

WILEY



Influences of Herbivory and Water on Willow in Elk Winter Range

Author(s): Linda C. Zeigenfuss, Francis J. Singer, Stephen A. Williams and Therese L. Johnson

Source: *The Journal of Wildlife Management*, Jul., 2002, Vol. 66, No. 3 (Jul., 2002), pp. 788-795

Published by: Wiley on behalf of the Wildlife Society

Stable URL: <https://www.jstor.org/stable/3803143>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

Wiley and Wildlife Society are collaborating with JSTOR to digitize, preserve and extend access to *The Journal of Wildlife Management*

INFLUENCES OF HERBIVORY AND WATER ON WILLOW IN ELK WINTER RANGE

LINDA C. ZEIGENFUSS,¹ U.S. Geological Survey, Midcontinent Ecological Science Center, 4512 McMurry Avenue, Fort Collins, CO 80525, USA

FRANCIS J. SINGER, U.S. Geological Survey, Midcontinent Ecological Science Center, and Natural Resources Ecology Lab, Colorado State University, Fort Collins, CO 80523, USA

STEPHEN A. WILLIAMS, Natural Resources Ecology Lab, Colorado State University, Fort Collins, CO 80523, USA

THERESE L. JOHNSON, National Park Service, Rocky Mountain National Park, Estes Park, CO 80517, USA

Abstract: Elimination of large predators and reduced hunter harvest have led to concerns that an increasing elk (*Cervus elaphus*) population may be adversely affecting vegetation on the low-elevation elk winter range of Rocky Mountain National Park, Colorado, USA. Beaver (*Castor canadensis*) and their impoundments also have declined dramatically (94%) in the same area over the past 50 years coincident with a 20% decline in willow (*Salix* spp.) cover. From 1994 to 1998, we studied vegetation production responses of willow communities to elk herbivory and water availability. We estimated willow production by measuring current annual growth of shrubs in 9.3-m² circular plots, and we measured herbaceous production by clipping vegetation within 0.25-m² circular plots. Elk herbivory suppressed willow heights, leader lengths, annual production, and herbaceous productivity of willow communities. Water impoundment had a positive effect on herbaceous plant production, but little effect on shrubs, possibly because water tables were naturally high on the study sites even without beaver dams. Nevertheless, the winter range environment previously included more riparian willow habitat because of more stream area (47–69%) due to larger beaver populations. Elk herbivory appears to be the dominant force determining vegetation productivity in willow sites, but the effects may be exacerbated by lowered water tables. Fewer elk or protection from browsing, and water enhancement for <10 years along with management to encourage elk movement away from willow communities, could possibly work as strategies to reestablish sustainable willow communities.

JOURNAL OF WILDLIFE MANAGEMENT 66(3):788–795

Key words: *Cervus elaphus*, Colorado, elk, grazing, herbivory, hydrology, Rocky Mountain National Park, *Salix*, willow.

Large mammalian herbivores can significantly influence plant species abundance, richness, and ecosystem processes (McNaughton 1984, Hobbs 1996). Habitat loss from development often concentrates animals on smaller ranges, increasing population densities and diminishing forage availability (Smith and Robbins 1994). National parks often are perceived as pristine (Krausman 1998); however, most national parks have been subject to human influence (Leopold et al. 1963). Large predators and some herbivores have been eliminated, intact complements of native habitats have been lost, and exotic plant species have been introduced (Huff and Varley 1999, Wright 1999).

The impact of ungulate herbivory on plant production is controversial. Some researchers have postulated that grazing optimization occurs and plant productivity increases in response to grazing—a result of overcompensation for tissues lost (McNaughton 1979, 1984; Dyer et al. 1991). However, the evidence of this theory for U.S. western rangelands is limited, and the importance of plant physiological characteristics and environ-

mental conditions in response to herbivory has been stressed (DeAngelis and Huston 1993, Painter and Belsky 1993, Patten 1993).

Decreases in willow communities that have occurred in the presence of high elk densities (>15 elk/km²) have been documented in the intermountain western United States, including Rocky Mountain National Park (RMNP), Colorado (Boyce 1989, Singer et al. 1994, Smith and Robbins 1994). Two causes have been proposed for willow declines in RMNP. First, elk are protected and large predators were eliminated. Large predators and Native Americans might have limited elk populations and protected willow communities in the past (Kay 1990, 1994; Hess 1993). Elk populations were maintained at lower levels through removals by park management from the 1930s to 1967, but have increased 3-fold from about 700 to about 3,000 in 2001, since cessation of elk removals in 1968 (Hess 1993).

Second, lowered water tables and plant stress due to declines of beaver and their dams, drainage of meadows by early park staff, and a slightly warmer (0.89 °C) and drier (approx. 1 cm less precipitation) climate may contribute to the willow declines (Singer et al. 1998). Willows become

¹ E-mail: linda_zeigenfuss@usgs.gov

established on disturbed sites with abundant water and are adapted for rapid vertical growth and large below-ground storage of nutrients (Bryant et al. 1983). An increasingly arid climate would reduce water availability to willows and other forage. Water stress may make plants more vulnerable to herbivory and reduce the ability to compensate for tissue losses. Physiologically stressed plants produce less resins and phenols compared to healthy plants (Kozlowski 1971; Singer et al. 1994, 1998), and may, as a result, be consumed preferentially by herbivores (Halls et al. 1994, Swihart and Picone 1998). Herbivory may interact with water stress to lower shoot:root ratios and reduce transpiration in leaf and stem tissues (Wright et al. 1989).

Our objectives were to test 3 hypotheses: (1) plant productivity has declined due to excessive elk herbivory, (2) plant production in willow sites will respond positively to increased water availability, and (3) willow canopy structure has been altered by high elk herbivory.

STUDY AREA

The RMNP straddles the Continental Divide in the Rocky Mountains of north-central Colorado, USA. Elk winter range in RMNP encompassed approximately 10,000 ha in 4 major valleys in the upper montane zone along the eastern boundary of the park near the town of Estes Park. Elevations ranged from 2,400 to 2,800 m. Valley bottom vegetation included sedges (*Carex* spp.), grasses, and riparian shrubs (willow, birch [*Betula* spp.]). Slopes contained ponderosa pine (*Pinus ponderosa*)–shrub, mixed conifer (ponderosa pine–Douglas-fir [*Pseudotsuga menziesii*]), lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), and upland grass–shrub (predominantly bitterbrush [*Purshia tridentata*]) vegetation types. Herbaceous consumption averaged 55% of annual production, and shrub consumption averaged 33% of current annual growth throughout the study period (F. J. Singer, unpublished data).

METHODS

Experimental Manipulations

We delineated vegetation communities in elk winter range using a geographic information system (GIS) and randomly selected 12 study sites located in riparian willow communities in Moraine and Horseshoe parks within RMNP. Predominant willow species throughout all areas were mountain willow (*Salix monticola*), plane-leaf

willow (*S. planifolia*), and Geyer willow (*S. geyeriana*) mixed with other shrubs, such as shrubby cinquefoil (*Dasiphora floribunda*), bog and river birches (*Betula pumila*, *B. occidentalis*), and alder (*Alnus incana* spp. *tenuifolia*). Eight of the sites were located in areas that beaver had abandoned and contained short, heavily browsed (approx. 34% of annual production consumed) willow. In half of these sites (2 in each drainage, $n = 4$), we attempted to raise the water table by placing sheet metal check dams in ephemeral stream channels that had previously held beaver impoundments, to impede the flow of runoff. This treatment, referred to as “short-watered,” was imposed in spring 1995. The rest of the short willow sites were left to their normal hydrologic regimes and referred to as “short-control.” The 4 remaining sites (2 in each drainage, $n = 4$) were located in areas with natural, mostly high, water tables that supported tall willow plants subject to less severe hedging (approx. 26% consumption) by elk and were referred to as “tall.”

We selected 2 paired plots (30.5 m $\times$ 45.7 m) at least 20 m apart at each site with similar willow cover and surface hydrology. We randomly chose 1 plot to be fenced to exclude elk. Exclosures were erected during August–November 1994. We conducted simulated browsing treatments during winter (Jan–Mar) each year. Each exclosure was divided into equal sections that were randomly assigned to either clipped treatments or ungrazed–unbrowsed treatments. In clipped sections, we clipped 75% of the current year’s growth (over twice the observed average level of 33% consumption of shrubs by elk) from all willow, birch, alder, and the herbaceous layer. The higher levels of clipping were intended to simulate greater herbivory that might occur with an additional increase in elk numbers. All clipped plant material was removed from clipped plots within the exclosures. Ungrazed–unbrowsed treatments were unmanipulated areas within the exclosures. The unfenced plots were left to unregulated herbivory.

Hydrological Monitoring

During summer 1994, we installed 81 shallow wells (<1–2 m depth) in the study sites to monitor natural fluctuations in water levels and those changes in water level induced by our damming treatments. These water wells consisted of 5-cm-diameter PVC pipe wells—50 in the Horseshoe Park sites, 31 in the Moraine Park sites. Well pipes were slotted along the entire underground length.

Wellheads were referenced to the same arbitrary plane of elevation. We determined depth of wells by the maximum depth that could be reached using a gas-powered auger or 0.5 m past the first sign of the water table, and varied from <1 m to just over 2 m below the surface. During the growing seasons from 1995 to 1998, we recorded groundwater levels ≥ 1 time/month at all sites. We evaluated the effect of dams on water levels by comparing levels at the paired undammed sites.

Shrub and Herbaceous Production

During 1994, we established 3 randomly selected circular plots (9.3 m²) in each treatment at each site to measure shrub production and structure. Plots were located at least 2.5 m from the fence to avoid fenceline effects of sun, wind, rain, and snow interception. During late summers of 1994–1996 and 1998, we collected data on shrub production, including species, canopy diameters (widest and perpendicular to widest diameter), plant height, number of stems, and percent of canopy dead (Singer et al. 1994). Several willows ($n = 2\text{--}4$) of the 3 predominant species—*S. monticola*, *S. planifolia*, and *S. geeyeriana*—in each treatment at each enclosure were tagged for more intensive measurement, including catkin counts (total $n = 157/\text{yr}$). We collected plant material removed from the tagged plants during annual clipping treatments to create log–log predictor regression models to estimate annual above-ground production (dependent variable) on canopy volume (independent variable) following Peek (1970). Within approximately 0.5 km of the study sites, we randomly selected 49 willows of all 3 species from a range of sizes to determine plant production during late summer 1995 and 1996. We used clipped current annual growth (CAG) from these plants to determine corrections for total plant production because winter-tagged plant samples contained twigs but not leaves.

We developed separate regression equations for each species in Moraine Park and Horseshoe Park for 1995 and 1996, and we pooled data from these 2 years to predict willow production for 1994 and 1998 because tagged plant production samples were not available for these years. To determine whether these equations were suitable to cover a range of willow morphology, we tested for differences in slopes of the regression lines between models for tall (>125 cm) and short (<125 cm) willows, unbrowsed and browsed willows, and Horseshoe and Moraine parks. We concluded that these regressions (r^2 values ranged from 0.75 to

0.92) adequately estimated willow current annual growth. We found no differences in slopes of the regression lines between models for tall and short, or unbrowsed and browsed willows.

We collected pretreatment herbaceous standing-crop biomass data by clipping 5 randomly located circular plots (0.25 m²) in late summer 1994 at each study site. During July–August 1995, 1996, and 1998, 3 of these plots were randomly placed in each treatment at each site to measure annual herbaceous production. In the grazed treatment, we sampled 0.25-m² plots from beneath 1-m² movable grazing exclosures that had been randomly placed at the beginning of the growing season. We clipped and sorted by species all graminoids and forbs within the plot to measure annual peak production. Litter also was collected from within each quadrat. We then oven-dried (55 °C for 48 hr) and weighed the vegetation to determine dry weight mass.

Statistical Analyses

We tested shrub production, height, canopy area, canopy volume, catkin production, and herbaceous production for differences between all treatments using SAS PROC MIXED (SAS Institute 2000), an analysis procedure that is a generalization of the standard linear model designed to analyze data generated from several sources of variation. This method allowed us to account and test for the effects caused by the different drainages (Moraine vs. Horseshoe) and random sites. When assumptions of equal variance were not met, we log-transformed variables. Due to small sample size and the impracticality of additional replication in the park, we accepted significance at the 90% confidence level ($P \leq 0.10$). Because water additions were limited in magnitude (12–37 cm) and duration (May and Jun only), we also investigated the response of all willows to depth to the water table.

RESULTS

Hydrological and Precipitation Conditions

Total precipitation for May through mid-June of the 1995 growing season was 20 cm above the 30-year average and combined with the heavy snowpack runoff, led to high water tables in our study sites. Total 1995 growing season precipitation was 14 cm above average. Totals for the next 3 growing seasons (1996–1998) were within 3 cm of the 30-year average. Rain gauge measurements in 1997 indicated similar rainfall patterns and totals for both drainages (27.4 cm and 26.5 cm).

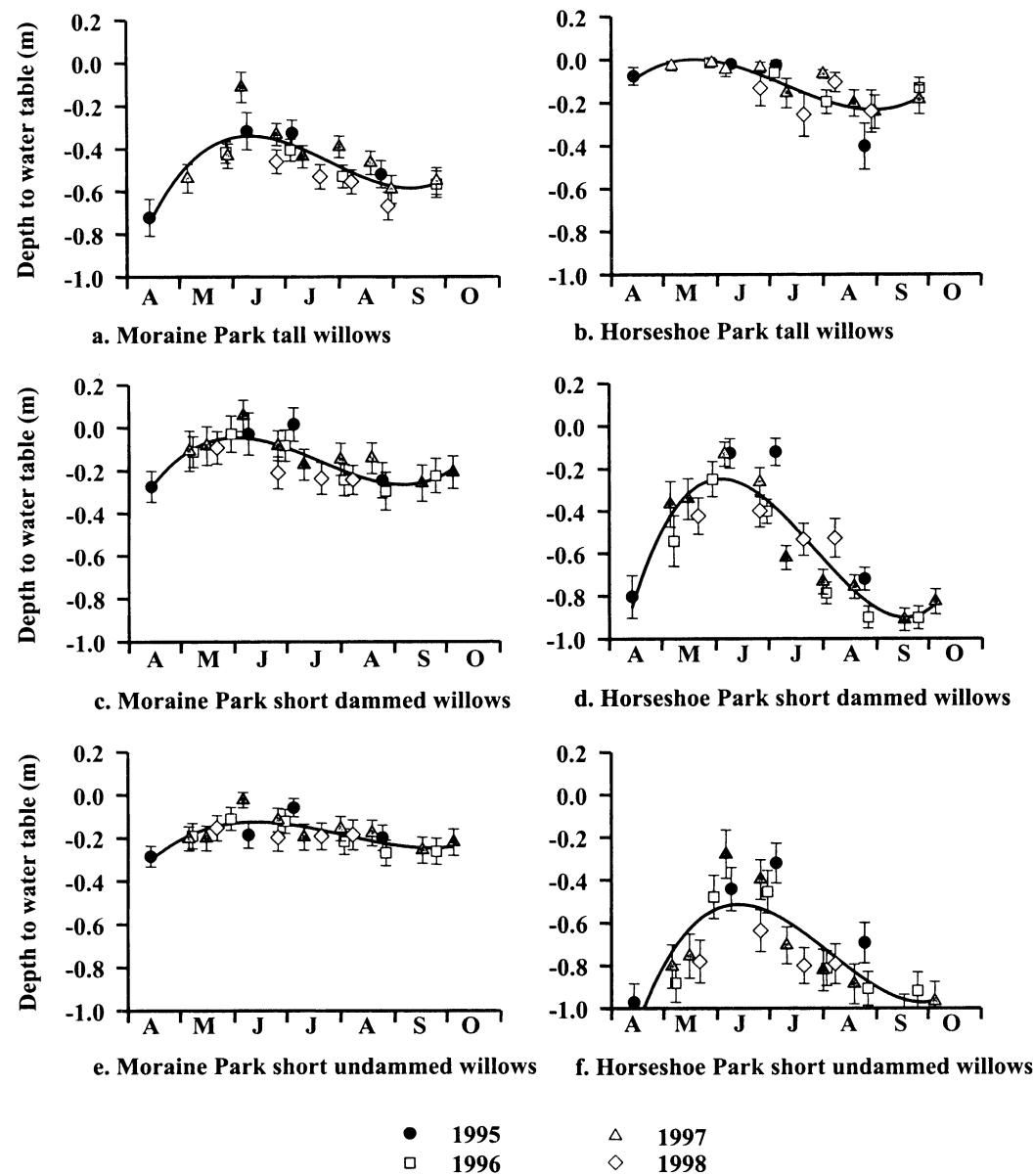


Fig. 1. Distance to groundwater (m) in: (a,b) tall willow sites, (c,d) short-watered willow sites, and (e,f) short-control willow sites in Moraine and Horseshoe Parks, Rocky Mountain National Park, Colorado, USA, 1995–1998. Tall willow sites were located in areas with natural, mostly high, water tables that supported tall willow plants subject to less severe hedging by elk; short-watered sites were similar to short-control except that sheet metal check dams were placed in ephemeral stream channels to impede the flow of runoff in an attempt to raise the water table; short-control sites were located in areas that beaver had abandoned and contained short, heavily browsed willow.

Dates of peak river levels varied from early June in 1998 to the end of June in 1995, as a function of melting of the annual snowpack at higher elevations (L. Zeigenfuss, personal observation). Fluctuations in groundwater levels from year to year were directly related to timing and volume

of snowpack melt and peak stream runoff (May–Jun) and variations in precipitation throughout the remainder of the growing season (Fig. 1). Even when low rainfall conditions occurred, groundwater levels at the study sites never averaged any lower than 1 m below the sur-

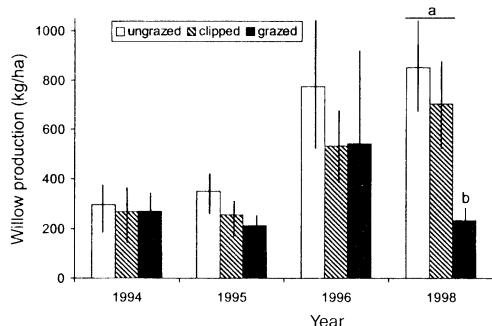


Fig. 2. Willow production (kg/ha) under different grazing treatments (different letters denote significant difference, $P < 0.02$) on elk winter range of Rocky Mountain National Park, Colorado, USA, 1994–1998. Bars represent 1 standard error.

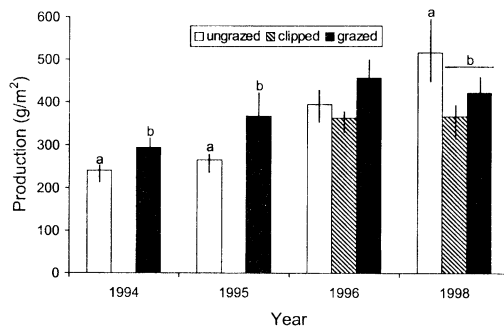


Fig. 4. Annual herbaceous production (g/m²) under different grazing treatments on elk winter range of Rocky Mountain National Park, Colorado, USA, 1994–1998 (different letters denote significant difference, $P < 0.10$). Bars represent 1 standard error.

face. These groundwater levels appeared to be high enough to be accessible to willows even during the dry months of July and August all years (Alstad et al. 1999). We hypothesized that tall willow sites would have higher groundwater levels than short willow sites (i.e., that higher water table contributed to the presence of taller willows). We also hypothesized that our check dams would raise groundwater levels resulting in higher water tables in short-watered than short-control sites. Sites in Horseshoe Park followed this pattern. However, in Moraine Park, the pattern for willow sites over the entire season was the reverse of predicted. The short willow sites had higher water tables than the tall willow sites (Fig. 1).

The check dams successfully held additional water at the sites only during the early growing season, but by early July, water no longer backed up behind the check dams, and there was no

longer a difference in mean groundwater levels between short-watered and short-control willow sites. Within each park, differences ($P \leq 0.058$) between groundwater levels in short-watered and short-control willow sites occurred only at the beginning of the growing season (May).

Plant Production Responses

Grazing by elk resulted in 67–73% lower willow production ($P = 0.017$) than clipped and ungrazed treatments by 1998 (Fig. 2). Willows browsed by elk were shorter than those protected or treated with clipping ($P \leq 0.002$) after only 2 years (Fig. 3). Willow catkin production (catkins/m³ of shrub canopy volume) was approximately 70% lower under clipped (21.2 ± 3.5 , $\bar{x} \pm \text{SE}$) and grazed (16.8 ± 6.1) than the ungrazed (69.0 ± 13.6) treatment. Elk were the primary ungulate herbivore on these sites, and although mule deer (*Odocoileus hemionus*) inhabit the winter range, neither deer nor deer pellets were observed in the sites during the study.

Herbaceous production in grazed and clipped treatments was 18–29% lower than in the ungrazed treatment by 1998 ($P = 0.016$; Fig. 4). We detected higher pretreatment biomass in those sites later selected for the grazing treatment, mainly in Horseshoe Park, but this difference was no longer significant by 1996. Less litter accumulated ($P \leq 0.009$) in grazed (60% less) and clipped plots (38% less) by 1996 and later.

The water impoundments did not have any impact on willow production (Fig. 5). Willow production ranged from 2 to 4 times greater in tall sites than either short-watered or short-control willow sites during 1994–1996 ($P \leq 0.001$); however, in 1998, this difference was not significant ($P =$

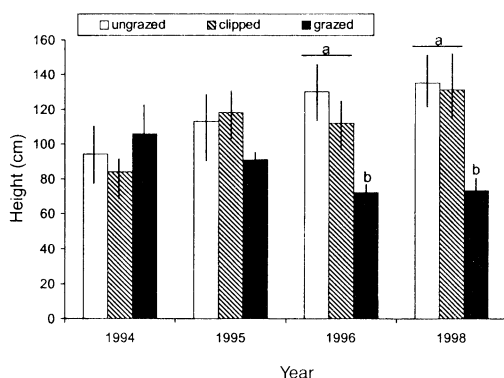


Fig. 3. Average heights (cm) of willows under different grazing treatments on elk winter range of Rocky Mountain National Park, Colorado, USA, 1994–1998. Bars represent 1 standard error.

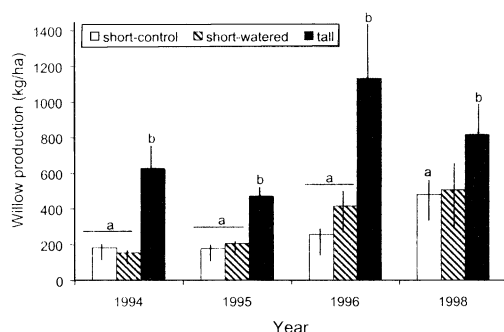


Fig. 5. Willow production (kg/ha) under different water treatments in willow communities on elk winter range of Rocky Mountain National Park, Colorado, USA, 1994–1998 (different letters denote significant difference, $P \leq 0.05$). Bars represent 1 standard error.

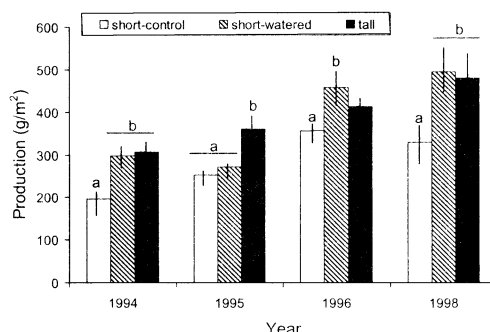


Fig. 6. Herbaceous production (g/m²) in willow sites with different water treatments on elk winter range of Rocky Mountain National Park, Colorado, USA, 1994–1998 (different letters denote significant difference, $P \leq 0.05$). Bars represent 1 standard error.

0.118) for short-watered sites. The height differences for tall and short willows selected at the start of the study were maintained, despite water impoundment, and heights were 1.5 times greater ($P < 0.036$) in tall sites than short-control or short-watered sites in all years.

Herbaceous production response to the water impoundment was difficult to interpret. At the onset of the study in 1994, herbaceous production was 52% greater in short willow sites destined for water impoundments than other short willow sites. However, in 1995, the first year of damming, herbaceous production was, on average, 30% greater ($P = 0.006$) in tall willow sites than in both grazed and ungrazed short willow sites. Following water impoundment, biomass in short-watered sites was significantly greater than in short-control sites ($P = 0.051$ and $P = 0.036$, respectively), and exceeded tall sites (although not significantly so) both years (Fig. 6). This effect may have been due to a priori site differences between short-control and short-watered sites, or a response to water impoundment on the sites.

Depth to water table in June and July was weakly correlated to herbaceous production and annual growth of willows, but the percent of variation explained was low (r^2 ranged from 0.04 to 0.06). For herbaceous plants, the association was positive, with consistently higher production with higher water tables. However, the influence of water on willow growth was difficult to interpret. While the highest production levels were achieved in sites with the highest water tables, overall, the association was slightly negative. When the data were categorized by drainage, we found that most of this negative association was attributed to the

Moraine Park sites, which had fewer wells, particularly in tall willow sites, and less variation in water table with no very dry sites.

DISCUSSION

The high level of elk herbivory in RMNP is the primary factor driving productivity decreases in willow communities. High elk herbivory is primarily responsible for the shorter stature of many willows. Although we found no interaction effect between herbivory and water table depth in our experimental manipulations, this may have been due to our small sample size ($n = 4$) and high sample variance, the naturally high water tables in the study area (even where beaver had abandoned formerly occupied sites), relatively short time frame (4 years post-treatment) for measurement of effects, and the relatively short-lived and small effect of our water impoundments. If the water tables had been lower (e.g., >2 m) and the dam treatment larger, we might have detected more positive responses by willows. Our inferences about water dynamics were limited by the smaller number of wells in Moraine Park, particularly in tall willow sites, and the fact that our sampling did not include dry years (1995–1998 had average or above-average annual precipitation). The importance of the amount of available water to plant production was further verified when we compared grazed sites in years of different growing season precipitation. Production was much lower during 1994, a year with lower-than-average precipitation.

Herbivory by ungulates can influence many aspects of plant structure, growth, and net primary productivity. The shift of some tall willow patches to shorter patches may influence insect,

bird, or small-mammal diversity. For example, higher songbird diversity was found in tall willow patches where the number of browsing moose (*Alces alces*) and browsing levels were reduced by sport hunting in the Jackson Valley than in the adjacent Grand Teton National Park where hunting was not allowed (Berger et al. 2001).

Net primary productivity can either increase or decrease as a result of ungulate herbivory (McNaughton 1979, Painter and Belsky 1993). In RMNP, elk herbivory reduced herbaceous and willow productivity. Based on observations of older exclosures in RMNP and Yellowstone National Park (Singer et al. 1994, 1998), we expect continued increases in canopy cover and annual production within protected sites for some years. Herbaceous production in protected sites may decrease as increasing shrub canopy takes over areas or shades out understory herbs.

Herbivory by elk reduced willow production more than higher levels of artificial clipping removals. Willow production and average heights were lower in clipped than unclipped treatments, and lowest in sites grazed by elk. The timing of clipping versus elk herbivory may explain the smaller negative response to clipping. Elk removed plant material during the spring, after the emergence of new shoots and leaves, and during winter, which was the period when the clipping treatments were conducted. However, winter clipping and browsing by elk had equivalent negative effects on seed production.

Hydrologic changes may be exacerbating the effects of elk herbivory in RMNP. Coincident with the elk population increase, stream surface areas decreased 47–69% and willow cover declined 20% (54–69% for tall willows) on the study area over the past 50 years (H. R. Peinetti, Natural Resources Ecology Laboratory, unpublished data). Beaver activity and their ponds have declined (94%) over the past 58 years on the study area (T. L. Johnson, unpublished data). The decline in beaver populations may contribute to declining willow populations through both reduced local water tables and through reduced recruitment sites. Recently abandoned beaver ponds often provide an ideal substrate for establishment of willow seedlings (Cottrell 1995) as does the stimulation of suckering in willow following beaver-cutting (Kindschy 1989). Several decades following beaver abandonment of dams, with no reoccupations, water and/or nutrient-stressed willows may become less able to recover from tissue losses caused by ungulate herbivory (Kozłowski 1971, Bryant and Kuropat 1980).

Other limiting factors to willows on the RMNP elk winter range may be the drainage of meadows by humans and the change to slightly warmer, drier conditions over the previous 9 decades (0.89 °C warmer, approx. 1 cm less precipitation; Singer et al. 1998). All of the meadows in the major elk-feeding areas experienced water diversions. In recent decades, >50% of these diversions have been eliminated (K. Czarnowski, National Park Service, personal communication). However, there is no way of knowing whether restoration of diverted water reverses changes to the ecosystem that may have occurred during years of lower water availability. Similarly, no information exists on whether the slight climate change to aridity, in conjunction with the high elk herbivory, could have contributed to the willow declines. This tendency to aridity was punctuated by a wetter period during the study years (Singer et al. 1998).

MANAGEMENT IMPLICATIONS

Reducing elk numbers and/or reducing elk concentrations will result in increases in willow productivity and heights of willow. Fencing some willow communities to encourage greater seed production and establishment, and to allow some individual willows to increase in size beyond the reach of elk, may also help sustain willow communities over the long term. Management of elk to decrease localized dense concentrations of animals could lead to lowered levels of consumption, and thus increased plant productivity and potentially a return to larger communities of tall, healthy willows.

Reintroduction or restoration of beaver populations to parts of this range, or artificial manipulations of hydrology in willow areas to simulate beaver ponds, could encourage willows by improving water relations, protecting some willows from herbivory due to standing water, and by providing new recruitment sites. While beaver ponds drown some willows and beaver may remove many of the stems, past beaver presence in the study area apparently resulted in a more-watered (50–70% more-watered) environment with substantially more riparian habitat, even in areas located away from ponds and between pond intervals. Simulated beaver cuttings (Kindschy 1989) to stimulate suckering, and plantings from cuttings, could be used to increase willow establishment.

ACKNOWLEDGMENTS

Funding for this project was provided by the National Park Service, Natural Resources Preser-

vation Program and United States Geological Survey, Biological Resources Division (USGS-BRD). We thank the numerous field and lab technicians from Rocky Mountain NP, Colorado State University, and USGS-BRD without whom this work could not have been done. B. Baker, D. Cooper, R. Monello, P. Krausman, and 2 anonymous reviewers provided very helpful comments on the manuscript.

LITERATURE CITED

- ALSTAD, K. P., J. M. WELKER, S. A. WILLIAMS, AND M. J. TRILICA. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: an isotopic study using $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. *Oecologia* 120:375–385.
- BERGER, J., P. B. STACEY, L. BELLIS, AND M. P. JOHNSON. 2001. A mammalian predator–prey imbalance: grizzly bear and wolf extinction affect avian Neotropical migrants. *Ecological Applications* 11:947–960.
- BOYCE, M. S. 1989. The Jackson elk herd: intensive wildlife management in America. Cambridge University Press, Cambridge, United Kingdom.
- BRYANT, J. P., F. S. CHAPIN, III, AND D. R. KLEIN. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate history. *Oikos* 40:357–368.
- , AND P. KUROPAT. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics* 11:261–285.
- COTTRELL, T. R. 1995. Willow colonization of Rocky Mountain mires. *Canadian Journal of Forest Research* 25:215–212.
- DEANGELIS, D. L., AND M. A. HUSTON. 1993. Further considerations on the debate over herbivore optimization theory. *Ecological Applications* 3:30–31.
- DYER, M. I., C. L. TURNER, AND T. R. SEASTEDT. 1991. Mowing and fertilizing effects on productivity and spectral reflectance in *Bromus inermis* plots. *Ecological Applications* 1:443–452.
- HALLS, S. C., D. R. GANG, AND D. J. WEBER. 1994. Seasonal variation in volatile secondary compounds of *Chrysothamnus nauseosus* (Pallas) Britt.; Asteraceae ssp. *hololeucus* (Gray) Hall & Clem. influences herbivory. *Journal of Chemical Ecology* 20:2055–2063.
- HESS, K., JR. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot, USA.
- HOBBS, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695–713.
- HUFF, D. E., AND J. D. VARLEY. 1999. Natural regulation in Yellowstone National Park's northern range. *Ecological Applications* 9:17–29.
- KAY, C. E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm. Dissertation, Utah State University, Logan, USA.
- . 1994. Aboriginal overkill: the role of Native Americans in structuring western ecosystems. *Human Nature* 5:359–398.
- KINDSCHY, R. R. 1989. Regrowth of willow following simulated beaver cutting. *Wildlife Society Bulletin* 17:290–294.
- KOZLOWSKI, T. T. 1971. Growth and development of trees. Volume I. Academic Press, New York, USA.
- KRAUSMAN, P. R. 1998. Conflicting views of ungulate management in North America's western national parks. *Wildlife Society Bulletin* 26:369–371.
- LEOPOLD, A. S., S. A. CAIN, C. M. COTTAM, I. N. GABRIELSON, AND T. L. KIMBALL. 1963. Wildlife management in the national parks. Transactions of the North American Wildlife and Natural Resources Conference 28:29–44.
- MCAUGHTON, S. J. 1979. Grazing as an optimization process: grass–ungulate relationships in the Serengeti. *American Naturalist* 134:1–19.
- . 1984. Grazing lawns: animals in herds, plant forms, and coevolution. *American Naturalist* 124:863–886.
- PAINTER, E. L., AND A. J. BELSKY. 1993. Application of herbivore optimization theory to rangelands of the western United States. *Ecological Applications* 3:2–9.
- PATTEN, D. T. 1993. Herbivore optimization and overcompensation: does native herbivory on western rangelands support these theories? *Ecological Applications* 3:35–36.
- PEEK, J. M. 1970. Relation of canopy area and volume to production of three woody species. *Ecology* 51:1098–1101.
- SAS INSTITUTE. 2000. SAS/STAT user's guide. Version 8. SAS Institute, Cary, North Carolina, USA.
- SINGER, F. J., L. MACK, AND R. G. CATES. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. *Journal of Range Management* 47:435–443.
- , L. C. ZEIGENFUSS, R. G. CATES, AND D. T. BARNETT. 1998. Elk, multiple factors, and persistence of willows in national parks. *Wildlife Society Bulletin* 26:419–428.
- SMITH, B. L., AND R. L. ROBBINS. 1994. Migrations and management of the Jackson elk herd. Resource Publication 199, National Biological Survey, Department of the Interior, Washington, D.C., USA.
- SWIHART, R. K., AND P. M. PICONE. 1998. Selection of mature growth stages of coniferous browse in temperate forests by white-tailed deer (*Odocoileus virginianus*). *American Midland Naturalist* 139:269–274.
- WRIGHT, R. G. 1999. Wildlife management in the national parks: questions in search of answers. *Ecological Applications* 9:30–36.
- WRIGHT, S. L., R. W. HALL, AND J. W. PEACOCK. 1989. Effects of simulated insect damage on growth and survival of red oak (*Quercus rubra*) seedlings. *Environmental Entomology* 18:235–239.

Received 27 October 2001.

Accepted 22 January 2002.

Associate Editor: Krausman.