $p < 0.06$, Figure 3). However, between 2004 and 2005 the exclosure effect was -13.8 (-26.2, -1.5) for *S. boothii,* indicating that plants outside of exclosures gained more height than those inside exclosures (Figure 3b). Exclosure effects between 2004 and 2005 were non-significant for *S. bebbiana* and *S. geyeriana*, indicating that plants inside exclosures gained about the same amount of height as control plants (Figure 3a & 3c, $p > 0.30$).

The effect of dams on *H* also depended on year for all species ($p < 0.004$). There was no effect of the dams on *H* until 2004 (year x dam interaction for consecutive pairs of years 2001- 2003: $p > 0.11$, Figure 3), when dams caused an increase of about 9 cm in all species over 2003 ($p < 0.004$, Figure 3). Dams caused an additional increase in *H* between 2004 and 2005 of 11.5 cm (1.6, 21.2) for *S. bebbiana,* 13.1 cm (0.8, 25.5) for *S. boothii,* and 6.5 cm (-2.1, 15.1) for *S. geyeriana.*

Height Increment

As expected, summer height increment (*I*) increased with increasing winter height loss (*L*, Figure 4). All models for *I* with substantial support in the data included a dam effect, indicating that additional water influences *I* (Table 3). The best model for all three study species allowed damming treatment to increase the intercept and the asymptote of a saturating function, indicating that effects of additional water on *I* are important when *L* is low as well as high (Table 3, Figure 4). For any given value of *L*, this model estimated that dams increased *I* by 12.0 cm (6.2, 17.8) in *S. bebbiana,* by 9.0 cm (3.3, 14.7) in *S. boothii,* and by 10.1 cm (5.6, 14.3) in *S. geyeriana* (Figure 4). The y-intercept in the absence of damming treatment is 13.4 (5.6, 21.1) for *S. bebbiana,* 10.2 (2.6, 17.7) for *S. boothii,* and 8.5 (2.7, 14.4) for *S. geyeriana.* Therefore, the effect of the dams was to roughly double *I* in the absence of height loss.

In contrast, no models including exclosure effects had substantial support in the data, indicating that exclosures have little effect on the relationship between *I* and *L* (Table 3). This result is interesting in light of the fact that in a simple ANOVA analysis of treatment effects on *I,* exclosures have a large negative effect [exclosure effect size, averaged over species: -19.8 cm (-27, -12.7)]. Apparently, there is no further effect of exclosures on *I* beyond the effect caused by reduced *L*.

Discussion

I have shown that rapid restoration of tall willows in the northern range in Yellowstone National Park depends on reducing browsing by elk and increasing the availability of water. Although removing browsing alone allowed increases in plant stature, these effects were not as great as the effects of elevated water tables and protection from browsing combined. These findings might be interpreted to mean that changes in stream morphology created by the absence of beaver may retard the recovery of willows following removal of browsing, but will not prevent recovery.

However, my data also suggests that the rate of height gain attributable to release from browsing has declined with time. For *S. bebbiana* and *S. boothii*, there was no height gain in the exclosed, undammed cell of the experiment between 2004 and 2005, and for *S. geyeriana*, height gain in this interval was not significantly different from control plots. Whether measured in spring or fall, heights in 2005 in the exclosed, undammed plots were well within the browse zone of elk [spring height/ fall height by species in 2005: *S. bebbiana:* 91.8 cm/ 128.5 cm; *S. boothii:* 111.1 cm/ 140.0 cm; *S. geyeriana:* 115.8 cm/ 129.4 cm].

In contrast, willows in the exclosed, dammed plots do not appear to have reached final height. For all three study species, spring heights in the exclosed, dammed plots were higher in 2005 than in 2004 [height difference 2005 contrasted with 2004: *S. bebbiana:* 25.2 cm (15.7, 34.7); *S. boothii:* 16.8 cm (5.5, 28.0); *S. geyeriana:* 14.5 cm

(6.7, 22.3)]. Furthermore, current heights in the exclosed, dammed plots are approaching the 200 cm browse zone threshold [spring height/ fall height by species in 2005: *S. bebbiana:* 149.5 cm/ 176.2; *S. boothii:* 140.5 cm/ 165.6 cm; *S. geyeriana:* 151.6 cm/ 170.2 cm].

These results, in conjunction with the observed effects of dams on summer height increment (I), support the idea that in the absence of browsing, water availability constrains the ultimate height of willows in Yellowstone. The hydraulic limitation hypothesis (Ryan & Yoder, 1997) predicts that the final height of a given tree species is determined by resource availability, particularly availability of water. This is believed to occur because shorter growth increments in water-limited trees have lower water conducting capacity, and this decreased ability to transport water constrains further growth and determines final stature (Ryan & Yoder, 1997). Growth increment in the absence of browsing appeared to be constrained by water availability in my experiment. When winter height losses are low ($L <$ 30 cm), the relationship between I and L is approximately linear with a slope of 1, and one may interpret the intercept as an estimate of annual height gain. Dams roughly doubled this value. It appears that following the cessation of browsing, willows without additional water grew by shorter height increments, and this led to earlier attrition in height gain and shorter ultimate stature in undammed, unbrowsed plots.

An unexpected result in my experiment was that dams also increased height in browsed plants. There was no effect of dams on H in browsed plots in 2002 or 2003, but in 2004 and 2005, dams caused height increases totaling 27 cm (Figure 3). What ecological conditions might explain this trend? Because I measured spring height, I cannot attribute taller values in 2004 to the much wetter conditions in the summer of that year (Table 2). I might expect a larger effect of dams on *H* following a dry year such as 2003, but there was no dam effect following the dry growing season of 2002, and a dam effect was apparent following the wet growing season of 2004. I conclude that the observed trends are not due to fluctuating ambient water availability, but to fluctuating browsing pressure. Browsing pressure was slightly lower in the winters preceding 2004 and 2005 than that of 2003, perhaps because thinner snowpacks allowed other forage to be more available to elk (Table 2) (Bellhouse & Rosatte, 2005). *H* increased in 2004 and 2005 in both water-ambient and water-elevated plots, but the effect was twice as large in plots with additional water. Apparently, increased water availability allowed willows to gain more height given a small decrease in browsing pressure. This result corroborates the findings of Ripple et al. (2001), who found that heights of aspen in areas with low elk-pellet counts were taller than those with high elk-pellet counts only in the wet meadow habitat type. In drier habitats, no height differences associated with herbivore use were seen.

Because annual effects on *H* result from the balance of *L* and *I*, two mechanisms are possible for increased height in browsed, dammed plots. Dams might decrease *L*, perhaps by increasing production of secondary defense compounds that make plants less palatable to herbivores (Singer et al., 1994), or dams might increase *I*. My data support the latter mechanism. First, I did not a difference in the percent of CAG consumed between dammed and undammed plots for any species ($p > 0.30$). Second, in the best-fit model for summer height gain, I observed a threshold, indicated by the intersection of the fit curves and the 1:1 line in Figure 4, determining whether *I* is sufficient to compensate for *L*. Beyond this threshold, plants lose stature. The effect of the dams was to move this threshold to the right, implying that increased water availability allows willows to maintain or increase height at higher levels of browsing. Therefore, I believe that dams allow plants to grow longer, thicker shoots that result in taller post-browsing heights when the same proportion of CAG is consumed. Slight reductions in browsing pressure then result in larger height increases in dammed plots.

Conclusion

My results suggest that reducing browsing in areas with low water table will not allow willow to grow sufficiently tall to escape browsing by elk and may not provide the large stem sizes needed to justify foraging costs for beaver. Without tall willow, restoration of the historic hydrologic regimen seems unlikely, and without a change in hydrology, willows will not be able to rapidly gain tall stature, resulting in a positive feedback maintaining the current, degraded state.

However, my data also indicate that willow recovery is likely in areas with higher water tables, where even a small reduction in browsing pressure may be sufficient for height gain. Several studies have found evidence for recovery of riparian woody vegetation due to lessened elk browsing in the presence of wolves (Beschta, 2003; Ripple & Beschta, 2003, 2004; Ripple, 2001a, b). These studies were conducted in or near the Lamar Valley in Yellowstone, where hydrologic changes have not occurred. My results lend support to previous findings suggesting that willow recovery is likely in areas with unaltered hydrologic conditions, such as the Lamar River. However, my results also imply that such a recovery is unlikely near smaller streams where high water availability depends on the presence of beaver. In such locations, mitigation of hydrologic conditions, in addition to reducing use by elk, may be necessary for willow recovery and restoration of historic willow/beaver mutualisms.

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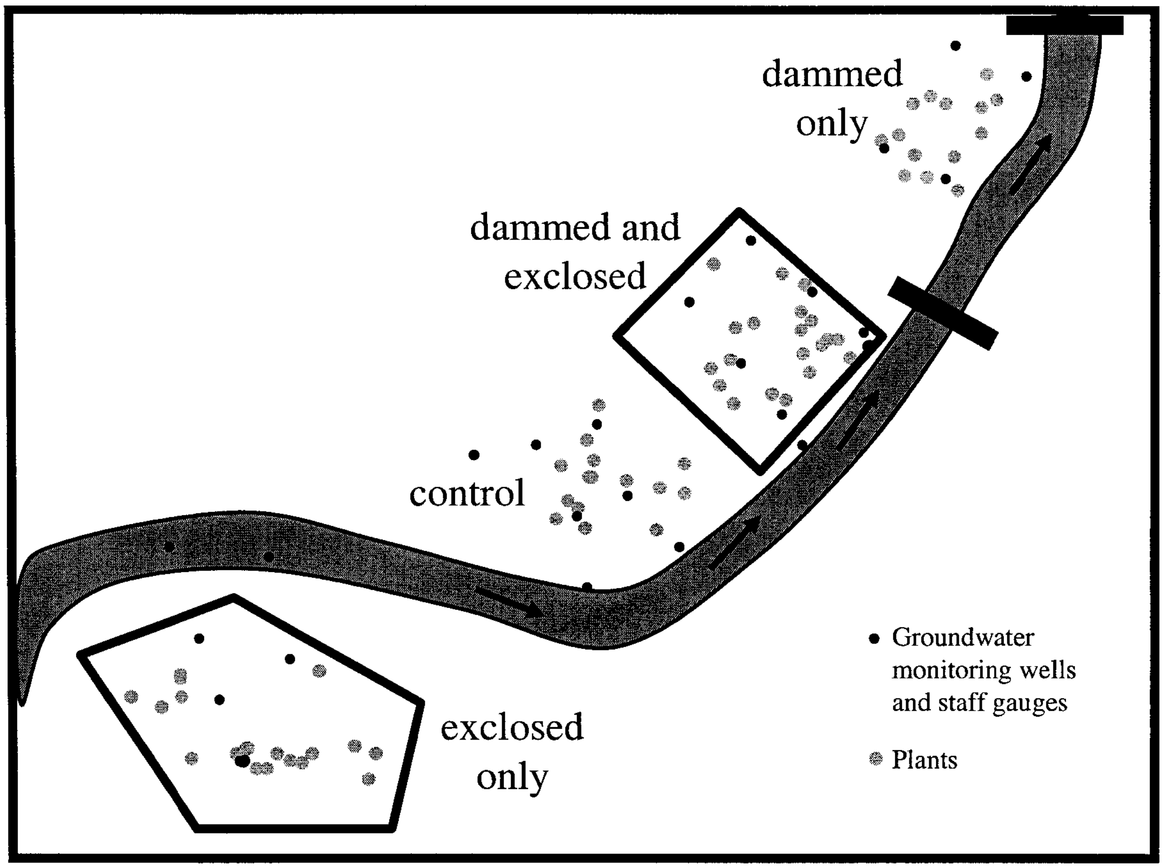


Figure 1. Layout of factorial experimental design at one of four study sites (Elk Creek).

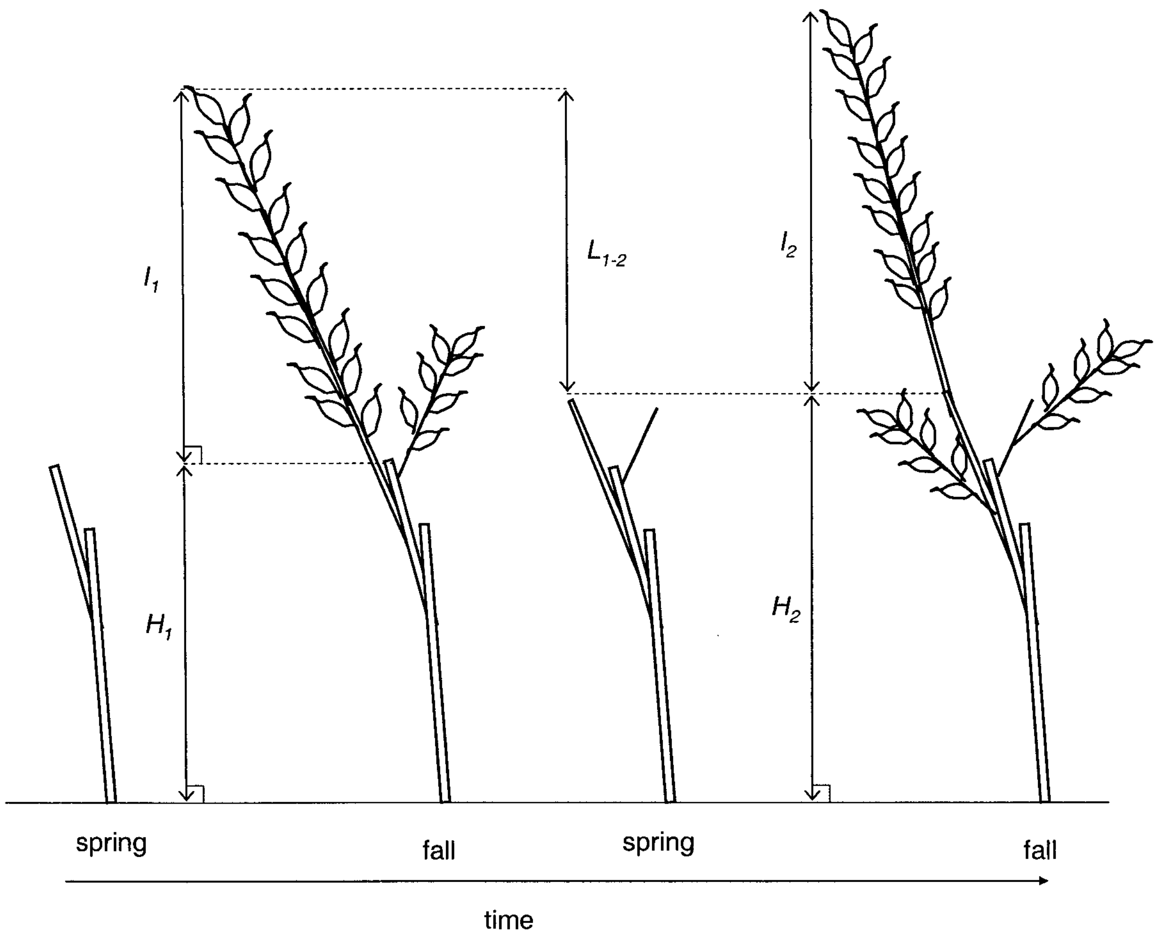


Figure 2. Height measurements taken in factorial experiment. Spring height (*H*) is identified in the fall by finding the maximum height of bud scars on the plant. Summer height increment (*I*) is the difference between total height and spring height. Height loss over the winter ($L_{1\text{-}2}$) is calculated as $(I_1 + H_1) - H_2$.

Table 1. Summary of functional forms for alternative Michalis-Menton models of summer height increment (*I*) in terms of winter height loss (*L*). In models with treatment effects, *T* represents the effect of either dam or exclosure treatment.

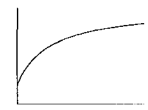
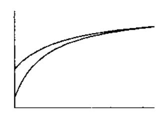
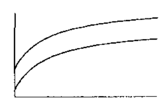
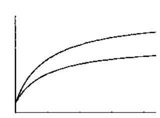
Model Description	Shape	Equation
No treatment effects		$I = \text{int} + \left(\frac{L * h_{\max}}{k + L} \right)$
Treatment effects on intercept only		$I = \text{int} + T + \left(\frac{L * (h_{\max} - T)}{k + T + L} \right)$
Treatment effects on intercept and asymptote		$I = \text{int} + T + \left(\frac{L * h_{\max}}{k + L} \right)$
Treatment effects on asymptote only		$I = \text{int} + \left(\frac{L * (h_{\max} + T)}{k + L} \right)$

Table 2. Summary of ecological conditions in the study sites. Snow and rain data are averages fro NOAA weather stations in Tower Junction and Mammoth, WY. Browsing intensity is the proportion of prior growing season's growth consumed, averaged across species and study sites. Snow data is summed over October through May, and rain data is summed over June through August. Water table depths are averaged over all undammed plots (n = 8) over May through September, and dam effect is the average difference between dammed and undammed plots in those months. Dams were constructed in fall of 2001, therefore 2001 should be regarded as pre-treatment data.

	2001	**2002**	**2003**	**2004**	**2005**
browsing intensity (percent CAG consumed)			70 ± 2	63 ± 3	65 ± 2
prior winter snow (m)	3.5	3.8	4.0	2.6	3.4
summer rain (mm)	85	90	58	124	167
ambient water table depth (m)	-1.3 ± 0.16	-1.17 ± 0.10	-1.18 ± 0.09	-1.24 ± 0.10	-1.08 ± 0.06
dam effect (m)	0.08 ± 0.13	0.36 ± 0.08	0.36 ± 0.09	0.40 ± 0.11	0.37 ± 0.06

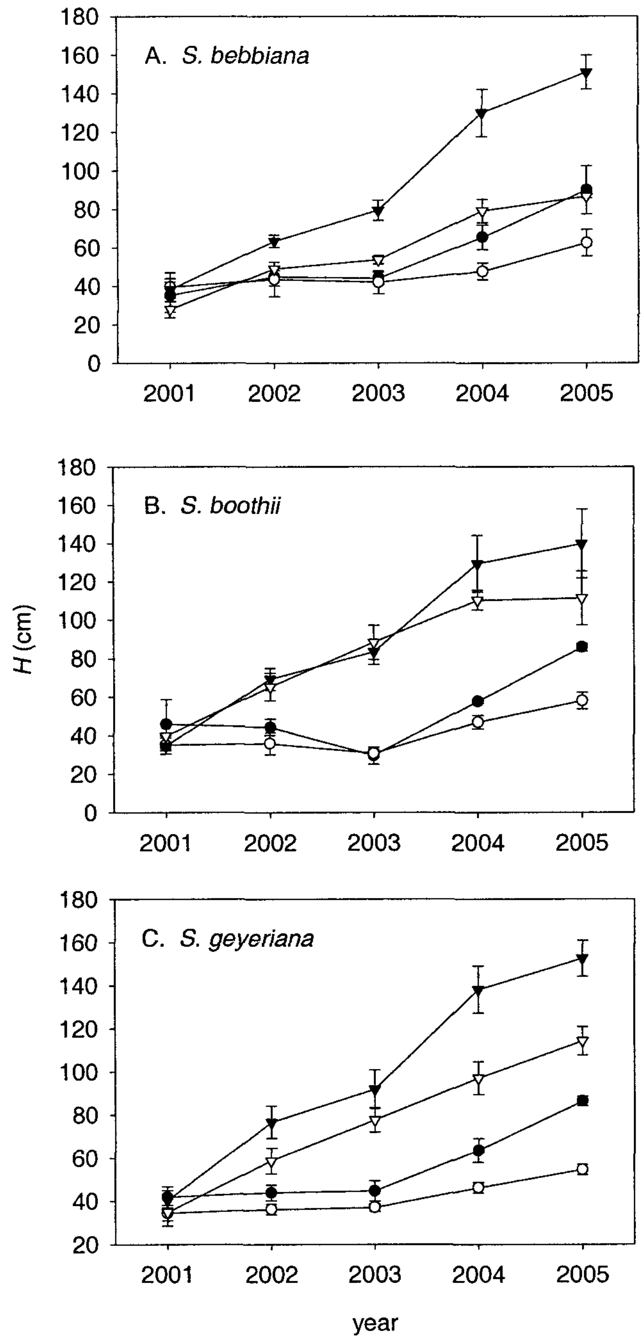


Figure 3. Mean spring heights (*H*) for three willow species in factorial experiment for control plots (○), exclosed only plots (∇), dammed only plots (●), and dammed and exclosed plots (▼). Error bars= SE. 2001 is pre-treatment data.

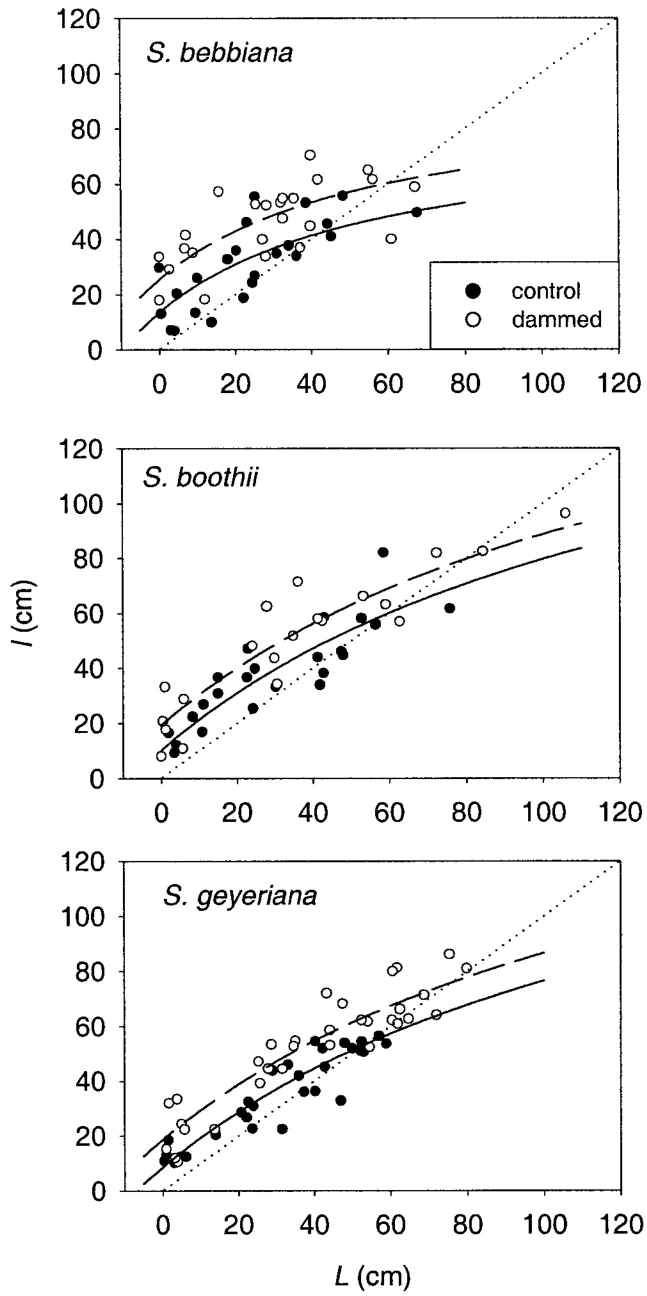
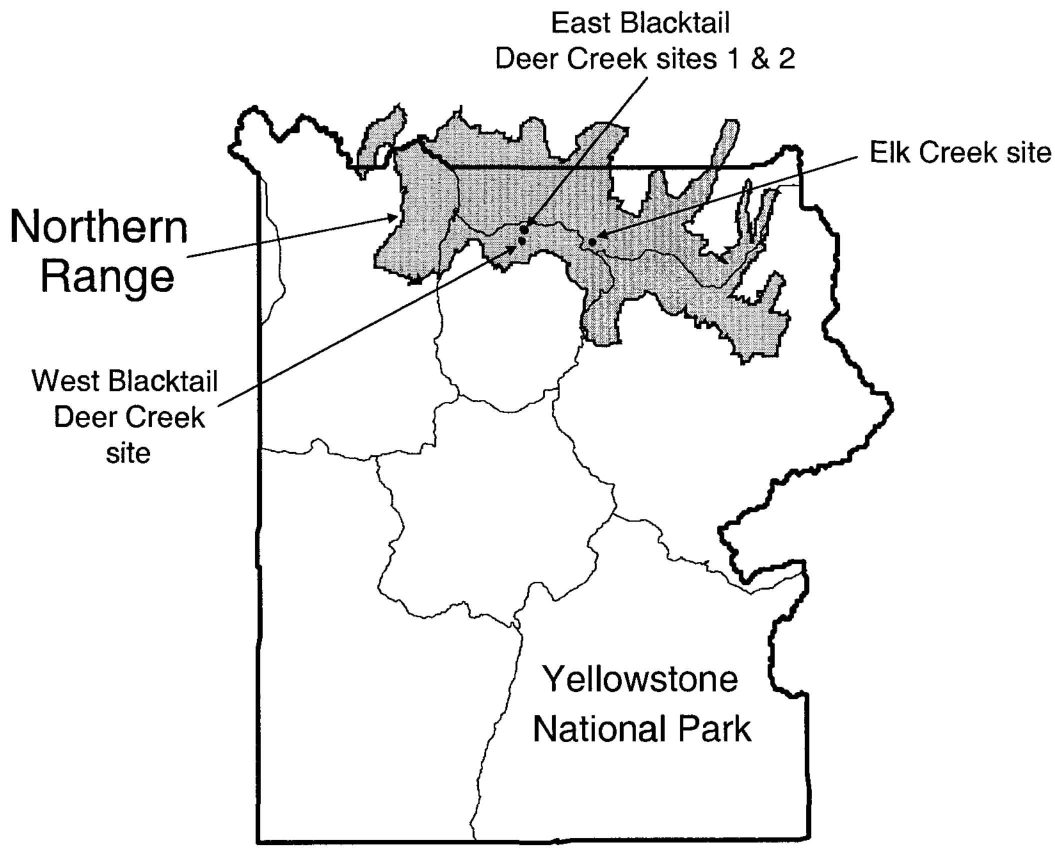


Figure 4. Summer height increment (*I*) for three willow species as a function of prior winter height losses (*L*). Lowest AIC_c model fit is shown: dashed lines: dammed plots; solid lines: control plots. Data for 4 years are included. All values above the dotted 1:1 line represent a net height increase.

Table 3. Strength of evidence for competing asymptotic models of summer height gain in terms of winter height loss. For all three study species, models allowing damming treatment to influence both the intercept and asymptote had most support in the data.

species	treatment effect included	Treatments influences allowed on	AIC_C	DeltaR	likelihood	w_r
S. bebbiana	**dam**	**Intercept and asymptote**	**359.7**	**0.00**	**1.00**	**0.71**
	dam	Intercept only	361.7	2.01	0.37	0.26
	dam	Asymptote only	366.1	6.46	0.04	0.03
	none	n/a	371.8	12.10	0.00	0.00
	exclosure	Asymptote only	372.4	12.75	0.00	0.00
	exclosure	Intercept and asymptote	373.6	13.95	0.00	0.00
	exclosure	Intercept only	374.2	14.46	0.00	0.00
S. boothii	**dam**	**Intercept and asymptote**	**320.8**	**0.00**	**1.00**	**0.56**
	dam	Asymptote only	321.9	1.10	0.58	0.32
	dam	Intercept only	324.7	3.95	0.14	0.08
	none	n/a	327.4	6.62	0.04	0.02
	exclosure	Asymptote	329.9	9.10	0.01	0.01
	exclosure	Intercept only	329.9	9.15	0.01	0.01
	exclosure	Intercept and asymptote	330.0	9.18	0.01	0.01
S. geyeriana	**dam**	**Intercept and asymptote**	**442.4**	**0.00**	**1.00**	**0.63**
	dam	Asymptote only	443.9	1.48	0.48	0.30
	dam	Intercept only	446.7	4.25	0.12	0.07
	exclosure	asymptote	459.0	16.63	0.00	0.00
	none	n/a	459.3	16.88	0.00	0.00
	exclosure	Intercept and asymptote	460.2	17.81	0.00	0.00
	exclosure	Intercept only	460.3	17.93	0.00	0.00

Appendix 1: Location of study sites in the northern elk wintering range of Yellowstone National Park.



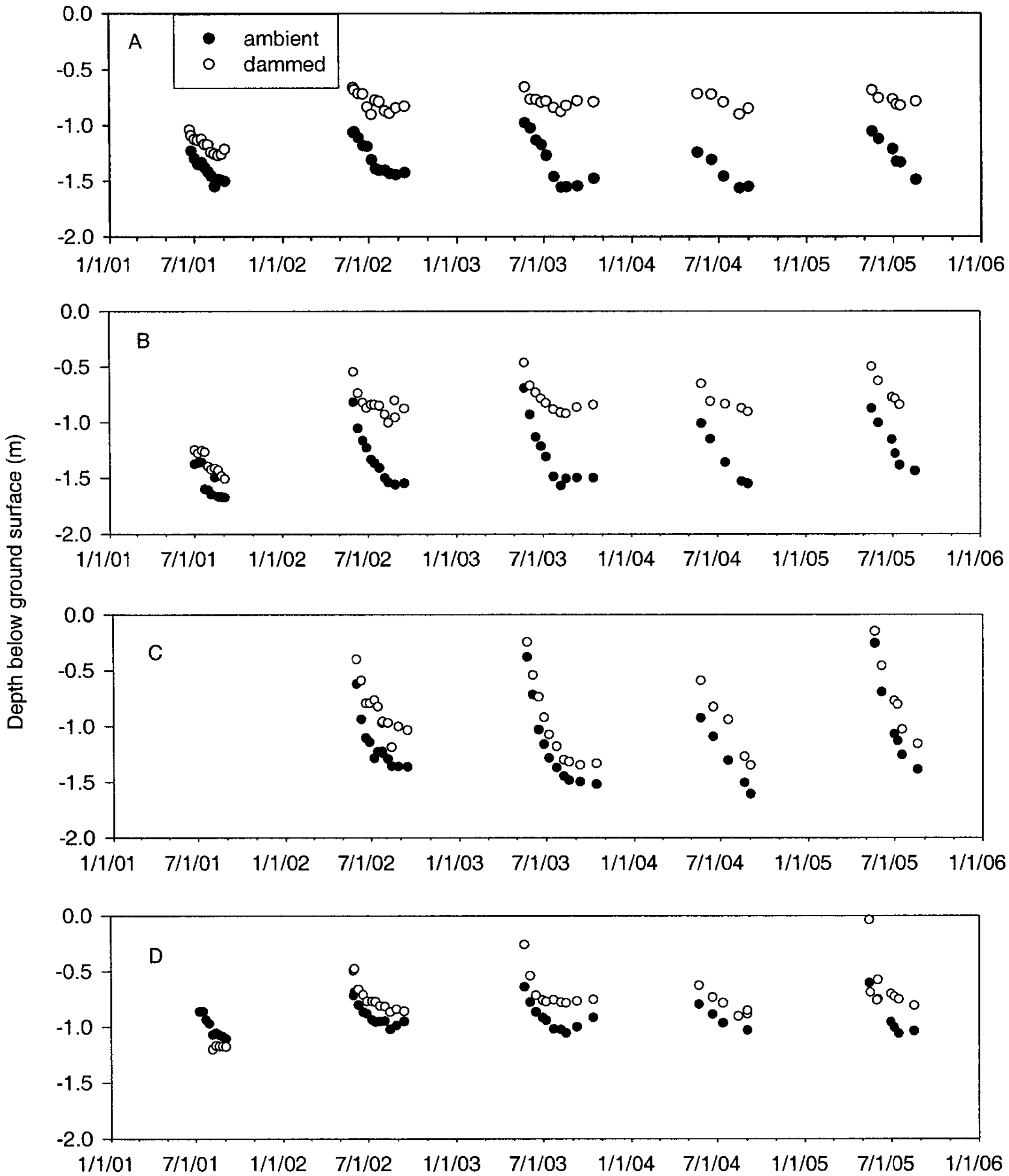
Appendix 2: Calculating browsing intensity in Yellowstone.

Equations are based on n = 60 samples per species for browsed shoots, and n = 300 samples per species for unbrowsed shoots. Length of each sample was measured to the nearest cm, and diameters at the base and browse point were measured on browsed shoots to the nearest mm. All samples were dried to a constant weight, and weighed without leaves. In constructing regressions, transformations were required to linearize the data and achieve homogeneity of variance. For browsed shoots, the transformation for weight was $\log(weight+1)$. For unbrowsed shoots, the transformation was $\sqrt[4]{weight}$. For unbrowsed shoots, length was a sufficient predictor variable. For browsed shoots, base diameter, the difference between base and browse point diameter (diameter increment) and a watershed dummy variable were used as predictor variables.

Table A1. Regression parameters for equations used in calculating browsing intensity.

Species	Shoot type	Equation predicting weight	Watershed Effect	R^2
S. bebbiana	unbrowsed	$-14,38+3.26*\log(length+40)$	n/a	0.96
	browsed	$0.23 + 0.144*(base\_diameter) + 0.157*(diameter\_increment) + watershed\_effect$	East Blacktail 1 and 2: -0.113 Elk Creek: -0.060 West Blacktail: 0.000	0.91
S. boothii	unbrowsed	$-14.13 + 3.20*\log(length + 40)$	n/a	0.98
	browsed	$0.140 + 0.180*(base\_diameter) + 0.094*(diameter\_increment) + watershed\_effect$	East Blacktail 1 and 2: -0.063 Elk Creek: 0.016 West Blacktail: 0.000	0.91
S. geyeriana	unbrowsed	$-13.33 + 2.98*\log(length + 40)$	n/a	0.97
	browsed	$= 0.282 + 0.146*(base\_diameter) + 0.065*(diameter\_increment) + watershed\_effect$	East Blacktail 1 and 2: -0.048 Elk Creek: -0.282 West Blacktail: 0.000	0.85

Appendix 3: Water table depths over the course of the experiment.



Water table depths over the course of the experiment in water-ambient and water-elevated plots at Elk Creek (A), Upper East Blacktail Creek (B), Lower East Blacktail Creek (C) and West Blacktail Creek (D). Each point is the average of 4-8 wells. Data from 2001 was taken before dams were installed.

CHAPTER 4

WATER TABLE EFFECT ON WILLOW PHYSIOLOGY CONSTRAINS EFFECTS OF FOOD WEB RESTORATION IN YELLOWSTONE NATIONAL PARK

Abstract

Anthropogenic disturbance to food webs resulting from removal of top predators can degrade ecosystems. Degradation can result from direct, trophic effects and from indirect effects on the physical environment. Consequently, restoration of degraded ecosystems often requires mitigating indirect effects. There is strong evidence that removal of wolves from the northern range of Yellowstone National Park has allowed abundant elk populations to degrade riparian woody plant communities. Exclusion of beaver and subsequent water table decline appears to be an important indirect effect of wolf removal. I conducted a factorial experiment to determine if changes in hydrology due to beaver exclusion will limit the recovery of willow populations under reduced elk browsing following wolf reintroduction in Yellowstone National Park, USA. Factors in the experiment included elk browsing and water table amendment. Browsing increased productivity of *Salix bebbiana* by 30%, of *S. geyeriana* by 69%, and of *S. boothii* by 37%. Water table elevation increased productivity of *S. geyeriana* by 32%, with non-significant effects on other species. Browsing had beneficial effects on *S. geyeriana*

water relations and photosynthesis, increasing 2003-2005 season-average midday water potential by 0.1 MPa, 2005 stomatal conductance by 42%, and 2005 photosynthesis by 23%. Reduced leaf-level photosynthesis in unbrowsed *S. geyeriana* plants did not appear to be offset by changes in leaf area (exclosure effect on 2005 leaf area $p = 0.43$). The effects of browsing on water relations appeared to be mediated by dramatic browsing-induced morphological changes that increased average shoot size and likely increased leaf-specific hydraulic conductivity. Water table elevation benefited *S. geyeriana*, increasing 2003-2005 season-average midday shoot water potential by 0.1 MPa, 2005 photosynthetic rate by 21%, 2005 stomatal conductance by 17%, and 2005 leaf area by 58%. Effects of treatments were additive, resulting in the most water stressed, least productive plants in the unbrowsed, water-ambient treatment, and the least water stressed, most productive plants in the browsed, water-elevated treatment. I conclude that willows are well-adapted to browsing and high water availability, and that removing browsing under conditions of low water availability is unlikely to result in vigorous willow stands. High willow productivity along small-order streams in the northern range appears to depend on the hydrologic effects of beaver. Because beaver and willow are mutualists, a positive feedback between low willow productivity and beaver absence may be stabilizing the current degraded state of riparian vegetation. The reintroduction of wolves and subsequent reduction in elk browsing may be insufficient for restoration willow in areas with low water table. In such areas, restoration may require mitigating the hydrologic regime in addition to reducing use by elk.

Introduction

Restoration is an increasingly important challenge for ecologists and managers. Anthropogenic disturbance to food webs occurring after loss of predators can exert profound effects on ecosystems (Binkley et al., 2006; Cote et al., 2004; Duffy, 2002; Soule et al., 2005) Degradation can result from direct, trophic effects that cascade through the community, but indirect effects on the physical environment may also occur. Consequently, restoration of degraded ecosystems may require mitigating indirect effects as well as direct ones.

There is strong evidence that removal of wolves from the northern range of Yellowstone National Park has allowed abundant elk populations to degrade riparian woody plant communities. Willows and other woody, deciduous species were historically abundant but have declined or disappeared in Yellowstone's northern elk (*Cervus elaphus* L.) wintering range over the past 80 years (Engstrom, 1991; Houston, 1982; Singer et al., 1994). During the period when wolves were absent from Yellowstone, elk browsing of riparian willows expanded (Houston, 1982) and little or no aspen recruitment occurred (Ripple & Larsen, 2000). Following wolf reintroduction in 1994, browsing pressure in some areas lessened (Ripple & Beschta, 2004), ostensibly due to the effect of wolves on elk foraging patterns (Fortin et al., 2005) and population size (White & Garrott, 2005).

The extent to which this trophic cascade will restore degraded willow communities is unclear (Smith et al., 2003) because indirect effects of wolf absence may prevent willow recovery in some areas of Yellowstone. Exclusion of beaver and subsequent water table decline appears to be an important indirect effect of wolf removal.

Recent work has shown that in the absence of wolves, elk may competitively exclude beaver (*Castor canadensis*) (Hebblewhite et al., 2005) by reducing willow standing crop (Baker et al., 2005). In Yellowstone, a decline in beaver activity concurred with willow decline. Damming by beavers was common in the northern range in the early 1900s (Warren, 1926), was greatly reduced by 1955 (Jonas, 1955), and was entirely absent by 1988 (Consolo Murphy & Hanson, 1990). Decades of beaver absence has led to an altered hydrologic regime in some parts of the park, as stream channels have eroded and water tables on adjacent terraces have declined (Wolf, 2004). Although beaver now occupy bank dens along larger streams in the northern range, they have not reestablished dams along small-order streams where they historically had a large influence on local water table (Warren 1926). Because water availability is essential for high willow productivity (Lindroth & Bath, 1999), and current beaver distribution is limited by availability of productive willow stands (Smith et al., 1996), eroded stream channels may prevent reestablishment of beaver colonies, restoration of the historic hydrologic regime, and recovery of willow.

To determine if the altered hydrologic regime will constrain willow recovery under reduced elk browsing, a more detailed understanding of the controls over willow growth and productivity is required. Riparian willows have exceptionally rapid leaf development rates (Cannell et al., 1987) and high leaf-level photosynthetic rates (Raven, 1992) under resource saturating conditions. These traits allow rapid recovery from disturbances, including browsing. For instance, in Oregon, winter beaver use of *Salix lasiandra* stems led to higher aboveground productivity the following growing season (Kindschy, 1985). In Rocky Mountain National Park, winter elk browsing caused *S.*

monticola to produce more shoot biomass per unit leaf area than protected plants (Peinetti et al., 2001). However, the same physiological attributes that confer high potential productivity, such as high stomatal conductance and transpiration rate, make willows sensitive to water stress (Wikberg & Ogren, 2004). Across landscapes, willow productivity is tightly linked to water availability (Lindroth & Bath, 1999).

Another important trait to consider is that willows undergo dramatic morphological changes in response to winter browsing. In a study of *S. monticola* and *S. planifola* in Rocky Mountain National Park, winter browsing by elk reduced the number of shoots per stem, increased shoot length, reduced the number of leaves per shoot, and increased average leaf size (Peinetti et al., 2001). Browsing also caused a tenfold increase in the number of epicormic shoots, or shoots developing from shoots older than one year (Peinetti et al., 2001), meaning that a larger fraction of leaf area is supplied by a water pathway crossing fewer age junctions. Recent work in the field of plant hydraulic architecture suggests that such changes may have a large effect on willow water relations. Larger stems tend to have a higher leaf-specific conductivity, meaning that they supply water to leaves at a higher rate under a given pressure gradient (Tyree & Ewers, 1991). Also, branch and age junctions are known to cause hydraulic constrictions (Ewers & Zimmermann, 1984; Joyce & Steiner, 1995; Tyree & Ewers, 1991; Zimmermann, 1978). Reduced hydraulic conductivity, in turn, is known to reduce stomatal conductance, photosynthesis, and growth (Brodribb & Feild, 2000; Hubbard et al., 1999; Ryan & Yoder, 1997). These patterns suggest that browsing may relieve water stress by facilitating a higher rate of water supply to leaves. Such a mechanism could cause reduced browsing to interact negatively with low water availability. If so, aboveground willow productivity would likely remain suppressed under current conditions in Yellowstone, and actions to mitigate the hydrologic conditions of floodplains might be warranted.

To inform restoration efforts, I sought to quantify the effects of water availability and browsing on willow productivity, and assess the mechanisms of those effects using morphological and physiological evidence. I manipulated herbivory and water table depth in a factorial field experiment to address the following questions: (1) How do browsing and water table influence aboveground willow productivity? (2) Does browsing alter shoot morphology and alleviate water stress? (3) Do browsing and increased water availability increase leaf-level photosynthetic rate and stomatal conductance?

Methods

Study area

I worked in the northern range of Yellowstone National Park, USA, a 100,000-hectare (ha) area used intensively by Yellowstone's largest elk herd during winter (Houston, 1982). Moose (*Alces alces* L.) and mule deer (*Odocoileus hemionus* Rafinesque) are also present and browse on willow, although at much lower rates than elk. Elevation ranges from 1925 to 2000 m above sea level. This semi-arid region receives 260 mm of precipitation annually, 45-65% of which falls during the growing season (Despain, 1987). The landscape consists of large areas of rolling hills of glacial till dominated by *Artemisia tridentata* Nutt. with an understory of *Elymus smithii* Rydb. and several other cool season grasses, interspersed with small wetlands and wet meadows dominated by *Carex aquatilis* and the willows *S. planifolia* and *S. wolfii*. Higher elevations, particularly north facing exposures, support stands of conifers such as *Pseudotsuga menziesii* Mirb., *Picea engelmanni* Parry ex Engelm., *Abies lasiocarpa* (Hook.) Nutt., and *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex Wats. as well as *Populus tremuloides* Michx. in a patchy distribution (Houston, 1982).

Riparian floodplains form networks that cover about 4% of Yellowstone's area. Riparian vegetation is dominated by the willow species *S. geyeriana, S. bebbiana, S. pseudomonticola* Ball, *S. boothii* Dorn, *S. wolfii* Bebb, and *S. exigua* Nutt. (Houston, 1982), with an understory of herbaceous plants. My study sites were located on terraces adjacent to 3rd or 4th order streams that had a recent decline in local water table, evidenced by stream downcutting through previously inundated, gleyed soils, and/or historical record of previous beaver ponding (Jonas, 1955; Warren, 1926). Ambient water tables in my study plots were less than 0.5 m below the surface in the spring, dropping to 1-2 m in late summer. The growth form of all willows in my study plots at the start of the experiment was short (< 1 m) with many browsed shoot stubs that had died back to the bud scar, indicating a history of heavy browsing (Keigley & Frisina, 1998).

Experimental design and sampling

My study was a factorial experiment with a randomized complete block structure. Treatments included two levels of herbivory (large herbivore browsing present and absent) imposed by exclosures, crossed with two levels of water table (ambient and elevated) imposed by simulated beaver dams.

There were four blocks on three drainages in the northern range (Appendix 1). Treatments were randomly assigned to plots within each block. Plots averaged 10 X 20 m in size, although plot size was allowed to vary in order to obtain sufficient numbers of willows for measurement. I monitored responses of three species, only one of which was found at all four sites: *S. bebbiana* (n = 3), *S. boothii* (n = 3), and *S. geyeriana* (n = 4).

Exclosures (2.4 m high) were constructed around exclosed plots in the summer of 2001 and completely eliminated browsing by large herbivores. I quantified browsing intensity outside exclosures as the percentage of current annual growth (*CAG*) consumed using the biomass comparison method on marked stems each year from 2003 to 2005 (Bilyeu et al., 2006). This method compares estimates of stem-level CAG prior to browsing with estimates of CAG remaining on the stem after winter browsing. Dry mass of intact shoots is estimated using a regression on stem length (calculated without leaves), and by a multiple regression using base diameter and the difference between browse point and base diameter for browsed shoots. Ambient browsing intensity during the course of the experiment was heavy, averaging 66% of current year's growth across species and years (Table 1).

Dams were constructed in fall of 2001 so that the pool was adjacent to plots that had been selected to receive the elevated water treatment. Dams were constructed from pine logs and square timbers that completely filled the stream channel. Pond-liner covered the structure and was secured to the upstream streambed to prevent water flow under or around the sides of the dam. To monitor the effect of the dams, I installed two to six groundwater monitoring wells in all plots in July and August of 2001. Wells were constructed of slotted 1.25-inch PVC pipe and were installed with hand augers to a depth approximately 30 cm below that of the water table depth, 120 to 280 cm deep. Following installation, wells were pumped dry several times to ensure proper flow between the well and adjacent soil. Water levels were recorded approximately every two weeks during the growing season using an electronic tape. Dams elevated water table depth by an average of 0.37 meters during the growing season (Table 1), but the effect size in August was as large as 90 cm at some sites in some years (Appendix 2). The observed pattern of attenuated water table decline late in the growing season in dammed plots is similar to that observed for natural beaver dams in the Rocky Mountains of Colorado (Westbrook et al., 2006). In each plot, seven plants of each species, where present, were selected by a spatially stratified, systematic protocol and permanently tagged in August of 2001. On each plant, at least 10%, but no fewer than three, rooted stems were selected for permanent marking using a game spinner placed over the center of the plant. Selection was stratified according to location within the plant, so that stems from the center, edge, and halfway between center and edge were equally represented. Each year, 2-year-old stems were tagged on plants noted as having a large percentage of new stems the previous year. The number tagged ensured that the proportion of new stems tagged was equivalent to the proportion of older stems tagged on the plant. This ensured that the average age of tagged stems did not increase with time, while preventing the tagging of first-year stems, which experience high mortality.

Overview of measurements

I quantified effects of browsing and water tables on current annual growth, shoot size distribution, maximum shoot diameter, average number of branch junctions between leaf and ground level, average leaf size, ratio of leaf area to shoot basal area, average leaf area per plant, midday shoot water potential, leaf-level stomatal conductance, and leaf-level photosynthesis in response to the factorial experiment. To aid in interpretation of morphological and physiological field data, I characterized the hydraulic properties of shoots of my three study species by constructing vulnerability curves.

Characterizing willow shoot hydraulic properties

Vulnerability curves describe how xylem function is lost with decreasing xylem pressure. In most plants, including willow, active photosynthesis requires simultaneous transpiration of water from leaves. This water supply water moves through the xylem under negative pressure. This pressure becomes increasingly negative as soil moisture or air humidity decrease, or temperature increases. If the pressure drops below a certain threshold, xylem vessels begin to cavitate and conducting capacity in the xylem is lost. I determined the vulnerability of shoot xylem to cavitation in *S. bebbiana, S. boothii,* and *S. geyeriana* in the fall of 2003. Large, current year shoots (basal diameter 3.4 to 4.3 mm, n = 5 per species) were selected in August of 2003 from areas within one mile of study plots, sealed in parafilm, refrigerated, and transported to the laboratory within 24 hr. Shoots were recut under water, attached to a tubing system, and flushed with deionized, filtered water for 20 minutes at 100 kPa to refill all xylem vessels. Maximum hydraulic conductivity (K_{max}) was then determined by measuring the mass flow rate of water through the shoot with a given pressure gradient (Sperry et al., 1988; Tyree & Ewers, 1991). Vulnerability curves were constructed using the centrifugation method (Alder et al., 1997) in which conductivity of a given shoot is repeatedly measured after being subjected to progressively decreasing xylem potentials. Percent loss conductivity (PLC) at each potential was calculated as the conductivity of the shoot at the given potential divided by K_{max}. Curves were plotted as PLC vs. potential, and I determined the potential causing a 50% loss of conductivity (p_{50}) by fitting a Weibull function to the curve for each shoot using the Solver function in Microsoft Excel. Species effects on PLC at each potential measured were analyzed using a repeated measures analysis of variance in PROC GLM (SAS/STAT software, Version 9.1 of the SAS System for Windows. Copyright © 2002-2003 SAS Institute Inc.).

I was interested in the effect of shoot size on conducting capacity and xylem vulnerability. For each shoot used in constructing vulnerability curves, I calculated area-specific conductivity (K_s), a measure of xylem porosity, as K_{max} divided by shoot basal cross-sectional area. I regressed shoot basal cross-sectional area against K_s to determine the effect of shoot size on conducting capacity (n = 14, species pooled). I also regressed shoot area against p_{50} to quantify the effect of shoot size on xylem vulnerability (n = 14, species pooled). Increased resistance to cavitation is generally coupled with reduced hydraulic conductance when water is not limiting (Alder et al., 1997; Tyree et al., 1994; Zimmermann, 1983). I regressed K_s against p_{50} to determine if there is a tradeoff between conducting capacity and vulnerability regardless of shoot size (n = 14, species pooled).

Measuring responses to the factorial experiment

PRODUCTIVITY

Current annual growth of new shoots, including leaves, was estimated non-destructively on all tagged stems in August of each year. Current-year shoots were identified by the presence of a single basal bud scar. I used a flexible, systematic sampling protocol for selecting shoots to measure in order to avoid human bias for selecting larger-than-average shoots (Rutherford, 1979). This method simultaneously provided a count of browsed and unbrowsed shoots (Fig. 1). Shoot number per stem ranged from 1 to nearly 1000, and I measured at least 6 or 10% of shoots per stem, whichever was greater. Each year, roughly 10,000 shoot length measurements were made. Length of each selected shoot was estimated visually to the nearest centimeter, and these estimates were periodically verified against shoots of known length to assure at least 90% accuracy. Dry mass of each measured shoot was determined by applying a length-dry mass regression created from shoots of each species collected from untagged plants from each drainage each study year (R^2 values: *S. bebbiana:* 0.965, n = 297; *S. boothii:* 0.973, n = 279; *S. geyeriana:* 0.974, n = 392, see Appendix 3.) Shoot dry mass estimates were averaged over each tagged stem and multiplied by the count of shoots to determine stem-level production. Plant-level production was calculated as the average production of tagged stems multiplied by the number of stems on each plant, plus any production of new stems. Production of new stems was calculated separately by applying the same length-dry mass regression function, as their morphology is that of large shoots. Average plant-level production was normalized by dividing by average initial plant canopy area to account for differences in plant size at the start of the experiment. Plant canopy area was estimated by measuring the longest diameter and diameter perpendicular to the longest diameter to the nearest centimeter, then assuming an elliptical canopy shape. *CAG* for each plot was calculated by dividing average plant-level productivity by average plant canopy area.

My methods quantified only new shoot and leaf biomass, not biomass added as increased girth on older portions of stems. As a plant grows taller, I expect a larger proportion of aboveground growth to be allocated to increased girth. If treatments cause plant height to increase, then a decline in *CAG* may simply reflect this change in architecture, and not an overall change in aboveground productivity. I was interested in discerning changes in *CAG* associated with changes in height from those not associated with height changes. Therefore, I regressed *CAG* against plant height for each species across treatments and years, and if the relationship was significant, I tested for treatment effects on the residuals to assess affects on *CAG* after the effect of height was removed.

MORPHOLOGY

I determined the distribution of shoot mass among shoots of different lengths for *S. bebbiana, S. boothii,* and *S. geyeriana* from 2002 to 2005. Using the regression relationships in Appendix 3, I calculated shoot masses for all possible integer shoot length values between 1 and 160 cm. Next, I created weighted histograms by weighting the number of shoots recorded of a given length by the mass of shoots of that length. I then calculated the percent of shoot mass contained in shoots less than 5 cm in length (*pct_mass5*) and analyzed treatment effects on this response.

Maximum shoot diameter (D_{max}) was recorded on all stems sampled for *CAG* in years 2003-2005, and values were averaged for each plot.

Average number of branch and age junctions between leaf and soil (*B*) for *S. geyeriana* and *S. bebbiana* in each treatment were estimated in 2004 for (n = 6) stems by randomly choosing 3 leaves per stem, then counting the number of terminal bud scar scales and branch points between the leaf and ground level.

Average area of individual leaves (*LS*), leaf area per unit shoot basal area (*La/Sa*), and average leaf area per plant (*L*) was determined for *S. geyeriana,* the most abundant species at my study sites, in 2005. First, I determined specific leaf area by tracing 60 leaves from inside and outside of exclosures, and collecting, drying, and weighing them. I cut out leaf tracings, weighed paper cutouts, and divided by the specific weight of the paper to find the area of each leaf. I tested for exclosure effects on the slope of the leaf weight/ leaf area relationship in SAS PROC GLM, and found no effect (exclosure slope effect $p = 0.49$). Therefore I pooled data from inside and outside of exclosures and created one regression ($R^2 = 0.98$), the slope of which I used as specific leaf area (135.24 $\pm$ 1.3 $cm^2\ g^{-1}$). Next, I sampled 110 *S. geyeriana* shoots in 2005 and measured shoot length, shoot basal diameter, and number of leaves. I dried and weighed shoots and leaves separately, then calculated leaf area for each sample by multiplying leaf weight by specific leaf area. I calculated *LS* by dividing leaf area by the number of leaves for each shoot sample, and calculated *La/Sa* by dividing leaf area by shoot cross-sectional basal area. Finding *L* required relating leaf area data from these samples to shoot length measurements taken for *CAG.* I created a regression for leaf area in terms of shoot length, which I found differed for shoots inside exclosures ($R^2 = 0.92$) and outside exclosures ($R^2 = 0.94$, see Appendix 4). I applied these regressions to each shoot length measurement taken for *CAG* data, then calculated plant-level leaf area in the same manner as plant-level production. Plant-level leaf area was averaged over each plot to find *L*.

PHYSIOLOGY

In the absence of stomatal regulation, water potential in the xylem drops as plants become increasingly drought stressed. I measured the water potential of freshly cut current year shoots (Ψ_s) using a Scholander-type pressure chamber (PMS instruments, Corvallis, OR). Water potentials were recorded at mid-day (12h -14h) under sunny conditions early in the growing season (June 25 – July 7) and late in the growing season (August 10 - August 25) in years 2003-2005 for *S. geyeriana* and in 2003 for *S. bebbiana*. Five plants per plot were sampled on each measurement date. Data was averaged over each plot each season.

In order to avoid loss of cell turgor pressure and prevent xylem cavitation, plants may close their stomata, thereby reducing water loss, but also reducing the availability of CO_2 for photosynthesis. I measured stomatal conductance (g_s) and photosynthesis (A) in *S. geyeriana* using a Li-6400 Portable Photosynthesis system in 2005 (Li-Cor instruments, Lincoln, NE). Measurements were made under sunny conditions on 2 sunlit, fully expanded leaves on 5 plants per study plot. Midday measurements were made between 11h and 14h on all study plots in last week of June and 3rd week of August, and values were averaged over each plot (n = 4). Vapor pressure deficit (D) was calculated using simultaneous measurements of leaf temperature, air temperature, and relative humidity with a sling psychrometer. Diurnal measurements of A and g_s were made for control and exclosed-only plots during the same sample periods. Measurements were taken at approximately 1.5 hr intervals between 8h and 18h, and values were averaged over each plot for 2 hour time blocks (n = 4). Exclosure effects were analyzed separately for each time point.

Statistics

I used analysis of variance for a randomized complete block experiment with a factorial layout to analyze responses to treatments (*CAG, pct_mass5,* D_{max}, *LS, La/Sa, L,* Ψ_s, *A,* and g_s) using the PROC MIXED model in SAS. Site was included as a random effect, and damming treatment, exclosure treatment, and their interaction were included as potential fixed effects. Measurements taken over multiple years were analyzed using a repeated measures analysis of variance with a compound symmetry covariance structure, with year and year-by-treatment interactions included as potential fixed effects in addition to treatment effects. For midday *A* and g_s, *D* was also included as a potential fixed effect. Interactions were dropped from models when non-significant at the $\alpha = 0.05$ level, and 95% confidence intervals on effect sizes of main effects were calculated (hereafter, CI). Confidence intervals that overlap zero indicate non-significant main effects at the $\alpha = 0.05$ level.

Results

Willow hydraulic properties

I did not observe differences by species in *PLC* at any of the measured xylem potentials ($p > 0.2734$, Figure 2). My vulnerability curves reveal that shoots of these willow species are vulnerable to cavitation at relatively low Ψ_s, reaching a 50% loss of conductivity at 1.85 ± 0.28 MPa. Across species, p_{50} was inversely correlated with K_s, indicating a tradeoff between vulnerability and conducting capacity ($R^2 = 0.61$, p = 0.0009). Even though my methods necessitated using the largest shoots available and the range of shoot sizes was therefore narrow, I observed a significant increase in p_{50} with increasing shoot cross-sectional area ($R^2 = 0.27$, p = 0.05, n = 14), indicating that smaller shoots are less vulnerable to cavitation. There was also a likely correlation between cross-sectional area and K_s ($R^2 = 0.25$, p = 0.07, n = 14), indicating that smaller diameter shoots are less porous to water flow on a per-area basis.

Productivity

Exclosures reduced *CAG* in *S. bebbiana* by 63.7 g/m^2 (95% CI: 7.0, 120.5), in *S. boothii* by 66.3 g/m^2 (95% CI: 2.8, 129.8), and in *S. geyeriana* by 101.3 g/m^2 (95% CI: 50.2, 152.3, Fig. 3). Dams increased *CAG* in *S. geyeriana* by 74.1 g/m^2 (95% CI: 23.0, 125.2, Fig. 3). I did not detect effects of year or interactions between year and treatment effects for any species. *CAG* declined with increasing plant height for *S. boothii* (R^2 = 0.16, p = 0.008), but not for *S. bebbiana* or *S. geyeriana.* The exclosure effect on *CAG* in *S. boothii* seemed to be due increased height inside exclosures, as removing the effect of plant height on *CAG* accounted for the negative effect of exclosures on *CAG* in this species (exclosure effect p < 0.73 for height-corrected *S. boothii* data).

Morphology

Treatments altered how shoot mass was allocated to shoots of different sizes in all species (*S. bebbiana,* Appendix 6; *S. boothii,* Appendix 7; *S. geyeriana,* Fig. 4, Appendix

5). Averaged over years, exclosures increased *pct_mass5,* or the proportion of mass allocated to shoots ≤ 5 cm in length, from 14.8% to 53.3% in *S. bebbiana* ($p < 0.0001$), from 3.0% to 30.4% in *S. boothii* ($p < 0.0001$), and from 12.4% to 51.9% in *S. geyeriana* ($p < 0.0001$, Fig. 4). The effect of exclosures depended on year in *S. boothii* (exclosure X year interaction $p = 0.0005$) and *S. geyeriana* (exclosure X year interaction $p = 0.02$) due to a smaller effect size of the exclosures in 2002 than in subsequent years. After 2002, the effect size of the exclosures on *pct_mass5* stabilized at 33.6 (95% CI: 27.8, 39.3) for *S. boothii* and 44.7 (95% CI: 38.2, 51.2) for *S. geyeriana* (Fig. 4), and there was no further interaction between exclosure and year (exclosure X year interaction 2003- 2005: $p > 0.34$). Dams had the opposite effect on shoot mass distribution. Dams decreased *pct_mass5* by 10.2 percentage points (95% CI: 0.88, 19.6) in *S. bebbiana,* and 12.5 percentage points (95% CI: 6.9, 18.1) in *S. geyeriana* (Fig. 4). There was no interaction between the dam effect and year, nor was there an interaction between the dam effect and the exclosure effect. These results indicate a shift in shoot diameter distribution towards a higher number of very small diameter shoots inside exclosures, and a fewer number in dammed plots, because shoot length and diameter are highly correlated ($R^2 = 0.81$, $p < 0.0001$ across species).

Exclosures decreased D_{max}, or maximum shoot diameter, by 1.6 mm (95% CI: 0.83, 2.3) in *S. boothii,* a decrease of 60%, and by 1.0 mm (95% CI: 0.62, 1.3) in *S. geyeriana,* a decrease of 39%. Dams increased D_{max} in *S. geyeriana* by 0.68 mm (95% CI: 0.33, 1.0). There was no interaction between dam and exclosure effects on D_{max}, nor any interactions between treatments and year.

Exclosures increased *B*, or the average number of age and branch junctions, for stems sampled in 2004. For *S. bebbiana,* exclosures increased *B* from 2.4 to 4.3 ($p = 0.015$) and for *S. geyeriana,* exclosures increased *B* from 2.2 to 3.7 ($p = 0.008$), indicating that exclosed plants have a more branched architecture. There was no effect of the dams on *B*, nor any interaction between treatments.

Exclosures reduced *S. geyeriana LS,* the average size of individual leaves ($p = 0.0038$), while dams increased *LS* ($p = 0.0014$, Fig. 5). There was no interaction between treatments on *LS.* There was no effect of exclosures *L,* average leaf area per plant ($p = 0.43$), implying that plants inside exclosures compensate for smaller leaf size by increasing number of leaves (Fig. 5). Dams increased *L* by 58% ($p = 0.037$, Fig. 5). There was no interaction between dam and exclosure effects on *L* ($p = 0.38$). There was no effect of exclosure treatment, dam treatment, or their interaction on *La/Sa,* the ratio of leaf area to sapwood area for individual shoots ($p = 0.15$).

Physiology

Exclosures caused a slight but significant decrease in Ψ_s across species, seasons, and years in a repeated measures factorial analysis [Exclosure effect size: *S. bebbiana:* -0.18 MPa (95% CI: 0.05, 0.32); *S. geyeriana:* -0.07 MPa (95% CI: 0.01, 0.13); Fig. 6]. Ψ_s was lower in 2003, a very dry year (Table 1), than in subsequent years [year effect in 2002 vs. average of 2003 and 2004: 0.48 MPa (95% CI: 0.42, 0.64)]. Ψ_s was higher in June than August ($p < 0.0001$, Fig 6), but there was no interaction between season and exclosure treatment. Dams caused an increase in Ψ_s across seasons and years of 0.12 MPa (95% CI: 0.06, 0.19) in *S. geyeriana,* and tended to increase Ψ_s in *S. bebbiana,* although the effect was not significant (Fig 6). There was no interaction between dam treatment and year or season, and no interaction between dam treatment and exclosure treatment.

Exclosures caused a decrease in *S. geyeriana* midday photosynthetic rate (*A*) in June of 5.1 μmol m^2/s (95% CI: 3.3, 6.9) and an increase in August of 1.8 μmol m^2/s (95% CI: -0.1, 3.8, $p = 0.06$, Fig. 7a). Dams caused an increase in *A* in June of 3.1 μmol m^2/s (95% CI: 1.3, 4.9) and an increase in August of 2.2 μmol m^2/s (95% CI: 0.1, 4.2, Fig. 7a). Treatments had similar effects on stomatal conductance (g_s). Exclosures decreased g_s by 0.15 mol m^2/s (95% CI: 0.11, 0.20) in June and by 0.07 mol m^2/s (95% CI: 0.03, 0.12) in August (Fig 7b). Dams increased g_s by 0.08 mol m^2/s (95% CI: 0.03, 0.12) in June and by 0.05 mol m^2/s (95% CI: 0.00, 0.09) in August (Fig. 7b). There was no effect of *D,* vapor pressure deficit, on midday *A* or g_s, as *D* was fairly constant during the midday time interval within a measurement period. There was no interaction between dam and exclosure effects on either *A* or g_s. Analysis of diurnal measurements on control and exclosed-only plots reveals that exclosures affect *A* and g_s throughout most of the day in June, while effects are less pronounced through the course of the day in August (Fig. 8).

Discussion

Excluding browsing reduced current annual growth and greatly altered plant morphology. Exclosures caused the fraction of biomass allocated to shoots smaller than 5 cm long to triple within 2 years, maximum shoot diameter and average leaf size to decrease, and number of branch points per stem to increase. Exclosures did not alter the ratio of leaf area to shoot basal area, and, concurring with an earlier study on willows in Rocky Mountain National Park (Peinetti et al., 2001), exclosures did not alter total leaf area. Excluding browsing also decreased midday water potential and reduced stomatal conductance and photosynthesis per unit leaf area throughout much of the day both early and late in the growing season.

An apparent paradox in these results warrants clarification. If the absence of browsing reduced total shoot and leaf productivity (i.e. *CAG*), but did not affect leaf area or specific leaf area, I can conclude that exclosures affect productivity by reducing shoot mass, but not leaf mass. If the ratio of total leaf area to total shoot mass is therefore altered, how is it possible that the ratio of shoot leaf area to shoot basal area remained the same? The relationship between shoot mass and shoot area is exponential, not linear (Appendix 7). Therefore, the fewer, larger shoots outside exclosures have more mass per unit basal area than the numerous, smaller shoots found inside exclosures.

Dams also affected most of the measured responses, increasing *S. geyeriana* productivity, maximum shoot diameter, average leaf size, and total leaf area. Dams also reduced water stress and increased stomatal conductance and photosynthetic rate in the early part of the growing season.

Thus, both elk browsing and increased water availability had beneficial effects on willow productivity, physiology, and morphology. Because there were no interactions between treatments in my experiment, willows in the water-elevated, browsed treatment had the highest productivity, lowest water stress, and highest photosynthetic rates. Willows in the water-ambient, unbrowsed treatment had the lowest productivity, most water stress, and lowest photosynthetic rates. These results support the idea that willows are well adapted to browsing, especially under conditions of high water availability, and suggest that removing browsing under conditions of low water availability may not allow willow recovery.

Experimental results suggest that browsing alleviates water stress by facilitating a more juvenile growth form characterized by fewer, longer, thicker shoots, allowing a higher rate of water supply to leaves. Although I did not measure leaf-specific conductivity (LSC) in the field, my data imply that LSC is reduced when plants are protected from browsing. In the sample of shoots used in constructing my vulnerability curves, which ranged from 3.4 to 4.3 mm in diameter, I found evidence that smaller diameter shoots are less porous to water flow. If this relationship extends to the much smaller shoot diameters found within exclosures (0.96 ± 0.37 mm), then the hydraulic capacity of shoots inside exclosures would be greatly reduced. Because the ratio of leaf area to shoot basal area was not different for browsed and unbrowsed plants, LSC would be reduced as well, concurring with the commonly observed pattern of reduced LSC in stems of smaller diameter (Tyree & Ewers, 1991). Such a mechanism could explain why willows respond well to browsing, and explain why unbrowsed willows occasionally resprout from the ground, suggesting a natural renewal of willow crowns (Kindschy, 1985).

Reduced LSC in smaller diameter shoots is consistent with the reduction in Ψ_s inside exclosures. With lowered LSC, the very small diameter shoots on unbrowsed plants would require a larger drop in pressure to supply water to their leaves at an adequate rate than the larger shoots of browsed plants. In August 2003, the driest year of my study, exclosures caused mid-day *S. geyeriana* water potentials to fall to -1.7 ± 0.5

MPa in exclosed, undammed plots. This value approaches the *p50* value of the vulnerability curve for *S. geyeriana*, implying nearly a 50% loss of conducting capacity. Such a loss of conductivity would be unusual, because plants typically regulate their stomata to avoid dramatic xylem cavitation, and study of *S. gooddingi* found no increase in cavitation during a drought (Pockman & Sperry, 2000). A more likely explanation is that the observed drop in vulnerability with decreasing shoot diameter extends to the very small diameter shoots inside exclosures, resulting in maintenance of xylem integrity at the measured water potentials. Because of the tradeoff between K_s and *p50*, this lessened vulnerability would be associated with lessened conductivity, requiring lower Ψ_s to support transpiration.

Although smaller diameter shoots may compensate for lower conducting capacity by lowering Ψ_s, my results suggest that reduced conducting capacity in the absence of browsing nonetheless limits willow growth. Two mechanisms appear to be at work. Stomatal conductance was lower in unbrowsed plants, implying that the reduction in Ψ_s was not sufficient to maintain the same rate of water flow to leaves as in browsed ones. Reduced leaf-level stomatal conductance and photosynthesis probably mean that seasonal carbon gain is lower inside exclosures, given that exclosures do not affect leaf area, and that differences in photosynthesis were seen both early and late in the growing season. Therefore, reduced photosynthesis may limit growth of unbrowsed plants. In addition, the role of hydraulic conductivity in limiting growth through constraints on turgor pressure has been suggested (Ryan et al., 2005). Turgor pressure is the driving force for cell expansion, and approximately equals the difference between Ψ_s and osmotic potential of leaf cells. Lower Ψ_s inside exclosures probably means that turgor pressure is reduced, which is consistent with the observed reduction in the average area of individual leaves. To maintain turgor, a plant may close stomata, but this limits carbon gain. With reduced conducting capacity, exclosed plants are forced into a tradeoff between turgor maintenance and photosynthesis under less severe atmospheric conditions than browsed plants. This explains why g_s was more affected by exclosures early in the growing season, when there would be a greater premium on leaf expansion than on photosynthesis.

In water-elevated plots, increased water availability allows for higher Ψ_s, increasing turgor and providing a greater force for cell expansion, resulting in larger average leaf size and longer shoots. More severe atmospheric conditions may be withstood before stomata must close, resulting in higher photosynthesis. Increased photosynthesis and increased leaf area probably result in greater seasonal carbon gain. Thus, water table elevation and browsing are similar in their effects on willow function, although the mechanisms by which they act differ. Both increase turgor and photosynthesis, but water table elevation does so by increasing water supply, while browsing does so by causing morphological changes that increase the rate of water flow through the plant.

As woody plants grow taller, there is a general trend of reduced productivity and photosynthetic rate (Ryan & Yoder, 1997). If the changes observed inside exclosures were accompanied by substantial height increases, I could attribute them to a natural progression of changing architecture and productivity with increasing height. However, in *S. bebbiana* and *S. geyeriana, CAG* and height were uncorrelated, and in *S. boothii* height explained only 11% of the variation in *CAG.* Furthermore, plants in the water-ambient, unbrowsed plots gained only 60 cm (95% CI: 45, 74) after four years of protection from browsing, with negligible height gain for 2 of the 3 study species in the last year of the experiment. Thus, it appears that under conditions of low water availability, unbrowsed willows develop stem morphology and productivity patterns typical of taller willows, even though they do not become tall.

Conclusion

Reduced aboveground growth inside exclosures was associated with morphological changes that exacerbated water stress and reduced productivity, while modest elevation of water table resulted in a substantial increase in willow productivity. Willows are apparently well-adapted to both browsing under conditions of high water availability; exactly the conditions created by beaver activity. I concur with the conclusion that beaver and willow are mutualists (Baker et al., 2005), and conclude that restoration of willow in many areas of Yellowstone can occur only with restoration of beaver populations. Because elk browsing on willows in the absence of wolves appears to disrupt beaver/willow mutualism (Baker et al., 2005; Hebblewhite et al., 2005), and wolf presence moderates elk use of willow, the reintroduction of wolves to Yellowstone is a critical first step in the restoration of degraded willow communities.

However, a reduction in elk browsing alone on water-stressed willows will likely not result in tall, productive willow stands, especially in areas with deep water tables. In the areas where prolonged absence of beaver activity has resulted in channel incision and water table decline, willow stands will likely not recover. Without productive willow, beaver may be unable to recolonize Yellowstone streams, resulting in a positive feedback that stabilizes riparian ecosystems in their current, degraded state. Mitigating this feedback may require increasing water availability to willows using artificial, temporary dams.

My results provide a counterbalance to earlier studies concluding that a trophic cascade following wolf reintroduction was resulting in a broad recovery of deciduous woody vegetation (Beschta, 2003; Ripple & Beschta, 2003, 2004; Ripple, 2001a, b). Some of the discrepancy in results may be attributed to study location. Studies finding evidence for recovery have been conducted almost exclusively along the Lamar River in Yellowstone, a large, low gradient river whose hydrologic regime was never influenced by beaver dams. Only one paper (Ripple & Beschta, 2004) addressed willow communities in an area historically occupied by beaver, and in this case, recovery was suggested through the use of comparative photographs that were mismatched by season; the pre-wolf picture was taken before bud break, and the post-wolf picture was taken at the end of the growing season. My results suggest that water availability is a key factor in determining which areas of Yellowstone have the potential for riparian ecosystem recovery. In areas such as the Lamar Valley, where the hydrologic regime has remained intact, wolf reintroduction may reduce elk/beaver interspecific competition and restore willow/beaver mutualisms. Alternatively, in areas that have undergone hydrologic change, such as Blacktail Deer Creek, Elk Creek, and Lost Creek, wolf reintroduction may be insufficient for willow recovery. As is commonly the case in restoration of degraded systems, recovery may require more effort than simply reversing the effects of the original stressor.

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Table 1. Summary of ecological conditions in the study sites. Snow and rain data are averages from NOAA weather stations in Tower Junction and Mammoth, WY. Browsing intensity is the proportion of prior growing season's growth consumed, averaged across species and study sites. Snow data is summed over October through May, and rain data is summed over June through August. Water table depths are averaged over all undammed plots (n = 8) over May through September, and dam effect is the average difference between dammed and undammed plots in those months. Dams were constructed in fall of 2001, therefore 2001 should be regarded as pre-treatment data.

	2001	**2002**	**2003**	**2004**	**2005**
browsing intensity (percent CAG consumed)			70 ± 2	63 ± 3	65 ± 2
prior winter snow (m)	3.5	3.8	4.0	2.6	3.4
summer rain (mm)	85	90	58	124	167
ambient water table depth (m)	-1.3 ± 0.16	-1.17 ± 0.10	-1.18 ± 0.09	-1.24 ± 0.10	-1.08 ± 0.06
dam effect (m)	0.08 ± 0.13	0.36 ± 0.08	0.36 ± 0.09	0.40 ± 0.11	0.37 ± 0.06

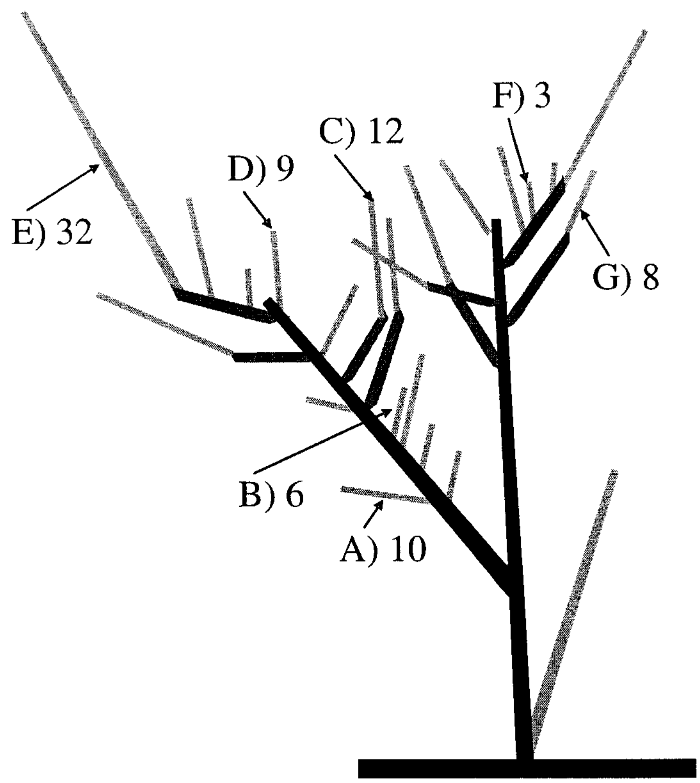


Figure 1. Diagram illustrating shoot sampling protocol for a stem. Letters indicate the order of measurements; numbers indicate lengths in cm. To adequately represent the shoot size distribution in this example, I chose a sampling ratio of 3, which means I recorded measurements on every third shoot encountered as I worked apically from the base of the stem, accommodating side branches by sampling lowest branches first. Here, 7 measurements were made, with 2 shoots apical of the last shoot sampled. The count of shoots was then calculated as 7*3+2=23.

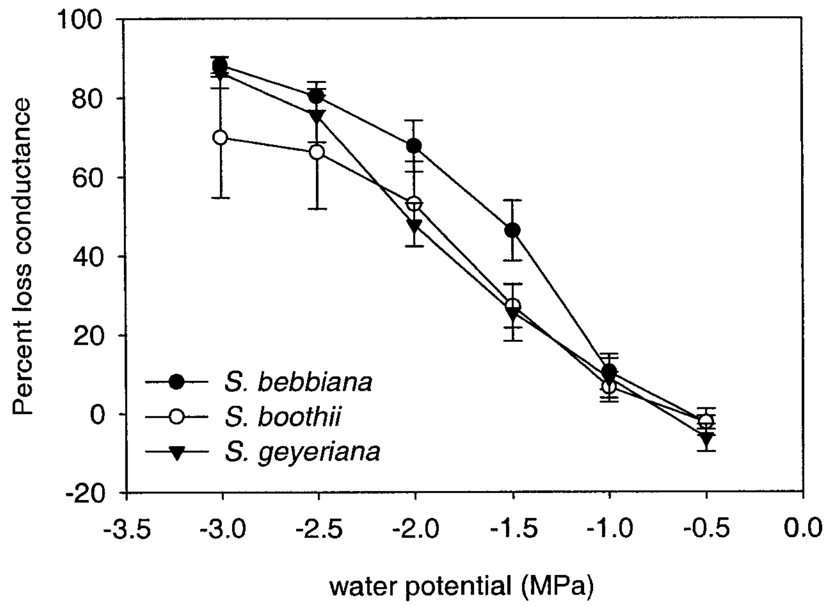


Figure 2. Vulnerability curves for large current-year shoots of three *Salix* species, *S. bebbiana* (n = 5), *S. boothii* (n = 4), and *S. geyeriana* (n = 5) collected in August of 2003.

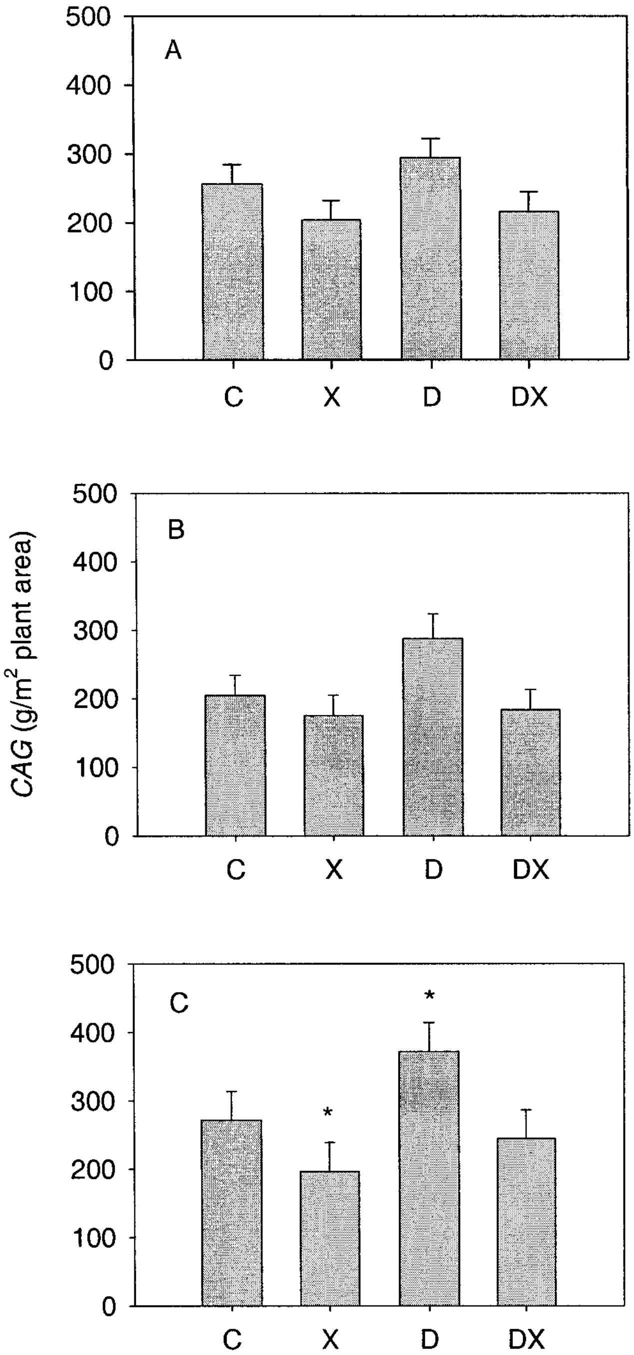


Figure 3. Current annual growth of (A) *S. bebbiana* (n = 3), (B) *S. boothii* (n = 3), and *S. geyeriana* (n = 4) in a factorial experiment with four plots: C = control, X = exclosed, D = dammed, and DX = dammed and exclosed. Values are least square means averaged over 4 years of treatment, with site effects removed. Stars denote treatments that are significantly different from control plots at the alpha = 0.05 level. In factorial analysis, exclosures significantly reduced CAG in all species ($p < 0.04$). Error bars = SE.

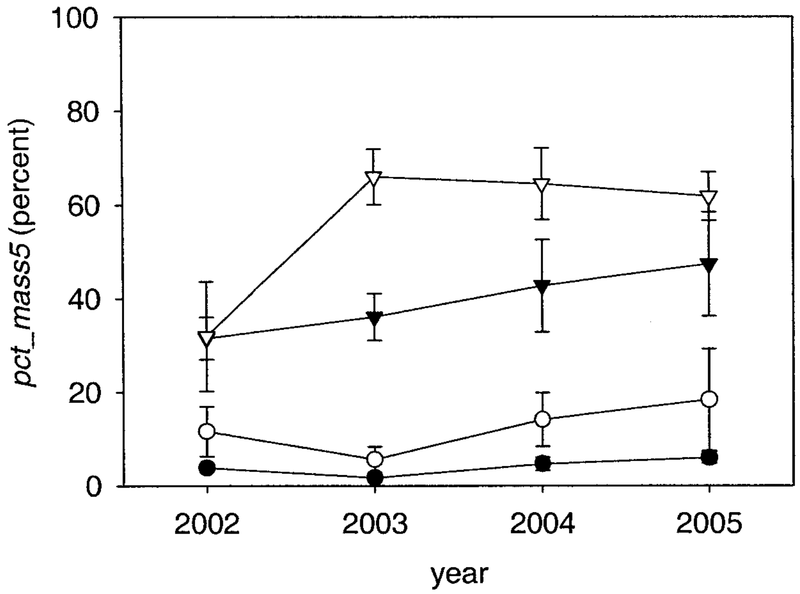


Figure 4. Percent of total shoot mass per stem contained in shoots smaller than 5 cm in length (*pct_mass5*) for *S. geyeriana* in a factorial experiment with four plots: control (○), exclosed only (∇), dammed only (●), and dammed and exclosed (▼). Error bars = SE, n = 4.

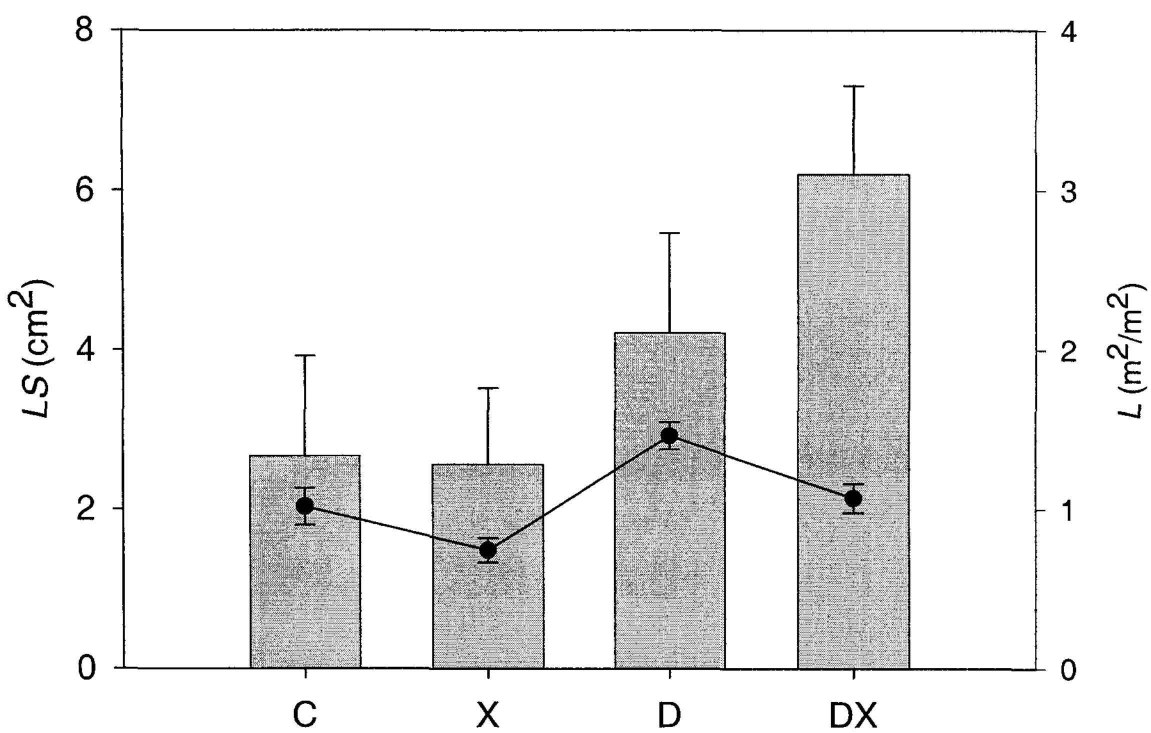


Figure 5. Average leaf size (*LS*, lines) and average leaf area per plant (*L*, bars) for *S. geyeriana* in August of 2005 in a factorial experiment with four plots: C = control, X = exclosed, D = dammed, and DX = dammed and exclosed. Error bars = SE. n = 4.

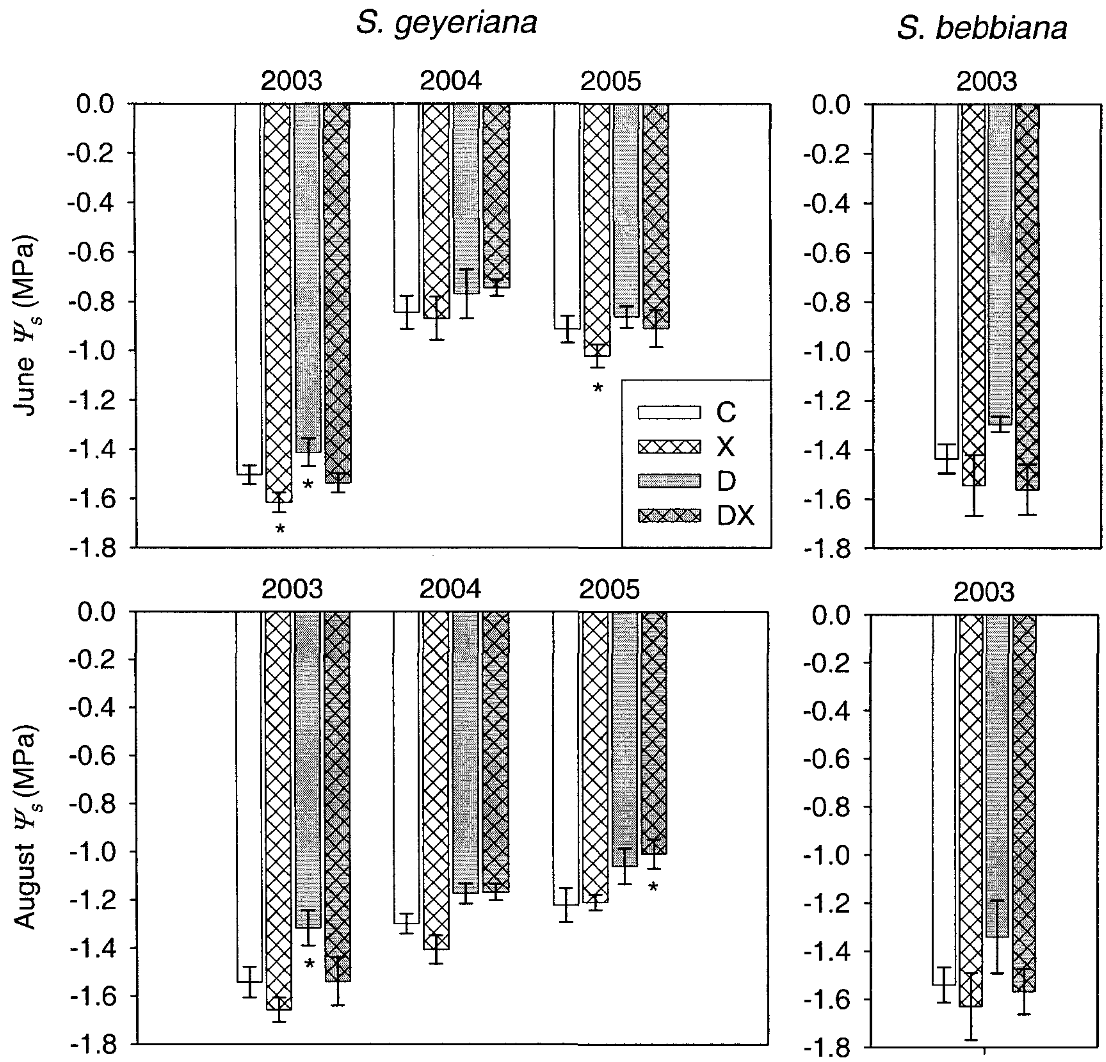


Figure 6. Midday leaf water potential (ψ_s) in June and August for *S. geyeriana* in 2003-2005 and *S. bebbiana* in 2003 in a factorial experiment with four plots: C = control, X = exclosed, D = dammed, and DX = dammed and exclosed. Exclosures and dams had significant effects on water potential across seasons and years in a repeated measures analysis. Stars denote means significantly different from control plots at the $\alpha = 0.05$ level for individual measurement periods. Error bars = SE. n = 4.

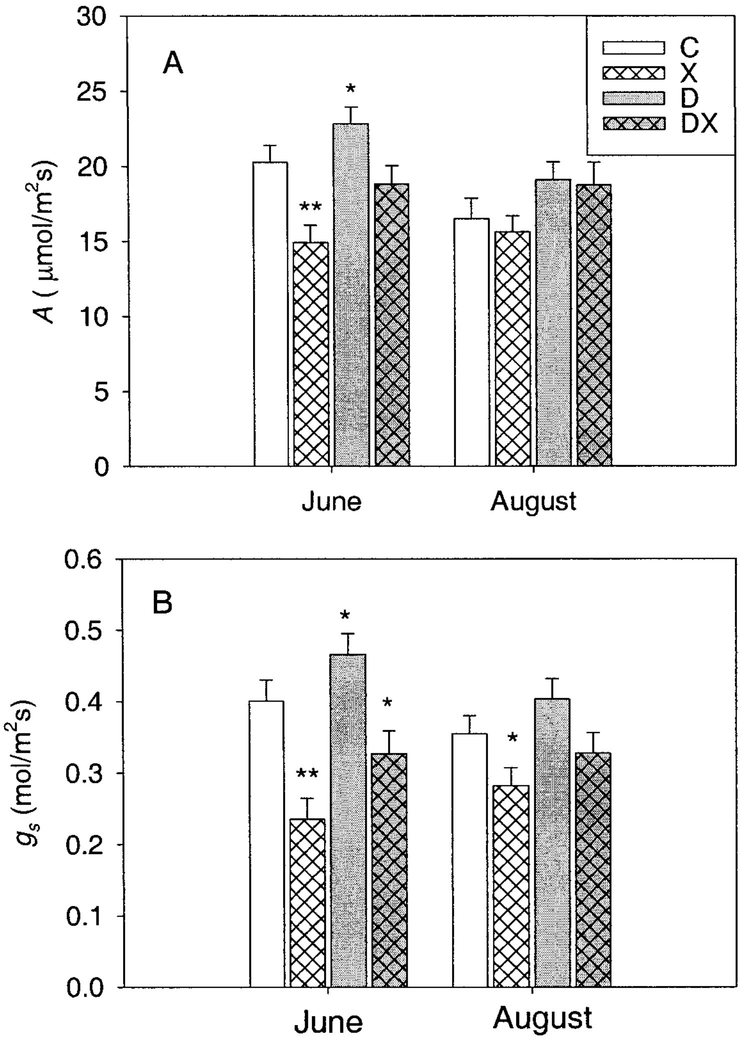


Figure 7. Midday leaf-level photosynthetic rate (*A*, panel A) and stomatal conductance (g_s, panel B) of *S. geyeriana* plants in a factorial experiment containing four plots: C = control, X = exclosed, D = dammed, and DX = dammed and exclosed. Stars denote treatments that are significantly different from control plots at the $\alpha = 0.05$ (*) and 0.001 (**) levels. Error bars = SE. n = 4.

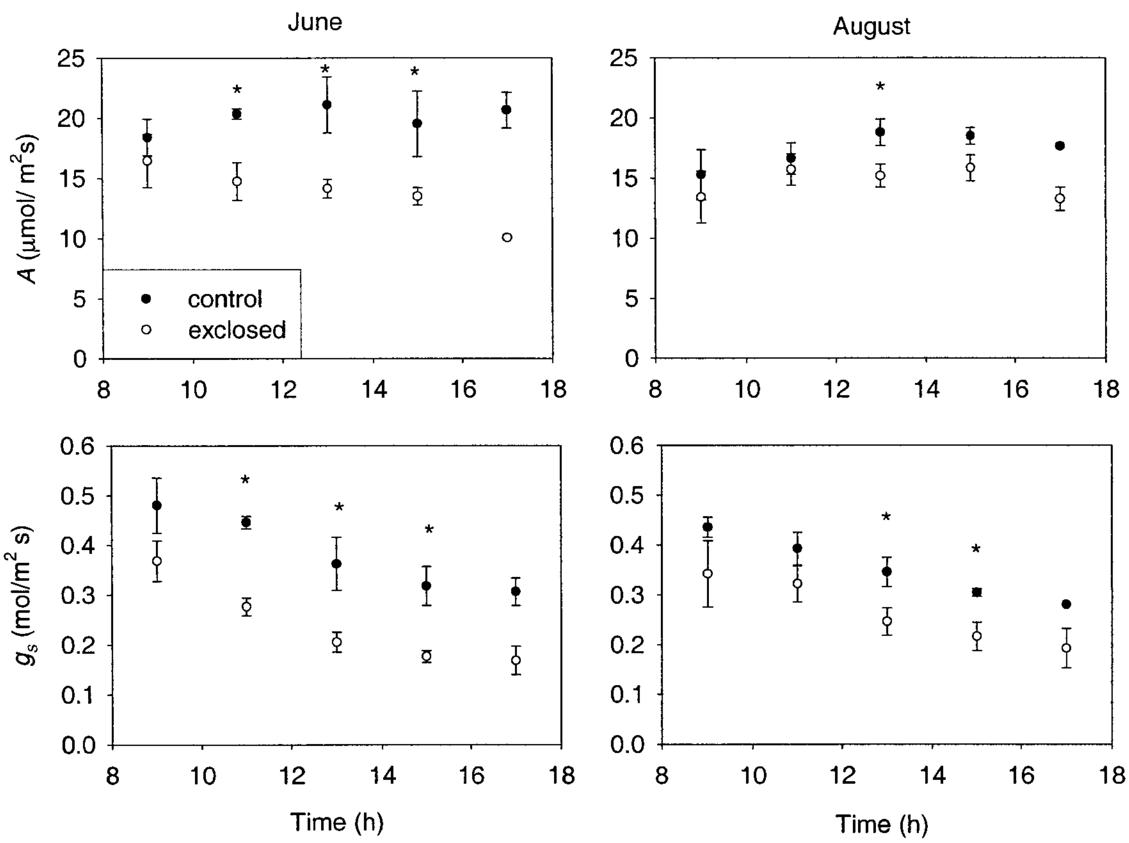
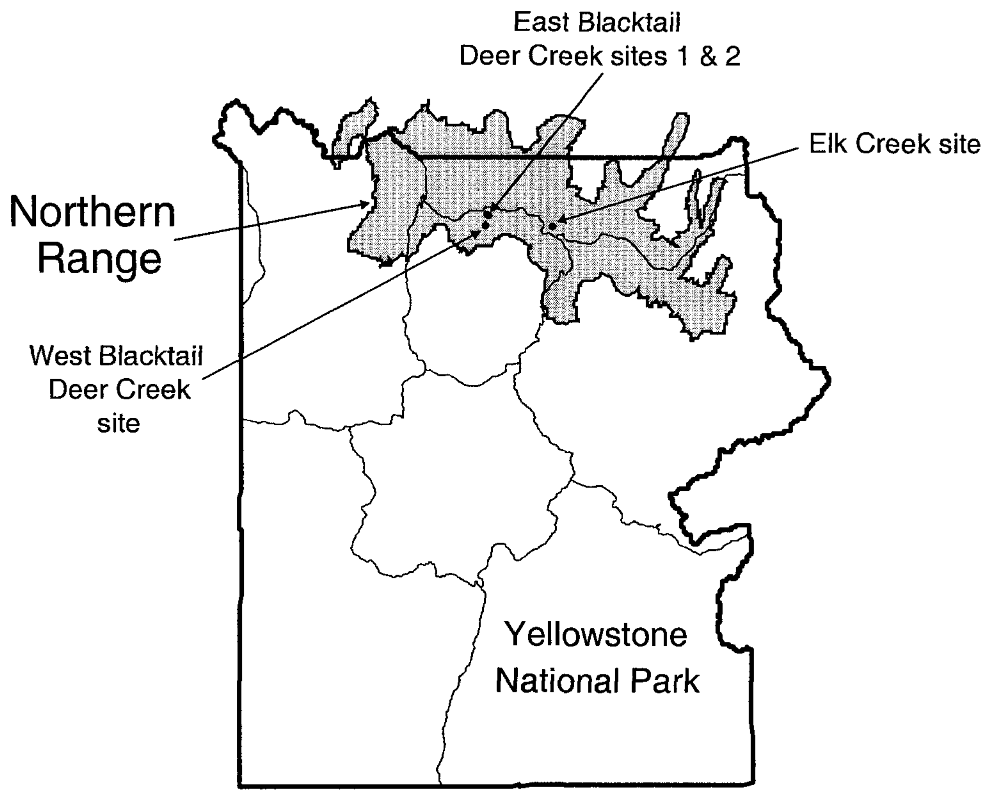
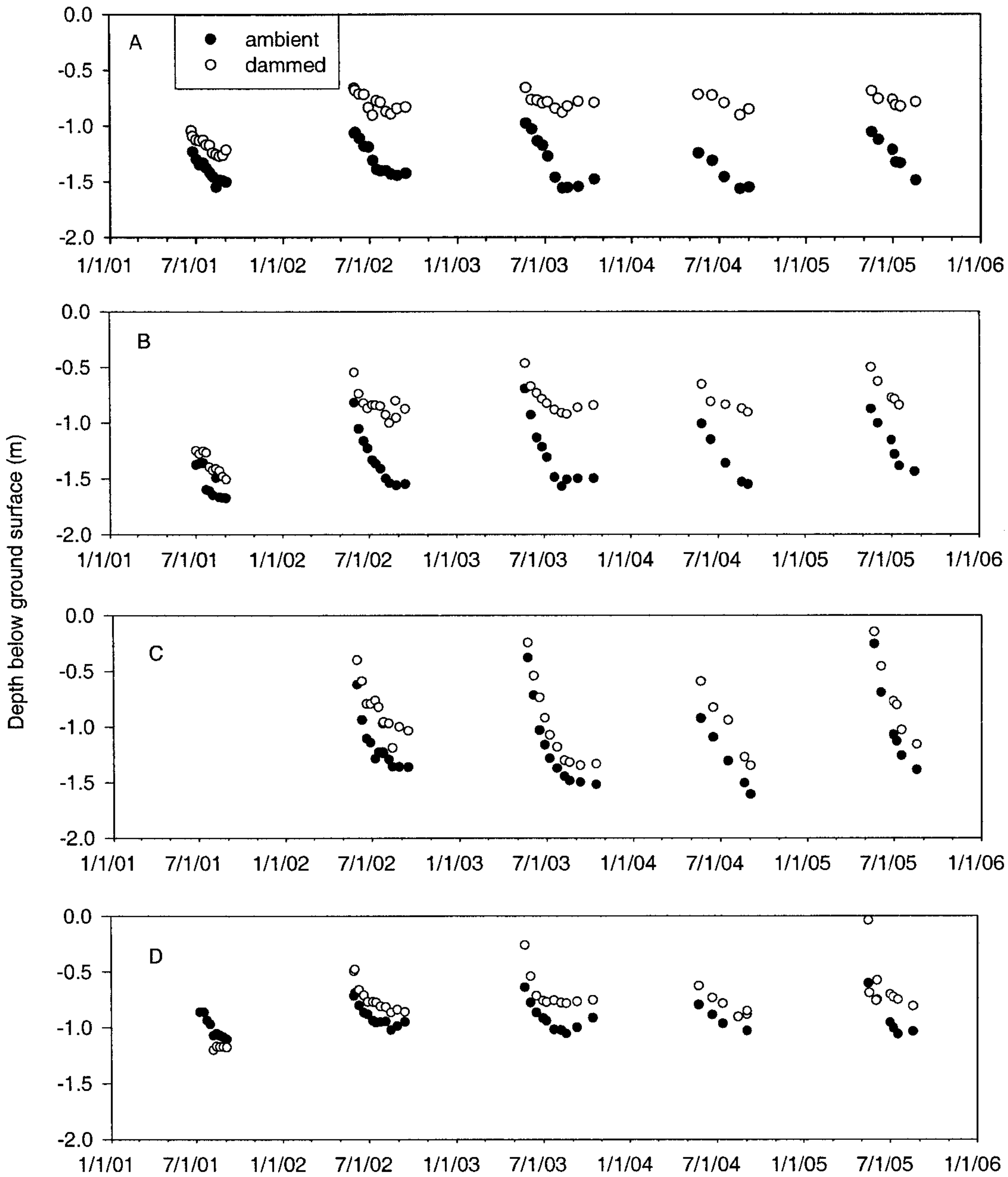


Figure 8. Diurnal trends in photosynthesis (A) and stomatal conductance (g_s) for control and exclosed *S. geyeriana*. Stars indicate significantly different means at the $\alpha = 0.05$ level. Error bars = SE. n = 4.

Appendix 1. Location of study sites in Yellowstone northern elk wintering range.



Appendix 2: Water table depths over the course of the experiment.



Water table depths over the course of the experiment in water-ambient and water-elevated plots at Elk Creek (A), Upper East Blacktail Creek (B), Lower East Blacktail Creek (C) and West Blacktail Creek (D). Each point is the average of 4-8 wells. Data from 2001 was taken before dams were installed.

Appendix 3: Regression equations used in calculating current annual growth (*CAG*).

To create an equation relating shoot length to dry weight, I sampled approximately 30 shoots of each species in each drainage each year 2002-2005. I measured the shoots in the field to the nearest cm, then dried them to a constant dry weight and weighed them with leaves. I transformed length and weight to linearize the data and achieve homogeneity of variance, then regressed the transformed variables in SAS PROC GLM. I tested for site-to-site and year-to-year differences in regressions, and found that only very marginal improvements in model fit were achieved by incorporating these differences in the shoot length/shoot mass regression. A simple model including only a parameter for shoot length outperformed more complex models in a model selection exercise.

By 2005, exclosures had caused changes in shoot lengths and I became concerned that the relationship between length and shoot dry mass might also differ by exclosure treatment. To test the extent to which this might change my estimates of CAG, I measured, collected, dried, and weighed 150 *S. geyeriana* shoots from inside and outside of exclosures in 2005. I tested for an exclosure effect on the slope of the mass/dry weight regression, and found a significant effect ($p = 0.0001$). Therefore, I applied treatment-specific shoot dry mass regressions to 2005 *S. geyeriana* shoot length data and compared these estimates with those made using a single regression. I found that using treatment-specific regressions caused estimates of CAG inside exclosures to increase by 4.8% (95% CI: 3.6, 5.8) and estimates outside exclosures to decrease by 1.3% (95% CI: 0.0, 2.4). Although the changes were significant, they were of sufficiently small magnitude that any substantial treatment effect on CAG would not be obscured by using a single regression across treatments, which would allow incorporation of regression data from all years. I applied a single regression for each species, incorporating log-transformed data from all years of the experiment, to my data.

A portion variable for shoots greater or less than 60 cm was significant for *S. geyeriana* ($p < 0.0001$) although not for *S. bebbiana* or *S. boothii*. Therefore, a stepwise regression was applied for *S. geyeriana* only. Regression parameters are summarized in Table A1. Regression fits are shown in Figure A1.

Species	portion	Intercept	Length effect	R^2
S. bebbiana	n/a	-9.3898	2.3303	0.965
S. boothii	n/a	-9.0515	2.2464	0.973
S. geyeriana	< 60 cm	-7.7272	1.8853	0.974
	> 60 cm	-10.8297	2.5664	

Table A1. Regression parameters for transformed variables. Transformation for shoot length was log (length +40). Transformation for weight was log (weight +0.45).

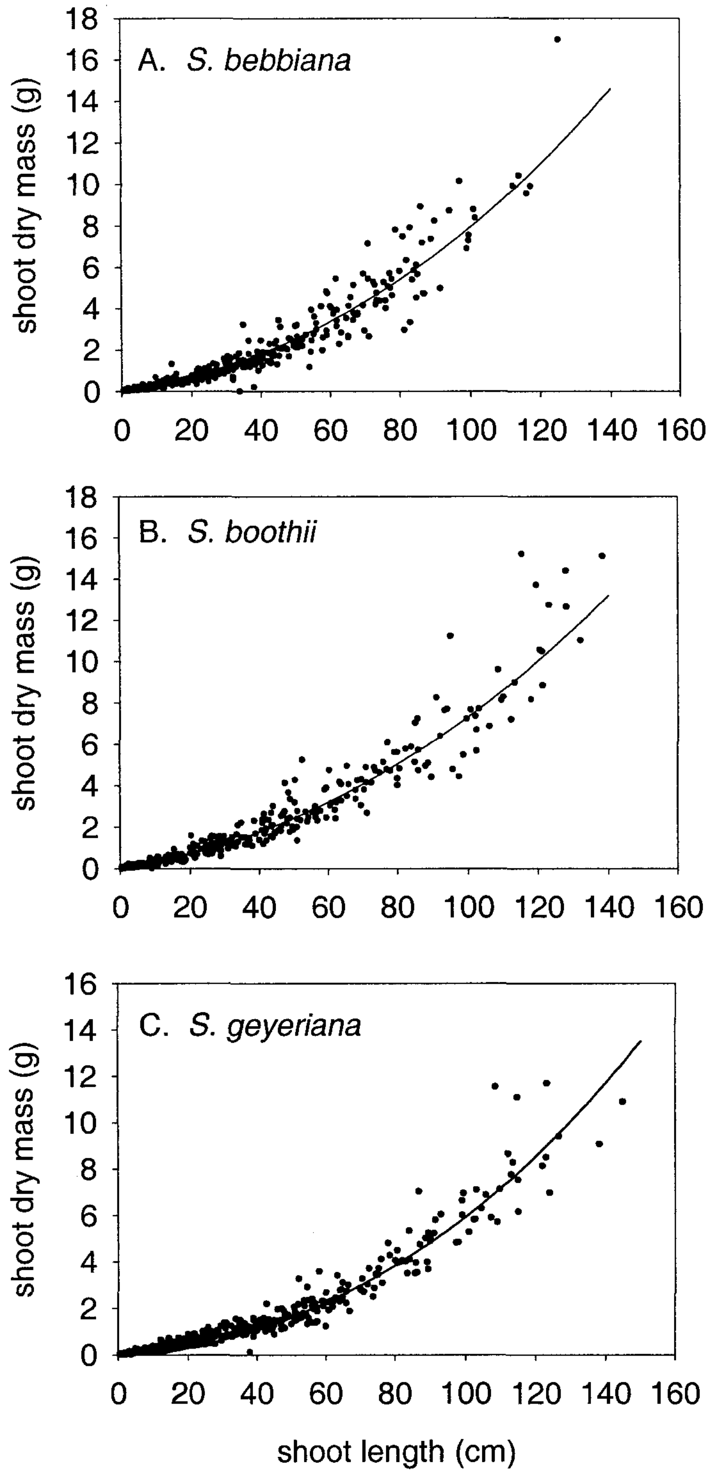
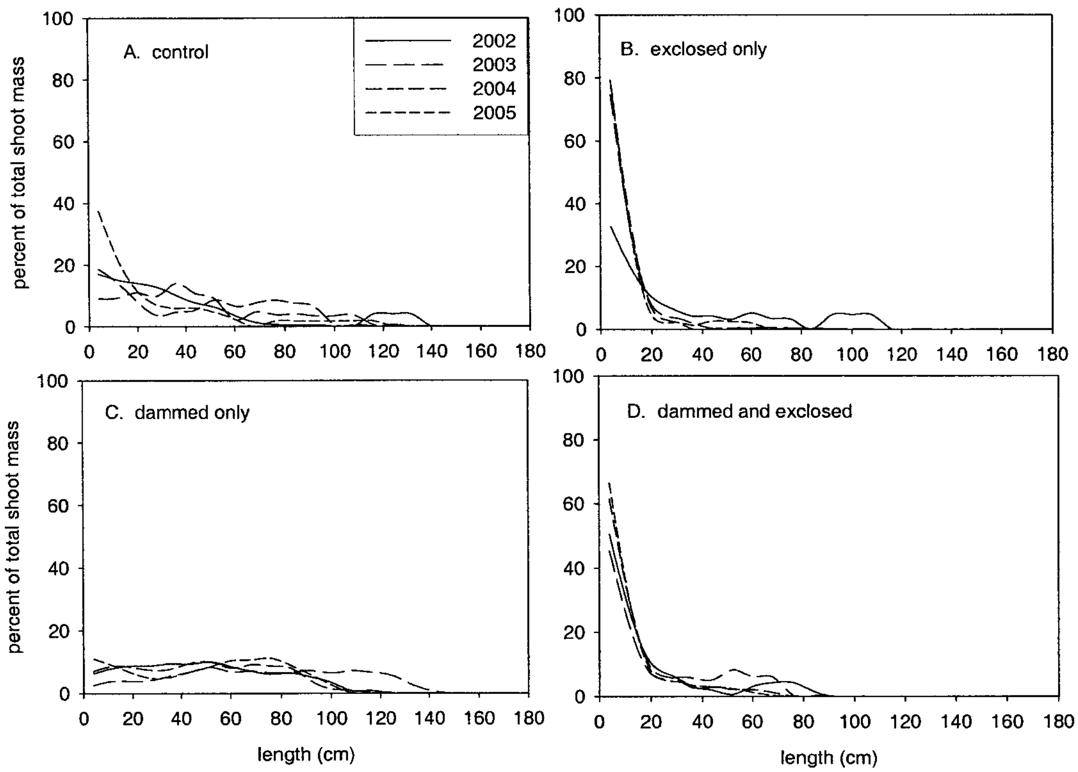


Figure A1. Shoot length/ dry mass regressions for three willow species.

Appendix 4: Table of regression parameters used in calculating log (leaf area) from shoot length measurements

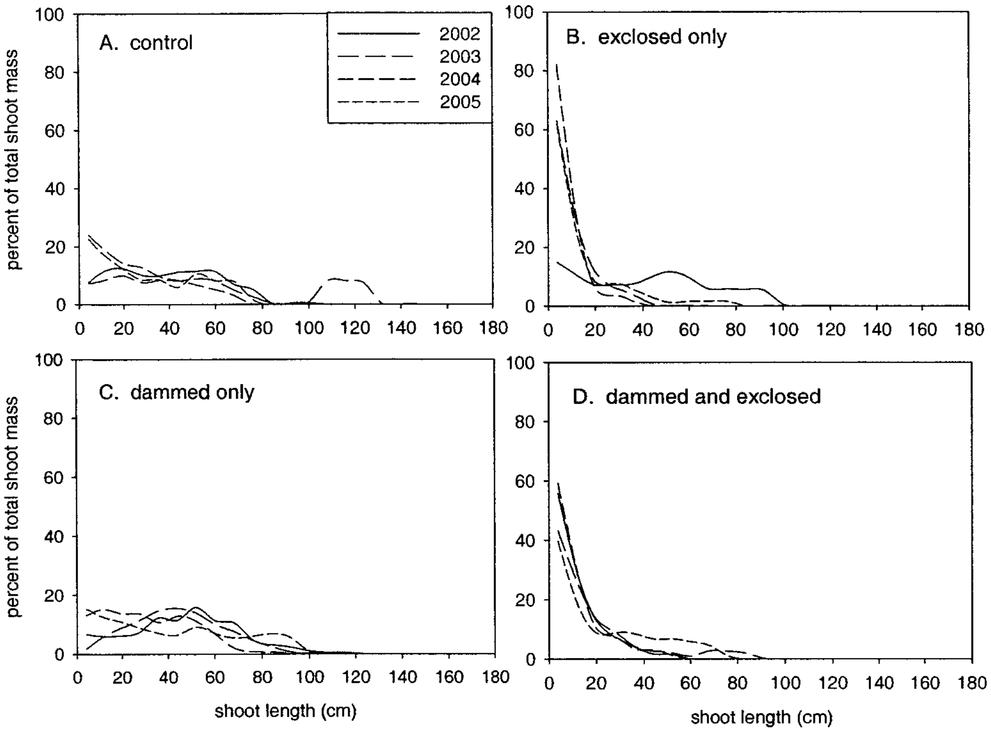
Species	treatment	Intercept	Log (shoot length)
S. geyeriana	exclosed	1.0901	0.8040
	unexclosed	0.7776	0.9670

Appendix 4: Distribution of *S. geyeriana* shoot mass by shoot length.



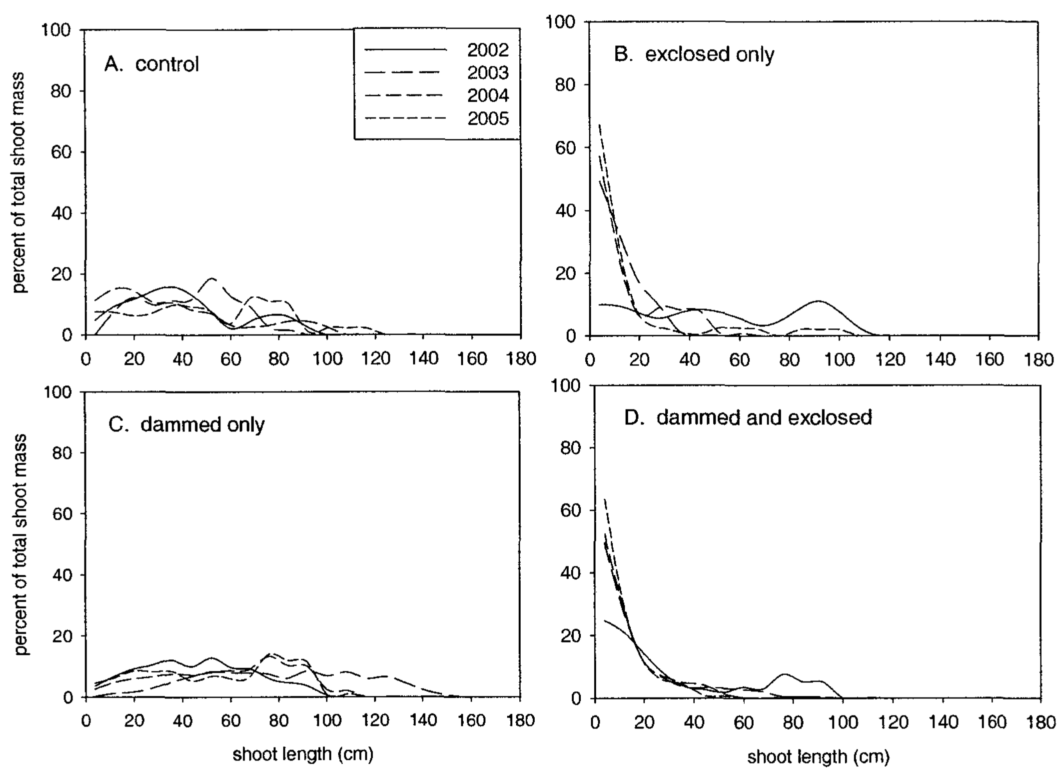
Distribution of *S. geyeriana* shoot mass by shoot length in four cells of a factorial experiment. Lines are smoothed over 3 bins of width 8 cm.

Appendix 5: Distribution of *S. bebbiana* shoot mass by shoot length.



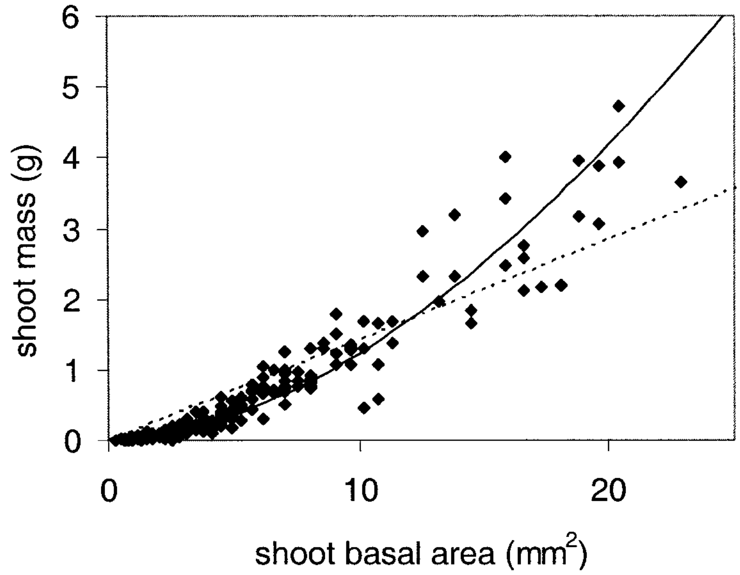
Distribution of *S. bebbiana* shoot mass by shoot length in four cells of a factorial experiment. Lines are smoothed over 3 bins of width 8 cm.

Appendix 6: Distribution of *S. boothii* shoot mass by shoot length.



Distribution of *S. boothii* shoot mass by shoot length in four cells of a factorial experiment. Lines are smoothed over 3 bins of width 8 cm.

Appendix 7: Relationship between *S. geyeriana* shoot basal area and shoot mass, showing linear and exponential fits to the data.



CHAPTER 5

SYNTHESIS

The controversy surrounding the degraded state of willows in Yellowstone's northern range highlights a common uncertainty over the causes of ecosystem degradation and the proper course of restoration. In many ecosystems, choice of management actions depends in a fundamental way on revealing the controls and feedbacks determining landscape configuration. This dissertation addresses critical steps in this challenge, starting with the development of a reproducible way to monitor a key stressor, browsing intensity, progressing to a field experiment to understand the controls over a key response, willow height, and finishing by the elucidation of a novel mechanism controlling willow responses. Each of these steps lends deeper understanding of why willows have declined, why they may remain suppressed in some areas, and where wolf restoration is likely to lead to willow recovery. By providing a deeper level of understanding, this process supports the manager in the difficult choice of what factors to mitigate for successful restoration.

Developing a reliable, sensitive measure of browse utilization first required developing a way to quantify available browse, or current annual growth. As shrubs, willows are amenable to neither to regressions based on weighing and clipping of whole plants, nor to neat allometric relationships based on trunk diameter. Furthermore, willow growth form changes in response to browsing and water availability, posing a unique difficulty to the researcher seeking a consistent protocol to quantify biomass across a wide range of environmental conditions. The solution presented here for measuring current annual growth is time-consuming, but allows both biomass and morphological changes to be tracked through time, offering insight into height and biomass responses to treatments. Comparing fall estimates of current annual growth to post-browsing estimates of remaining growth allowed for a straightforward way to assess browsing intensity. The discrepancy between this estimate and estimates by other methods demonstrates the importance of careful scaling; in order to accurately scale up measurements taken at the level of the shoot, the researcher must consider herbivore foraging preferences. By accounting for this scaling issue, I found that browsing intensity is considerably higher than previously reported for Yellowstone's northern range, lending credence to the argument that heavy elk browsing may competitively exclude beaver. I was also able to discern subtle year-to-year differences in browsing pressure, which, in conjunction with the factorial experiment, allowed me to quantify how high water table promotes willow height gain when browsing pressure is slightly reduced.

The factorial experiment also allowed me to quantify the importance of high water table to willow height gain when large herbivore browsing is eliminated entirely. I found strong evidence that willow height is limited by water availability in the absence of browsing. In areas where beaver abandonment has caused water table decline, this height is probably not tall enough to allow willows to escape the browse zone of elk or to provide the material needed by beaver to justify foraging costs. Therefore, the experiment allowed me to demonstrate the presence of a threshold in water availability beyond which the restoration of historic willow/beaver mutualism is unlikely to result from a reduction in elk browsing alone. The precise value of this threshold is an important remaining subject for research.

While height results from the factorial experiment clearly demonstrated the importance of high water table in allowing willows to grow tall, they do not satisfy the question of why willows fail to get tall without a high water table. Although the end result is most important, understanding the mechanism behind it solidifies confidence in that result. In a system where different researchers have proposed different reasons for the degraded state of riparian vegetation, including climate change, elk overbrowsing, and beaver decline, only a synthetic understanding of the mechanisms controlling willow growth and height gain can provide the confidence needed to make an informed choice of mitigation efforts. I believe I can supply that understanding. Rapid willow growth appears to depend on high turgor pressure in the uppermost buds of the plant. As a willow grows from year to year in the absence of browsing, turgor pressure in the apical buds decreases. This happens because the yearly accumulation of bud scars constricts water flow, causing turgor pressure to drop before water reaches the top of the plant. If water table is high, there will be sufficient pressure to overcome these constrictions, and turgor pressure at the top of the plant will remain adequate for cell expansion and continued growth until the plant reaches normal stature. If water table is low, pressure will be less sufficient to overcome hydraulic constrictions, turgor pressure at the top of the plant will be less adequate for cell expansion, and growth will cease before the plant reaches normal stature.

Earlier attrition in growth in water-stressed willows has important implications for restoration of willow/beaver mutualisms. Results from an agricultural study indicate that when willows are grown under high water availability, yield after three years is greater than the sum of three years' annual harvest (Kopp et al., 1997), implying that growth does not decrease until after at least three years. In willows with ambient water table in my study, decreased growth was evident after only one year of protection from browsing. Taken together, these results imply that the effect of water stress is to reduce the optimum browsing return interval. Given adequate water, willows are more productive when periodically coppiced than when harvested annually. With reduced water, willows are dependant on annual browsing in order to maintain productivity. This shift in optimum browsing interval may affect the competitive balance between elk and beaver. Water-stressed willows may provide a useable resource for elk, which may browse the same areas every year, but because productivity drops off so quickly in the absence of browsing, they are less suitable for use by beaver, which have longer return intervals to a given area and require larger standing crops to justify and supply dam-building efforts. If the growth and stature of water-stressed willows is sufficiently lessened, beaver will not recolonize, and historic beaver/willow mutualisms will not be restored.

My research indicates that the case of degraded willow communities in Yellowstone is an example of how positive feedbacks stabilize landscape configurations and confound restoration efforts. If, as I believe, the absence of wolves allowed elk to browse willow intensively and resulted in the exclusion of beaver, then the reintroduction of wolves and subsequent reduction in elk browsing constitutes removal of the original stressor that caused the shift in landscape configuration. However, in areas where productive willow historically depended on hydrologic changes brought about by beaver, a positive feedback between low water table, low willow productivity, and beaver absence appears to be stabilizing the current landscape configuration. In these areas, I recommend mitigation of the hydrologic regime through the use of temporary, artificial beaver dams for efficient restoration of the historic landscape configuration. These should raise water tables on adjacent terraces to near ground level, and should be constructed to last approximately 10 years in order to allow sufficient time for willows to grow tall under ambient browsing pressure. Such a management effort, in conjunction with reduced elk browsing following wolf reintroduction, would likely allow willow populations in areas historically occupied by beaver to grow tall, produce seed, support riparian bird populations, and promote beaver recolonization.

Reference

Kopp, R.F., Abrahamson, L.P., White, E.H., Burns, K.F., & Nowak, C.A. (1997) Cutting cycle and spacing effects on biomass production by a willow clone in New York. *Biomass & Bioenergy*, **12**, 313-319.