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# Effects of grazing, topography, and precipitation on the structure of a semiarid grassland

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## Abstract

Structural aspects of the shortgrass steppe plant community, functional groups, and species populations were examined in response to long-term heavy grazing and exclosure from grazing, contiguous wet or dry years, and an environmental gradient of topography. Of the three factors, relatively greater differences in community similarity were observed between catena positions, particularly on the ungrazed treatments. Grazing was intermediate between catena position and short-term weather in shaping plant community structure. Grazed treatments and ridgetops had a less variable species composition through fluctuations in weather.

An increase with grazing of the dominant, heavily grazed species was observed. Basal cover and density of total species was also greater on grazed sites. The more uniform grazing lawn structure of the grazed plant communities had an influence on segregation of plant populations along topographical gradients. Segregation was less on grazed catenas, but diversity and the abundance of introduced and opportunistic-colonizer species was also less.

Although the shortgrass steppe community was relatively invariant, less abundant species were dynamic and interactions occurred with respect to grazing, weather, and catena position. The effects of grazing may be mitigated by favorable growing seasons but magnified in unfavorable years in populations that are adapted to favorable sites. Grazing can be considered a disturbance at the level of the individual but it may or may not be a disturbance at the level of the population, and it is not a disturbance at the level of the community in this particular grassland.

*Nomenclature:* the Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

## Introduction

The semiarid shortgrass steppe of North America has a relatively long history of heavy grazing pressure compared with other grassland types in North America (Stebbins 1981). The diverse pre-Pleistocene fauna, and large herds of bison and antelope in pre-settlement times had a large influence on the overall physiognomy (Mack & Thompson 1982). Currently, grazing by domestic cattle is an important component of energy flow in the shortgrass steppe. Laurenroth & Milchunas (1989) calculated that total aboveground and belowground herbivory is primarily by, and approximately equally divided among, ruminants, arthropods, and nematodes. However, cattle account for 84% of the aboveground herbivory and consume 40% of the aboveground net primary production (ANPP) in moderately grazed pastures.

In addition to grazing by large herbivores, precipitation and topography are also important determinants of plant community structure in this semiarid region. These three factors may interact in a complex manner. For example, ANPP is frequently limited by the availability of soil water (Lauenroth *et al.* 1978). This results in large fluctuations in ANPP from wet to dry years (Sims & Singh 1978; Lauenroth 1979). Swales often are more productive than ridgetops (Lauenroth & Milchunas, unpubl.), possibly due to higher fertility (Schimel *et al.* 1985) and more favorable soil water conditions. Cattle grazing behavior studies indicate that swales are grazed more heavily than ridgetops during the growing season (Senft *et al.* 1985).

Previous studies of the effects of grazing on the shortgrass steppe suggested no difference, or only minor differences, in the species composition of long-term heavily grazed versus ungrazed communities (Klipple & Costello 1960; Hyder *et al.* 1966, 1975). However, these studies did not consider topographic effects. Even though the coevolution of plants and large herbivores may have produced a plant community that is tolerant of grazing, sampling without regard to topography may mask plant community responses. Gradients in resource availability and intensity of grazing with topography can affect both competitive relationships among plants as well as the manner in which the communities respond to short-term fluctuations in weather.

The objective of this study was to assess the effects of 45 yr of controlled, heavy grazing by cattle and exclosure to grazing on the basal cover and density of species in plant communities along catenas following periods of wet or dry years. The interactions, and relative importance, of grazing, topography, and precipitation in determining vegetation structure are examined at the levels of organization of the plant community, functional groups, and populations. The responses at these levels of organization are discussed in terms of fast or slowly changing independent variables and the evolutionary history of the shortgrass steppe.

## Methods

The study was conducted at the Central Plains Experimental Range (CPER) lat. 40°49′N, long. 107°47′W, located in the northern portion of the shortgrass steppe region in northcentral Colorado, approximately 56 km northeast of Fort Collins, Colorado. During the past 43 years, mean annual precipitation was 310 mm, ranging from 115 mm to 595 mm. Approximately 85% of the precipitation occurs during May, June and July. Mean air temperatures are 15.6 °C in summer and 0.6 °C in winter.

Light, medium, and heavy grazed treatments (each 130 ha) and grazing exclosures were established in 1939. Only the heavily grazed treatment was used in this study. The original grazing exclosure in the heavily grazed pasture was not used because of its small size and location on a single catena position. Instead, ungrazed rangeland was sampled in a 12-m × 1.6-km strip contiguous with heavily grazed range. This permitted side by side sampling of grazed and ungrazed treatments on the same soils/topographic units. This strip, ungrazed since 1939, perpendicularly transverses three catenas in a north-south direction. The three ridgetops are at a similar elevation, whereas the swales are 6, 8, and 21 m lower than their associated ridgetops. The term *ridgetop* may be a misnomer since the topography is gently rolling. The strip was used twice a year in the 1930's to drive cattle from private land to a nearby road. Stocking rates in heavily grazed range averaged 0.72 ha/yearling heifer/month (Bement 1969). From 1939 to 1962, the stocking rate varied from year to year depending on the number of cattle necessary to attain 60% use of maximum standing herbage (averaged over the 130 ha pasture) over a six month period spanning the growing season. From 1962, 22.5 g/m$^2$ of herbage were left at the end of the summer grazing season. Based on 9 yr of data, aboveground maximum standing crop ranged from 50 to 155 g/m$^2$ ($\bar{X}$ = 101 g/m$^2$) (Shoop unpubl.). This means that herbage removal ranged from ca 55 to 86% ($\bar{X}$ = 78%).

A description of soil profiles based on 5 cores in each grazing treatment for each topographic unit indicated a high degree of similarity between grazing treatments within a topographic unit, but that catena replicate − 2 has a shallower depth to shale (~75 cm). Differences between swale and ridgetops are not as great as the classical concept of a catena may imply because of the strong influence of geologically recent eolian processes. However, aboveground primary production averages 68 g/m$^2$ on ridgetops and 112 g/m$^2$ on swales (Lauenroth & Milchunas, unpubl.) and organic C, N, and P are three times greater in soils of swales than of ridgetops (Schimel 1985).

16 sampling locations were located 3 m apart along each of 3 randomly located transects within each of 3 replicate swales and 3 replicate ridgetops in each grazed and ungrazed treatment (16 plots × 3 transects × 3 reps × 2 topounits × 2 grazing treatments = 576 locations). Transects on the grazed side of the fence were placed between 15 and 27 m away from the fence, since cattle tend to walk the fencelines. Density and basal cover were estimated as follows: density by counting all individuals in 0.25 m$^2$ circular quadrats (total = 1152 quadrats), and basal cover by recording hits of a 10-point frame (total = 11520 points). Cactus density was recorded as the number of live cladodes in each 0.25 m$^2$ quadrat. The density of shrubs was determined by counting individuals in ten 63 m$^2$ quadrats in each of the 12 treatment units. Individuals for all species refers here to tillers or basal stems emerging from the soil surface, because many species of the shortgrass steppe are rhizomatous, or otherwise clonal. An index to the grazing intensity at each catena location was obtained by counting fecal pats in ten 63 m$^2$ plots.

All sampling was performed in 1984 and 1986 at the time of peak standing crop. 1984 was a slightly wetter than average year following a wet year and 1986 was a relatively dry year following a dry year. Precipitation from early spring (April) to the time of vegetation sampling in late July was 210 mm in 1984 and 139 mm in 1986, compared with a 43 yr mean of 197 mm (SD = 75 mm). Thus, precipitation in 1984 was 7% above, and in 1986 was 29% below, the long-term mean. Although not indicated by the growing season means, a period of drought in which vegetation senesced occurred in both 1985 and 1986. Prior to 1985, favorable growing seasons of above average precipitation occurred for a period of six years. We use the terms relatively wet or dry years because they do not represent the extremes of precipitation.

Analysis of variance was performed on the data sets, with significant differences ($P \leq 0.05$) between means identified by Least Significant Range (LSR) values (Sokal & Rohlf 1969). The assumption of randomly located treatment and catena locations was obviously violated, since all grazed treatments were on the same side of the fence and swales always followed ridgetops. However, the physical layout permitted comparison of adjacent grazed and ungrazed treatments on the same swales or ridgetops. Three possible error terms (replicate, transect, and plot) were tested for significance, starting from the bottom of the hierarchial arrangement, and pooled whenever possible.

Similarity indices were used for several of the community level comparisons of plant density in relation to grazing treatment, topography, and precipitation. Whittaker's index of association (1952) was chosen because it was responsive to less abundant species and was stable in bootstrapping, i.e., confidence intervals were small compared with those obtained with other indices. Because all indices are more responsive to dominants, and because the shortgrass steppe is heavily dominated by *Bouteloua gracilis*, we computed similarity values without *B. gracilis* and without transforming the data. Similarity values represent all other species comprising greater than 5% of the plant density on any one treatment-rep in the absence of *B. gracilis*.

Confidence intervals for similarity indices were computed using the bootstrap percentile method (Efron 1981), with 1000 bootstrap replications sampled in two stages to mimic the transect sampling of quadrats that was used. Variability between transects, as well as between quadrats within transects, is accounted for in this bootstrap sampling procedure. The 95% confidence intervals should be used conservatively, however, because simulation studies have indicated that percentile method confidence interval coverage rates are typically low (Schenker 1985). Nominal 95% confidence intervals may have coverage rates closer to 90%.

Indices of diversity (Shannon & Weaver 1949), richness (# species/quadrat and total # species) evenness (Pielou 1966), and dominance (Simpson 1949) were calculated for each grazing treatment-topographic position-year combination.

## Results

Our organizational approach will be to proceed from the level of the community to functional groups, to individual populations. Basal cover assesses the major components of the community because small or rare species are seldom encountered. Density weights all individuals equally, thereby indicating more subtle changes in community structure. Community-level attributes will be described using basal cover, and then with indices of similarity, dominance, and diversity based on density data. We first define grazing intensities along the toposequences of the heavily grazed grassland.

### *Grazing intensities*

Grazing intensities, as indicated by density of fecal pats, were significantly greater on swales than on ridgetops (Table 1), averaging 150 and 50% of the mean, respectively. The decomposition of fecal pats in the shortgrass region may take more than 6 yr (Lussensop *et al.* 1982). Thus counts of fecal pats provide an estimate of relative grazing intensity integrated over several years. Grazing intensities on swales that were three times as great as on ridgetops, based on studies of cattle behavior, were also reported for nearby pastures (Senft *et al.* 1985).

### *Community structure*

The shortgrass communities at the CPER are dominated by *Bouteloua gracilis*, *Opuntia polyacantha*, litter and bare ground (Fig. 1). These four components accounted for more than 95% of the cover on all locations. *B. gracilis* constitutes approximately 90% of the plant basal cover, with the remaining 10% divided between *O. polyacantha* and all other species.

*Table 1.* Grazing intensity index based upon fecal pat density for swales and ridgetops in the heavily grazed pasture. Differences between topographic positions (LSR = 4) were significant and between replicates (LSR = 5) were not.

| Replicate | Cow dung density | | | |
|---|---|---|---|---|
| | Swale | | Ridgetop | |
| | Density (#/63 $m^2$) | % of overall mean | Density (#/63 $m^2$) | % of overall mean |
| North | 14 | 140 | 6 | 60 |
| Middle | 16 | 160 | 4 | 40 |
| South | 15 | 150 | 5 | 50 |
| $\bar{x}$ | 15 | 150 | 5 | 50 |

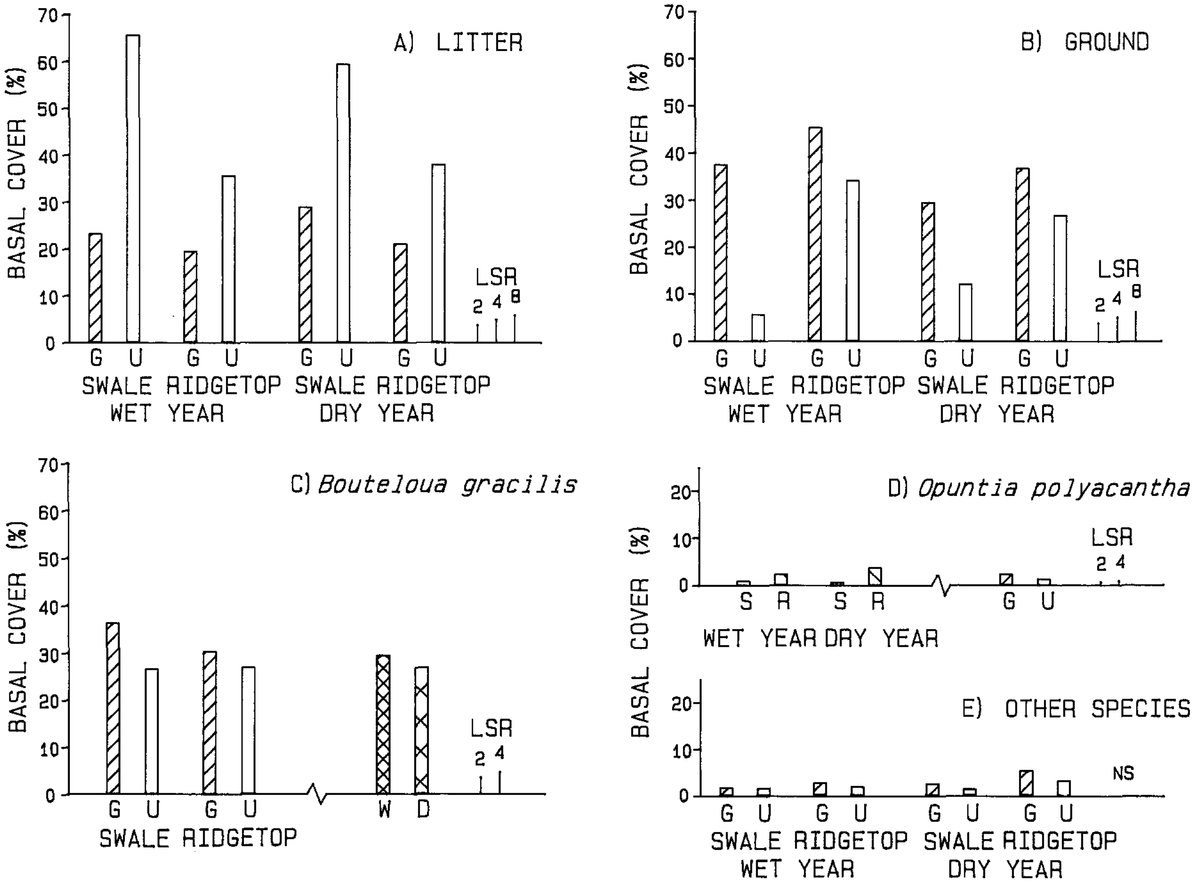

*Fig. 1.* Basil cover (%) of the shortgrass steppe on grazed (G) and ungrazed (U) swales (S) and ridgetops (R) in wet (W) and dry (D) years. USE $LSR_2$ for significance test when crossing any one treatment within the other two treatments, $LSR_4$ when crossing any two treatment categories within a third, and $LSR_8$ when comparing between all three treatment categories. A broken x-axis represents a two-way interaction followed by a main effect, or three main effects. All main effects may or may not be significant, use $LSR_2$ values to test.

*B. gracilis*, the primary forage species grazed by cattle, increased in basal cover with grazing on the grazed swales (Fig. 1). There were no significant differences between wet and dry years or between ungrazed swales and ridgetops. *O. polyacantha*, a cactus which is not grazed and deters grazing of other nearby plants, was more abundant on ridgetops and increased during dry years on ridgetops. *O. polyacantha* obtained a slightly greater basal cover under grazing, but cladode density was not significantly different between grazed and ungrazed sites. The largest differences in cover were observed for litter and bare ground. Litter was much greater on ungrazed sites and on swales versus ridgetops except on grazed sites during the wet year.

Community-level differences were assessed by comparisons of similarity between grazing treatments, catena position, and wet and dry years. The similarities of grazed versus ungrazed treatments within a catena position and year averaged greater than 0.8 (value of 1.0 indicates complete similarity) in all cases but one (Fig. 2A). 47 yr of heavy grazing had only a small influence on community structure. The effects of grazing did not differ significantly between wet and dry years on the same swale or ridgetop replicate. Grazing had a greater effect on swales than on ridgetops in three out of six within-year comparisons.

The similarity of swales versus ridgetops within grazing treatment and year is an indication of the degree of segregation of plant populations along the topographic gradient. The segregation of plant populations was generally greater on ungrazed sites (Fig. 2B). Plant communities along the catenas on the grazed sites were very uniform. Comparisons of each site in the wet year with the same site in the dry year indicated very little change (Fig. 2C).

Diversity was greatest for the ungrazed swales in both wet and dry years (Table 2). All other within-year comparisons were similar. Diversity was lowest in the dry year in all cases, although this was significant only on grazed swales. The difference in diversity were a function of the generally greater richness of ungrazed sites and lower dominance on ungrazed swales.

*Functional group structure*

Grasses are the dominant life-form of shortgrass steppe plant communities. The response of grasses as a group (including sedges) to the three

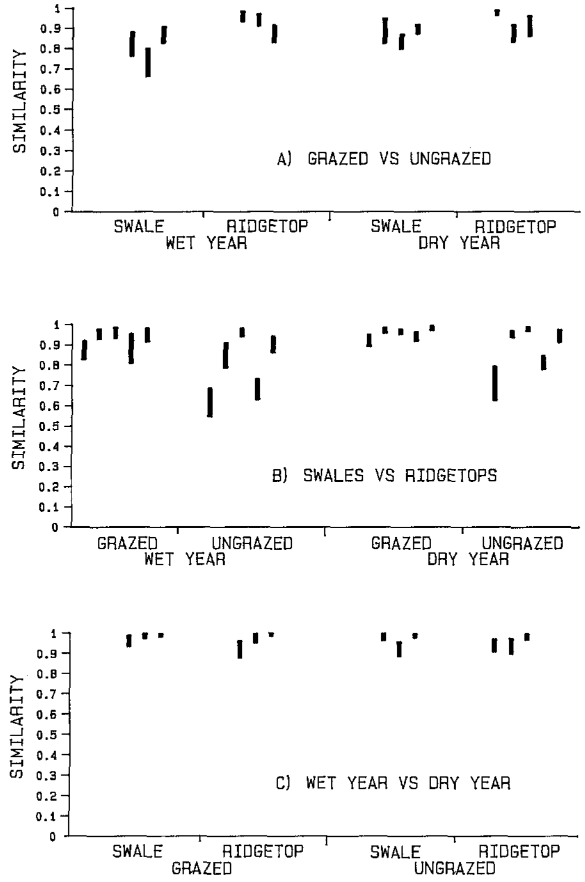

*Fig. 2.* Similarities of (A) grazed versus ungrazed treatments within topographic positions and years, (B) swale versus ridgetop communities within grazing treatments and years, and (C) wet year versus dry year comparison of same community for grazing treatments and topographic positions. A similarity value of 1.0 indicates completely alike and 0.0 completely different. Range of a similarity value represents 95% confidence interval by bootstrapping. The Whittaker (1952) index of association was computed with density data.

*Table 2.* Indices of diversity, richness, evenness, and dominance of heavily grazed and ungrazed swales and ridgetops of the shortgrass steppe during wet and dry years.

| Community attribute | Year | Index value | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Grazed | | | | Ungrazed | | | |
| | | Swale | | Ridgetop | | Swale | | Ridgetop | |
| | | $\bar{x}$ | (SD) | $\bar{x}$ | (SD) | $\bar{x}$ | (SD) | $\bar{x}$ | (SD) |
| Diversity (exp H′) | Wet | 1.33 | (0.06) | 1.31 | (0.08) | 1.50 | (0.10) | 1.31 | (0.04) |
| | Dry | 1.26 | (0.03) | 1.27 | (0.05) | 1.46 | (0.07) | 1.28 | (0.03) |
| Richness (Total # spp.) | Wet | 18.7 | (5.0) | 18.0 | (2.7) | 25.7 | (4.9) | 27.0 | (1.7) |
| | Dry | 14.7 | (8.3) | 15.0 | (3.6) | 18.0 | (1.7) | 19.7 | (4.9) |
| Evenness (J′) | Wet | 0.10 | (0.02) | 0.09 | (0.02) | 0.13 | (0.02) | 0.08 | (0.01) |
| | Dry | 0.09 | (0.01) | 0.09 | (0.01) | 0.11 | (0.02) | 0.08 | (0.01) |
| Dominance (C) | Wet | 0.88 | (0.03) | 0.89 | (0.05) | 0.83 | (0.04) | 0.90 | (0.02) |
| | Dry | 0.90 | (0.01) | 0.90 | (0.03) | 0.84 | (0.02) | 0.91 | (0.02) |

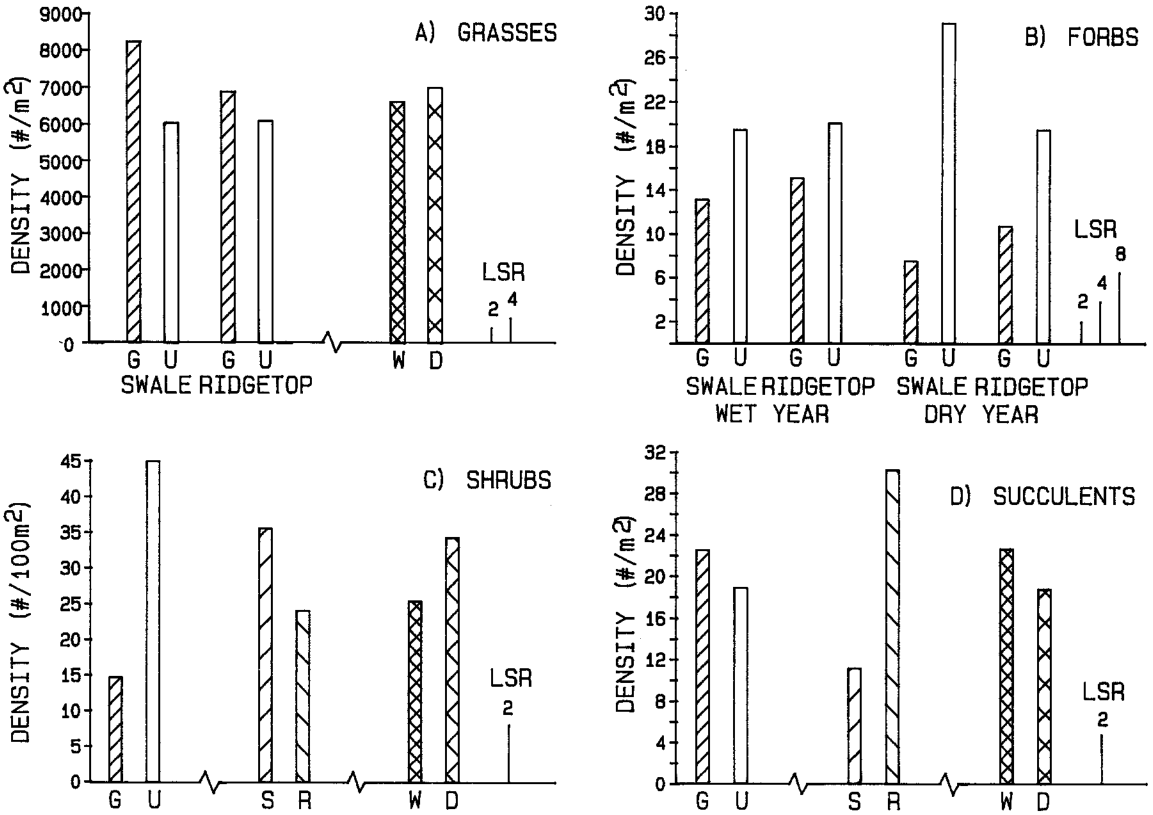

*Fig. 3.* Functional group densities (# of individuals/$m^2$ or /100 $m^2$ for shrubs) of shortgrass steppe plant communities in grazed (G) and ungrazed (U), swales (S) and ridgetops (R), wet year (W) and dry year (D). See Fig. 1 for statistical explanations.

experimental variables was similar to that of the dominant species, *B. gracilis*, with the exception of the greater density of grasses in the dry year (Fig. 3A). The increase in grasses in the dry year was primarily because of greater numbers of the sedge *Carex eleocharis* and the annual grass *Festuca octoflora*. *C. eleocharis* is drought and grazing tolerant and *F. octoflora* is a cool-season annual that matured prior to the 1986 dry period. Grasses obtained a greater density on grazed sites and were most abundant on the grazed swales.

Forb density was greatest on ungrazed sites, in the wet year versus dry year on grazed sites, and in dry year on ungrazed swales (Fig. 3B). Shrubs and half-shrubs were most abundant on the ungrazed treatments, in swales, and in the dry year (Fig. 3C). The only significant difference observed for succulents was greater cladode density on ridgetops (Fig. 3D).

### *Population structure*

The two most abundant species of the shortgrass steppe, *B. gracilis* and *O. polyacantha*, were addressed above (Figs 1C and 3D). In this section, we examine four additional important species and four species that are common on disturbed areas where all or part of the cover of *B. gracilis* was killed due to an outbreak of root feeding white-grubs or various water or nutrient enrichment treatments (Milchunas *et al.* ms.).

*Agropyron smithii* was the most severely affected by the 47 yr of heavy grazing (Fig. 4A). Highest densities occurred on swales, and it was these swale populations that were most affected in the dry year. *Gutierrezia sarothrae* is an unpalatable half-shrub. However, it attained greatest density on ungrazed sites (Fig. 4B). *Sphaeralcea coccinea* and *Gaura coccinea* are examples of how grazing,

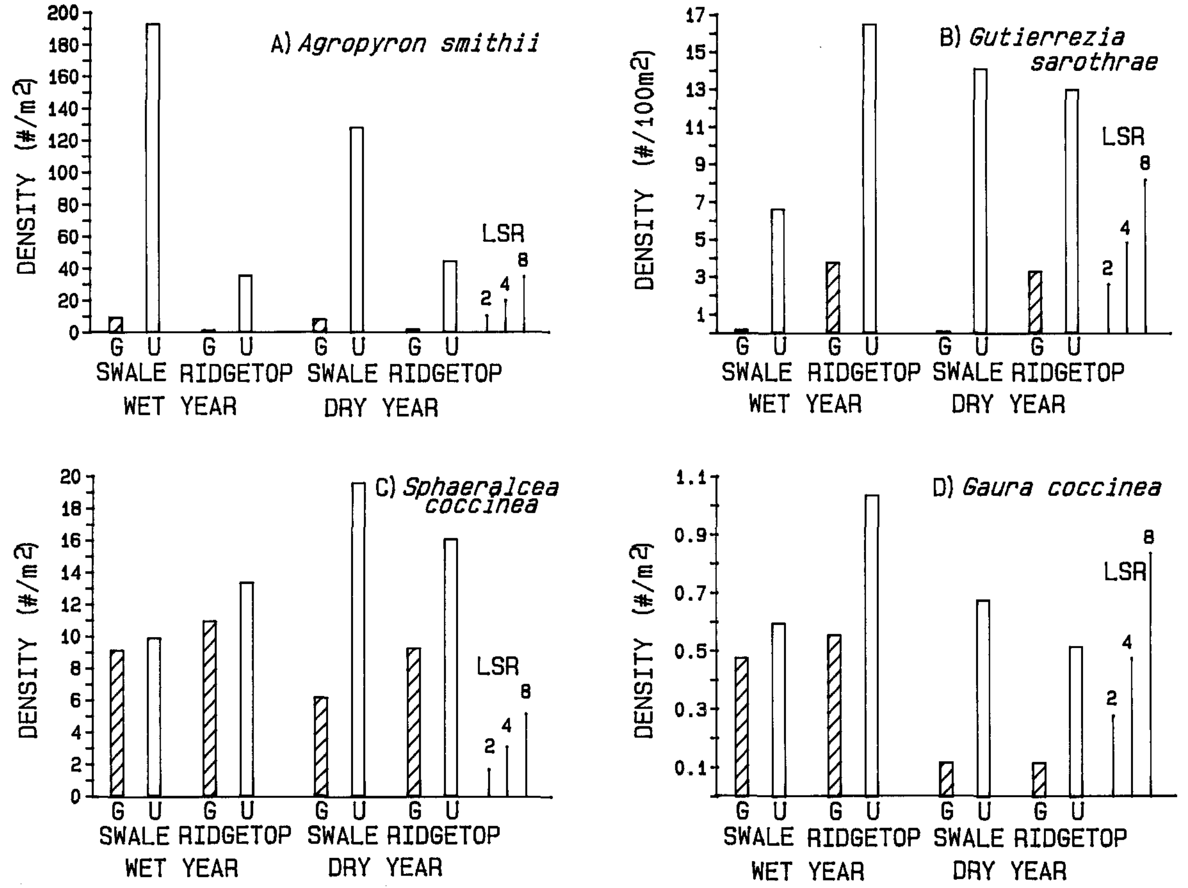

*Fig. 4.* Densities of 4 important species of the shortgrass steppe by grazing treatment, topographic position, and wet or dry year. Notation and statistical explanation same as in Fig. 1.

precipitation, and topography interactively influence plant populations. *Sphaeralcea coccinea* densities in the wet year were slightly but significantly increased on ungrazed sites only on the ridgetops (Fig. 4C). The additional stress of grazing in a dry year decreased *S. coccinea* densities, whereas *S. coccinea* was favored in the dry year in the absence of grazing. *Gaura coccinea* populations appeared to be sensitive to grazing and to dry conditions (Fig. 4D). In the dry year, *G. coccinea* decreased on all ridgetops but not on ungrazed swales, and densities were very low on grazed sites. For the two most common forbs on the site and for total forbs, the differences between the grazed and ungrazed treatments were greater in the dry year and this was most apparent in populations inhabiting the more favorable swales rather than those on the more xeric ridgetops.

Four apportunistic-colonizer species occurred on the study area at densities sufficient for statistical analysis. All opportunistic colonizers except *A. longiseta* were found at highest densities on the ungrazed treatments (Fig. 5). Only *S. hystrix* and *O. coronopifolia* differed between wet and dry years.

Although chosen based on their high densities on other heavily disturbed areas, the classification of a species as an opportunistic-colonizer species is somewhat subjective. A better defined category is introduced species (exotics). The densities of introduced species on the ungrazed treatments were 0.52 and 0.48 individuals/m$^2$ for swales and ridgetops, compared with 0.28 and 0.12 individuals/m$^2$ for the grazed swales and ridgetops. A total of 6 introduced species were identified on the ungrazed treatments and only 2 on the grazed.

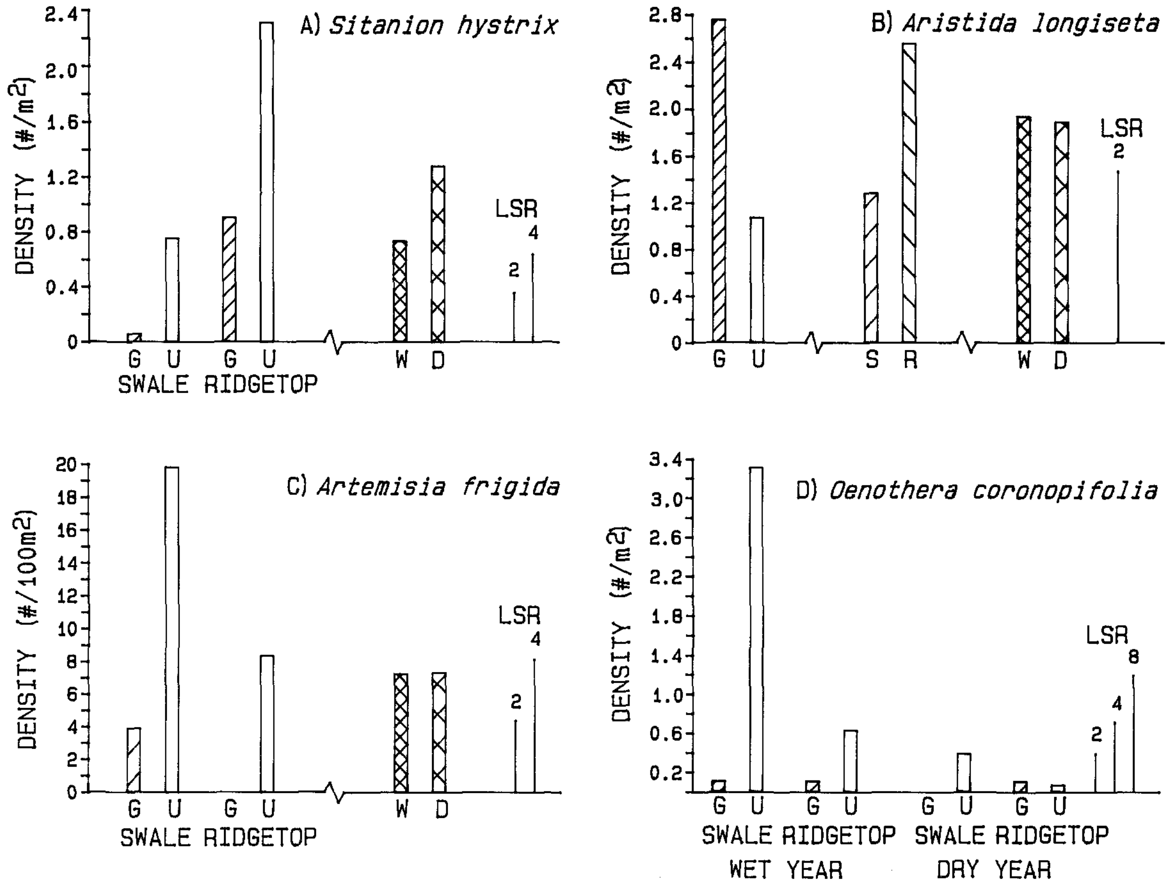

*Fig. 5.* Densities of 4 opportunistic-colonizer species of the shortgrass steppe by grazing treatment, topographic position, and wet or dry year. Notation and statistical explanation same as in Fig. 1.

Contrastingly, identical sampling procedures on roadsides adjacent to the treatments resulted in density counts of introduced species that averaged 55 and 61 individuals/m$^2$ for swales and ridgetops, with 6 and 12 introduced species encountered, respectively.

## Discussion

Changes in the shortgrass steppe community structure at the CPER in response to 47 yr of grazing treatments were most evident in litter and bare ground. An increase in basal cover of the dominant, heavily grazed *B. gracilis* was also observed. This increase was not associated with a decrease in total plant basal cover. Total basal cover of plants was 30% greater, and total density was 25% greater on the grazed than on ungrazed sites. The shortgrass steppe has a long evolutionary history of grazing (Stebbins 1981; Mack & Thompson 1982). Heavily grazed areas of the shortgrass steppe can be characterized as *grazing lawns* (sensu McNaughton 1984). Changes in the community at this level of resolution may result in additional subtle changes because both the direct effect of grazing and the indirect effects of altered competitive relationships among plants shape the subsequent structure of the community.

The effects of grazing were increasingly evident as the level of observation proceeded from the community, to functional groups, to individual species populations. Only small differences were observed at the level of the community. Of these, relatively greater differences in similarity occurred between swales and ridgetops, particularly on the ungrazed treatments. Grazing was intermediate between catena position and short-term weather cycles in shaping community structure.

Segregation of plant populations along catenas was found to be less on grazed catenas, but diversity was lower and total density and basel cover were greater. These responses are contradictory when viewed in terms of the usual manner in which plant communities respond to disturbance. The intermediate disturbance hypothesis (Grime 1973; Connell 1978; Fox 1979) and the Huston (1979, 1985) hypothesis predict increased diversity as competition is reduced at intermediate levels of disturbance, followed by decreased diversity through population reduction at heavy levels of grazing. The heavy intensity of grazing in this study probably resulted in population reduction via direct injury to sensitive species. However, the increase in total plant density and basal cover and the decrease in opportunistic-colonizer species with grazing suggests that levels of plant competition may not be reduced. As a measure of potential competition, the three-dimensional distribution of belowground biomass indicated no difference in crown biomass with grazing and slightly less (7%) root biomass on the heavily grazed swales (Milchunas & Lauenroth in press). However, there were large differences in the horizontal uniformity of root and crown biomass. The belowground grazing lawn structure of the grazed sites suggests that sparsely occupied patches conducive to seedling establishment occur less frequently on grazed sites.

We expected that the grazed treatments, and ridgetops with less favorable soil water conditions, would display less stable species composition through fluctuations in precipitation. Years of above average precipitation would enrich species composition to the potential levels found on more favorable sites, and dry years would be relatively more stressful on unfavorable sites. Differences in community similarity after 6 wet and 2 dry years were small and were relatively uniform across grazing treatments and topographic position. Differences after periods of wet and dry years were also relatively less than the differences between topographic position or grazing treatments when viewed at the levels of functional groups or species. However, all responses were greater at finer levels of observation. This suggests that the main components of the communities varied little with respect to short-term weather cycles and lesser components responded on a short time-scale. Although the wet-dry year comparison does not represent the extremes of long-term records, there was a significant difference in net primary production between the wet (104 g/m$^2$) compared to the dry (70 g/m$^2$) year (Lauenroth & Milchunas unpubl.). Grassland primary production closely tracks annual precipitation (Sims & Singh 1978; Lauenroth 1979), whereas inertia in species composition may result in tracking climate changes at some greater time-scale. In general, the community and the dominant species were influenced more by slow changing variables. Topography changes very slowly. Grazing is managed to minimize year-to-year variability and is a force the community has experienced through evolutionary time.

Although the shortgrass steppe community at the CPER was relatively invariant, less abundant species were dynamic with respect to grazing, precipitation, and topographic position. We hypothesized that a plant species may respond differently to grazing in wet years and in different sites as levels of grazing injury and different soil moisture deficits interactively determine abundances. While the response of some species fit the categories of increasers or decreasers with grazing, other species displayed complex interactions with grazing, precipitation, and topography. For example, *Sphaeralcea coccinea* and *Gaura coccinea* were not sensitive to grazing on swale sites during a wet year. They were sensitive to grazing during a dry year, and the sensitivity to grazing during the dry year was greatest on the swale sites. The effects of grazing may be mitigated by favorable growing seasons but magnified in unfavorable years in populations that are adapted to favorable sites.

An increase in the abundance of introduced species or annuals is commonly reported in grazed, rather than ungrazed, grasslands with short evolutionary histories of grazing, such as in

South America (Sala *et al.* 1986), Australia (Biddiscombe 1953; Moore & Biddiscombe 1964), Europe (Rosén 1982; Titlyanova *et al.* 1988), and North America west of the Rocky Mountains (Mack & Thompson 1982). In this study the densities of introduced species and of opportunistic-colonizer species on ungrazed sites were three times as great as on grazed sites. This suggests that the lack of grazing is more like a disturbance in this community that has evolved with heavy grazing. Based upon these data alone, we cannot definitely accept or reject this hypothesis since other less abundant species also increased on the ungrazed treatments. However, comparisons of these grazed and ungrazed plant communities with other types of disturbances indicated that the structure of the ungrazed sites were more similar to disturbed communities over a wide range of disturbance levels (Milchunas *et al.* ms.). Many of the introduced species that occur on the artificially, heavily disturbed treatments and along disturbed roadsides adjacent to the grazing treatments do not invade the native grazed grassland. Similar observations were reported by Belsky (1987) for Serengeti grasslands.

The response of the shortgrass steppe plant communities to grazing is unusual even when compared with other plant communities of long evolutionary history of grazing. Relatively greater differences in plant community structure between grazed and ungrazed sites were observed in subhumid grasslands of the North American Great Plains compared with those observed at this semiarid location (Collins & Barber 1985; Collins *et al.* 1987; Ketling 1954, Penfound 1964, Heitschmidt *et al.* 1985). McNaughton (1979, 1983) assessed plant communities inside and outside 12-yr exclosures in several Serengeti grasslands and observed that organization and structural properties changed radically due to protection from grazing. We attribute the different responses to grazing of the shortgrass steppe and the Serengeti to be the result of convergent selection pressures imposed by grazing and semiaridity versus divergent selection pressures imposed by grazing and canopy competition in more mesic environments (Milchunas *et al.* 1988). Adaptations to semiaridity also confer a degree of tolerance or avoidance to grazing (Coughenour 1985). Although the Serengeti is often considered semiarid, precipitation and primary production in the driest plant communities of the Serengeti are twice that of the shortgrass steppe. Researchers in African grasslands often report decreased diversity in exclosures as a few canopy competitors eventually become dominant (McNaughton 1979, 1983; Thornton 1971; Spence & Angus 1970; Halton & Smart 1984; Heady 1966). Grazing exclosures at the CPER were more diverse and we did not observe large changes in canopy structure or species composition. Convergent selection pressures of semiaridity and grazing in the shortgrass steppe have resulted in a community with a high degree of tolerance to both grazing pressure and yearly fluctuations in precipitation.

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