Chapter 11

Biodiversity and Productivity at an Undisturbed Spring in Comparison with Adjacent Grazed Riparian and Upland Habitats

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Springs and associated wetland and riparian ecosystems are among the most productive, biologically diverse, and threatened habitats, particularly in the arid southwestern United States (Knopf et al. 1988; Johnson 1991; Williams and Danks 1991; Erman 1992; Ferrington 1995; Noss et al. 1995; Botosaneanu 1998; Glennon 2002). Although Odum's (1957) studies of Silver Springs in Florida laid much of the foundation of ecosystem ecology, patterns of wetland and riparian productivity, biodiversity, and essential ecological processes at springs in arid regions have received scant attention. Stevens and Ayers (2002) reported that springs wetlands make up less than 0.01 percent of the area of Grand Canyon in Arizona yet support nearly 11 percent of the plant species in the overall landscape, as well as many invertebrate and bird species and facultative plant, herpetofaunal, and mammal species. Thus, springs may function as keystone ecosystems that, given their generally small size, exert disproportionately large impacts on the biodiversity and ecological processes of the surrounding landscapes.

Although much progress has been made on evaluations of riparian ecosystem ecology and health (e.g., Vannote et al. 1980; U.S. Department of the Interior 1993, 1998; Pellant et al. 2000; Stevens et al. 2005), there have been too few systematic inventories or assessments of springs in the West to address basic questions about geomorphologic commonalities, basic ecological processes, biota, degree of impairment, assessment protocols, or the landscape-scale importance of springs in comparison with adjacent upland habitats. Inventory and research on the ecology of spring ecosystems are needed, as are studies describing and assessing the impacts of human activities, such as livestock grazing, on such systems. Here we characterize basic ecological properties of an ungrazed spring ecosystem in southern Utah, in comparison with those on adjacent grazed riparian and upland ecosystems. Such baseline knowledge of spring ecosystem processes is essential for informed habitat management and restoration.

Human activities have greatly reduced the ecological integrity of many riparian and spring ecosystems in the West (Erman 1992). Overall estimates of riparian habitat loss range from 40 percent to 90 percent among the southwestern states (Dahl 1990). Although the extent of alteration of spring ecosystems has not been explored, the Grand Canyon Wildlands Council (2002) reported that 80–93 percent of the springs within several large land-management units in Arizona had been severely altered by human activities. Springs and other western riparian habitats are focal points of competing exploitative uses, such as timber harvest, recreation, water diversion, and livestock grazing (Thomas et al. 1979; Johnson et al. 1985). Livestock grazing continues to exert pervasive adverse influences on springs and other riparian habitats because riparian zones provide water, shade, and succulent vegetation (Bauer and Burton 1990; Chaney et al. 1990; Fleischner 1994; Stevens et al. 2005). Although springs and other riparian habitats are highly altered throughout the West, undiverted springs are ecologically resilient and may respond positively to improved management practices. Because of their biological importance, threatened status, and potential resilience, the protection and restoration of spring ecosystems should become a high priority for land-management and conservation agencies.

Productivity is an important ecological variable (Odum 1957; Bonham 1989), not only affecting ecosystem function and dynamics but also influencing biodiversity (Huston 1979; Zervas 1998). Unfortunately, research on riparian recovery has been focused primarily on vegetation structure, with less attention given to primary productivity and invertebrate (food-base) population dynamics. Previous investigations on the effects of livestock grazing impacts on riparian habitats have revealed that grazing reduces the number, total biomass, and condition of shrubs and trees, but such measurements have not been well quantified (Stevens et al. 2005). Similarly, differences in productivity between spring and upland sites have not been quantified in the western United States.

We studied patterns of biodiversity, productivity, and the impacts of grazing in 2002 at the undisturbed Seaman Spring and in adjacent grazed riparian areas and uplands in Grand Staircase–Escalante National Monument, Utah. Our purpose was to determine basic ecological characteristics (biodiversity and productivity) of this spring system and explore the impacts of grazing on those processes. To do this, we gathered information on plant, invertebrate, and vertebrate species diversity, abundance, and composition and quantified differences in organic standing mass and estimated net aboveground annual primary productivity along a springs-to-upland ecological gradient. We provide some of the first comparative productivity estimates for a rheocrene spring gradient in western North America.

Methods

Study Site

Seaman Spring is located in the southwest corner of Grand Staircase–Escalante National Monument, in Kane County, Utah. The spring emerges on the floor of a small, structurally controlled canyon in the pinyon pine–juniper zone at an elevation of 1,867 meters. The parent rock is Mesozoic sandstone. The climate is highly variable, with average springtime high temperatures of about 26°C, 34–35°C in summer, and 13–15°C in winter, with winter lows well below freezing. Rainfall occurs bimodally, with winter and summer precipitation peaks. Seaman Spring has a flow of about 5.5 liters per minute and is a bicarbonate/magnesium spring with moderate water quality (table 11.1) in relation to data presented in Mundorff (1971) for southwestern Utah.

Study Design

We divided the Seaman Spring site into three reaches of approximately equal length and area and also studied an adjacent upland site with equivalent slope and aspect. These four study sites were designated as follows:

REF: The reference site, the spring source riparian habitat that has received little or no grazing

WG: A wet grazed spring riparian habitat that has received relatively high grazing intensity

TABLE 11.1. Water quality data from Seaman Spring, August–September 2002

Water quality variable	Mean
Flow—field	5.5 L/min
Specific conductance—field	724.33 μmho/cm
pH—field	7.83
Temperature—field	19.83°C
Alkalinity (carbonate, as $CaCO_3$)	366.50 mg/L
Bicarbonate	447.00 mg/L
NO_2, NO_3, NH_3	0.00 mg/L
Phosphorus	0.03 mg/L
Dissolved solids	429.00 mg/L
Hardness (Ca, Mg)	377.73 mg/L
Calcium	63.58 mg/L
Magnesium	53.25 mg/L
Potassium	3.43 mg/L
Sodium	24.05 mg/L
Iron	265.75 μg/L
Manganese	107.75 μg/L
Chloride	26.65 mg/L
Arsenic	6.83 μg/L
Barium	259.50 μg/L
Chromium	7.43 μg/L
Selenium	1.23 μg/L

Note: $N = 3$ samples; data provided courtesy of J. Vanderbilt, Grand Staircase–Escalante National Monument.

DG: A dry riparian reach that has received relatively high grazing intensity

UG: A dry upslope shrubland and woodland site that has received relatively high grazing intensity

REF is naturally excluded from grazing by steep hillslopes and a large rockfall. Livestock grazes freely on the other three experimental sites.

Data Collection

We compared plant and invertebrate biodiversity, standing plant and litter biomass per square meter and net annual productivity (measured in grams of carbon per square meter per year dry weight) with that of grazed wet and dry riparian systems and with the grazed upland habitat. Total dry organic standing mass (TDOSM) and estimated net aboveground annual primary productivity (NAAPP) were measured on plots in a stratified random design. We clipped and sorted all existing vegetation from twelve randomly selected and georeferenced plots (100 cm^2) in each study reach from ground cover (<1 m tall, comprising grasses and herbs) and from shrub and canopy cover (>1 m tall) strata. A 5-meter-tall survey rod was held vertically and used to measure where to clip shrub and canopy cover. The tree trunk or branch material too large to clip was estimated by relating measured wood mass-to-volume relationships from samples of the same species. We air-dried clipped vegetation to a constant mass at low humidity. Because this was the first year of monitoring, we clipped growth from the 2002 growing season, as well as growth from previous seasons. We separated green (2002) growth from woody growth and litter (pre-2002) and adjusted some upland samples (e.g., *Juniperus* sp. and *Pinus* spp. needles) for green growth that persists for more than one year. Vegetation was dried and weighed and productivity calculated, following the standard clipping methods of Bonham (1989) and Brower and colleagues (1998). This method allowed us to distinguish total organic standing biomass from estimated NAAPP. The NAAPP samples represent cumulative estimates of 2002 estimated NAAPP, and we recognize that these values are conservative underestimates because of losses attributable to seasonality and both invertebrate and vertebrate herbivory.

Plant cover, demography, and vigor were measured by visual estimation of percent cover by stratum and demography of the dominant native and nonnative plant species in each study site. These data were recorded on a site vegetation sketch map. The percentage of the total native plants on site that were healthy, in marginal condition (less than 50 percent of an individual plant wilted, burned, or dead), in poor condition (more than 50 percent of an individual plant wilted, burned or dead), or dead was visually estimated by three researchers and averaged.

We inventoried plants and aquatic and terrestrial macroinvertebrates, and we recorded but do not present data on herpetofauna, avifauna, and mammals. We searched intensively for all species of plants on each site. Two to five individuals or diagnostic portions of any unrecognized plants were collected for identification, and all taxa encountered were recorded. We visually estimated the percent cover of each native and non-native species in four strata: ground cover (annual deciduous nonwoody and <2 m tall); shrub cover (woody perennial, 1–4 m tall); midcanopy (woody perennial, 4–10 m tall); and high (woody perennial, >10 m tall) canopy cover classes.

Aquatic macroinvertebrates were inventoried in each reach using quantitative kick net sampling (0.09 m^2) and spot sampling, with particular emphasis on aquatic Mollusca, various Coleoptera (especially Dytiscidae, Dryopidae, Hydrophilidae, Haliplidae, and Elmidae), semiaquatic Hemiptera, and Diptera (especially Tipulidae, Simuliidae, and Chironomidae).

Terrestrial macroinvertebrates were inventoried by collecting two to five individuals or diagnostic portions of all species encountered or by recording other taxa observed. Netting and other spot collecting were conducted with particular emphasis on Isopoda, various Coleoptera (especially Carbidae), and semiaquatic Hemiptera and Diptera (especially Chironomidae and Empididae). In addition, fifty sweeps with an aerial sweep net were performed at each study site for a quantitative comparison of terrestrial invertebrate species richness and abundance. Invertebrate specimens were mounted on pins in the field (especially mosquitoes and mirid bugs) or preserved dry (hard-bodied invertebrates) or in 70 percent ethyl alcohol (soft-bodied forms), labeled, and transported to the laboratory for preparation. Host plant and habitat affinities were recorded for all specimens. Invertebrate specimens are housed at the Museum of Northern Arizona in Flagstaff.

Analyses

We compiled the above data and analyzed data using nonparametric statistical tests because data were non-normally distributed. We conducted nonparametric Kruskal-Wallis and Mann-Whitney statistical tests with sequential Bonferroni corrections to compare TDOSM, estimated NAAPP, wood production, and leaf litter between sites. Statistical analyses were conducted using the statistical analysis computer program SPSS Version 6.0 (Norusis 1993).

TABLE 11.2. Plant species composition of different sites at Seaman Spring

Site	Date	Native species (*N*)	Non-native species (*N*)	Exotic species (%)	Total species (*N*)
UG	8/11/02	17	2	11	19
DG	8/12/02	16	0	0	16
WG	8/13/02	19	8	30	27
REF	8/14/02	17	4	19	21

Note: UG = grazed upland; DG = dry grazed riparian; WG = wet grazed riparian; REF = spring source, riparian with no detectable grazing.

Results

Vegetation

Plant species diversity, vegetation cover characteristics, plant vigor, and proportion of exotic species varied greatly between study sites. Overall, the two sites with surface water (REF and WG) had the highest plant species richness, as well as the highest proportion of exotic species (table 11.2). Nearly one-third of the plant species in the wet grazed site at Seaman Spring were non-native. This was 11 percentage points higher than that in the ungrazed reference site, where 19 percent of the flora was non-native (table 11.2).

Vegetation structure also varied considerably by study site. The REF site was the only site with a strong representation of all cover strata (fig. 11.1). The WG site had a noticeable absence of shrub, midcanopy and tall canopy cover; however, it had abundant low ground cover of wetland grasses, sedges, and rushes. The dominant stratum for both the dry UG and DG sites was the shrub layer, and those sites had little to no ground cover, midcanopy, or high canopy cover.

Invertebrate Biodiversity

Similar to the plant diversity data, the wet riparian sites (WG and REF) had far higher abundance and species richness of terrestrial invertebrates than did the dry sites. The WG site had the highest overall abun-

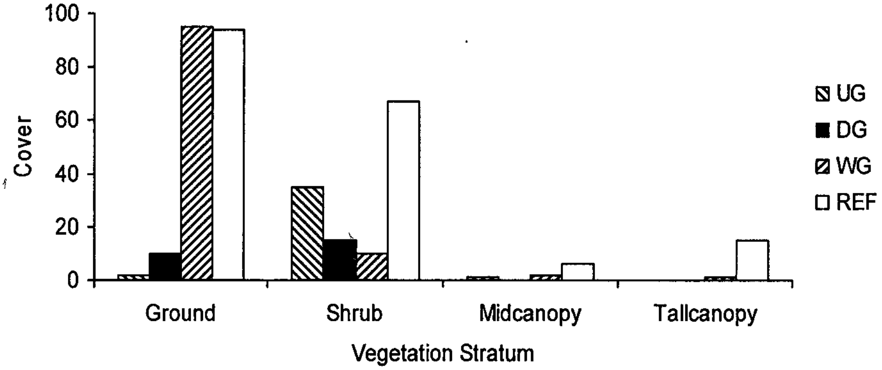

Figure 11.1. Percent cover of each vegetation stratum for each site at Seaman Spring visually estimated by three observers over the total area of the site.

dance of terrestrial invertebrates, but morphotype richness was statistically equivalent to that of the REF site. The higher value on WG was attributable to Diptera associated with cow manure.

The fifty-sweeps data revealed great differences among sites in terrestrial invertebrate abundance, morphotype richness, and order dominance. The wet riparian sites (REF, WG) had a much larger proportion of Diptera than did the dry sites (table 11.3; fig. 11.2). WG also had a higher proportion of Homoptera than did the reference site. REF had a higher proportion of insect predators (Hymenoptera and Arachnida), indicating a more trophically integrated assemblage than that on the WG site. Predatory insects (carabid and cicindelid beetles, spiders, asilid flies, etc.) occupy higher trophic levels and may be more likely to disappear from impaired ecosystems. The dominant insect order in the dry grazed reach was herbivorous, nonpredatory Coleoptera. A high abundance of leaf-feeding Coleoptera may indicate a drought-stress-induced nutrient concentration in heavily browsed riparian shrubs.

Our fifty-sweeps sampling (table 11.4) produced no invertebrates in the UG site. This does not mean there are no insects in the uplands surrounding Seaman Spring, but it does indicate that insect abundance is extremely low in that habitat as compared to the riparian sites. Unfortunately, the absence of ungrazed upland habitats precludes our assessment of the impacts of grazing on invertebrate biodiversity in uplands in this region.

TABLE 11.3. Percent composition of terrestrial invertebrates collected in fifty-sweep samples by site at Seaman Spring

	Dominant insect order		
Site	First	Second	Third
UG	—	—	—
DG	Coleoptera (36)	Hymenoptera (18)	Diptera (18)
WG	Diptera (84)	Homoptera (12)	Coleoptera (2)
REF	Diptera (80)	Hymenoptera (9)	Arachnidae (4)

Note: UG = grazed upland; DG = dry grazed riparian; WG = wet grazed riparian; REF = spring source, riparian with no detectable grazing.

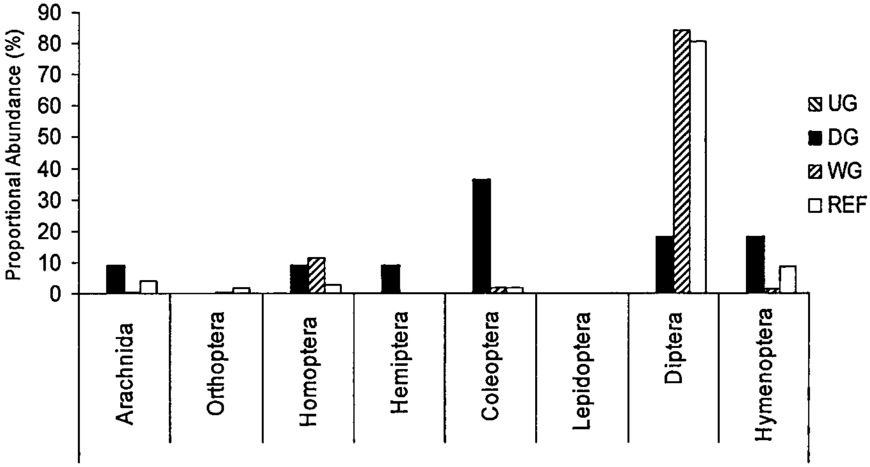

Figure 11.2. Proportional abundance (percentage of total insects collected) of eight invertebrate orders by study site at Seaman Spring. Data were collected from fifty sweeps of each study site with an aerial insect net.

Ecological Processes—Productivity

Large and significant differences existed in TDOSM, estimated NAAPP, wood production, and leaf litter between sites (Kruskal-Wallis $p < .001$, $\chi^2 > 24.89$, df = 3 for each variable). TDOSM was defined as all plant material, including green leaves and ground cover of plants as well as the woody stems of shrubs and trees, in addition to litter. The REF site had up to thirty-four times greater TDOSM than did the dry sites and an order of magnitude higher values than did the WG site (fig. 11.3, table 11.5; Mann-

TABLE 11.4. Morpho-species richness and abundance of terrestrial invertebrates by site at Seaman Spring

Site	Area (m^2)	Total richness	Richness/ m^2	Abundance/ m^2
UG	650	0	0	0
DG	750	9	0.003	0.015
WG	718	58	0.08	1.41
REF	710	56	0.08	0.145

Note: Fifty-sweeps data. Abbreviations: UG = grazed upland; DG = dry grazed riparian; WG = wet grazed riparian; REF = spring source, riparian with no detectable grazing.

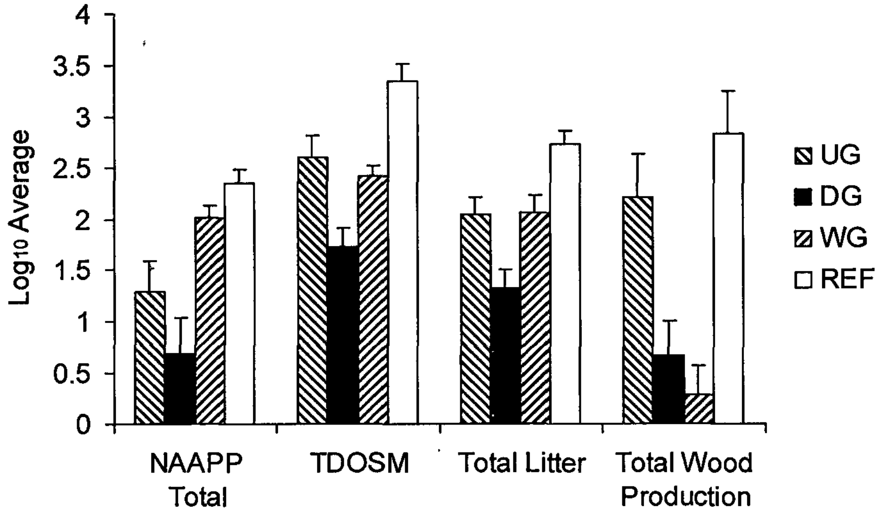

Figure 11.3. Log_{10} average NAAPP, total biomass, leaf litter, and total wood production for each study site at Seaman Spring. Error bars represent one standard error.

Whitney $U < 17.00$, $p < .001$, $n = 12$ per site for all comparisons). TDOSM is a useful indicator of stored, produced, and decomposing carbon in these ecosystems. Ecosystems with higher TDOSM generally have higher levels of net above- and below-ground productivity, more available nitrogen, and higher levels of litter decomposition.

Mean estimated NAAPP differed greatly between sites as well (tables 11.5, 11.6; figs. 11.3, 11.4; Kruskal-Wallis $\chi^2 = 29.79$, $p < 0.0001$, df = 3). Wet

TABLE 11.5. Comparison of mean total dry organic standing biomass among study sites in 2002

Category	DG	UG	WG	REF
Productivity (g C/m²/yr)	14.1	97.9	124.8	281.6
Shrub, canopy stems (g C/m²)	57.1	330.0	15.4	2,501.0
Litter (g C/m²)	31.4	191.2	154.7	687.9
TDOSM (g C/m²)	102.6	619.4	294.9	3,470.5

Note: Twelve samples taken at each site. Statistically significant differences exist ($p << .05$) between all sites for each variable except between total productivity in WG and REF, litter UG-WG, shrub and canopy stems DG-WG. Abbreviations: UG = grazed upland; DG = dry grazed riparian; WG = wet grazed riparian; REF = spring source, riparian with no detectable grazing.

TABLE 11.6. Comparison of mean estimated net aboveground annual primary productivity among study reaches in 2002

	Reach			
Category	DG	UG	WG	REF
Ground cover (g C/m²/yr)	3.9	22.7	120.2	122.3
Shrub and canopy leaves (g C/m²/yr)	10.3	75.2	4.5	159.3
Total productivity (g C/m²/yr)	14.1	97.9	124.8	281.6

Note: Twelve samples taken in each reach. NAAPP and ground cover NAAPP were significantly different between all reaches (except WG and REF) at $p << .05$. Shrub and canopy cover NAAPP differed significantly among all sites. Abbreviations: UG = grazed upland; DG = dry grazed riparian; WG = wet grazed riparian; REF = spring source, riparian with no detectable grazing.

riparian sites were two to twenty times more productive than upland and dry sites. Estimated NAAPP did not differ significantly between the WG and REF sites; however, estimated NAAPP in WG was due primarily to ground cover, while that on the REF site was more balanced between ground cover and shrub and canopy cover layers (table 11.6; figs. 11.3, 11.4). Multistoried vegetation provides better wildlife habitat, as ground, shrub, and canopy layers provide diverse cover, invertebrate and bird food and habitat, and leaf fall that contributes to stream invertebrate diversity (Vannote et al. 1980).

Measurements of litter and other fallen and decaying vegetative matter revealed significant differences between sites, with the REF site having significantly higher levels of litter than other sites (table 11.5, fig. 11.3; Kruskal-Wallis $\chi^2 = 28.5$, $p < 0.0001$, df = 3). The WG site had no

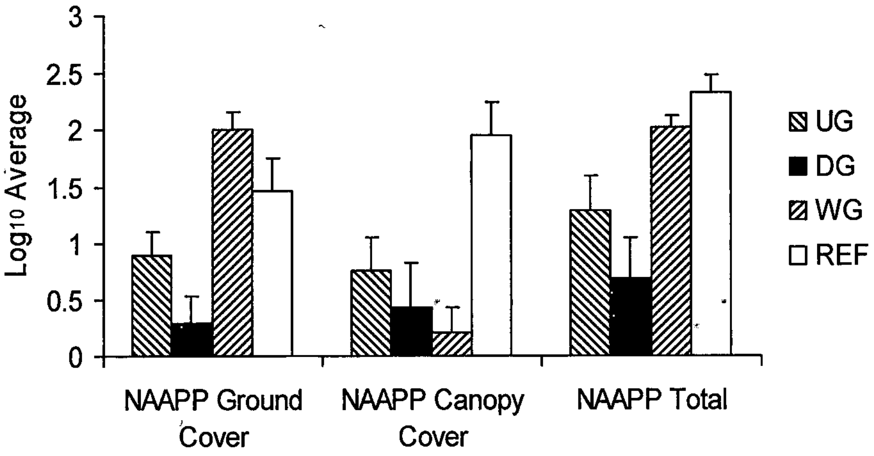

Figure 11.4. Mean estimated $\log_{10}$ of NAAPP by vegetation stratum for each site at Seaman Spring. Error bars represent one standard error.

more litter than did the upland site (Mann-Whitney $U = 70$, $p = 0.908$, $n = 24$). This was because reduction in shrub and canopy layers prevented litter deposition. Fallen canopy leaves and wood made up a large proportion of the litter in the REF site, and WG had comparatively little canopy cover. Cow manure made up a minor but conspicuous component of the litter in WG, and that source of litter was absent in the REF site. Carbon storage in woody stems was highest in the REF site by one to two orders of magnitude over other sites (Kruskal-Wallis $\chi^2 = 25.4$, $p = 0.0001$, df = 3).

Discussion

Our data indicate that spring ecosystems are focal points of biodiversity, non-native plant invasion, productivity, and organic matter accumulation. Wet riparian sites (WG, REF) had higher plant species richness and two to three times higher vegetative cover than did the upland grazed (UG) and grazed dry riparian (DG) sites. Wet riparian sites also were more prone to exotic plant species invasions and had 8–30 percent higher exotic species richness than did dry sites, a finding consistent with those of Stohlgren and colleagues (1999, 2003) and Stevens and Ayers (2002). Grazing disturbance of wet riparian sites may further increase the exotic plant diversity: WG had 30 percent non-native species, whereas the REF site had 19 percent non-native species.

Vegetation structure on sites varied in relation to water availability, as well as grazing disturbance. The ungrazed REF site was the only site that had a strong representation of all structural vegetation levels, including ground, shrub, midcanopy, and high canopy cover. Such factors influence not only microclimate, microhabitat structure, and wildlife habitat and food resource availability, but also ecological processes such as NAAPP, carbon storage, and probably decomposition. The REF site had far higher litter and wood standing mass values because of the extensive cover of shrubs and trees that created canopy cover, woody stem carbon storage, and leaf litter.

Grazing can greatly alter or reduce riparian ecosystem structure. Marcuson (1977) found that differential browsing by livestock reduced the number and total biomass of shrubs and trees in riparian habitats, and Glinski (1977) demonstrated that livestock strongly reduced Fremont cottonwood (*Populus fremontii*) seedling establishment. Knopf and Cannon (1982) similarly demonstrated that grazing significantly altered the size, shape, volume, and quantities of live and dead willow stems. The impacts of grazing on tree production have a critical impact on the riparian ecosystem because of the importance of the woody vegetation to wildlife habitat and its effects on riparian microclimate (Kauffman and Krueger 1984; Stevens et al. 2005).

Structural vegetation differences, some of which were attributable to grazing impacts, affected productivity at Seaman Spring and are likely to influence other basic ecological processes. The REF and WG sites had significantly higher estimated NAAPP levels than did the UG and DG sites. Productivity differed between the WG and REF sites not in the quantity of estimated NAAPP but rather in where carbon was being produced (ground cover versus canopy cover, respectively). Because litter levels differed greatly among sites, decomposition rates are likely to differ considerably as well because the litter layer is where decomposition is likely to be most rapid.

Terrestrial invertebrate assemblages likewise differed between sites. Wet riparian sites had higher abundance and greater morpho-species richness than did upland and dry sites, by more than two orders of magnitude. Some of the differences in the terrestrial invertebrate assemblages between the WG and REF sites were directly attributable to grazing and manure distribution. For example, WG had a greater relative abundance of Diptera, while REF had a greater abundance of predatory insects, suggesting a more complex trophic structure on the ungrazed site. Such patterns indicate that invertebrate production and potential food resources for terrestrial and aquatic vertebrates are greater in riparian and perhaps spring ecosystems and that dewatering spring-fed channels may substantially reduce and change the invertebrate food base for wildlife.

Our studies of Seaman Spring provided considerable insight into fundamental ecological processes at an undisturbed spring ecosystem in comparison with adjacent grazed wet riparian, dry riparian, and upland habitats. However, most springs in the Grand Staircase–Escalante National Monument and throughout the West have been highly modified for livestock use and culinary water supplies. It is increasingly difficult to find undisturbed springs study sites, such as Seaman Spring, at which to conduct basic research on ecological processes. Such sites are important laboratories for research into ecological processes and restoration potential of these unique, highly productive, biologically diverse, and poorly understood ecosystems.

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