

Elk browsing increases aboveground growth of water-stressed willows by modifying plant architecture

Danielle B. Johnston · David J. Cooper ·
N. Thompson Hobbs

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Abstract In the northern elk wintering range of Yellowstone National Park, USA, wolf (*Canis lupus*) removal allowed elk (*Cervus elaphus*) to overbrowse riparian woody plants, leading to the exclusion of beaver (*Castor canadensis*) and a subsequent water table decline in many small stream valleys. Reduced elk browsing following wolf reintroduction may or may not facilitate willow (*Salix* sp.) recovery in these areas. To determine if the effect of elk browsing on willow interacts with that of beaver abandonment, we manipulated elk browsing and the water table in a factorial experiment. Under the condition of an ambient (low) water table, elk browsing increased shoot water potential (Ψ_s), photosynthesis per unit leaf area (A), stomatal conductance per unit leaf area (g_s), and aboveground current annual growth (CAG) by 50%. Elk browsing occurred entirely during dormancy and did not affect total plant leaf area (L). Improved water balance, photosynthetic rate, and annual aboveground productivity in browsed willows appeared to be due to morphological changes, such as increased shoot diameter and decreased branching, which typically increase plant hydraulic conductivity. An elevated

water table increased Ψ_s , A , g_s , CAG, and L , and eliminated or lessened the positive effect of browsing on CAG for most species. Because low water tables create conditions whereby high willow productivity depends on the morphological effects of annual elk browsing, removing elk browsing in areas of water table decline is unlikely to result in vigorous willow stands. As large willow standing crops are required by beaver, a positive feedback between water-stressed willow and beaver absence may preclude the reestablishment of historical conditions. In areas with low water table, willow restoration may depend on actions to promote the re-establishment of beaver in addition to reducing elk browsing.

Keywords Compensation · Herbivory · Leaf-specific conductivity · Plant hydraulic architecture · *Salix* sp.

Introduction

The restoration of ecosystems altered by human activity has emerged as a fundamental challenge for contemporary ecologists and land managers. Successful restoration demands an understanding of the feedbacks that may retard the restoration of desired conditions (Suding et al. 2004). When ecosystems are altered by the removal of top predators, changes can result from trophic feedbacks that cascade through the community (Binkley et al. 2006) as well as from indirect feedbacks operating through other consumers and the physical environment (vandeKoppel et al. 1997; Hebblewhite et al. 2005). Consequently, the restoration of ecosystems altered by predator removal may require mitigating indirect as well as direct effects.

The removal of wolves from the Northern Range of Yellowstone National Park in the early twentieth century is

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D. B. Johnston (✉)
Colorado Division of Wildlife,
711 Independent Avenue, Grand Junction, CO 81505, USA
e-mail: danielle.bilyeu@state.co.us

D. B. Johnston · N. T. Hobbs
Natural Resource Ecology Laboratory,
Colorado State University, Fort Collins, CO 80523, USA

D. J. Cooper · N. T. Hobbs
Department of Forest, Rangeland,
and Watershed Stewardship, Colorado State University,
Fort Collins, CO 80523, USA

reported to have allowed elk (*Cervus elaphus* L.) to degrade riparian willow- and cottonwood-dominated plant communities (Houston 1982; Engstrom et al. 1991; Singer et al. 1994). Following the reintroduction of the wolf in 1994, elk browsing pressure in some riparian areas diminished (Ripple and Beschta 2004), likely due to the effect of wolves on elk foraging patterns (Fortin et al. 2005). The extent to which reduced elk browsing following wolf reintroduction will restore degraded willow communities is unclear (Smith et al. 2003) because the indirect effects of wolf absence may prevent or delay willow recovery in some areas of Yellowstone (Bilyeu et al. 2007b). However, the absence of the wolf has led to the competitive exclusion of beaver (*Castor canadensis* Kuhl; Hebblewhite et al. 2005) as intense elk browsing in riparian areas prevents the accumulation of the large standing crops required to support persistent beaver populations (Baker et al. 2005). Beaver activity was common in Yellowstone's Northern Range in the early 1900s (Warren 1926), greatly reduced by 1955 (Jonas 1955), and entirely absent by 1988 (Consolo Murphy and Hanson 1990). Decades of diminished beaver activity has allowed the erosion of fine-grained sediments that had accumulated over several millennia on the floodplains historically influenced by beaver dams (Wolf et al. 2007). Thus, erosion of the stream channel, and a resulting decline in water table on adjacent floodplain terraces, may be regarded as an indirect effect of the removal of wolves from the system (Wolf et al. 2007).

Following the re-introduction of the wolf, beaver have reoccupied large river systems in Yellowstone, such as Slough Creek and the Lamar River, where stream hydrologic regimes have remained unchanged because the streams are too wide for beavers to dam. However, beaver have not returned to most of their former habitat where their dams historically had a large influence on floodplain processes. Experimental results have shown that low water tables in areas of former beaver dam-building activity limit the rate of willow height gain both in the absence of browsing and under ambient elk browsing pressure (Bilyeu et al. 2007b). Because beaver in Yellowstone depend on willow (Smith et al. 1996), water stress suppression of willows in areas with low water tables may explain the delay in beaver re-establishment. Stream erosion and lowered water tables appear to have retarded the redevelopment of the beaver/willow mutualism that once supported vigorous willow communities in these areas, a mutualism consisting of a positive feedback between high water table, rapid willow height gain, and beaver presence.

Although the effects of the water table on the rate of willow height gain is an important driver of current ecosystem dynamics (Bilyeu et al. 2007b), a mechanistic understanding of the controls over willow productivity is required to determine the likelihood of long-term ecosystem recovery.

In particular, an understanding of how the water table and winter elk browsing interact to influence willow water stress and productivity is needed (Committee on Ungulate Management in Yellowstone National Park 2002). Prior research has shown that winter browsing can reduce water stress in willow (Singer et al. 1994; Alstad et al. 1999) and stimulate willow productivity (Kindschy 1985; Peinetti et al. 2001), but the mechanism by which this occurs, as well as the conditions under which it occurs, is unknown.

In this study, we analyzed the effect of winter elk browsing on willow water relations and aboveground productivity under alternative hydrologic conditions representing the presence versus the absence of beaver. We manipulated elk herbivory and water table depth in a factorial field experiment and assessed willow physiological and morphological responses to determine the mechanisms of treatment effects on productivity. We assessed the evidence for one previously suggested mechanism for reduced water stress in browsed willows – that of leaf area reduction, which could improve the root/shoot ratio for remaining transpiring tissues (Singer et al. 1994; Alstad et al. 1999). We also assessed evidence for a novel mechanism by which browsing-induced changes in plant hydraulic architecture promote higher leaf water potential. In this paper we address the following questions: (1) does browsing alleviate water stress and increase the photosynthetic rate and stomatal conductance of willows and, if so, does the effect depend on the depth of the water table? (2) does winter browsing reduce leaf area during the subsequent summer? (3) does browsing cause changes in plant hydraulic architecture, such as increased shoot diameter or reduced number and age of branch junctions, which are likely to increase leaf-specific conductivity (Zimmermann 1978; Ewers and Zimmerman 1984; Tyree and Ewers 1991; Joyce and Steiner 1995)? (4) do typical plant hydraulic architecture relationships, such as reduced conductivity in shoots of smaller diameter, hold true for willow? (5) does browsing increase aboveground productivity and, if so, does the effect depend on the depth of the water table?

Methods

Study area

We worked in the Northern Range of Yellowstone National Park, USA, a 100,000-ha area used intensively by Yellowstone's largest elk herd during the winter (Houston 1982). This area ranges from 1925 to 2000 m a.s.l. and receives 260 mm of precipitation annually, 45–65% of which falls during the growing season (Despain 1987). Riparian floodplains cover approximately 4% of the area and are dominated by the willow species *Salix geyeriana* Anderss, *S.*

bebbiana Sang, *S. pseudomonticola* Ball, *S. boothii* Dorn, *S. wolfii* Bebb, and *S. exigua* Nutt. (Houston 1982), with an understory of herbaceous plants. Our study sites were located on terraces adjacent to third- or fourth-order streams that had shown a recent decline in local water table, as evidenced by stream downcutting through previously inundated, gleyed and mottled soils and/or historical records of previous beaver ponding (Warren 1926; Jonas 1955). Ambient water tables in our study plots were less than 0.5 m below the surface in the spring, dropping to 1–2 m in late summer. The willows in our study plots at the start of the experiment were short in stature, (<1 m) with many browsed shoot stubs that had died back to the bud scar, indicating a history of heavy browsing (Keigley and Frisina 1998).

Experimental design and sampling

Our study was a randomized complete block with a factorial layout ($n = 4$). Treatments included two levels of herbivory (large herbivore browsing present and absent) imposed by the exclosures, crossed with two levels of water table (ambient and elevated) imposed by simulated beaver dams (for locations and construction details, see Bilyeu et al. 2007b). Exclosures successfully eliminated browsing by large herbivores. Browsing intensity outside of the exclosures, measured by the biomass comparison method (Bilyeu et al. 2007a), averaged 66% of current annual growth (CAG) removed from 2003 to 2005 (Bilyeu et al. 2007b). Dams elevated the water table depth by an average of 0.37 m during the growing season (Table 1), and an observed pattern of attenuated water table decline late in the growing season (Bilyeu et al. 2007b) resembled that of natural beaver dams in the Colorado Rocky Mountains (Westbrook et al. 2006).

Because different willow species respond differently to water stress (Wikberg and Ogren 2004) and herbivory (Stolter et al. 2005), we assessed species-specific responses

to the treatments for the three dominant willows at our sites: *S. bebbiana* ($n = 3$), *S. boothii* ($n = 3$), and *S. geyeriana* ($n = 4$). *Salix bebbiana* tolerates slightly drier conditions than *S. geyeriana*, and *S. geyeriana* is slightly more drought tolerant than *S. boothii*, with the latter only found in areas with water tables near the soil surface (Brunsfield and Johnson 1985). All three species are commonly consumed by beaver and elk.

For each species in each plot, seven plants, defined as a spatially discrete group of rooted stems, were selected using a spatially stratified, systematic protocol (Bilyeu et al. 2007b) and permanently tagged in August of 2001. For each selected plant, 10% (but not fewer than three) of the rooted stems were selected for permanent marking using a stratified random sampling procedure (Bilyeu et al. 2007b). Additional stems were tagged each year to ensure that the average age of the tagged stems did not increase with time (Bilyeu et al. 2007b). On each tagged stem in August of each year, all current-year shoots were identified. Current-year shoots of willows are easily identifiable because they rarely branch, have a single, basal bud scar, and bear all of the leaves. Current-year shoots at our study sites ranged in length from less than 1 cm to over 100 cm and numbered from one to over 1000 per stem. We selected a subset of shoots on each stem to measure using a systematic sampling protocol, which simultaneously provided a count of shoots (Bilyeu et al. 2007a). At least six or 10% of shoots, whichever was greater, were measured on each stem. We visually estimated the length of the selected shoots to the nearest centimeter and verified these estimates against shoots of known length to ensure at least 90% accuracy. Approximately 10,000 shoot length measurements were made each year.

Plant material for characterizing willow shoot hydraulic parameters was collected in August of 2003 from areas within 1.5 km of the study plots. We sampled only shoots larger than 3.4 mm in basal diameter ($n = 5$ per species) due

Table 1 Summary of ecological conditions at experimental sites

Ecological conditions ^a	2001	2002	2003	2004	2005
Browsing intensity (percentage 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 ^b	0.36 ± 0.08	0.36 ± 0.09	0.40 ± 0.11	0.37 ± 0.06

CAG, Current annual growth

^a 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 are summed from October through to May, and rain data are summed from June through to August. The depths of the water table are averaged over all undammed plots ($n = 8$) from May through September, and dam effect is the average difference between dammed and undammed plots in those months

^b Dams were constructed in the fall of 2001; therefore, data from 2001 should be regarded as pre-treatment data

to methodological constraints in measuring hydraulic conductivity.

Physiology and morphology measurements

We measured the water potential of freshly cut current-year shoots (Ψ_s) of five plants per plot using a Scholander-type pressure chamber (PMS instruments, Corvallis, OR) at mid-day (1200–1400 hours) under sunny conditions early in the growing season (June 25–July 7) and late in the growing season (August 10–25). *Salix geyeriana* was measured in 2003–2005, and *S. bebbiana* was measured in 2003 only. Data were averaged over each plot for each sample period and each year for each species.

We measured stomatal conductance (g_s) and photosynthesis (A) per unit leaf area in *S. geyeriana*, the most abundant species at our study sites, using a Li-6400 Portable Photosynthesis system in 2005 (Li-Cor instruments, Lincoln, NE). Measurements were made under sunny conditions on two sunlit, fully expanded leaves on five plants per study plot. Midday measurements were made between 1100 and 1400 hours on all study plots in the last week of June and third week of August, and values were averaged over each plot ($n = 4$). Vapor pressure deficit (VPD) was calculated using simultaneous measurements of leaf temperature with the Li-6400 and 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 2-h intervals between 800 and 1800 hours, and the values were averaged over each plot for each time interval ($n = 4$).

We quantified treatment effects on the average area of individual leaves (LS, cm²), leaf area per unit shoot basal area (La/Sa, cm² mm⁻²), and average leaf area per plant (L, m²) for *S. geyeriana* in 2005. This required finding the specific leaf area (SLA) and ensuring that browsing did not affect it. We found the area and dry mass of 60 *S. geyeriana* leaves taken from inside and outside of the exclosures and tested for an exclosure effect on the slope of the relationship between leaf area and leaf weight using SAS PROC GLM ($n = 60$; SAS/STAT software, ver. 9.1 of the SAS System for Windows 2002–2003; SAS Institute, Cary, NC). As no effect of exclosures was found ($P = 0.49$), we pooled data and created one regression ($r^2 = 0.98$) with a slope of 135.24 ± 1.3 cm² g⁻¹, which we used as SLA. We next sampled ten *S. geyeriana* shoots per plot in August of 2005 and measured shoot length, shoot basal diameter, and number of leaves. We dried and weighed the shoots and leaves separately and calculated leaf area for each sample by multiplying leaf weight by SLA. Average leaf size, LS, was calculated by dividing leaf area by the number of leaves for each shoot sample, and La/Sa was calculated by dividing leaf area by the shoot cross-sectional basal area. We found

leaf area per plant, L, by relating leaf area relationships to the shoot length measurements taken on tagged stems. We created a regression for leaf area in terms of shoot length, which we found differed for shoots inside ($r^2 = 0.92$) and outside ($r^2 = 0.94$) the exclosures. We applied treatment-specific regressions to each shoot length measurement to find the leaf area per shoot, found the average leaf area per shoot for each stem, then multiplied this average by the sampling ratio for the stem to find stem-level leaf area. Total plant leaf area, L, was calculated as the average leaf area of tagged stems multiplied by the number of live stems on each plant.

We determined the average number of branch and age junctions between leaf and soil (NumBranch) for *S. geyeriana* and *S. bebbiana* in 2004 for three randomly chosen stems per plot. We randomly choose three leaves per stem and counted the number of terminal bud scar scales and branch points between the leaf and ground level. We averaged NumBranch over each plot.

We quantified treatment effects on shoot diameter by determining the diameter of the largest shoot on each tagged stem (D_{\max} , mm) in the period 2003–2005. Maximum shoot diameter was chosen instead of average shoot diameter because it is less affected than the average by the number of small, temporary shoots on the stem. Because browsing reduces the number of competing growing points in woody plants, it usually reduces the number of shoots per stem (Rooke et al. 2004). Unbrowsed willows contain a larger number of very small shoots, which may be shed during dormancy (Raven 1992). We were primarily interested in treatment effects on the diameter of shoots that would be likely to be retained through winter and subsequently supply water to new shoots the following growing season. We therefore focused on the largest, usually apical, shoot on each stem. Values for D_{\max} were averaged for each plot.

Willow shoot hydraulic properties

We determined relationships among the shoot hydraulic properties of our study species by constructing vulnerability curves in August of 2003 in the laboratory. Sampled shoots were sealed in Parafilm, refrigerated, and transported to the laboratory within 24 h. The shoots were recut under water, attached to a tubing system, and flushed with deionized, filtered water for 20 min at 0.1 MPa 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 and Ewers 1991). Shoots were subjected to progressively decreasing xylem potentials using the centrifugation method (Alder et al. 1997). Percentage loss in 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 versus potential, and we determined the potential causing a 50% loss of conductivity (p_{50}) by fitting a Weibull function to the curve for each shoot by minimizing the sums of squared errors 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 SAS PROC GLM. For each shoot, we calculated area-specific conductivity (K_s), which is a measure of xylem porosity, as K_{\max} divided by shoot basal cross-sectional area. We regressed shoot basal cross-sectional area against K_s to determine the effect of shoot size on conducting capacity ($n = 14$, species pooled). We also regressed shoot area against p_{50} to quantify the effect of shoot size on xylem vulnerability ($n = 14$, species pooled). To test for a tradeoff between increased resistance to cavitation and high hydraulic conductance when water is not limiting (Zimmermann 1983; Tyree et al. 1994; Alder et al. 1997), we regressed K_s against p_{50} ($n = 14$, species pooled).

Aboveground productivity

To estimate the current annual growth of new shoots, including leaves, we applied a regression between length and dry mass (r^2 values: *S. bebbiana* 0.97, $n = 297$; *S. boothii* 0.97, $n = 279$; *S. geeyeriana* 0.97, $n = 392$) to each measured shoot, averaged these values for each stem, and then multiplied these by the count of shoots on the stem. Plant-level values were calculated as the average current annual growth of tagged stems multiplied by the number of live stems on each plant. Average plant-level current annual growth was multiplied by the total count of plants in each plot and then divided by plot area to find current annual growth per plot (CAG; g/m^2). There was large plot-to-plot variability in CAG prior to treatment installation. Therefore, we normalized CAG data before analysis by calculating the percentage change in CAG pre- and post-treatment, and multiplying percentage change +1 by the average pre-treatment CAG value for each species. We determined treatment effects on CAG of shoots 3 cm in length or less, those greater than 3 cm but less than 16 cm, and those greater than 16 cm by summing the masses of shoots on tagged stems in each length category. We divided the mass of each category by the total mass of shoots on tagged stems to determine the proportion of total shoot mass attributable to each category.

Statistics

We used analysis of variance for a randomized complete block experiment with a factorial layout to analyze responses to treatments (Ψ_s , A, g_s LS, La/Sa, L, Num-

Branch, D_{\max} CAG) 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 and/or months were analyzed using a repeated measures analysis of variance with a compound symmetry covariance structure, as the covariance parameter estimate for an autoregressive covariance structure with a lag of 1 was found to be close to zero for all species and responses, except for D_{\max} , where the autoregressive parameter was retained. Year, month, year-by-treatment interaction, and month-by-treatment interaction were included as potential fixed effects in addition to treatment effects. For midday A and g_s , VPD was also included as a potential fixed effect. In calculating the effect sizes of treatments, interactions were dropped from models when non-significant at the $\alpha = 0.05$ level. We report results as estimates of effect sizes (ES) and 95% confidence intervals produced from ESTIMATE statements in SAS PROC MIXED. Confidence intervals that do not overlap zero indicate significant effects at the $\alpha = 0.05$ level.

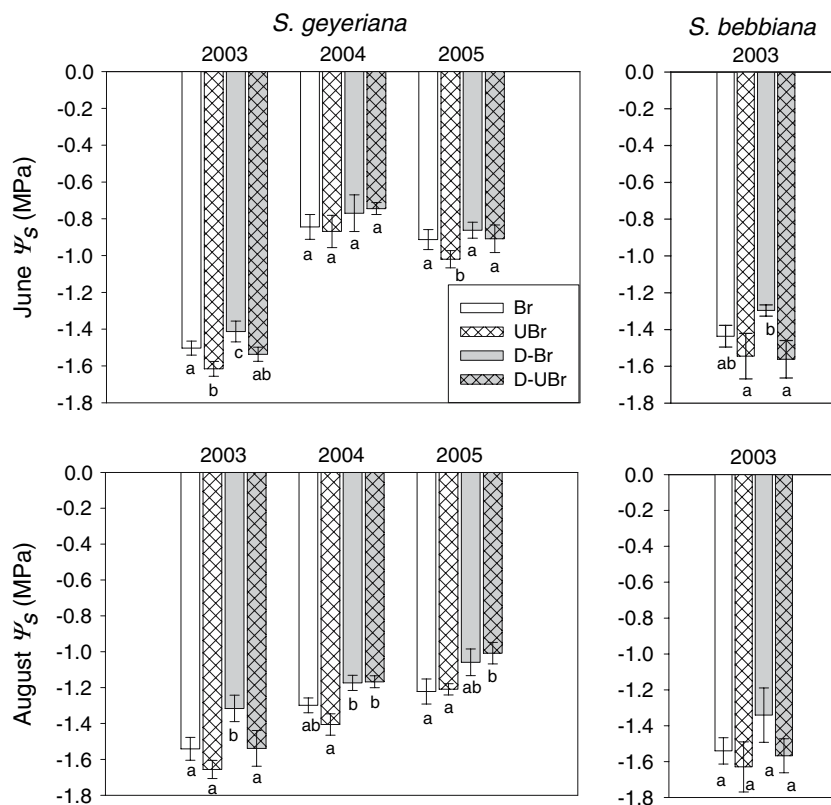
Results

Physiology and morphology measurements

Midday Ψ_s of *S. bebbiana* was higher in browsed plots than in unbrowsed ones during 2003 (browsing ES 0.18 ± 0.13 MPa; Fig. 1), indicating that winter browsing reduced water stress. There was no effect of month on Ψ_s for *S. bebbiana* in 2003 ($P = 0.41$), nor was there a significant effect of the dams ($P = 0.13$). Similarly, browsing reduced water stress in *S. geeyeriana*, (browsing ES = 0.07 ± 0.4 MPa), but the magnitude of this reduction depended on year (year \times exclosure interaction $P = 0.06$; Fig. 1). A significant main effect of year ($P < 0.0001$) was attributable to a lower Ψ_s in 2003 than in subsequent years (year ES in 2003 vs. average of 2004 and 2005 = 0.48 ± 0.05 MPa), and browsing had a larger effect in 2003 than in later years (browsing ES in 2003 vs. average of 2004 and 2005 = 0.11 ± 0.09 MPa). The dam treatment also reduced stress in *S. geeyeriana* (dam ES = 0.13 ± 0.04 MPa). The effect of dams did not depend on year ($P = 0.95$), but was likely larger in August than in June (dam \times season ES = 0.09 ± 0.09 MPa). There was no interaction between dam treatment and browsing treatment for *S. geeyeriana* ($P = 0.70$).

Midday A of *S. geeyeriana* was higher in browsed than unbrowsed plots in June (browsing ES = $5.1 \pm 1.8 \mu\text{mol m}^{-2} \text{s}^{-1}$) and likely also higher in August (browsing ES = $1.8 \pm 1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig. 2a). The dam treatment also increased A in both June (dam ES = 3.1 ± 1.8

Fig. 1 Midday leaf water potential (ψ_s) in June and August for *Salix geyeriana* in 2003–2005 and *S. bebbiana* in 2003 in a factorial experiment with four treatments: *Br* browsed, *Ubr* unbrowsed, *D-Br* dammed and browsed, *D-Ubr* dammed and unbrowsed ($n = 4$). Bars not sharing letters indicate significantly different means within a sample period ($\alpha = 0.05$). Error bars Standard error



$\mu\text{mol m}^{-2} \text{s}^{-1}$) and August (dam ES = 2.2 ± 2.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Fig. 2a). Midday *S. geyeriana* g_s was higher in browsed than unbrowsed plots in both June (browsing ES = 0.15 ± 0.05 $\text{mol m}^{-2} \text{s}^{-1}$) and August (browsing ES = 0.07 ± 0.05 $\text{mol m}^{-2} \text{s}^{-1}$; Fig. 2b). The dam treatment also increased g_s in both June (dam ES = 0.08 ± 0.05 $\text{mol m}^{-2} \text{s}^{-1}$) and August (dam ES = 0.05 ± 0.04 $\text{mol m}^{-2} \text{s}^{-1}$; Fig. 2b). There was no interaction between browsing treatment and dam treatment on either A or g_s , and there was no effect of VPD on midday A or g_s ; VPD was fairly constant during the midday time interval within a measurement period. Photosynthetic rate per leaf area (A) was higher in browsed than unbrowsed plots between 1100 and 1500 hours in June and at 1300 hours only in August ($P < 0.05$; Fig. 3), while g_s was higher in browsed than unbrowsed plots between 1100 and 1500 hours in June and between 1300 and 1500 hours in August ($P < 0.05$; Fig. 3).

Salix geyeriana LS was larger in browsed than unbrowsed plots (browsing ES = 0.7 ± 0.4 cm^2) and larger in plots with than without the dam treatment (dam ES = 0.8 ± 0.4 cm^2 ; Fig. 4). There was no interaction between treatments on LS ($P = 0.54$). There was no effect of browsing on L for *S. geyeriana* ($P = 0.43$), implying that unbrowsed plants compensate for smaller leaf size by increasing leaf number (Fig. 4). Average leaf area per plant (L) was higher in plots with the water table treatment (dam ES = 1.3 ± 1.2 m^2), showing an increase of 58% (Fig. 4).

There was no interaction between dam treatment and browsing treatment on L ($P = 0.38$). There was also no effect of browsing treatment, dam treatment, or their interaction on La/Sa, the ratio of *S. geyeriana* leaf area to sapwood area, for individual shoots ($P > 0.15$).

The NumBranch was 76% lower in browsed than unbrowsed plots for *S. bebbiana* (browsing ES = 1.9 ± 1.5) and 68% lower in browsed than unbrowsed plots for *S. geyeriana* (browsing ES = 1.5 ± 1.1 ; Fig. 5). There was no effect of the dams on NumBranch nor any interaction between treatments for either species ($P > 0.08$).

D_{max} was 60% larger in browsed than unbrowsed plots for *S. boothii* (browsing ES = 1.6 ± 0.8 mm) and 30% larger in browsed than unbrowsed plots for *S. geyeriana* (browsing ES = 1.0 ± 0.4 mm; Fig. 6). The D_{max} was higher in plots with the water table treatment for *S. geyeriana* (dam ES = 0.7 ± 0.4 mm; Fig. 6). Treatment effects on *S. bebbiana* were non-significant ($P > 0.17$). There was no interaction between dam treatment and browsing treatment on D_{max} nor interactions between treatments and year for any species.

Willow shoot hydraulic properties

There were no differences by species in terms of PLC at any of the measured xylem potentials ($P > 0.27$; Fig. 7a); therefore, we pooled data over species for subsequent analysis. Our vulnerability curves reveal that shoots of these willow

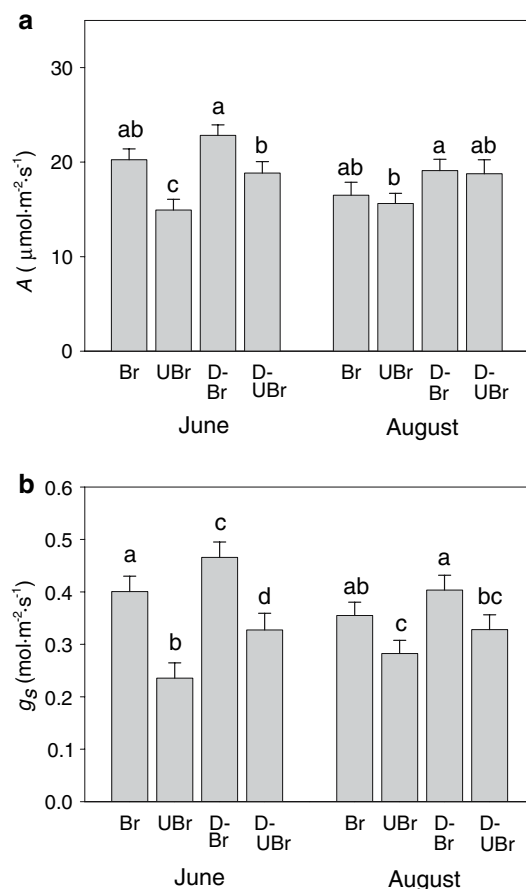


Fig. 2 Midday leaf-level photosynthetic rate (A ; **a**) and stomatal conductance (g_s ; **b**) of *S. geyeriana* plants in 2005 in a factorial experiment with four treatments: *Br* browsed, *UBr* unbrowsed, *D-Br* dammed and browsed, *D-UBr* dammed and unbrowsed ($n = 4$). Bars not sharing letters indicate significantly different means within a sample period ($\alpha = 0.05$). Error bars SE

species are vulnerable to cavitation at a relatively low Ψ_s , reaching a 50% loss of conductivity at 1.85 ± 0.28 MPa. Water potential incurring a 50% loss of conductivity (p_{50}) was inversely correlated with K_s , indicating a tradeoff between vulnerability and conducting capacity ($r^2 = 0.61$, $P = 0.001$; Fig. 7b). Even though measuring hydraulic conductivity necessitated using the largest shoots available and the range of shoot sizes was therefore narrow, we observed a significant increase in p_{50} with increasing shoot cross-sectional area ($r^2 = 0.27$, $P = 0.05$), indicating that smaller shoots are less vulnerable to cavitation. There was also a likely correlation between cross-sectional area and K_s ($r^2 = 0.25$, $P = 0.07$), indicating that shoots smaller in diameter are less porous to water flow on a per-area basis.

Aboveground productivity

There was a significant interaction between treatments on CAG of *S. bebbiana* ($P = 0.004$). The CAG of browsed plots was higher than that of unbrowsed plots in the

absence of the water table treatment ($ES = 5.9 \pm 3.4$ g/m²), but there was no effect of browsing in plots with the water table treatment ($P = 0.49$; Fig. 8a). While CAG was higher in plots with the water table treatment in the absence of browsing ($ES = 7.9 \pm 3.4$ g/m²), the water table treatment had no effect on CAG in browsed plots ($P = 0.63$). Browsing increased CAG mainly by increasing the productivity of shoots longer than 16 cm (browsing ES on long shoots = 4.5 ± 1.0 g/m²; Fig. 8a). Similarly, the increased productivity of long shoots contributed to the positive effect of the water table treatment on productivity (dam ES on long shoots = 2.6 ± 1.1 g/m², Fig. 8a). For *S. bebbiana*, a significant interaction between dam treatment and year ($P = 0.02$) was due to the higher productivity in dammed plots in 2004 and 2005 relative to 2002 and 2003 (dam ES difference for 2004 and 2005 vs. 2002 and 2003: 7.0 ± 4.8 g/m²; Fig. 8a).

For *S. boothii* and *S. geyeriana*, there was no significant interaction between dam treatment and browsing treatment on total CAG ($P > 0.18$). The CAG was higher in browsed than unbrowsed plots for *S. boothii* (browsing ES = 2.9 ± 1.8 g/m²) and *S. geyeriana* (browsing ES = 8.5 ± 6.0 g/m²; Fig. 8b, c). For both species, increased productivity of long shoots accounted for a large portion of the positive effects of browsing and water table elevation on productivity ($P < 0.0001$, Fig. 8b, c). A significant interaction between browsing treatment and year for *S. geyeriana* ($P = 0.001$) was due to a larger effect of browsing treatment on large-shoot productivity in 2003 than in other years (browsing ES on long shoots 03 vs. other years = 8.3 ± 4.4 g/m²; Fig. 8c).

The productivity of shoots less 3 cm in length was higher in the absence of browsing for all species ($P < 0.0001$; Fig. 8a–c).

Discussion

The elevated water table increased CAG of all three of the willow species studied, indicating that aboveground willow productivity in our study areas was water-limited. Browsing increased the CAG of all study species in the absence of the water table treatment; therefore, reduced elk browsing may exacerbate the negative effects of a low water table on aboveground willow productivity.

Similar to our Yellowstone findings, Alstad et al. (1999) found that browsing reduced water stress in *S. monticola* in the Colorado Rocky Mountains. However, contrary to Alstad's suggestion that this effect was caused by reduced leaf area, and similar to Peinetti's et al. (2001) findings for this same species, we found that winter browsing had no effect on whole-plant leaf area the following growing season. Our data support an alternative, novel mechanism by which

Fig. 3 Diurnal trends in photosynthesis (A) and stomatal conductance (g_s) for control and exclosed *S. geyeriana* with ambient water table ($n = 4$). Stars indicate significantly different means at the $\alpha = 0.05$ level. Error bars SE

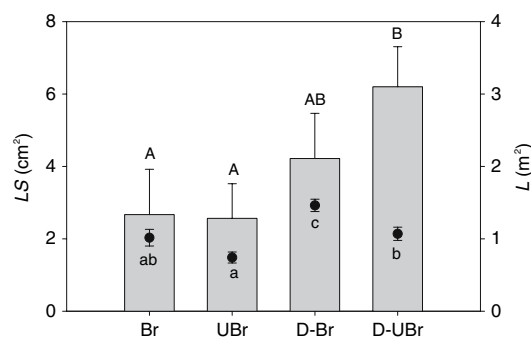
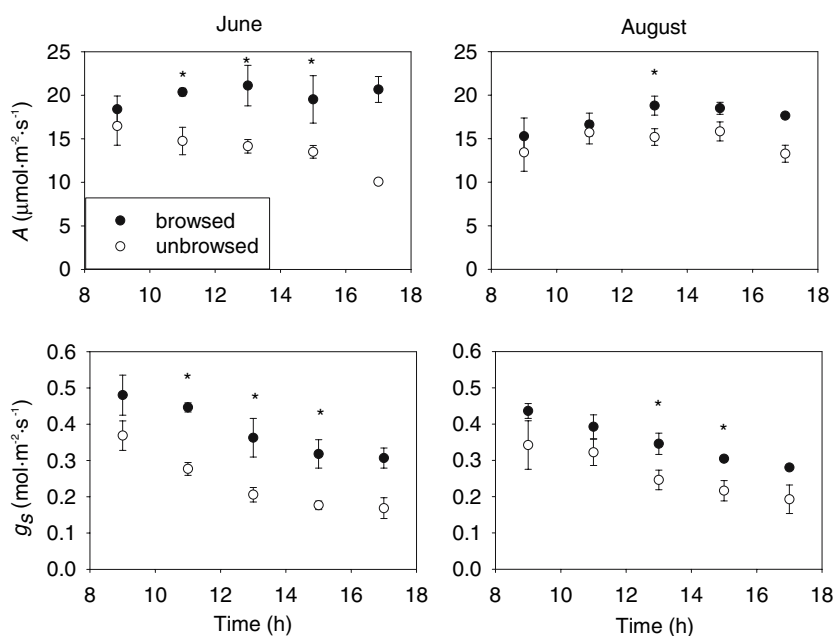


Fig. 4 Average leaf size (LS ; filled circles) and average leaf area per plant (L ; bars) for *S. geyeriana* in August of 2005 in a factorial experiment with four treatments: *Br* browsed, *UBr* unbrowsed, *D-Br* dammed and browsed, *D-UBr* dammed and unbrowsed ($n = 4$). Bars not sharing capital letters and filled circles not sharing lower case letters indicate significantly different treatment means ($\alpha = 0.05$). Error bars = SE

browsing may improve water relations in woody plants. Winter elk browsing reduced the number and age of branch junctions between leaves and soil, junctions which are known to reduce stem hydraulic conductivity (Zimmermann 1978; Ewers and Zimmerman 1984; Tyree and Ewers 1991; Joyce and Steiner 1995). Browsing also increased maximum shoot diameter, which is associated with an increased porosity of shoots to water flow in our study species as well as in many others (Tyree and Ewers, 1991). These morphological changes facilitate increased whole-plant conductivity (K_h). The ratio of K_h to leaf area, leaf-specific conductivity (LSC), therefore increased in browsed plants.

Increased LSC has important ramifications for growth because it allows plants to maintain higher water potential

at the leaf for a given rate of water supply, which may facilitate both photosynthesis and the maintenance of cell turgor. The plant's stomates may remain open under more severe environmental conditions, thereby allowing more CO_2 to be incorporated per unit leaf area (Meizner and Grantz 1990; Ryan and Yoder 1997; Hubbard et al. 1999, 2001; Brodrigg and Feild 2000). The plant's need to divert resources for osmotic adjustment is diminished (Woodruff et al. 2004), which allows the plant to more easily maintain higher cell turgor pressure which, in turn, provides a higher driving force for cell expansion (Lockhart 1965) and promotes larger leaf size (Tardieu et al. 1999). Therefore, the higher photosynthetic rates, increased stomatal conductance, larger average leaf size, and longer shoots of browsed willows are consistent with increased LSC. Increased LSC without loss of leaf area is the likely mechanism for increased aboveground productivity of browsed willows.

There is a general trend for woody plants to have reduced hydraulic conductivity, water potential, photosynthetic rate, and productivity as they near their final heights (Ryan and Yoder 1997). If the decreased water potential, photosynthesis, and CAG in unbrowsed willows were accompanied by substantial height increases, we could attribute these changes to a normal progression of changing architecture with increasing height. However, we found no evidence for decreasing CAG with increasing height for any of the species studied. Height and CAG were uncorrelated for *S. boothii* ($P = 0.33$), whereas they were positively correlated for *S. bebbiana* and *S. geyeriana* ($P < 0.04$). In the absence of the dam treatment, unbrowsed willows gained only 49 cm (95% CI = 33, 65) during 4 years of protection from browsing (Bilyeu et al 2007b), while unbrow-

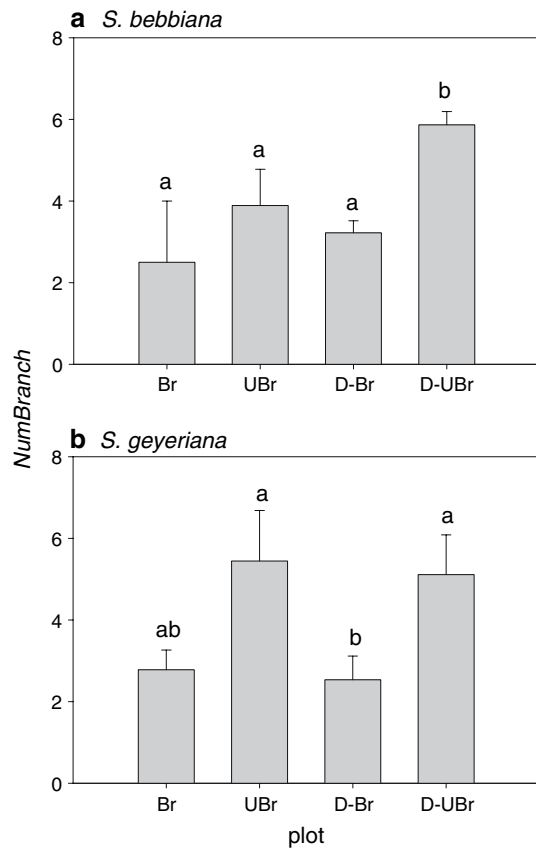


Fig. 5 Average number of age and branch junctions (*NumBranch*) between leaves and ground level for two *Salix* species in 2004 in response to a factorial experiment with four treatments: *Br* browsed, *UBr* unbrowsed, *D-Br* dammed and browsed, *D-UBr* dammed and unbrowsed ($n = 4$). Bars not sharing letters indicate significantly different means ($\alpha = 0.05$). Error bars SE

sed willows with the dam treatment gained 87 (72, 102) cm. Therefore, under conditions of low water availability, eliminating browsing suppressed aboveground productivity without allowing willows to become tall.

We suggest that continued height gain in willow depends on maintaining a high xylem water potential in plant apical buds to support the development of long shoots. In the absence of browsing, the water potential in apical buds decreases from year to year because the yearly accumulation of bud scars and branch points constricts water flow and causes the water potential to drop before it reaches the plant's apex. If the water table is high, xylem water potential nonetheless remains adequate at the plant's top for photosynthesis, turgor maintenance, and continued growth until the plant reaches normal stature. If the water table is deep, shoots with lower conductivity form near the top of the plant; these constrain further height gain before the plant reaches normal stature. In this case, tall willows cannot develop, and high productivity depends on winter browsing to remove the hydraulic constrictions to water flow.

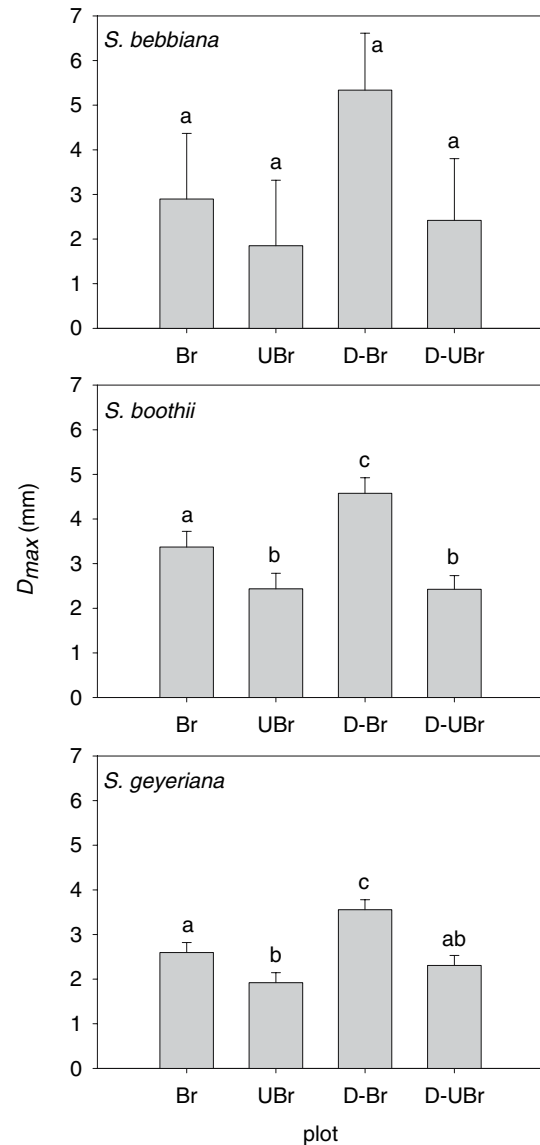


Fig. 6 Average diameter of the largest shoot per stem (D_{max}) of three *Salix* species in response to a factorial experiment with four treatments: *Br* browsed, *UBr* unbrowsed, *D-Br* dammed and browsed, *D-UBr* dammed and unbrowsed ($n = 4$). Values represent means taken over the years 2003–2005. Bars not sharing letters indicate significantly different means ($\alpha = 0.05$)

The water table treatment in our study appeared to be sufficient to counteract reduced conductivity in the absence of browsing only for *S. bebbiana*, the species with the highest water stress tolerance. The water table treatment allowed *S. bebbiana* to maintain similar aboveground productivity in browsed and unbrowsed plots, to become more productive with time, and to gain height dramatically in the absence of browsing (Bilyeu et al. 2007b). In contrast, the water table treatment did little to promote CAG or height (Bilyeu et al. 2007b) of unbrowsed *S. boothii*, the species with the lowest water stress tolerance. For *S. geyeriana*, interannual differences in water availability impacted the

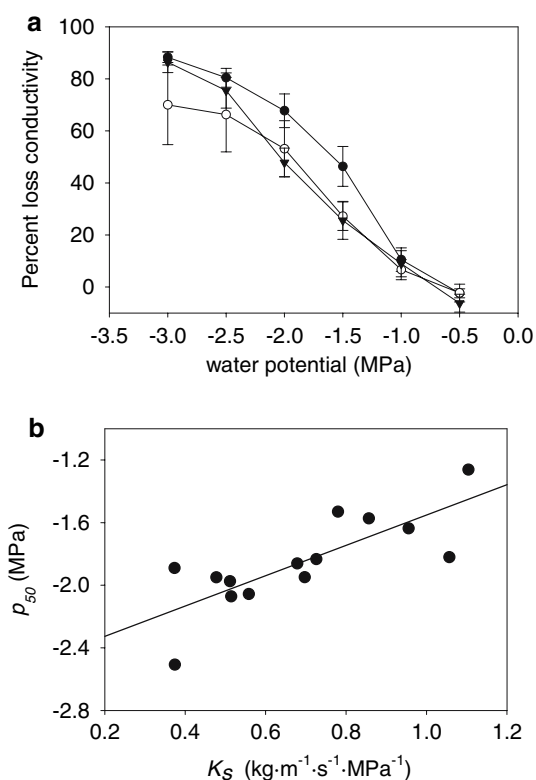


Fig. 7 **a** Vulnerability curves for large, current-year shoots of three *Salix* species, *S. bebbiana* ($n = 5$), *S. boothii* ($n = 4$), and *S. geyeriana* ($n = 5$), collected in August of 2003. **b** Maximum specific conductivity (K_s) versus the water potential incurring a 50% loss of conductivity (p_{50}) for large, current-year *Salix* shoots; species were pooled ($r^2 = 0.61$, $P = 0.001$, $n = 14$)

effect of browsing. For example, browsing had a larger effect on both water potential and long shoot productivity in 2003, the driest year of the study, than in other years. These patterns suggest that browsing increases aboveground productivity when willows are water stressed and that this stress depends on water table, the water stress tolerance of the species, and rainfall.

In our study plots with deep water tables, decreased rates of growth of unbrowsed willows were evident after only 1 year of protection from browsing. In contrast, when willows are grown under conditions of high water availability, they maintain their productivity for at least 3 years (Kopp et al. 1997). The early attrition in the growth of water-stressed willows could influence the competitive balance between elk and beaver. Elk can utilize water-stressed willows because they browse the same areas every year and do not require large willow standing crops. However, water-stressed willows may not provide the tall stems that are critical for beaver. The larger standing crops needed by beaver can accrue only in the presence of a water table sufficiently high for willow species to maintain productivity from year to year without heavy elk browsing, such as the dammed and exclosed treatment provided for *S. bebbiana* in this experiment.

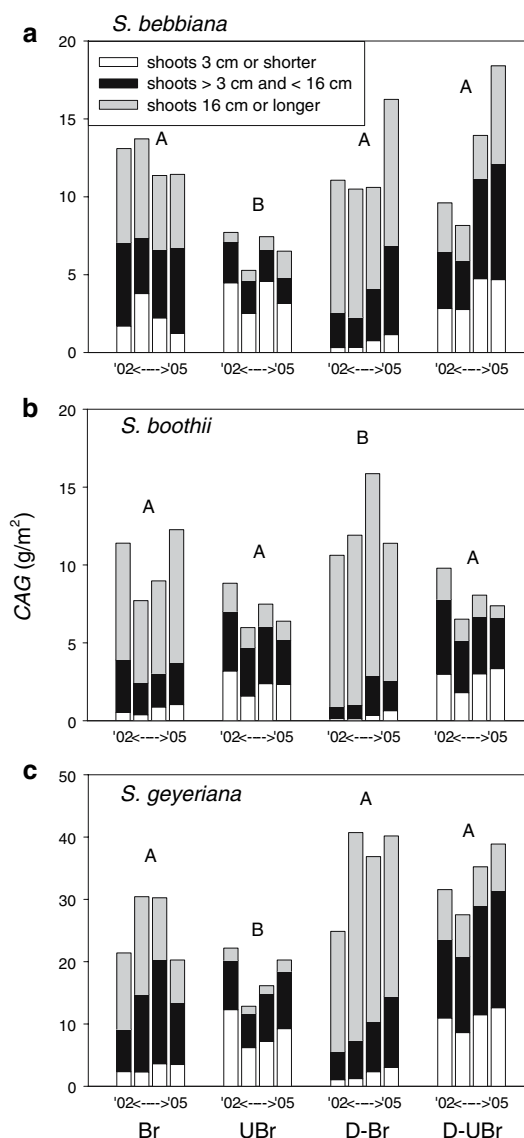


Fig. 8 Current annual growth (CAG) of new shoots and leaves for three *Salix* species (**a** *S. bebbiana*, **b** *S. boothii*, **c** *S. geyeriana*) in response to 4 years (2002–2005) of a factorial experiment with four treatments: *Br* browsed, *UBr* unbrowsed, *D-Br* dammed and browsed, *D-UBr* dammed and unbrowsed ($n = 4$). Groups of bars not sharing letters indicate significant differences between treatments when ls-means were taken over years ($\alpha = 0.05$). Note differing Y axis scales

Conclusion

We have shown that eliminating elk browsing in areas with deep water tables decreases willow aboveground productivity and that productive, tall willows are likely to recover only if the water table rises. Because higher water tables cannot occur without beaver dams, the restoration of tall willows along small streams in Yellowstone can occur only with restored beaver activity. The mutualistic relationship between beavers and willows (Baker et al. 2005) suggests that the current lack of beaver is due to a lack of tall

willows. Therefore, a positive feedback between deep water tables, low willow productivity, and beaver absence precludes re-establishment of the beaver/willow mutualisms that historically influenced the hydrologic regime and ecosystems of small streams on Yellowstone's Northern Range.

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 re-introduction of wolves to Yellowstone was a critical first step in the restoration of degraded willow communities. However, in areas where the prolonged absence of beaver activity has resulted in channel incision and water table decline (Wolf et al. 2007), reduced elk browsing may not facilitate willow recovery. Restoration of the historical positive feedback between productive willow, beaver presence, and high water table that formerly supported vigorous willow communities may require promoting beaver re-establishment in addition to reducing elk browsing. This could involve the use of artificial, temporary dams, alterations to the stream channels, providing aspen or willow for beaver use, or a combination of these approaches. As is commonly the case in the restoration of degraded systems (Suding et al. 2004), recovery may require mitigating secondary effects as well as reversing the direct effects of the original stressor.

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