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MONITORING TEMPORAL CHANGE IN RIPARIAN VEGETATION OF GREAT BASIN NATIONAL PARK

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ABSTRACT.—Disturbance in riparian areas of semiarid ecosystems involves complex interactions of pulsed hydrologic flows, herbivory, fire, climatic effects, and anthropogenic influences. We resampled riparian vegetation within ten 10-m × 100-m plots that were initially sampled in 1992 in 4 watersheds of the Snake Range, east central Nevada. Our finding of significantly lower coverage of grasses, forbs, and shrubs within plots in 2001 compared with 1992 was not consistent with the management decision to remove livestock grazing from the watersheds in 1999. Change over time in cover of life-forms or bare ground was not predicted by scat counts within plots in 2001. Cover results were also not well explained by variability between the 2 sampling periods in either density of native herbivores or annual precipitation. In contrast, Engelmann spruce (*Picea engelmannii*) exhibited reduced abundance at all but the highest-elevation plot in which it occurred in 1992, and the magnitude of change in abundance was strongly predicted by plot elevation. Abundance of white fir (*Abies concolor*) individuals increased while aspen (*Populus tremuloides*) individuals decreased at 4 of 5 sites where they were sympatric, and changes in abundance in the 2 species were negatively correlated across those sites. Utility of monitoring data to detect change over time and contribute to adaptive management will vary with sample size, observer bias, use of repeatable or published methods, and precision of measurements, among other factors.

Key words: riparian ecosystems, monitoring, woody vegetation, Great Basin National Park, livestock removal, disturbance.

Natural disturbance in riparian areas is intimately tied to the timing, magnitude, frequency, and duration of stream flows, as well as to the geomorphic characteristics of the system (Yount and Niemi 1990, Gregory et al. 1991). Anthropogenic disturbances can alter stream flow and geomorphic processes and affect the distribution and composition of riparian plants by inducing changes in floodplain characteristics (Harris 1986, Auble et al. 1994). Changes in plant communities, in turn, may affect stability of stream channels and flood response. These changes also may influence vulnerability to invasion of exotic plants and the value of riparian areas for both wildlife and recreation. In the face of natural and anthropogenic disturbances, functioning watersheds are critical for ecological integrity of semiarid regions because they provide numerous ecosystem services, including (1) a high-quality, dependable supply of water; (2) moderation of the effects of flooding, drought, and climate change; (3) recharge of stream systems and groundwater aquifers; (4)

maintenance of diverse and productive vegetation that buffers sediment pulses, moderates stream temperatures through shading, and provides habitat for a diversity of wildlife; and many others (Postel and Carpenter 1997).

Although riparian areas comprise one of the most drastically altered community types over the last 150 years on federal lands in the Intermountain West of North America, they remain the most biologically diverse (Naiman et al. 1993, Hann et al. 1997). Their position at the interface of aquatic and terrestrial habitats brings together diverse geomorphic features, a consistent supply of water and nutrients, and contrasting landscape elements (Naiman et al. 1993). As a result of this concentration of resources, as well as increased humidity, higher transpiration rate, greater shade, and increased air movement relative to surrounding upland habitats, up to 75% of species within semiarid mountain ranges may use riparian areas disproportionately (Bull 1978, Thomas 1979). Riparian areas also act as corridors for dispersal or

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migration for many taxa, including carnivores, ungulates, birds, bats, and plants (Bull 1978, Gregory et al. 1991).

Free-roaming cattle often concentrate activity in riparian areas because these areas possess abundant shade, water, and nutrient-rich forage. Herbivory by native grazers likely played a less significant role in Great Basin landscapes during the Pleistocene and early to mid-Holocene than does contemporary livestock grazing (Mack and Thompson 1982, Grayson 1993). Introduction of domestic sheep, cattle, and horses by Anglo-Americans led to higher grazing intensities, especially in the late 1800s and early 1900s (Mack and Thompson 1982). In many areas grazing by domestic livestock can significantly alter characteristics of woody riparian vegetation such as height, density, connectedness, habitat complexity, and species composition (Rickard and Cushing 1982, Schulz and Leninger 1990, Green and Kauffman 1995, Jansen and Robertson 2001). Nonetheless, many areas exist in the Great Basin where removal of livestock may not improve ecological integrity because transitions to altered ecosystem states (e.g., encroaching junipers, areas of widespread invasion by exotic species, exceeded geomorphic thresholds) have prevented the possibility of return to previous conditions (Archer and Smeins 1991, Laycock 1994, Miller and Wigand 1994).

After numerous studies of riparian restoration and decades of livestock management in semiarid riparian systems, there remains uncertainty about the multiple effects of livestock grazing with varying grazing seasons, duration, periodicity (amount of rest), and stocking rate, as well as the short- and long-term consequences of removing such grazing. This research represents an effort to evaluate short-term variability in riparian vegetation in relation to removal of cattle grazing from Great Basin National Park (GBNP).

Our intent was to compare composition and structure of vegetation in 10 permanent plots established in 1992 between 2 sampling dates, 1992 and 2001, to see if change had occurred. We also tested whether successional relationships observed during 1992 sampling remained evident in 2001. An underlying goal was to assess the degree to which removal of domestic cattle grazing from the park in 1999 affected woody riparian vegetation. However, constraints of having only 2 sampling points (1 during

grazing [1991] and another 2 years after grazing was removed in 1999) and a lack of experimental controls weaken the ability of managers to interpret the impacts of management actions on resources. In the context of analysis and interpretation of our results, we provide monitoring recommendations for land managers who desire to use monitoring in adaptive management.

METHODS

In 1992, Smith et al. (1994), as part of a larger study, established 10 permanent plots in 4 watersheds of the Snake Range to address hypotheses about change over time in structure and composition of riparian communities, and about how this change varied among drainages and sites. Through repeated sampling of these plots over time, researchers could "potentially document long-term successional processes in the Park" (Smith et al. 1994:63). The plots were explicitly designed for monitoring over time and had been permanently marked.

We (EAB, DAP, and assistants) performed fieldwork in GBNP from 21 July through 20 August 2001. Unless stated otherwise, methods described herein pertain to 2001 sampling. In addition to garnering all relevant information from the 1994 report, we worked with collaborators on the previous research before, during, and after our 2001 sampling to maximize comparability between the 2 sampling dates. In 2001 our primary goals were to (1) provide a 2nd set of measurements of the plots, 9 years after the 1st sampling in 1992; (2) implement standard methods for our sampling and document them in sufficient detail to facilitate precise comparisons with subsequent sampling; (3) expand the components sampled within the plots to account for recent increased attention to taxa such as bryophytes, lichens, and rare plants; and (4) determine, to the degree possible, to what extent observed differences were consistent with anticipated vegetational changes following removal of cattle grazing from the park in 1999.

Smith et al. (1994) presented 3 types of data from the 10 permanent plots: (1) percent cover of forbs, grasses (thus excluding *Carex* and *Juncus*), shrubs, and bare ground, as well as species richness of shrubs; (2) frequency distributions (histograms) of DBH size classes for

TABLE 1. Mean stream gradient, drainage area, and hydrogeomorphology of 4 target watersheds. Gradient and drainage areas were obtained via GIS analyses in ArcInfo.

Watershed (creek name)	Mean stream gradient (%)	Drainage area (ha)	Range of elevations of mainstem (m)	Hydrogeomorphic units present ^a
Strawberry	8.7	1921	2080–2774	ACG, AV, AFV, AFD
Lehman	10.7	2174	2000–3073	IMV, LOV
Baker	11.0	3006	2056–3239	IMV, ABC, LOV, AFD
Snake	8.4	5827	1893–3200	IMV, AFV, ACG, TBV

^aFrom Frissell and Liss (1993). Listed in order of occurrence on mainstem from highest to lowest elevations within GBNP. Some units appear in ≥ 2 disjunct segments within a drainage. ABC = alluviated canyon, boulder-bedded; ACG = alluviated canyon, gravel- and cobble-bedded; AFD = alluvial fan delta; AFV = alluvial-fan-influenced valley; AV = alluvial valley; IMV = incised moraine-filled valley; LOV = leveed outwash valley; TBV = terrace-bound valley.

the most abundant tree species in each plot; and (3) relative cover of bare ground, forbs, grasses, *Carex* and *Juncus*, and shrubs (both combined and for individual shrub species). These 3 analyses, along with 4 relationships the authors observed in their analyses, formed the foundation for our comparison across sampling periods. These 4 relationships were believed to relate to long-term successional processes and included (1) high values of bare ground correlated with reduced vegetative diversity, shrub cover, and tree recruitment; (2) age structuring of *Populus* individuals related to site conditions; (3) abbreviated distribution of *P. engelmannii* at low elevations, but natural succession toward this species at high elevations; (4) apparent competition between white fir (*Abies concolor*) and aspen (*Populus tremuloides*) (Smith et al. 1994). Given the removal of livestock, we predicted that bare ground would decrease and tree recruitment, plant species richness, and cover of shrubs and especially grasses would increase across sites.

STUDY AREA

Research was conducted adjacent to streams in 4 watersheds on the eastern side of the southern Snake Range in east central Nevada in GBNP. Plots were established along Strawberry, Lehman, Baker, and Snake Creeks, because roads adjacent to these streams should facilitate resampling by U.S. National Park Service staff over time. The plots ranged in elevation from 1948 to 3060 m, but elevations within these drainages vary from 3968 m at Wheeler Peak down to the Snake Valley floor at 1510 m. Stream gradients of all 4 creeks were similar. The hydrogeomorphology for the upper reaches of 3 of the 4 creeks was that of an incised, moraine-filled valley, whereas Strawberry Creek was classified as an alluvial sys-

tem and resembled the downstream reaches of Snake and Baker Creeks (Table 1). Active channel width in midsummer averaged 1–3 m, but the channel was significantly braided in many locations (E. Beever personal observation). The highest-elevation plots exhibited traits characteristic of Rosgen's (1985) "A" classification for stream channels, and lower plots most closely resembled either "A" or "B" streams. Mean precipitation on the east side of the Snake Range varies from 65.5 cm \cdot yr⁻¹ at 3182 m elevation, to 33.3 cm \cdot yr⁻¹ at 2081 m elevation, to 19.3 cm \cdot yr⁻¹ at the valley floor (Garrison, UT; 1518 m elevation; Western Regional Climate Center online data, Reno, NV).

Although watersheds varied in plant species composition, upland vegetation bordering riparian corridors typically transitioned from salt-scrub to big sagebrush communities below the park boundary, to pinyon juniper–big sagebrush (*Pinus monophylla*–*Artemisia tridentata*), ponderosa pine (*Pinus ponderosa*), white-fir–douglas-fir (*A. concolor*–*Pseudotsuga menziesii*), mountain mahogany (*Cercocarpus* spp.), aspen (*P. tremuloides*), and Engelmann spruce (*P. engelmannii*) communities as elevation increased. Soils in the park generally and the study watersheds in particular derive primarily from granitic or limestone parent rock material (Blake 1992). Although the Brokit Series encompassed only 0.6% of the park area, it has been assigned to all riparian areas in the park, despite notable spatial heterogeneity in riparian vegetation and likely in associated soils (Smith et al. 1994, Beever personal observation). Cattle grazed the area of the park from the 1860s (Eddleman and Jaindl 1994) until the National Park Service terminated permits in 1999 due to conflicts with other park uses. When using the benchmark of 45% utilization of grasses and forbs at the allotment scale, Eddleman and Jaindl (1994:41) found that

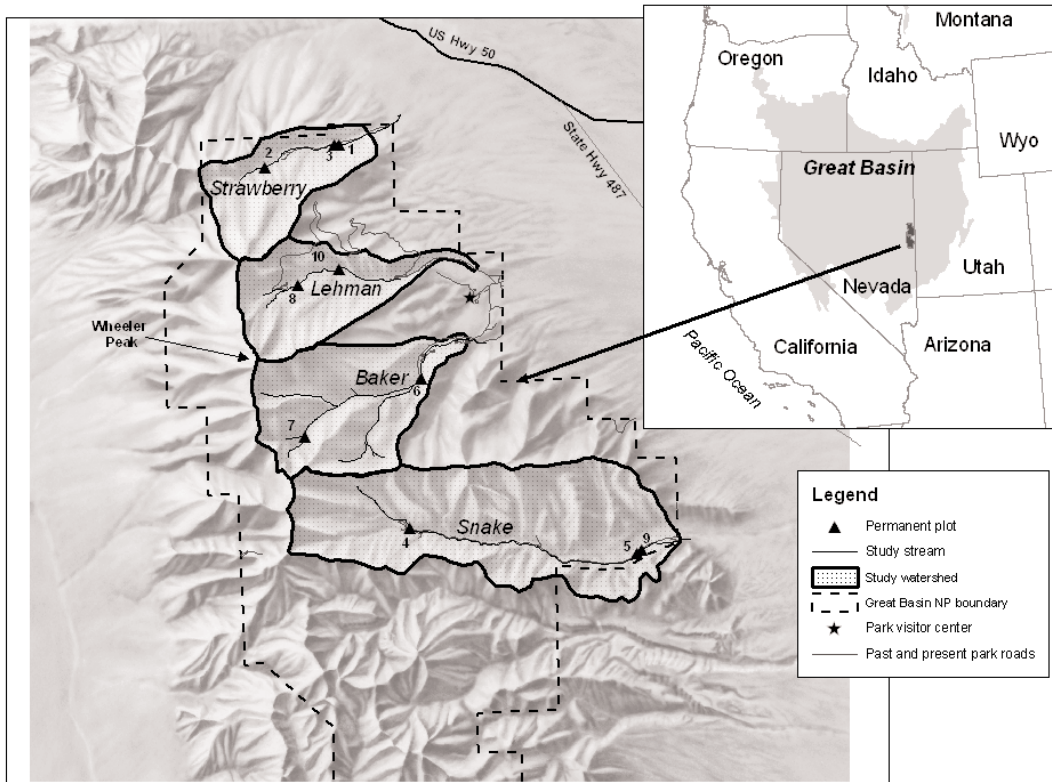


Fig. 1. Inset: Location of the Snake Range within the Basin and Range ecoregion (central and northern combined; U.S. EPA 2000) and relative to the western United States. Main map: Location of the 10 permanent plots in 4 target watersheds in the southern half of the Snake Range, east central Nevada.

stocking levels were “near the maximum levels in all allotments,” but that use was highest on slope gradients $< 15\%$ and within 1.6 km of water. Consequently, they found that “riparian areas [were] overgrazed and many [were] in poor condition (1994:43)” due to historic degradation as well as current poor distribution and movement of animals. However, overuse of riparian areas still occurred even when herding and salting were used (Eddleman and Jaindl 1994). Other than domestic cattle, herbivores in our target watersheds include pronghorn antelope, mule deer, elk, a few bighorn sheep, an occasional mountain goat, domestic sheep (at high elevations only), and a diverse guild of lagomorphs, insects, and granivorous rodents.

FIELDWORK

Ten 10-m \times 100-m plots, each bisected by a 100-m transect, were established in the flood-

plains of the 4 creeks across a broad range of elevations and community types in 1992 (Fig. 1, Table 2). To relocate 1992 plots, we conducted intensive on-site searches for the plots’ copper endpoint stakes. Nonetheless, we experienced great difficulty in precisely locating the endpoints of the 1992 plots. Thus, our interpretation of changes in riparian ecosystem vegetation was partially confounded by this and other sources of error (see Beaver et al. 2002). We replaced all missing stakes (on $n = 5$ plots) and recorded locations of all stakes with a differentially corrected GPS unit, providing horizontal precision of ~ 1.1 m.

Once the 100-m main transect axis was established, 5-m line-intercept transects were placed at right angles (angle was sighted with a compass) to the main axis, on alternating sides of the main axis. The first 5-m transect began on the left side of the main axis (looking from 0 toward 100 m), at the 5-m position (Fig. 1). One exception to the abovementioned procedure

TABLE 2. Summary of abiotic and biotic characteristics for each of 10 permanent plots.

Plot name	Elevation (m)	Community type ^a	Distance of main axis from active channel (m) ^b	Hydrogeomorphic unit ^c	Cattle defecations
Strawberry 1	2213	<i>Betula occidentalis</i> , <i>Rosa woodsii</i>	0–8	AV	7
Strawberry 2	2463	<i>Populus tremuloides</i> , <i>Abies concolor</i>	3–12	AV	
Strawberry 3	2231	<i>P. tremuloides</i> , <i>A. concolor</i> , <i>R. woodsii</i> , <i>Salix</i> spp.	0–9	AV	18
Snake 4	2475	<i>P. tremuloides</i> , <i>Symphoricarpos oreophilus</i>	3–11	AFV	12
Snake 5	1961	<i>Populus angustifolia</i> , <i>B. occidentalis</i> , <i>R. woodsii</i>	6–19	TBV	22
Baker 6	2404	<i>P. tremuloides</i> , <i>A. concolor</i> , <i>R. woodsii</i> , <i>Salix</i> spp.	4–14	AFV	6
Baker 7	3060	<i>Picea engelmannii</i>	0–15	IMV	49
Lehman 8	2914	<i>P. tremuloides</i> , <i>P. engelmannii</i> , <i>Pinus flexilis</i>	3–17	IMV	17
Snake 9	1948	<i>P. angustifolia</i> , <i>B. occidentalis</i> , <i>R. woodsii</i>	4–12	TBV	36
Lehman 10	2691	<i>P. tremuloides</i> , <i>P. engelmannii</i> , <i>Pseudotsuga menziesii</i> , <i>A. concolor</i>	6–15	IMV	0
Mean values	2436				18.6

^aPer Smith et al. (1994)

^bValues vary along the 100-m transect due to contrast between linear transect and naturally sinuous stream.

^cFrom Frissell and Liss (1993). See Table 1 for explanations of abbreviations.

was Snake 9, where all 20 transects occurred on the streamside of the main axis, as in 1992. Because the primary goal was measuring vegetative cover, we did not correct the transect length (5 m) for slope gradient.

Along each 5-m transect we recorded basal coverage (at the soil surface), understory canopy coverage, and overstory (tree) canopy coverage. Basal and understory interceptions in 2001 were recorded to the nearest 1 mm, but overstory interceptions could be estimated only to the nearest 1 cm. Smith et al. (1994) generally identified nonwoody plants to life-form (i.e., grass, forb, and *Carex-Juncus*). In 2001 we identified all plants to genus, and to species where possible, using Hickman (1993). For basal measurements we moved items obstructing the view of plant bases to obtain accurate measurements. For understory line intercepts, grass cover was measured by counting individual blades of grass (of each species) crossing the tape, then multiplying the total number by an average width (0.1–0.4 cm) of each blade, determined by measuring widths of numerous single blades of each species. We chose this approach because grass

interceptions were frequently not continuous. A gap of >5 cm was required to interrupt a continuous interception of a forb, shrub, or sedge/rush, but the minimum interception required to record a species' presence was 1 mm. For overstory sampling, a gap of >20 cm had to be present within the canopy of a given species to interrupt a continuous interception, and a minimum interception of 5 cm was required to record a species on a transect.

Within each plot we measured the DBH of trees at 1.5 m aboveground, rather than measuring at 1 m aboveground as did Smith et al. (1994). Thus, 2001 measurements were 0% to ~8% larger (depending on tree species and DBH, as well as slope gradient) than 1992 measurements, independent of tree growth. In 1992 Smith et al. (1994) measured DBH to the nearest 1 cm by placing a ruler tangential to the tree trunk, whereas in 2001 we measured to the nearest 0.01 cm with a DBH tape. These likely influenced comparisons only mildly, however, due to the broad width of our DBH categories. Greater than half of the tree's base had to be within the plot for the tree to be tallied or measured. We were unable to identify

TABLE 2A. Tree data and bare-ground data for each of 10 permanent plots.

Plot name	Tree data			Bare ground data				Litter cover percentage
	Tree species richness	Total seedlings + saplings	Total DBH values	Bare ground, 1992	Bare ground, original definition	Exposed soil surface		
Strawberry 1	7	444	1154	48	71.0	0.00		87.51
Strawberry 2	5	586	811	55	75.3	1.52		94.14
Strawberry 3	4	1127	2049	36	75.5	4.90		82.92
Snake 4	6	44	352	55	70.9	1.45		93.22
Snake 5	1	101	190	60	62.0	2.17		95.65
Baker 6	4	667	1267	58	83.9	0.00		96.67
Baker 7	1	15	142	76	89.0	0.27		81.52
Lehman 8	2	44	145	75	79.5	1.42		76.62
Snake 9	5	23	310	32	64.5	5.44		89.70
Lehman 10	4	225	413	78	88.9	1.47		89.29
Mean values	3.9	327.6	683.3	57.3	76.1	1.86		88.72

TABLE 2B. Cover by life-form and understory summary data, from sampling during 1992 and 2001, for each of 10 permanent plots.

Plot name	Cover by life-form (%)					Understory summary data			
	Forb cover, 1992	Forb cover	Grass cover, 1992	Grass cover	Shrub cover, 1992	Shrub cover	Understory species richness	Understory cover, 1992 (%)	Understory cover (%)
Strawberry 1	10	8.7	13	8.6	28	9.7	36	51	29.08
Strawberry 2	33	17.4	2	1.4	11	5.9	39	46	24.79
Strawberry 3	17	8.8	8	8.9	32	6.7	37	57	24.55
Snake 4	13	4.8	6	3.1	24.5	18.3	29	45.5	29.05
Snake 5	11	12.3	1	1.2	30	24.5	15	42	37.98
Baker 6	34	6.5	3	2.6	12	1.7	33	49	16.13
Baker 7	8	3.1	0.5	0.9	0.5	0.4	29	22.5	11.19
Lehman 8	8	10.5	1	0.7	1	0.6	36	25	21.89
Snake 9	8	2.1	6	1.1	52	32.3	19	66	35.41
Lehman 10	11	6.1	0.5	0.1	8	4.5	26	21.75	13.07
MEAN VALUES	15.3	8.0	4.1	2.9	19.9	10.5	30	42.6	24.31

to species *Juniperus* and *Salix* individuals, except for *S. exigua*, the only narrow-leaved willow in GBNP. In 2001 sampling only, for each *Betula occidentalis* clump, we tallied the number of stems at 1.5 m height, and measured DBH of the 3 largest stems and 4 randomly selected stems, to create frequency histograms of distributions of their diameters within a clump. While measuring DBH values, in 2001 only, we also tallied the number of cattle defecations occurring within each plot, counting as single defecations instances when animals defecated while moving. We assumed that these tallies reflected intensity of recent livestock grazing. In addition, we took 4 digital photographs of each plot along the main transect axis, 1 from each endpoint toward the 50-m mark, and 1 from the 50-m mark toward each end of the main line.

ANALYSIS

For basal coverage in 2001 sampling, “litter” represented total cover minus cover of rock, moss, water, plant bases, trunks, roots, lichens on rock, dead trees, bryophytes, and bare ground (defined as exposed soil surfaces). Bare ground was recorded only if the intercepted patch was >1 cm long. Smith et al. (1994) did not distinguish in their field sampling of permanent plots between truly bare ground (i.e., exposed soil surface) and unvegetated areas. Rather, they defined bare ground as $[1 - (\text{forb cover}) - (\text{grass cover}) - (\text{shrub cover}) - (\text{Carex-Juncus cover})]$. This original definition of bare ground does not reflect the sum of bare soils plus litter, as litter can also occur under vegetation (compare 2001 values in Table 3). Overlapping canopies of different species frequently occurred; in such cases, we tallied the full lengths of both species. We analyzed relationships applicable to shrubs using all species considered shrubs by Hickman (1993) and, for direct comparability with initial analyses, using the list of species considered shrubs by Smith et al. (1994; the last 17 species listed in Table 3).

For DBH sampling in 2001, we defined seedlings as independent tree sprouts noticeable above ground surface, but <0.46 m tall. Saplings were 0.46–1.0 m tall. We used the same size classes as did Smith et al. (1994) for comparing distribution of DBH values for dominant tree species, except that we did not measure

diameter of *Betula occidentalis* canopies. Thus, no DBH comparisons between sampling periods were made for this species. Smith et al. (1994) measured diameters only to the nearest cm; thus, we placed DBH values that fell between the bounds of adjacent classes in the lower category (e.g., the 11–20 cm category held values from 11.00 cm to 20.99 cm).

For statistical comparisons between 1992 and 2001 data, we applied paired *t* tests, with each plot paired across years. We tested purported relationships (e.g., with elevation, bare ground) using simple (linear) and multiple linear regressions. For these regressions we analyzed data using the variables (e.g., bare ground, shrub identities) defined in Smith et al. (1994) for greater comparability and the methods of 2001. To assess effect of livestock grazing on recovery of riparian ecosystem components, we used regressions to test whether number of cattle defecations detected in our standardized surveys significantly predicted the magnitude of change in the [2001/1992] ratio of cover of each life-form.

RESULTS

Comparisons of 1992 and 2001 Data: Bare Ground, Life-forms, and Shrub Species

When we used the definition adopted by Smith et al. (1994), bare ground comprised an average of 1.33 times more cover in 2001 than in 1992 (Table 3). However, truly bare ground, defined by exposed soil surface, averaged only 1.9% across plots (range = 0%–5.4%) in 2001, whereas litter averaged 88.7% and was as high as 96.7% of basal cover (Table 3). Whereas both forb cover and shrub cover in 2001 averaged 53% of the 1992 cover values, grass cover in 2001 averaged nearly 70% and was not significantly different from 1992 values (Table 3). Shrub cover in 2001 was >1.88 times higher at all Snake Creek sites than at any site from other drainages, which was not true in 1992 (Smith et al. 1994). Snake Creek sites exhibited particularly high cover of Woods' rose (*Rosa woodsii*), skunkbrush (*Rhus trilobata*), and snowberry (*Symphoricarpos oreophilus*) in 2001. Cover values for all life-forms except forbs and all “shrub” species except *Salix exigua* and *Clematis ligusticifolia* were significantly correlated between the 2 sampling periods (Table 3). When considering only the 17 species

TABLE 3. Value of various parameters, across 10 permanent plots established in 1991 in watersheds associated with Strawberry, Baker, Lehman, and Snake Creeks. Values are from plot measurements (mean \pm 1s) taken in 1992 (as in Smith et al. 1994), and in 2001 (Beever and Pyke). For each parameter, N represents the number of permanent plots on which that parameter occurred. The rightmost "probability" column represents the P -value for a paired t test, whereas the other "probability" column represents the P -value of Fischer's r to z transformation for each correlation.

Variable	UNLV (1992) value	N	USGS (2001) value	N	Average ratio 2001/1992	Probability (P)	Correlation	Probability (P)
Bare ground, 1994 definition	57.30 \pm 5.04	10	76.05 \pm 2.96	10	1.327	0.0008	0.669	0.032
Truly bare ground	—	10	1.86 \pm 0.60	10	0.032	<0.0001	-0.671	0.032
Litter	—	—	88.72 \pm 2.10	10	—	—	—	—
Forb cover (%)	15.30 \pm 3.16	10	8.03 \pm 1.45	10	0.525	0.028	0.470	0.18
Grass cover (%)	4.10 \pm 1.30	10	2.86 \pm 1.02	10	0.698	0.09	0.870	0.0004
Shrub cover (%)	19.90 \pm 5.15	10	10.46 \pm 3.46	10	0.526	0.008	0.865	0.0005
Species richness of shrubs	4.00 \pm 0.83	10	4.90 \pm 0.82	10	1.225	0.029	0.911	<0.0001
Species richness of forbs	—	—	16.80 \pm 2.23	10	—	—	—	—
Understory cover (G+F+S; %)	42.58 \pm 4.76	10	24.31 \pm 2.84	10	0.571	0.0007	0.657	0.037
Relative cover, <i>Carex-juncus</i> (%)	3.28 \pm 1.85	4	2.60 \pm 1.01	7	0.793	0.57	0.836	0.0014
Relative cover, AMEALN (%)	0.00 \pm 0.00	0	0.03 \pm 0.02	3	N/A	0.23	—	—
Relative cover, ARTTRI (%)	0.50 \pm 0.39	3	0.62 \pm 0.53	3	1.230	0.46	0.991	<0.0001
Relative cover, CHRNAU (%)	0.10 \pm 0.10	1	0.05 \pm 0.05	1	0.540	0.34	1.000	0.99
Relative cover, CHRVIS (%)	0.10 \pm 0.07	2	0.09 \pm 0.09	1	0.920	0.91	0.667	0.033
Relative cover, CLELIG (%)	0.30 \pm 0.21	2	0.19 \pm 0.17	2	0.633	0.61	0.448	0.20
Relative cover, CORSER (%)	0.30 \pm 0.21	1	0.02 \pm 0.02	2	0.077	0.20	0.781	0.006
Relative cover, EQUSP (%)	0.50 \pm 0.50	1	0.25 \pm 0.13	6	0.508	0.58	0.643	0.043
Relative cover, JUNCOM (%)	0.25 \pm 0.13	3	0.23 \pm 0.16	4	0.904	0.79	0.847	0.001
Relative cover, MAHREP (%)	0.40 \pm 0.40	1	0.18 \pm 0.15	4	0.448	0.39	0.995	<0.0001
Relative cover, PRUVIR (%)	0.60 \pm 0.40	2	—	—	—	—	—	—
Relative cover, RHUTRI (%)	3.25 \pm 2.26	2	1.90 \pm 1.43	2	0.585	0.17	0.980	<0.0001
Relative cover, ROSWO (%)	5.75 \pm 2.72	6	4.37 \pm 1.54	7	0.760	0.42	0.856	0.0007
Relative cover, RUBIDA (%)	0.30 \pm 0.30	1	0.12 \pm 0.12	1	0.413	0.34	1.000	<0.0001
Relative cover, SALEXI (%)	1.75 \pm 1.49	1	0.05 \pm 0.05	2	0.029	0.28	0.042	0.91
Relative cover, SALSPP (%)	3.22 \pm 2.17	2	2.77 \pm 1.50	5	0.858	0.74	0.799	0.004
Relative cover, SARVER (%)	0.02 \pm 0.02	1	0.00 \pm 0.00	0	0.000	0.34	**	—
Relative cover, SYMORE (%)	2.67 \pm 1.73	5	1.74 \pm 1.31	6	0.653	0.13	0.972	<0.0001

**Correlation could not be assessed due to lack of variance in 2001 data.

identified as shrubs in the 1992 data, species richness across plots was significantly higher in 2001.

Although Smith et al. (1994) did not discuss overstory cover, the number of overstory (tree) species occurring across all transects within plots in 2001 ranged from 1 to 7 (mean = 3.9) species. One to 3 more species may have occurred at middle-elevation plots due to *Salix* and *Juniperus* trees that we were not able to identify as separate species. Species richness of understory plants ranged from 15 to 39 (mean = 29.9) species and exhibited more of a bell-shaped relationship with elevation ($r^2_{\text{adj}} = 0.41$, $P = 0.07$) than a linear relationship ($r^2_{\text{adj}} = 0.07$, $P = 0.24$).

Cattle defecations in 2001 averaged 18.6 per plot, but ranged from 0 to 49. Number of defecations did not linearly predict the (2001/1992) ratio of cover of bare ground, grasses, forbs, shrubs, or all understory species. This remained true whether analyzed in simple regressions ($P > 0.10$ for all regressions) or in multiple linear regressions that accounted for the effect of elevation ($P_{\text{defecns}} > 0.15$). We performed the latter regressions because both cover and species richness (SR) of shrubs in 2001 declined with increasing elevation (cover: $F_{1,9} = 12.1$, $r^2 = 0.60$, $P = 0.008$; SR: $F_{1,9} = 23.5$, $r^2 = 0.75$, $P = 0.001$), as in 1992 (Smith et al. 1994). Monotonically decreasing SR with increasing elevation has been observed in plants, vertebrates, and insect taxa (Stevens 1992), and numerous hypotheses have been proposed to explain the mechanism of this relationship (reviewed in Fleishman et al. 1998).

We observed 27 differences in presence of individual species identified as shrubs by Smith et al. (1994). Sixteen of those differences occurred on plots ($n = 5$) where we could not locate both original stakes, whereas only 11 differences occurred on plots ($n = 5$) that were precisely relocated. Five of the 27 differences were apparent losses of shrub species from plots, whereas the other 22 differences were shrubs that we detected in 2001 that were not detected in 1992. Three of the 5 apparent losses were shrubs represented with $\leq 1\%$ cover in 1992, and the other 2 were losses of *Salix* spp. (willows) from Strawberry 3. Horsetails (*Equisetum* spp.) were added at 5 plots, and the next most common additions were *Carex-juncus*, broad-leaved *Salix* spp., *Mahonia repens* (Oregon grape), and *Amelanchier*

alnifolia (serviceberry), all new in 2001 in 3 plots (Table 3). Of the 17 individual shrub species graphed in Smith et al.'s (1994) Appendix 4, only 4 species (*Chrysothamnus nauseosus*, *C. ligusticifolia*, *Rhus trifolium*, and *Rubus idaeus*) occurred in 2001 solely in all plots in which they were observed in 1992.

DBH Measurements

The distribution of tree diameters in 2001 was biased more heavily toward the smallest size class than in the 1992 data for both *A. concolor* and *P. engelmannii*. The proportion of individuals with DBH <2 cm increased from 1992 to 2001 at 4 of 5 (10-m \times 100-m) plots (and remained the same at the 5th) for *A. concolor*, and at 3 of 4 plots for *P. engelmannii* (Appendix). In contrast, relative frequency of smallest size class *Populus* species was not higher in 2001 than in 1992; the proportion of individuals with DBH <2 cm decreased at both sites for *P. angustifolia*, and at 3 of 6 sites for *P. tremuloides* (with increases at remaining sites of only 1%, 5%, and 12% absolute increases; Appendix). In addition, the distribution of the largest-diameter trees migrated 1–2 classes upward for *A. concolor* at all 4 plots possessing the species where both stakes were relocated, as well as for *P. engelmannii* and *P. tremuloides* at 1 site each (Appendix). In contrast, all larger-diameter *P. engelmannii* individuals were lost from plot 6, and *P. tremuloides* appeared to have been totally lost from plot 3. Distributions of DBH values remained similar to those observed in 1992 for *Populus tremuloides* in plots 4 and 10, *P. angustifolia* in plot 5, and *P. engelmannii* in Lehman 8 (Appendix).

The number of *A. concolor* individuals increased from 1992 to 2001 at 4 of 5 plots but decreased by 81% at the remaining mid-elevation site (Appendix). In contrast, the number of *P. tremuloides* individuals decreased from 1992 to 2001 at 5 of 6 plots; the decrease ranged from 8% to 100% (Appendix). Although the number of *P. angustifolia* individuals increased at plot 9, the number decreased at the adjacent site by 73% (Appendix).

Revisitation of Successional Phenomena Observed in 1992

High values of bare ground were suspected by Smith et al. (1994) to lead to reduced tree recruitment, shrub species richness, and shrub cover. Bare ground did not predict the total

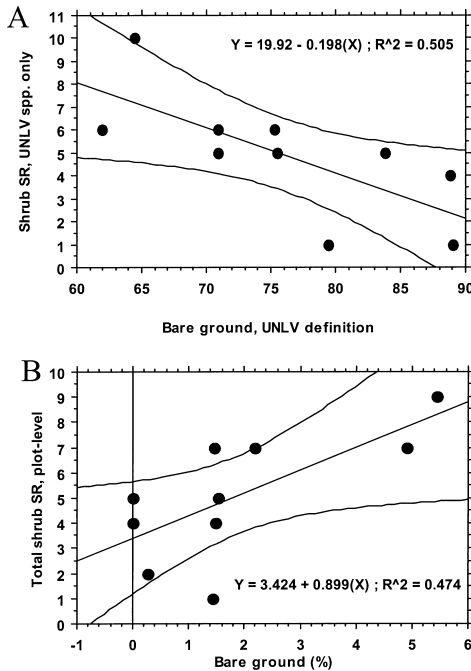


Fig. 2. Relationship of species richness of shrubs to percent cover of bare ground within 10-m \times 100-m permanent plots in 4 watersheds on the east slope of the Snake Range. Dotted lines represent 95% CI on slope. **A**, Only species considered shrubs in 1992 sampling (Smith et al. 1994) were regressed against the 1992 definition of bare ground [1 - (forb cover) - (grass cover) - (shrub cover) - (*Carex-Juncus* cover)]; **B**, life-forms follow Hickman (1993) and bare ground represents exposed soil surface.

number of seedlings and saplings in plots in 2001, when defining bare ground either as unvegetated ground or as exposed soil surface ($F_{1,9} < 0.3$, $r^2 < 0.03$). Using species defined as shrubs by Smith et al. (1994), we observed in 2001 the same inverse relationship between species richness (SR) of shrubs and cover of unvegetated ground ($F_{1,9} = 8.2$, $r^2 = 0.51$, $P = 0.021$; Fig. 2A) as in 1992. Interestingly, however, as amount of exposed soil surface increased, so did SR of shrubs in 2001, using species identified as shrubs by Hickman (1993; $F_{1,9} = 7.2$, $r^2 = 0.47$, $P = 0.028$; Fig. 2B) or by Smith et al. (1994; $F_{1,9} = 4.2$, $r^2_{\text{adj}} = 0.26$, $P = 0.08$). In both cases of this relationship to SR, however, the strength of the relationship was driven largely by high values of shrub SR at Strawberry 3 and Snake 9 plots. Given that bare ground was defined as the absence of vegetative cover and the result that shrub

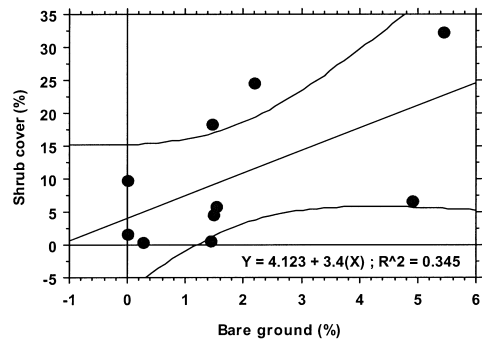


Fig. 3. Relationship of shrub cover to percent cover of bare ground, defined as exposed soil surface, at 10 permanent plots. Life-forms for shrubs followed Hickman (1993). Dotted lines represent 95% CI on slope.

cover dwarfed grass and forb cover (Table 3), shrub cover not surprisingly decreased with increasing amounts of bare ground (original definition) in 2001 ($F_{1,9} = 21.6$, $r^2 = 0.73$, $P = 0.002$). However, shrub cover **increased** with increasing amounts of exposed soil surface, although not as sharply ($F_{1,9} = 4.2$, $r^2 = 0.35$, $P = 0.07$; Fig. 3).

Second, recruitment of *Populus* varied among plots, demonstrated by an L-shaped distribution of DBH values of *P. angustifolia* (DBH <2 cm were most common) at plot 9 in 1992, whereas in plots 4 and 5 moderate-sized (DBH 11–20 cm) individuals were most common. On a coarse level, the comparison continued to hold during 2001, but results varied across plots and species. The distribution of *P. angustifolia* at plot 9 was again heavily biased toward smaller trees, as over 50% of the trees had DBH <2 cm and 84% of the trees had DBH <11 cm (Appendix). The distribution of *P. tremuloides* sizes at plot 4 was again bell- (rather than L-) shaped, but the center of the distribution had increased such that individuals of 11–20 cm, 21–30 cm, and 31–40 cm diameter were all about equally abundant. Distribution of *P. angustifolia* was again not L-shaped at plot 5, as 76.3% of *P. angustifolia* trees had DBH values >11 cm. However, in contrast to 1992 results, trees with DBH 21–30 cm were twice as abundant as any other size class at plot 5 (Appendix). Relative to 1992, both plots with *P. angustifolia* exhibited a decrease in the number of individuals in each of the 2 smallest DBH size classes.

Third, *P. engelmannii* was relatively rare at lower elevations in 1992, reached its maximum density between 2650 and 2850 m elevation, and appeared to be outcompeting *A. concolor* and *P. tremuloides* at higher elevations (Smith et al. 1994). Number of *P. engelmannii* individuals decreased from 1992 to 2001 at the 3 lowest-elevation plots (2409–2914 m; at all of which we located both stakes) and increased only at the highest-elevation (3060 m) site (Appendix). The log ratio of number of individuals encountered in 2001 compared with 1992 was strongly and linearly predicted by plot elevation ($F_{1,3} = 269.2$, $r^2 > 0.99$, $P = 0.004$). At plot 10, where the apparent competition was noted in 1992, the distribution of DBH values for *P. tremuloides* migrated to slightly larger DBH values, although the number of individuals dropped by 52% (Appendix). In contrast, distribution of *A. concolor* moved more heavily toward smallest-size trees, yet number of individuals increased by 15%. *P. engelmannii*, although its abundance decreased by 54%, exhibited 6 individuals with DBH >41 cm in 2001, compared with none in 1992. At plot 6, frequency distributions for all 3 remained similar in 2001 to those observed in 1992 (Appendix).

Fourth, *A. concolor* was believed to be invading and competing strongly with *P. tremuloides* at high elevations (Smith et al. 1994). This supposition was inferred from data in 1992 from 2 of 10 plots: (1) plot 10 possessed many *A. concolor* seedlings, yet few *P. tremuloides* seedlings and saplings; and (2) at plot 4, there were only a few small *A. concolor* individuals and very few large trees in the plot. In sampling during 2001, the relationship at plot 10 remained true, but only among the most immature individuals; there were 149 *A. concolor* seedlings in the plot, compared to 16 *P. tremuloides* seedlings (Appendix). However, the plot contained only 1 more *A. concolor* sapling (13 vs. 12) than *P. tremuloides* saplings. Furthermore, the plot contained 95 *P. tremuloides* trees older than saplings and seedlings, compared to only 25 *A. concolor* trees with DBH > 0. At plot 4 in 2001, the distribution of *A. concolor* DBH values differed strongly from the 1992 distribution. In 2001, 84.4% of the *A. concolor* trees in plot 4 occupied the smallest (<2 cm) size class, in contrast to a unimodal distribution of DBH values, centered on the 11–20 cm class, in the 1992 data. When we added 1 *P. tremu-*

loides individual to the 2001 total at plot 3 to allow a logarithm, log change in number of *A. concolor* individuals in the plot from 1992 to 2001 was inversely correlated with log change in number of *P. tremuloides* individuals in the plot where the species were sympatric in 1992 ($r = -0.96$, $P = 0.007$). In contrast, the log of the ratio of individuals observed in 2001 versus 1992 was not related to elevation for either *A. concolor* or *P. tremuloides* ($r^2 < 0.4$, $P > 0.25$ for each species).

DISCUSSION

Disturbance has been defined by researchers in numerous ways (e.g., White and Pickett 1985, Petraitis et al. 1989, Pickett et al. 1989), with definitions varying in terms of their inclusiveness of spatio-temporal scales as well as ecosystem components and processes. In addition to intensive use by livestock, riparian areas in the Great Basin have been affected during the last 100 years by impoundments for agriculture, heavy recreational use, introduction of exotic plant and animal species, fire exclusion, mining, dams, channelization, insect and disease outbreaks, and by factors that were also the dominant historic disturbances—periodic floods and fires, beaver dams, and periodic ungulate browsing. In GBNP the dominant disturbances in riparian systems over the last 2 centuries have included sheep and cattle grazing, mining, and recreation.

Riparian areas comprise landscape elements of the northern Intermountain West that have been particularly altered over the last 2 centuries. This alteration has been suggested to have arisen primarily because of improper livestock grazing practices (i.e., during summer, for too great a duration, or in too great a number; Hann et al. 1997). Kauffman and Krueger (1984), Trimble and Mendel (1995), and Belsky et al. (1999) reviewed a broad range of impacts of livestock grazing on riparian systems and provided considerations for management. In similar fashion Platts (1991) reviewed impacts on instream conditions, focusing particularly on fishes. Relevant to our study, for example, excessive livestock grazing may alter riparian ecosystems by accelerating erosion, stream incision, and siltation; compacting soils and thus reducing infiltration; widening and shallowing the streambed; altering timing and volume of water flows; and decreasing vigor and biomass

and altering species composition and diversity of riparian vegetation (Kauffman and Krueger 1984, Belsky et al. 1999).

Although season, duration, livestock type and class, distribution, and stocking rates may all be manipulated to attempt recovery of riparian areas (Kauffman and Krueger 1984), most cases of successful riparian restoration in the Intermountain West have excluded livestock for 2 or more years (Hann et al. 1997, Dobkin et al. 1998, Homyack and Giulano 2002, Krueger et al. 2003). This period of exclusion often facilitates recovery due to improved management in subsequent years. Nonetheless, some authors have found that removal of livestock grazing from riparian areas produces either no detectable improvement in aspects of riparian condition (Buckhouse et al. 1981) or improvement only after significant time lags (Kondolf 1993). Furthermore, research in central Nevada riparian systems suggests that, at least in some watersheds, effects of current management practices (such as grazing management) are overshadowed by residual effects of past (paleo- and historic) climate change on hillslope processes and sediment regimes (Chambers et al. 1998, Miller et al. 2001, 2004). We sought to test whether vegetative characteristics differed across 10 permanently marked sites during 2 periods that had received similar precipitation and intensity of other ungulates but differed in their grazing (grazed vs. 2 years' rest from grazing).

Permanent Plots

Smith et al. (1994:72) reported that riparian areas of GBNP "can be considered in fair ecological condition," but that the condition varied among reaches from "near-pristine" to "degraded." They concluded that "the primary impacts on riparian ecosystems of the Park appear directly related to livestock grazing." These authors proposed several hypotheses to revisit with subsequent sampling.

COMPARISONS OF 1992 AND 2001 DATA.—Our method of sampling appeared to produce consistently more conservative estimates of cover, as cover of all life-forms and all shrubs except *Artemisia tridentata* was notably lower in 2001 than in 1992 (Table 3). Although the logic behind this conclusion is only indirectly supported by the data, the smaller apparent decreases in cover of grasses in 2001 (relative to decreases in forbs and shrubs) may mean that

some increase in grasses may have occurred between 1992 and 2001. Increase of grasses after removing grazing would be the most likely change if livestock grazing were exerting persistent influence that did not cause riparian systems to cross ecological thresholds (sensu Tausch et al. 1993, Laycock 1994), because diets of cattle are composed of up to 95% grasses (Hanley and Hanley 1982). However, comparisons of life-forms were compromised by the fact that we could not exactly replicate the methods used to record interceptions in the 1992 sampling.

Given the sources of error that often occur in repeat sampling of plots (e.g., slightly different transect locations sampled; see Beever et al. 2002), we cannot be confident that all changes in presence of individual shrub species reflect true additions or losses to plots. On the other hand, assuming that plots were originally placed in locations representative of nearby areas, even for those transects where we could relocate only 1 endpoint, measurements should not be excessively influenced by small deviations in transect location. The degree of heterogeneity at small spatial scales in plant community characteristics will determine how greatly the imprecise relocation of monitoring plots will affect results. Nonetheless, using the same suite of species defined as shrubs for 1992 sampling, we did observe an increase of an average of 22.5% greater SR of shrubs (mean = 4.9 vs. 4.0 species) in 2001 compared with 1992, consistent with our prediction of system response to grazing removal. The apparent addition of willow to 3 new plots in 2001 sampling is similarly consistent with the fact that cattle in many riparian areas often heavily utilize willows, as do native ungulates (Singer et al. 1994, Patten 1998, Peinetti et al. 2001).

FOUR RELATIONSHIPS RELATED TO LONG-TERM SUCCESSIONAL PROCESSES.—Although extent and distribution of bare ground can play critical roles in ecosystem function of both riparian corridors and associated uplands, our ability to detect any change over time in bare ground was confounded by 2 main attributes of the 1992 sampling. First, bare ground was defined as the absence of forbs, shrubs, grasses, sedges, and rushes, but was not distinguished from litter. Second, line-intercept sampling methods were not precisely described or referenced against any published source; consequently, we struggled to replicate the methodology used

in 1992. Because soil properties, erosion potential, and biotic properties often differ dramatically between areas of exposed soil and litter-covered ground, we distinguished the 2 in our 2001 sampling.

Smith et al. (1994) postulated that high levels of bare ground at low-elevation sites probably reflect a substantial grazing impact on vegetation. While we observed even higher amounts of bare ground (using the original definition) than that observed in 1992, we cannot say with confidence to what degree this resulted from methodological differences in line-intercept sampling or from authentic system response to livestock removal. This difference was not well explained by precipitation patterns, as precipitation was 6.8% higher in the 12 months before 2001 sampling than in 1992 (Fig. 4). Neither tree recruitment nor SR of shrubs was consistently related to amount of bare ground in 2001, although shrub SR was inversely proportional to elevation. Whereas bare ground is itself a response to disturbances and management actions rather than a direct cause-and-effect agent on the vegetation attributes we revisited, bare ground and vegetation may interact in feedback loops (e.g., through greater desiccation, sheet and rill erosion, and higher wind speeds; Davenport et al. 1998). In addition to livestock effects, inverse relationships of bare ground to shrub SR and tree recruitment could also be caused by higher levels of allelopathy or other interspecific competition among plants, independent of grazing.

Reanalysis of the age structure of trees (as seen through the distribution of DBH values) at Snake 9 versus Snake 4 and Snake 5 yielded results broadly similar to those observed in 1992 sampling. The most notable exception was that distributions of tree sizes shifted upward to larger size classes, suggesting maturation of larger trees without concomitant die-off. Otherwise, all 3 cases of *Populus* species highlighted by Smith et al. (1994) demonstrated results similar to those of 1992, despite the fact that we could not precisely relocate 2 of the 3 plots. The persistence of this result across plots is consistent with the strong relationship of *Populus* recruitment to hydrologic regime and geomorphic constraints (rather than solely to management effects), common for riparian obligates such as *P. angustifolia* (Stromberg and Patten 1991, Auble et al. 1994, Chambers et al. 2004).

Specifically, recruitment of *Populus* individuals will be affected not only by survival of germinants experiencing browsing by domestic and native herbivores, but also by the distribution and suitability of benches of stream channels as germination sites. The maintenance and magnification of a bell-shaped distribution at plot 5 two years after livestock removal suggests that the high degree of channel incision within the 100-m plot length may have compromised recruitment of *P. angustifolia* there (see Yount and Niemi 1990). Highly divergent recruitment patterns of *P. angustifolia* in plots adjacent to each other (note also trends in total individuals at plots 5 and 9; Appendix) and in the same hydrogeomorphic unit are somewhat unexpected and underscore that variability in processes such as recruitment and establishment occurs at numerous spatial scales.

Picea engelmannii occurred rarely at low elevations in 1992 and appeared to be outcompeting *A. concolor* and *P. tremuloides* at higher elevations (Smith et al. 1994). Under scenarios of climate change, distributions of most species are broadly predicted to move either upslope or to more northern latitudes. Although the proportion of individuals in the smallest size class increased at 3 of 4 *P. engelmannii* plots, the total number of individuals declined in all but the highest-elevation plot (Appendix). Elevation strongly predicted change in abundance across the 4 plots ($r^2 > 0.99$), providing stronger support for a climate-related response in *P. engelmannii*. Stronger support yet was provided by comparing walking surveys in 0.2-mile segments in the 4 watersheds in 2002 (Beever unpublished data) to elevational distributions of the 7 species reported by Smith et al. (1994). Whereas the lower end of the elevational distribution did not increase for *Pinus monophylla*, *P. angustifolia*, *A. concolor*, *P. tremuloides*, or *P. flexilis* (except for modest increases at 1 site each in *P. flexilis* and *A. concolor*), the lower limit of *P. engelmannii* increased by 175–200 m in 3 of 4 watersheds. *Pinus engelmannii* in the Snake Range is associated with higher-elevation habitats that have shorter growing seasons, deep shade, and cooler microsites (Smith et al. 1994). Thus, reductions of *P. engelmannii* at lower elevations are consistent with the trends of both (1) increased temperatures (Mote et al. 2005) and

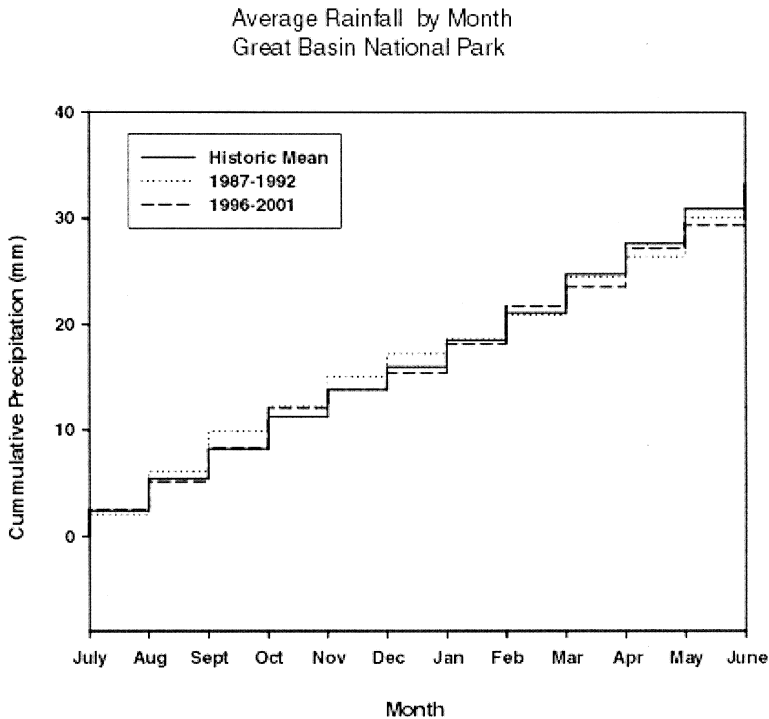


Fig. 4. Five-year averages of cumulative monthly precipitation in the periods before the initial (1992) and repeat (2001) sampling at Park Headquarters of GBNP, 2081 m elevation, Snake Range, NV. Also shown is the 56-year average of precipitation. Data source: Western Regional Climate Center online data, Reno, NV.

earlier snowmelt and streamflow (Stewart et al. 2005) in the Great Basin and across the West during the 20th century; and (2) decreased snow-water equivalent (SWE; measured 1 March and 1 April) amounts in Baker Creek at elevations of 2505 m, 2805 m, and 2902 m during 1942–2001 (G. Baker, GBNP ecologist, April 2005 unpublished report). More specifically, April SWE has decreased by 22%, 26%, and 15% at those elevations, and March SWE has decreased by 20%, 32%, and 31%, as noted in regional-scale, climate-driven trends across much of the West, reported by Mote et al. (2005). The magnitude of shift (175–200 m in 9 years) in the lower-elevation boundary far exceeds the migration expected for trees in the Swiss Alps (8–10 m per decade; Grabherr et al. 1994); however, this was the only tree species whose distribution exhibited notable upward migration. Furthermore, the bioclimatic envelope for this species may not have been well established at the time of the 1992 sampling, such that the lowest-elevation trees were “stand-

ing dead.” These types of elevationally explicit data sets will prove invaluable for assessing ecosystem response to climate change in the future.

Although we did not consistently observe the aspects of relationships noted by Smith et al. (1994) between mature and young individuals of *A. concolor* and *P. tremuloides* at Lehman 10 and Snake 4, other 2001 data nonetheless suggest an antagonistic relationship between the 2 species. Differences in abundance of smallest size class individuals in 1992 did not translate into differential recruitment into larger size classes at those plots (Appendix). However, the 2 species exhibited opposite directions in change in total abundance at all 5 sites, and these changes correlated strongly with changes in the other species but not with elevation. Across the Intermountain West, *P. tremuloides* becomes established quickly in disturbed sites, particularly after fire, but is replaced over time by *A. concolor* or other conifers under fire suppression. The park is currently moving toward reincorporation of fire into the disturbance

regime through active management. Because we were able to precisely relocate 4 of 5 plots having both species, we suggest that this relationship reflects a true biological phenomenon on the landscape rather than a source of error. Monitoring a greater number of locations could further clarify this relationship.

Alternative Explanations for Observed Differences Between Sampling Periods

The fact that tallies of cow defecations within plots did not predict magnitude of change in cover of any life-form suggests either that tallies poorly reflected grazing intensity (e.g., if the system were flushed with peak flows, or if microsite conditions created variability across sites in rates of decay of defecations during the period since grazing removal) or that grazing effects were overshadowed by hydrogeomorphic and clinal constraints on plant composition. For example, some soil types or hydrogeomorphic units associated with vegetative communities may be naturally more vulnerable to grazing and other disturbance than others. Frissell and Liss (1993) found that Strawberry and Snake Creeks possessed a geomorphology that was inherently more prone to system alteration. In contrast, riparian corridors in Baker and Lehman Creeks were extensively armored with boulders and cobbles, providing stability to the system. Depending on the response variable, 10 plots may provide insufficient power to detect disturbance-related relationships across areas of broad environmental heterogeneity.

Another source of change in riparian systems (reviewed by Trombulak and Frissell 2000)—the presence of dirt roads near sampled reaches of streams—may also have confounded our analysis of change relative to change in livestock management. Although dirt roads exist in all 4 of our target drainages, roads were within 0.25 km of the active channel at only the 2 pairs of low-elevation sites (sites 1, 3, 5, and 9), a nonrandom subsample of the biophysical conditions found across all sites (and thus inappropriate for analysis of road effects).

Our sampling represented a single sampling event 2 years after cessation of grazing, which may be insufficient time for vegetative recovery in riparian zones of semiarid ecosystems. In their thorough review of case studies of recovery, Yount and Niemi (1990) found that

most lotic systems recovered quite rapidly from disturbance due to their high flushing rates, the availability of upstream and downstream refugia for recolonization, and life-history characteristics of species that allow rapid repopulation of affected areas. In contrast, recovery was protracted when disturbances resulted in alterations to the physical habitat (e.g., mining activity, clear-cut logging, channelization; Yount and Niemi 1990). Relative to the timing of our 2nd sampling, numerous authors have reported significant recovery in 1 or more parameters of riparian vegetation in similar time frames (<2 years after protection from grazing; e.g., Davis 1982, Case and Kauffman 1997, Auble and Scott 1998, Dobkin et al. 1998, Homyak and Giulano 2002). Rates of vegetation and channel recovery in any given stream reach may be strongly affected by factors such as watershed stability, climate, subsurface moisture availability, soil organic content, condition and proximity of propagule sources, and degree of channel incision (Sarr 2002, Chambers et al. 2004).

Relatively rapid recovery in some riparian ecosystems contrasts markedly with the unpredictable trajectories of recovery in arid and semiarid upland communities, where productivity is much lower, plant recruitment more sporadic, and dynamics are characterized by thresholds, nonlinear recovery, and multistate systems (Tausch et al. 1993, Laycock 1994). Regardless of how disturbance is defined, long-term data are required to assert recovery within riparian areas, which can provide information on the frequency and rates of change rather than simply point estimates (Gore et al. 1990). Additionally, ecologists are becoming increasingly aware that livestock-grazing disturbance must be investigated in concert with other influences such as precipitation, fire, and fluctuations in density of native herbivores (Drewa and Havstad 2001).

Precipitation during the previous year(s) will clearly affect the magnitude, duration, and timing of stream flows in montane riparian systems, as well as the productivity and diversity of upland vegetation, though likely with different time scales and lags. However, precipitation at none of 3 temporal scales we investigated strongly supported the vegetative differences we observed between sampling periods, and trends were in fact opposite those

that would be predicted by our results at 2 temporal scales. On the most proximate level of causation, precipitation in GBNP ranged from 24% to 28% higher (rather than lower) during the months of sampling (July and August) in 2001 compared with 1992. On a slightly longer scale, precipitation occurring in the 12 months before 1992 sampling totaled 32.7 cm, 7% lower (rather than higher) than the 34.9 cm of precipitation received during the 12 months before 2001 sampling (Western Regional Climate Center, online data, Park Headquarters weather station at 2082 m; Fig. 1). Riparian shrubs and trees depend more on the amount of winter snowpack and subsequent spring runoff and aquifer recharge than on summer precipitation, and so precipitation from October to April/May would be most critical for their productivity. Again, precipitation patterns were counterintuitive to our finding of lower shrub cover in 2001 than 1992, as precipitation during October–May was 42% higher before 2001 than before 1992 sampling.

On relatively longer time scales, precipitation levels during the 5 years previous to each sampling period were nearly indistinguishable from each other (33.35 cm · yr⁻¹ during 1987–1992, vs. 32.99 cm · yr⁻¹ during 1996–2001) and the 56-year average (33.27 cm · yr⁻¹; Fig. 4). Furthermore, slightly lower precipitation during the latter period may have resulted simply from its larger number of days of missing data (3.8 d · yr⁻¹, compared to 1 d · yr⁻¹ during 1987–1992), though both frequencies are relatively small. Because vegetation dynamics do not scale linearly with precipitation, it is difficult to predict what types of variability in vegetative parameters we would expect in these systems without other long-term data sets. However, interannual changes in cover of trees and perennial shrubs under variable precipitation should be comparatively small.

It is possible that removal of nonnative herbivores from GBNP was compensated by subsequently higher densities of native herbivores, thus preventing system recovery. Historic records of elk (*Cervus elaphus*) in eastern Nevada are fragmentary, but we do know that they were first introduced to the region in the adjacent Schell Creek Range in 1932 and were first reported in the southern Snake Range in 1976 (C. Baughman, Nevada Division of Wildlife, personal communication). Elk are rarely found in eastside drainages of the Snake Range,

and there probably have never been >50 animals in the entire south Snake Range (C. Baughman personal communication). Up to 30–40 elk may occupy drainages near Strawberry Creek during summer months, but this number varied little between 1992 and 2001.

Censusing and population modeling of mule deer (*Odocoileus hemionus*) by the Nevada Division of Wildlife became more fine-grained between 1992 and 2001. The data collected for both sampling dates estimated that mule deer populations within a 5-mountain-range area approximated 18,600 animals in 1992 but only 11,700 animals in 2001. Assuming that the proportion of animals in the Snake Range relative to the other 4 ranges was similar, this would produce an estimated total of 5800 deer in the Snake Range in 1992. This value is 1.6 times higher than the estimate from mountain range-specific census data of 3600 animals in 2001. Thus, disparities between riparian vegetation data in 2001 and 1992 that were not consistent with predictions of vegetation change following livestock removal (e.g., lower shrub cover, lower grass cover) do not correspond to fluctuations in native herbivore numbers during that period. Furthermore, Trimble and Mendel (1995) suggested that variability in numbers of native herbivores may have more influence on trends in upland rather than riparian communities, whereas cattle often exert greater relative pressure in the riparian corridor itself.

Implications for Future Efforts

Monitoring is an essential element of ecosystem management, in that it is intended to detect long-term environmental change, provide insights to the potential ecological consequences of the change, and help decision makers determine if and how management practices should be amended (Noon et al. 1999).

We sought to address to what degree long-term monitoring can be used to address hypotheses about plant community relationships and vegetation change. Also of interest is comparing the percent change over time that a given method can detect, and how that compares to what percent change is ecologically relevant. Our results suggest that the utility of monitoring will depend on the precision of the data, the question being addressed, and the short-term variability of the response variable, among other things. With the types of data we

collected, comparisons that can most robustly and meaningfully be interpreted are changes in relative proportions of different life-forms, shrub and tree densities, size structuring of trees, and relationships among these. For management-based monitoring to be maximally effective in filtering out the effects of expected intrinsic variability or cycles (i.e., noise) from the effects of human-induced patterns of change (i.e., signal), monitoring activities should follow several guidelines. Adequate replication within the domain of interest, in combination with concomitant sampling of "control" or benchmark sites, can help clarify indicator dynamics. In their assessment of needs for multiscale monitoring of vegetation in the park relative to changing management and abiotic conditions, Eddleman and Jaindl (1994) noted that methods should index vegetation attributes at scales of 10–15 years to accurately detect true vegetation change.

Repeatability is the single-most important aspect of successful monitoring, but it is elusive because budgets are restricted and vary greatly over time, and because changes in monitoring personnel inevitably lead to observer bias. Repeatability in space can be improved by (1) placing permanent markers at ends of plots or transects that cannot be easily detected and removed by the general public or natural processes (e.g., floods); (2) recording plot locations with differentially corrected GPS or a handheld GPS unit with WAAS (Wide Area Augmentation System); (3) using traditional orienteering techniques to triangulate plot vertices (see Harrelson et al. 1994); and (4) taking pictures from defined locations. Repeatability in time can be improved by standardizing or including covariates in analyses factors such as sampling date and time, as well as atmospheric conditions (e.g., moon phase, weather). Although these temporal conditions affect vegetation monitoring in many systems only through their effect on phenology, many animals respond strongly to them. Repeatability of techniques used in the field can be improved by following published guidelines for well-established methods, noting explicitly any deviations from the standard method.

Because ecosystem interactions operate within a hierarchy (Noss 1990), it is critical that monitoring and evaluation address questions and trends at various spatial scales. Hierarchi-

cal structuring and organization are particularly evident in stream networks (Frissell et al. 1986, Gregory et al. 1991). For example, using Bray-Curtis ordination and cluster analysis, Baker (1989) found that riparian vegetation in 115 plots in the southern Rocky Mountains reflected complex interactions of macroscale abiotic gradients (e.g., elevation and geology) with microscale (valley morphology) characteristics. Although not strictly hierarchical, the original placement of the 10 permanent plots permits analysis to a limited extent within vegetation associations of the same drainage ($n = 2$ pairs), across different associations within the same drainage, and across 4 drainages of the Snake Range.

Future Research Directions

Because semiarid ecosystems generally do not exhibit succession to climax communities in the Clementsian sense (Tausch et al. 1993, Laycock 1994), research is needed to improve our understanding of the conditions under which transitions between different vegetation states occur in diverse communities and the inputs of resources (i.e., active restoration treatments) needed to shift ecosystems from less desirable states to one of many other possible metastable configurations. For desert streams Fisher (1990) argued that the concept of ecosystem resilience and resistance to disturbance, rather than succession to a climax state, better represents system dynamics. Determining how ecosystem patterns and processes in semiarid regions respond to bulk grazing by cattle, horses, and elk constitutes a major focus area of future research needs. Few studies exist on how landscape-level patterns in riparian vegetation affect viability of wildlife populations. Many research needs for riparian areas related to scale remain, including (1) effects of homogeneous vs. heterogeneous distributions of disturbance, (2) how local disturbances or restoration efforts affect ecosystem function and structure in a regional context, and (3) importance of size and location of critical vs. noncritical patches of disturbance at different spatial scales and temporal frequencies (Gore et al. 1990).

Given that many of the ecological issues related to land use and environmental quality may be ameliorated with effective management of riparian corridors (Naiman et al. 1993),

monitoring in managed areas should focus at least partially within riparian zones. Geomorphology can strongly affect both floral and faunal assemblages within riparian areas (Huryn and Wallace 1987, Harris 1988). Consequently, we recommend stratifying by hydrogeomorphic zones (Frissell and Liss 1993) and dominant woody vegetation to capture dominant gradients in community composition. Other authors have described quantitative yet easily implemented methods for monitoring change in riparian vegetation in managed ecosystems that may be useful alternatives to the system of permanent plots described in this research. For example, the 3 sampling methods presented by Winward (2000) provide practitioners with information about extent of various plant communities along the riparian "greenbelt" and across stream sections, as well as in density of individual woody species within a 1.83×221.3 -m plot along the greenbelt. Similarly, Herrick et al. (2005) describe methods that record the channel profile and the shape of the soil surface in uplands, and cover of individual species along the greenline. Indicators that may be monitored with these 2 methods include total canopy cover, cover of stabilizing species, total woody cover, and bank angle and width-depth ratios (Herrick et al. 2005). Both frameworks view change through the lens of inherent site capacity and utilize methods that not only characterize plant composition but also index ecosystem function by analyzing vegetation in concert with hydromorphology of the adjacent stream. Ecologists are increasingly beginning to understand the interconnectedness of riparian and adjacent upland communities (e.g., Gregory et al. 1991); future riparian monitoring should thus integrate these communities. In these systems such monitoring may be used as a starting point to define baseline conditions, understand the range of current variability in riparian vegetation parameters, and detect undesirable short-term changes within reserve areas and adjacent ecosystems.

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LITERATURE CITED

- ARCHER, S., AND F.E. SMEINS. 1991. Ecosystem-level processes. Pages 109–140 in R.K. Heitschmidt and J.W. Stuth, editors, *Grazing management: an ecological perspective*. Timber Press, Portland, OR.
- AUBLE, G.T., J.M. FRIEDMAN, AND M.L. SCOTT. 1994. Relating riparian vegetation to present and future streamflows. *Ecological Applications* 4:544–554.
- AUBLE, G.T., AND M.L. SCOTT. 1998. Fluvial disturbance patches and cottonwood recruitment along the upper Missouri River, Montana. *Wetlands* 18:546–556.
- BAKER, W.L. 1989. Macro- and micro-scale influences on riparian vegetation in western Colorado. *Annals of the Association of American Geographers* 79:65–78.
- BEEVER, E.A., D.A. PYKE, J.E. HERRICK, J. BELNAP AND J.C. CHAMBERS. 2002. Soil and vegetation changes related to livestock removal at Mojave National Preserve and Great Basin National Park. NRPP annual report to Great Basin National Park.
- BELSKY, A.J., A. MATZKE, AND S. USELMAN. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. *Journal of Soil and Water Conservation* 54:419–431.
- BLAKE, E.W. 1992. Soil survey of Great Basin National Park, Nevada (parts of Humboldt National Forest, Nevada, South Part Soil Survey). USDA Soil Conservation Service, Reno, NV.
- BUCKHOUSE, J.C., J.M. SKOVLIN, AND R.W. KNIGHT. 1981. Streambank erosion and ungulate grazing relationships. *Journal of Range Management* 34:339–340.
- BULL, E.L. 1978. Specialized habitat requirements of birds: snag management, old growth, and riparian habitat. Pages 74–82 in R.M. DeGraaf, editor, *Proceedings of the workshop on nongame bird habitat management in coniferous forests of the western United States*. General Technical Report PNW-GTR-64, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, LaGrande, OR.
- CASE, R.L., AND J.B. KAUFFMAN. 1997. Wild ungulate influences on the recovery of willows, black cottonwood and thin-leaf alder following cessation of cattle grazing in northeastern Oregon. *Northwest Science* 71:115–126.
- CHAMBERS, J.C., K. FARLEIGH, R.J. TAUSCH, J.R. MILLER, D. GERMANOSKI, D. MARTIN, AND C. NOWAK. 1998. Understanding long- and short-term changes in vegetation and geomorphic processes: the key to riparian restoration. Pages 101–110 in D.F. Potts, editor, *Proceedings: Rangeland Management and Water Resources, 27–29 May 1998*, American Water Resources Association and Society for Range Management, Reno, NV.
- CHAMBERS, J.C., R.J. TAUSCH, J.L. KORFMACHER, J.R. MILLER, AND D.G. JEWETT. 2004. Effects of geomorphic processes and hydrologic regimes on riparian vegetation. Pages 196–231 in J.C. Chambers and J.R. Miller, editors, *Great Basin riparian ecosystems: ecology, management, and restoration*. Island Press, Covelo, CA.

- DAVENPORT, D.W., D.D. BRESHEARS, B.P. WILCOX, AND C.D. ALLEN. 1998. Viewpoint: sustainability of piñon-juniper ecosystems—a unifying perspective of soil erosion thresholds. *Journal of Range Management* 51:231–240.
- DAVIS, J.W. 1982. Livestock vs. riparian habitat management—there are solutions. Pages 175–184 in *Wildlife-livestock relations symposium: Proceedings* 10. University of Idaho Forest, Range, and Experiment Station, Moscow.
- DOBKIN, D.S., A.C. RICH, AND W.H. PYLE. 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. *Conservation Biology* 12:209–221.
- DREWA, P.B., AND K.M. HAVSTAD. 2001. Effects of fire, grazing, and the presence of shrubs on Chihuahuan Desert grasslands. *Journal of Arid Environments* 48: 429–443.
- EDDLEMAN, L.E., AND R. JAINDL. 1994. Range analysis for Great Basin National Park. Oregon State University Cooperative Park Studies Unit, Cooperative Agreement 9000-8-0006, Subagreement 14, NPS/PNROSU/NRTR-94/02, 1 of 5 volumes.
- FISHER, S.G. 1990. Recovery processes in lotic ecosystems: limits of successional theory. *Environmental Management* 14:725–736.
- FLEISHMAN, E., G.T. AUSTIN, AND A.D. WEISS. 1998. An empirical test of Rapoport's rule: elevational gradients in montane butterfly communities. *Ecology* 79: 2482–2493.
- FRISSELL, C.A., AND W.J. LISS. 1993. Valley segment classification for the streams of Great Basin National Park, Nevada. Report prepared for the Cooperative Park Studies Unit, College of Forestry, Oregon State University, Corvallis.
- FRISSELL, C.A., W.J. LISS, C.E. WARREN, AND M.D. HURLEY. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10:199–214.
- GORE, J.A., J.R. KELLY, AND J.D. YOUNT. 1990. Application of ecological theory to determining recovery potential of disturbed lotic ecosystems: research needs and priorities. *Environmental Management* 14:755–762.
- GRABHERR, G., M. GOTTFRIED, AND H. PAULL. 1994. Climate effects on mountain plants. *Nature* 369:448.
- GRAYSON, D.K. 1993. The desert's past: a natural prehistory of the Great Basin. Smithsonian Institution Press, Washington, DC.
- GREEN, D.M., AND J.B. KAUFFMAN. 1995. Succession and livestock grazing in a northeastern Oregon riparian ecosystem. *Journal of Range Management* 48:307–313.
- GREGORY, S.V., F.J. SWANSON, W.A. MCKEE, AND K.W. CUMMINS. 1991. An ecosystem perspective of riparian zones. *BioScience* 41:540–551.
- HANLEY, T.A., AND K.A. HANLEY. 1982. Food resource partitioning by sympatric ungulates on Great Basin rangeland. *Journal of Range Management* 35:152–158.
- HANN, W.J., J.L. JONES, M.G. KARL, P.F. HESSBURG, R.E. KEANE, D.G. LONG, J.P. MENAKIS, ET AL. 1997. Landscape dynamics of the Basin. Pages 337–1055 in T.M. Quigley and S.J. Arbedbide, technical editors, An assessment of ecosystem components in the Interior Columbia Basin and portions of the Klamath and Great Basins. General Technical Report PNW-405, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.
- HARRELSON, C.C., C.L. RAWLINS, AND J.P. POTYONDY. 1994. Stream channel reference sites: an illustrated guide to field technique. General Technical Report RM-GTR-245, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- HARRIS, R.R. 1986. Occurrence patterns of riparian plants and their significance to water resource development. *Biological Conservation* 38:273–286.
- _____. 1988. Associations between stream valley geomorphology and riparian vegetation as a basis for landscape analysis in the eastern Sierra Nevada, California, USA. *Environmental Management* 12:219–228.
- HERRICK, J.E., J.W. VAN ZEE, K.M. HAVSTAD, L.M. BURRETT, AND W.G. WHITFORD. 2005. Monitoring manual for grassland, shrubland, and savanna ecosystems. USDA-ARS Jornada Experimental Range, Las Cruces, NM. 2 volumes.
- HICKMAN, J.C., EDITOR. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley.
- HOMYACK, J.D., AND W.M. GIULIANO. 2002. Effect of stream-bank fencing on herpetofauna in pasture stream zones. *Wildlife Society Bulletin* 30:361–369.
- HURYN, A.D., AND J.B. WALLACE. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. *Ecology* 68:1932–1942.
- JANSEN, A., AND A.I. ROBERTSON. 2001. Relationships between livestock management and the ecological condition of riparian habitats along an Australian floodplain river. *Journal of Applied Ecology* 38:63–75.
- KAUFFMAN, J.B., AND W.C. KRUEGER. 1984. Livestock impacts on riparian ecosystems and streamside management implications . . . a review. *Journal of Range Management* 37:430–438.
- KONDOLF, G.M. 1993. Lag in stream channel adjustment to livestock enclosure, White Mountains, California. *Restoration Ecology* 1:226–230.
- KRUEPER, D., J. BART, AND T.D. RICH. 2003. Response of vegetation and breeding birds to the removal of cattle on the San Pedro River, Arizona (U.S.A.). *Conservation Biology* 17:607–615.
- LAYCOCK, W.A. 1994. Implications of grazing v. no grazing on today's rangelands. Pages 250–280 in M. Vavra, W.A. Laycock, and R.D. Pieper, editors, Ecological implications of livestock herbivory in the West. Society for Range Management, Denver, CO.
- MACK, R.N., AND J.N. THOMPSON. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* 119:757–773.
- MILLER, J., D. GERMANOSKI, K. WALTMAN, R. TAUSCH, AND J. CHAMBERS. 2001. Influence of late Holocene processes and landforms on modern channel dynamics in upland watersheds of central Nevada. *Geomorphology* 38:373–391.
- MILLER, J.R., D. GERMANOSKI, R.J. TAUSCH, AND J.C. CHAMBERS. 2004. Fluvial geomorphic responses to Holocene climate change. Pages 49–87 in J.C. Chambers and J.R. Miller, editors, Great Basin riparian ecosystems: ecology, management, and restoration. Island Press, Covelo, CA.
- MILLER, R.F., AND P.E. WIGAND. 1994. Holocene changes in semiarid pinyon-juniper woodlands. *BioScience* 44:465–474.
- MOTE, P.W., A.F. HAMLET, M.P. CLARK, AND D.P. LETTENMAIER. 2005. Declining mountain snowpack in western North America. *Bulletin of the American meteorological Society* 86:39–49.

- NAIMAN, R.J., H. DECAMPS, AND M. POLLOCK. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3:209–212.
- NOON, B.R., T.A. SPIES, AND M.G. RAPHAEL. 1999. Conceptual basis for designing an effectiveness monitoring program. Pages 21–48 in B.S. Mulder, B.R. Noon, T.A. Spies, M.G. Raphael, C.J. Palmer, A.R. Olsen, G.H. Reeves, and H.H. Welsh, technical coordinators, The strategy and design of the effectiveness monitoring program for the Northwest Forest Plan. General Technical Report PNW-437, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.
- NOSS, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355–364.
- PATTEN, D.T. 1998. Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* 18: 498–512.
- PEINETTI, H.R., R.S.C. MENEZES, AND M.B. COUGHENOUR. 2001. Changes induced by elk browsing in the aboveground biomass production and distribution of willow (*Salix monticola* Bebb): their relationship with plant water, carbon, and nitrogen dynamics. *Oecologia* 127:334–342.
- PETRAITIS, P.S., R.E. LATHAM, AND R.A. NIESENBAUM. 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology* 64:393–418.
- PICKETT, S.T.A., J. KOLASA, J.J. ARMESTO, AND S.L. COLLINS. 1989. Patch dynamics and the design of nature reserves. *Biological Conservation* 13:27–37.
- PLATTS, W.S. 1991. Livestock grazing. Pages 389–424 in W.R. Meehan, editor, *Influences of forest and rangeland management on salmonid fishes and their habitat*. Special Publication 19, American Fisheries Society, Bethesda, MD.
- POSTEL, S., AND S. CARPENTER. 1997. Freshwater ecosystem services. Pages 195–214 in G.C. Daily, editor, *Nature's services: societal dependence on natural ecosystems*. Island Press, Covelo, CA.
- RICKARD, W.H., AND C.E. CUSHING. 1982. Recovery of streamside woody vegetation after exclusion of livestock grazing. *Journal of Range Management* 35: 360–361.
- ROSCEN, D.A. 1985. A stream classification system. Pages 91–95 in *Riparian ecosystems and their management*. First North American Riparian Conference, publication RM-120, Rocky Mountain Forest and Range Experiment Station.
- SARR, D.A. 2002. Riparian livestock enclosure research in the western United States: a critique and some recommendations. *Environmental Management* 30: 516–526.
- SCHULZ, T.T., AND W.C. LENINGER. 1990. Differences in riparian vegetation structure between grazed areas and enclosures. *Journal of Range Management* 43: 295–299.
- SINGER, F.J., L.C. MARK, AND R.C. CATES. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. *Journal of Range Management* 47:435–443.
- SMITH, S.D., K.J. MURRAY, F.H. LANDAU, AND A. SALA. 1994. The woody riparian vegetation of Great Basin National Park. Contribution CPSU/UNLV 050/03, Cooperative National Park Resources Studies Unit, National Biological Survey, University of Nevada, Las Vegas.
- STEVENS, G.C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *American Naturalist* 140:893–911.
- STEWART, I.T., D.R. CAYAN, AND M.D. DETTINGER. 2005. Changes toward earlier streamflow timing across western North America. *Journal of Climate*. In press.
- STROMBERG, J.C., AND D.T. PATTEN. 1991. Instream flow requirements for cottonwoods at Bishop Creek, Inyo County, California. *Rivers* 2:1–11.
- TAUSCH, R.J., P.E. WIGAND, AND J.W. BURKHARDT. 1993. Viewpoint: plant community thresholds, multiple steady states, and multiple successional pathways: legacy of the Quaternary? *Journal of Range Management* 46:439–447.
- THOMAS, J.W., TECHNICAL EDITOR. 1979. *Wildlife habitats in managed forests of the Blue Mountains of Oregon and Washington*. U.S. Department of Agriculture, Forest Service, with U.S. Department of the Interior, Bureau of Land Management, and the Wildlife Management Institute, Washington, DC.
- TRIMBLE, S.W., AND A.C. MENDEL. 1995. The cow as a geomorphic agent—a critical review. *Geomorphology* 13:233–253.
- TROMBULAK, S.C., AND C.A. FRISSELL. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- U.S. ENVIRONMENTAL PROTECTION AGENCY. 2000. *Level III ecoregions of the continental United States*. National Health and Environmental Effects Research Laboratory, Corvallis, OR. Revised March 2000.
- WHITE, P.S., AND S.T.A. PICKETT. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3–13 in S.T.A. Pickett and P.S. White, editors, *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, FL.
- WINWARD, A.H. 2000. *Monitoring the vegetation resources in riparian areas*. General Technical Report RMRS-47, USDA Forest Service, Rocky Mountain Research Station, Ogden, UT.
- YOUNT, J.D., AND G.J. NIEMI. 1990. Recovery of lotic communities and ecosystems from disturbance—a narrative review of case studies. *Environmental Management* 14:547–569.

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APPENDIX. Distribution of tree sizes (cm), by species, at 9 plots in 4 watersheds in Great Basin National Park, Snake Range, eastern Nevada. Seedlings and saplings are defined in the text. Values in each cell represent the number of individuals in that size class in that 10-m × 100-m plot. Plot # refers to sites in Figure 1. Data from 1992 sampling were collected by Smith et al. (1994), and 2001 data were collected by USGS personnel.

Plot #	Creek	Elevation (m)	Tree species ^a	Sample date	# seedlings	# saplings	# <2 cm DBH	# trees 2-10	# trees 11-20	# trees 21-30	# trees 32-40	# trees 41-50	# trees 51-60	# trees >60 cm	Total # of individuals
6	Baker	2405	ABICON	1992	—	—	427	38	59	16	0	0	0	0	540
6	Baker	2405	ABICON	2001	473	28	516	42	57	40	5	1	0	0	661
10	Lehman	2691	ABICON	1992	—	—	107	44	11	0	0	0	0	0	162
10	Lehman	2691	ABICON	2001	149	13	164	15	6	1	0	0	0	0	186
4	Snake	2475	ABICON	1992	—	—	24	73	97	48	0	0	0	0	242
3	Strawberry	2231	ABICON	1992	—	—	13	9	2	1	0	0	0	0	25
3	Strawberry	2231	ABICON	2001	619	8	627	3	2	1	0	0	0	0	633
2	Strawberry	2463	ABICON	1992	—	—	276	55	15	7	7	4	4	0	368
2	Strawberry	2463	ABICON	2001	260	107	382	26	13	6	3	7	5	1	443
7	Baker	3060	PICENG	1992	—	—	7	24	20	21	17	6	2	2	99
7	Baker	3060	PICENG	2001	5	10	21	22	41	21	13	14	7	3	142
6	Baker	2405	PICENG	1992	—	—	19	13	6	2	1	0	0	0	41
6	Baker	2405	PICENG	2001	6	0	6	0	0	0	0	0	0	0	6
10	Lehman	2691	PICENG	1992	—	—	84	44	38	26	8	0	0	0	200
10	Lehman	2691	PICENG	2001	24	7	33	13	12	20	8	4	1	1	92
8	Lehman	2914	PICENG	1992	—	—	13	40	33	15	8	5	9	9	132
8	Lehman	2914	PICENG	2001	3	7	12	34	27	13	3	6	4	9	108
9	Snake	1948	POPANG	1992	—	—	38	38	11	10	4	3	1	1	106
9	Snake	1948	POPANG	2001	10	7	21	22	41	21	13	14	7	3	142
5	Snake	1961	POPANG	1992	—	—	89	58	92	78	17	7	0	0	341
5	Snake	1961	POPANG	2001	6	3	19	3	18	37	13	3	0	0	93
6	Baker	2405	POPTRE	1992	—	—	484	203	62	31	0	0	0	0	780
6	Baker	2405	POPTRE	2001	44	116	331	136	11	11	2	0	0	0	491
10	Lehman	2691	POPTRE	1992	—	—	74	76	84	13	5	3	0	0	255
10	Lehman	2691	POPTRE	2001	16	12	32	23	45	18	3	1	1	0	123
8	Lehman	2914	POPTRE	1992	—	—	35	3	0	0	0	0	0	0	38
8	Lehman	2914	POPTRE	2001	10	23	33	3	0	0	0	0	0	0	35
4	Snake	2475	POPTRE	1992	—	—	6	16	31	29	16	1	1	1	101
4	Snake	2475	POPTRE	2001	1	0	2	12	36	33	36	7	3	0	129
3	Strawberry	2231	POPTRE	1992	—	—	88	9	4	0	0	0	0	0	101
3	Strawberry	2231	POPTRE	2001	0	0	0	0	0	0	0	0	0	0	0
2	Strawberry	2463	POPTRE	1992	—	—	366	175	17	6	0	0	0	0	564
2	Strawberry	2463	POPTRE	2001	130	84	247	59	9	2	3	0	0	0	320

^aABICON = *Abies concolor*; PICENG = *Picea engelmannii*; POPANG = *Populus angustifolia*; POPTRE = *P. tremuloides*