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LIVESTOCK EXCLUSION AND BELOWGROUND ECOSYSTEM RESPONSES IN RIPARIAN MEADOWS OF EASTERN OREGON

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Abstract. Ecological restoration of riparian zones that have been degraded by decades of overgrazing by livestock is of paramount importance for the improvement of water quality and fish and wildlife habitats in the western United States. An increasingly common approach to the restoration of habitats of endangered salmon in the Columbia Basin of the Pacific Northwest (USA) is to exclude livestock from streamside communities. Yet, few studies have examined how ending livestock grazing changes ecosystem properties and belowground processes in herbaceous-dominated riparian plant communities (meadows). Along the Middle Fork John Day River, Oregon, we compared ecosystem properties of dry (grass and forb-dominated) and wet (sedge-dominated) meadow communities at three sites that had been managed for sustainable livestock production with three sites where livestock had been excluded for 9–18 years as a means of riparian and stream restoration. Profound differences in the belowground properties of grazed and exclosed communities were measured. In dry meadows, total belowground biomass (TBGB consisting of roots and rhizomes) was ~50% greater in exclosures (1105 and 1652 g/m^2 in the grazed and exclosed sites, respectively). In exclosed wet meadows, the TBGB was 62% greater than in the grazed sites (1761 and 2857 g/m^2, respectively). Soil bulk density was significantly lower, and soil pore space was higher in exclosed sites of both meadow types. The mean infiltration rate in exclosed dry meadows was ~13-fold greater than in grazed dry meadows (142 vs. 11 cm/h), and in wet meadows the mean infiltration rate in exclosures was 233% greater than in grazed sites (24 vs. 80 cm/h). In exclosed wet meadows, the rate of net potential nitrification was 149-fold greater (0.747 vs. 0.005 μg NO_3-N·[g soil]$^{-1}$·d^{-1}), and the rate of net potential mineralization was 32-fold greater (0.886 vs. 0.027 μg N·[g soil]$^{-1}$·d^{-1}, respectively) when compared to grazed sites, though changes observed in dry meadows were not significant. Livestock removal was found to be an effective approach to ecological restoration, resulting in significant changes in soil, hydrological, and vegetation properties that, at landscape scales, would likely have great effects on stream channel structure, water quality, and the aquatic biota.

Key words: ecological resilience; ecological restoration; infiltration rates; livestock effects; N dynamics; Oregon (USA) meadow communities, dry and wet; riparian zones; root biomass; soil properties.

Introduction

Throughout the semiarid forest and rangeland landscapes of the western United States, riparian zones are focal points for the maintenance and restoration of biological diversity as well as other ecosystem services such as water quality. Of the wildlife species that occur in Oregon and Washington, ~70% utilize riparian zones as habitat (Kauffman et al. 2001). Considering that riparian zones and wetlands only cover 1–2% of western forest and rangeland landscapes, their value associated with biological diversity can not be understated (Kauffman and Krueger 1984). Riparian vegetation also exerts strong influences on stream habitats. Riparian zones are important sources of nutrient and energy inputs, affect channel complexity, and influence water quality and temperature (Gregory et al. 1991, Naiman and Decamps 1997).

Many of the attributes and ecosystem functions of riparian zones that contribute to the high productivity and biodiversity of wildlife species are of great economic value to human society. For example, broad floodplains formed through the millennia are valuable not only for their complex wildlife habitats and linkages to the aquatic biota, but also for their nutrient-rich soils; the most productive lands in terms of agriculture, forage for livestock, and forest growth for wood are riparian zones and wetlands (Kauffman et al. 2001). Livestock grazing is the most widespread land use throughout the interior Pacific Northwest and In-

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termountain West, and most of the forests, grasslands, shrub steppes, and riparian zones have been, or currently are, grazed by livestock (Dwire et al. 1999). Livestock grazing has had widespread ecological effects, including loss of native species, changes in species composition, soil deterioration, degradation of fish habitat, and changes in ecosystem structure and function (Kauffman and Krueger 1984, Fleischner 1994, Rhodes et al. 1994, Belsky et al. 1997, Dwire et al. 1999, Kauffman and Pyke 2001).

Few studies have described how livestock affect belowground biomass and soil properties in riparian zones (Bohn and Buckhouse 1985, Wheeler et al. 2002). Livestock have apparent effects on the composition and structure of riparian plant communities dominated by willows (*Salix* spp.), cottonwoods (*Populus* spp.), or other woody species, and they may have subtle effects on the composition and structure of herbaceous-dominated wet and dry meadows (Kauffman et al. 1983, 2002, Schulz and Leininger 1990, Green and Kauffman 1995). However, we hypothesized that soils, belowground processes, and vegetation features in riparian meadows may be influenced in ways that could affect ecosystem function and important linkages to adjacent aquatic ecosystems. Alterations in belowground structure and processes of riparian zones could potentially influence the adjacent stream ecosystems through changes in root mass, soil structure, infiltration rates, and N turnover rates. These are important linkages because riparian–stream ecosystems in the Pacific Northwest are important habitats of many salmonid populations currently listed as threatened or endangered.

How herbivory affects ecosystem properties is related to the type of animal grazing and the season, intensity, and duration of grazing (Briske and Richards 1994). Many studies have shown that herbivores increase N cycling (Holland and Detling 1990, Hobbs 1996, Frank and Groffman 1998). However, many of these studies have largely examined the effects of wild herbivores on ecosystems where levels of defoliation and/or influences on soil physical properties are quite low. Conversely, introductions of large exotic herbivores (cattle) have been shown to negatively affect ecosystem structure and processes (Dwire et al. 1999, Kauffman and Pyke 2001).

Because the structure and composition of many riparian zones have the potential to recover rapidly following cessation of livestock grazing (Brookshire et al. 2002, Kauffman et al. 2002), rest from livestock grazing or corridor fencing is a common stream-improvement practice on degraded western riparian zones. Yet few studies have examined the effects of livestock exclusion on belowground structure and soil features of floodplain communities dominated by grasses or sedges. Information on how the removal of exotic herbivores affects belowground structure and processes of these plant communities would have widespread applicability for development of restoration and improved management strategies. Our objectives were to investigate potential differences in some belowground ecosystem attributes including infiltration rates, belowground biomass, and soil properties (bulk density, porosity, soil organic matter, potential net N mineralization) in two common herbaceous-dominated riparian plant communities (wet and dry meadows) where grazing had not occurred for 9–18 years and where livestock management had remained constant over the same time period.

Study Site

The study was conducted in riparian ecosystems along the upper reaches of the Middle Fork John Day River in the Blue Mountains of northeastern Oregon, USA. The Middle Fork Subbasin drains approximately $\sim$2100 km^2 and travels 120 km before it enters the North Fork John Day River (Oregon Water Resources Department 1986). All study sites were located in floodplain meadows ranging in elevation from 1066 to 1323 m in elevation. Uplands are dominated by mixed-conifer forests of lodgepole pine (*Pinus contorta*) and ponderosa pine (*Pinus ponderosa*) on south slopes, and Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), western larch (*Larix occidentalis*), and ponderosa pine on north slopes.

Two common herbaceous-dominated plant communities were selected for analysis. The first was the ''wet meadow'' dominated by the sedge *Carex nebrascensis*. This widely distributed plant community is typically located within active channels, swales, or in low areas within the floodplain (Crowe and Clausnitzer 1997). Other common species in this community type included *Carex utriculata* and *Scirpus microcarpus*. Wet meadows are usually inundated during high flows associated with winter rain-on-snow events or spring runoff. Soils are reduced (anaerobic) for much of the growing season when water tables are near or above the soil surface (Dwire et al. 2000, Dwire 2001). The second plant community type sampled was the ''dry meadow'' dominated by the exotic grass *Poa pratensis*. This community type is widespread where overgrazing and other major disturbances have degraded the native vegetation (Crowe and Clausnitzer 1997). Other common species in this community type included *Achillea millefolium*, *Carex microptera*, and *Fragaria virginiana*. Dry meadows are typically situated along elevated terraces within the floodplain and are flooded only during infrequent high-flow events. Soils are rarely reduced or anaerobic (Green and Kauffman 1989, Dwire et al. 2000, Dwire 2001). Soils in all sampled areas were Entisols (Cryofluvent subgroup) formed from mixed alluvial sediments derived from basalts and volcanic ash. Surface soil textures were largely silt loams to loams. A gravel-cobble layer occurred at depths of 80–160 cm.

We sampled soil and plant properties in six floodplain meadow complexes along the upper reaches of the Middle Fork John Day River. Each of the sampled sites contained both dry and wet meadows. The sites were distributed along the upper ~30-km section of the river. Three sites (the exclosed treatment) were not grazed by cattle. The Summit Creek exclosure was a cattle exclosure constructed in 1978. The Boulder Creek and Dunstan homestead sites were grazed until 1990 when the Nature Conservancy purchased the Dunstan ranch and halted cattle grazing. While livestock were excluded, wild herbivores, principally elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) and many small mammals and insects continued to use the sites. As is common in many small exclosures, accidental grazing has occurred in the Summit Creek exclosure on several occasions. The other three sampled sites (the grazed treatment) had been continuously managed for cattle grazing. One site (Grazed Summit Creek, Malheur National Forest) was managed on a deferred grazing system where it is grazed early in the summer months one year and late summer the next. The other two grazed sites (Big Meadow and Salmon Pool) were located on private lands, and were grazed season-long each year (~1 July to 15 September), which is typical of livestock grazing management practices on broad floodplains in the region. The ecological conditions of the grazed riparian meadows and the livestock management of these sites were judged to be typical representations for riparian zones of this region.

The sampled grazed and exclosed communities were selected on the basis of similar geomorphic positions, soils, and dominant species. Livestock grazing and hay production had been a dominant land use in floodplain meadows of the Middle Fork John Day since the late 1800s. Because of their proximity to one another, we assumed that all sites had similar land-use histories and that the variables measured in this study were similar in the grazed and exclosed sites at the time when livestock exclosures were built.

METHODS

All measurements were collected at the end of the growing season, late August to early September, 1996 and 1997. Sampling at this time facilitated measurements of ecosystem conditions after livestock had utilized the areas for the current year. We selected this time frame for sampling because we observed that it is most reflective of conditions that exist throughout most of the year (late summer till spring) and including those times when there is an increased amount of interaction between the river and its adjacent floodplain via high flows and runoff.

Biomass

Total belowground plant biomass (TBGB) consisting of live and dead roots and rhizomes was sampled along a randomly established transect in dry- and wet-meadow communities at each site in 1996. Every 5 m along a 20-m transect, a soil core 10 cm in diameter and 40 cm in depth was extracted with a soil augur (n = 5 cores per site). Each core was separated into four 10-cm segments based on depth, placed in a paper bag, and transported to the laboratory. In the laboratory, the roots were extracted from the soil core with a Hydropneumatic Elutriation System (Gillison's Variety Fabrication, Benzonia, Michigan, USA). After extraction and oven-drying at 60°C, roots were separated into three categories: fine roots <1-mm diameter, roots >1-mm diameter, and rhizomes.

Total aboveground biomass (TAGB) was collected by clipping all material in ten 25 × 25 cm (0.0625 m^2) microplots placed every 5 m along a randomly established transect bisecting each sampled plant community in 1997. In the field, TAGB was separated into litter (dead and detached) and standing biomass (current year's growth). The samples were oven-dried at 60°C until a constant weight was achieved for dry-mass determination.

Soil properties

Samples for the determination of surface (0–10 cm depth) soil bulk density and soil organic matter were collected along the same transects used for collection of root biomass (n = 5 soil samples per sampled community). Adjacent to each point where roots were sampled, soil bulk density was measured via extraction of a core of known volume (184 cm^3). These cores were transported to the laboratory and dried at 60°C for 4 d to obtain dry masses.

Soil organic matter (SOM) was calculated by the loss-on-ignition method modified from that given in Nelson and Sommers (1996). Five 20-g samples collected in the same area as the bulk density samples from each site were combusted in a muffle furnace at 430°C for 1 h, then 500°C for 5 h. Samples were then cooled for 4 h in a desiccator and re-weighed to determine organic matter loss.

Soil pore space or porosity (in percentage) is a measure of the amount of water that can be stored per unit volume of soil when saturated (Hillel 1971). Soil pore space was calculated from bulk density and SOM results. To calculate soil pore space, we assumed that mineral components had a particle density of 2.65 g/cm^3 and organic matter had a density of 1.35 g/cm^3 (Hillel 1971). Soil bulk density divided by sample particle density would yield the percentage of the sample occupied by solid materials. Porosity would equal 1 minus the percentage volume occupied by minerals and soil organic matter.

Available nitrogen and potential N mineralization

Mineral forms of N (NO_3-N and NH_4-N) and potential N mineralization were determined from soil samples collected in August 1997. At 5-m intervals along 20-m transects established within each sampled community, soil samples consisting of a core to a depth of 10 cm were placed in an ice chest and transported to

TABLE 1. Aboveground and belowground (roots and rhizomes) biomass for grazed and exclosed dry and wet meadows measured at the end of the grazing season, Middle Fork John Day River, Oregon, USA.

Source location of biomass	Dry meadow: Biomass (g/m^2) Grazed	Dry meadow: Biomass (g/m^2) Exclosed	Dry meadow: *P*	Wet meadow: Biomass (g/m^2) Grazed	Wet meadow: Biomass (g/m^2) Exclosed	Wet meadow: *P*
Aboveground						
Standing (green)	201 ± 90	544 ± 123	0.05	414 ± 87	708 ± 106	0.12
Litter	87 ± 44	371 ± 29	0.05	120 ± 58	372 ± 201	0.27
Total	288 ± 114	915 ± 131	0.03	534 ± 144	1080 ± 265	0.13
Belowground						
0–10 cm	780 ± 83	1030 ± 169	0.20	898 ± 133	1542 ± 242	0.03
10–20 cm	160 ± 22	271 ± 41	0.03	461 ± 58	679 ± 101	0.07
20–30 cm	104 ± 12	163 ± 22	0.03	278 ± 42	423 ± 105	0.22
30–40 cm	62 ± 9	188 ± 74	0.11	123 ± 27	213 ± 32	0.04
Total	1105 ± 109	1652 ± 223	0.04	1761 ± 183	2857 ± 321	0.007

Note: Data are means ± 1 SE for three sites.

the laboratory for analysis (n = 5 cores per sampled community). Soil samples were passed through a 2-mm sieve and a subsample of each was dried to constant weight for moisture determination. In the laboratory, a subsample of each sample was immediately analyzed for mineral forms of N colorimetrically in 2 mol/L KCl soil extract solutions using an Alpkem RFA-300 rapid-flow analyzer (Alpkem Corporation, Clackamas, Oregon, USA). Net potential nitrification and mineralization were determined via laboratory aerobic incubations of 50-g soil samples placed in 100-mL plastic cups with perforated lids (Hart et al. 1994). Samples were maintained at field moisture capacity (by mass) and incubated for 14 days at ~25°C before extraction with KCl. Potential net N mineralization rate was calculated by subtracting the initial mineral N concentrations from the 14-d incubated concentrations. Potential net nitrification was calculated in the same manner, subtracting initial concentrations of NO_3-N from the 14-d incubation concentrations.

Infiltration rates

Soil infiltration rates were measured in 1997 using a constant-head single-ring infiltrometer (Branson et al. 1972). Infiltration rates were collected at five locations within each sampled wet and dry community. The infiltration rings were steel cylinders 7.5 cm in diameter and 20 cm in height. Each ring was inserted 10 cm in the ground. During sampling, a 2-cm constant head was maintained above the ground surface. Sample areas were pre-wet prior to measurement of infiltration rates to eliminate differences in antecedent moisture content. Depending on the infiltration rate, measurements were taken every 30 s to 1 min and until a constant infiltration rate had been achieved for at least 10 min.

Differences between livestock-grazed and exclosed sites for all factors were tested with a Mann-Whitney test of two samples. Sites were the tested replicates. Wet- and dry-meadow sites were analyzed separately.

RESULTS

Biomass

Total aboveground biomass (TAGB) in the exclosed dry and wet meadows was 915 and 1080 g/m^2, respectively (Table 1). At the end of the grazing season, mean TAGB in the grazed dry meadow was 288 g/m^2 or 31% of that of the exclosed sites. In the grazed wet meadows, mean TAGB was 534 g/m^2 or 49% of that of the exclosed wet meadow sites. The higher biomass in grazed wet meadows compared to grazed dry meadows is a reflection of both the greater productivity in the wet meadows as well as the greater preference for dry meadows by cattle. In addition to differences in TAGB between grazed and exclosed sites, there were differences in the proportion of the TAGB found in litter and standing biomass. In dry meadows, litter composed 30% of the TAGB in grazed sites and 41% in the exclosed sites. In the wet meadows, litter composed 22 and 34% of the TAGB in the grazed and exclosed sites, respectively.

We found highly significant differences in the biomass of roots and rhizomes (total belowground biomass, TBGB) between the grazed and exclosed sites (Table 1). In dry meadows, mean TBGB was 50% greater in exclosed sites compared to grazed sites: 1105 g/m^2 in grazed sites and 1652 g/m^2 in the exclosed sites. The TBGB in exclosed wet meadows was 2857 g/m^2 compared to 1761 g/m^2 in grazed wet meadows (a 62% difference in biomass).

Within all communities and sites, the biomass of roots and rhizomes located only in the top 10 cm of soil was greater than the total aboveground biomass (Table 1). For example, the mean biomass of the 0–10 cm soil layer in exclosed wet meadows was 1542 g/m^2 compared to a TAGB of 1080 g/m^2. The top 10 cm of soil also contained most of the belowground biomass. The belowground biomass in the 0–10 cm soil layer in dry meadows comprised >62% of the TBGB and in wet meadows comprised >51% of the TBGB. In con-

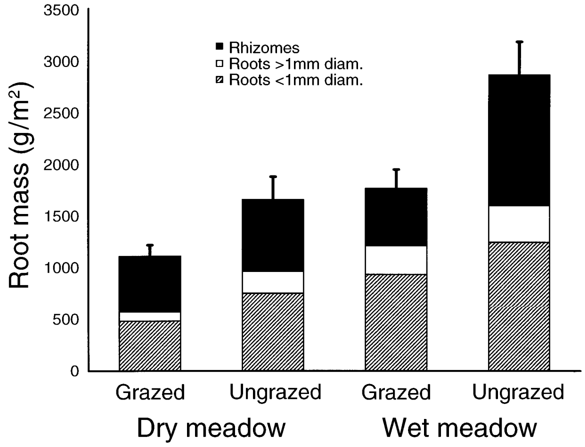

FIG. 1. The biomass distribution of roots partitioned by size class for grazed and exclosed dry and wet meadows in riparian zones of the Middle Fork John Day River, Oregon, USA. Data are based on the mean and 1 SE of three sites for each community and treatment. Results are reported on an oven-dry mass basis. Mean organic-matter concentrations, necessary to calculate data on an ash-free dry-matter basis (AFDM) are 80.5 ± 0.6%, 89.1 ± 0.6%, and 91.6 ± 0.3% for wet-meadow fine roots, roots >1 mm, and rhizomes, respectively. Mean organic-matter concentrations are 81.3 ± 2.1%, 91.6 ± 0.4%, and 92.1 ± 0.4% for dry-meadow fine roots, roots >1 mm, and rhizomes, respectively (J. B. Kauffman, *unpublished data*).

trast, belowground mass of the 30–40 cm depth comprised only 6–11% of the TBGB in dry meadows and ≈7% in wet meadows. Nevertheless, comparing belowground biomass of the 30–40 cm soil depth between grazed and exclosed sites, we found exclosed sites exceeded grazed sites by >126 g/m^2 in dry meadows and ≈90 g/m^2 in wet meadows. While the belowground biomass was consistently higher in exclosed sites than grazed sites at all depths, the proportional distribution of root biomass by depth was similar in the grazed and exclosed sites (Table 1).

Fine roots (<1-mm diameter) and rhizomes comprised >80% of the TBGB at all sites (Fig. 1). Fine-root biomass was ~56% greater in exclosed dry meadows compared to grazed dry meadows (748 and 479 g/m^2, respectively). In wet meadows, fine-root biomass was ~34% greater in exclosed sites compared to grazed sites (1239 and 927 g/m^2, respectively). Roots >1-mm diameter comprised 8–13% of the TBGB in dry meadows and 12–16% of the TBGB in wet meadows. Comparing grazed to exclosed sites, there were no significant differences in the proportion of the TBGB composed of fine roots, roots >1-mm diameter, or rhizomes.

Soil properties

Soils were less compacted in the exclosed sites compared to the grazed sites. Soil bulk density was significantly lower in exclosed sites of both dry and wet meadows (Table 2). In dry meadows, the soil bulk density was 16% lower in exclosed sites compared to the grazed sites (0.84 and 1.00 g/cm^3, respectively). In wet meadows, soil bulk density was 32% lower in exclosed sites compared to grazed sites (0.67 and 0.99 g/cm^3, respectively). In contrast, there were no significant differences in the soil organic matter between grazed and exclosed sites. Soil organic-matter of the surface soils in dry meadows ranged from 11 to 16% for the grazed sites and from 14 to 17% for exclosed sites. Soil organic-matter concentration in the top 10 cm of soil in wet meadows ranged from 12 to 17% for the grazed sites and from 11 to 24% for exclosed sites. Soil pore space, and hence water-storage capacity, was significantly different between the grazed and exclosed sites for both dry and wet meadows (Table 2). In dry meadows, ~6% more of the soil volume was comprised of pore space in exclosed sites compared to grazed sites. In wet meadows, soil pore space occupied ~12% more of the soil volume in exclosed sites (i.e., 60% and 72% in grazed and exclosed sites, respectively). These differences in soil bulk density and soil pore space suggest a greater degree of recovery from livestock compaction in exclosed wet meadows than dry meadows.

Concentrations of mineral forms of N were low at all sites (Table 2). Livestock exclusion did not result in a reduction of the concentration of available N, as there

TABLE 2. Soil properties of grazed and exclosed meadow communities along the Middle Fork John Day River, Oregon, USA.

Soil properties	Dry meadow			Wet meadow		
	Grazed	Exclosed	*P*	Grazed	Exclosed	*P*
Soil bulk density (g/cm^3)	1.00 ± 0.04	0.84 ± 0.04	0.05	0.99 ± 0.04	0.67 ± 0.05	0.05
Soil organic matter (%)	13.4 ± 1.5	15.5 ± 1.1	0.51	12.4 ± 0.8	17.2 ± 3.8	0.42
Soil pore space (%)	59.6 ± 1.4	65.7 ± 1.3	0.05	60.1 ± 1.4	72.2 ± 1.2	0.05
NH_4-N (μg/g soil)	3.94 ± 0.76	5.45 ± 3.17	0.99	5.36 ± 1.01	4.53 ± 1.97	0.66
NO_3-N (μg/g soil)	0.44 ± 0.09	1.96 ± 1.15	0.66	1.53 ± 0.54	3.81 ± 2.53	0.66
Net potential nitrification (μg NO_3-N·(g soil)$^{-1}$·d^{-1})	0.061 ± 0.043	0.195 ± 0.132	0.28	0.005 ± 0.007	0.747 ± 0.615	0.05
Net potential mineralization (μg NH_4-N+ NO_3-N·(g soil)·d^{-1})	0.099 ± 0.048	0.139 ± 0.018	0.51	0.027 ± 0.019	0.886 ± 0.534	0.05

Note: Data are means ± 1 SE.

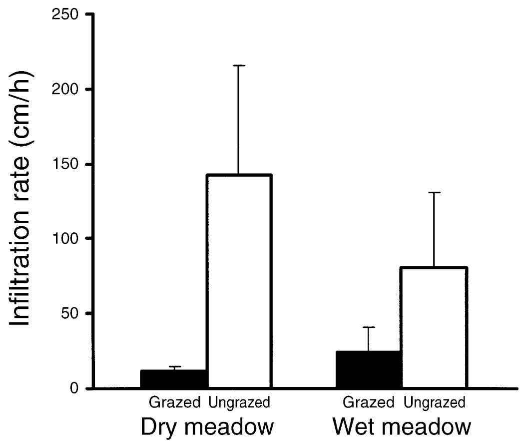

FIG. 2. Infiltration rates for grazed and exclosed dry meadows along the Middle Fork John Day River, Oregon, USA. Data are based on the mean and 1 SE of three sites for each community and treatment. Differences on infiltration rates between grazed and ungrazed sites are significant at $P = 0.0001$ in dry meadows and $P = 0.0002$ in wet meadows.

were no significant differences in the concentration of soil NH_4-N or NO_3-N between grazed and exclosed sites (Table 2). Site variation was greater within treatments than between treatments. Rates of net potential nitrification and mineralization were significantly greater in exclosures compared to grazed sites for wet meadows but not for dry meadows. In the sampled wet meadows, the rate of net potential nitrification was 149-fold greater (0.747 vs. 0.005 μg NO_3-N·g soil^{-1}·d^{-1}), and the rate of net potential mineralization was 32-fold greater (0.886 vs. 0.027 μg N·g soil^{-1}d^{-1}, respectively) in the exclosed compared to grazed sites.

Infiltration rates

Infiltration rates were consistently greater in the exclosed sites compared to the grazed sites (Fig. 2). In dry meadows, mean infiltration rates were over 11-fold greater in exclosed sites compared to grazed sites ($P < 0.001$). Infiltration rates ranged from 6 to 19 cm/h in grazed sites and from 36 to 283 cm/h in exclosed sites (a mean of 11 cm/h in grazed and 142 cm/h in the exclosed sites). Similarly, in wet meadows mean infiltration rates were over 3-fold greater in exclosed sites compared to grazed sites. Mean infiltration rates in wet meadows were 24 and 81 cm/h in grazed and exclosed sites, respectively ($P = 0.002$). In addition to significant differences between treatments, there were significant interactions between locations and treatments ($P < 0.001$). The lowest infiltration rates in dry meadows were at the Summit Creek site where an exclosure fence separated the grazed and exclosed communities. The exclosed dry meadow had an infiltration rate that was 6-fold greater than in the grazed side of the fence (i.e., 36 cm/h compared to 6 cm/h in the exclosed and grazed sites, respectively).

DISCUSSION

There were dramatic differences in belowground ecosystem processes and properties between the grazed and exclosed riparian meadows. Total plant biomass (roots + aboveground biomass) was 1593 and 2567 g/m^2 in grazed and exclosed dry meadows, respectively. The mean total plant biomass in wet meadows was 2295 and 3937 g/m^2 in grazed and exclosed sites, respectively. Thus, total plant biomass in exclosures was 61% greater in dry meadows and 71% greater in wet meadows.

Our estimates of root biomass are similar to those few studies that have measured root biomass in similar riparian plant communities. Root biomass in the top 10 cm of *Poa pratensis*-dominated dry meadows of Yellowstone National Park was similar (250–1147 g/m^2) (Frank and Groffman 1998) to that reported for this study (grazed, 780 g/cm^2 and exclosed, 1030 g/m^2). In Northeastern Oregon, Otting (1999) found root biomass at two sites to a 40-cm depth in ungrazed dry meadows (*Poa pratensis* and *Deschampsia cespitosa*-dominated communities) was 1237 and 1632 g/m^2. This is similar to our estimates of 1105 g/cm^2 (grazed) to 1652 g/m^2 (exclosed) (Table 1). In contrast, Manning et al. (1989) found that a moderately cattle-grazed dry meadow dominated by *Poa nevadensis* in Nevada had a root mass to a depth of 40 cm of only 555 g/m^2. In the same floodplain meadows, they reported that root mass of *Carex nebrascensis*-dominated communities averaged 3382 g/m^2, which was greater than our estimates of 1761 g/m^2 (grazed) to 2857 g/m^2 (exclosed). In Northeastern Oregon, Otting (1999) reported that root biomass in two ungrazed *Carex*-dominated wet meadows (sites with a high groundwater level) were 2784 and 4375 g/m^2.

Large herbivores can increase N cycling rates through mechanisms such as increasing available forms of N via urine and fecal inputs and lowering the C:N ratios of plant materials and soil organic matter, which would reduce microbial immobilization rates (Floate 1981, Risser and Parton 1982). It has been hypothesized that areas frequently and repeatedly grazed will have decreased C inputs from roots resulting in decreased N immobilization, increased N availability, and increased N mineralization rates (Holland and Detling 1990). Therefore, one would expect N availability to decrease within exclosures. However, we found no differences in N availability between grazed and ungrazed riparian meadows and significantly higher rates of net potential N mineralization and nitrification in the exclosed wet meadows (Table 2). Studies reporting increased N mineralization rates due to grazing were often in upland sites that were only grazed by wild herbivores (Holland and Detling 1990, Frank and Groffman 1998), or where domestic cattle grazing was light to moderate (Risser and Parton 1982, Shariff et al. 1994). Hypotheses relating to increases in N cycling due to herbivory fail to consider how large herbivores affect soil physical processes. Based upon our results, we hypothesize that the differences in soil physical properties between grazed and exclosed sites exerted stronger influences on N dynamics than effects of reduced belowground C allocation or fecal and urine inputs. Additional studies are needed to understand how the physical actions of large herbivores such as cattle affect ecological processes in productive ecosystems such as riparian meadows.

The influences of livestock exclusion on soil infiltration rates in this study are consistent with results presented in a review of livestock impacts on infiltration rates of upland soils by Gifford and Hawkins (1978). They concluded that infiltration rates in ungrazed areas were statistically different from those in grazed areas at any grazing intensity. Many studies have found that soil compaction increases linearly with increases in grazing intensity (Kauffman and Krueger 1984). Gifford and Hawkins (1978) reported that light grazing reduced infiltration rates to 75% of rates in ungrazed areas, and heavy grazing reduced infiltration rates to 50% of rates in ungrazed sites. Our study examined whether this loss is reversible. In this study, the mean infiltration rate in exclosed dry meadows was 1190% greater than in grazed dry meadows and the mean rate in exclosed wet meadows was 233% greater than that in grazed sites (Fig. 2). This indicates that recovery of soil properties can be quite dramatic even following over a century of heavy livestock grazing. In a northeastern Oregon riparian zone, Bohn and Buckhouse (1985) also reported that infiltration rates improved in exclosures over a seven-year period, implying that recovery from historically high levels of livestock grazing was occurring.

An important question in the ecological restoration of riparian areas is the temporal scale of recovery following implementation of restoration. Comparing grazed to exclosed sites, the degree of change among the measured ecosystem properties differed. Many studies have reported decreases in root biomass when the aboveground shoots are grazed during the growing season (Richards 1984). In the time frame described in this study, it appears that declines in root biomass were reversed in riparian meadows following cessation of livestock grazing. Soil organic matter was not significantly different between grazed and exclosed communities but may be trending in that direction. Differences in infiltration rates were highly significant between grazed and exclosed sites. However, the time required for recovery of infiltration rates is poorly defined. Gifford and Hawkins (1978) found that infiltration rates in grasslands were still recovering after 13 years of rest from grazing. The dramatic differences in soil belowground properties between the grazed and the exclosed riparian plant communities indicated that livestock elimination is an effective means of ecological restoration.

Implications for livestock management

We did not measure the quantity of biomass removed by cattle in this study. We sampled aboveground biomass and other ecosystem properties with the objective of describing the conditions at the end of the growing season. We sampled at this time because this is the structure that exists throughout the winter to early spring when overland flows from precipitation or runoff and high flows from overbank flooding interact most strongly with the riparian communities (i.e., the time periods and seasonal events where interactions between riparian communities and the stream are greatest). If we assume that annual aboveground productivity in grazed communities was the same as in the exclosed communities, then the utilization of herbage was 64% in the dry meadows and 42% in the wet meadows. Utilization at these levels is at the high end of levels recommended for sustained riparian conditions on public lands in the western United States (25 to 65% utilization rates; Clary 1995). However, through examination of other ecosystem attributes measured in this study, it is likely that aboveground productivity was lower in grazed than exclosed plant communities. Differences in rates of N transformations are correlated to levels of primary productivity (Vitousek and Howarth 1991, Hart et al. 1994). The greater rates of N transformations in the exclosures may contribute to a greater aboveground productivity. The greater root biomass in the cattle exclosures would also indicate a greater volume of the soil is occupied by roots, thereby increasing nutrient and water uptake. In a simulated grazing and compaction study in riparian zones, Clary (1995) found decreased biomass in sedge-dominated communities following increased soil compaction. Biomass was also decreased in sedge-dominated communities due to defoliation at treatment levels where residual stubble heights were 1–10 cm. Therefore, it is likely that primary production was lower in grazed sites than exclosed sites. As such, the utilization level of the grazed sites was likely lower than our estimates based on differences in TAGB (total aboveground biomass) between the grazed and exclosed sites and within the range recommended for utilization on public lands. If this is true, then utilization levels recommended by federal land-management agencies could result in ecosystem changes similar to what was described in this study (i.e., soil compaction, lower rates of infiltration, and lower root biomass).

Implications for watershed/stream management

Plants often respond to defoliation through reduced allocation of C to belowground tissues (Jaramillo and Detling 1988, Holland and Detling 1990, Briske and Richards 1994). The effects of greater root mass in the exclosed sites suggest potentially important changes in ecosystem functions. For example, roots form an important source of organic carbon and may be an important source of dissolved organic carbon to stream ecosystems (Dwire 2001). *C. nebrascensis* reproduces vegetatively via tillers produced from rhizomes. Rhizome mass in exclosures was 1263 g/m^2 compared to 556 g/m^2 in grazed sites. The greater rhizome mass suggests a greater reproductive potential in exclosures. Roots and rhizomes stabilize streambanks and reduce erosion of stream channels (Smith 1976). Fine-root biomass was ~56% greater in exclosed dry meadows compared to grazed dry meadows (Fig. 1). In wet meadows, fine-root biomass was ~34% greater in exclosed sites compared to grazed sites. The increase in fine-root biomass was particularly apparent at the deeper layers. For example, in wet meadows fine-root biomass at the 30–40 cm depth in exclosures was almost twice that of grazed areas (66 g/m^2 and 129 g/m^2 in grazed and exclosed sites, respectively). This is important because Manning et al. (1989) reported that roots < 0.9 mm in diameter may account for ~95% of the root length density in riparian zones. Smith (1976) found an inverse relationship between rates of stream channel erosion and root abundance. The significantly higher mass of fine roots in exclosed communities may increase the capacity of streambanks to resist erosion.

Many studies have reported decreased soil bulk density and/or increased soil pore space in sites excluded from cattle grazing (Orr 1960, Aldefer and Robinson 1962, Clary and Medin 1990). Our results are similar to those of Orr (1960) who suggested that soils of *Poa pratensis*-dominated meadows excluded from grazing for 7 to 17 years had experienced a sufficient time for recovery in terms of bulk density and pore space. Increased soil pore space results in a greater volume of soil water present when soils are saturated. The potential differences in soil water storage due to differences in soil pore space are not trivial. Based upon the results of this study we calculated that saturated soils of the surface 10 cm of a single hectare of exclosed dry meadow would contain 61 000 L more water than an equivalent grazed hectare. Under saturated conditions, a hectare of wet meadows with the pore space measured in the exclosed communities of this study would contain 121 000 L more water than those with the pore space of the grazed wet-meadow communities. Based upon a GIS analysis of aerial photos of the 30-km riparian zone sampled in this study, there were 145 ha of dry meadows and 64 ha of wet meadows (C. Heider and J. B. Kauffman, *unpublished data*). Our results suggest that if the entire area was excluded from livestock, the surface 10 cm of soil in the meadows alone (about 60% of the riparian-zone cover) could potentially store 16.6×10^6 L more of water than if the area were grazed by cattle. And, this estimate does not include the entire soil profile. This increase in soil water likely influences ecosystem productivity, soil temperature, biogeochemistry, and stream flows.

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