Ecological Applications, 10(5), 2000, pp. 1384–1399
© 2000 by the Ecological Society of America

PLANT–HERBIVORE–HYDROPERIOD INTERACTIONS: EFFECTS OF NATIVE MAMMALS ON FLOODPLAIN TREE RECRUITMENT

DOUGLAS C. ANDERSEN[1,3] AND DAVID J. COOPER[2]

[1]*United States Geological Survey, D-8220, P.O. Box 25007, Denver, Colorado 80225-007 USA*
[2]*Department of Earth Resources, Colorado State University, Fort Collins, Colorado 80523 USA*

Abstract. Floodplain plant–herbivore–hydroperiod interactions have received little attention despite their potential as determinants of floodplain structure and functioning. We used five types of exclosures to differentially exclude small-, medium-, and large-sized mammals from accessing Fremont cottonwood (*Populus deltoides* Marshall subsp. *wizlizenii* (Watson) Eckenwalder) seedlings and saplings growing naturally on four landform types at an alluvial reach on each of two rivers, the Green and Yampa, in Colorado and Utah. The two study reaches differed primarily as a result of flow regulation on the Green River, which began in 1962. Landforms were a rarely flooded portion of the alluvial plain, geomorphically active slow- and fast-water channel margin sites on the Yampa reach, and an aggrading side channel on the Green. Small-mammal live-trapping and observational data indicated that, with minor exceptions, the kinds of mammals eating cottonwood within each reach were identical. We monitored condition and fates of individual cottonwood plants from October 1993 through the 1997 growing season. Differences in survival and growth were noted both within and between reaches, and both due to, and independent of, mammalian herbivory. Comparisons of cottonwood growth and survivorship among exclosures and between exclosures and controls indicated that a small mammal, *Microtus montanus,* reduced seedling and sapling survivorship at the Green River reach, but to a lesser extent (seedlings) or not at all (saplings) on the Yampa reach. In contrast, reductions in sapling height increment attributable to medium- and large-sized herbivores were detected only at the Yampa site. We suggest that these differences are a result of (1) flow regulation allowing *Microtus* populations to escape the mortality normally accompanying the large, snowmelt-driven spring flood, as well as regulation promoting a herbaceous understory favorable to voles, and (2) greater browsing pressure from overwintering deer and elk at the Yampa reach, unrelated to flow regulation. Within areas used by foraging beaver, the probability of a sapling being cut by beaver was similar on the two reaches. This study suggests that changes in riparian plant–herbivore relationships due to shifts in river hydrology may be a common and important consequence of river regulation.

Key words: alluvial arid-land rivers; browsing; Dinosaur National Monument; Fremont cottonwood growth; Green River; mammalian herbivory; Microtus montanus; *plant–herbivore–hydroperiod interactions; population dynamics;* Populus deltoides; *regulated river; riparian vegetation; Yampa River.*

INTRODUCTION

Riverine riparian zones are recognized as vital ecosystem components at spatial scales ranging from the landscape to the biosphere (Malanson 1993, Naiman et al. 1993, Ward et al. 1999). The ongoing degradation and loss of these systems (e.g., Sparks 1992, Dynesius and Nilsson 1994) has focused attention on the need for both basic and applied research on riparian community development and maintenance (National Research Council 1992). Naiman and Rogers (1997) suggest that riparian community structure results from a hierarchy of processes, led by physical factors (Junk et al. 1989, Bayley 1995, Hupp and Osterkamp 1996, Power et al. 1996, Hughes 1997, Naiman and Décamps 1997), and followed by biological and physical alterations directly generated through animal activity. In most cases, however, the form and magnitude of effects due to riparian animals are unknown. For example, with the exception of beaver (*Castor canadensis*), the role of native herbivores in structuring North American floodplain plant communities under natural flow regimes has received little attention (Bryant 1988, Kay 1994, Keigley 1997).

This gap in our basic knowledge of riparian systems underlies the poor understanding of the overall ecological effects of river management. Whereas a large number of studies have shown that damming a river results in downstream changes in the physical factors (e.g., flows and fluvial processes) that affect riparian vegetation structure (Tabacchi et al. 1996), very few have addressed how river regulation can influence riparian systems through effects on resident terrestrial animals (Nilsson and Dynesius 1994). In particular, no

Manuscript received 28 April 1999; revised 17 September 1999; accepted 25 October 1999; final version received 18 November 1999.

[3] E-mail: doug_andersen@usgs.gov

study to our knowledge has evaluated effects of a primary structure-altering activity, herbivory, interacting with a modified river flow regime.

Flow regulation could modify plant–herbivore–hydroperiod (PHH) interactions at least two ways. First, a change in hydroperiod can induce physiological stress in a floodplain plant (Osmond et al. 1987), which in turn reduces its resistance or tolerance to herbivore damage (Mattson and Haack 1987, but see Karban and Myers 1989). Secondly, a change in hydroperiod can modify herbivore foraging behavior or population density, e.g., by increasing survivorship rates in floodplain populations (Hoslett 1961, Sheppe and Haas 1981) or disrupting reproductive processes (Nefdt 1996).

In this paper, we address the question of whether shifts in PHH relationships could be responsible, at least in part, for the decline in floodplain trees noted along some regulated rivers in the western United States (Johnson et al. 1976, Bradley and Smith 1986, Rood and Mahoney 1990, Stromberg and Patten 1992, Rood and Mahony 1995, Rood et al. 1995). We focus on PHH linkages involving mammals, assessing effects by monitoring young trees differentially protected from various combinations of these herbivores along two alluvial river reaches that differ markedly in level of regulation.

Study Sites

We worked in the upper Colorado River Basin, along the regulated Green River and the free-flowing Yampa River within Dinosaur National Monument (DNM) in northeastern Utah and northwestern Colorado (Fig. 1). These rivers, which originate in the Rocky Mountains and then descend through semiarid regions, are characterized by large snowmelt-driven fluctuations in discharge and large sediment loads (Andrews 1986). Our study sites were in alluvial valleys, known locally as "parks," that supported a similar suite of herbivorous mammal species: Deerlodge Park (DLP; elevation ~1705 m) on the Yampa River, and Island Park (IP; ~1510 m) on the Green River, downstream from its confluence with the Yampa (Fig. 1). The active channel is primarily sand in both reaches. Immediately adjacent upland is semidesert shrubland that grades into piñon–juniper woodland on surrounding ridges. We chose sites for intensive study within each reach subjectively, based primarily on accessibility and the requirement that they harbored physiognomically similar stands of young (<2 m tall) Fremont cottonwood trees (*Populus deltoides* Marshall subsp. *wizlizenii* (Watson) Eckenwalder; plant taxonomy follows Weber and Wittmann [1966]), the dominant structural component of the riparian community.

The Island Park site (Fig. 2) was an aggrading 18–24 m wide side channel (Fig. 2B) whose floor featured a continuous canopy of cottonwood saplings in 1993, when we began the study. Herbaceous cover was sparse under the saplings, but high along the channel margins.

We worked at three sites differing in landform attributes within Deerlodge Park (Fig. 2A). The topographically highest site (DL1) was a nearly level floodplain surface (hereafter, "plain") that had been inundated only three times in the 50 years prior to initiation of the study: in 1957, 1974, and 1984. Clusters of saplings were intermixed among scattered mature cottonwood (>150 years old), and herbaceous cover was well developed. The second Deerlodge site (DL2) was within an aggrading portion of the active channel margin (hereafter, "slow-water margin") where herbaceous cover was sparse. We considered this site to be most similar in physical attributes to the IP site. The third site (DL3; Fig. 2A) was located within the active channel where flood current velocity was higher than that at DL2. Surface topography at DL3 (hereafter, "fast-water margin") was complex and modified annually. Herbaceous cover was very sparse in 1993.

Historic human influence on conditions at our study sites was largely through livestock grazing. Outside of river regulation at IP, current disturbance is minimal. Livestock grazing has been allowed within IP, but not DLP, since 1986. We never saw evidence of livestock in the vicinity of our IP study site. In contrast, trespassing cattle probably lightly grazed the DL1 area during most years of the study (1993–1997).

Both IP and DLP are important winter range for mule deer and elk. Several hundred elk, and even larger numbers of mule deer were occasionally seen in the vicinity of DLP during winter (S. Petersburg, *personal communication*). Numbers at IP were lower, with sightings of up to 130 elk and somewhat fewer mule deer.

Details of historic and current hydrologic regimes of these rivers are presented elsewhere (Cooper et al. 1999). The flow patterns of the Yampa and Green rivers above their confluence were quite similar prior to the 1963 closure of Flaming Gorge Dam on the Green. Mean annual discharge of the Green River near Greendale (Fig. 1) and of the Yampa River at DLP was 58.1 and 54.6 m^3/s, respectively (Andrews 1986). Flood peaks typically ranged between 400–600 m^3/s and occurred between 15 May and 15 June. The magnitude of the flood peak on the Green River in IP, downstream from the Yampa/Green confluence, has been reduced by ~25% since closure of Flaming Gorge Dam.

Methods

Mammalian herbivore communities

Herbivorous mammals potentially present at DLP and IP were identified using published distribution maps and habitat affinities (Durrant 1952, 1963, Armstrong 1972, Bogan et al. 1988, Fitzgerald et al. 1994), and unpublished data from DNM files. Concurrent livetrapping studies at DLP (Falck 1996, Miller 1998) and IP (D. C. Andersen, *unpublished data*) documented the kinds and abundances of small mammals actually present, but we relied on observations made incidental to

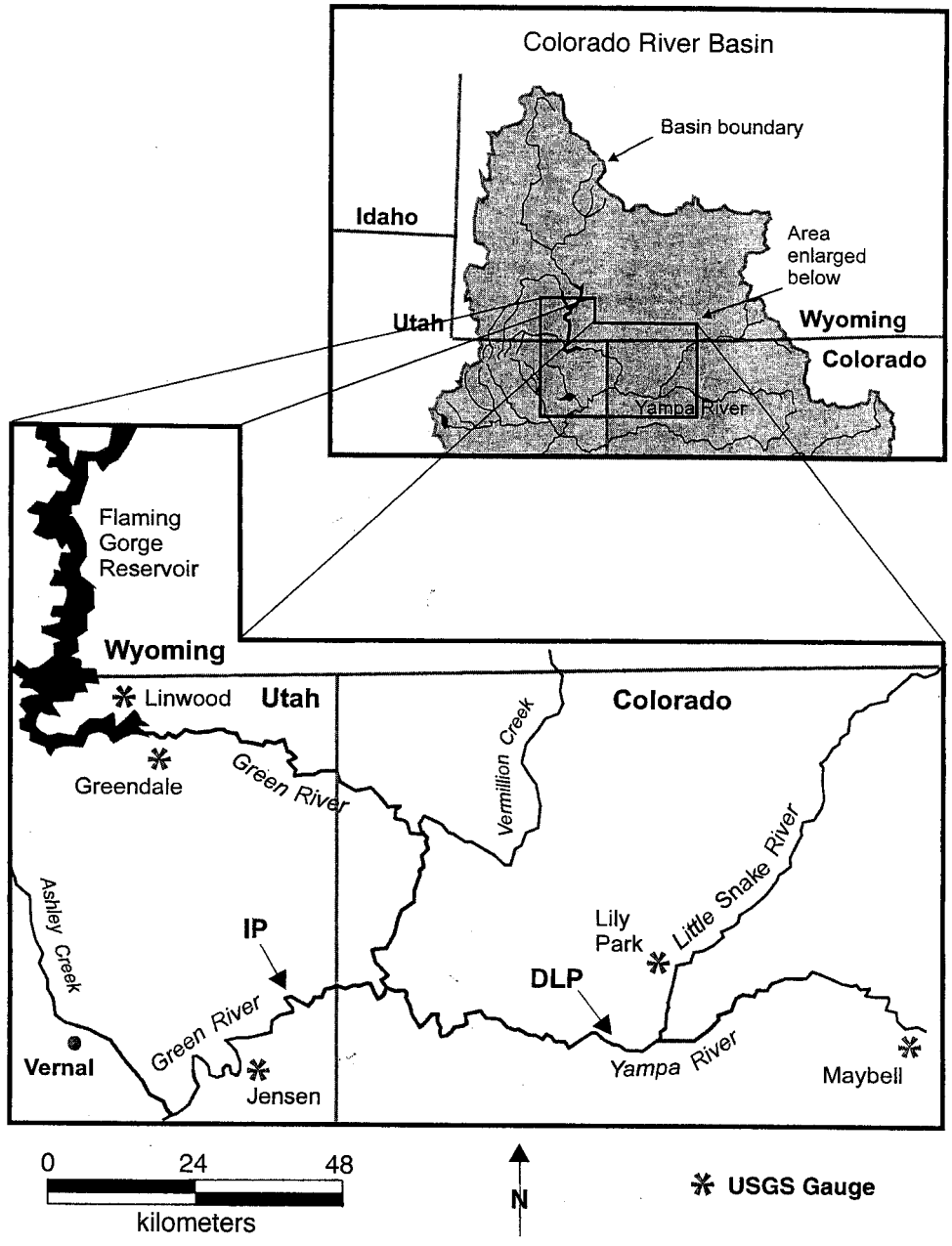

FIG. 1. Study reach locations within the upper Colorado River Basin at Island Park (IP) on the Green River, downstream of Flaming Gorge Dam and Reservoir, and Deerlodge Park (DLP) on the Yampa River in northwestern Colorado. The location of USGS gauging stations (starred) used in estimating flows are also shown.

field work to verify presence of larger mammals. We made no systematic attempt to survey for, or monitor levels of, herbivory by insects or other taxa.

Capture–recapture trapping at IP (1 grid, 4 sessions) and DLP (2 grids, 5 sessions) was used to assess small-mammal densities. The grids, which were uniformly large (Fig. 2), were first trapped in 1994 after the spring flood. Subsequent sessions were conducted both prior to and following the flood in 1995. Details of methods are in Falck (1996) and Miller (1998).

Effects of mammalian herbivores

We quantified effects from mammalian herbivores on cottonwood growth and survivorship using exclosures. We established four treatments by protecting groups of plants from different combinations of large, medium, and small mammals (Table 1). Small mammals (e.g., mice and voles) had their access to plants precluded by hardware cloth; medium-sized mammals (e.g., rabbits and beaver) were excluded using either hardware cloth or 1.2 m tall ranch wire, and large mam-

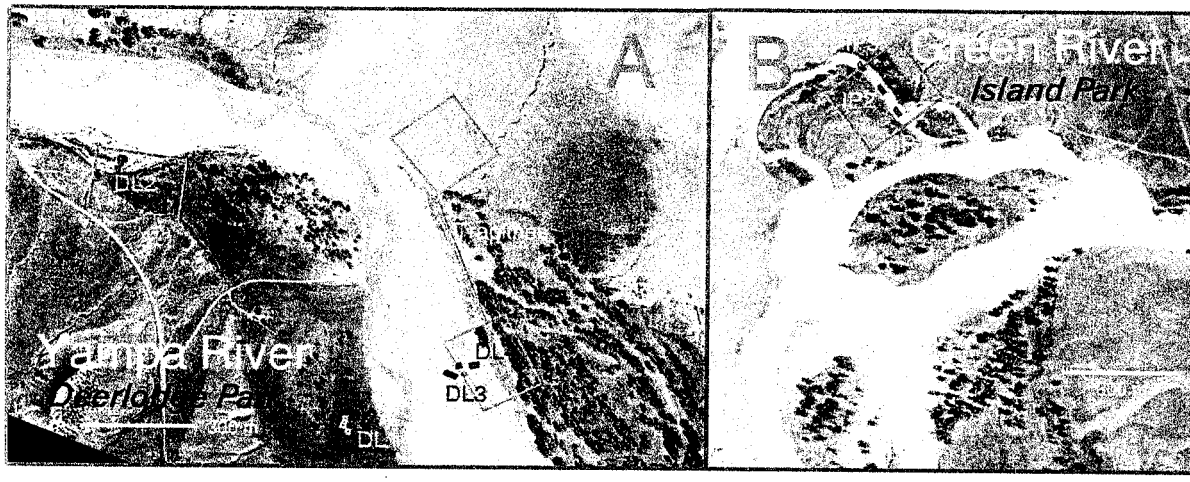

FIG. 2. (A) Rectified aerial image of Deerlodge Park (Yampa River reach) showing locations of exclosures and outlines (green rectangles) of three small-mammal trapping grids. Exclosure set DL1 is on the rarely flooded "plain," DL2 is at the "slow-water margin" and DL3 and DL4 are at the "fast-water margin." Rows of small-mammal traps (the wide green line) linked an upland grid to the grid assessing the small-mammal community at DL3. The image was generated from photographs taken in September 1995. Dark spots on the floodplain are individual large, mature cottonwood trees. Flow is from lower right to upper left. (B) Rectified aerial image of the Island Park side channel site (Green River reach) showing the locations in the channel of exclosure sets IP1, IP2, and IP3 (red) and the small-mammal trapping grid (outlined in green). The image was created from an aerial photograph taken 22 August 1984, shortly after the record spring flood and when the channel contained flowing water and an exposed bed free of vegetation. Dark spots are mature cottonwood trees. Flow is from right to left.

mals (e.g., deer and elk) were stopped by either hardware cloth or a ~2.5 m tall fence of either barbed wire or barbed wire above ranch wire (Table 1). Plants inside control areas, which were not fenced, were accessible to groups of all sizes.

Exclosures, as well as control areas, were configured as either small or large. The H and HH exclosures (see Table 1 for configuration coding rationale) were small (~1.2 m on a side and ~1 m tall) and included sides buried ~20 cm and a hardware cloth lid. All other exclosures were "large" and included open tops, but actual size varied, in part due to physical constraints imposed by the IP site: 4.5 × 3.6 m (IP), 5 × 5 m (DLP), or 10 × 20 m (DLP).

The large B+R and small HH exclosures nominally provided the same treatment (Table 1: plants protected from medium- and large-sized mammals), but in fact the treatments differed slightly. The B+R exclosure's ranch wire was a barrier to adult, but not necessarily young, cottontails, whereas even young rabbits were excluded in the HH treatment. Analogously, the barbed wire of the B exclosure may not have been a barrier to very young ungulates.

No type of exclosure, with the possible exception of HH (Table 1), provided a herbivore with complete refuge from predators. Small predators known to be present (e.g., short-tailed weasel, *Mustela erminea*) could easily pass through the ranch wire.

Three replicates of each treatment were constructed within the IP channel in autumn 1993. For convenience, a B, B+R, and R exclosure were built as a contiguous set, in a linear arrangement. A control area of similar size (LC) was added to each set, and the same spatial sequence (LC:B:B+R:R) was used at three locations along the channel, designated IP1, IP2, and IP3 (Fig 2B). The small H and HH exclosures and small control areas (SC) were disjunct; a group consisting of one of each was placed near each of the IP large exclosure sets and assigned the same locational identifier. Only one SC plot was established in 1993; the other two were established in April 1994.

A set of large exclosures consisting of a B, R, and B+R was also constructed in a contiguous manner at DLP, but the associated control area was disjunct (<50 m from the other members of the set). A single set was established at each of the plain (DL1), slow-water margin (DL2), and fast-water margin sites (DL3) in autumn 1994 (Fig. 2A). Thus, the B, R, and B+R treatments were replicated within the DLP reach, but not on any DLP landform. Treatments involving small exclosures were confined to one landform, the slow-water margin. Three replicates, each made up of a spatially proximate H, HH, and a small control area (SC), were placed around the DL2 large exclosure set in February 1995.

When it became apparent in 1996 that migration of the flood channel would destroy exclosure set DL3, another B+R exclosure (of unique size, 10 × 20 m) was constructed nearby as a partial replacement. That exclosure, together with nearby, previously unmonitored saplings selected as controls, constituted set DL4 (Fig. 2A).

We centered a single 1-m^2 plot within each small

TABLE 1. The eight possible presence/absence (P/A) combinations for three size groups of mammalian herbivores at a locality, and the five combinations (four exclosure treatments plus a nonfenced control) used to evaluate effects of herbivory in this study.

Size group status (presence/absence)			Configuration code	Exclosure size†	Exclosure materials and design
Large	Medium	Small			
A	A	A	H	small	hardware cloth (1.3-cm mesh) sides and lid
A	A	P	HH	small	hardware cloth sides and lid, with 3-cm holes at ground level
			B+R	large	barbed wire (3 strands, ~30-cm spacing) above ~1.2 m ranch wire
A	P	P	B	large	barbed wire to ~2.5 m height (7 strands, ~30-cm spacing)
A	P	A	not tested		
P	A	A	not tested		
P	P	A	not tested		
P	A	P	R	large	ranch wire (5 × 10 cm mesh) ~1.2 m high
P	P	P	SC		small† control; no fence present
			LC		large† control; no fence present

Notes: The "only small mammals present" (AAP) treatment was created in two configurations, and control areas could also differ in size. Configuration codes are based on fencing materials and design (note letters in bold).

† Small = ~1 m on side; large = at least 4 m on a side.

exclosure and SC control, and a rectangular array of 12 (IP) or 25 (DLP) disjunct plots (25 x 50 cm) within each large exclosure and LC control (except DL4, see below). Three parallel plots (1 x 18.5 m) separated by 1.5 m were placed in the B+R exclosure of DL4. Plot locations were permanently marked using metal pins and, in some cases, baling twine stretched at ground level. We mapped the location of each live woody stem emerging from the ground within each plot, and classified it by species and condition. Because Fremont cottonwood does not spread vegetatively (Braatne et al. 1996), each mapped cottonwood stem was entered as a unique point in a geographical information system and treated as an individual plant in all analyses. The within-plot censuses conducted in large exclosures and large control areas are the basis for estimates of initial plant density.

We measured plant height (ground surface to tip) to the nearest centimeter using a retractable steel tape. During subsequent censuses, each plant was remeasured and its condition reassessed, and all new plants appearing inside plots added to the monitored population. We augmented sample sizes in 1996 by adding plants located outside plots (typically <1 m from a plot edge) to the population of monitored plants. No plants were individually marked until 1996, when white plastic electrical ties were attached to ~25% of the saplings. All DL4 control saplings were marked with a 1.5 cm diameter metal tag attached by wire or plastic tie.

We performed separate analyses to test for effects of herbivory on cottonwood seedlings (hereafter, "SL") and saplings ("SP"). We classified each plant having a thin (≤3 mm at ground level), unbrowsed primary stem <40 cm tall as a seedling, i.e., a plant that had experienced ≤1 growing season. Root systems of such plants excavated at nearby locations supported the seedling classification, as did seedling height growth data collected in concurrent studies (Cooper et al. 1999). In a few cases, extremely rapid growth during the subsequent growing season indicated the "seedling" was actually a sprout, and it was reclassified. A short, unbrowsed plant with primary stem >3 mm in diameter was assumed to be a sprout emerging from an older root system. We classified these plants and all plants ≥40 cm tall as saplings. In the rare instance where two or more tall stems were separated by <1 cm at ground level, we assumed the stems represented a single sapling, and only the tallest stem was monitored.

Refining sources of mammalian herbivory.—We compared survivorship and growth among treatments and controls to assess effects of the three size classes of mammalian herbivores (Table 1). We differentiated browsing damage (due solely to mammals) from injury due to insects or physiological stress by the presence of a clipped or torn primary stem or branch. We assumed damage by mice or voles would show the same form in the large exclosures as in HH. We used tooth marks to confirm this assumption, and also to differentiate among cases of injury in large exclosures potentially due to small- or medium-sized mammals. Although no resident mammal's dietary preference for Fremont cottonwood is precisely known, use of other *Populus* species, particularly aspen (*P. tremuloides*), by mammals is well documented (Finley 1958, Spencer 1984, Barnes et al. 1989, Keigley 1997). Combined with knowledge of both the mammalian herbivores present and how flooding affects their populations, the tree damage data allow us to infer whether regulation could be responsible for observed differences in cottonwood survival or growth.

Effects of mammals on plant survivorship.—We used log-linear modeling to test for the presence of an effect from mammalian herbivores on the survivorship of young cottonwoods in the large exclosures. We performed separate analyses for each combination of plant age class (seedlings, saplings) and reach (DLP, IP), modeling cell frequencies within four-way tables gen-

erated using the binary variable Fate (alive or dead) and explanatory categorical variables: treatment (Extype), location (Set), and monitoring period (Period). Statistical acceptability of models was based on the criterion that the P value for the Pearson χ^2 value >0.05 (Engelman 1996). The presence of an interaction term linking an explanatory variable and Fate in the most parsimonious, statistically acceptable model indicates that survivorship is determined, at least in part, by that explanatory variable. We used χ^2 to isolate specific differences within or between factors deemed important based on the log-linear analysis. An estimate of age-specific cottonwood survivorship through a particular time interval (ϕ) was then calculated as the proportion of those plants originally present (n_0) that were alive at the end of the interval (n_f), pooling treatments or locations not significantly different. Where appropriate, raw data are presented in the text as (n_f/n_0), along with the calculated ϕ value, in order to show sample size. Equality of survivorship among treatments was tested using χ^2 on fate data for populations pooled across replicates (= sets). Although pooling ignored potential spatial variability (addressed via the log-linear modeling), it increased statistical power otherwise constrained by small sample sizes. In cases where equality was rejected, we conducted pairwise Fisher's exact tests to determine which exclosure types were different, using a two-tailed test statistic with a Bonferroni correction [$\alpha = (0.05/n)$, where n is the number of tests performed]. We also conducted Cochran's test of linear trend (Wilkinson and Engleman 1996:61) using types ordered as discussed below. Finally, the exclosures at IP and DLP were established and occasionally censused at different points in time. Thus, we directly compared ϕ values for a given period among exclosure types within a reach, but converted ϕ values to a per year basis for other comparisons. Chi-square tests involving derived annual rates are based on n_f and $n_{(0\text{-}f)}$ values calculated by applying annual rates to n_0. We used an arcsine square-root transform on the annual rates prior to conducting ANOVA.

We hypothesized that herbivory would reduce survivorship, and thus predicted ϕ values associated with small exclosures at each study reach would show a ranking of $\phi_H > \phi_{HH} > \phi_{SC}$, where the subscript refers to exclosure size and type (see Table 1). We predicted the rank of ϕ values for sets of large exclosures would be $\phi_{B+R} > \phi_R \approx \phi_B > \phi_{LC}$, with the most uncertainty concerning the relative values of ϕ_R and ϕ_B. We expected $\phi_{SC} = \phi_{LC}$ and $\phi_{HH} = \phi_{B+R}$ at each reach, and we expected ϕ_H values to be similar at IP and DL2, assuming that factors other than herbivory were similar.

Effects of mammals on plant growth.—We calculated the growth increment, γ, of a plant surviving through a particular time period as the difference between height measurements on the two occasions delineating the period. Negative γ values could result where browsing removed the shoot apex or dieback occurred. We corrected γ values within each location for changes in soil surface elevation due to erosion or sediment deposition using the mean change measured at sets of sediment stakes (marker pins or wood lath) placed in or near exclosures. Excluding beaver-cut stems, we predicted the ranking of mean height increments, adjusted as appropriate for initial plant height (see *Environmental conditions: Initial vegetation structure*) to parallel that for survivorship, e.g., within each set of large exclosures, $\gamma_{B+R} > \gamma_R \approx \gamma_B > \gamma_{LC}$ (most protected > intermediate > least protected). We tested the prediction using ANOVA. We included initial plant height as a covariate because of the known increase in growth increment with sapling age (Braatne et al. 1996:71).

Means are presented as $\bar{X} \pm$ SE, with n in parentheses. Statistical analyses were performed using SYSTAT 6.0.1 for Windows (SYSTAT 1996) or ABstat 6.02 (ABstat 1989).

Results

Mammalian herbivore assemblages

Up to 15 species of mammalian herbivores were actually or very likely using the riparian areas at IP and DLP (Falck 1996; D.C. Andersen, *unpublished data*). The "large mammal" group consisted of mule deer (*Odocoileus hemionus*), moose (*Alces alces*; a single observation at IP), and elk (*Cervus elaphus*), all of which browse cottonwood, plus pronghorn (*Antilocapra americana*; observed in the floodplain only at DLP), which probably do not normally eat cottonwood. Medium-size species that eat cottonwood were beaver (*Castor canadensis*) and cottontail rabbits (*Sylvilagus audubonii* and/or *S. nuttallii*). Eight "small" mammals were trapped: the deer mouse (*Peromyscus maniculatus*), piñon mouse (*P. truei*), bushy-tailed wood rat (*Neotoma cinerea*), western harvest mouse (*Reithrodontomys megalotis*), Ord's kangaroo rat (*Dipodomys ordii*), Great Basin pocket mouse (*Perognathus parvus*), and montane vole (*Microtus montanus*). Food preference data gleaned from the literature indicated only four of these species were likely to eat cottonwood: the folivorous montane vole and bushy-tailed woodrat, and the omnivorous deer mouse and piñon mouse. Of these, only the montane vole and deer mouse were present at crude densities exceeding 1 individual/ha at the study sites (Table 2). Voles were relatively uncommon on the DLP grids, and few were captured near exclosures (M. Falck, *personal communication*). In contrast, many individuals at IP were captured in the channel and near exclosures. Deer mice tended to be more abundant at DLP (Table 2), but were captured near exclosures at both reaches.

Nonmammalian herbivores noted to be present in or near exclosures included cottonwood leaf beetles (*Chrysomela scripta* Fabricus) at both reaches, Canada Geese (*Branta canadensis*) at DLP, and carp (*Cyprinus carpio*) at IP.

TABLE 2. Crude density estimates (individuals/ha) for the most common small-mammal species captured in the riparian zone of the study reaches at Island Park (IP) and Deerlodge Park (south bank, DL2; north bank, DL3).

Species	Trophic code	Study reach and grid	Trapping session: 1994 July–August	1995 April	1995 May–June	1995 June	1995 July–August
Peromyscus maniculatus	O	DL2	18	3	10	20	16
		DL3	81	11	10	16	27
		IP	16	...	5	5	5
Microtus montanus	F	DL2	...	1	...	2	2
		DL3	4	...	...	...	...
		IP	8	...	3	8	12
Reithrodontomys megalotis	G	DL2	9	...	...	...	<1
		DL3	...	...	...	...	...
		IP	1	...	...	...	...
Dipodomys ordii	G	DL2	...	2	1	1	1
		DL3	17	9	13	3	2
		IP	5	...	...	...	...
Perognathus parvus	G	DL2	...	...	...	...	...
		DL3	...	...	...	...	...
		IP	2	...	<1	<1	<1

Notes: Density was calculated by dividing the number of unique individuals captured during a session by the area enclosed by the grid (without any buffer area). Grid locations are shown in Fig. 2. An ellipsis indicates no captures. Codes for trophic categories are: F, folivore; O, omnivore; G, granivore.

Environmental conditions

Initial vegetation structure.—On a reach basis, the initial densities of live cottonwood saplings at IP ($\bar{X}$ = 4.0 ± 0.8 plants/m^2) and DLP ($\bar{X}$ = 5.4 ± 1.0 plants/m^2) were not significantly different (1994 data: t = 1.12, df = 22, P = 0.27). Initial densities varied among locations within each reach, however. Sapling density declined along the IP channel in 1993 from 7.0 plants/m^2 at IP1 to 1.0 plants/m^2 at IP3 (ANOVA; F = 16.1, df = 2,9, P = 0.001). There was similar variation among DLP landforms, from plain (9.0 plants/m^2) through slow-water margin (5.5 plants/m^2) to fast-water margin (3.0 plants/m^2) (F = 3.46, df = 2,9, P = 0.077). About 12% of sapling-sized (≥40 cm tall) plants in IP large exclosures were willow (*Salix exigua*), whereas exclosures at DLP contained few woody plants other than cottonwood. Saltcedar (*Tamarix ramosissima*) saplings were present at both IP and DLP, but uncommon within the exclosures or control areas.

The initial (1993) mean height of cottonwood saplings in the IP channel varied inversely with density. Bonferroni pairwise comparisons following ANOVA (F = 5.42, df = 2,79, P = 0.006) indicated mean sapling height in IP1 ($\bar{X}$ = 79 ± 4.8 cm, n = 47) was significantly (P = 0.027) less than that in IP2 (103 ± 7.7 cm, n = 29), and the latter was marginally (P = 0.051) less than that in IP3 (107 ± 20.8 cm, n = 9). Most (75%) saplings had been browsed, but only one had been cut by a beaver.

Initial (1994) heights of cottonwood saplings also differed among the three landforms monitored at DLP, but in a manner unrelated to density. Saplings at the slow-water margin (DL2, $\bar{X}$ = 62 ± 3.3 cm, n = 75) were significantly shorter than those growing on the plain (DL1, $\bar{X}$ = 109 ± 5.6 cm, n = 112) or fast-water margin ($\bar{X}$ = 117 ± 11.8 cm, n = 35). Pre-study sapling browse damage (nonbeaver) at DLP was more common at the slow-water margin (30%) than at the plain (6%) or fast-water margin site (8%). Evidence of pre-study beaver damage was only present in DL1: 12% of the live saplings there featured a main (vertical) stem that originated from a beaver-cut stump.

Hydrology.—Details of hydrology within the study reaches are provided in Cooper et al. (1999). Briefly, peak flood flows at DLP were 498, 216, 520, 571, and 607 m^3/s for the years 1993 to 1997, respectively. The peak stage in DLP during the unusually low 1994 spring flood was ~1 m lower than the peak stage observed in 1993 or 1995, whereas the unusually large 1997 peak stage was probably >60 cm higher than the 1993 peak.

The channel containing the Island Park exclosures was dry throughout the 1994 flood season. In contrast, the 1995 flows through IP resulted in complete inundation of all exclosures for at least four weeks (21 May through 23 June). Both deer mice and montane voles were trapped in the channel prior to the 1995 flood.

All or most of the three Deerlodge sites also escaped inundation during the unusually low 1994 flood. Trapping indicated that the area surrounding DL2 harbored numerous deer mice and a few voles, but most voles were captured >75 m from an exclosure. The area surrounding DL3 held numerous deer mice, but no voles. Only the 1997 spring flood inundated the Deerlodge plain (DL1: Fig. 2A), although groundwater rose to within 20 cm of the ground surface during the 1996 flood. No trapping took place at DL1, but voles were observed moving through the dense ground cover pres-

ent within the exclosures. Each of the 1995–1997 floods on the Yampa resulted in inundation of DL2 (including all small-mammal exclosures) and DL3.

Seedling survivorship in the Island Park channel

The 1993 cohort.—Seedling survival through winter 1993–1994 differed among the small treatments and the single small control ($\chi^2 = 21.0$, df = 2, $P < 0.001$). Survivorship was lower in the control than in either H or HH treatments, matching our prediction (Table 3), but no difference was detected between the two treatments (sets pooled: two-tailed Fisher's exact test, $P = 0.80$). A significant difference between seedling survival in H and HH treatments was detected during the 1994–1995 period (one-tailed Fisher's exact test, $P = 0.051$). Low seedling survivorship from September 1993 to April 1994 in the H exclosure at IP2 (Set 2; Table 3), unrelated to mammalian herbivory, masked the reduction in ϕ(SL) due to small mammals when the entire two-year (1993–1995) period was considered (one-tailed Fisher's exact test, $P = 0.11$). All three small control plots were lost when buried under an unexpectedly deep (~20 cm) 1995 spring flood sediment deposit.

Seedlings in the B+R treatments, vulnerable only to small mammals, furnished additional evidence for a small-mammal effect at IP during 1993–1995. Only 1 of the 15 seedlings originally present survived (Table 3), an improbable event using ϕ(SL) estimated from fully protected seedlings in small exclosures (ϕ_H[SL] = [8/29] = 0.28; binomial probability = 0.04).

Medium- and large-sized mammals did not reduce ϕ(SL) at IP below the rate due to small mammals. Seedling survival through 1993–1995 was universally low (Table 3); no effect of exclosure type was detected ($\chi^2 = 1.42$, df = 3, $P = 0.70$; Cochran's $\chi^2 = 0.204$, df = 1, $P = 0.65$). The 1993–1995 ϕ(SL) values associated with large and HH exclosures were not significantly different (Table 3: pooled value 0.34 yr^{-1}, $n_0 = 76$).

The 1994–1996 cohorts.—No germinants appeared in IP plots during 1994. Only 1 new seedling (1995 cohort) was found in an IP small exclosure in 1995, and only 9 were noted present in the large exclosures; all 10 were dead at the 1996 census (Table 3). No new (1996 cohort) seedlings were found in or near any of the IP exclosures during the October 1996 census.

Physical evidence of herbivory by small mammals

The small control (SC) plot at IP held 46 5–15 cm tall seedlings in October 1993. The April 1994 census showed 37 of these plants to be missing, one dead, and all 8 live plants browsed to a 1–4 cm height. Removal of the upper stem was at least partially due to mice or voles, because 4 of 16 surviving seedlings in the HH of Set 1, accessible only to those species, had been similarly browsed to a 5–10 cm height. Each of three live willow seedlings present had also been browsed. The willow seedlings featured basal or root sprouts, but no sprouting was apparent among the browsed cottonwood. There was no evidence of browsing within the closed H exclosures.

Sapling survivorship in the Island Park channel

No effect of location on survivorship in the large control plots (LC) was detected through the 24-month 1993–1995 period ($\chi^2 = 2.67$, df = 2, $P = 0.26$), the 11-month 1995–1996 period, or the 13-month 1996–1997 period ($\chi^2 = 0.04$, df = 2, $P = 0.98$) (Table 3). Based on pooled data, the estimated survivorship of unprotected Island Park saplings through each of these periods was ϕ_{LC}(SP) = 0.86, 0.92, and 0.92 yr^{-1}, respectively. These rates are not statistically different ($\chi^2 = 4.00$, df = 2, $P = 0.14$).

Effect of medium- and large-sized mammal herbivory.—The most parsimonious log-linear model of the sapling survivorship data collected in the Island Park large exclosures (variable Fate) included all categorical explanatory variables [treatment (Extype), location (Set), and time (Period)] plus all interaction terms with the exception of the single four-way term. Thus, whether a sapling lived or died during a particular interval was influenced by the type of exclosure, and the effect of exclosure type varied both in space and through time. A subsequent test for a linear trend among fates of saplings in LC, B, R, and B+R exclosures through 1993–1995 indicated a nonzero slope (Cochran $\chi^2 = 5.27$, df = 1, $P = 0.02$), but the pattern among treatments was opposite of that predicted, with $\phi_{LC}(SP) > \phi_{B+R}(SP)$ (Table 3). No difference in ϕ(SP) values was detected among treatments for the 1995–1996 period ($\chi^2 = 0.46$, df = 3, $P = 0.93$; Cochran $\chi^2 = 0.22$, df = 1, $P = 0.64$).

A treatment effect on (SP) again became apparent at IP in the final 13-month 1996–1997 period (Table 3; $\chi^2 = 7.35$, df = 3, $P = 0.06$; Cochran $\chi^2 = 1.77$, df = 1, $P = 0.18$). Survivorship rates within B and B+R exclosures were equivalent (one-tailed Fisher's exact test, $P = 0.8$; pooled ϕ[SP] = $[55/76]^{(12/13)} = 0.74$ yr^{-1}), as were rates within LC and R exclosures (one-tailed Fisher's exact test, $P = 0.35$; pooled ϕ[SP] = $[70/79]^{(12/13)} = 0.89$ yr^{-1}). The unanticipated lower survivorship of saplings exposed to ungulate herbivory (LC and R plots) may reflect localized small-mammal herbivory (see *Girdling of saplings . . .*). The proportion of saplings surviving through 1996–1997, regardless of treatment, tended to be lower in IP2 than in either IP1 or IP3, and was dramatically so for saplings within the adjacent B and B+R plots: 8/27 in IP2 vs. 46/49 in IP1 and IP3 (two-tailed Fisher's exact test, $P < 0.001$).

Effect of small-mammal herbivory.—Protection from small mammals had no effect on sapling survival during the seven-month September 1993 to April 1994 period (one-tailed Fisher's exact test, $P = 0.34$; Table 3). However, small mammals significantly reduced sapling survivorship during the subsequent 18-month pe-

TABLE 3. Survivorship estimates for cottonwood saplings [ϕ(SP)] and seedlings [ϕ(SL)] at Island Park (IP) and Deerlodge Park (DLP) within five types of exclosures and control plots (without fencing).

Exclosure configuration	Reach	Period	Saplings		
			Set 1	Set 2 or pooled	Set 3
Small–closed (H)	IP	Sep 1993–Apr 1994		**0.93** (14/15)^{f}	
Small–holes (HH)	IP	Sep 1993–Apr 1994		1.00 (29/29)^{f}	
Small controls (SC)	IP	Sep 1993–Apr 1994		...	
Small–closed (H)	IP	Apr 1994–Sep 1995		**0.93** (13/14)^{o}	
Small–holes (HH)	IP	Apr 1994–Sep 1995		0.48 (14/29)^{p}	
Small–closed (H)	IP	Sep 1993–Sep 1995		**0.87** (13/15)^{l}	
Small–holes (HH)	IP	Sep 1993–Sep 1995		0.48 (14/29)^{m}	
Large control (LC)	IP	Sep 1993–Sep 1995		0.74 (14/19)^{d}	
Large–barbed (B)	IP	Sep 1993–Sep 1995		0.69 (9/13)^{d}	
Large–ranch (R)	IP	Sep 1993–Sep 1995	0.20 (3/15)^{b}	0.55 (6/11)^{bc} [0.41 (12/29)]^{d}	1.00 (3/3)^{c}
Large-barbed+ranch (B+R)	IP	Sep 1993–Sep 1995		**0.44** (8/18)^{d}	
Small–closed (H)	DLP	Feb 1995–Oct 1995		**0.57** (17/30)^{u}	
Small–holes (HH)	DLP	Feb 1995–Oct 1995		0.50 (14/28)^{u}	
Small control (SC)	DLP	Feb 1995–Oct 1995	0.80 (12/15)^{s}	0.42 (10/24)^{t} [0.56 (22/39)]^{u}	... (0)
Large control (LC)	DLP	Oct 1994–Oct 1995		0.75 (50/67)^{r}	
Large–barbed (B)	DLP	Oct 1994–Oct 1995		0.69 (35/51)^{r}	
Large–ranch (R)	DLP	Oct 1994–Oct 1995	0.10 (1/10)^{ii}	0.70 (7/10)^{jj} [0.55 (16/29)]^{r}	0.89 (8/9)^{jj}
Large–barbed+ranch (B+R)	DLP	Oct 1994–Oct 1995		**0.77** (58/75)^{r}	
Small–closed (H)	IP	Sep 1995–Oct 1996		**0.93** (14/15)^{j}	
Small–holes (HH)	IP	Sep 1995–Oct 1996		0.64 (16/25)^{k}	
Large control (LC)	IP	Sep 1995–Aug 1996		0.93 (13/14)^{e}	
Large–barbed (B)	IP	Sep 1995–Aug 1996		0.89 (8/9)^{e}	
Large–ranch (R)	IP	Sep 1995–Aug 1996		0.85 (11/13)^{e}	
Large–barbed+ranch (B+R)	IP	Sep 1995–Aug 1996		**0.89** (8/9)^{e}	
Small–closed (H)	DLP	Oct 1995–Oct 1996		0.82 (14/17)^{hh}	
Small–holes (HH)	DLP	Oct 1995–Oct 1996		0.87 (13/15)^{hh}	
Small control (SC)	DLP	Oct 1995–Oct 1996		0.92 (23/25)^{hh}	
Large control (LC)	DLP	Oct 1995–Oct 1996	0.55 (23/42)^{p}	0.93 (26/28)^{q} [0.75 (70/93)]^{y}	0.91 (21/23)^{q}
Large–barbed (B)	DLP	Oct 1995–Oct 1996		0.79 (46/58)^{y}	
Large–ranch (R)	DLP	Oct 1995–Oct 1996		0.95 (21/22)^{y}	
Large-barbed+ranch (B+R)	DLP	Oct 1995–Oct 1996		**0.73** (60/82)^{y}	
Large control (LC)	IP	Aug 1996–Oct 1997		0.91 (40/44)^{g}	
Large–barbed (B)	IP	Aug 1996–Oct 1997	1.00 (11/11)^{i}	0.29 (4/14)^{h} [0.69 (22/32)]^{g}	1.00 (7/7)^{i}
Large–ranch (R)	IP	Aug 1996–Oct 1997		0.86 (30/35)^{g}	
Large–barbed+ranch (B+R)	IP	Aug 1996–Oct 1997	**0.86** (19/21)^{i}	**0.31** (4/13)^{h} [**0.75** (33/44)]^{g}	**1.00** (10)^{i}
Large control (LC)	DLP	Oct 1996–Oct 1997		0.96 (255/267)^{kk}	
Large–barbed (B)	DLP	Oct 1996–Oct 1997		0.94 (84/89)^{kk}	
Large–ranch (R)	DLP	Oct 1996–Oct 1997		0.97 (34/35)^{kk}	
Large–barbed+ranch (B+R)	DLP	Oct 1996–Oct 1997		**0.95** (235/247)^{kk}	

Notes: Entries are organized by monitoring period and are based on sample populations pooled across sets where χ^2 tests indicated that no significant difference existed. In cases where differences were detected, the estimate for each set is also shown (above the bracketed pooled estimate), with statistically different values having different trailing superscript letters. Number of surviving plants, n_f, and original size of the sample population, n_0, are shown as n_f/n_0 in parentheses. Tabulated estimates for different exclosure types, within each age class and period, having the same superscript letter are not statistically different based on χ^2 tests of data pooled across sets. Survivorship within the most protected exclosure type within a series is shown in boldface. See Table 1 for exclosure configuration code information.

riod (April 1994 to September 1995) [one-tailed Fisher's exact test, $P = 0.003$; $\phi_H[SP] = [13/14]^{(12/18)} = 0.95$ yr^{-1}; $\phi_{HH}[SP] = [12/26]^{(12/18)} = 0.60$ yr^{-1}). Exposure to small mammals also reduced sapling survivorship during the subsequent 1995–1996 period (one-tailed Fisher's exact test, $P = 0.040$; $\phi_H[SP] = [14/15]^{(12/11)} = 0.93$ yr^{-1}; $\phi_{HH}[SP] = [16/25]^{(12/11)} = 0.61$ yr^{-1}).

Survivorship in the two forms of treatment exposing saplings solely to small mammals, B+R and HH, was equivalent at IP, matching our prediction. ANOVA indicated that period (1993–1995 *vs.* 1995–1996) but not exclosure type (HH vs. B+R) had an effect on proportion surviving within these exclosures (Period: $F = 5.36$, df = 1,7, $P = 0.054$; Type: $F = 1.48$, df = 1,7 $P = 0.26$). There was a significant interaction effect, with the values of $\phi_{B+R}(SP)$ and $\phi_{HH}(SP)$ tending to reverse their relative ranks over the two periods (Table

TABLE 3. Extended.

Seedlings		
Set 1	Set 2 or pooled	Set 3
0.79 (15/19)[z]	**0.12** (1/8)[aa]	**0.50** (1/2)[zaa]
	[**0.59** (17/29)][bb]	
	0.91 (21/33)[bb]	
	0.17 (8/46)[cc]	
	0.50 (8/16)[dd]	
	0.19 (4/21)[dd]	
	0.28 (8/29)[gg]	
0.00 (0/26)[ee]	0.33 (1/3)[ff]	0.75 (3/4)[ff]
	[0.12 (4/33)][gg]	
	0.09 (1/11)[a]	
	0.22 (2/9)[a]	
	0.13 (1/8)[a]	
	0.07 (1/15)[a]	
	0.14 (15/109)[v]	
	0.04 (5/118)[x]	
	0.01 (1/112)[x]	
	0.32 (10/31)[ee]	
	0.06 (2/36)[ff]	
	0.63 (5/8)[ee]	
	0.43 (3/7)[ee]	
	...	
	0.00 (0/1)	
	...	
	0.00 (0/2)	
	0.00 (0/4)	
	0.00 (0/3)	
	0.00 (0/15)	
	0.00 (0/5)	
	0.0 (0/10)	
	1.00 (1/1)	
	...	
	...	
	0.14 (1/7)	

3). Survivorship rates through the two periods calculated on the basis of pooled sample populations were identical: $\phi_1(SP) = (22/47)^{(12/24)} = 0.68\ yr^{-1}$, and $\phi_2(SP) = (24/34)^{(12/11)} = 0.68\ yr^{-1}$.

Medium- and large-sized mammals did not reduce sapling survivorship beyond that due to small mammals. Estimates of sapling survivorship within exclosures accessible only to small mammals, $\phi_{HH}(SP)$, were less than estimates for unprotected controls accessible to all mammals, $\phi_{LC}(SP)$, during both the 1993–1995 and 1995–1996 periods (Table 3).

Girdling of saplings by Island Park small mammals

Partial or complete girdling of the basal portion of IP cottonwood saplings was first noted at the September 1995 census. Girdled saplings were found in both small (HH, accessible only to small mammals) and large exclosures. Most (31 of 35) saplings classified as partially girdled in 1996 were located in IP2, and most (23) of those were in the adjacent R and B+R treatments. No girdling was apparent in the completely closed H exclosures at IP.

Seedling survivorship in Deerlodge Park

The 1994 cohort.—The most parsimonious log-linear model for seedling survivorship through 1994–1995 within the large exclosures at DLP included main effects plus the (Extype × Fate) interaction. Thus, the fate of a seedling depended upon which mammals it was exposed to, but not on location. Although survivorship differed among treatments ($\chi^2 = 15.6$, df = 3, $P = 0.001$), the trend was not as predicted; survival was lowest in the B exclosures (Table 3).

Seedlings at DL2 protected in H exclosures exhibited higher survivorship through February–October 1995 than seedlings exposed to small mammals (Table 3; $\chi^2 = 16.9$, df = 2, $P < 0.001$). No location effect was detected among the small DLP treatments.

The 1995 cohort.—Hundreds of seedlings germinated within the H and HH exclosures at the slow-water margin following the 1995 spring flood. Only 20 of these plants, all in one set, lived through the 3–4 mo to the October 1995 census, indicating that factors other than rodent herbivory were primarily responsible for the very low early survivorship. None of these seedlings, nor any in SC plots, survived to October 1996 (Table 3).

Sapling survivorship in Deerlodge Park

Effect of herbivory by medium- and large-sized mammals.—The most parsimonious log-linear model of the 1994–1995 sapling survivorship data generated from the large exclosures at Deerlodge Park contained all main effects (Set, Extype, and Fate) plus a single interaction term, (Set × Fate). Thus, sapling survivorship varied among locations, but not with treatment; exposure to medium- and large-sized mammals apparently did not affect the fate of saplings during this period. The location effect was due to low survival in the R treatment at DL1 (Table 3; $\chi^2 = 13.3$, df = 2, $P = 0.001$), which led to a low 1994–1995 survivorship rate at the plain site ($0.59\ yr^{-1}$ [66/111]) relative to the slow-water (0.82 [61/74]) and fast-water margin sites (0.86 [32/37]). A location effect on survival through 1995–1996 was again due to a low value at the plain site, but focused on the LC plot ($\chi^2 = 17.3$, df = 2, $P < 0.001$). Survivorship rates for 1995–1996 were 0.63 (69/110), 0.88 (91/103), and 0.88 (37/42) yr^{-1} for DL1, DL2, and DL3, respectively. The most parsimonious log-linear model for the 1996–1997 period included only two main factors (Fate and Location) and no interaction term, indicating survivorship was equal across locations and independent of treatment (Table 3).

TABLE 4. Summary of survivorship rates (yr^{-1}) for seedlings and saplings at Island Park on the regulated Green River and at Deerlodge Park on the unregulated Yampa River.

Environmental condition	Island Park, Green River		
	1993–1995†	1995–1996	1996–1997
Saplings			
No mammals present‡	0.93 $[(13/15)^{12/24}]^a$	0.94 $[(14/15)^{12/13}]^a$	...
Only small mammals present§	0.68 $[(22/47)^{12/24}]^b$	0.73 $[(24/34)^{12/13}]^b$	0.78 $[(33/44)^{12/14}]$
All mammals present‖	0.76 $[(35/61)^{12/24}]^b$	0.90 $[(32/36)^{12/11}]^a$	0.85 $[(92/111)^{12/14}]$
Seedings			
No mammals present	0.53 $[(8/29)^{12/24}]^a$	...	
Only small mammals present	0.32 $[(5/48)^{12/24}]^b$	...	
All mammals present	0.38 $[(4/28)^{12/24}]^a$	...	

Notes: Survivorship rates are for locations pooled and, where no differences were found, treatments pooled (see footnotes for groupings). Survivorship rates are derived from entries in Table 3; the pertinent expression is shown in brackets and indicates initial population size. Different letters following tabulated values within a period–age class category indicate they are statistically different (pairwise comparisons in cases where change is in predicted direction, using one-tailed Fisher's exact test and $\alpha = 0.08$).

† Rates in 1993–1994 and 1994–1995 are assumed to be equal.

‡ Treatment H.

§ Treatment HH, B+R (in years lacking HH data), or pooled HH and B+R.

‖ Pooled treatments LC and SC, or those plus B and/or R.

¶ Based on small exclosures at slow-water margin (DL2).

At a finer spatial scale (within the slow-water margin site), a location effect on sapling survivorship was evident among the small exclosures, but only during the nine-month, February–October 1995 period (two-tailed Fisher's exact test, $P = 0.024$; Table 3).

Effect of small-mammal herbivory.—We found no effect from small mammals on sapling survivorship at the slow-water margin. Chi-square analysis comparing number of surviving cottonwood saplings in the HH exclosures to the number expected on the basis of $\phi_H(SP)$ values (Table 3) indicated that exposure to small mammals had no effect on survivorship of saplings over the nine-month February 1995 to October 1995 period ($\chi^2 = 1.02$, df = 1, $P = 0.31$). Nor did we detect a difference between the HH and small control for that period ($\chi^2 = 0.26$, df = 1; $P = 0.61$). Analyses for the October 1995–October 1996 period produced similar results (HH vs. H: $\chi^2 = 0.37$, df = 1, $P = 0.54$; HH vs. SC: $\chi^2 = 0.49$, df = 1, $P = 0.48$).

Comparative survivorship in Island Park and Deerlodge Park

In summary, small mammals reduced sapling survivorship at IP by ~25% below the level for plants protected from all mammalian herbivores during each of 1993–1995 and 1995–1996 (Table 4). Small mammals had no detectable effect on sapling survivorship at the comparable slow-water margin site at DLP (Table 4). Further, the additional presence of medium- and large-sized mammals had no detectable effect at either IP or DLP (Table 4). Neither reach had consistently higher survivorship among control saplings, and mean survivorship over the study period was similar: 0.81 yr^{-1} and 0.80 yr^{-1} for IP and DLP, respectively.

Small mammals reduced seedling survivorship at IP during 1993–1995 by ~40%, and at DL2 over spring and summer 1995 by ~80% (Table 4). We detected no reduction in seedling survivorship attributable to medium- or large-sized mammals on either reach.

Height increases

Effect of herbivory on height growth increment (γ) of IP saplings.—Height increments of IP saplings during 1993–1995 were influenced by exclosure type ($F = 4.91$; df = 3,31; $P < 0.01$) but not location ($F < 0.01$; df = 1,31; $P = 0.95$) ($n = 40$ plants, ANOVA with initial height as a covariate and sets IP2 and IP3 pooled $n = 16$ and 6, respectively). Bonferroni pairwise comparisons indicated only $\bar{\gamma}_R$ and $\bar{\gamma}_{LC}$ were significantly different (Table 5). However, the mean increments, adjusted for the covariate, did not trend in the predicted direction of $\bar{\gamma}_{B+R} > \bar{\gamma}_B \approx \bar{\gamma}_R > \bar{\gamma}_{LC}$ (Table 5). Several control plants lost ~100 cm of height, damage we attributed to browsing by large mammals because of the height at which stems were clipped.

Neither exclosure type ($F = 0.165$; df = 3,39; $P = 0.919$) or location ($F = 0.590$, df = 1,39, $P = 0.45$) affected height increments for 1995–1996 (ANOVA with IP2 and IP3 pooled and initial height as a covariate). Nor was an effect detected for either exclosure type ($F = 0.85$; df = 3,99; $P = 0.47$) or location ($F = 2.13$, df = 2,99, $P = 0.12$) over the 1996–1997 period (IP2 and IP3 separate, initial height as covariate). No consistent trend was evident across exclosure types or periods (Table 5). Examination of the 1996–1997 data indicated unusually small mean adjusted growth increments for the saplings in the R ($\bar{\gamma}_R = 34$ cm) and B ($\bar{\gamma}_B = 7$ cm) exclosures of IP2. This group included a large number of saplings whose bases had been partially girdled by small mammals.

Effect of herbivory on growth increments of DLP saplings.—We restricted ANOVA examining effects of location and treatment on the 1994–1995 height increment to DL1 and DL2, and ignored R exclosures be-

TABLE 4. Extended.

Deerlodge Park, Yampa River					
1994–1995		1995–1996		1996–1997	
0.43	$[(17/30)^{12/8}]$	0.82	$(14/17)^a$	...	
0.65	(67/103)	0.75	$(73/97)^a$	0.95	(235/247)
0.63	(118/186)	0.81	$(160/198)^a$	0.95	(373/391)
0.05¶	$[(15/109)^{12/8}]^a$	<0.07¶	(<1/15)		
0.009¶	$[(5/118)^{12/8}]^b$	<0.08¶	(<1/12)		
0.10	(<18/198)	...			

cause of the few stems uninjured by beaver. Analysis of the remaining 110 saplings (lowest cell $n = 16$) indicated that both location ($F = 4.57$, df = 1,103, $P = 0.035$) and exclosure type ($F = 4.25$, df = 2,103, $P = 0.017$) affected mean height increment (Table 5). The covariate (initial height) was also significant ($F = 4.73$, df = 1,103, $P = 0.032$). Although the largest mean growth increment was consistently in the B+R exclosure as predicted, the smallest was never in the control area. Thus, the hypothesis that the mean growth increments would differ as $\gamma_{B+R} > \gamma_B \approx \gamma_R > \gamma_{LC}$ was not supported.

Only the large control plots harbored sufficient saplings ($n \geq 20$) to test for a location effect over 1995–1996; none was detected ($F = 1.389$, df = 2,55, $P = 0.26$). ANOVA performed on the pooled locations indicated a significant effect due to exclosure type ($F = 3.670$, df = 3,164, $P = 0.014$), with $\bar{\gamma}_{B+R} > \bar{\gamma}_{LC}$ as predicted (Table 5).

The loss of all but the large control plot of DL3 and addition of DL4 (LC and B+W plots) necessitated a modified analysis for DLP growth increments over 1996–1997. One-way ANOVA (with initial height as covariate) comparing the four LC plots indicated no significant location effect ($n = 234$ plants, $F = 0.28$, df = 3,229, $P = 0.84$). Two-way ANOVA (with initial height as covariate) comparing LC, B, and B+R treatments at DL1 and DL2 (there were no saplings in the R treatment at DL1) also indicated no location effect but a significant exclosure effect, trending in the predicted manner (Table 5).

Herbivores generally affected 3-yr height increments of Deerlodge Park saplings (i.e., growth over the entire study period) in the predicted manner, the exception being a low $\bar{\gamma}_R$ value (Table 5). These results are based on ANOVA performed on height change over 1994–1997 for 95 saplings within DL1 and DL2, which indicated a significant treatment effect ($F = 15.8$, df = 3,86, $P < 0.001$) but no location effect ($F = 0.606$, df = 1,86, $P = 0.44$). The effect of the covariate (initial height) was not significant ($F = 0.009$, df = 1,86, $P = 0.92$).

Beaver herbivory

Beaver cut 19 of the 119 monitored cottonwoods accessible to them (i.e., plants within LC and B exclosures) in Island Park during the four years between September 1993 and September 1997. Stems in IP1, IP2, and IP3 were cut. An estimate of the probability of a sapling being cut by a beaver, P_{BC}, based on these figures is 0.043 yr^{-1}. During the three years between September 1994 and September 1997, Deerlodge Park beaver cut no monitored plants at DL1, which was inundated solely in 1997, and only one plant at DL2, which was entirely inundated each spring. Beaver cut 16 of the 125 accessible plants at DL3, also inundated each year, during the two years prior to its destruction. The DL3 data produce an estimate of $P_{BC} = 0.066$ yr^{-1}, whereas the data pooled across sets (17 of 454 plants cut during two years of exposure) leads to $P_{BC} = 0.019$ yr^{-1}.

DISCUSSION

Our results demonstrate that herbivory by native mammals can be a significant determinant of tree seedling survivorship in particular floodplain environments, and more generally, of sapling survivorship and growth. They also suggest that the hydrologic regime interacts with floodplain topography and the spatial relationships among floodplain landforms and upland to determine the extent to which each herbivore species can affect riparian vegetation structure.

Small mammals reduced per capita seedling survivorship (ϕ[SL]) at both IP and DLP (Table 3). The proportional reduction in ϕ(SL) was larger at DLP than IP (Table 4), but the ecological significance of this is clouded by the different time periods monitored, the larger initial sample populations at DLP, and our inability to discriminate between additive and compensatory sources of mortality. Assuming mortality due to small-mammal herbivory is additive, the 10-fold higher survivorship of fully protected seedlings at IP compared to DLP implies small mammals had a greater short-term impact at IP, but one nevertheless of questionable long-term consequence. Given 100 seedlings at each reach, exposed for one year to risk from small mammals and the other factors operating there (Table 4), small mammals would be responsible for 21 deaths at IP, but only 4 at DLP. Even so, 32 seedlings would survive at IP, whereas only one would survive at DLP.

There was no unambiguous evidence for a detrimental effect on seedlings due to larger mammals at either reach (Table 3). Whether medium- and large-sized mammals reduce seedling survivorship at DLP remains unclear because of the unexpected survivorship pattern among the large exclosures. The low 1994–1995 value in the DLP barbed wire exclosures (Table 3) relative to the control, for example, could be due to either localized herbivory by small- or medium-sized mammals, localized mortality due to agents other than mammals, or experimental error that resulted in protection reducing, rather than increasing, ϕ(SL). The large difference between seedling survivorship within

TABLE 5. Adjusted least-squares mean height increments (cm) for saplings in the large exclosures at the IP and DLP study reaches.

Period	Deerlodge Park, Yampa River				Island Park, Green River			
	γ_{B+R}	γ_B	γ_R	γ_{LC}	γ_{B+R}	γ_B	γ_R	γ_{LC}
1993–1995	...	...	...	...	61 (8)^{ab}	74 (9)^{ab}	101 (13)^{a}	22 (10)^{b}
1994–1995	49 (44)^{a}	25 (32)^{b}	...	40 (34)^{ab}	...	...	...	...
1995–1996	42 (52)^{a}	34 (42)^{ab}	24 (16)^{ab}	24 (59)^{b}	49 (12)	38 (8)	52 (15)	54 (13)
1996–1997	31 (97)^{a}	22 (83)^{ab}	...	17 (95)^{b}	51 (32)	37 (19)	55 (27)	39 (34)
1994–1997	142 (34)^{a}	88 (24)^{b}	26 (12)^{bc}	80 (25)^{c}	...	...	...	...

Notes: Number of plants measured is in parentheses. Within any reach–period combination, values lacking a superscript letter or with the same superscript letter are not significantly different. The forms of the ANOVAs (with initial height as a covariate) producing the tabulated values differ; see *Methods* for details.

the large vs. small control plots at DL2 (separated by <50 m) does not clarify the issue.

Mammals reduced sapling survivorship (ϕ[SP]) at IP, but not at DLP (Table 3), providing support for the hypothesis that native mammals have a larger detrimental effect on ϕ(SP) along a regulated river than along a similar reach on an unregulated river. Significant differences in ϕ(SP) among the large exclosures at IP were not in the predicted order, indicating the presence of either unanticipated forms of herbivory, or more likely, experimental error involving larger mammals (discussed below).

Trapping data combined with observational data and life history information suggest that the mammals damaging cottonwood at IP and DLP were the montane vole, beaver, one or both rabbit species, and the two (DLP) or three (IP) cervid species present. A young cottonwood's risk of injury from any of these species would be influenced by the hydrologic regime. Even short-duration flooding involving only a few centimeters of water temporarily removes nonclimbing, nonaquatic small-mammal herbivores, in our case voles and rabbits, from a site. Floodwaters a few decimeters deep promote visitation by aquatic species (e.g., beaver), but probably still do not hinder browsing by ungulates if the substrate offers a firm footing. The duration of inundation is likely of little consequence relative to risk from small mammals or ungulates, but is of major importance with respect to beaver and other species attracted by the presence of water. As depth of flooding further increases, ungulates are also eliminated, but aquatic species remain a threat. The location of a tree with respect to the river/floodwater margin influences its vulnerability to beaver (McGinley and Whitham 1985), regardless of inundation pattern or the nature of surrounding herbaceous vegetation. In contrast, the nature of ground-level vegetation is more important than location relative to the river in determining a young cottonwood's risk of injury from voles and rabbits. The cover provided by a dense herbaceous layer (voles) or nearby shrubs (rabbits) would enhance risk from these taxa. Although the preference for Fremont cottonwood as a food item is not known for montane voles or either rabbit species, it seems likely to be high, particularly in winter.

It is reasonable to conclude that regulation of the Green River, with its attendant reduction of the flood peak and expansion of floodplain vegetation in Island Park (Grams 1997), has promoted expansion of vole populations there. Voles were relatively abundant at IP but rare at DLP (Table 2). The physical evidence suggests that most of the reduction in cottonwood survivorship at IP was due to voles clipping seedlings and girdling saplings. Montane voles are known to consume bark and twigs (Johnson and Johnson 1982, Fitzgerald et al. 1994), and their territorial behavior (Jannett 1982) could lead to differential feeding activity over small distances. Although no locational effect was detected, survival of only 4 of 10 saplings in IP small-mammal exclosure Set 2 during the 1996–1997 period is highly unlikely (binomial probability $P < 0.001$) if the true probability of surviving is assumed to equal ϕ_H(SP) = 0.93. Small exclosure Set 2 was located near large exclosure Set 2, where survival was also relatively low during 1996–1997. Both sets were in an area where extensive nonlethal, ground-level bark removal attributable to voles was noted.

Beaver cut plants at a higher rate at DL3 than within the IP channel, but they showed large variation in their foraging activities among the DLP landforms. There was no obvious linkage between the observed pattern of beaver damage and river regulation. Also, beaver appeared to have little direct effect on sapling survivorship. In most cases (e.g., 10 of 11 at DLP during 1995–1996), plants cut by beaver remained alive. Fremont cottonwood saplings, like those of other floodplain poplars (Rood et al. 1994), appear to be both tolerant of and resilient to stem damage, including herbivory. McGinley and Whitham (1985) studied beaver–Fremont cottonwood interactions in southern Utah and noted that foraging was concentrated on trees nearest the river, where it led to those trees having a shrub-like growth form. We have aged potentially mature (>40-yr-old) cottonwood plants at both DLP and IP that had also been maintained in a shrub-like form (<2 m tall) by the combined activities of beaver and ungulates. Intense herbivory by beaver has been shown to reduce stand density and basal area of aspen (*P. tremuloides*), while promoting the importance of less preferred species (Johnston and Naiman 1990).

Rabbits may be of greater importance than beaver as a direct source of seedling mortality. *Sylvilagus audubonii* will eat willow, and presumably cottonwood (Orr 1940, in Chapman et al. 1982). These animals consume seedling shoots as well as sapling leaves during the growing season, and seedlings as well as branch tips within their reach during winter. Rabbit abundance was not quantified, but sightings indicated they were common at both IP and DLP.

Deer and elk (and possibly moose at IP) were solely responsible for removing the shoot apex of saplings >100 cm tall. River regulation would primarily affect the intensity of herbivory by ungulates indirectly, by reducing the number and size of patches on which new cottonwood cohorts could appear. This would tend to concentrate browsing on fewer, smaller areas. We have observed deer crossing the flowing river in both Island Park and Deerlodge Park, indicating neither river is a complete barrier to ungulate movement. Further, because flood peak is reached in May or later, after animals have initiated migration to higher elevation summer ranges (Garrott et al. 1987), even a large natural flood has no direct effect on animal welfare. The presence of chemical feeding deterrents, known to operate in other members of the genus *Populus* (Basey et al. 1990), may also affect patterns of herbivory by ungulates, as well as those of the smaller herbivores. Fremont cottonwood produces flavone glycosides (Whitham et al. 1996), but neither its variability, inducibility, or effectiveness against mammalian herbivores has been studied. Whether regulation affects the overall quantity or quality of winter forage used by deer or elk, their propensity to cross the river, or their vulnerability to predators, is unknown. Chronic severe ungulate browsing has been postulated to be responsible for deaths and shrub-like growth form of cottonwoods (*P. trichocarpa* and *P. angustifolia*) within Yellowstone National Park (Kay 1994, Keigley 1997).

We detected reductions in height growth attributable to mammalian herbivores other than beaver in all periods at DLP but only in the earliest period at IP. At IP, the mean height increase of unprotected saplings over 1993–1995 was less than that of any group of protected saplings, but significantly so only for plants in R exclosures (Table 5). There was no evidence for a strong effect from rabbits, which would have been manifested as γ_R and/or γ_{B+R} values exceeding γ_B. At DLP, the 1994–1997 analysis (Table 5) indicated that height increase among unprotected saplings was less than that of saplings protected by barbed wire (i.e., from ungulates) and those, in turn, added less than saplings protected by ranch wire-plus-barbed wire (e.g., from ungulates, including fawns and calves, and adult rabbits). Together with our observation that large numbers of mule deer and elk use DLP in winter, these results suggest that large mammalian herbivores play a more significant role at DLP than at IP.

Our failure to detect growth reductions due to specific size groups of herbivores at IP may in part be due to exclosure design. The unexpectedly low values of γ_B and γ_{B+R} suggest that young deer or elk entered B exclosures through the barbed wire, and then moved into the adjacent B+R exclosure. Once in an exclosure, an animal may have actually browsed more intensively than it would have outside the exclosure, if the fence restricted the travel that normally accompanies feeding. An alternative explanation is that moderately injured plants increased in height more than uninjured plants, an overcompensatory response that has been suggested to occur in silvicultural field experiments (Reichenbacker et al. 1996).

The results of this study underscore the need to understand plant–animal interactions in the context of the natural flow regime in order to clarify the effects of river regulation on riparian systems. Bradley and Smith (1986) looked for differential effects due to browsing and beaver cutting in a comparison between a regulated and an unregulated reach of the Milk River, but concluded survival had not been differentially affected. Although the authors imply their sites were grazed by cattle as well as native species, their estimates of browsing level (46% and 69% of "young cottonwoods," respectively) and beaver damage are comparable to those we found. In contrast, Cordes et al. (1997) suggest that bison herds historically limited recruitment into populations of cottonwood (*P. deltoides*) along the Red Deer River in Alberta, Canada.

Management implications

Regulation of snowmelt-driven rivers may typically increase the susceptibility of young floodplain trees to mammalian herbivory. In the regulated reach we examined, a reduced peak discharge during the spring flood led to a reduction in the area inundated. This removed one of the factors constraining the distribution and abundance of a herbivore, the montane vole. Because of reduced flood-caused mortality and unimpeded herbaceous vegetation development (promoted by regulation-induced substrate stability), vole densities rose and populations expanded into areas of previously unsuitable habitat. Both changes increased the likelihood that a sapling would be damaged or killed by voles. It is less clear whether regulation can also increase a floodplain tree's risk of injury from medium-sized mammals through effects on their demographics or individual behavior; an investigation of beaver–cottonwood–hydrology linkages at our study sites is underway. Whether regulation increases risk to damage from ungulates is problematical. If so, it would likely be manifested through changes in plant quality or spatial relationships (e.g., size and extent of stands) rather than herbivore numbers. Ungulates, like the other herbivore species, do not forage uniformly across the riparian landscape (Senft et al. 1987).

A river management strategy of periodically mimicking the natural flow regime is likely to aid in res-

toration of normal riparian community interactions. This, in turn, would aid in restoration of ecosystem function (Molles et al. 1998). In our case, using a series of managed, high-discharge floods to create the environmental conditions needed for successful cottonwood seed germination and initial establishment (Cooper et al. 1999) is likely to simultaneously reduce browsing by small mammals and thereby promote an environment conducive to plant survival and undelayed attainment of sexual maturity. However, the complexity of plant–herbivore–hydroperiod interactions argues for caution in extrapolating from small to large mammals, from small mammals to nonmammalian herbivores, and even from snowmelt-driven to other types of river systems.

Acknowledgments

Initial funding for this project was provided by the U.S. Bureau of Reclamation. We thank the Superintendent of Dinosaur National Monument for permission to work within the Monument, and Steve Petersburg for facilitating our field work. Rick Wydoski was instrumental in establishing and maintaining the exclosures, and along with Mark Nelson, Andrew Montano, and Kathleen Groves, helped census plants. Miles Falck, Michael Miller, and Mark Nelson helped with trapping in Island Park. Mark Nelson, Michael Scott, Michael Bogan, Miles Falck, Ken Wilson, and the assigned reviewers provided constructive comments on various drafts of the manuscript.

Literature Cited

ABstat. 1989. ABstat 6.02 for PC-DOS. Anderson-Bell, Arvada, Colorado, USA.

Andrews, E. D. 1986. Downstream effects of Flaming Gorge Reservoir on the Green River, Colorado and Utah. Geological Society of America Bulletin **97**:1012–1023.

Armstrong, D. M. 1972. Distribution of mammals in Colorado. Monograph of the University of Kansas Museum of Natural History **3**:1–415.

Barnes, T. G., E. J. Keyser III, and R. L. Linder. 1989. Survey of animal damage and feeding selectivity of rabbits in eastern South Dakota shelterbelts. Pages 154–159 *in* Proceedings of the Ninth Great Plains Wildlife Damage Control Workshop. U.S. Forest Service General Technical Report **RM-171**.

Basey, J. M., S. H. Jenkins, and G. C. Miller. 1990. Food selection by beavers in relation to inducible defenses of *Populus tremuloides*. Oikos **59**:57–62.

Bogan, M. A., R. B. Finley, Jr., and S. J. Petersburg. 1988. The importance of biological surveys in managing public lands in the western United States. Pages 254–261 *in* R. C. Szaro, K. E. Severson, and D. R. Patton, technical coordinators. Management of amphibians, reptiles, and small mammals in North America. U.S. Forest Service General Technical Report **RM-166**.

Braatne, J. H., S. B. Rood, and P. E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. Chapter 3. Pages 57–85 *in* R. F. Stettler, H. D. Bradshaw Jr., P. E. Heilman, and T. M. Hinckley, editors. Biology of *Populus* and its implications for management and conservation. NRC Research Press, Ottawa, Ontario, Canada.

Bradley, C. E., and D. G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. Canadian Journal of Botany **64**:1433–1442.

Bryant, J. P. 1988. Feltleaf willow–snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. Ecology **68**:1319–1327.

Chapman, J. A., J. G. Hockman, and W. R. Edwards. 1982. Cottontails. Pages 83–123 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of North America. Johns Hopkins University Press, Baltimore, Maryland, USA.

Cooper, D. J., D. M. Merritt, D. C. Andersen, and R. A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, U.S.A. Regulated Rivers: Research and Management **15**: 419–440.

Cordes, L. D., F. M. R. Hughes, and M. Getty. 1997. Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: the Red Deer River, Alberta, Canada. Journal of Biogeography **24**:675–695.

Durrant, S. D. 1952. Mammals of Utah. University of Kansas Museum of Natural History Publication **6**:1–549.

Durrant, S. D. 1963. Mammals of Dinosaur National Monument. University of Utah Miscellaneous Papers **1**:69–77.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science **266**:753–762.

Engelman, L. 1996. Loglinear models. Pages 497–525 *in* SYSTAT 6.0 for Windows: Statistics. SPSS, Chicago, Illinois, USA.

Falck, M. 1996. Small mammal population dynamics in riparian zones of regulated versus unregulated rivers in northwestern Colorado. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Finley, R. B., Jr. 1958. The wood rats of Colorado: distribution and ecology. University of Kansas, Museum of Natural History Publication **10**:213–552.

Fitzgerald, J. P., C. A. Meaney, and D. M. Armstrong. 1994. Mammals of Colorado. Denver Museum of Natural History and University Press of Colorado, Niwot, Colorado, USA.

Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management **51**:634–643.

Grams, P. E. 1997. Geomorphology of the Green River in Dinosaur National Monument. Thesis. Utah State University, Logan, Utah, USA.

Hoslett, S. A. 1961. Effects of floods on mammal distribution. Proceedings of the Iowa Academy of Science **68**:260–264.

Hughes, F. M. R. 1997. Floodplain biogeomorphology. Progress in Physical Geography **21**:501–529.

Hupp, C. R., and W. R. Osterkamp. 1996. Riparian vegetation and fluvial geomorphic processes. Geomorphology **14**:277–295.

Jannett, F. J., Jr. 1982. Nesting patterns of adult voles, Microtus montanus, in field populations. Journal of Mammalogy **63**:495–498.

Johnson, M. L., and S. Johnson. 1982. Voles. Pages 326–354 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of North America. Johns Hopkins University Press, Baltimore, Maryland, USA.

Johnson, W. C., R. L. Burgess, and W. R. Keammerer. 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. Ecological Monographs **46**:59–84.

Johnston, C. A., and R. J. Naiman. 1990. Browse selection by beaver: effects on riparian forest composition. Canadian Journal of Forest Resources **20**:1036–1043.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Pages 110–127 *in* D. P. Dodge, editor. Proceedings of the International Large River Symposium. Canadian Special Publication,

Fisheries and Aquatic Science 106, Ottawa. Ontario, Canada.

Karban, R., and J. H. Myers. 1989. Induced plant responses to herbivory. Annual Review of Ecology and Systematics **20**:331–348.

Kay, C. E. 1994. The impact of native ungulates and beaver on riparian communities in the Intermountain West. Natural Resources and Environmental Issues **1**:23–44.

Keigley, R. B. 1997. An increase in herbivory of cottonwood in Yellowstone National Park. Northwest Science **71**:127–136.

Malanson. G. P. 1993. Riparian landscapes. Cambridge University Press, Cambridge, UK.

Mattson, W. J., and R. A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. BioScience **37**:110–118.

McGinley, M. A., and T. G. Whitham. 1985. Central place foraging by beavers (*Castor canadensis*): a test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). Oecologia **66**:558–562.

Miller, M. S. 1998. Ecology of deer mice (*Peromyscus maniculatus*) and Ord's kangaroo rat (*Dipodomys ordii*) in riparian zones of regulated versus unregulated rivers in northwestern Colorado. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Molles, M. C., Jr., C. S. Crawford, L. M. Ellis, H. M. Valett, and C. N. Dahm. 1998. Managed flooding for riparian ecosystem restoration. BioScience **48**:749–756.

Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics **28**:621–658.

Naiman, R. J., H. Décamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications **3**:209–212.

Naiman, R. J., and K. H. Rogers. 1997. Large animals and system-level characteristics in river corridors. BioScience **47**:521–529.

National Research Council. 1992. Restoration of aquatic ecosystems. National Academy Press, Washington, D.C., USA.

Nefdt, R. J. C. 1996. Reproductive seasonality in Kafue lechwe antelope. Journal of Zoology **239**:155–166.

Nilsson, C., and M. Dynesius. 1994. Ecological effects of river regulation on mammals and birds: a review. Regulated Rivers: Research and Management **9**:45–53.

Orr, R. T. 1940. The rabbits of California. Occasional Papers of the California Academy of Science **19**:1–227.

Osmond, C. B., M. P. Austin, J. A. Berry, W. D. Billings, J. S. Boyer, J. W. H. Dacey, P. S. Nobel, S. D. Smith, and W. E. Winner. 1987. Stress physiology and the distribution of plants. BioScience **37**:38–48.

Power, M. E., W. E. Dietrich, and J. C. Finlay. 1996. Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. Environmental Management **20**:887–895.

Reichenbacker, R. R., R. C. Schultz, and E. R. Hart. 1996. Artificial defoliation effect on *Populus* growth, biomass production, and total nonstructural carbohydrate concentration. Environmental Entomology **25**:632–642.

Rood, S. B., C. Hillman, T. Sanche, and J. M. Mahoney. 1994. Clonal reproduction of riparian cottonwoods in southern Alberta. Canadian Journal of Botany **72**:1766–1774.

Rood, S. B., and J. M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. Environmental Management **14**:451–464.

Rood, S. B., and J. M. Mahoney. 1995. River damming and riparian cottonwoods along the Marias River, Montana. Rivers **5**:195–207.

Rood, S. B., J. M. Mahoney, D. E. Reid, and L. Zilm. 1995. Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta. Canadian Journal of Botany **73**:1250–1260.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. BioScience **37**:789–799.

Sheppe, W., and P. Haas. 1981. The annual cycle of small mammal populations along the Chobe River, Botswana. Mammalia **45**:157–176.

Sparks, R. E. 1992. Risks of altering the hydrologic regime of large rivers. Pages 119–152 *in* N. J. Cairns, B. R. Niederlehner, and D. R. Orvos, editors. Predicting ecosystem risk. Volume XX. Advances in modern environmental toxicology. Princeton Scientific, Princeton, New Jersey, USA.

Spencer, A. W. 1984. Food habits, grazing activities, and reproductive development of long-tailed voles, *Microtus longicaudus* (Merriam) in relation to snow cover in the mountains of Colorado. Pages 67–90 *in* J. F. Merritt, editor. Winter ecology of small mammals. Special Publication of the Carnegie Museum of Natural History Number **10**.

Stromberg, J. C., and D. T. Patten. 1992. Mortality and age of black cottonwood stands along diverted and undiverted streams in the eastern Sierra Nevada, California. Madroño **39**:205–223.

SYSTAT. 1996. SYSTAT 6.0 for Windows: statistics. SPSS, Chicago, Illinois, USA.

Tabacchi, E., A.-M. Planty-Tabacchi, M. J. Salinas, and H. Décamps. 1996. Landscape structure and diversity in riparian plant communities: a longitudinal comparative study. Regulated Rivers: Research and Management **12**: 367–390.

Ward, J. V., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research and Management **15**:125–139.

Weber, W. A., and R. C. Wittmann. 1996. Colorado flora: western slope, revised edition. University Press of Colorado, Niwot, Colorado, USA.

Whitham, T. G., K. D. Floate, G. D. Martinsen, E. M. Driebe, and P. Keim. 1996. Ecological and evolutionary implications of hybridization: *Populus*-herbivore interactions. Chapter 11. Pages 247–275 *in* R. F. Stettler, H. D. Bradshaw Jr., P. E. Heilman, and T. M. Hinckley, editors. Biology of *Populus* and its implications for management and conservation. NRC Research, Ottawa, Ontario, Canada.

Wilkinson, L., and L. Engelman. 1996. Tests and measures for two-way tables. Pages 43–96 *in* SYSTAT 6.0 for Windows: Statistics. SPSS, Chicago, Illinois, USA.