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BEAVER HERBIVORY OF WILLOW UNDER TWO FLOW REGIMES: A COMPARATIVE STUDY ON THE GREEN AND YAMPA RIVERS

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ABSTRACT.—The effect of flow regulation on plant-herbivore ecology has received very little attention, despite the fact that flow regulation can alter both plant and animal abundance and environmental factors that mediate interactions between them. To determine how regulated flows have impacted beaver (*Castor canadensis*) and sandbar willow (*Salix exigua*) ecology, we first quantified the abundance and mapped the spatial distribution of sandbar willow on alluvial sections of the flow-regulated Green River and free-flowing Yampa River in northwestern Colorado. We then established 16 and 15 plots (1 m × 2.7 m) in patches of willow on the Green and Yampa Rivers, respectively, to determine whether rates of beaver herbivory of willow differed between rivers (Green versus Yampa River), seasons (fall–winter versus spring–summer), and years (spring 1998–spring 1999 versus spring 1999–spring 2000). Areal extent of willow was similar on each river, but Green River willow patches were smaller and more numerous. Beavers cut more stems during fall and winter than spring and summer and cut over 6 times more stems (percentage basis) on the Green River than on the Yampa River. We attribute the between-river difference in herbivory to higher availability of willow, greater beaver density, and lower availability of young Fremont cottonwood (*Populus deltoides* subsp. *wislizenii;* an alternative food source) on the Green River. Flow regulation increased willow availability to beaver by promoting the formation of island patches that are continuously adjacent to water and feature a perimeter with a relatively high proportion of willow interfacing with water.

Key words: Castor canadensis, *foraging behavior, herbivory, regulated flows,* Salix exigua.

Patterns of herbivory are influenced by many factors including the abundance and distribution of plants and herbivores and environmental factors that mediate interactions between them (Gessaman and MacMahon 1984, Huntly 1991, Augustine and McNaughton 1998). The regulation of river flow (i.e., the managed release of flows from large dams) strongly affects abundance and distribution of riparian plants (Nilsson et al. 1991, Stromberg et al. 1991, Auble et al. 1994, Naiman and Decamps 1997, Poff et al. 1997) and movement, behavior, distribution, and density of mammals living in riparian zones (Miller 1999, Andersen et al. 2000, Breck et al. 2001, Falck et al. 2003). Because of these effects, regulated flows should also alter the ecological relationships between mammalian herbivores and plants that are closely tied to riparian ecosystems.

Andersen and Cooper (2000) addressed this issue by comparing the impact of mammalian herbivores feeding on tree saplings on ecologically matched free-flowing and flow-regulated rivers. Noting that a small mammal, *Microtus montanus*, reduced seedling and sapling survivorship more on the regulated than on the free-flowing river, they attributed the difference to the elimination of large floods that periodically decimated riparian small mammal populations along the free-flowing river. Their study highlighted the importance of understanding the role of flow regimes when attempting to clarify ecological relationships between plants and herbivores in floodplain ecosystems.

On many rivers in western North America, beavers (*Castor canadensis*) and willow (*Salix* spp.) maintain a close ecological association in that willow can be an important forage species for beavers (Hall 1960, Baker and Cade 1995) and the foraging activity of beavers can affect growth patterns and density of willow (Kindschy 1985, 1989). Little is known about how these interactions are influenced by river flow regime. Considering that flow regulation can alter both the distribution of willow (Stromberg et al. 1991, Merritt and Cooper 2000) and the abundance of beavers (Breck et al.

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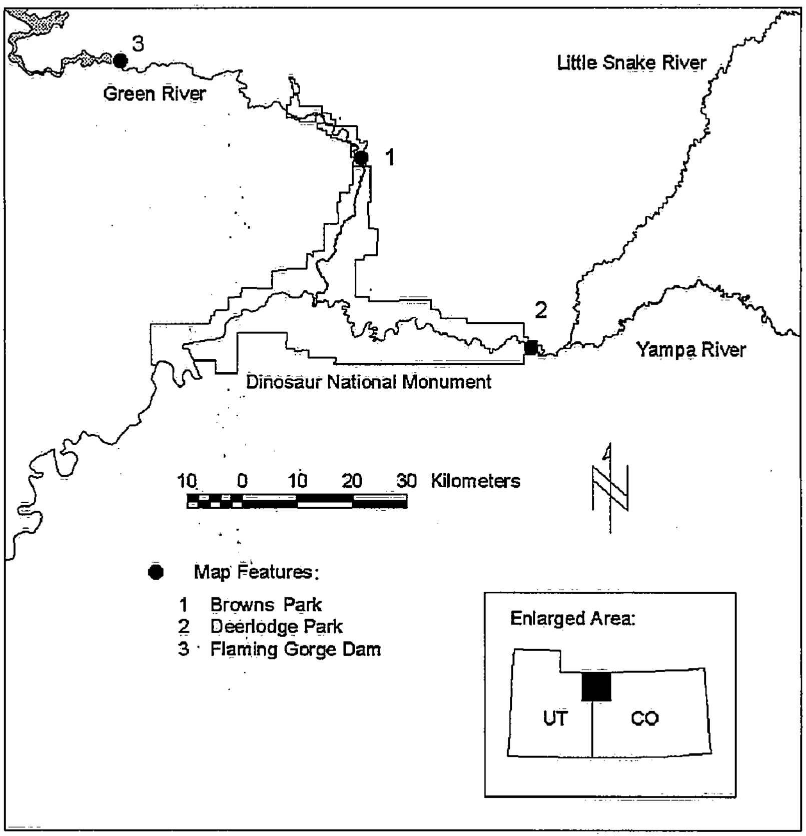

Fig. 1. Location of study areas and Flaming Gorge Dam on the Green and Yampa Rivers in northwestern Colorado, 1998–2000.

2001), it is likely that ecological links between beavers and willow will also be altered.

In this study our objective was to determine if and how flow regulation altered patterns of herbivory by beavers on willow. To do this, we studied beaver–sandbar willow (*Salix exigua*) dynamics on 2 rivers matched in most attributes except the nature of their flow: one was free-flowing and the other regulated. We quantified abundance and mapped spatial distribution of sandbar willow on each river and then quantified differences in percentage of willow stems cut by beavers between rivers, seasons, and years. We also compared estimates of total amount of willow biomass removed by beavers.

STUDY AREA

We conducted our study on a 10-km section of the Green River in Browns Park National Wildlife Refuge and an 8.6-km section of the Yampa River in Deerlodge Park (Fig. 1). At these locations both rivers are 6th-order tributaries of the Colorado River and historically were influenced by snowmelt-driven spring floods. The Yampa River is free-flowing and maintains its meandering form through Deerlodge Park. Flows of the Green River at Browns Park have been regulated by Flaming Gorge Dam since late 1962; as a result, the river is in transition from a meandering to a braided system (Merritt and Cooper 2000). The main premise of our study design was that prior to completion of Flaming Gorge Dam, the Green and Yampa Rivers featured similar flow regimes (Fig. 2) and maintained similar riparian ecosystems. Details of the ecosystems and the validity of our assumptions are in Cooper et al. (1999), Andersen and Cooper (2000), and Merritt and Cooper (2000).

On the Yampa River annual spring floods maintain the distribution of vegetation. Patches

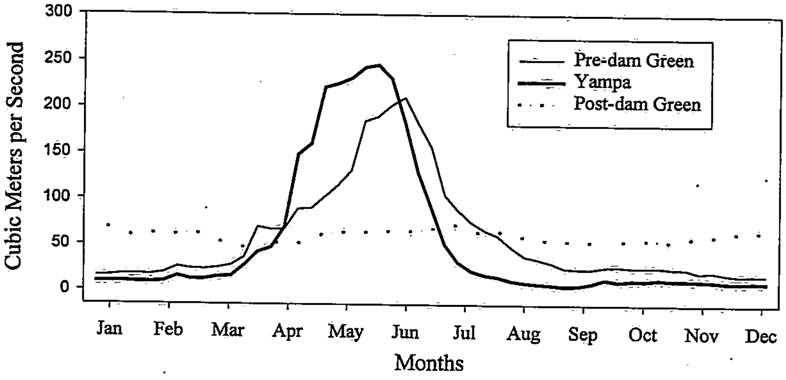

Fig. 2. Average yearly flow for the Green River (pre-dam 1940–1962 and post-dam 1962–1995) and Yampa River (1940–1995). Peak and base flows on each river were similar prior to the completion of Flaming Gorge Dam. Flow regulation since 1962 on the Green River has resulted in elimination of the peak flow and increase in base flow.

of sandbar willow are found at the edge of the active channel (i.e., the portion of the channel kept free of perennial vegetation by the spring floods), and patches of young Fremont cottonwood (*Populus deltoides* subsp. *wislizenii*), another important forage species for beavers, are found on vertically accreting bars within the active channel (Cooper et al. 1999). During periods of flooding (April–July), willow and cottonwood patches may be inundated, depending upon the size of the flood peak, making both species more accessible to beavers. By August the Yampa River drops to its base flow, which exposes large sandbars that separate the river from vegetation. Locations of sandbars and subsequently the location of the base flow channel vary from year to year.

On the Green River flow regulation has altered the distribution of plants by altering the magnitude of peak and base flows, erosion and deposition processes, and associated edaphic conditions (Merritt and Cooper 2000). Two important changes have been the formation of islands in mid-channel and the elimination of point bar dynamics. As a result, sandbar willow has shifted from a primarily bank species to a primarily island species, patches of young cottonwood trees are rare, and upland vegetation is establishing to the edge of the active channel (Merritt and Cooper 2000).

METHODS

Willow Abundance and Distribution

On each river section we quantified the number of willow patches, size of each patch, and total area of willow patches per kilometer of river. We defined a willow patch as any area where willow was the dominant woody species and measured at least 3 m deep (perpendicular to the river). We quantified the number of willow patches by surveying the length of each study area. Surveys were conducted on the ground by walking the length of both shores and paddling the length of each river section. We determined the size of each willow patch by pacing the length and width of each patch at several locations depending on patch size and shape. Patch location and dimensions were plotted in GIS coverages generated from aerial photographs taken in July 1997 and August 1995 on the Green and Yampa Rivers, respectively. Two patches were considered distinct if separated by ≥20 m. We used ArcView to quantify number of patches, total area of willow on each river section, mean patch size, and percentage of willow area on islands. An island was defined as any area within the active channel with vegetation. To develop a comparable estimate between rivers, we divided the number of patches and total area of patches by the length of the study reach for each river.

Willow Plots

In December 1997 we established 16 plots on the Green River and 15 plots on the Yampa River. The plots were 1 × 2.7 m (W × L) and had a midpoint located 1.5 m from the active channel margin. We placed plots close to the active channel because our observations indicated that beavers were utilizing willow principally in areas close to water. To select plot locations, we started from the upstream end of each willow patch and randomly selected a point within the first 25 m along the river's edge to place the first plot. The remaining plots were spaced evenly from this point, with 50 m separating plots. Thus, the number of plots in a willow patch increased with patch length. If a patch was less than 25 m long (measured along the bank), we placed a single plot in the patch at a randomly selected point along the river's edge. We dispersed plots throughout the study length of each river and attempted to place at least 1 plot on every patch of willow, but logistics limited us to approximately 75% of the willow patches on each river.

In each plot we collected data on size and number of available live stems and size and number of beaver-cut stems at 5 points in time (mid-April 1998, 1999, 2000 and mid-September 1998, 1999). During each survey cut stems were marked with tacks and/or paint to prevent their being counted again in subsequent surveys. We used dial calipers to measure stem diameters at 3 cm aboveground to the nearest 0.5 mm. Generally, branching of stems did not occur until well above 3 cm aboveground. However, when branching occurred at a height <3 cm, we considered each branch as a separate stem. Stems <7 mm were not counted. We measured stems cut by beaver at the level of the cut or 3 cm aboveground, whichever was less. Very occasionally, a branch from a stem was cut. In this case we recorded diameter of the cut branch and measured live stem at the same height as the cut branch. Both measurements were used as independent measurements in the analyses. We used data from the 1st (April 1998) survey to calculate mean density of willow stems (number of live stems per area of plot) for each river and performed a 2-sample t test to test for statistical differences between rivers. We report actual significance levels for tests.

During fall and winter on the Yampa River, many of our plots were separated from the base flow channel by large sandbars that became exposed as river flows decreased. We suspect this influenced foraging activity of beavers and thus we recorded whether or not the base flow channel ran adjacent to plots. If water from the base flow channel was within 1 m of a plot, we considered the plot adjacent to water; otherwise it was recorded as not adjacent to water. We calculated the mean percentage of stems cut in plots adjacent and not adjacent to water on the Yampa River during fall–winter periods combined across years. We applied an arcsine transformation to the portion of stems cut in each plot and used a t test on the transformed data to test for statistical difference between plots adjacent and not adjacent to water. We report untransformed means followed by their asymmetrical confidence limits (Sokal and Rohlf 1981:419).

From early June through early July 1999, a controlled "flood" was created on the Green River in Browns Park that featured a peak discharge rate 2.2 times greater than the mean post-dam annual peak. This flood was the first relatively large flood (>250 $m^3 \cdot s^{-1}$) on the Green River since 1986 and deposited a few to 50 cm of sediment in different locations along the river in Browns Park (S. Breck personal observation). This sediment accretion resulted in the loss of 6 plots for the mid-September 1999 and mid-April 2000 surveys.

Analyses of Percent Willow Cut

We used likelihood-based methods (Buckland et al. 1997, Burnham and Anderson 1998) to quantify strength of evidence for alternative models explaining patterns of willow herbivory between rivers. The approach has been formalized in techniques for selecting among competing models of ecological phenomena (Buckland et al. 1997, Hilborn and Mangel 1997, Burnham and Anderson 1998) and is measured by Akaike's Information Criterion (AIC; Akaike 1973). Estimating "weight," or probability a given model is the best approximation to truth among the models considered, is a means for reporting the relative support for alternative models, where the sum of weights from the candidate list of models is 1. Thus, a model with a weight of 1 has complete support, a model with a weight of 0 no support (Burnham and Anderson 1998).

We used data from all the surveys, with the exception of stems cut prior to the April 1998 survey which were excluded from analysis, to investigate the relationship between the percentage of willow cut by beavers and 3 independent variables: season (fall–winter or spring–summer), river (Green or Yampa), and year (spring 1998–spring 1999 or spring 1999–spring 2000). We predicted that the percentage of stems cut would be greater during fall–winter

TABLE 1. Results of the AIC model selection procedure (see Methods) to determine the model that best explains patterns of willow cutting by beavers on the Green and Yampa Rivers in northwestern Colorado, September 1998–April 2000. NPAR is the number of parameters, QAICc is a version of Akaike's information criteria adjusted for overdispersion, ΔQAICc is QAIC differences relative to the smallest QAIC value in the set, and weight is an estimate of the likelihood of each model (Burnham and Anderson 1998). Variables in models are season (September–April and April–September), river (Green and Yampa Rivers) and year (spring 1998–spring 1999 and spring 1999–spring 2000). An asterisk (*) indicates an interaction between 2 variables and | indicates all possible combinations of the 3 variables.

Model	NPAR	QAICc	ΔQAICc	Weight
season river	3	–249.78	0	0.94
year river season	4	–243.06	6.72	0.03
season river season*river	4	–242.87	6.91	0.03
river	2	–195.47	54.30	0.00
year river	3	–190.02	59.76	0.00
year river year*river	4	–188.96	60.81	0.00
season	2	–126.27	123.51	0.00
year season	3	–121.92	127.86	0.00
intercept	1	–107.14	142.64	0.00
year	2	–103.86	145.92	0.00
season|river|year	8	–3.51	246.26	0.00

(Jenkins and Busher 1979, Hill 1982) and on the Green River because of the spatial distribution of willow. We generated a linear model that reflected these predictions as well as other competing models that included interaction terms and other combinations of the 3 variables (see Table 1 for a complete list of models).

We used Proc GENMOD with the log-linear link option that assumes a poisson distribution (SAS 1999) to analyze each model and create output required to calculate AIC values. The small-sample correction of AIC adjusted for overdispersion (QAICc; see Lebreton et al. 1992, Burnham and Anderson 1998:53) was used to generate a weight for each model.

Biomass Removal

To estimate the amount of food biomass removed by beavers, we applied Baker and Cade's (1995) model that converts measures of sandbar willow stem diameter and density to estimates of amount of food ($g \cdot m^{-2}$). We used measurements of live stems from the fall 1998 and 1999 surveys to calculate the mean amount of food biomass ($g \cdot m^{-2}$) available to beavers. We then used measurements of cut stems from the spring 1999 and 2000 surveys to calculate the mean amount of food biomass removed ($g \cdot m^{-2}$) during the intervals fall 1998–spring 1999 and fall 1999–spring 2000. We tested for differences in the amount of food biomass available and utilized between rivers using a 2-sample t test with plots as replicates. We performed a separate test for each time period (i.e., fall 1998–spring 1999 and fall 1999–spring 2000).

RESULTS

Willow Abundance, Distribution, and Density

Total area occupied by willow patches ($m^2 \cdot km^{-1}$) was almost identical on the 2 rivers (Green River: 10,630 $m^2 \cdot km^{-1}$, Yampa River: 10,607 $m^2 \cdot km^{-1}$). Patches were more numerous (4.0 per km) and, on average, smaller (3700 m^2) on the Green River than on the Yampa River (2.9 per km and 4146 m^2). The percentage of willow area on islands was 3.6 times greater on the Green River (51%) than the Yampa River (14%). Mean density of stems in plots ($\pm s$) was lower on the Green (10.1 ± 2.6 stems $\cdot m^{-2}$, $n = 16$) than the Yampa River (15.2 ± 2.6 stems $\cdot m^{-2}$, $n = 14$), but the difference was not statistically significant ($t = -1.29$, $P = 0.205$).

Patterns of Willow Cutting by Beaver

Based on QAICc weights (Table 1), percentage of willow stems cut by beavers over the study duration was overwhelmingly supported by the model showing a difference between rivers and seasons. Over the 2-year study, the proportion of willow stems cut ($\bar{x} \pm s_{\bar{x}}$) by beavers was more than 6 times greater on the Green River (36.9% ± 0.05) than on the Yampa River (5.8% ± 0.02), and over 2 times greater during fall and winter (28.5% ± 0.05) than during spring and summer (11.3% ± 0.03; Fig. 3). Averaging the percentage of stems cut over an entire year, we found little difference between years, 19.2% ± 0.04 and 20.8% ± 0.05

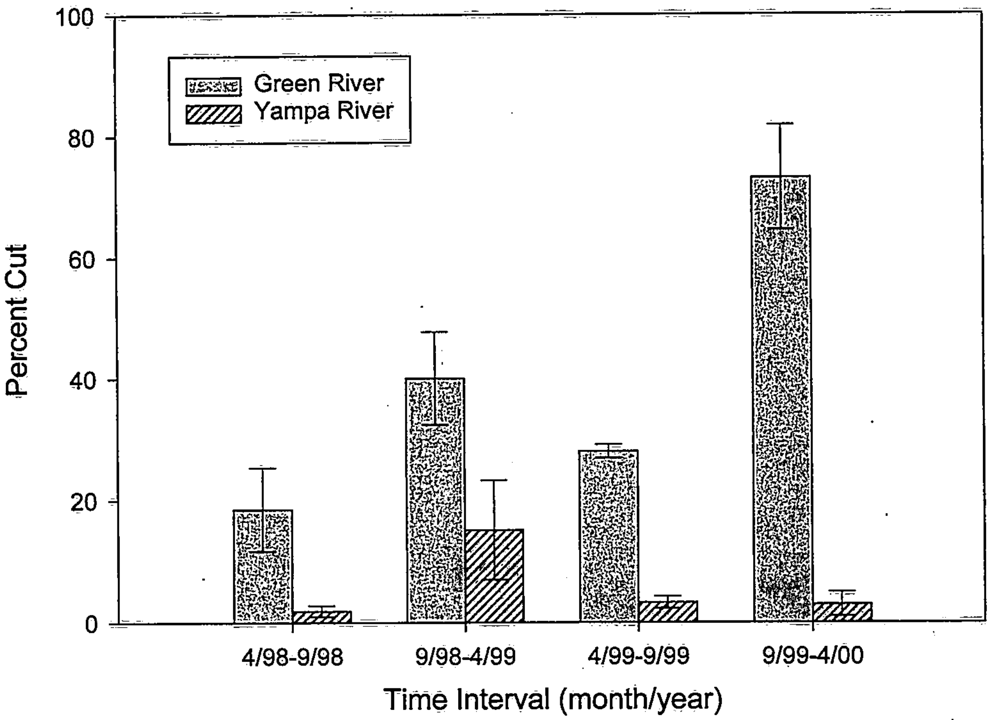

Fig. 3. Percentage of willow stems cut by beavers ($\bar{x} \pm s_{\bar{x}}$) in plots on the Green and Yampa Rivers in northwestern Colorado during 4 consecutive time intervals (2 during spring–summer months and 2 during fall–winter months).

in the 1st and 2nd year, respectively, which explains why the variable "year" was not in the top model. On the Yampa River during fall–winter periods, the base flow channel ran adjacent to 2 of 15 plots in the 1st year and 3 of 15 plots in the 2nd year. Mean percentage of stems cut in plots adjacent to the base flow was much higher (44.5%, 7.7%–81.2%, $n = 5$) than in plots far from the base flow (1.9%, 0.0%–4.7%, $n = 25$; $t = -5.31$, $P < 0.001$).

Willow Biomass

In fall 1998 and 1999, mean amounts of food biomass available to beavers on the Yampa River were greater than on the Green River, but the differences were not statistically significant (Table 2). Conversely, the amount of food removed by spring 1999 and spring 2000 was 2.8 and 15.6 times greater, respectively, on the Green River than on the Yampa River (Table 2).

DISCUSSION

At the time of our study, the areal extent of willow patches was similar between rivers, and we could not detect a statistical difference in either stem density within patches or in willow biomass density. The primary difference between willow distribution and abundance on the rivers was in its spatial arrangement. Most willow on the Green River was on islands and, because of that river's relatively stable flow regime, never far from the river's edge. In contrast, most willow on the Yampa was located along the river bank, and during low flow periods some patches were far from water. We believe this difference in spatial arrangement directly affected availability of willow to beavers and, combined with other changes associated with regulated flows, explains differences in patterns of herbivory we documented between rivers.

Over the course of the study, beavers removed over 6 times more willow stems (percentage basis) from plots on the Green River than on the Yampa River (36.9% versus 5.8%, respectively). Greater herbivory on the Green River is also reflected in the amount of food biomass removed. For example, from fall 1998 through spring 1999, beavers removed 2.8

TABLE 2. Amounts of willow biomass ($g \cdot m^{-2}$) available in fall and removed by the following spring for the Green and Yampa Rivers. Differences between rivers were compared using a 2-sample t test. Fewer plots were sampled in fall 1999 on the Green River because of a flood that caused sediment to bury 6 plots.

	Green River		Yampa River		
	($\bar{x} \pm s_{\bar{x}}$)	n	($\bar{x} \pm s_{\bar{x}}$)	n	P
Available fall 1998	142.7 ± 30.9	16	198.7 ± 29.4	15	0.201
Removed by spring 1999	76.6 ± 22.8	16	27.8 ± 16.5	15	0.097
Available fall 1999	101.8 ± 19.9	10	173.0 ± 34.8	15	0.134
Removed by spring 2000	70.3 ± 19.7	10	4.5 ± 3.5	15	0.001

times more food biomass and 2.6 times more stems (percentage basis) on the Green River. Similarly, from fall 1999 through spring 2000, beavers removed 15.6 times more food biomass and 24 times more stems (percentage basis) on the Green River.

Three factors possibly help explain the greater amount of willow cut by beavers on the Green River. First, beaver density was slightly higher on the Green River (0.5 colonies $\cdot$ river km^{-1}) than on the Yampa River (0.35 colonies $\cdot$ river km^{-1}; Breck et al. 2001). However, assuming a linear relationship between density of beavers and amount of willow cut, higher beaver densities on the Green River cannot alone account for difference in amount of willow cut.

Second, abundance of Fremont cottonwood, a preferred forage for beaver (S. Breck personal observation), was lower on the Green River. This forced beavers to rely more on willow for forage. Breck et al. (2003) documented that total abundance of young Fremont cottonwood was over 5 times greater on the Yampa River than on the Green River and that individual Yampa River beavers, on average, cut more cottonwood than Green River beavers. Hall (1960) documented similar relationships between beavers, aspen, and willow, where beavers preferred aspen, but if unavailable increased their dependence on willow.

Finally, availability of willow was higher on the Green River primarily because stable flows (Fig. 2) and an altered spatial distribution of willow (i.e., 51% of the total area of willow on the Green River was on islands compared to 14% on the Yampa River) created a situation where willow was in close proximity to water year-round. Willow close to water should be associated with less predation risk and smaller energetic cost during foraging (Basey and Jenkins 1995), making it a more attractive forage than willow (or other species) far from water. In contrast, on the Yampa River during fall and winter when beavers did most of their cutting, location of willow relative to the river was dependent upon location of the base flow channel. Cutting activity was substantial (44.5% of stems cut) in plots where the base flow channel ran adjacent to willow but very light (1.9% of stems cut) in plots where the base flow channel was not adjacent.

Greater accessibility of willow and subsequent impacts on trophic dynamics between beavers and willow on the Green River may have important ecological ramifications. For example, greater willow accessibility appears to support higher beaver densities on the Green River (Breck et al. 2001), despite almost 5 times fewer cottonwood trees on the Green River. As the Green River continues to change from a meandering system to a braided system, more islands are likely to develop (Merritt and Cooper 2000), which should in turn increase the total amount of willow present. More easily accessible willow may in turn promote further increases in density of beavers on the Green River. Ecological ramifications of higher densities of beavers could be important for species like cottonwood, whose population on the Green River is susceptible to beaver herbivory (Breck et al. 2003).

Consequences of beaver herbivory to the structure of willow patches are unclear. The greater herbivory on the Green River may be causing lower stem density there, at least within the first 3 m of willow patches (10.1 ± 2.6 and 15.2 ± 2.6 stems $\cdot$ m^{-2} on the Green and Yampa Rivers, respectively). On the other hand, willow on the Green River may be able to compensate for herbivory better than willow on the Yampa River because growing conditions for willow appear to have been improved by river regulation (Merritt and Cooper 2000, Breck unpublished data).

Overall, the 6-fold increase in percentage of stems removed suggests that beavers have become a more important force in the ecology of willow on the regulated Green River than on the free-flowing Yampa River. Whether this postulated shift in importance among resident riparian herbivores is a general pattern accompanying shifts in flow regimes is unknown. Taken together, however, our comparative assessment of beaver herbivory and shifts in importance hypothesized for both small mammal and insect herbivores (Andersen and Cooper 2000, Andersen and Nelson 2002), at these and other sites on the Green and Yampa Rivers, suggest that this is an important area for research on numerous rivers and streams now regulated throughout the world.

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