

## HOW GRAZING AND SOIL QUALITY AFFECT NATIVE AND EXOTIC PLANT DIVERSITY IN ROCKY MOUNTAIN GRASSLANDS

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**Abstract.** We used multiscale plots to sample vascular plant diversity and soil characteristics in and adjacent to 26 long-term grazing exclosure sites in Colorado, Wyoming, Montana, and South Dakota, USA. The exclosures were 7–60 yr old ( $31.2 \pm 2.5$  yr, mean  $\pm 1$  SE). Plots were also randomly placed in the broader landscape in open rangeland in the same vegetation type at each site to assess spatial variation in grazed landscapes. Consistent sampling in the nine National Parks, Wildlife Refuges, and other management units yielded data from 78 1000-m<sup>2</sup> plots and 780 1-m<sup>2</sup> subplots. We hypothesized that native species richness would be lower in the exclosures than in grazed sites, due to competitive exclusion in the absence of grazing. We also hypothesized that grazed sites would have higher native and exotic species richness compared to ungrazed areas, due to disturbance (i.e., the intermediate-disturbance hypothesis) and the conventional wisdom that grazing may accelerate weed invasion. Both hypotheses were soundly rejected. Although native species richness in 1-m<sup>2</sup> subplots was significantly higher ( $P < 0.05$ ) in grazed sites, we found nearly identical native or exotic species richness in 1000-m<sup>2</sup> plots in exclosures ( $31.5 \pm 2.5$  native and  $3.1 \pm 0.5$  exotic species), adjacent grazed plots ( $32.6 \pm 2.8$  native and  $3.2 \pm 0.6$  exotic species), and randomly selected grazed plots ( $31.6 \pm 2.9$  native and  $3.2 \pm 0.6$  exotic species). We found no significant differences in species diversity (Hill's diversity indices,  $N1$  and  $N2$ ), evenness (Hill's ratio of evenness,  $E5$ ), cover of various life-forms (grasses, forbs, and shrubs), soil texture, or soil percentage of N and C between grazed and ungrazed sites at the 1000-m<sup>2</sup> plot scale. The species lists of the long-ungrazed and adjacent grazed plots overlapped just  $57.9 \pm 2.8\%$ . This difference in species composition is commonly attributed solely to the difference in grazing regimes. However, the species lists between pairs of grazed plots (adjacent and distant 1000-m<sup>2</sup> plots) in the same vegetation type overlapped just  $48.6 \pm 3.6\%$ , and the ungrazed plots and distant grazed plots overlapped  $49.4 \pm 3.6\%$ . Differences in vegetation and soils between grazed and ungrazed sites were minimal in most cases, but soil characteristics and elevation were strongly correlated with native and exotic plant diversity in the study region. For the 78 1000-m<sup>2</sup> plots, 59.4% of the variance in total species richness was explained by percentage of silt (coefficient = 0.647,  $t = 5.107$ ,  $P < 0.001$ ), elevation (coefficient = 0.012,  $t = 5.084$ ,  $P < 0.001$ ), and total foliar cover (coefficient = 0.110,  $t = 2.104$ ,  $P < 0.039$ ). Only 12.8% of the variance in exotic species cover ( $\log_{10}$ cover) was explained by percentage of clay (coefficient = -0.011,  $t = -2.878$ ,  $P < 0.005$ ), native species richness (coefficient = -0.011,  $t = -2.156$ ,  $P < 0.034$ ), and  $\log_{10}N$  (coefficient = 2.827,  $t = 1.860$ ,  $P < 0.067$ ). Native species cover and exotic species richness and frequency were also significantly positively correlated with percentage of soil N at the 1000-m<sup>2</sup> plot scale. Our research led to five broad generalizations about current levels of grazing in these Rocky Mountain grasslands: (1) grazing probably has little effect on native species richness at landscape scales; (2) grazing probably has little effect on the accelerated spread of most exotic plant species at landscape scales; (3) grazing affects local plant species and life-form composition and cover, but spatial variation is considerable; (4) soil characteristics, climate, and disturbances may have a greater effect on plant species diversity than do current levels of grazing; and (5) few plant species show consistent, directional responses to grazing or cessation of grazing.

**Key words:** competitive exclusion; exotic species richness; grazing exclosures; intermediate disturbance; mountain grasslands; multiscale vegetation sampling; native plant diversity; Rocky Mountains; soil characteristics; species composition overlap; species-specific responses.

## INTRODUCTION

For over half a century, investigators have used exclosures (i.e., areas fenced to exclude wildlife or domestic livestock) as a means to evaluate the effects of grazing (Daubenmire 1940a, Reardon 1996). Such studies are vitally important to rangeland conservationists because of increased concerns about protecting native plant diversity (Bock et al. 1993, Stohlgren et al. 1997a, b) and preventing exotic species invasion and spread of noxious weeds (Ellison 1960, Mack 1981, Stohlgren et al. 1999). Comparisons of vascular plant diversity of grazed and ungrazed sites can also yield important theoretical insights on the role of herbivory and competition in structuring plant communities (Harper 1969, McNaughton 1983, Belsky 1986). Commonly, small plots or transects are placed on either side of a fence in a paired-plot or two-sample comparison of vegetation or soil (e.g., Smith 1960, Heady 1968, West et al. 1979, Chew 1982, Bock et al. 1984, Facelli et al. 1989, Milchunas and Lauenroth 1993, Dormaar et al. 1994, Reardon 1996).

Exclosure studies have produced inconsistent and questionable results, because most exclosures are small (<1 ha), long-term grazing rates in adjacent rangeland are usually unknown, and studies have quantified grazing effects inconsistently (Daubenmire 1940a, Fisser 1970, Fleischner 1994, Woodward et al. 1994). The "long-term ungrazed" condition is thought to be atypical for landscapes that evolved with grazing (Milchunas et al. 1988, Milchunas and Lauenroth 1993). Exclosures sometimes attract grazing animals; hence, grazing effects are accentuated adjacent to the exclosures. Exclosures may also differentially concentrate small herbivores and granivores (McNaughton 1983).

We focus on the issues important to statistical inferences in exclosure studies. First, most studies are poorly replicated (Webster 1992). Exclosures are expensive to construct so they tend to be small and few and, thus, are compromised by edge effects, unique local conditions, or poor representation of larger scale processes (Daubenmire 1940a, Woodward et al. 1994, Hughes 1996). Large exclosures cover wider environmental conditions and incorporate larger scale processes (e.g., patchy small-mammal disturbance and seed dispersal effects), but their expense prohibits extensive replication. We are left with a few, small exclosures in different management units that were usually established to evaluate changes in forage production rather than plant diversity.

Most published studies using large exclosures involved pseudoreplication, in which many small plots or transects were used on either side of a fence and statistical inferences were made about the "grazing effect" on the larger, unsampled landscape (Webster 1992). In our literature review of 28 exclosure studies, we found that 17 studies had a true sample size of  $n = 1$  exclosure (e.g., Robertson 1971, Tiedemann and

Berndt 1972, Smeins et al. 1976, Chew 1982, Orr and Evenson 1991, Dormaar et al. 1994, Frank et al. 1995, Lavado et al. 1996), whereas 20 studies relied on fewer than five exclosures (e.g., Evanko and Peterson 1955, West et al. 1979, Collins and Adams 1983, Schultz and Leininger 1990, Cid et al. 1991, Coughenour 1991, Chaneton and Lavado 1996). The problems of pseudoreplication have been reviewed by Hurlbert (1984) and Webster (1992).

We especially draw attention to three concerns limiting statistical inferences about potential grazing effects on plant diversity that have received little attention: subjective location of exclosures, poor sampling techniques, and inadequate assessment of spatial heterogeneity in the larger landscape. Most exclosures are subjectively located near roads and in flat terrain. This is what Krebs (1989) calls "accessibility sampling." None of the studies that we reviewed detailed the sample population (i.e., all potential sites from which the exclosure sites were selected). Questions arise as to whether local measurements of plant diversity are really typical of landscape-scale measurements of plant diversity (Brown and Allen 1989, Collins and Glenn 1997, Stohlgren et al. 1997a). Local species richness, for example, may be poorly correlated with landscape-scale species richness, because species overlap and species richness are highly dependent on scale (e.g., Collins and Glenn 1997, Stohlgren et al. 1997a, 1999). Thus, it is difficult to extrapolate information from subjectively selected sites to the broader landscape (Krebs 1989).

Most exclosure studies used poor sampling techniques, particularly with respect to plant diversity. For example, an evaluation of exclosures and grazed sites in Yellowstone National Park relied on actual measurements on only 3.5 m<sup>2</sup> per site (four 81.28 × 81.28 cm chart quadrats per site) at only five sites (Reardon 1996). Evanko and Peterson (1955) measured 3.0 m<sup>2</sup> per treatment (30 20 × 50 cm plots/treatment along a transect). An evaluation of grazed and ungrazed sites in Alberta, Canada (Dormaar et al. 1994) relied on just 1.5 m<sup>2</sup>/treatment (15 0.1-m<sup>2</sup> plots, 10 m apart on a transect). It is unlikely that such small sample units tell a complete story. In a comparison of small-plot and point-sampling techniques, Stohlgren et al. (1999) found that the commonly used Daubenmire (1959) transects (20 × 50 cm quadrats), and Parker (1951) transects (2 cm diameter loops), routinely missed about half of the vascular plant species found in 1000-m<sup>2</sup> plots. This was due to small total sampling area, spatial autocorrelation effects, and missing patches of high or distinctive plant diversity. Replicate transects also failed to capture significant components of the flora such as locally rare species and patchily distributed exotic plant species. Multiscale vegetation plots, which included a larger sampling area (1000-m<sup>2</sup> plots), more adequately described plant diversity in a variety of habitats and vegetation types in the Central Grasslands

(Stohlgren et al. 1999). We did not find any enclosure studies that used well-replicated, large-plot designs in several vegetation types.

Lastly, nearly all enclosure studies confined sampling to a small area within a much larger area of concern. The most extreme example we found was a series of 10 2-ha enclosures established in eastern Oregon. Only one 6.1 × 6.1 m detailed chart plot was measured within each enclosure that had different external grazing regimes (Sneva et al. 1984). The problem of tiny sampling areas is compounded when investigators attempt to evaluate different "treatment" effects without replicate enclosures (Webster 1992). The major assumption is that the "main effect" detected by plant diversity or soil studies in paired plots or transects is due solely to the different grazing regimes on either side of a fence line (e.g., Bock et al. 1984, Hughes 1990, 1996, Dormaar et al. 1994, and nearly all enclosure studies that we reviewed). Do small plots capture all of the spatial variation in plant composition at the sites, or do they exaggerate differences between sites?

Because of these sampling problems, it has been difficult to synthesize information from enclosure studies, and the effects of grazing (or cessation of grazing) on plant diversity have remained elusive. Recognizing these problems, we designed a study that used standardized, multiscale sampling techniques (Stohlgren et al. 1995, 1999) with improved replication (multiple enclosures at several areas in four states). Furthermore, we randomly selected plot locations inside and adjacent to the enclosures, with a third plot randomly located in a grazed area in the same vegetation type at each site. The third plot provided a means to assess spatial variation in grazed landscapes.

Our objectives were to: (1) examine several aspects of plant communities at multiple spatial scales in long-term grazed and ungrazed sites in several management areas; (2) determine the relative roles of grazing, soil characteristics, and climate in determining patterns of species richness; and (3) develop broad generalizations about the effects of grazing and cessation of grazing on plant diversity in typical grasslands in the Rocky Mountains. We hypothesized that native species richness would be lower in enclosures than in grazed sites, due to competitive exclusion in the absence of grazing (Grime 1973, Harper 1977). We also hypothesized that grazed sites would have higher native and exotic species richness than ungrazed sites for two reasons. First, grazing might reduce plant biomass and competition, and increase available nutrient and water resources, resulting in greater establishment of various plant species than in long-term ungrazed sites (i.e., the intermediate-disturbance hypothesis; Grime 1973, Connell 1978, Fox 1979). Second, there is the long-standing paradigm, supported by studies in other regions, that grazing accelerates weed invasion (Daubenmire 1940b, Ellison 1960, Mack 1981, D'Antonio and Vitousek 1992, Hobbs and Huenneke 1992, Fleischer 1994). If

grazed and ungrazed sites differed significantly in native or exotic species richness, cover, diversity, etc., and if they differed consistently among management areas, then grazing or cessation from grazing might be considered a major determinant of plant diversity. The comparison of long-term enclosures to long-grazed sites from highly productive to less productive habitats (Huston 1979) should accentuate differences in plant diversity and recovery from grazing in Rocky Mountain grasslands.

## METHODS

### *Study areas and sampling design*

We surveyed Federal land management agencies in Colorado, Wyoming, Montana, and South Dakota, USA, for potential study sites (Fig. 1). Criteria for selection included >12 yr of continued protection from grazing (after McNaughton 1983), and moderate to moderately heavy grazing outside the enclosures in typical Rocky Mountain grasslands. We sampled 20 enclosures that met these criteria in Yellowstone and Grand Teton National Parks and Bighorn Basin Resource Area in Wyoming; Rocky Mountain National Park and Uncompahgre and Gunnison Resource Areas in Colorado; Charles M. Russell National Wildlife Refuge and Custer National Forest/Pryor Mountain Wild Horse Range in Montana; and Wind Cave National Park in South Dakota (Tables 1 and 2). Three large enclosures at Gunnison, Uncompahgre, and Rocky Mountain contained multiple vegetation types, so additional plots were established in and adjacent to them. This created 26 enclosure sites in all. The sites were primarily montane grasslands, upper plains grasslands, and shrublands ranging in elevation from 776 m to 2675 m. The enclosures averaged  $31.2 \pm 2.5$  yr old (mean  $\pm$  1 SE; range 7–60 yr). The study sites probably were at least moderately grazed in historic and pre-settlement times (Buchholtz 1983, Coughenour and Singer 1996). The primary grazers varied by site (Table 2). Although exact grazing intensity could not be determined for the sites, discussions with resource managers and field observations of plant cover and height confirm that the sites are at least moderately grazed annually.

Climatic data were gathered from the nearest long-term (>30 yr) weather station for each management unit. Variables included long-term mean minimum and maximum temperature in January and July, winter/spring precipitation (October to June), and summer/fall precipitation (July to September).

Three multiscale vegetation plots were placed at each enclosure site. Modified-Whittaker plots (see *Vegetation sampling*) were randomly placed inside and adjacent to each enclosure. Where the topography varied considerably inside or outside enclosures, plots were paired on similar aspects, slopes, and elevations. Edges of fences were avoided by at least 2 m. A third plot for each enclosure pair was randomly located within

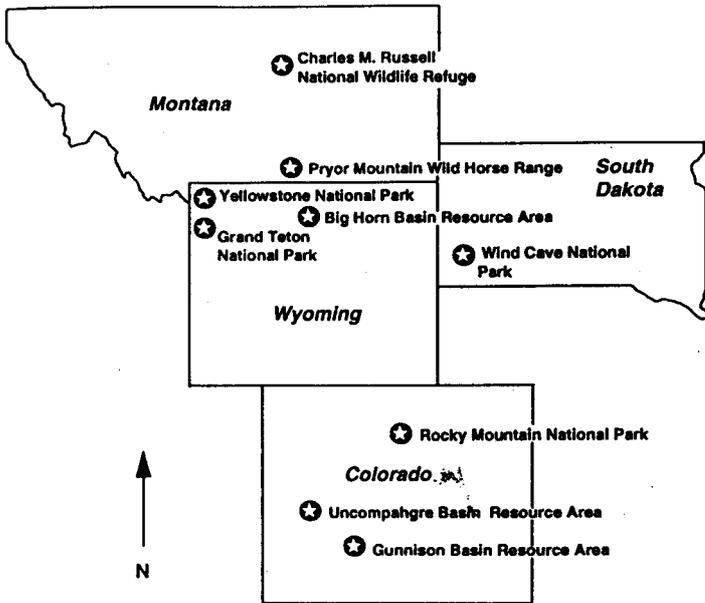


FIG. 1. Map of the study areas in the western United States.

1.5 km of the enclosure, in the similarly grazed landscape, in the same vegetation type, and with a similar slope, aspect, and elevation. The paired plots on either side of the fenced enclosures averaged  $100 \pm 10$  m apart (mean  $\pm 1$  SE), whereas the two grazed plots averaged  $940 \pm 230$  m apart.

#### Vegetation sampling

The modified-Whittaker plot was  $20 \times 50$  m, placed with the long axis along the major elevation or moisture gradient to maximize plant diversity in the plot (Stohlgren et al. 1995). Nested in each plot were 10  $0.5 \times 2$  m ( $1\text{-m}^2$ ) subplots systematically spaced along the inside border, two  $2 \times 5$  m ( $10\text{-m}^2$ ) subplots in alternate corners, and a  $5 \times 20$  m ( $100\text{-m}^2$ ) subplot in the plot center. Foliar cover for each species and percentage of bare ground were estimated to the nearest percent in the 10  $1\text{-m}^2$  subplots, and cumulative plant species were

noted in the  $10\text{-m}^2$  subplots, the  $100\text{-m}^2$  subplot, and the  $1000\text{-m}^2$  plot. We sampled each site as close to the phenological maximum (peak biomass) as possible. In 1996, we sampled in Yellowstone 9–19 July, Grand Teton 9–16 July, and Wind Cave 10–12 July, Rocky Mountain National Park 26–29 July, and Charles M. Russell 6–11 Aug. In 1997, we sampled at Gunnison from 24 June to 2 July, Uncompahgre 13–17 July, Custer National Forest/Pryor Mountain Wild Horse Range 24–28 July, and Bighorn Basin 7–9 Aug.

Plant species that could not be identified in the field were collected and identified at the herbarium at Colorado State University (Department of Biology). Fewer than 5% of the specimens encountered could not be identified to species, due to phenological stage or missing flower parts. In these cases, plants were identified to genus and treated as individual species. Ancillary data recorded for each plot included: UTM location

TABLE 1. Maximum ( $T_{\max}$ ) and minimum ( $T_{\min}$ ) temperatures for January and July, and seasonal precipitation at grazing enclosure study areas.

Site†	$T_{\max}$ (°C)		$T_{\min}$ (°C)		Precipitation (cm)	
	Jan	Jul	Jan	Jul	Oct–Jun	Jul–Sep
Bighorn Basin	0.3	25.4	-12.0	9.7	353.8	22.4
Charles Russell	-2.8	30.4	-16.7	11.9	122.5	11.4
Grand Teton	-3.7	25.3	-19.0	4.4	405.1	13.0
Gunnison	-2.6	27.1	-21.1	5.4	146.7	11.2
Rocky Mountain	3.5	25.7	-8.7	7.8	101.6	14.7
Uncompahgre	3.7	33.8	-11.1	12.7	51.7	6.6
Wild Horse	0.3	25.4	-12.0	9.7	353.8	22.4
Wind Cave	3.1	31.8	-11.8	13.9	120.2	14.7
Yellowstone	0.9	26.6	-9.3	10.7	190.0	18.7

† Site locations are: Bighorn Basin Resource Area, Wyoming; Charles M. Russell National Wildlife Refuge, Montana; Grand Teton National Park, Wyoming; Gunnison Resource Area, Colorado; Rocky Mountain National Park, Colorado; Uncompahgre Basin Resource Area, Colorado; Pryor Mountain Wild Horse Range, Custer National Forest, Montana; Wind Cave National Park, South Dakota; Yellowstone National Park, Wyoming.

TABLE 2. Descriptions of enclosure study areas, including number of plots (*n*), enclosure age, size, elevation, and major vegetation type, the primary grazers of pre- and post-European settlement, and estimated number of grazers per season.

Site and enclosure name	Age <i>n</i> (yr)	Size (ha)	Elev. (m)	Vegetation association†	Pre-European primary grazers‡	Post-European primary grazers‡	Current estimated grazers per season§
Bighorn Basin Paint Rock Canyon	6	14	2.7	1902	Agr spi/Art tri	elk, mule deer	cattle, wildlife 450 cattle (sp, fa)
Charles Russell Agate Ridge	3	31	4	842	Agr smi/Art tri	bison, elk	cattle 698 cattle, Jun-Sep same pasture
Opuntia Spring Creek	3	30	4	800	Agr smi/Art tri	bison, elk	cattle same pasture
Bell Ridge	3	30	16	776	Agr smi/Art tri	bison, elk	cattle 405 cattle, May-Jul
BLM	3	13	3.3	892	Agr smi/Art tri	bison, elk	cattle 8000 cattle, May-Nov
Grand Teton Davis Hill	3	33	0.35	2191	Agr spi/Art tri	bison, elk	moose, elk, mule deer, cattle 12 000 elk, 400 bison, moose, cattle (wi)
Uhl Hill	3	33	0.37	2152	Ely sp./Art tri	bison, elk	moose, elk, mule deer, cattle 12 000 elk, 400 bison, moose, cattle (wi)
Gunnison Woods Gulch	9	43	12.6	2530	Sti let/Art tri	mule deer, elk, bison	cattle 220 cattle, May-Jun
Rocky Mountain Aspen	3	27	39	2675	Poa pra/Pop tre	Rocky Mt. big- horn sheep, elk	elk, mule deer 700 elk, deer (wi)
Beaver Meadows	6	34	4.2	2566	Agr spp./Art tri	Rocky Mt. big- horn sheep, elk	elk, mule deer 700 elk, deer (wi)
Deer Ridge	3	33	0.39	2585	Agr spp./Art tri	Rocky Mt. big- horn sheep, elk	elk, mule deer 700 elk, deer (wi)
Uncompahgre County Line	9	60	14.6	1646	Hil jam/Atr con	mule deer, ante- lope, rabbit	domestic sheep 3600 sheep (wi)
Wild Horse Forest Service	3	34	0.01	2317	Fes ida/Pin fle	Rocky Mt. big- horn sheep, elk, mule deer	wild horses 120 wild horses (su)
Penn's Cabin	3	34	1.1	2573	Phl hoo/Fes ida	Rocky Mt. big- horn sheep, elk, mule deer	wild horses 120 wild horses (su)
Wind Cave Campground	3	31	80.9	1325	Poa pra/Amo can	bison, elk, mule deer, prairie dog	bison, elk, prairie dog 325 bison, 300 elk, 10 prairie dog towns/440 ha (yr rd)
Cottonwood	3	7	1.7	1124	Pso ten/Poa pra	bison, elk, mule deer, prairie dog	bison, elk, prairie dog 325 bison, 300 elk, 10 prairie dog towns/440 ha (yr rd)
Yellowstone Blacktail	3	34	2	2056	Fes ida/Art tri	elk	elk, bison elk and bison, 20/ha (wi)
Junction Butte	3	38	2	1909	Fes ida/Art tri	elk	elk, bison elk and bison, 20/ha (wi)
Lamar	3	34	2	2074	Fes ida/Art tri	elk	elk, bison elk and bison, 20/ha (wi)

† Full scientific names for the coded species are given in the Table 6 footnote.

‡ Mule deer are included as browsers, not grazers.

§ Data on approximate number of grazers and the season of grazing were obtained from personal communications with agency wildlife biologists. Seasons are abbreviated as sp, spring; su, summer; fa, fall; wi, winter; yr rd, year-round.

and elevation from a global positioning system, slope, and aspect.

### Species richness comparisons

For each management area, we used ANOVA to test for differences in native and exotic species richness and cover, and exotic species frequency between excluded sites, adjacent grazed sites, and the randomly located grazed sites in the same vegetation types. We also combined data from all management units for a summary ANOVA of ungrazed, grazed-adjacent, and grazed-distant plots. All statistical analyses were conducted with SYSTAT (version 6.0, SPSS, Chicago, Illinois, USA), and  $P < 0.05$  was used to determine significance in all tests. Tukey's test was used as a means comparison test when the  $F$  test was significant. We analyzed 1-m<sup>2</sup> subplot data and 1000-m<sup>2</sup> plot data separately to assess the scale dependency of the results (Stohlgren et al. 1999). The same ANOVA approach was used to compare differences in species composition, diversity, evenness, and cover by life-form group. Exotic species richness and cover data, and distances between plots were not normally distributed, so those values were log<sub>10</sub>-transformed prior to analysis.

### Species composition, diversity, and evenness

Jaccard's Coefficient (Krebs 1989) was used to compare species overlap (1000-m<sup>2</sup> plot data) between excluded plots and adjacent plots, adjacent plots and the randomly located grazed plots in the same vegetation types, and excluded plots and the randomly located plots. A comparison of species lists for two sites resulting in a similarity coefficient of 1.0 would indicate complete overlap (i.e., identical species lists), whereas a value of 0.0 would indicate no overlap. We selected Jaccard's Coefficient over other similarity indices because all species are equally important, and we have found that >50% of all species sampled have <1% cover and few species have >5% cover (Stohlgren et al. 1997a, 1999). We have found that, in vegetation types with high evenness, Jaccard's Coefficient is an appropriate measure of similarity (Stohlgren et al. 1997a, b).

We used two diversity indices and one evenness index recommended by Ludwig and Reynolds (1988).  $N1$  is an index of the number of abundant species, whereas  $N2$  measures the number of very abundant species. We measured foliar cover as a measure of abundance, so the diversity indices measure the number of high-cover species and very high-cover species, respectively. These indices complement the comparisons of total species richness or Jaccard's Coefficients between grazed and ungrazed sites by downweighting locally rare species. Thus, higher  $N1$  or  $N2$  values would indicate higher dominant species diversity. Following Ludwig and Reynolds (1988),  $N1$  was calculated as

$$N1 = e^{H'}$$

where  $H'$  (Shannon's index) for a sample was defined as

$$H' = -\sum_{i=1}^S \left[ \left( \frac{n_i}{n} \right) \ln \left( \frac{n_i}{n} \right) \right]$$

where  $n_i$  was the cover of the  $i$ th species of  $S$  species in the sample and  $n$  is the total cover of all species in the sample.  $N2$  is calculated as

$$N2 = 1/\lambda$$

where  $\lambda$  (Simpson's index) for a sample was defined as

$$\hat{\lambda} = \sum_{i=1}^S \frac{n_i(n_i - 1)}{n(n - 1)}$$

We used the modified Hill's ratio ( $E5$ ; Ludwig and Reynolds 1988) as an index of evenness, where

$$E5 = \frac{(1/\lambda) - 1}{e^{H'} - 1} = \frac{N2 - 1}{N1 - 1}$$

$E5$  approaches zero as one species becomes increasingly dominant in foliar cover, so higher  $E5$  values indicate greater evenness in foliar cover among species.

### Soil sampling and analysis

Five soil samples were taken in each modified-Whittaker plot (in the corners and the plot center) and were combined. The surface litter, if present, was removed, and the top 15 cm of soil was sampled with a 2.5-cm soil core. Particle size analysis was based on the standard hydrometer method (Gee and Bauder 1986). Samples were air-dried for 48 h, sieved with a standard Number 10 (2-mm pore size) sieve, ground in a standard three-ball grinder, and then oven-dried at 55°C for 24 h. Samples were analyzed for percentage of total carbon and percentage of total nitrogen using a LECO-1000 CHN Analyzer (LECO Corporation, St. Joseph, Michigan, USA), following the methods of Carter (1993).

Multiple regression was used to determine the relationship of the number and cover of native or exotic plant species to soil characteristics for all 1000-m<sup>2</sup> plots in the study region. We tested the significance of each predictor with  $t$  values (i.e., against the null hypothesis that the slope is 0). We used stepwise forward multiple regressions to assess the ability of native species richness and cover, soil characteristics, elevation, and climate variables to predict exotic species richness. Soil characteristics included total N, total C, and percentages of sand, silt, and clay (only two soil texture variables were added into each model to reduce multicollinearity). The forward linear regression models included only variables meeting the  $P < 0.15$  criterion (Neter et al. 1990). Data distributions that were strongly skewed were transformed prior to analysis. Log<sub>10</sub> transformations were used on percentage of N and exotic species cover to improve normality.

TABLE 3. Mean (1 SE in parentheses) number and cover of native and exotic species in 1-m<sup>2</sup> subplots in ungrazed exclosures (UG), grazed-adjacent plots (G-A), and grazed-distant plots (G-D) in nine study sites.

Site	n†	No. native species			No. exotic species			Cover of native species (%)			Cover of exotic species (%)		
		UG	G-A	G-D	UG	G-A	G-D	UG	G-A	G-D	UG	G-A	G-D
Bighorn Basin	20	6.1 (0.5)	6.4 (0.4)	7.4 (0.5)	4.1 (0.3)	4.6 (0.2)	3.6 (0.2)	28.7 (4.0)	30.8 (2.0)	28.4 (1.8)	19.0 (2.9)	16.4 (2.0)	19.0 (3.6)
Charles Russell	50	4.5 (0.5)	4.4 (0.3)	3.5 (0.2)	0.1 (0.1)	0.1 (0.0)	0.1 (0.0)	18.1 (1.8)	20.8 (1.8)	14.0 (2.3)	0.1 (0.1)	0.1 (0.1)	0.2 (0.1)
Grand Teton	20	8.8 (0.6)	11.8 (0.8)	10.1 (0.9)	0.1 (0.1)	0.2 (0.1)	0.4 (0.2)	58.4 (8.3)	48.2 (5.0)	55.8 (6.0)	0.2 (0.2)	1.7 (1.2)	1.1 (0.6)
Gunnison	30	8.2 (0.4)	9.9 (0.4)	9.0 (0.4)	0.6 (0.1)	0.4 (0.1)	0.3 (0.1)	38.3 (3.7)	38.7 (2.7)	31.5 (3.1)	1.7 (0.5)	0.4 (0.1)	0.2 (0.1)
Rocky Mountain	40	7.6 (0.6)	10.8 (0.5)	12.9 (0.7)	1.1 (0.2)	1.1 (0.3)	1.0 (0.2)	66.5 (7.5)	60.6 (3.7)	64.2 (5.5)	24.8 (4.9)	15.5 (5.2)	3.6 (1.0)
Uncompahgre	30	1.9 (0.2)	2.7 (0.2)	2.4 (0.2)	1.1 (0.1)	1.1 (0.1)	1.3 (0.1)	9.0 (0.9)	13.2 (1.0)	13.6 (1.0)	7.6 (0.7)	8.3 (0.8)	1.8 (0.9)
Wild Horse	20	16.2 (1.3)	14.9 (1.4)	18.8 (1.2)	0.4 (0.1)	0.8 (0.2)	0.1 (0.1)	54.6 (4.5)	65.5 (8.0)	66.7 (3.6)	1.8 (0.9)	7.5 (2.0)	0.0 (0.0)
Wind Cave	20	6.5 (0.5)	7.4 (0.6)	6.8 (0.8)	2.2 (0.2)	2.8 (0.2)	3.2 (0.2)	36.7 (4.8)	36.7 (4.6)	31.2 (4.4)	22.1 (3.1)	28.4 (4.1)	29.1 (4.8)
Yellowstone	30	8.8 (0.6)	10.9 (0.6)	10.8 (0.5)	0.2 (0.1)	0.4 (0.1)	0.4 (0.1)	62.9 (6.0)	46.6 (3.5)	46.0 (3.5)	0.3 (0.1)	0.3 (0.1)	0.8 (0.4)
All areas‡	260	7.1 <sup>a</sup> (0.3)	8.3 <sup>b</sup> (0.3)	8.5 <sup>b</sup> (0.3)	0.9 (0.1)	1.1 (0.1)	0.9 (0.1)	40.1 (2.1)	38.6 (1.6)	37.1 (1.8)	8.4 (1.0)	7.5 (1.0)	5.4 (0.7)

† Number of subplots per treatment.

‡ Entries followed by different superscripts (a, b) indicate that native species richness was significantly different between grazed and ungrazed sites ( $F = 6.3$ ;  $df = 2, 777$ ;  $P < 0.002$ ) at  $\alpha = 0.05$  with Tukey's test.

## RESULTS

### Species richness, cover, and frequency

Plant species richness, cover, and frequency varied at multiple spatial scales throughout the study region. At the 1-m<sup>2</sup> scale, native species richness ranged from  $1.9 \pm 0.2$  species/m<sup>2</sup> in the ungrazed sites of the Uncompahgre area to  $18.8 \pm 1.2$  species/m<sup>2</sup> in the grazed sites of the Wild Horse area (Table 3). However, there were only a few consistent differences found between grazed and ungrazed sites in the number and cover of native and exotic species in any of the management areas. For example, native species richness in Grand Teton averaged  $8.8 \pm 0.6$  native species/m<sup>2</sup> (mean  $\pm$  1 SE) in exclosures, whereas grazed-adjacent plots averaged  $11.8 \pm 0.8$  and grazed-distant plots averaged  $10.1 \pm 0.9$  native species/m<sup>2</sup>. There also was consistently greater richness and cover of exotic species in grazed sites in Grand Teton compared to the ungrazed exclosures. The cover of native species was higher in the Yellowstone exclosures than in grazed sites, but the reverse was true of the Wild Horse area (Table 3).

For all of the management areas combined, the 1-m<sup>2</sup> subplots in exclosures had significantly fewer native species than both adjacent grazed sites and randomly selected grazed sites. On average, exotic species represented ~10–12% of the total number of species per square meter and 13% (grazed-distant plots) to 17% (ungrazed-exclosure plots) of the foliar cover. The cov-

er of exotic species in grazed-distant sites was almost significantly different from ungrazed sites ( $F = 2.3$ ,  $P < 0.07$ ). This relationship was heavily influenced by the 24.8% mean cover of exotic species in exclosures in Rocky Mountain National Park. Grazed and ungrazed sites did not differ significantly in exotic species richness or native species cover (Table 3).

Frequency distributions were used to compare the packing of native and exotic plant species in 1-m<sup>2</sup> subplots in grazed and ungrazed sites. In the study region (all 1-m<sup>2</sup> subplots combined), ungrazed sites tended to have lower native plant diversity than grazed sites (Fig. 2). The frequency distributions of exotic species were similar. The frequency distributions of grazed sites (i.e., grazed-adjacent and grazed-distant sites combined) were consistently different from the ungrazed sites for native and exotic species (Fig. 2).

In addition to the 1-m<sup>2</sup> "subplot" scale data, the nested-plot design allowed comparisons of grazed and ungrazed sites at the 1000-m<sup>2</sup> "plot" scale. Mean native species richness in 1000-m<sup>2</sup> plots ranged from  $9.0 \pm 2.0$  species/plot in the grazed sites of the Uncompahgre to  $50.0 \pm 9.0$  species/plot in the grazed sites of the Wild Horse area (Table 4). Mean exotic species richness in 1000-m<sup>2</sup> plots ranged from  $0.5 \pm 0.5$  species/plot in grazed and ungrazed sites of the Wild Horse area to  $8.5 \pm 0.5$  species/plot in the grazed sites of Bighorn Basin. The frequency of exotic species (out of 10 subplots in each plot) ranged from <10% in un-

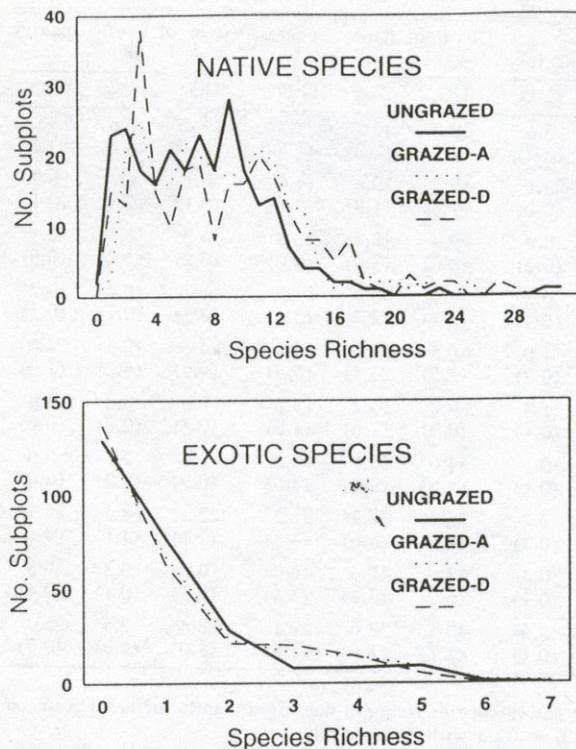


FIG. 2. The frequency distributions of native and exotic species richness in 1-m<sup>2</sup> subplots in ungrazed exclosures, grazed-adjacent sites, and grazed random points.

grazed plots at the Charles Russell area to 100% in grazed plots in Wind Cave, Uncompahgre, and Bighorn Basin areas (Table 4).

Also at the 1000-m<sup>2</sup> scale, many strong similarities were found between grazed and ungrazed plots (Table

4). For the 26 exclosure sites, native species richness in 1000-m<sup>2</sup> plots averaged  $31.5 \pm 2.5$  species/plot in exclosures compared to  $32.6 \pm 2.8$  species/plot in adjacent grazed sites and  $31.6 \pm 2.9$  species/plot in randomly selected grazed sites. There was variable, but slightly higher, species richness in grazed plots in the Rocky Mountain, Grand Teton, Gunnison, Wild Horse, and Bighorn Basin areas, but it was inconsistent at other areas. Surprisingly, mean exotic species richness and frequency were essentially the same for ungrazed plots as for adjacent and distant grazed plots (Table 4).

At the 1000-m<sup>2</sup> scale, exotic species richness was positively correlated to native species richness at the  $P = 0.1$  level of significance, but little of the variation was explained ( $F = 3.0$ ;  $r^2 = 0.04$ ,  $df = 76$ ). Exotic species frequency was strongly correlated with exotic species richness ( $F = 74.4$ ;  $r^2 = 0.49$ ,  $P < 0.001$ ). For the 59 plots with exotic species in them, exotic species frequency was positively and significantly correlated with native species richness, but little variation was explained ( $F = 486$ ;  $r^2 = 0.08$ ,  $P < 0.03$ ).

#### Species composition, diversity, and evenness

On average, the species lists of the long-ungrazed exclosures and adjacent grazed 1000-m<sup>2</sup> plots overlapped by  $57.9 \pm 2.8\%$  (Fig. 3). Species composition overlap was similar between the exclosure plots and grazed-distant plots, and between the grazed-adjacent and grazed-distant plots. The distance between plots within each sampling area had a significant effect on species composition overlap. For all pairs of plots for each exclosure, species composition overlap significantly decreased with increasing distance apart (Fig. 4). Thus, the species lists of any two 1000-m<sup>2</sup> plots only 100 m apart would be expected to overlap just

TABLE 4. Mean (1 SE in parentheses) number of native and exotic species in 1000-m<sup>2</sup> plots and frequency of exotic species (in 10 1-m<sup>2</sup> subplots) in ungrazed exclosures (UG), grazed-adjacent (G-A), and grazed-distant (G-D) plots in nine study sites.

Site	No. exclosures	No. native species			No. exotic species			Freq. of exotic spp.		
		UG	G-A	G-D	UG	G-A	G-D	UG	G-A	G-D
Bighorn Basin	2	26.5 (2.5)	28.5 (0.5)	29.5 (3.5)	7.0 (0.0)	7.0 (1.0)	8.5 (0.5)	10.0 (0.0)	10.0 (0.0)	10.0 (0.0)
Charles Russell	5	20.8 (4.8)	21.2 (3.7)	17.6 (3.0)	1.8 (0.7)	0.8 (0.4)	0.8 (0.4)	0.8 (0.8)	1.2 (0.6)	1.0 (0.8)
Grand Teton	2	34.5 (0.5)	40.5 (2.5)	40.5 (3.5)	2.5 (2.5)	4.0 (2.0)	3.5 (1.5)	0.5 (0.5)	2.5 (2.5)	2.5 (2.5)
Gunnison	3	33.0 (1.7)	34.7 (0.9)	33.7 (2.7)	1.3 (0.3)	1.7 (0.3)	1.0 (0.0)	6.0 (1.7)	4.3 (0.9)	2.7 (0.9)
Rocky Mountain	4	40.8 (3.1)	44.2 (5.8)	44.5 (7.1)	4.2 (1.2)	3.8 (2.2)	4.2 (0.9)	6.2 (1.9)	3.8 (2.2)	6.8 (0.6)
Uncompahgre	3	9.3 (1.2)	9.0 (2.0)	9.3 (0.3)	3.0 (0.0)	3.0 (0.6)	3.7 (0.7)	9.7 (0.3)	10.0 (0.0)	10.0 (0.0)
Wild Horse	2	45.2 (5.5)	50.0 (9.0)	49.0 (7.0)	0.5 (0.5)	1.0 (1.0)	0.5 (0.5)	3.5 (3.5)	5.0 (5.0)	0.5 (0.5)
Wind Cave	2	41.5 (1.5)	35.5 (4.5)	33.0 (11.0)	6.0 (1.0)	7.5 (0.5)	7.0 (0.0)	10.0 (0.0)	10.0 (0.0)	10.0 (0.0)
Yellowstone	3	42.7 (3.5)	41.3 (6.5)	40.7 (6.4)	3.0 (1.5)	1.7 (0.9)	3.3 (1.3)	2.3 (1.5)	4.0 (2.0)	3.3 (0.9)
All areas	26	31.5 (2.5)	32.6 (2.8)	31.6 (2.9)	3.1 (0.5)	3.0 (0.6)	3.2 (0.5)	5.0 (0.8)	5.0 (0.8)	4.8 (0.8)

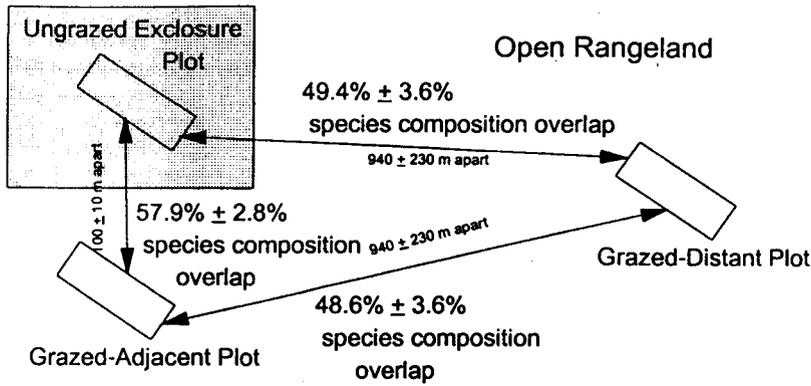


FIG. 3. Schematic diagram and mean ( $\pm 1$  SE) species composition overlap among ungrazed enclosures, grazed-adjacent sites, and grazed-distant sites.

58.3%, on average, regardless of the grazing regime. For the pairs of grazed plots accompanying each enclosure, species composition overlap also significantly decreased with distance ( $J = -0.14 \times \log_{10}[\text{distance in meters apart}] + 0.86$ ;  $r^2 = 0.17$ ,  $df = 24$ ,  $P < 0.04$ ). About 28% of the variance in species composition overlap between enclosure plots and distant grazed plots could be attributed to the distance between them ( $J = -0.18 \times \log_{10}[\text{distance in meters apart}] + 0.99$ ;  $r^2 = 0.278$ ,  $df = 24$ ,  $P < 0.006$ ).

For all management areas combined, there were no significant differences between grazed and ungrazed plots in diversity or evenness, although mean diversity values were greater by about one dominant species per plot in grazed sites (Table 5). Mean  $N1$  diversity index values ranged from  $23.5 \pm 5.1$  for grazed plots at Wild Horse to  $2.8 \pm 0.1$  in ungrazed plots in the Uncompahgre area. Mean  $N2$  diversity index values were consistently lower than  $N1$  values for all areas except the Charles Russell and the grazed-distant plots at Wild Horse. Evenness values ranged from  $1.2 \pm 0.4$  for ungrazed plots at the Charles Russell to  $0.5 \pm 0.01$  at the Gunnison area. Four management units (Grand Teton, Wind Cave, Rocky Mountain, and Uncompahgre) had slightly higher plant diversity in grazed sites, whereas three management areas (Charles Russell, Gunnison,

and Bighorn Basin (by  $N1$ ) had slightly lower plant diversity in grazed sites. Only two management areas (Wind Cave and Rocky Mountain) had consistently higher evenness in grazed sites (Table 5).

*Species-specific responses to grazing*

Few plant species showed consistent, directional responses to grazing or cessation from grazing. Examples

TABLE 5. Mean (1 SE in parentheses) Hill's diversity index values ( $N1$  and  $N2$  species equivalents) and mean (1 SE in parentheses) modified Hill's ratio for evenness ( $E5$ ) in ungrazed (UG), grazed-adjacent (G-A), and grazed-distant (G-D) 1000-m<sup>2</sup> plots.

Area	Type	$N1$	$N2$	$E5$
Bighorn Basin	UG	11.8 (0.2)	10.0 (0.3)	0.83 (0.04)
	G-A	11.7 (2.2)	10.5 (4.3)	0.84 (0.23)
	G-D	10.7 (1.0)	8.2 (2.6)	0.72 (0.19)
Charles Russell	UG	6.6 (1.6)	8.8 (4.2)	1.22 (0.36)
	G-A	5.8 (1.4)	6.4 (2.8)	0.99 (0.22)
	G-D	4.6 (0.6)	7.0 (2.4)	1.48 (0.53)
Grand Teton	UG	9.7 (1.4)	7.2 (1.1)	0.72 (0.02)
	G-A	16.3 (1.1)	15.8 (0.1)	0.98 (0.07)
	G-D	11.0 (4.3)	7.3 (2.8)	0.62 (0.01)
Gunnison	UG	6.9 (0.4)	4.6 (0.3)	0.61 (0.04)
	G-A	6.3 (1.0)	3.9 (0.7)	0.52 (0.04)
	G-D	6.4 (1.0)	3.8 (0.4)	0.52 (0.01)
Rocky Mountain	UG	10.6 (2.7)	8.3 (2.8)	0.68 (0.11)
	G-A	15.5 (2.4)	12.5 (2.8)	0.78 (0.05)
	G-D	16.4 (3.2)	15.6 (4.2)	0.87 (0.15)
Uncompahgre	UG	2.8 (0.1)	2.6 (0.1)	0.87 (0.06)
	G-A	4.3 (0.6)	4.0 (0.6)	0.92 (0.01)
	G-D	3.4 (0.3)	2.9 (0.3)	0.80 (0.02)
Wild Horse	UG	18.1 (2.8)	16.4 (1.2)	0.91 (0.08)
	G-A	16.4 (4.5)	14.1 (4.7)	0.83 (0.06)
	G-D	23.5 (5.1)	23.5 (6.1)	0.99 (0.05)
Wind Cave	UG	7.7 (1.1)	5.1 (0.8)	0.60 (0.03)
	G-A	9.1 (1.4)	6.8 (0.9)	0.73 (0.02)
	G-D	10.2 (2.9)	8.0 (1.9)	0.77 (0.04)
Yellowstone	UG	11.7 (1.7)	8.9 (1.5)	0.73 (0.06)
	G-A	11.1 (2.6)	8.7 (3.3)	0.70 (0.12)
	G-D	12.1 (2.4)	10.1 (2.6)	0.79 (0.12)
All areas	UG	9.0 (0.9)	7.8 (1.1)	0.83 (0.08)
	G-A	10.1 (1.1)	8.7 (1.1)	0.82 (0.05)
	G-D	10.2 (1.3)	9.3 (1.4)	0.90 (0.11)

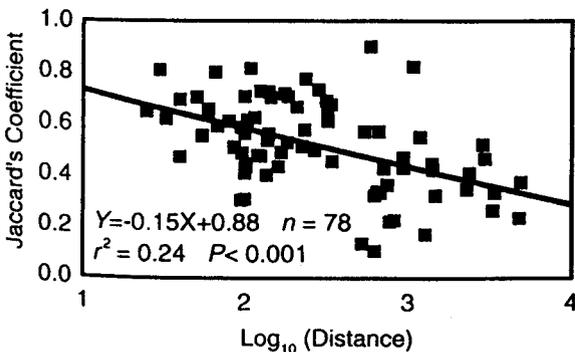


FIG. 4. Relationship of species composition overlap ( $J$ ) and distance between the plots (within a management area).

TABLE 6. The top four dominant plant species and their percentage cover, inside (in) and outside (out) wildlife exclosures and at distant points (dist) at the study site exclosure areas. Species in boldface type are introduced exotic species.

Site and exclosure	Location	Species 1		Species 2		Species 3		Species 4	
		Code	% Cover						
<b>Bighorn Basin</b>									
Paint Rock 1	in	<b>Poa pra</b>	10.2	Art tri	7.0	<b>Bro tec</b>	5.6	Agr spi	3.2
	out	Gri squ	19.6	<b>Bro tec</b>	11.5	<b>Poa pra</b>	5.2	Sti let	3.5
	dist	Agr spi	8.7	Gut sar	7.3	Sti com	5.3	<b>Bro tec</b>	3.8
Paint Rock 2	in	Agr spi	11.4	<b>Poa pra</b>	8.3	Sti com	7.3	<b>Bro tec</b>	5.8
	out	Gri squ	5.8	<b>Bro tec</b>	5.2	Agr spi	4.5	Chr vil	4.2
	dist	<b>Bro tec</b>	20.5	Agr spi	5.7	Chr vil	5.2	Ant sp.	2.6
<b>Yellowstone</b>									
Blacktail	in	Fes ida	9.5	Agr spi	7.5	Art tri	7.5	Lup ser	5.2
	out	Sti ric	19.3	Agr spi	10.9	Ger vis	5.0	Fes occ	2.9
	dist	Sti com	6.4	Art tri	5.0	Lup ser	4.6	Fes occ	3.9
Lamar	in	Art tri	15.8	Sym occ	12.0	Agr spi	4.7	Pru vir	4.1
	out	Koe nit	7.0	Ast mis	2.6	Fes ida	2.4	Sol mis	2.1
	dist	Art tri	10.9	Agr spi	6.0	Lup ser	4.7	Fes ida	4.5
Junction Butte	in	Fes ida	24.6	Ely cin	9.9	Art tri	8.7	Chr nau	5.0
	out	Lup ser	23.3	Art tri	12.0	Fes ida	4.6	Gut sar	3.1
	dist	Sti ric	22.4	Art tri	11.8	Lup ser	5.6	Pen pro	4.6
<b>Wind Cave</b>									
Campground	in	<b>Poa pra</b>	21.8	Amo can	8.0	Ros ark	6.8	Art tri	4.8
	out	<b>Poa pra</b>	19.7	Sti com	12.6	Agr sp.	7.3	<b>Bro jap</b>	6.9
	dist	<b>Poa pra</b>	16.5	Ele sp.	8.0	<b>Bro jap</b>	8.0	Amo can	6.5
Cottonwood	in	Pso ten	22.3	<b>Poa pra</b>	15.4	<b>Bro jap</b>	5.1	Tra bra	5.1
	out	<b>Bro jap</b>	14.1	Pso ten	13.2	<b>Poa pra</b>	13.0	Sym occ	4.2
	dist	<b>Poa pra</b>	13.6	Pso ten	12.6	Mel off	9.6	<b>Bro jap</b>	6.3

Notes: Species codes (including Table 2): Agr smi and Agr spi, *Agropyron smithii* and *A. spicatum*; Amo can, *Amorpha canescens*; Ant sp., *Antennaria* sp.; Art lud and Art tri, *Artemisia ludoviciana* and *A. tridentata*; Ast mis, *Astragalus miser*; Atr con, *Atriplex confertifolia*; Bro jap and Bro tec, *Bromus japonicus* and *B. tectorum*; Chr vil, *Chrysopsis villosa*; Chr nau, *Chrysothamnus nauseosa*; Ele sp., *Eleocharis* sp.; Ely cin and Ely sp., *Elymus cinereus* and *E. sp.*; Fes ida and Fes occ, *Festuca idahoensis* and *F. occidentalis*; Ger vis, *Geranium viscosissimum*; Gri squ, *Grindelia squarrosa*; Gut sar, *Gutierrezia sarothrae*; Hil jam, *Hilaria jamesii*; Koe nit, *Koeleria nitida*; Lup ser, *Lupinus sericeus*; Mel off, *Melilotus officinalis*; Pen pro, *Penstemon procerus*; Phl hoo, *Phlox hoodii*; Pin fle, *Pinus flexilis*; Poa pra, *Poa pratensis*; Pop tre, *Populus tremuloides*; Pru vir, *Prunus virginiana*; Pso ten, *Psoralea tenuiflora*; Ros ark, *Rosa arkansana*; Sol mis, *Solidago missouriensis*; Sti com, *Stipa comata*, *S. lettermannii*, and *S. richardsonii*; Sym occ, *Symphoricarpos occidentalis*; Tra bra, *Tradesantia bracteata*.

of dominant species cover from Yellowstone, Bighorn Basin, and Wind Cave show highly inconsistent responses to grazing (Table 6). For example, *Festuca idahoensis* was the dominant species inside the Blacktail and Junction exclosures in Yellowstone, with 9.5% and 24.6% cover, respectively. The species had much lower foliar cover in grazed plots near those exclosures. However, for the Lamar site, cover of *Festuca idahoensis* was higher in grazed plots relative to ungrazed plots. Typical of the response by most species in all management units, the cover of *Agropyron spicatum* varied greatly at the three exclosure sites at Yellowstone, with inconsistent patterns in grazed or ungrazed plots.

The cover of *Agropyron spicatum* at Bighorn Basin was also variable. It averaged 11.4–3.8% cover inside exclosures, 4.5% to <3.5% in adjacent plots, and 8.7–5.7% at the random points. The cover of the native species *Grindelia squarrosa* (curly-cup gum weed), was low in ungrazed plots and grazed-distant plots, but high in grazed-adjacent plots. The cover of another exotic grass, *Bromus tectorum* (cheatgrass), was also highly variable in the Bighorn Basin area, due to patchy distributions.

The exotic, sod-forming Kentucky bluegrass, *Poa pratensis*, was one of the few dominant species with a consistent pattern: it had higher cover in ungrazed plots at Bighorn Basin and Wind Cave. In contrast, the foliar cover of the exotic annual grass, *Bromus japonicus*, was as much as three times greater in sites grazed by bison, elk, and deer than in ungrazed plots. The frequency (number of 1-m<sup>2</sup> subplots) of *Bromus japonicus* was nearly twice as great in grazed vs. ungrazed plots.

For all management areas, the four dominant species at the exclosure sites were different for each exclosure, adjacent plot, and randomly selected plot. Where plots had species in common, they often switched the order of dominance and were variable in cover. Patchy shrub species (e.g., *Artemisia tridentata*) and locally rare species had even more inconsistent patterns between grazed and ungrazed sites.

#### Responses of plant life-forms

We found variable, insignificant differences in life-form composition between grazed and ungrazed plots in each management area (Table 7). For example, the cover of forbs was consistently higher in grazed than in ungrazed plots in four of nine management areas,

TABLE 7. Mean (1 SE in parentheses) life-form cover (%), and mean bare ground (%) by management area and grazing regime (UG, ungrazed; G-A, grazed-adjacent; G-D, grazed-distant).

Area	Type	Forb cover	Grass cover	Shrub cover	Bare ground
Bighorn Basin	UG	12.0 (0.8)	28.2 (7.2)	6.8 (2.8)	52.1 (8.8)
	G-A	25.6 (7.4)	20.6 (2.9)	0.6 (0.4)	54.3 (7.8)
	G-D	14.0 (3.0)	29.0 (4.1)	4.2 (3.0)	50.2 (2.4)
Charles Russell	UG	2.6 (0.7)	10.9 (2.5)	4.7 (1.2)	79.8 (5.6)
	G-A	2.1 (0.6)	11.5 (2.3)	7.0 (4.1)	74.9 (6.2)
	G-D	1.6 (0.7)	7.5 (3.3)	4.8 (3.1)	80.7 (8.4)
Grand Teton	UG	11.9 (3.0)	14.2 (4.8)	32.1 (4.3)	59.2 (33.4)
	G-A	25.8 (6.9)	17.4 (7.6)	13.1 (4.8)	78.4 (12.4)
	G-D	24.4 (10.7)	15.8 (3.0)	23.5 (3.0)	85.0 (28.8)
Gunnison	UG	6.3 (2.1)	12.4 (0.7)	21.4 (2.7)	57.1 (2.0)
	G-A	7.4 (0.5)	6.9 (0.6)	24.6 (3.9)	44.0 (18.2)
	G-D	5.4 (1.0)	5.3 (1.0)	20.8 (3.7)	67.5 (2.6)
Rocky Mountain	UG	39.5 (18.2)	46.1 (8.3)	26.8 (11.4)	...
	G-A	32.8 (5.9)	34.8 (10.6)	10.0 (6.1)	...
	G-D	26.4 (5.2)	29.7 (12.4)	10.8 (4.5)	...
Uncompahgre	UG	0.9 (0.2)	16.5 (2.7)	0.6 (0.3)	82.2 (1.9)
	G-A	2.2 (0.3)	16.1 (1.1)	2.6 (0.6)	78.8 (1.2)
	G-D	2.5 (1.0)	19.1 (0.5)	0.4 (0.1)	76.5 (2.7)
Wild Horse	UG	40.6 (7.2)	15.8 (2.6)	0.0 (0.0)	35.3 (10.5)
	G-A	45.6 (12.4)	27.2 (7.2)	0.0 (0.0)	29.2 (9.6)
	G-D	47.3 (1.8)	18.5 (1.5)	0.0 (0.0)	36.4 (5.6)
Wind Cave	UG	10.1 (1.7)	29.1 (3.8)	19.1 (3.8)	51.6 (1.2)
	G-A	4.6 (0.6)	47.2 (12.6)	12.4 (5.4)	53.9 (18.0)
	G-D	10.9 (2.4)	35.3 (9.1)	14.3 (1.7)	66.6 (10.8)
Yellowstone	UG	14.5 (1.2)	23.2 (7.4)	21.9 (8.0)	61.3 (5.6)
	G-A	19.0 (5.1)	20.5 (8.6)	7.4 (3.9)	66.2 (21.5)
	G-D	9.8 (3.3)	23.1 (3.1)	10.8 (2.6)	59.4 (13.5)
All areas	UG	14.8 (3.8)	21.9 (2.8)	14.6 (2.9)	53.7 (5.8)
	G-A	16.6 (3.1)	21.2 (3.0)	8.9 (1.9)	52.8 (6.3)
	G-D	13.9 (2.8)	19.1 (2.7)	9.5 (1.8)	57.3 (6.1)

lower in two management areas, and inconsistent in three management areas. For percentage of bare ground, five of nine management areas had similar or inconsistent values for grazed and ungrazed plots. The frequency of forbs in 1-m<sup>2</sup> subplots was consistently higher in grazed plots (adjacent = 15.1 ± 1.6%, distant plots = 13.8 ± 1.7%) vs. ungrazed plots (12.9 ± 1.5%). The frequency of grasses in 1-m<sup>2</sup> subplots also was consistently higher in grazed plots (adjacent = 6.6 ± 0.5%, distant plots = 6.8 ± 0.5%) compared to ungrazed plots (6.3 ± 0.5%). In contrast, the frequency of shrubs in 1-m<sup>2</sup> subplots was consistently lower in grazed plots (adjacent = 2.3 ± 0.3%, distant plots = 2.1 ± 0.4%) compared to ungrazed plots (2.7 ± 0.4%). However, none of the frequency means was significantly different between grazed and ungrazed plots.

Some management areas had more consistent patterns of life-form changes than others. Grazed plots in Grand Teton National Park, for example, had consistently higher cover and frequency of forbs and grasses, more bare ground, and lower cover and frequency of shrubs compared to ungrazed plots (Table 7; frequencies not shown). Grazed plots in the Rocky Mountain area had consistently lower cover of forbs, grasses, and shrubs, but higher frequency of forbs and grasses than

did ungrazed plots. In the Yellowstone, Grand Teton, Rocky Mountain, and Bighorn Basin areas, and for all management areas combined, forb and grass frequency increased as shrub frequency decreased in grazed plots. Still, none of the comparisons of life-form composition differed significantly between grazed and ungrazed plots, and similarities and inconsistencies dominated most comparisons (Table 7).

#### Soil and climate characteristics

Soil texture (percentages of sand, silt, and clay) and soil fertility (percentages of N and C) did not vary significantly between grazed and ungrazed plots (Table 8). However, soil characteristics varied greatly among management areas. For example, mean percentage of sand varied from <30% in the Charles Russell area to >65% in Rocky Mountain. Mean soil N ranged from 9–10% in Uncompahgre to >25% in Wind Cave. Mean soil percentage of C also varied considerably within the study region.

Although the differences in vegetation and soils characteristics between grazed and ungrazed plots were minimal, soil characteristics and elevation were strongly correlated with plant diversity in the study region (Table 9). For the 78 1000-m<sup>2</sup> plots, 59.4% of the vari-

TABLE 8. Soil characteristics (top 15 cm) by grazing regime (UG, ungrazed; G-A, grazed-adjacent; G-D, grazed-distant) for the management areas.

Management area	Grazing regime	Sand (%)	Silt (%)	Clay (%)	N (%)	C (%)
Bighorn Basin	UG	41.0 (1.3)	25.3 (2.1)	33.6 (0.8)	0.32 (0.04)	4.01 (0.44)
	G-A	45.6 (5.1)	20.4 (3.3)	34.0 (1.8)	0.25 (0.03)	2.44 (0.16)
	G-D	50.5 (0.4)	18.9 (0.3)	30.6 (0.1)	0.25 (0.10)	2.84 (1.46)
Charles Russell	UG	17.2 (5.2)	26.0 (1.5)	56.0 (5.8)	0.21 (0.01)	1.87 (0.18)
	G-A	14.5 (6.4)	22.7 (4.1)	62.8 (9.4)	0.18 (0.02)	1.44 (0.17)
	G-D	27.7 (8.5)	24.0 (2.1)	48.3 (8.7)	0.18 (0.01)	1.55 (0.09)
Grand Teton	UG	55.2 (10.6)	21.0 (3.8)	23.7 (6.8)	0.14 (0.01)	2.19 (0.88)
	G-A	56.2 (5.6)	20.9 (0.1)	22.8 (5.7)	0.13 (0.03)	1.01 (1.09)
	G-D	53.0 (7.6)	22.4 (3.2)	24.6 (4.4)	0.06 (0.10)	1.40 (1.49)
Gunnison	UG	50.2 (3.5)	16.6 (3.9)	33.3 (7.1)	0.10 (0.01)	1.19 (0.12)
	G-A	53.8 (5.8)	15.1 (2.3)	31.1 (5.3)	0.10 (0.02)	0.95 (0.09)
	G-D	52.4 (1.0)	4.2 (3.6)	43.4 (4.3)	0.11 (0.02)	1.23 (0.23)
Rocky Mountain	UG	71.2 (4.1)	17.9 (3.2)	11.0 (0.9)	0.14 (0.06)	2.20 (0.79)
	G-A	66.8 (6.7)	19.2 (2.7)	14.0 (4.2)	0.22 (0.11)	3.42 (1.24)
	G-D	69.5 (1.7)	15.4 (0.5)	15.1 (1.8)	0.14 (0.06)	3.42 (1.36)
Uncompahgre	UG	53.9 (1.3)	2.3 (1.2)	44.0 (0.5)	0.09 (0.01)	2.49 (0.35)
	G-A	48.9 (1.4)	8.8 (0.4)	42.9 (1.7)	0.10 (0.01)	2.13 (0.16)
	G-D	51.4 (1.2)	0.4 (0.4)	50.3 (0.5)	0.10 (0.01)	2.56 (0.26)
Wild Horse	UG	27.9 (2.9)	21.0 (8.1)	51.1 (10.9)	0.28 (0.04)	2.82 (0.38)
	G-A	25.0 (7.4)	27.7 (0.7)	47.3 (6.7)	0.42 (0.08)	4.10 (0.89)
	G-D	25.6 (3.6)	27.1 (0.8)	47.4 (4.4)	0.24 (0.04)	2.72 (0.48)
Wind Cave	UG	35.7 (5.2)	30.6 (0.9)	33.7 (6.1)	0.26 (0.06)	2.74 (0.80)
	G-A	35.3 (2.6)	31.0 (6.1)	33.7 (3.5)	0.28 (0.10)	3.08 (1.17)
	G-D	36.7 (8.6)	36.0 (8.5)	27.2 (0.1)	0.26 (0.06)	2.84 (0.91)
Yellowstone	UG	50.9 (2.5)	28.3 (1.4)	20.8 (2.5)	0.27 (0.05)	3.02 (0.37)
	G-A	50.4 (3.6)	29.9 (1.4)	19.7 (3.4)	0.47 (0.09)	5.79 (1.21)
	G-D	64.1 (12.2)	14.2 (7.9)	21.7 (4.8)	0.29 (0.04)	3.40 (0.53)
All areas	UG	44.4 (3.9)	20.8 (1.8)	34.7 (3.4)	0.19 (0.02)	2.24 (0.20)
	G-A	43.1 (3.9)	21.2 (1.6)	35.7 (3.8)	0.23 (0.03)	2.65 (0.38)
	G-D	48.1 (3.7)	17.2 (2.3)	34.9 (3.2)	0.18 (0.02)	2.41 (0.28)

TABLE 9. Results of stepwise multiple linear regressions and simple regressions of plant richness, cover, and frequency and soil characteristics.

Dependent variable and predictors	Coefficient	<i>t</i>	<i>P</i>	<i>R</i> <sup>2</sup>	df	<i>F</i>	<i>P</i>
<b>Multiple regressions</b>							
Total species				0.594	3, 74	36.06	<0.001
Constant	-6.479	-1.326	0.019				
Total cover	0.110	2.104	0.039				
Soil percentage silt	0.647	5.107	0.001				
Elevation	0.012	5.084	0.001				
Native species cover				0.571	3, 74	32.795	<0.001
Constant	-26.178	-2.969	0.004				
No. native species	0.507	2.279	0.026				
Soil percentage silt	0.044	1.668	0.100				
Elevation	0.023	4.864	0.001				
No. exotic species				0.150	2, 75	6.60	<0.002
Constant	3.689	4.537	0.001				
Soil percentage clay	-0.046	-2.919	0.005				
Log <sub>10</sub> percentage N	13.876	2.079	0.041				
Log <sub>10</sub> exotic species cover				0.128	3, 74	3.623	<0.017
Constant	1.087	4.029	0.001				
Log <sub>10</sub> percentage N	2.827	1.860	0.067				
No. native species	-0.011	-2.156	0.034				
Soil percentage clay	-0.011	-2.878	0.005				
Frequency of exotic species				0.193	5, 72	3.436	<0.008
Constant		0.526	0.601				
Log <sub>10</sub> percentage N	27.690	2.397	0.019				
No. native species	-0.078	-1.782	0.079				
Native species cover	-0.056	-2.240	0.028				
Soil percentage sand	0.047	1.524	0.132				
Elevation	0.002	2.126	0.037				
<b>Simple regressions</b>							
Log <sub>10</sub> exotic species				0.129		11.25	
Constant	0.213	1.849	0.068				
Total cover	0.007	3.354	0.001				
Total cover				0.065		5.252	
Constant	35.029	5.092	0.001				
Log <sub>10</sub> N	180.776	2.292	0.025				
Exotic species cover				0.054		4.316	
Constant	2.167	0.783	0.436				
Log <sub>10</sub> N	65.939	2.078	0.041				

ance in total species richness was explained by percentage of silt, elevation, and total foliar cover ( $F_{3,74} = 36.1$ ,  $P < 0.001$ ). Total foliar cover was, in turn, significantly positively correlated with soil percentage of N ( $\log_{10}N$ ;  $r = 0.36$ ,  $F = 5.3$ ,  $P < 0.025$ ). About 58% of the variance in native plant species richness could be explained by percentage of silt and elevation ( $F_{2,75} = 51.5$ ,  $P < 0.001$ ). Grazed and ungrazed plots behaved similarly using the same model, with 51.4% (ungrazed) and 66.1% (grazed-distant) of the variance explained. The model used to predict native species cover performed equally well for grazed and ungrazed plots, with 57.2% to 67.2% of the variance explained.

The regression models explained less variance for exotic species diversity in the study region. About 13% of the variance in exotic species cover ( $\log_{10}cover$ ) was explained by percentage of clay, native species richness, and  $\log_{10}N$  ( $F_{3,74} = 3.6$ ,  $P = 0.017$ ). Exotic species

frequency (in 1-m<sup>2</sup> subplots) and foliar cover were also significantly positively correlated to soil percentage of N (Table 9).

For the nine management units in four states, species richness and cover were strongly linked to climate. Mean exotic species cover was positively correlated with mean maximum January temperature ( $r = 0.62$ ,  $P = 0.07$ ,  $n = 9$ ). Total plant cover was significantly negatively correlated with mean maximum July temperature ( $r = -0.50$ ,  $P = 0.019$ ), and total species richness was significantly positively correlated with total plant cover ( $r = 0.78$ ,  $P = 0.013$ ,  $n = 9$ ).

#### DISCUSSION

We acknowledge several assumptions and caveats of the present study. Ours is an observational study, and the "effects of grazing" are not directly measured on vegetation or soils. The primary assumptions of exoc-

sure studies are that: (1) the vegetation and soils were initially similar on the grazed and ungrazed plots; and (2) vegetation and soil differences measured in subsequent years are presumed to be caused primarily by grazing in the grazed plots and by cessation of grazing in exclosed sites. It was reassuring to find similar soil textures and total percentages of N and C in grazed and ungrazed plots (Table 8) as a more consistent basis for assessing differences in vegetation among treatments. However, we realize (and our data strongly confirm) that no two sites are botanically identical, grazing is inherently heterogeneous, and current vegetation patterns represent a complex response to site-specific environmental factors, historic land uses, and species-specific responses to many natural processes. Still, because soil characteristics among treatments were similar, the long-term exclosures should have shown any differences in plant diversity between ungrazed and grazed plots due to cessation of grazing and continued grazing, respectively.

We measured each site only once. Most of our grassland sites peak in biomass and plant species richness simultaneously in the early summer. However, we may have missed some early- or late-season plant species in a few of the dry sites (e.g., Uncompahgre, Charles Russell) and some plant species that occur in atypically wet or dry years. In any case, the sets of three plots in grazed and ungrazed sites at each exclosure were measured within two days of each other, providing a valid comparison of the main grazing effect. We are confident that many of the problems of previous exclosure studies were overcome by using consistent vegetation and soils sampling methods, larger sampling areas, additional randomly placed plots in grazed sites, and increased replication. The broad generalizations that follow stem from the overwhelming similarities that we found, rather than from the exaggerated differences that we expected.

#### *Broad generalizations*

*Grazing probably has little effect on native species richness at landscape scales in these Rocky Mountain grasslands.*—We hypothesized that native species richness would be lower in exclosures than in grazed plots, due to competitive exclusion in the absence of grazing. The average age of  $31.2 \pm 2.5$  yr old for the exclosures should have allowed ample time for succession and the sequestering of dominance by a few highly competitive species (e.g., Grime 1973, Harper 1977). At the 1-m<sup>2</sup> scale, there was significantly lower richness of native species in ungrazed exclosures than in grazed sites (Table 3), a difference of  $\sim 1.5$  species/m<sup>2</sup> (<20% difference). However, as the spatial scale increased to 1000-m<sup>2</sup> plots, the differences between grazed and ungrazed sites were radically reduced. At the 1000-m<sup>2</sup> scale, mean native species richness differed between long-ungrazed and grazed plots by only 0.3–3.5% (Table 4). Thus, higher native species richness in grazed sites at

the 1-m<sup>2</sup> scale can be attributed to higher species packing, with locally common plant species filling open sites throughout the 1000-m<sup>2</sup> plots in grazed sites. Because species richness was nearly identical at the larger plot scales (1000-m<sup>2</sup> plots), species richness is probably unaffected by grazing at landscape scales in these vegetation types.

Studies in other habitats have shown decreases in species richness on grazed sites (Rummell 1951, pine habitat; Reynolds and Trost 1980, sagebrush desert). Some studies in other habitats have shown increases in species richness following a cessation of grazing (Winegar 1977, riparian habitat; Chew 1982, desert grassland vegetation), whereas some have shown no major differences (Evanko and Peterson 1955, habitats similar to those of our sites; Smeins et al. 1976, drier sites in Texas; Cid et al. 1991, habitats similar to our sites; Hughes 1996, drier sites in Arizona). Some studies have shown decreases in species richness at small scales, but little change at larger scales (Collins and Adams 1983, prairie sites in Kansas; Facelli et al. 1989, wetter sites in Argentina; see Tables 3 and 4).

There are several possible mechanisms that may maintain similar species richness in grazed and ungrazed sites. It may be that 31 years, on average, is not long enough for competitive exclusion to be demonstrated. This seems highly unlikely, given that 12 years was long enough to show drastic reductions in species richness in the Serengeti (McNaughton 1983), and 13 years was long enough to show major changes in life-form composition in old-field succession in tallgrass prairie in Oklahoma (Collins and Adams 1983). Still, the moderate-to-high diversity of species in many management units should have allowed for some highly competitive species to dominate exclosure sites (Horn 1975, Connell 1978, Fox 1979). In most management areas, we also observed an equally rich variety of growth forms (tall perennial shrubs to short annual herbs), functional groups (C3 and C4 grasses), and physiological types (rhizomatous types, obligate seeders). It may be that grazing at current and past levels is not as strong a regulator of species richness in Rocky Mountain grasslands as it is in other areas (e.g., the Serengeti; McNaughton 1979). These grasslands may lack dominant competitors, with or without grazing, or they may be controlled more by belowground competition than by aboveground interactions (see Milchunas et al. 1988). Another possibility is that local extinction and immigration rates are similar in grazed and ungrazed sites in Rocky Mountain grasslands. Gibson and Brown (1991) showed that sheep grazing increased species' colonization rates, but local extinction rates were similar on grazed and ungrazed sites of British limestone grassland. Glenn and Collins (1992) found that grazing had little impact on immigration and extinction rates of plant species in tallgrass prairies in Kansas, and the same may be true in Rocky Mountain grasslands.

*Grazing probably has little effect on the accelerated spread of most exotic plant species at landscape scales.*—We also hypothesized that grazed plots would have higher exotic species richness and cover than ungrazed sites, due to disturbances associated with grazing (i.e., greater bare ground and the intermediate-disturbance hypothesis) and the typical claim that grazing may accelerate weed invasion. Again, we assumed that the vegetation and soils were initially similar on the grazed and ungrazed plots prior to the construction of the exclosures. The similarities in soil characteristics (Table 8), exotic species richness, cover, and frequency (Tables 3 and 4) between pairs of grazed plots in this study support this assumption. At the 1-m<sup>2</sup> scale, the number and cover of exotic species were similar in grazed and ungrazed sites (Table 3). The ungrazed plots consistently had slightly higher cover of exotic species, but this was due primarily to Rocky Mountain National Park, where control efforts may have reduced the cover of exotic species in some of the grazed sites (J. Connor, National Park Service, *personal communication*). At the 1000-m<sup>2</sup> scale, mean exotic species richness between long-ungrazed and grazed plots differed by <3.5% (Table 4). Of the nine study areas that we examined, only Wind Cave National Park had consistently higher exotic species richness in grazed than ungrazed sites. Likewise, the frequency of exotic species was extremely similar between grazed and ungrazed plots (Table 4). Thus, assuming similar pre-exclosure conditions in the study sites, there is very little evidence that either continuous grazing at current levels or cessation from grazing radically alters exotic species richness, cover, or frequency in these vegetation types. In another study, we showed that long-term grazing by cattle in the shortgrass steppe of Colorado resulted in little invasion by weeds (Stohlgren et al. 1999).

Other studies in various habitats have shown that exotic plant species invade sites with or without grazing. In mixed prairie in North Dakota, the cover of *Poa pratensis* inside an exclosure increased from 0% in 1916 to 56% in 1994 (Frank et al. 1995). The cover of *Poa pratensis* in grazed sites was 29% in moderately grazed sites and 0% in heavily grazed sites, but it may have been undersampled with 10 1-m<sup>2</sup> plots per treatment. Schulz and Leininger (1990) reported that *Poa pratensis* cover was greater in grazed riparian sites, whereas *Poa palustris*, another exotic grass, was greater in long-ungrazed riparian sites. Diffuse knapweed (*Centaurea diffusa*), which occupies  $>1.2 \times 10^6$  ha of the western United States (Lacey 1989), has been shown to invade pristine, ungrazed, native plant communities (Lacey et al. 1990) and long-ungrazed sites (Sheley et al. 1997). Smith and Schmutz (1975) reported rapid increases in Lehmann lovegrass (*Eragrostis lehmanniana*), an exotic perennial grass, in long-ungrazed desert grasslands in Arizona. In contrast, Mack (1981) strongly suggested that overgrazing

and disturbance were key factors in the spread of *Bromus tectorum* and other weeds in the historically lightly grazed perennial grasslands in Washington, Idaho, Oregon, Nevada, Utah, and British Columbia. Robertson (1971) found that *Bromus tectorum* could increase in sites protected from grazing, but the area previously had been heavily grazed. We also found *Bromus tectorum* in grazed and ungrazed plots, with higher cover generally in grazed plots (Table 6). One study reported a decrease in the cover of exotic species in the absence of grazing, but that occurred as light levels were reduced in a more forested area (Woodward et al. 1994). In short, many exotic species invade grazed and ungrazed sites, and we found little evidence to suggest that grazing at current levels accelerates the spread of most species of weeds in these vegetation types (Tables 3 and 4).

*Grazing affects local plant species and life-form composition and cover, but spatial variation is considerable.*—Similarities in species richness (Table 4), similarities in diversity and evenness (Table 5), and differences in species composition between grazed and ungrazed sites, and between grazed-adjacent and grazed-distant sites (Fig. 3) suggest that these vegetation types may have a "free substitution rule" for many species. That is, local extinctions are balanced by local immigration, both primarily by other native species, as the number of exotic species is generally low and similar among treatments. Because species composition overlap increases with spatial scale (Stohlgren, *unpublished data*), the substitute species are likely to be part of the same landscape-level species pool.

One fairly consistent pattern is that shrub cover and frequency tended to decrease slightly in grazed plots relative to ungrazed plots (Table 7). However, greater shrub cover inside exclosures did not necessarily translate into less forb and grass cover (Table 7). Other studies in similar habitats (Schulz and Leininger 1990, Coughenour 1991, Singer 1996) and elsewhere (Smith 1960, Tiedemann and Berndt 1972, Smith and Schmutz 1975, Collins and Adams 1983, Bock et al. 1984, Sneva et al. 1984, Kindschy 1987) have shown that cessation of grazing can increase the cover and frequency of shrubs. Still, there are some exceptions. Hughes (1980, 1983) found higher shrub frequency on grazed sites in desert shrub communities in Arizona, and Smeins et al. (1976) found no significant increase in shrub cover in Texas after 25 years of protection from grazing. Three of nine management areas in our study region had inconsistent results among grazed and ungrazed sites, and the Charles Russell area had greater shrub cover in grazed plots (Table 7). Although forb and grass cover is often lower in grazed sites (Table 7; Hughes 1983, Bock et al. 1984, Cid et al. 1991), as would be expected with herbivory, higher frequency of forbs and grasses in grazed sites may allow greater resilience and recovery when grazing pressure is reduced.

Woodward et al. (1994) reported a decrease in the

cover of forbs and grasses in the absence of grazing in Olympic National Park, Washington, presumably due to decreased light levels in exclosures as a result of succession. In Yellowstone National Park, Coughenour (1991) found that the cover of grasses was increased in some exclosures and decreased in others. Reardon (1996) reported increased forb cover on grazed areas at some sites in Yellowstone National Park, but few major differences between grazed and ungrazed sites overall. Our sampling techniques of foliar cover, which covered about five times the commonly sampled area of previous studies, also found no consistent differences in the cover of forbs, grasses, shrubs, or bare ground in Yellowstone National Park and elsewhere (Table 4). We suspect that small quadrat sample areas and sample sizes have exaggerated the differences reported in many grazing studies. For example, the significant differences in native species richness between grazed and ungrazed sites at the 1-m<sup>2</sup> scale (Table 3) were insignificant at the 1000-m<sup>2</sup> scale (Table 4). Given the many vegetation studies that recognized high spatial variability (e.g., Young 1943, Evanko and Peterson 1955, Belsky 1983, Collins and Adams 1983, Brown and Allen 1989, Frank and McNaughton 1993), it is difficult to understand why so many studies evaluating change in plant diversity relied on paired-plot studies using small quadrats without many replicates.

Plant distributions are influenced by complex spatial and temporal parameters such as environmental gradients, seed dispersal, site occupancy, lag effects, patchy nutrient and water resources, competition, disturbance at multiple scales, selective herbivory, disease and pathogens, and species-specific demography. The Collins and Barber (1985) description of grassland communities seems equally true of the vegetation types that we studied: biotic factors include large-scale effects of grazing, superimposed on small-scale effects of burrowing, excavation, or wallowing. Pacala and Crawley (1992) theorized that spatial variability in herbivory could create ephemeral, local refuges for each plant species if there is not a negative correlation between a plant's palatability and its competitive ability. Our results suggest that, at current levels of grazing, high spatial variability (i.e., well-dispersed populations and seeds) may be all that is necessary to maintain plant diversity at landscape scales.

Even within so-called "homogeneous" vegetation types, plant species are commonly distributed in patches. In this study and others (Stohlgren et al. 1995, 1997a, 1998, 1999), we found that: (1) about 50% of the vascular plant species had <1% foliar cover; (2) only a few dominant species were shared among plots within a vegetation type; and (3) plant frequency (i.e., the number of times a plant species occurred in 1-m<sup>2</sup> subplots) was extremely variable, suggesting that plant species distributions were patchy at 1000-m<sup>2</sup> scales (see also McNaughton 1983, Collins and Barber 1985). The consequence of low species overlap (Figs. 3 and 4;

Table 6), besides the obvious claim that no two plots are alike, is that investigators are obliged to evaluate how spatial heterogeneity influences study results. It is unlikely that sweeping generalizations about treatment effects can be made by surveying a few square meters on either side of a fence line, as has commonly been the case in exclosure studies.

*Soil fertility, climate, and other factors have a greater effect on plant species diversity than does grazing.*—Our work demonstrates that current levels of grazing may have little effect ( $\pm 10\%$ , roughly, at 1000-m<sup>2</sup> scales) on species richness (Table 4), foliar and life-form cover (Tables 3 and 7), plant diversity (Table 5), and selected soil characteristics (Table 8) in these vegetation types in the Rocky Mountains. Yet, species richness ranged from ~12 species/1000-m<sup>2</sup> plot (Uncompahgre) to >50 species/1000-m<sup>2</sup> plot (Wild Horse), or greater than a fourfold difference. Obviously, other factors have more of a controlling influence on plant diversity than do livestock and wild ungulate herbivory at these regional scales.

At the regional scale (i.e., for these rangeland types in the four-state study region), soil characteristics and elevation play a major role in determining the richness and cover of native and exotic plant species (Table 9). In the Rocky Mountains, grazed sites high in soil nitrogen and carbon tend to have higher native and exotic species richness and cover than sites low in soil fertility (Table 9; also see Stohlgren et al. 1998). Soil fertility and water availability are known to overshadow the effects of grazing in many areas (Hongo et al. 1995).

Often, exclosure studies have shown that increased or decreased precipitation can have greater effects than herbivory in altering plant productivity and species richness (Chew 1982, Milchunas et al. 1989, Coughenour 1991, Orr and Evenson 1991). For the nine management areas studied in four states, we found that mean exotic species cover was strongly positively correlated with mean maximum January temperature, with less cover in high-elevation, cooler habitats. Meanwhile, total cover was significantly negatively correlated with mean maximum July temperatures, with less cover in lower-elevation, hot, dry habitats. Because total plant cover and total number of species are positively correlated in these sites at all spatial scales, species richness at landscape and regional scales may be largely controlled by climate, rather than by grazing.

It may be that important resources such as light, nitrogen, and water remain at relatively similar levels in grazed and ungrazed sites in most of the management units, prohibiting rapid growth by some species in the absence of grazing or extirpation of species in grazed sites. Plant diversity may not be controlled by ungulate herbivory (Crawley 1983, McNaughton et al. 1989) or competitive exclusion (Grime 1973, Harper 1977) as much as it is by other factors.

Disturbances such as rodent activity (Whicker and Detling 1988, Cid et al. 1991, Hulme 1996), insect

outbreaks (Sneva et al. 1984), intermittent fire (Walker and Peet 1984, Collins and Barber 1985, Hart and Hart 1997), and occasional flooding (DeFerrari and Naiman 1994) probably play a significant role in maintaining plant diversity. We observed slightly more rodent activity inside exclosures. Evaluating other disturbances and factors was beyond the scope of this study. Milchunas et al. (1990) found that plant diversity at one site in the shortgrass steppe in Colorado increased with increased levels of perturbation, whereas a study by Collins and Barber (1985) in tallgrass prairie supported the intermediate disturbance hypothesis. More research is needed on these other disturbances in montane meadows.

*Few plant species show consistent, directional responses to grazing and cessation of grazing.*—We found that the vast majority of species showed inconsistent responses to grazing and protection from grazing, due to high spatial variability (Table 6). We question whether the terms “increaser” and “decreaser” (Weaver and Hansen 1941, Ellison 1960) are useful concepts for even a few plant species at landscape and regional scales. *Bromus tectorum* (Mack 1981) and *Bromus japonicus* (Table 6) may indeed spread faster in grazed and disturbed sites. However, Daubenmire (1940b) classified *Festuca idahoensis* and *Agropyron spicatum* as decreasers under grazing in southeastern Washington, whereas we found that the cover of *Festuca idahoensis* was higher in grazed than in ungrazed plots, and the cover of *Agropyron spicatum* varied greatly in and around the three exclosures in Yellowstone. Our use of a third plot randomly located in the same vegetation type strongly suggests that the natural patchiness of vegetation, spatially heterogeneous and selective grazing, and inconsistent responses to grazing make it very difficult to classify plant species in simplistic ways that will have meaning for landscapes and regions (Table 6).

Consistent, directional changes in species cover and frequency in grazed plots compared to adjacent, exclosed sites is usually considered evidence of the “grazing effect.” Our study shows that it is difficult to attribute this effect to grazing alone. Because the responses of most species differ by site (Table 6; Evanko and Peterson 1955), it is difficult to isolate the effects of grazing on plant diversity from differences due to other biotic and environmental factors (Table 9).

#### MANAGEMENT IMPLICATIONS

Our research led to five broad generalizations about current levels of grazing on these vegetation types in the Rocky Mountains: (1) grazing probably has little effect on native species richness at landscape scales; (2) grazing probably has little effect on the accelerated spread of most exotic plant species at landscape scales; (3) grazing affects local plant species and life-form composition and cover, but spatial variation is considerable; (4) soil fertility, climate, and other factors may

have a greater effect on plant species diversity than does grazing; and (5) few plant species show consistent, directional responses to grazing and cessation of grazing. Land managers may be somewhat relieved that plant species diversity in these vegetation types in Rocky Mountain grasslands is fairly resilient to grazing and cessation of grazing. Nature's abilities to increase plant frequencies when foliar cover decreases due to grazing, and to freely substitute many species within landscapes under a wide variety of grazing regimes (Table 2), may add to the redundancy of species distribution patterns (Stohlgren et al. 1997a) and a hedge against extirpation and extinction. We found no evidence that current levels of grazing have led to a loss in plant species richness and diversity at landscape scales in the vegetation types and management areas that we surveyed. At local scales, exotic species may replace native species, a situation that may call for immediate control measures, especially in the case of noxious weeds.

Other biomes with different evolutionary histories may have very different responses to grazing (Mack and Thompson 1982, Milchunas and Lauenroth 1993). In many cases in our study region, dead tissues are removed by grazing because the plants are grazed when they are dormant (Coughenour 1991); thus, few measurable effects on diversity and productivity have been shown in Rocky Mountain grasslands. However, because few exclosures exist in riparian zones, wetlands, and rare habitats, additional research is needed in these habitats. Other effects of grazing, such as mechanical damage to soils and trees, soil erosion, and gullyng, may be more pronounced in rare habitat types and riparian zones (Fleischner 1994, Belsky and Blumenthal 1997), and these should be regionally studied. A new system of large exclosures, as suggested by Bock et al. (1993), is needed to fully evaluate grazing effects in rare habitat types and riparian zones.

It is unlikely that the similarities and differences that we found between grazed and ungrazed sites were due to small plot and sample sizes. First, all of the exclosure studies that we reviewed actually measured far less ground area than we measured. Typically, studies that relied on the 20 × 50 cm Daubenmire quadrat and transect methods measure only 2–8 m<sup>2</sup> (one to four 20-quadrat transects per treatment). Small quadrats and transect techniques generally are designed to maximize precision (Daubenmire 1959, 1968, Coughenour 1991). Given the very high spatial variation reported in our study, we believe that the emphasis on precision has resulted in low accuracy (i.e., incomplete information on plant diversity and a poor understanding of spatial variation). Small quadrat and transect techniques generally miss about half of the native and exotic species in a 1000-m<sup>2</sup> area (Stohlgren et al. 1998). We surveyed species cover and frequency in 30–50 m<sup>2</sup>, and native and exotic species richness in 3000–5000 m<sup>2</sup> per grazing treatment in each management unit. Other inves-

tigators (e.g., Gibson and Brown 1991, Glenn and Collins 1992) have effectively used multiscale techniques to assess plant species dynamics in rangelands. Still, most previous enclosure studies have compounded sampling error with poor methods and experimental error with poor replication. Plant diversity studies are further confounded by high spatial variation. Management areas using small-quadrate methods would do well to overlay a much larger plot to adequately characterize native and exotic species richness and cover (Stohlgren et al. 1998).

The other two major differences between this study and previous studies are increased replication and the evaluation of spatial variation in grazed sites in each management area, without which broad generalizations about the effect of grazing on plant diversity could be erroneous. It is highly unlikely that the error term in unreplicated enclosure studies is represented by the sampling error, as stated in Dormaar et al. (1994: 29). Even with increased replication, simple paired-site designs on either side of a fence line need to evaluate the effects of spatial variation.

The existing grazing enclosures have provided important insights on the effects of grazing on plant diversity patterns. We owe thanks to the plant ecologists, land managers, and maintenance workers for their foresight and investment in long-term research. A comparison using only grazed sites would not have yielded these insights. Every effort should be made to maintain the present enclosures and to establish additional enclosures in rare habitats and riparian zones. New enclosure sites should be randomly selected and carefully surveyed for pretreatment data. The multiscale vegetation sampling methods used here helped to isolate the effects of spatial scale from the effects of grazing and cessation of grazing.

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