

INTERACTION OF BEAVER AND ELK HERBIVORY REDUCES STANDING CROP OF WILLOW

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Abstract. Populations of beaver and willow have not thrived in riparian environments that are heavily browsed by livestock or ungulates, such as elk. The interaction of beaver and elk herbivory may be an important mechanism underlying beaver and willow declines in this competitive environment. We conducted a field experiment that compared the standing crop of willow three years after simulated beaver cutting on paired plants with and without intense elk browsing (~85% utilization rate). Simulated beaver cutting with intense elk browsing produced willow that was small (biomass and diameter) and short, with far fewer, but longer, shoots and a higher percentage of dead biomass. In contrast, simulated beaver cutting without elk browsing produced willow that was large, tall, and leafy, with many more, but shorter, shoots (highly branched) and a lower percentage of dead biomass. Total stem biomass after three years was 10 times greater on unbrowsed plants than on browsed plants. Unbrowsed plants recovered 84% of their pre-cut biomass after only two growing seasons, whereas browsed plants recovered only 6%. Thus, the interaction of beaver cutting and elk browsing strongly suppressed the standing crop of willow. We predict that a lack of willow suitable as winter food for beaver can cause beaver populations to decline, creating a feedback mechanism that reduces beaver and willow populations. Thus, intense herbivory by ungulates or livestock can disrupt beaver–willow mutualisms that naturally occur in less competitive environments.

Key words: beaver; *Castor canadensis*; compensatory growth; elk; herbivory; livestock; plant–herbivore interaction; Rocky Mountain National Park (USA); *Salix monticola*; standing crop; ungulate; willow.

INTRODUCTION

Compensatory growth, defined as the positive response of plants to injury, helps plants to tolerate damage from abiotic and biotic causes, such as fire, wind, commercial harvest, and herbivores ranging in size from insects to large mammals (McNaughton 1983). Plant response to herbivory varies in form and magnitude depending on how plants are grazed or browsed (Belsky 1986, Milchunas and Lauenroth 1993, Brookshire et al. 2002). Large mammals often repeatedly browse shoot tissue from the tops of woody plants, a model system widely used to develop and test theory about mechanisms of compensatory growth. In response to mammalian herbivory, woody plants can shunt carbon stores from roots to shoots; increase leaf N, photosynthetic rate, and growth rate; and increase branching in response to released apical dominance (Hobbs 1996, Strauss and Agrawal 1999).

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Beaver (*Castor canadensis*) are central-place foragers that cut and remove entire stems at or near the ground surface. They often cut all stems from preferred shrubs growing near their winter food caches, dams, and lodges, but become more selective as foraging distances increase (Baker and Hill 2003). In response to beaver cutting, red willow (*Salix lasiandra*) increased stem production in proportion to the number of stems cut per plant, with a stem elongation rate of 3.3 cm/d on cut plants compared with 0.4 cm/d on uncut controls (Kindschy 1985, 1989). Beaver cutting of sprouting woody species is most analogous to coppicing, an ancient forestry practice that involves cutting trees down close to the ground to induce production of basal sprouts, which are allowed to grow until suitable for harvest; woodlands systematically coppiced in this manner can remain productive for centuries (Hardesty and Box 1988, Del Tredici 2001). Traditional logging, fire, wind, and floodwater also can remove entire stems from plants; thus they share some characteristics and effects with beaver cutting (Spiller and Agrawal 2003).

Historically, a beaver–willow community dominated many riparian landscapes in North America. Seton (1929) estimated that beaver numbered 60–400 million before European settlement. Beaver modify their environment by cutting willow for food and construction material, by building dams that raise the water table, and by building ponds that trap sediment and increase N availability to willow (Naiman et al. 1988). These modifications benefit willow by creating bare, moist soil for seed germination, by increasing late-season moisture regimes for seedling survival, and by increasing stem turnover rate (asexual reproduction). The sprouting ability of willow and the ability of beaver to shift their foraging upstream or downstream if needed as willow recovers suggest that beaver and willow can persist indefinitely within the same stream reach (Hall 1960). Because beaver facilitate willow establishment and survival processes, and willow is important as food and construction material for beaver (Baker and Hill 2003), we suggest that beaver and willow are mutualists.

Despite their legendary abundance, most beaver populations were decimated by fur trappers during the 1700s and 1800s to support the European fashion for felt hats (Baker and Hill 2003). Although beaver reintroduction helped populations to recover throughout much of their former range, beaver–willow communities have declined or have failed to recover in riparian environments that have become heavily browsed by livestock or ungulates since European settlement. Large herbivores congregate in these areas because they lack disturbance from large predators and provide water and productive vegetation (Belsky et al. 1999). These additional herbivores directly compete with beaver for willow, which is highly palatable and selected for by livestock and ungulates, such as elk (*Cervus elaphus*). We suggest that this new level of competition is unnatural to beaver–willow mutualisms, which probably evolved under relatively low herbivory in a more predator-rich environment. Thus, the interaction of beaver and elk herbivory may be an important mechanism underlying beaver and willow declines in this new competitive environment, and represents a model system where intense disturbance can alter plant–herbivore interactions and ecosystem processes.

Here, we present experimental evidence that intense browsing by elk can suppress the standing crop of simulated beaver-cut willow. This suppression can drive declines or prevent restoration of beaver–willow communities in heavily browsed environments.

METHODS

Study area

We chose a beaver–willow community in Rocky Mountain National Park (RMNP), Colorado, USA that was heavily browsed by elk as our model plant–herbivore system. Study sites were in Moraine Park (el-

evation 2500 m) and Horseshoe Park (elevation 2600 m), which were broad, flat alluvial valleys dominated by willow (*Salix monticola*, *S. geeyeriana*, *S. planifolia*) and alder (*Alnus tenuifolia*) with a herbaceous understory of *Carex* and grass that averaged ~30 cm in height during late summer. Beaver were once abundant in the study area but declined dramatically after 1940; for example, population estimates in Moraine Park were 315 in 1939–1940, 102 in 1964, 12 in 1980, and six in 1999. Elk were reintroduced to RMNP in 1913–1914 after nearly being extirpated by the late 1800s. They had increased to ~1200 animals in 1940, when Packard (1947) first noted beaver and elk competition for willow. Control efforts reduced the elk population to 500 until 1968, when a policy of natural regulation altered management and elk increased to ~3000 by the late 1990s (Singer et al. 1998). Elk utilization of riparian willow averaged ~85% of leaders browsed annually in 1968–1992 (Zeigenfuss et al. 1999: Fig. 11) as the elk population increased to six times its 1968 level (Lubow et al. 2002: Table 1), evidence that willow utilization rates were both very high and independent of elk population levels for many years. In a comparison of 1937/1946 and 1996 aerial photographs, Peinetti et al. (2002) found that tall willow (>3 m) cover declined by 54% in Moraine Park and 65% in Horseshoe Park. Short willow plants (<1.5 m) have dominated the study area for several decades, probably a result of a change in individual plant stature rather than in willow species composition. Thus, beaver and willow populations have both declined in heavily browsed environments within RMNP.

Experimental design

We experimentally tested the effects of elk browsing on willow (*S. monticola*, a tall shrub) three years after simulated beaver cutting. Morphology, biomass, N, and recovery were compared for 712 stems on plants paired inside (unbrowsed) and outside (browsed) five elk exclosures (treatment replicate) in RMNP (exclosure numbers 3–7 in Moraine and Horseshoe Parks). Elk exclosures were 30 × 46 m in size and were erected in August–November 1994 by randomly locating adjacent paired willow sites in elk winter range and randomly selecting one site for exclosure treatment and the other as a paired control left available to elk (Peinetti et al. 2001, Zeigenfuss et al. 2002). In May 1997, one plant was randomly selected from “the most frequent size type (canopy volume and height)” inside and outside the five exclosures (10 plants in total) and cages were placed around outside plants to protect them from elk browsing during the 1997 growing season (Peinetti et al. 2001:335). In September 1997, all stems (age 7–10 years) from paired treatment and control plants were cut and removed at the ground level, effectively simulating beaver cutting as the initial condition for this study. Neither 1997 shoot biomass nor total aboveground woody biomass differed for browsed

and unbrowsed treatments, which showed, respectively, that browsed plants had probably recovered the biomass removed by elk during the previous winter (Peinetti et al. 2001) and that paired plants probably began this study with a similar initial condition. Paired treatment and control plants also were likely to be in similar hydrologic environments, as they were <20 m apart and were a similar distance from streams. In addition, previous studies in the same areas found that the water table was high enough to be accessible to mature willow (Alstad et al. 1999) and that depth to water table had no effect on willow response to elk browsing (Zeigenfuss et al. 2002). After three years, we again removed all stems (29 August–7 September 2000) from the 10 paired plants to compare treatment effects. Biomass removed by elk (the offtake component of compensatory growth) was not estimated, as we were interested in the *consequences* of elk browsing to beaver. Thus, we compared the standing crop of simulated beaver-cut willow plants that remained after three years of growth in browsed and protected environments.

Sampling and analysis procedures

Whole stems were aged, measured (basal stem diameter and height from cut end to tip of tallest leader), and cut into segments. Segments were sorted into age cohorts (1998, 1999, or 2000), browsed or unbrowsed, and live or dead. Age cohort was determined from the presence of nodes, sympodial branching patterns, leaf presence, and condition of bark (Alliende and Harper 1989, Peinetti et al. 2001); stems and stem segments could be from one of only three possible years, which simplified age cohort classification. Estimates of segment length were obtained from a size-based, stratified random sample of six stems from each of the 10 plants. To include radial growth in the proper year, we adjusted biomass values for 1998 and 1999 by the proportion of annual radial growth, which we developed from width measurements of growth rings on a random sample of 15 stem segments from each age cohort. For example, 1998 stem segments had annual radial growth from 1998, 1999, and 2000. To ensure statistical independence, we randomly selected five different stem segments from this sample and measured ring widths for each of the three years via an integrated system consisting of a Velmex TA Unislide system with ACURite linear encoder and QC 1100 digital readout device (Velmex, Bloomfield, New York, USA), stereoscope, and Measure 2JX software (Version 3.1, Voortech Consulting, Holderness, New Hampshire, USA). Stem segments and leaves from all 712 stems were oven-dried at 65°C until dry and then weighed to compute biomass. Percentage of biomass recovery was estimated by comparing aboveground biomass before and after simulated beaver cutting ($100 \times \text{Biomass}_{2000} / \text{Biomass}_{1997}$) for the same 10 plants. However, because Peinetti et al. (2001) had temporarily fenced control plants to preclude elk browsing during the 1997 growing season, we sub-

tracted biomass of current annual growth (CAG) from both data sets before computing biomass recovery. Percentage N was estimated from 0.1-g samples of dried, ground stem segments and leaves using a LECO CHN1000 analyzer (LECO, St. Joseph, Michigan, USA). All statistical tests were constructed using paired *t* tests. Data were examined for normality using normal probability plots and the Shapiro-Wilk statistic (Shapiro and Wilk 1965), and were \log_e -transformed where necessary.

RESULTS

Browsing effects on stem morphology

Simulated beaver-cut willow plants located outside enclosures were heavily browsed by elk during the study: utilization rates (percentage of leaders clipped) were $86.4 \pm 4.8\%$ ($\bar{x} \pm 1$ SE) for extant year 1998 stems and $92.6 \pm 4.1\%$ for extant year 1999 stems. These data are consistent with previous studies in RMNP that showed elk utilization of willow averaged ~85% annually during 1968–1992 (Zeigenfuss et al. 1999). We found that the utilization rate of extant year 2000 stems was $64.6 \pm 5.9\%$ in early fall 2000, which indicates that substantial summer browsing had occurred before elk concentrated on winter ranges.

Mean number of stems/plant for all three years combined did not significantly differ for unbrowsed and browsed plants; however, the age distribution of stems suggested a strong treatment effect (Table 1a). Year 1998 stems composed 98% of unbrowsed plants but only 58% of browsed plants. Thus, plants protected from elk responded with vigorous sprouting in the first year and added new growth to existing stems in successive years. In contrast, browsed stems probably responded to released apical dominance either by sprouting a new basal stem from the collar (regeneration tissue located between roots and stems just below the soil surface, Del Tredici 2001), which increased stem turnover rate, or by lateral branching of dormant buds located directly below the point of browsing.

Mean stem height was four times greater on unbrowsed plants than on browsed plants (Table 1b). Maximum stem height of browsed plants was only 31.7 cm, and variation among stems was low. Because the height of surrounding herbaceous vegetation in late summer was also ~30 cm, these results suggest that elk were attracted to willow stems after they had emerged from the herbaceous canopy.

Mean stem diameter was greater on stems protected from elk browsing (Table 1c). Stem diameter increased with age for both browsed and unbrowsed plants (Table 1c), but browsed plants did not increase height as they aged (Table 1b). After three years, unbrowsed stems were tall and relatively thin, whereas browsed stems had developed a short and stout form (diameter relative to height was greater).

TABLE 1. Effects of elk browsing on willow (*Salix monticola*) standing crop three years after simulated beaver cutting (fall 1997) inside (unbrowsed) and outside (browsed) elk enclosures ($n = 5$) in Rocky Mountain National Park, Colorado, USA; values are means \pm SE.

Plant trait, by year	Unbrowsed	Browsed	Difference	<i>P</i>
a) No. stems/plant				
1998	69.4 \pm 21.1	41.2 \pm 15.4	27.6 \pm 23.6	0.306
1999	1.7 \pm 0.3	15.2 \pm 4.5	-16.3 \pm 7.2	0.152
2000	0.0	14.0 \pm 6.2	NA	NA
1998–2000	70.4 \pm 21.3	71.0 \pm 21.2	-0.6 \pm 30.8	0.985
b) Stem height (cm)				
1998	111.2 \pm 9.7	26.9 \pm 2.5	84.3 \pm 9.2	<0.001
1999	67.9 \pm 9.1	25.0 \pm 2.4	41.3 \pm 9.0	0.044
2000	NA	28.8 \pm 3.7	NA	NA
1998–2000	110.5 \pm 9.7	26.8 \pm 2.6	83.7 \pm 9.2	<0.001
c) Stem diameter (mm)				
1998	8.1 \pm 0.7	5.6 \pm 0.4	2.5 \pm 0.7	0.022
1999	4.4 \pm 0.6	3.9 \pm 0.3	0.5 \pm 0.3	0.187
2000	NA	3.2 \pm 0.2	NA	NA
1998–2000	8.0 \pm 0.7	4.7 \pm 0.4	3.3 \pm 0.6	0.005
d) No. segments/stem				
1998	1.0 \pm 0.0	1.0 \pm 0.0	0.0 \pm 0.0	0.712
1999	3.6 \pm 0.4	1.9 \pm 0.1	1.7 \pm 0.4	0.023
2000	25.0 \pm 2.6	3.7 \pm 0.5	21.3 \pm 2.3	0.003
e) Segment length (cm)				
1998	64.2 \pm 4.9	8.5 \pm 1.5	54.5 \pm 6.2	<0.001
1999	20.2 \pm 1.8	9.0 \pm 2.1	11.2 \pm 3.0	0.021
2000	5.5 \pm 0.8	15.2 \pm 3.5	-9.8 \pm 4.0	0.071
f) Biomass (g)				
1998	251.0 \pm 122.7	14.2 \pm 4.1	236.0 \pm 123.6	0.007
1999	414.9 \pm 219.7	34.3 \pm 8.7	380.6 \pm 221.4	0.013
2000 woody	659.2 \pm 402.9	80.5 \pm 24.0	578.6 \pm 412.9	0.098
2000 leaves	351.4 \pm 172.4	31.5 \pm 12.0	319.7 \pm 176.5	0.023
1998–2000	1717.8 \pm 907.2	173.4 \pm 48.6	1544.4 \pm 924.9	0.029
g) N (%)				
1998	0.47 \pm 0.09	0.65 \pm 0.07	-0.18 \pm 0.07	0.076
1999	0.60 \pm 0.04	0.77 \pm 0.04	-0.17 \pm 0.03	0.009
2000 woody	0.87 \pm 0.09	0.85 \pm 0.06	0.02 \pm 0.11	0.877
2000 leaves	1.80 \pm 0.11	1.97 \pm 0.13	-0.16 \pm 0.21	0.475

Notes: Year indicates origination year for sections a–c and growth year for sections d–g. NA = not available (no stems present). Biomass and N values for 2000 woody exclude leaves; biomass values for 1998–2000 include leaves. Year 2000 represents current annual growth (CAG). Willow plants were sampled 29 August–7 September 2000. Differences are computed as unbrowsed minus browsed.

Branching was nearly seven times greater on unbrowsed stems (mean 25.0 segments/stem) than on browsed stems (3.7 segments/stem) after three years (year 2000, Table 1d), perhaps because browsing by elk had reduced the number of growing points on plants (Danell and Bergstrom 1989).

Mean segment length was greater on unbrowsed plants for year 1998 and year 1999 stem segments, but greater on browsed plants for CAG (year 2000, Table 1e). Differences were most dramatic in the first year after cutting (1998), when unbrowsed stem segments were an average of 64.2 cm in length and browsed stems were an average of 8.5 cm in length. This may indicate either that elk browsing arrested vertical growth by removing the shoot tip during the first growing season, or that elk browsing after the growing season removed a substantial portion of CAG. In contrast, segment length of CAG shoots was nearly three times

greater on browsed (15.2 cm) than on unbrowsed plants (5.5 cm), a very significant difference considering that, on browsed plants, elk had already removed some length from 65% of the shoots during the summer before measurement. This pattern of fewer but longer shoots on browsed plants is consistent with studies of moose (*Alces alces*) browsing on birch (*Betula*) in Sweden and may suggest that plants had allocated more photosynthates to fewer shoot segments in response to herbivory (Danell and Bergstrom 1989).

Browsing effects on stem biomass

Mean total biomass (1998–2000) was ~10 times greater on unbrowsed plants than on browsed plants (Table 1f). Treatment differences were consistent for all years, with the greatest contrast between unbrowsed and browsed plants occurring in the first year (1998), when biomass averaged 251.0 g on unbrowsed plants

TABLE 2. Effects of elk browsing on recovery of willow (*Salix monticola*) stems (no. stems/plant) and biomass (g) three years after simulated beaver cutting (fall 1997) inside (unbrowsed) and outside (browsed) elk exclosures ($n = 5$) in Rocky Mountain National Park, Colorado, USA; values are means ± 1 SE.

Plant trait, by year	Unbrowsed	Browsed	Difference	<i>P</i>
a) Stem recovery (%)				
1998	148.4 \pm 25.5	78.5 \pm 21.4	69.9 \pm 24.1	0.044
1998–1999	151.0 \pm 26.3	106.7 \pm 26.1	44.3 \pm 29.1	0.203
1998–2000	151.0 \pm 26.3	132.9 \pm 25.9	18.2 \pm 35.9	0.640
b) Biomass recovery (%)				
1998	63 \pm 20	3 \pm 1	59 \pm 19	0.038
1998–1999	84 \pm 28	6 \pm 1	77 \pm 27	0.046
1998–2000	93 \pm 32	NA	NA	NA

Notes: Year indicates origination year for section a and growth year for section b. NA = not available; see *Methods*. Willow plants were sampled 29 August–7 September 2000. Recovery (%) is computed as $100 \times \text{fall 2000/fall 1997}$. Differences are computed as unbrowsed minus browsed.

but only 14.2 g on browsed plants. Leaf biomass also was ~ 10 times greater on unbrowsed plants than on browsed plants, which was consistent with differences in stem height and other morphometrics. The percentage of total biomass composed of dead tissue (not separable by age cohort) was four times greater ($P = 0.031$) on browsed plants ($16.1 \pm 4.1\%$) than on unbrowsed plants ($4.1 \pm 0.9\%$). This suggests that elk browsing may increase the mortality of stems or shoots, either as a direct result of browsing, or as plants shift growth away from browsed shoots (which then die back) to new basal stems arising from the collar (Table 1a) or to elongate unbrowsed leaders (Table 1e).

Browsing effects on N

Percentage N was greatest in leaves and decreased with age of the stem segment for both browsed and unbrowsed stems (Table 1g). Percentage N in older stem segments (1998 and 1999) was higher on browsed than on unbrowsed plants, which is consistent with the general pattern that browsing increases N in above-ground plant biomass (Hobbs 1996). Percentage N in CAG did not differ for either woody material or leaves, which suggests that plants already may have translocated N away from active growing tissues for winter storage in roots and older portions of above-ground plant tissues. This explanation is consistent with observed phenological evidence, because leaf color had already turned from green to yellow/brown when plants were cut.

Browsing effects on stem recovery

In a comparison of standing crop before and after simulated beaver cutting, we found that unbrowsed plants recovered 148.4% of their pre-cut number of stems after one year (1998), whereas browsed plants recovered only 78.5% of stems after one year, but had recovered 132.9% of stems after three years (1998–2000), and at that point did not significantly differ from unbrowsed plants (Table 2a). In contrast, elk browsing

had a large and sustained effect on recovery of stem biomass. After two years (1998–1999), unbrowsed plants had recovered 84% of their pre-cut biomass and browsed plants had recovered only 6% (Table 2b). Thus, recovery of standing-crop biomass was rapid and vigorous following simulated beaver cutting, but was strongly suppressed by intense elk browsing.

DISCUSSION

Intense elk browsing for three years following simulated beaver cutting resulted in willow standing crop that was small, short, and relatively unbranched, with a higher percentage of dead biomass and longer, but far fewer, shoots. In contrast, simulated beaver cutting in the absence of elk browsing resulted in plants that were large, tall, highly branched, and leafy, with a lower percentage of dead biomass and shorter, but many more, shoots. Aboveground biomass was 10 times greater on unbrowsed plants than on browsed plants. Unbrowsed plants had recovered 84% of their pre-cut standing-crop biomass after only two years, whereas browsed plants had recovered only 6%. Thus, the interaction of beaver cutting and intense elk browsing strongly suppressed the height and biomass of willow standing crop, which was much more substantial in the absence of elk browsing.

Elk herbivory effects on N content of simulated beaver-cut willow

Herbivory can increase plant N via increased demand by browsed stems and increased availability in the soil due to urine and feces deposition (Hobbs 1996). We found that percentage N of 1- and 2-year-old stem segments was higher on plants browsed by elk than on unbrowsed plants, but percentage N of leaf and woody CAG did not differ. Previous studies in RMNP found higher leaf N on elk-browsed willow in June, but these effects had diminished by September (Alstad et al. 1999, Peinetti et al. 2001). In studies of moose browsing on birch in Sweden, the leaves of moderately

browsed plants contained more N than did slightly browsed plants in July, but differences had diminished by October (Danell et al. 1985). Thus, our results confirm that browsing increases stem N, but effects diminish as plants enter senescence in late summer. Hobbs (1996:701) listed six studies that suggested either "increased allocation of nitrogen to leaves" or "increased uptake of nutrients by roots" as mechanisms that contribute to compensatory growth following plant defoliation. Our findings suggest that the interaction of beaver cutting and intense elk browsing can negate the positive effects of increased N on standing crop, as we found that browsed plants were much smaller than unbrowsed plants even though they had a higher N content.

Herbivore effects on standing crop and mechanisms of compensatory growth

Elk.—Compensatory growth mechanisms may be influenced by how woody plants are browsed. Large herbivores browse the tips of leaders, which removes mostly CAG. A large percentage of leaf and woody biomass remains intact, which contributes to the growth of new shoots via photosynthesis. Browsing frequency can be high because shoot regrowth rapidly becomes suitable as forage. Released apical dominance can activate dormant buds below the point of browsing or can increase the number and size of lateral shoots, which increases branching and growth rates (Honkanen and Haukioja 1998). When new shoots are within reach of elk, then repeated browsing may create hedged plants, which often can maintain high forage productivity. However, browsing can reduce or eliminate sexual reproduction in willow, maintain plants in a vegetative or juvenile growth phase, and reduce plant fitness (Kay 1994). Summer elk browsing is especially detrimental to beaver because summer growth may provide a high percentage of beaver food on stems procured in the fall for a winter food cache (Baker and Cade 1995) and because summer browsing can be more detrimental to compensatory growth mechanisms than dormant-season use (Danell et al. 1994).

Beaver.—Beaver typically cut entire stems near ground level rather than the tips of leaders. Frequency of beaver cutting is relatively low compared to ungulate browsing because it takes several years for regrowth to become large enough to justify the cost of procuring a stem in terms of predation risk, energy expended, and transport to a safe eating site, winter food cache, dam, or lodge (Baker and Hill 2003). In addition, beaver may avoid juvenile sprouts because they can contain higher concentrations of phenolic glycosides or other defensive chemicals (Basey et al. 1990). Willow can rapidly recover stems cut by beaver (Kindschy 1985, 1989). In our study, willow regained 151% of stems and 84% of biomass in only two years following complete removal of all stems (Table 2). Because the frequency of herbivory is usually low and plants can rap-

idly recover lost biomass and height, beaver-cut plants are more likely to reach sexual maturity and produce seed than are plants browsed by elk.

Beaver and elk interaction.—The combined effects of beaver cutting and intense elk browsing strongly suppressed the standing crop of willow in our study. After three years, browsed plants had averaged only 12% of CAG woody biomass, 9% of leaf biomass, and 10% of total biomass relative to paired unbrowsed control plants (Table 1), and after two years had recovered only 6% of their pre-cut biomass (Table 2b). In a previous study, these same plants recovered equally from elk herbivory: CAG, leaf biomass, and woody biomass were similar for browsed and unbrowsed treatments under similar elk densities in the absence of beaver cutting (Peinetti et al. 2001). In an African browsed environment, where the large herbivore density was 10 animals/km² and greater kudu (*Tragelaphus streliceros*) was the dominant species, the deciduous tree *Combretum apiculatum* showed exact compensation to clipping (simulated browsing), but strong undercompensation to cutting (stem removal to simulate fire or stem breakage, which also simulated beaver) (Bergstrom et al. 2000). In this experiment, trees either were clipped via a 55% one-time reduction in number of annual shoot tips <6 mm in diameter, or were cut at 0.5 m above ground, and then compared to unclipped/uncut controls after all three treatments were subjected to large herbivore browsing for eight months. The biomass of clipped trees was similar to controls, but biomass of cut trees was only 15% of controls, evidence that browsing strongly suppressed cut trees. This analogous system suggests that our results may have some general application, as we found that the combined effects of beaver cutting and intense elk browsing strongly suppressed the standing crop of willow that was evident when either herbivore operated independently.

What mechanisms explain how willow can tolerate either complete, infrequent cutting by beaver, or partial, frequent browsing by ungulates, but not both? The ability of willow to vigorously sprout following complete removal of aboveground biomass suggests that it has a high level of nutrients stored in roots, which can be rapidly shunted from roots to shoots following herbivory (Strauss and Agrawal 1999). However, this mechanism probably reduces root reserves and places plants in a stressed state until new sprouts can recover the stem and leaf tissue necessary for photosynthesis, which is a prerequisite of other compensatory growth mechanisms such as increased photosynthetic rate, leaf N, and growth rate. Also, when beaver cut tall stems, they can place regrowth under the canopy of surrounding herbaceous vegetation where further herbivory can prevent new stems from escaping competition for light and increasing their growth rates (Raven 1992). In our study, all three age cohorts of browsed willow averaged <30 cm in height and plants continued to sprout new

stems each growing season, which suggests that browsed plants were unable to gain a competitive advantage for light above the herbaceous canopy. Alternatively, if some stems or shoots on a plant escape beaver or elk herbivory, then the plant may compensate for partial stem or shoot loss via a more complete suite of mechanisms than is available under more intense herbivory. Thus, individual shoots, stems, plants, and populations are likely to exhibit a range of morphologies that reflect their particular browsing history and the compensatory growth mechanisms available in response to herbivory.

Beaver alter future plant–herbivore interactions when they cut the stems of woody plants. Breaking apical dominance can improve plant quality for herbivores because it increases the number of vigorously growing shoots, which are rich in nutrients and sugars and poor in proteinaceous material (Honkanen and Haukioja 1998). Intense disturbance to plants by beaver, other herbivores, coppicing, fire, or floodwater can enhance plant susceptibility to herbivory via induced neotany, increased leaf size but reduced toughness, and reduced levels of defense (Spiller and Agrawal 2003). For example, elk and grasshoppers were attracted to arroyo willow (*S. lasiolepis*) that had vigorously sprouted following a fire, probably because regrowth was more succulent and nutritious (Stein et al. 1992).

When beaver cut tall woody plants, they increase stem turnover rate and place regrowth within easy reach of herbivores. Although large herbivores can break stems and make existing food or regrowth available to themselves and other species (Bergstrom 1992), beaver cutting can greatly enhance the process of shrub height reduction in browsed environments, with effects that can cascade to a new suite of herbivores. In Africa, megaherbivores (elephants, *Loxodonta africana*) break and trample woody vegetation as they browse, which places regrowth within easy reach of mesoherbivores and creates a trophic cascade of altered plant–herbivore interactions and competition among herbivores (Fritz et al. 2002). Thus, beaver herbivory represents a model system where intense disturbance alters future plant–herbivore interactions.

Interaction of beaver and large herbivores as an ecological driver

Given our experimental evidence, we offer a series of predictions about the interaction of beaver cutting and intense elk browsing as the cause of declining beaver–willow ecosystems. We suggest that beaver and willow are mutualists, and this mutualism collapses in heavily browsed environments where asymmetrical competition favors elk over beaver. We refer to elk and willow for simplicity, but suspect that these mechanisms apply equally well to other large ungulates or livestock, to other woody plant species that are benefited by beaver, and to other systems where anthro-

pogenic or natural disturbance mimics the effects of beaver cutting.

First, we predict that when beaver cut willow in a heavily browsed environment, they can drive a tall willow community into an alternative state consisting of short, hedged plants that are vegetatively productive but less likely to mature and produce seed. Lacking sexual reproduction, this state will persist only until plants die of old age or other causes, which may take many decades. Second, we predict that elk browsing decreases the suitability of willow as beaver food by reducing the biomass of twigs and bark on stems and their preference by beaver, leading to beaver declines where willow limits populations. In these systems, willow that provides adequate biomass of twigs and bark is *necessary* for beaver as a winter food supply, but short or heavily browsed willow (or no willow) is *sufficient* for elk, because elk can subsist on herbaceous forage in areas lacking deep winter snow (Skovlin 1982). Thus, in riparian systems where elk are overabundant, they will outcompete and exclude beaver. Third, we predict that when beaver populations decline, wetlands will lose key willow establishment and survival processes provided by beaver dams and canals, such as increased sediment deposition and soil moisture, and higher water tables spread across larger areas. Loss of these functions will decrease the distribution and abundance of willow and will contribute to the eventual collapse of beaver-engineered wetlands, with effects cascading throughout the ecosystem. Fourth, we predict that the carrying capacity for elk is altered by the presence or absence of beaver. Where beaver dams and canals create landscapes dominated by open water, then beaver declines will probably increase elk carrying capacity in a process equivalent to the agricultural practice of wetland drainage to increase livestock forage production. Beaver may also increase carrying capacity for elk in dry environments where dams raise the water table and increase productivity enough to overcompensate for surface area lost to beaver ponds. Thus, we predict that when beaver cut tall willow, and intense elk browsing suppresses the height and biomass of willow available to beaver, then the interaction of beaver and elk herbivory will create a feedback mechanism that decreases beaver and willow, but either increases or decreases elk depending on local conditions.

RESEARCH AND MANAGEMENT IMPLICATIONS

Further research is necessary to determine the level of additional herbivory that beaver–willow communities can tolerate before willow becomes unsuitable to beaver. As a guide to recognize trends, we suggest that a beaver–willow community is likely to be *stable* if ungulate or livestock utilization of willow is absent or limited to the perimeter of the community and interior stems are mostly full height; *declining* if herbivory has penetrated the interior of the community and suppressed regrowth of beaver-cut stems; and *recovering*

if interior or perimeter plants show evidence of previous hedging, but include many unbrowsed leaders.

Trapping, disease, and other limiting factors may cause beaver populations to decline, in addition to competition with other herbivores. If beaver decline, then the distribution and abundance of willow may decline in areas formerly influenced by beaver. Where beaver and willow have both declined, how can we determine cause and effect? It may be important to consider that suitable willow may be necessary for beaver, but beaver are sufficient for willow, because willow can establish and persist without beaver. Thus, the location and success of willow establishment and survival processes relative to beaver activity and browsing pressure by other herbivores may provide clues for deciphering cause and effect on the landscape.

How can managers restore a beaver–willow mutualism, given that browsing by elk (or other herbivores) has suppressed willow height and biomass enough to preclude beaver? Because willow utilization rates may remain high under a wide range of elk population levels, elk control via culling, hunting, or fertility reduction may not reduce competition with beaver unless elk numbers are severely reduced. Redistribution of elk, in combination with population control, may be necessary to reduce or eliminate elk use of willow. Fencing can protect willow from elk, but riparian pastures must be large enough to sustain a beaver colony. Herding or hazing livestock away from riparian willow has been effective on western rangelands (B. W. Baker, *personal observation*), and may have application for wild ungulates. Predation risk also can reduce elk use of riparian areas. In Yellowstone National Park (YNP), USA, a 70-year absence of wolves (*Canis lupus*) as apex predators coincided with a period of poor cottonwood (*Populus angustifolia* and *P. trichocarpa*) recruitment, which suggests that elk had lost their fear of browsing in riparian areas (Beschta 2003). After wolves were reintroduced to YNP, areas with higher predation risk (low visibility and/or presence of escape barriers) had young cottonwood that was taller and less browsed by elk (Ripple and Beschta 2003). Recent observations in YNP suggest that the release of willow is even stronger than cottonwood in areas of wolf use, and corresponds to areas of new colonization by beaver (D. W. Smith, *personal communication*). We suggest that the presence of ponds, dams, and canals built by beaver will further impede elk escape from wolves in riparian areas, because microtopography that restricts visibility or escape can increase predation risk to elk (Ripple and Beschta 2003). The positive effects of wolves on release of willow from elk browsing probably overcompensate for wolf predation of beaver, and result in a net benefit to beaver. If willow is completely protected from elk browsing via high predation risk, fencing, or other methods, then the use of fire to remove existing stems may benefit subsequent beaver restoration, because new willow shoots that arise from be-

low ground are likely to be more palatable and productive as beaver food than shoots released from the tips of severely hedged stems.

We conclude that the interaction of beaver cutting and intense elk browsing can strongly suppress the standing crop of willow, especially willow height and biomass. We predict that a lack of willow stems that are suitable as winter food for beaver will cause beaver populations to decline, creating a feedback mechanism that reduces beaver and willow populations and either increases or decreases elk populations, depending on local conditions. Thus, intense herbivory by ungulates or livestock can disrupt beaver–willow mutualisms that naturally occur in less competitive environments.

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