

Relationships between groundwater use, water table, and recovery of willow on Yellowstone's northern range

DANIELLE B. JOHNSTON,^{1,3} DAVID J. COOPER,^{2,†} AND N. THOMPSON HOBBS^{1,2}

¹Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523 USA

²Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, Colorado 80523 USA

Abstract. Excessive levels of herbivory, incision of stream channels, and climate warming are believed to be responsible for the decline of woody deciduous plants in riparian zones in western North America, declines that are likely to be associated with diminished biological diversity. In the northern elk wintering range of Yellowstone National Park, USA, overbrowsing by elk (*Cervus elaphus*), lowered water tables resulting from stream incision, and loss of activity by beaver (*Castor canadensis*) have been implicated in the decline of willow (*Salix* sp.) communities. Reducing elk browsing appears sufficient for willow recovery in some areas, but where water table changes have been dramatic, recovery may be slow or absent. The importance of water table changes is disputed because experimental results demonstrate water table limitations, but water table depth has failed to explain variation in willow height at landscape scales. One explanation for this apparent discrepancy is that willows that have survived intensive browsing by elk have maintained access to groundwater despite declining water tables. Using stable isotopes of water, we examined the relationships between groundwater use, water table depth, and height of heavily browsed *Salix geyeriana*. *Salix geyeriana* groundwater use varied from 30% to 80%, and was higher later in the growing season, when soil water was less available and shoot water potentials were lower. Late season groundwater use explained 26% of the variation in total height of willows ($P = 0.002$), with taller plants using more groundwater. Water table depth explained only 8% of the variability in total height ($P = 0.051$), with shorter willows having deeper water table depths. Groundwater use and water table depth were uncorrelated. Height recovery following a winter of heavy browsing was related to groundwater use, but not groundwater depth. We suggest that access to deeper water sources alleviates late season water stress, allowing for more rapid height recovery and higher total plant height. Variability in groundwater access may account for variability in height recovery at landscape scales.

Key words: beaver; elk; restoration ecology; riparian vegetation; *Salix geyeriana*; stable oxygen isotopes; water sources; Yellowstone.

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³ Present address: Colorado Division of Wildlife, 711 Independent Ave, Grand Junction, Colorado 81505 USA.

† **E-mail:** davidc@warnercnr.colostate.edu

INTRODUCTION

Willows (*Salix* sp.) are the dominant plants of many riparian ecosystems, providing organic matter to streams (Kauffman and Krueger 1984), sustaining aquatic invertebrates (Kennedy

et al. 2000), and offering habitat to many species of wildlife (Bryant and Kuropat 1980). Tall willow communities have particularly high habitat value for mammals (Baker et al. 2005, Stephenson et al. 2006) and birds (Tremblay et al. 1997, Scott et al. 2003). In many areas of the

North American Rocky Mountains the abundance and distribution of willow communities has declined during the past century (Houston 1982, Cooper et al. 2006). Several factors have been implicated in these declines, including excessive herbivory (Kauffman and Krueger 1984, Kay and Wagner 1994, Peinetti et al. 2001) and degradation in the quality of riparian habitat for willows resulting from a drying climate (Cooper et al. 2006), river regulation (Busch and Smith 1995), and/or beaver extirpation (Wolf et al. 2007). Designing the best restoration practice in a particular ecosystem requires understanding the processes driving the decline (Suding et al. 2004). For instance, debate lingers about the importance of water table changes to the recovery of tall willow communities in the northern elk (*Cervus elaphus* L.) winter range in Yellowstone National Park, USA.

Heavy elk browsing has been implicated in the decline of tall willow communities in Yellowstone (Kay and Chadde 1991, Ripple and Larsen 2000, Larsen and Ripple 2005, Wolf et al. 2007), and the extirpation of wolves (*Canis lupus* L.) in the 1930s has been suggested to have increased elk browsing to levels that created and maintained short statured willows (Beschta 2003, Ripple and Beschta 2003, Beschta 2005). Following wolf reintroduction in 1994, elk browsing on willow has decreased in some areas and tall willows are reported to have recovered (Beschta and Ripple 2010).

During the time that wolves were absent, beaver (*Castor canadensis* Kuhl.) activity declined (Jonas 1955) and finally ceased (Consolo Murphy and Hanson 1990). Beaver require large standing crops of willow and/or aspen for dam building and foraging (Baker and Hill 2003). The suppressed willow communities created by heavy elk browsing may have competitively excluded beaver (Baker et al. 2005, Hebblewhite et al. 2005). Beaver and willow form a symbiotic relationship as beaver use willows for dam building, and the dams raise local water tables and stimulate willow productivity (Lindroth and Bath 1999, Baker et al. 2005, Westbrook et al. 2006, Johnston et al. 2007). Where beavers had historically altered local water tables on the northern range, beaver abandonment was accompanied by channel incision through up to 2 m of alluvial sediments (Wolf et al. 2007). There

is clear experimental evidence that deep water tables in these areas limit willow height gain even in the absence of elk browsing (Bilyeu et al. 2008). However, a survey of northern range riparian zones found no correlation between willow height and water table depth (Ripple and Beschta 2006). This absence of correlation is important because it was used to support the idea that spatial variation in height recovery of willows in Yellowstone is due to a “behavioral trophic cascade” as opposed to spatial variation in water availability (Ripple and Beschta 2006). For instance, the absence of rapid height recovery of willows in dryer upland sites was ascribed to elk preference for open upland habitat, which allowed wolves to be seen from a distance, as opposed to water stress resulting from deeper water tables in the uplands.

Thus, two competing views of the role of water availability in explaining spatial variation in willow height are motivated by the results of Ripple and Beschta (2006) and Bilyeu et al. (2008): (1) water availability in willow habitat in Yellowstone does not limit willow growth or (2) availability of water influences willow growth, but is poorly correlated with water table depth. In this paper, we evaluate these explanations. Our objective was to understand the role of water availability in determining height growth of browsed willows. Specifically we sought to determine if access to ground water accelerated height recovery in willows following a winter of browsing. Height was chosen as a response variable because of the importance of willow height for providing adequate habitat for beaver and birds (Olechnowski and Debinski 2008), and because willows that reach 2 m or more may escape elk browsing (Keigley 1998), allowing seed production (Kay and Chadde 1991), and providing high quality structural materials for dam building by beaver. Height recovery was chosen as a response variable because the height of willows in our study area (0.7 m in spring) was well below the typical stature of 3–5 m for the study species (Brunsfeld and Johnson 1985). In this context, height recovery indicated that plants are able to compensate for tissue loss due to browsing by growing large, hydraulically efficient shoots that best support photosynthesis and continued growth (Johnston et al. 2007, Bilyeu et al. 2008).

We measured the proportion of groundwater used by each plant in June and August by comparing the oxygen isotope ratio of plant xylem water to that of groundwater and rainwater. Stable isotopes of hydrogen and oxygen have been used successfully to determine the water uptake patterns of riparian plants in the intermountain west (Alstad et al. 1999, Snyder and Williams 2000, Chimner and Cooper 2004). This is possible because groundwater and rainwater often have distinct isotopic signatures, and plants do not distinguish between different isotopes of water upon uptake (Dawson and Ehleringer 1991). The composition of plant xylem water therefore reflects the relative contribution of the sources (Dawson 1996). June and August were selected as measurement times because these months typically represent the lowest and highest periods of water stress during the growing season in our study area.

We also measured height gain over the growing season, plant height at the end of the growing season, and the water table depth at each plant in early August. We hypothesized that willow height variables would be correlated with the proportion of groundwater used, but not with water table depth. We compared the predictive power of groundwater use versus groundwater depth in determining willow height.

METHODS

Study area

The study stream, the east fork of Blacktail Deer Creek (Fig. 1), is located in the northern range of Yellowstone National Park, a 100,000 ha region used intensively by Yellowstone's largest elk herd during winter (Houston 1982; Fig. 1). The area receives 260 mm of precipitation annually, 45–65% of which falls during the growing season (Despain 1987). Upland areas are steppe or shrub steppe, dominated by *Artemisia tridentata* Nutt., and riparian ecosystems are dominated by the willow species *Salix geyeriana* Anderss., *S. bebbiana* Sarg., *S. boothii* Dorn, *S. wolfii* Bebb., *S. pseudomonticola* Ball, and *S. exigua* Nutt. (Houston 1982).

Topography of the study area was a ~50 m wide, flat valley bottom bordered by steep, unforested slopes rising ~30 m to the Blacktail

Plateau. Channel erosion followed by bank collapse created a dichotomy with willows on remnant stream terraces and on slumped banks within the incised channel (Wolf 2004). Collapsed banks varied from 1 to 2 m in height, resulting in variable depth to groundwater for individual plants. Willows had many browsed shoots that had died back to the bud scar, indicating a history of heavy browsing (Keigley 1998). In the study area, nearly all browsing occurs during winter. *Salix geyeriana*, the most common willow in the study area, was selected for analysis.

Plant selection

Plants were selected systematically in each of four height classes: 0–0.49, 0.5–0.99, 1.00–1.49, and >1.5 m at the time of leaf out. Every 30 m along the stream, a target size class was selected, and the nearest *S. geyeriana* plant in that size class was tagged for measurement. We also made use of 12 plants located near groundwater monitoring wells that had been installed for a companion study (Johnston et al. 2008). About nine plants in each size class were selected.

Water table depth

Water table depth was measured on 20 August 2004. For plants located within 2 m of the stream, water table depth was estimated as the height of the plant's base above the stream stage. A level was used to measure this height. For plants located further from the stream, water table depth was estimated using depth to the water table measurements in groundwater monitoring wells located within 1 m of the plant, following the methods of Bilyeu (2008). About half of the groundwater depths were determined using groundwater monitoring wells.

Plant height

Plant total height and the height gain during the 2004 growing season was measured on 20 August 2004, after terminal leaves had expanded, but before leaf drop. Total height was measured perpendicular to the ground surface. Height gained during the 2004 growing season (height recovery) was measured by identifying the maximum height of bud scars on the plant, and then subtracting this value from total height (Keigley 1998, Bilyeu et al. 2008).

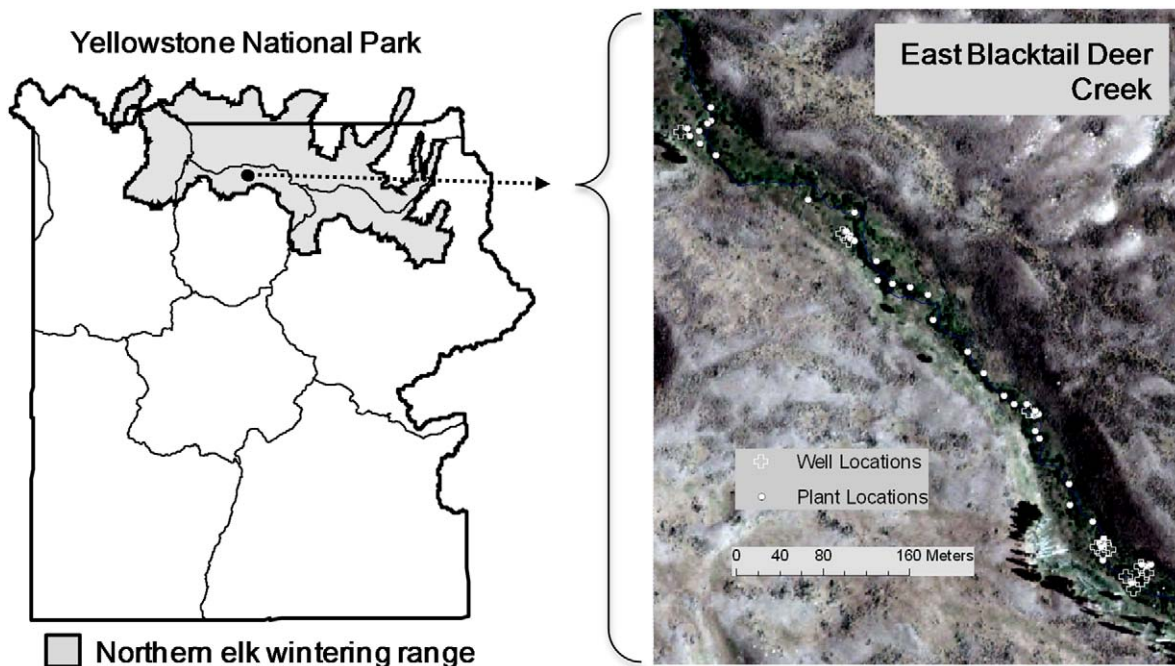


Fig. 1. Map of sampled plants and groundwater monitoring wells along East Blacktail Deer Creek.

Soil wetness and plant water stress

To characterize near-surface soil water availability, we sampled soils in five locations on 23 June and 15 August 2004. Three soil cores were taken in each location. Cores were taken from 5–40 cm in depth, double-bagged in zippered plastic bags, and placed in a cooler on ice. Gravimetric soil water content was determined by weighing, drying to a constant weight, and reweighing each sample.

To characterize plant water stress, we measured the water potential of one randomly selected, freshly cut current-year shoot from each study plant using a Scholander type pressure chamber (PMS instruments, Corvallis, OR, USA) at midday (12:00–14:00) under sunny conditions on 23 June and 15 August 2004. Data were averaged over each sample date.

Groundwater use

Samples of rainwater, groundwater, stream water, and plant tissues were collected on 23 June and 15 August 2004. Rainwater ($n = 2$) was collected from plastic rain gauges installed the prior month. The rain gauges contained cooking oil to prevent evaporation. Groundwater ($n = 11$) was sampled from groundwater monitoring

wells using a hand pump. The well casing was purged twice before the sample was collected. Stream water was collected in four locations. Plant tissues were sampled from two-year-old shoots with suberized stems. Three 20-cm-long shoot sections were sampled per plant. All samples were placed immediately in airtight containers in a cooler on ice, transported within 4 h to a freezer, and kept frozen until analyzed.

Cryogenic vacuum distillation was used to extract water from plant tissue (Ehleringer 1989) following procedures outlined in Alstad and Welker (1999). Extracted water was pipetted to storage containers, sealed, and frozen until analyzed for $\delta^{18}\text{O}$.

Water samples were equilibrated with CO_2 following procedures outlined in Alstad and Welker (1999). The $^{18}\text{O}:^{16}\text{O}$ ratio of the CO_2 was measured using a multi-prep sampler connected to a dual-inlet VG-Optima mass spectrometer (VG Instruments, Manchester, UK; Ehleringer 1989). We expressed $^{18}\text{O}:^{16}\text{O}$ ratio of plant, rain, and ground waters as $\delta^{18}\text{O}$ (‰) relative to the standard of V-SMOW (Vienna Standard Mean Ocean Water) using the equation $\delta^{18}\text{O}$ (‰) = $[(^{18}\text{O}:^{16}\text{O})_{\text{samp}} / (^{18}\text{O}:^{16}\text{O})_{\text{stan}} - 1] \times 1000$, where $^{18}\text{O}:^{16}\text{O}_{\text{samp}}$ was the $^{18}\text{O}:^{16}\text{O}$ ratio of the sample,

and $^{18}\text{O}:^{16}\text{O}_{\text{stan}}$ was the $^{18}\text{O}:^{16}\text{O}$ ratio of the standard.

Rain water, groundwater, and stream water $\delta^{18}\text{O}$ values were calculated by a simple average. We determined groundwater use (%) using a two-end-member mixing model of the form $\text{Groundwater use} = (\delta^{18}\text{O}_{\text{plan}} - \delta^{18}\text{O}_{\text{rain}}) / (\delta^{18}\text{O}_{\text{gw}} - \delta^{18}\text{O}_{\text{rain}})$, where $\delta^{18}\text{O}_{\text{plan}}$ was the measured $\delta^{18}\text{O}$ value for the plant xylem water, $\delta^{18}\text{O}_{\text{rain}}$ was the average $\delta^{18}\text{O}$ of rain water and $\delta^{18}\text{O}_{\text{gw}}$ was the average $\delta^{18}\text{O}$ of groundwater (Dawson 1993). June and August groundwater use were calculated independently.

Browsing intensity

We quantified browsing intensity using the biomass comparison method (Bilyeu et al. 2007) for seven plants in each of two locations; one near the upper extent of the sampled reach, and one near the lower end.

Statistical analysis

Browsing intensity for sampling locations on the upper vs. lower portions of the stream were compared using ANOVA in SAS PROC MIXED (SAS Institute Inc., Cary, NC, USA).

Correlations were calculated for: August groundwater use vs. water table depth; June groundwater use, August groundwater use, and water table depth vs. height recovery; and June groundwater use, August groundwater use, and water table depth vs. total plant height using SAS PROC GLM.

We used Akaike's Information Criterion, adjusted for small sample size (AIC_c ; Burnham and Anderson 2002) and Akaike weights (w_i) to estimate the strength of evidence in data for alternative models of August groundwater use vs. water table depth on height recovery and plant height. We tested four models: (1) water table depth as the sole predictor, (2) groundwater use as the sole predictor, (3) both water table depth and groundwater use as predictors, and (4) water table depth, groundwater use, and their interaction as predictors. AIC_c , maximum likelihood estimates of model parameters, and confidence intervals on model parameters were obtained by maximum likelihood fitting in SAS PROC MIXED.

Means are reported with 95% confidence intervals.

RESULTS

Average $\delta^{18}\text{O}$ values of rainwater were $-12.3 \pm 1.4\text{‰}$ in June and $-10.9 \pm 1.4\text{‰}$ in August (Fig. 2). Stream water values were $-18.6 \pm 0.3\text{‰}$ in June and $18.1 \pm 0.2\text{‰}$ in August. Groundwater values were $-18.9 \pm 0.3\text{‰}$ in June and $-18.3 \pm 0.8\text{‰}$ in August. Willow xylem water values were $-15.7 \pm 0.9\text{‰}$ in June and -16.5 ± 0.3 in August (Fig. 2).

The mixing model predicted that *S. geyeriana* acquired $51.5 \pm 13.2\%$ of its water from groundwater in June, and $75.6 \pm 4.1\%$ in August (Fig. 3). Gravimetric soil water content was $34.3 \pm 1.9\%$ in June and $26.7 \pm 2.1\%$ in August (Fig. 3). Shoot water potential was -0.86 ± 0.05 MPa in June and -1.27 ± 0.04 MPa in August.

Browsing intensity over the winter of 2003–4 averaged $63.3 \pm 15.4\%$ of current annual growth. We detected no difference in browsing intensity for locations in the upper vs. lower portions of the study stream reach ($F_{1,13} = 0.26$, $P = 0.619$).

Height recovery and June groundwater use were uncorrelated ($R^2 = 0.06$, $P = 0.110$). Height recovery increased with a higher proportion of groundwater use in August ($R^2 = 0.25$, $P = 0.002$; Fig. 4A) and was uncorrelated with August water table depth ($R^2 = 0.02$, $P = 0.334$; Fig. 4B). Total plant height increased with both June groundwater use ($R^2 = 0.13$, $P = 0.014$) and August groundwater use ($R^2 = 0.26$, $P = 0.001$; Fig. 4C). There was a negative relationship between total plant height and August water table depth ($R^2 = 0.08$, $P = 0.051$; Fig. 4D).

The best-fit model for explaining height recovery contained only August groundwater use, although the model containing both groundwater use and water table depth also had support in the data (Table 1). The best-fit model for total plant height contained water table depth and groundwater use (Table 2). There was no correlation between water table depth and August groundwater use ($R^2 = 0.02$, $P = 0.39$).

DISCUSSION

Use of groundwater influenced end of growing season height and height recovery following a winter of browsing. *Salix geyeriana* plants with the greatest proportion of groundwater use had the greatest total height. This relationship was

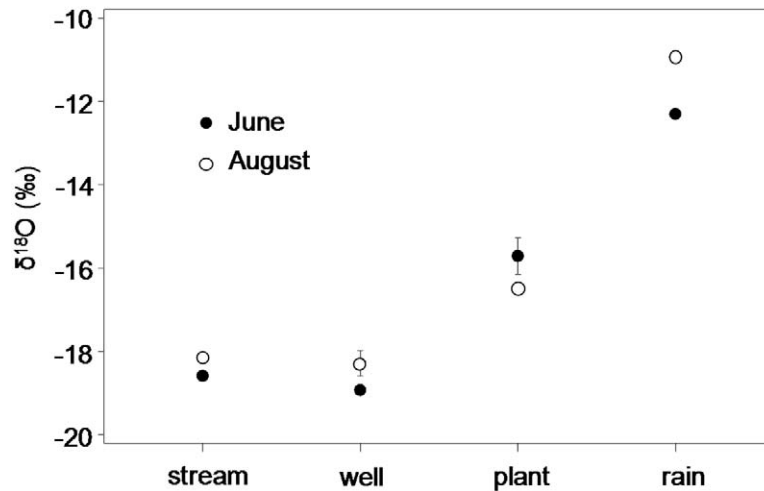


Fig. 2. Mean $\delta^{18}\text{O}$ values (\pm SE) for stream water, groundwater, *Salix geyeriana* xylem water, and rainwater in late June (solid circles) and mid August (open circles) of 2004 on East Blacktail Deer Creek, Yellowstone National Park.

evident for groundwater use both early and late in the growing season. Willows were 16.4 cm taller for every 10% increase in the proportion of groundwater used in August, and August groundwater use explained 26% of the variability in willow height. In addition, *S. geyeriana* plants with greater late season groundwater use also had greater height recovery following a winter of heavy browsing. Late season groundwater use explained 25% of the variability in height recovery.

Salix geyeriana groundwater use was higher late in the growing season when water availability in upper soil layers and shoot water potential were both lower. The August xylem pressure potentials corresponded to an approximate 25% loss of hydraulic conductance in *S. geyeriana* shoots (Johnston et al. 2007). Therefore, the plants experienced considerable late season water stress. Because willow productivity is known to be water limited, the most likely explanation for greater height gain in plants using more groundwater is that groundwater use alleviates water limitations to growth (Dawson and Pate 1996).

Water table depth was only weakly related to *S. geyeriana* height. Over the range of water table depths in this study, plant height was 3.7 cm shorter for every 10% decrease in water table depth, and water table depth explained only 8%

of the variability in plant height. Model selection results indicated that groundwater use is a more important predictor of height than water table depth, as models containing only groundwater use outperformed those containing only water table depth.

Groundwater use was not correlated with

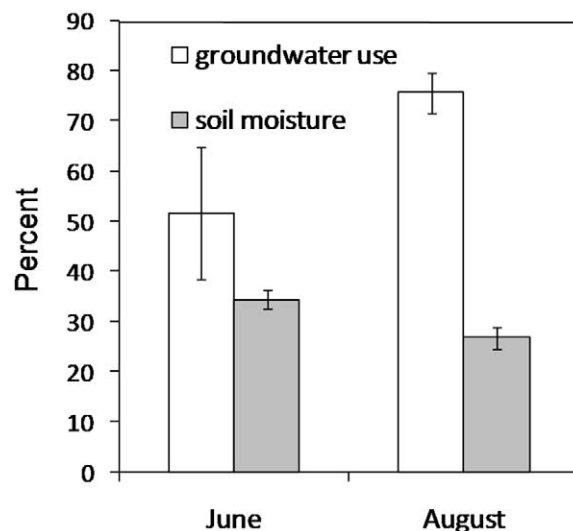


Fig. 3. Percent groundwater use by *Salix geyeriana* (open bars) and percent soil moisture 5–40 cm (grey bars) in June and August of 2004 on Blacktail Deer Creek, Yellowstone National Park. Error bars = SE.

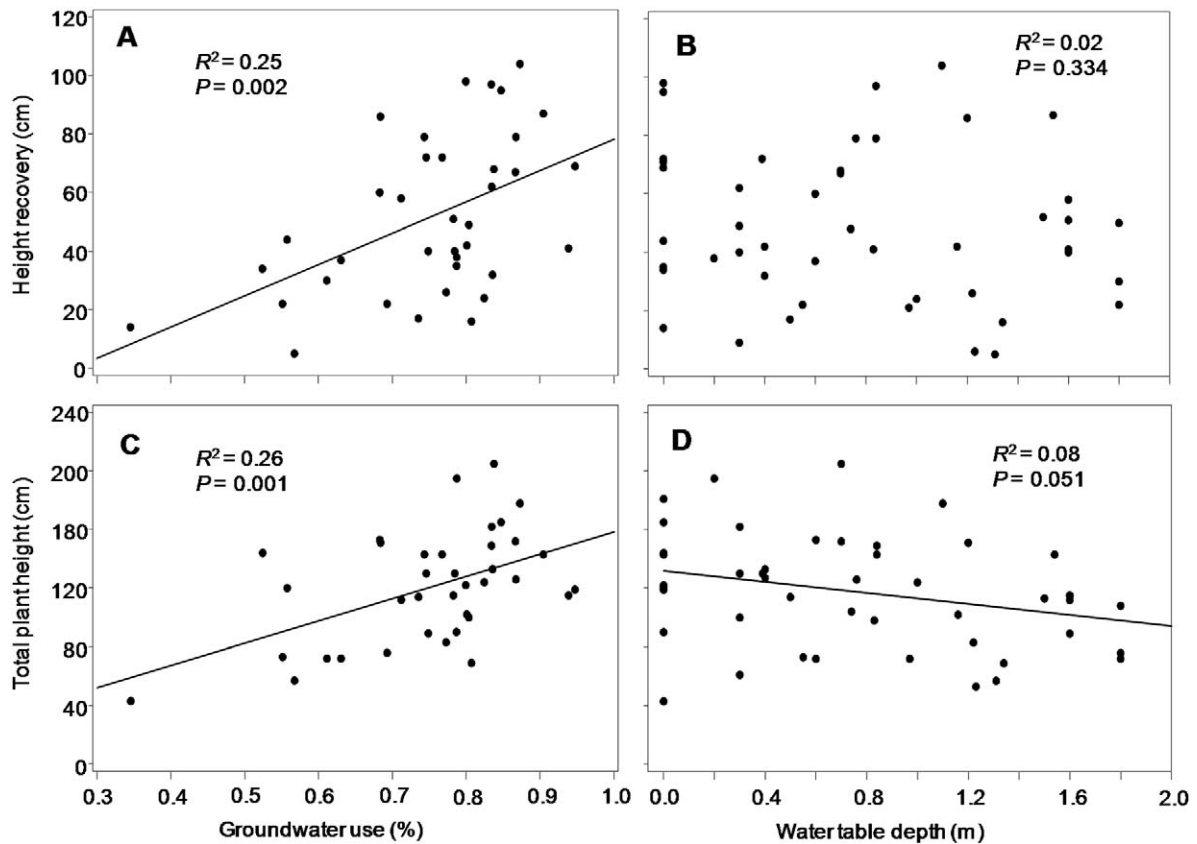


Fig. 4. Relationships between *Salix geyeriana* August groundwater use and August groundwater depth vs. height recovery and total plant height for *Salix geyeriana* on East Blacktail Deer Creek, 2004.

Table 1. Strength of evidence for competing models of height recovery as a function of groundwater use (*GWU*) and/or groundwater depth (*WTD*).

Parameters included in model	AIC _c value	Δr	Likelihood	W _r
<i>GWU</i>	343.9	0.00	1.00	0.49
<i>WTD</i> and <i>GWU</i>	344.3	0.40	0.82	0.40
<i>WTD</i> , <i>GWU</i> , and their interaction	347	3.10	0.21	0.10
<i>WTD</i>	436.2	92.30	0.00	0.00

Table 2. Strength of evidence for competing models of plant height as a function of groundwater use (*GWU*) and/or groundwater depth (*WTD*).

Parameters included in model	AIC _c value	Δr	Likelihood	W _r
<i>WTD</i> and <i>GWU</i>	365.7	0.00	1.00	0.66
<i>WTD</i> , <i>GWU</i> , and their interaction	368.0	2.30	0.32	0.21
<i>GWU</i>	368.9	3.20	0.20	0.13
<i>WTD</i>	467.8	102.10	0.00	0.00

water table depth. One explanation for this result is that groundwater use may be primarily a function of prior root development rather than of

current conditions. Our study was conducted in an area where water tables had declined due to the absence of beaver dams on the study stream.

Plants that experienced the decline more slowly or were healthier at the onset of the decline may have better adjusted to changing conditions. In a laboratory study, better taproot development and higher willow survival was found for a slow rather than fast water table decline (Amlin and Rood 2002). The history of water table change and root development may be more important than a plant's current position relative to the water table.

Many factors can influence rate of height gain in willows including genetic variation among individuals, pre-browsing height, browsing intensity (Singer et al. 1994), availability of nutrients (Houle 1999), and plant age (Ryan and Yoder 1997). We did not attempt to quantify these additional sources of variation. However, the operation of these additional influences cannot explain why groundwater use, taken alone, would account for 25% of the variation in height recovery. This is in contrast to the traditionally measured variable, water table depth, which explained none of the variation in height recovery. One explanation is that plants which were able to grow deeper roots as water tables declined may be better able to respond to current browsing pressure as a result of their ability to use groundwater late in the growing season.

This suggests that we should refine our thinking on willow water limitations, in that it may be a plant's ability to access the water table, and not water table depth, which ultimately limits willow growth. At certain points in time, the two may be tightly correlated; for instance, the ability of willow seedlings to access groundwater is probably largely a function of water table depth. The same may not be true for populations of older willows that experienced a decline in water table decades ago. In these populations, plants that were unable to adapt to changing conditions may have already died. Those remaining may have adjusted more or less successfully to the decline by altering their root architecture. In spite of this adjustment, raising the water table causes increased growth and height (Bilyeu et al. 2008). This implies that adjustment to deep water tables has a cost that may be relieved by water table elevation. It follows that a weak correlation between water table depth and height should not be taken as

evidence that water availability fails to limit height growth of willow on some portions of Yellowstone's northern range.

In our study area, willow stature was critical to its fitness. Willow catkins form on two-year-old or older shoots, and heavily browsed willow branches produce virtually no catkins or seed (Kay and Chadde 1991). Tall willows are more likely to promote the return of beaver, which would allow the historic symbiotic relationship between beaver and willow to be reestablished. Our data suggest that willows better able to exploit groundwater resources are most likely to grow tall enough to escape elk browsing, produce seed, and facilitate beaver colonization. Willows less able to access groundwater may require a larger rise in water table level, or larger reduction in elk browsing, to recover tall stature.

Earlier work (Ripple and Beschta 2006) used the absence of a correlation between water table depth and willow height growth to support the idea that spatial variation in height recovery of willows could not be explained by variation in plant water relations, but instead was due to spatial variation in browsing intensity induced by behavioral effects of wolves on elk foraging. However, recent work offered compelling evidence refuting the operation of a behaviorally mediated trophic cascade in Yellowstone (Creel and Christianson 2009, Kauffman et al. 2010), thereby renewing the question of why some willows have increased in height, while others have not. Our results suggest a parsimonious explanation: browsed willows with greater access to groundwater grow taller than those with less access to groundwater.

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