J. Range Manage.
52:637-645 November 1999

Plant responses to pocket-gopher disturbances across pastures and topography

JOANNE M. CARLSON AND THOMAS O. CRIST

Authors are research assistant and assistant professor, Department of Zoology, Miami University, Oxford, Ohio 45056.

Abstract

Pocket gophers are important disturbance agents in rangelands, yet little is known about how plant responses to gopher disturbances vary with grazing and topography. We measured the spatial distribution of soil mounds created by the northern pocket gopher (*Thomomys talpoides attenuatus* Hall and Montague) in shortgrass steppe, and sampled plant cover and species composition on gopher mounds at 3 topographic positions within 2 pastures that were lightly and heavily grazed by cattle. Measurements were taken during 1996 and 1997 in each pasture along a 75 x 900-m transect that spanned the same topographic gradient: a south-facing slope, a north-facing slope, and an upland plain. Pocket-gopher mounds were more numerous in the lightly grazed pasture but mounds were larger in the heavily grazed pasture. An estimated 1-6% of the total area was disturbed on uplands and south-facing slopes, and <1% was disturbed on north-facing slopes. Plant cover on mounds was generally higher in the heavily grazed than in the lightly grazed pasture, primarily due to a greater cover of the dominant perennial grass, blue grama (*Bouteloua gracilis* [H.B.K.] Lag ex Griffiths). Detrended correspondence analysis also showed that pasture had a greater effect on plant species composition on mounds than topography or yearly variation. Our results demonstrate that topography affected the spatial distribution of pocket-gopher disturbances, and pasture influenced the pool of plant species colonizing mounds. It is therefore important to assess animal-disturbance effects and plant responses to disturbances on rangelands within the broader context of topography and grazing.

Key Words: *Bouteloua gracilis,* cattle grazing, disturbance area, plant community, shortgrass steppe, Thomomys talpoides

Resumen

Los ardillones abazón (pocket gophers) son importantes agentes de disturbios en las áreas de pastoreo, pero sin embargo se sabe poco de como responden las plantas a estos disturbios, que pueden variar con el pastoreo y la topografía. Medimos las distribución espacial de los montículos de arena creado por el ardillón abazón norteño (*Thomomys talpoides attenuatus* Hall and Montague) en la hierba corta de la estepa, y tomamos muestras de las plantas y las composiciones de especies en montículos de los ardillones en tres posiciones topográficos en dos áreas de pastoreo que estaban ligeramente y extremadamente usados como campo de pasto para ganado. Se tomaron muestras durante 1996 y 1997 en cada área de pastoreo en un marco midiendo 75 por 900-m trasectado que se expande en el mismo declive topográfico: un pendiente mirando hacia el sur, un pendiente mirando hacia el norte, y un llano tierra arriba. Los montículos de los ardillones abazón eran más numerosos en las áreas de pastoreo que estaban ligeramente pastados pero los montículos en las áreas que estaban extremadamente pastados eran más grandes. Entre 1-6% del áreas total tenía disturbios tierra arriba y en los pendientes mirando hacia el norte. La cobertura de plantas en los montículos era generalmente más alto en las áreas de pastoreo extremado en comparación a las áreas de pastoreo ligero, primordialmente por la incrementada cobertura de la hierba perrenial, gamma azul (*Bouteloua gracilis* [H.B.V.] Lag ex Griffiths). Análisis correspondiente intendenciada (Detrended Correspondence Analysis) también apuntó a que la intensidad del pastoreo tenía un mayor efecto en las composiciones de especies de plantas en los montículos que en la topografía o variación anual. Nuestros resultados demuestran que la topografía afectó la distribución espacial de los disturbios de los ardillones abazón y el pastoreo influenció la variedad de especies de plantas colonizando los montículos. Por consiguiente, es importante valorar los efectos de los animales y su impacto/disturbio en la correspondencia de las plantas a estos disturbios en áreas de pastoreo en un contexto mayor topográfico y de campo de pasto.

Grazing affects plant community heterogeneity and species diversity in semiarid grasslands (Lauenroth et al. 1994). In the western Great Plains, grazing can result in an increased dominance of grazing-tolerant perennial grasses such as blue grama (*Bouteloua gracilis* [H.B.K.] Lag ex Griffiths) (Milchunas et al. 1988, 1990, Lauenroth et al. 1994). Greater cover of *B. gracilis*, coupled with a reduction in grazing-intolerant

The authors wish to thank the USDA-ARS for use of the Central Plains Experimental Range. Paul Stapp and Mark Lindquist provided advice and logistical support in the field, and Mary Ashby helped with plant identification. Dave Golden, Jon Gering, Bob Parmenter, Douglas Andersen, and Jeff Powell provided comments on previous drafts of the manuscript. Special thanks to Nicolás Fernández for providing a spanish translation of the abstract. Our research was supported by the USDA Competitive Grants Program (No. 95031420) and the Miami University Summer Scholars Program.
Manuscript Accepted 15 Feb. 1999.

species, decreases plant species diversity and patch heterogeneity in heavily grazed areas of shortgrass steppe (Lauenroth et al. 1994). Soil disturbance by soil-dwelling animals or fecal deposition by livestock causes mortality of competitively dominant *B. gracilis* (Coffin and Lauenroth 1989) and opens sites for colonization by other plant species (Milchunas et al. 1990). Broad-scale effects such as grazing therefore interact with small-scale disturbance processes to influence the plant community diversity and spatial heterogeneity in grassland systems (Collins 1987, Steuter et al. 1995).

Small-mammal disturbances alter soil nutrient levels and plant species composition (Platt 1975, Huntly and Inouye 1988, Whicker and Detling 1988, Guo 1996). Pocket gophers (*Thomomys* spp. and *Geomys* spp.) are particularly important as disturbance agents because they are locally abundant and have a widespread distribution in coniferous forests, alpine meadows, and grasslands (Mielke 1977, Andersen and MacMahon 1985, Grant et al. 1980, Huntly and Inouye 1988, Cortinas and Seastedt 1996). Gopher mounds often have higher levels of soil nutrients (Inouye et al. 1987), reduced soil evaporation, and increased soil water permeability compared to undisturbed areas (Grant et al. 1980, Williams et al. 1986). The alteration of soil characteristics in pocket-gopher disturbances affects plant community composition. Plant diversity on gopher mounds is often greater than surrounding areas (Huntly and Inouye 1988) because disturbance reduces competition with dominant plant species and favors colonization by opportunistic species (Hobbs and Mooney 1985, Williams et al. 1986, Martinsen et al. 1990). As a result, annuals and perennial forbs generally increase on disturbance patches in grasslands (Huntly and Inouye 1988, Martinsen et al. 1990) and it can take up to 10 years for dominant grasses to recolonize a disturbance (Vaughan 1967, Coffin and Lauenroth 1988).

Soil disturbance and burrowing activities are closely linked to food consumption in pocket gophers (Reichman et al. 1982, Andersen and MacMahon 1985). Pocket gophers tunnel as part of their foraging and search behavior so that the spatial pattern of disturbance is linked to movement behavior as well as population abundance (Reichman et al. 1982, Benedix 1993, Andersen 1996). Forbs and succulents are a major part of gopher diets (Vaughan 1967, Andersen and MacMahon 1981, Hunt 1993, Steuter et al. 1995), although significant quantities of perennial grasses are used in shortgrass steppe and mixed-grass prairie (Vaughan 1967, Foster and Stubbendieck 1980).

Past studies have elucidated the mechanisms of plant responses to gopher disturbances, but few investigations have considered how broad-scale factors of grazing and topography affect plant responses to disturbance in rangelands (e.g. Steuter et al. 1995). Here, we present our findings from a 2-year study of the spatial variability in soil disturbance by the northern pocket gopher (*Thomomys talpoides attenuatus* Hall and Montague) and the plant responses to gopher disturbance across grazing regime and topography in shortgrass steppe. We examined 3 aspects of gopher disturbance and plant responses to gopher mounds as they varied over grazing intensity and topographic position: (1) the size, frequency, and distribution of pocket-gopher mounds; (2) total plant cover and dominance by *B. gracilis* on gopher mounds; and (3) the species richness and composition of plants on gopher mounds.

Methods

Study Site

Our study was conducted at the Central Plains Experimental Range (CPER), about 40 km northeast of Fort Collins, Colo. The 6,000-ha area is the site of a long-term grazing study managed by the USDA-ARS, and is comprised of 130-ha pastures that have been lightly, moderately, or heavily grazed by cattle since 1939. Lightly grazed pastures have about 20% of the above-ground production removed by cattle, moderate grazing at 40% removal, and heavy grazing at 60% removal (Lauenroth and Milchunas 1992). Topography varies from upland plains to gentle slopes and swales. Mean monthly temperatures vary from -5°C in January to 22°C in July and mean annual precipitation is 311 mm (Lauenroth and Milchunas 1992). Precipitation from April through July differed markedly in the 2 years of our study, with 252 mm in 1996 and 137 mm in 1997. The 43-yr mean at the site is 197 mm, so that precipitation was 28% above normal in 1996 and 30% below normal in 1997 (cf. Milchunas et al. 1989).

We measured the spatial distribution of pocket-gopher activity within two, 75 x 900 m transects, 1 located in a lightly grazed pasture (23W) and one in a heavily grazed pasture (23E). Pastures were adjacent and each transect spanned the same topographic sequence: a south-facing slope, a lowland swale, a north-facing slope, and an upland plain. Soils vary from sandy loams on uplands to clay loams in swales. Similar soil series are represented along the topographic sequence in the lightly grazed and heavily grazed pastures (see Crist and Wiens 1996).

The dominant perennial grass is *B. gracilis*, but three-awn (*Aristida longiseta* Nutt.), buffalo grass (*Buchloe dactyloides* [Nutt.] Engelm.), needlegrass (*Stipa comata* Trin. and Rupr.), and wheatgrass (*Agropyron smithii* Rydb.) are also common. Prickly pear cactus (*Opuntia polyacantha* Haw.) is abundant and numerous perennial forbs are scattered among the dominant grasses. Shrubs include fringed sage (*Artemisia frigida* Willd.), rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britt.), and broom snakeweed (*Gutierrezia sarothrae* [Pursh.] Britt. and Rusby). *B. gracilis* cover is generally higher and shrub cover is lower in the heavily grazed than in the lightly grazed pasture (Crist, unpublished data).

Pocket-Gopher Disturbances

Pocket gophers created surface mounds and burrow systems in distinct clusters of 20–30 m in diameter. Clusters of mounds and burrows were usually discontinuous and rarely overlapped, perhaps because only one adult is usually found within a cluster of mounds (R. R. Parmenter, personal communication) and individuals interact to produce burrow spacing patterns (Reichman et al. 1982). During July 1996, we mapped the locations of all clusters along each transect by placing a stake within the center of each cluster and recording its position using a total station surveying instrument (Nikon, C-100). This sample period follows the peak activity in burrowing and mound formation by pocket gophers at this site

(Vaughan 1967). Few pocket-gopher disturbances were found in the swale, so we focused our sampling efforts on the south- and north-facing slopes and on uplands within each transect.

At each topographic position, a subset of clusters was randomly chosen for more detailed measurements. A total of 12 clusters (2 clusters x 3 topographic positions x 2 pastures), were measured in 1996, and 24 clusters (4 clusters x 3 topographic positions x 2 pastures) were measured in July 1997. Within each cluster, we recorded the distance and compass direction of each gopher mound from the center stake, and estimated the size of each mound within the cluster. Mound size was determined by measuring the diameter along 2 perpendicular axes, and area was calculated assuming an ellipse.

We then estimated the total ground surface area disturbed by pocket gophers in each combination of topography and grazing by the following: total number of clusters x average number of mounds per cluster x the average mound area within a cluster. Because we did not map clusters of mounds along transects again in 1997, we used the same total number of clusters for each topographic position in estimates of disturbance area for both 1996 and 1997.

Vegetation Sampling

In 1996, two clusters of pocket-gopher mounds were randomly selected at each of the 3 topographic positions. Vegetation sampling was conducted on five randomly selected mounds within each cluster for a total of 10 mounds in each topographic position. We used a 0.5 x 0.5-m quadrat placed over the center of the gopher mound to record the basal cover of each plant species. Values were rounded to the nearest 1% and species with negligible cover were assigned a value of 1%. The quadrat occasionally included some of the plants near the edge of the mounds; these plants are still influenced by the mound disturbance, however, as "background" levels of plant biomass occur at diameters of >50 cm around gopher mounds at this site (Grant et al. 1980). The relative age of each mound sampled was noted as new (freshly turned soil), recent (<1 yr, with little or no vegetation), or old (>1 yr, with numerous plants). Because mounds were randomly sampled, we did not control for mound age; however, most of the mounds sampled were recently formed (<1 yr) except those that were resampled in 1997 (which were >1-yr old).

Plant sampling of gopher mounds was conducted in the same manner in 1997 except that we added 2 clusters of mounds at each topographic position and sampled 3 mounds (rather than 5) within each cluster. Thus, there was total of 12 mounds (4 clusters x 3 mounds per cluster) within each topographic position and pasture. Of these, 6 mounds (3 mounds within 2 of the 4 clusters) were the same as those sampled in 1996. Therefore, 36 of the 60 mounds sampled in 1996 were measured again as part of the 72 mounds sampled in 1997. This provided some continuity in yearly comparisons but permitted a broader sampling of gopher mounds in 1997.

Data Analysis

We conducted a nested analysis of variance (ANOVA; Neter et al. 1990) to determine differences in mean mound areas and plant community variables between pastures and among topographic positions. Analyses were performed using mounds nested within clusters (5 in 1996, 3 in 1997), and clusters nested within topographic position (2 in 1996, 4 in 1997). Separate analyses were conducted for mound area, total plant cover, *B. gracilis* cover, and species richness in 1996 and 1997. Analysis of variance for a nested design involves hypothesis tests using different error terms: the effects of pasture and topography were tested using clusters as replicates, and the effect of clusters within topographic position were tested using mounds as replicates (Neter et al. 1990).

Finally, we used detrended correspondence analysis (DCA) to examine overall changes in plant species composition on gopher mounds among pastures, topographic positions, and years. Correspondence analysis is a reciprocal averaging technique that maximizes the weighted averages of the species abundances across sites (ter Braak 1987). The resulting multivariate ordination axes often have a conspicuous "arch effect" and may require detrending (ter Braak 1987; Palmer 1993). We performed DCA by taking the average cover of each species within a topographic position so that site scores represent the weighted average of species cover values at 3 topographic positions, 2 pastures and 2 years (12 site scores total). The DCA was conducted using PC-ORD software (McCune and Mefford 1995).

Results

The estimated fraction of the total area disturbed by pocket gophers varied between 0.1–5.6% across topographic positions, pastures, and years (Table 1). Estimates of disturbance area were generally greater on south-facing slopes and uplands than on north-facing slopes due primarily to a larger number of disturbances (Table 1, Fig. 1). A greater variability was obtained for estimates of disturbance area in the heavily grazed

Table 1. The estimated area disturbed by the northern pocket gopher according to pasture and topography during 1996 and 1997. SF=south-facing slope, NF=north-facing slope, UP=upland plain. Values in parentheses are ±1 SE.

Pasture	Topo-Position	Total Area	No. Clusters	Year	Mound Area Per Cluster	Total Mound Area	% Area Disturbed
		(m^2)			(m^2)	(m^2)	%
Heavy	SF	14,400	31	1996	25.9 (0.3)	803	5.6
				1997	4.2 (0.6)	130	0.9
	NF	15,900	4	1996	8.7 (3.6)	35	0.2
				1997	5.4 (2.2)	22	0.1
	UP	21,075	32	1996	7.3 (0.7)	234	1.1
				1997	12.4 (2.4)	397	1.9
Light	SF	12,150	46	1996	3.4 (0.7)	156	1.3
				1997	5.0 (1.1)	230	1.9
	NF	16,200	36	1996	3.4 (0.1)	122	0.8
				1997	3.9 (2.6)	140	0.9
	UP	28,875	57	1996	4.4 (0.7)	251	0.9
				1997	5.8 (1.1)	331	1.1

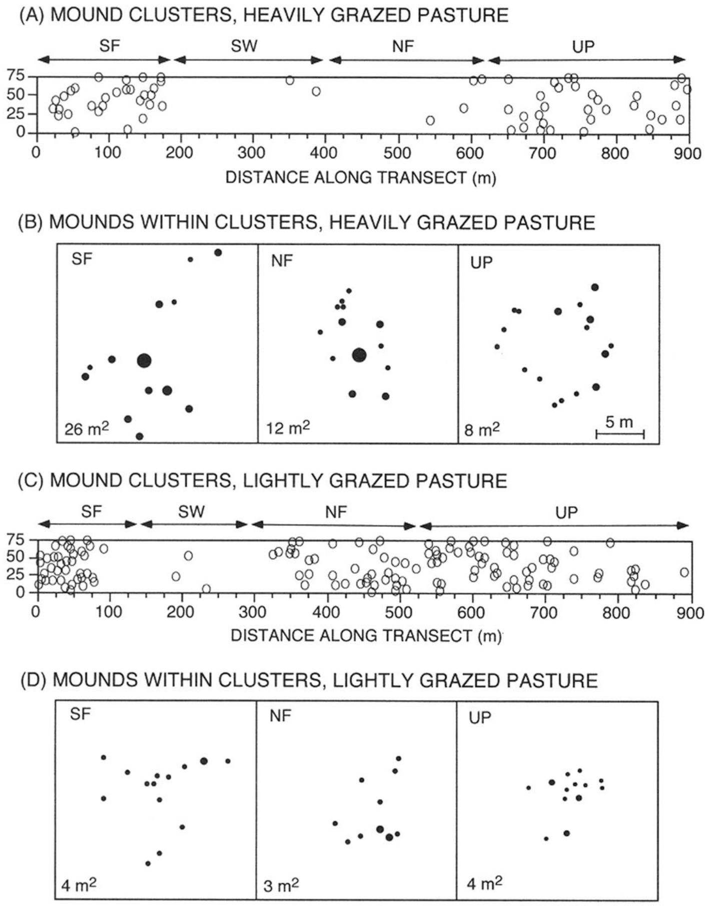

Fig. 1. The spatial distribution of pocket-gopher disturbances along a topographic gradient in 2 pastures. Topographic positions are south-facing slope (SF), swale (SW), north-facing slope (NF), and upland plain (UP). (A and C) Locations of clusters of mounds along 75 x 900-m transects. (B and D) Locations and sizes of mounds within 1 of the clusters sampled in 3 topographic positions (total area of mounds within each cluster is in the lower left).

(0.1–5.6%) than in the lightly grazed pasture (0.8–1.9%). Pocket gopher mounds and clusters were more numerous in the lightly grazed pasture (Table 1, Fig. 1) but mounds were generally larger in the heavily grazed pasture. The effect of pasture on mound size was significant in 1996 but not in 1997 (Table 2, Fig. 2), and the effect of topography on mound size was not significant in either year although there was a trend towards smaller mounds on uplands in 1996 (Table 2, Fig. 2).

Total plant cover on gopher mounds was greater in 1996 (42–57%) than in 1997 (16-23%). There was a weak but non-significant interaction between pasture and topography on plant cover in 1996 (Table 2) because mounds on the south- and north-facing slopes had a greater cover in the heavily grazed pasture, whereas mounds on uplands had a slightly greater cover in the lightly grazed pasture (Fig. 3). In 1997, however, mounds in the heavily grazed pasture had significantly greater plant cover than in the lightly grazed pasture (Table 2, Fig. 3).

Cover of the dominant perennial grass, *Bouteloua gracilis*, was greater on gopher mounds in 1996 (4-23%) than in 1997 (3–10%) (Fig. 4). About half of the decrease in total plant cover on mounds from 1996 to 1997 can therefore be explained by reduced cover of *B. gracilis*. There was a significant effect of topography in 1996 (Table 2), with both pastures showing a large decrease in *B. gracilis* cover from south-facing to north-facing slopes and a smaller decrease from north-facing slopes to uplands (Fig. 4). A significant effect of cluster also occurred (Table 2) in 1996, suggesting that there was considerable variation in *B. gracilis* cover on mounds within a topographic position. In 1997, *B. gracilis* cover on mounds within the heavily grazed pasture was significantly greater than on mounds in the lightly grazed pasture (Fig. 4).

A total of 35 and 34 plant species were recorded on gopher mounds during 1996 and 1997, respectively, representing a total of 47 different species. Mean plant-species richness per mound was similar (5–8 species) across pastures and topography in both years (Fig. 5), but there was significant variation in species richness among mounds located in different clusters during 1997 (Table 2). Although overall species richness was similar across pasture and topography, plant species composition clearly differed. The DCA showed that the plant species on gopher mounds were most strongly affected by pasture (Fig. 6). The DCA axis 1 primarily differentiated pasture and, to a lesser extent, topographic position. Yearly differences are largely represented along the DCA axis 2. Site scores from the heavily grazed pasture showed the greatest movement between years, thus reflecting the greater change in plant cover between years than was observed in the lightly grazed pasture (Fig. 6a). Overall, the first 2 ordination axes of the DCA explained 43% of the variation in the plant species data. A third axis explains nearly half (49%) of the total variation.

Different plant species were associated with gopher mounds depending on pasture and topography (Fig. 6b). The DCA species score for *B. gracilis* was most closely related to the site scores of the heavily grazed pasture on the south-facing slopes (Fig. 6b), which is consistent with mean cover values (Fig. 4). *Aristida longiseta* and *Sitanion hystrix* (Nutt.) J. G. Sm. were highly associated with the 1997 site scores for the heavily grazed upland and the lightly grazed upland, respectively (Fig. 6b). These patterns are consistent with previous findings for off-mound vegetation, which showed that *A. longiseta* had a greater cover in grazed uplands and *S. hystrix* was more common in ungrazed uplands (Milchunas et al. 1989). *Stipa comata* was associated with gopher mounds on lightly grazed uplands in 1996, and *Buchloe dactyloides* had greater cover in lightly grazed areas in 1997 (Fig. 6b). *Agropyron smithii* and *Sporobolus cryptandrus* (Torr.) A. Gray were more common on gopher mounds sampled on north-facing slopes of the

Table 2. Analysis of variance of pocket-gopher mound areas (log-transformed), total basal plant cover, basal cover of *Bouteloua gracilis*, and plant-species richness in 1996 and 1997. Values are F-statistics for the effects of pasture and topography using Error a (variation among clusters of mounds), and the effect of clusters of mounds using Error b (variation among mounds within clusters). In 1996, 5 mounds were randomly sampled within 2 clusters of mounds at each of 3 topographic positions (south- and north-facing slopes and upland) located in lightly and heavily grazed pastures (60 mounds). In 1997, a total of 3 mounds were randomly sampled within 4 clusters in each combination of topography and grazing (72 mounds).

Source of Variation	df	Mound Area	Total Cover	*B. gracilis* Cover	Plant Species Richness
1996					
Pasture	1	8.506*	0.705	1.082	2.989
Topography	2	3.542†	0.313	5.396*	1.395
Pasture x Topography	2	1.429	4.852†	0.059	2.684
Error a (clusters)	6	0.721	0.532	2.486*	1.580
Error b (mounds)	48				
Total	59				
1997					
Pasture	1	3.372†	10.469**	12.980**	0.924
Topography	2	0.075	0.109	2.515	0.452
Pasture x Topography	2	0.345	0.502	0.566	0.128
Error a (clusters)	18	1.075	0.665	0.542	1.905*
Error b (mounds)	48				
Total	71				

†0.05<†P<0.10, *P<0.05, **P<0.025

heavily grazed pasture in 1996 (Fig. 6b). The association of *A. smithii* with more mesic locations is consistent with the findings of Milchunas et al. (1989), but their study showed *A. smithii* to have greater cover in ungrazed plant communities. *Gaura coccinea* Nutt. ex Pursh and *Sphaeralcea coccinea* (Pursh.) Rydb. are perennial forbs that were primarily found on gopher mounds on the south-facing slope of the heavily grazed pasture (Fig. 6b). Four perennial shrubs (*Chrysothamnus nauseosus*, *Gutierrezia sarothrae, Eriogonum effusum* Nutt. and *Artemisia frigida*) and *Opuntia polyacantha* were all more commonly associated with pocket gopher mounds on uplands in the lightly grazed pasture (Fig. 6b). In contrast, the common annual plants on gopher mounds—a grass (*Vulpia octoflora* Walt. and 2 forbs (*Euphorbia glyptosperma* Engelm. and *Plantago patagonica* Jacq.)—were largely found in the heavily grazed pasture in 1996 (Fig. 6b).

Discussion

The size and frequency of disturbances by pocket gophers were highly variable among pastures, topography, and year. Pocket gophers were most important on south-facing slopes and uplands, where the area disturbed was generally >1%. In contrast, north-facing slopes in both pastures had <1% of the area disturbed, and swales had virtually no disturbance by pocket gophers. A significantly larger mound size in the heavily grazed than in the lightly grazed pasture translated into a larger proportion of the total area disturbed only on the south-facing slope where disturbances were frequent. In general, however, the estimated area disturbed was similar between pastures because larger mounds in the heavily grazed pasture compensated for the greater number of smaller disturbances in the lightly grazed pasture. At the same site, Grant et al. (1980) estimated that pocket gophers disturbed 8% of the ground surface area in the heavily grazed pasture, 2.5% of the area in lightly grazed pasture, and 6.5% in an ungrazed exclosure.

Our findings, and those of Grant et al. (1980), suggest that factors other than grazing such as soil characteristics or plant species composition also have important roles in determining the size and frequency of disturbance by pocket gophers. The yearly changes in mound size and total area disturbed suggest that differences in precipitation (252 mm in 1996, 137 mm in 1997) affected patterns of pocket-gopher disturbance, perhaps due to changes in plant productivity. A higher food availability in 1996 than in 1997 could have led to increased pocket-gopher abundance or altered the size and arrangement of burrows (Vaughan 1967, Reichman et al. 1982, Hunt 1993, Andersen 1996).

The spatial patterns of disturbance might also be related to food preferences of pocket gophers. Vaughan (1967) examined the diet of the northern pocket gopher in shortgrass steppe, and found that *O. polyacantha* comprised >50% of the yearly food intake. Forbs, such as *S.*

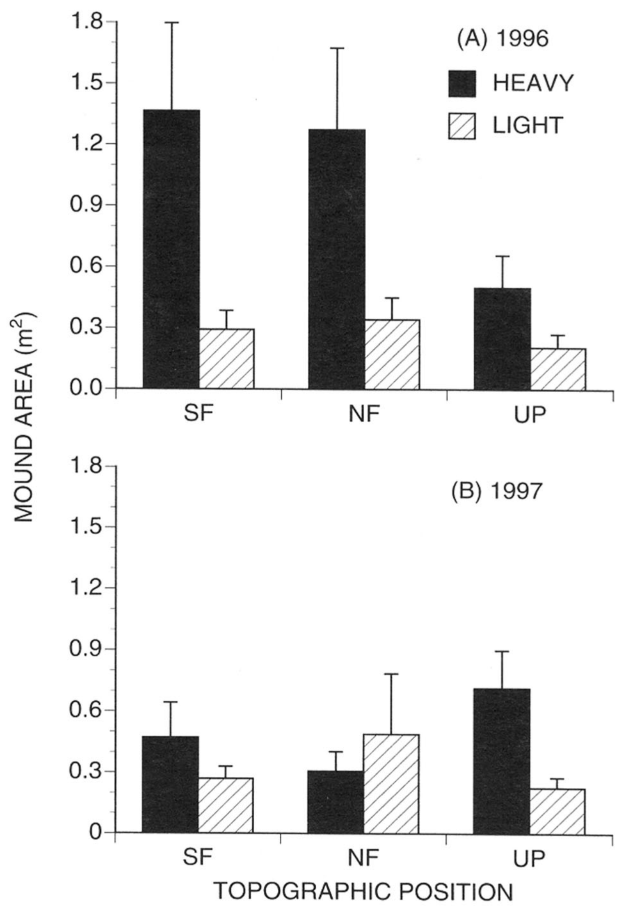

Fig. 2. Mean areas (±1 SE) of gopher mounds at 3 topographic positions in heavily and lightly grazed pastures during (A) 1996 (n = 60) and (B) 1997 (n = 72).

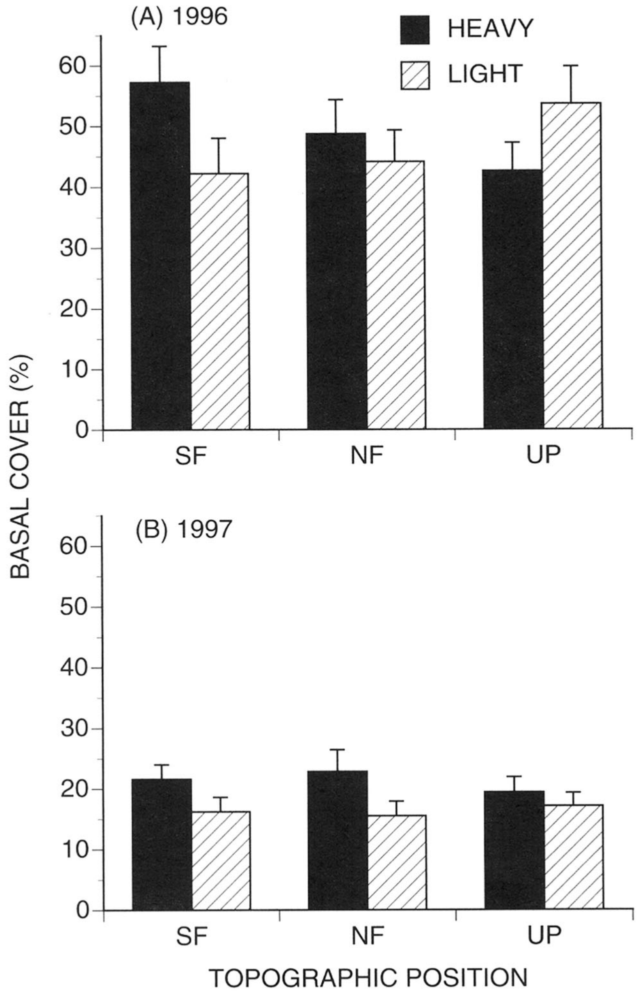

Fig. 3. Mean basal cover (±1 SE) of all plants on pocket gopher mounds at 3 topographic positions in heavily and lightly grazed pastures during (A) 1996 and (B) 1997.

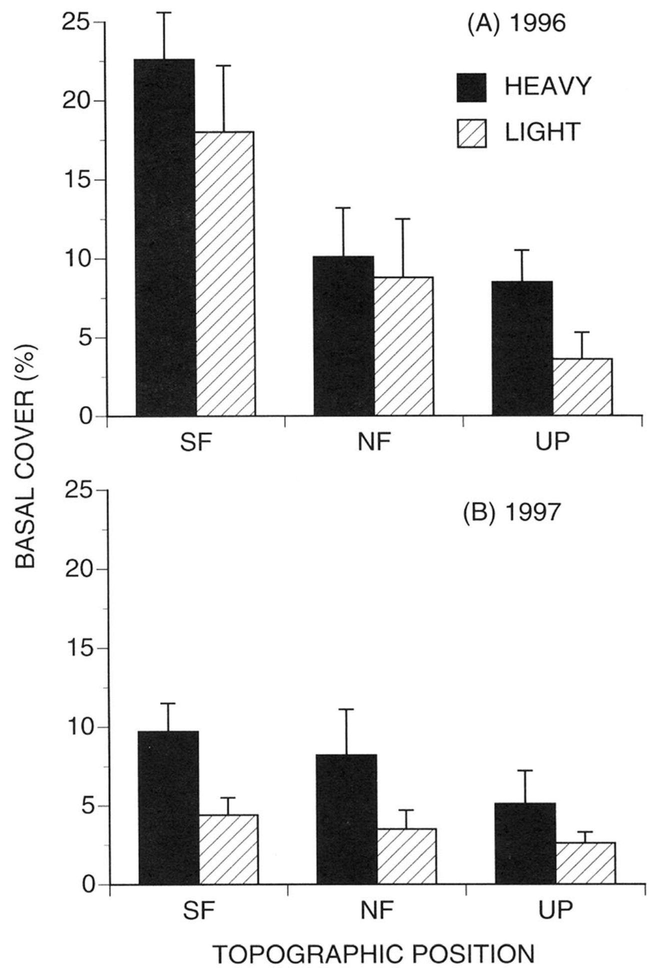

Fig. 4. Mean basal cover (±1 SE) of blue grama (*B. gracilis*) on pocket gopher mounds at 3 topographic positions in heavily and lightly grazed pastures during (A) 1996 and (B) 1997.

coccinea, were also important in pocket-gopher diets (see also Andersen and MacMahon 1981, Hunt 1993, Steuter et al. 1995) and perennial grasses, such as *B. gracilis*, were primarily consumed in June when grasses peak in green biomass (Vaughan 1967). For several reasons, however, the strong preference of pocket gophers for *O. polyacantha* might be more important than the consumption of grasses in determining the size and distribution of gopher disturbances. First, *O. polyacantha* is most common on slopes and uplands (Milchunas et al. 1989) where gopher disturbances are abundant. Second, among all plant samples, mound size was negatively related to *O. polyacantha* cover ($r=-0.37$ in 1996, $df=59$, $P<0.01$; $r=-0.24$ in 1997, $df=71$, $P<0.05$), but was unrelated to *B. gracilis* cover ($r=0.09$ in 1996 and $r=-0.12$ in 1997; $P>0.30$). This suggests that search area—and therefore disturbance size—is smaller in patches with greater cover of *O. polyacantha*, which is consistent with observed patterns of area-restricted search by pocket gophers in preferred food patches (Hunt 1993, Andersen 1996). Lastly, overall food availability to pocket gophers is likely greater in cactus patches because *O. polyacantha* also deters cattle grazing of nearby plants (Milchunas et al. 1989). Given the potentially important relationships among cattle grazing, cactus cover, and pocket gophers as disturbance agents, these interactions clearly deserve further attention in semiarid rangelands.

Our findings on *B. gracilis* responses to gopher disturbances across pastures and topography are consistent with previous studies which found that heavy livestock grazing in the shortgrass steppe results in increased dominance by *B. gracilis* (Milchunas et al. 1989, Lauenroth et al. 1994). Topographic position also affected the response of *B. gracilis* to pocket-gopher disturbance; there was a marked decrease in *B. gracilis* cover on upland gopher mounds, especially during 1996. Upland areas may have less cover of *B. gracilis* than slopes due to a coarser soil texture, decreased water availability, or a lower grazing intensity by cattle (Coffin and Lauenroth 1988, Milchunas et al. 1989). Because overall plant cover on gopher mounds was similar across topographic positions (Fig. 3, Table 2), a decreased dominance of *B. gracilis* on uplands (Fig. 4) therefore corresponded with increased cover of perennial grasses

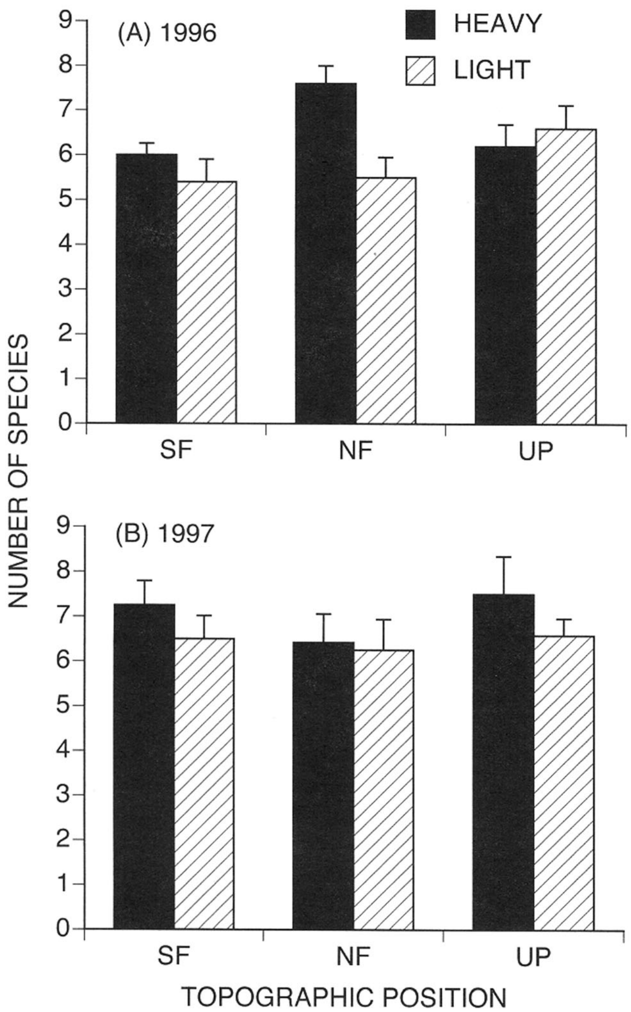

Fig. 5. Mean plant-species richness (±1 SE) on pocket gopher mounds at 3 topographic positions in heavily and lightly grazed pastures during (A) 1996 and (B) 1997.

such as *A. longiseta* and *S. comata*, and perennial shrubs such as *A. frigida* (Fig. 6b). Species replacement of *B. gracilis* on uplands is especially clear in the greater plant cover observed on upland mounds within the lightly grazed pasture in 1996 (Fig. 3), which explains the weak interaction of pasture and topography on plant cover (Table 2).

Gopher disturbances had a lower basal cover of *B. gracilis* (5–22% in 1996, 3–10% in 1997; Fig. 4) compared to the surrounding plant community (20–35%; Coffin and Lauenroth 1988, Milchunas et al. 1989). Although *B. gracilis* was still the dominant plant on gopher mounds, the fraction of the total plant cover attributable to *B. gracilis* was considerably less (21% on lightly grazed mounds both years, and 27% on heavily grazed mounds in 1996 and 29% in 1997) than in off-mound samples of the plant community (cf. 90%; Milchunas et al. 1989). Survival and recovery of *B. gracilis* on disturbance patches depends upon the size of disturbance relative to individual plants (Coffin and Lauenroth 1988). Small disturbances such as cattle fecal pats that are similar in size to *B. gracilis* plants (mean basal cover of 0.03–0.04 m^2; Aguilera and Lauenroth 1993) increases the likelihood that plants will re-establish on the disturbance by tillering. If disturbances are larger, however, such as the pocket-gopher mounds studied here (0.3–1.3 m^2; Fig. 2), then recolonization depends to a greater degree on seedling establishment (Coffin and Lauenroth 1988) because of the slow rates of vegetative expansion of *B. gracilis* (Samuel and Hart 1995). We found several isolated *B. gracilis* plants on gopher mounds, suggesting that seedling establishment is important in colonization of pocket-gopher disturbances by *B. gracilis*. Whether colonization is by vegetative growth or seedling establishment, however, broad-scale factors likely affected *B. gracilis* establishment on gopher disturbances in our study because *B. gracilis* shows an increased lateral expansion when grazed (Milchunas et al. 1989, Lauenroth et al. 1994) and seedling establishment is strongly influenced by soil texture (Coffin and Lauenroth 1994).

Pocket-gopher mounds did not differ in overall plant-species richness despite the variation in *B. gracilis* cover (Fig. 4) and plant species composition (Fig. 6) across topography and pasture. Several studies have shown a higher plant diversity on gopher mounds compared to off-mound vegetation (Foster and Stubbendieck 1980, Hobbs and Mooney 1985, Williams et al. 1986, Inouye et al. 1987, Martinsen et al. 1990). We did not sample plants in areas adjacent to gopher mounds in this study. Plant cover data were obtained in 1996, however, from 0.25 m^2 quadrat samples at 20-m intervals along the 900-m transects. In these off-mound plant samples, a mean of 7.8 species per plot was found in the lightly grazed pasture, and was significantly greater than the 4.9 per plot in the heavily grazed pasture (paired $t=7.50$, $P<0.001$). We found an overall mean of 5.8 species per plot on gopher mounds in the lightly grazed pasture and 6.6 per plot on mounds in the heavily grazed pasture (Fig. 5). Although the latter difference is not significant (Table 2), the trend is reversed from the pattern of off-mound richness. Thus, patterns of plant diversity on and off gopher mounds appear to interact with the effects of pasture.

Pasture produced the largest separation of DCA site scores for plant species composition among the 3 effects of pasture, topography, and year (Fig. 6a). Within pasture, site scores for topographic positions were consistently ordered from south-facing to north-facing slopes to uplands (Fig. 6a), which suggests that plant species composition on gopher mound differed most between south-facing slopes and uplands. The perennial plant species on gopher mounds are consistent with grazing-induced changes in the surrounding plant community (Fig. 6b). A greater cover of grazing-tolerant grasses such as *B. gracilis* and *A. longiseta* on mounds in the heavily grazed pasture are consistent with the off-mound responses of these species. Similarly, a greater cover of perennial shrubs such as *A. frigida* on mounds in the lightly grazed pasture are also consistent with pasture differences in the surrounding plant community (Milchunas et al. 1989).

Yearly variation in plant species composition on gopher mounds was likely due to several factors, including mound age, colonization of annual plants, and selective plant mortality. A relatively wide separation of the site score for mounds on the lightly-grazed south-facing slope during 1996 compared to other topographic positions was due to a greater mound cover of annual forbs such as *P. patagonica* and *E. glyptosperma*. Along with an annual grass, *V. octoflora*, these annuals were most abundant in the heavily grazed pasture

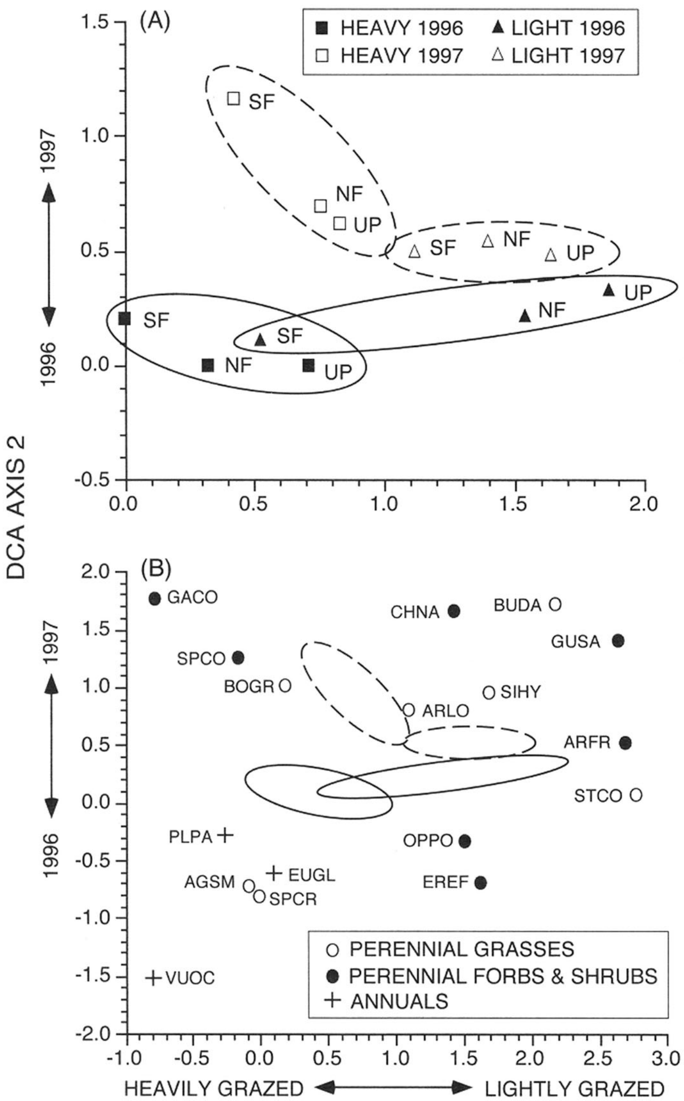

Fig. 6. (A) Detrended correspondence analysis (DCA) plot of site scores for plants on gopher mounds by pasture, topographic position, and year. (B) DCA plot of species scores with ellipses that enclose the site scores shown in A. All 47 plant species sampled on gopher mounds were analyzed, and shown are the 17 most common species (overall basal cover >1%). Perennial grasses: *Agropyron smithii* (AGSM), *Aristida longiseta* (ARLO), *Bouteloua gracilis* (BOGR), *Buchloe dactyloides* (BUDA), *Sitanion hystrix* (SIHY), *Sporobolus cryptandrus* (SPCR), *Stipa comata*. Perennial forbs, shrubs, and succulents: *Artemisia frigida* (ARFR), *Chrysothamnus nauseosus* (CHNA), *Eriogonum effusum* (EREF), *Gaura coccinea* (GACO), *Gutierrezia sarothrae* (GUSA), *Opuntia polyacantha* (OPPO), *Sphaeralcea coccinea* (SPCO). Annuals: *Vulpia octoflora* (VUOC), *Euphorbia glyptosperma* (EUGL), *Plantago patagonica* (PLPA).

in 1996. The greater movement of the site scores for the heavily grazed than for the lightly grazed pasture between 1996 and 1997 was also due to a decrease in cover of these annuals on gopher mounds. The greater number of annuals on mounds in 1996 than in 1997 could be because we sampled fewer newly-formed mounds in 1997 (36 of 72 were those sampled in 1996), which might favor annual plant establishment. A greater number of older mounds could explain fewer annuals and a smaller size of mounds observed in 1997 (Fig. 2); mound age, however, does not explain a lower plant cover in 1997 than in 1996 (Fig. 2) since plant cover increases with mound age (Foster and Stubbendieck 1980). We therefore attribute fewer annuals and a decrease in perennial plant cover on mounds between years to a wet spring and summer in 1996 and a relatively dry growing season in 1997.

Conclusions and Management Implications

Our study shows how the broad-scale effects of pasture and topography can influence the variation in the gopher disturbance regime as well as patterns of plant responses to gopher disturbance. Topography primarily affected the numbers of gopher mounds, which were most common on south-facing slopes and uplands. We note that another disturbance agent, the western harvester ant (*Pogonomyrmex occidentalis* Cresson), also has greater nest densities in these topographic positions (Crist and Wiens 1996). In shortgrass steppe, the combined effects of these 2 animals on disturbance area and plant productivity may therefore be considerably greater than that described here for pocket gophers alone. As with harvester ants, however, the effect of pocket gophers may be to redistribute rather than reduce plant productivity because increases in plant productivity adjacent to mounds may compensate for the lost productivity in the disturbance patch (Rogers and Lavigne 1974, Grant et al. 1980). Nonetheless, pocket-gopher disturbances can favor the establishment of plant species that are less palatable to livestock as forage (Foster and Stubbendieck 1980). We found that the species composition of plants on pocket-gopher mounds was most strongly influenced by pasture. Mounds in the heavily grazed pasture showed: (1) a larger average size, (2) a greater cover of *B. gracilis*, and (3) a greater yearly variation due to an increased cover of annuals and a decreased cover of perennial shrubs.

Past studies of animal disturbances in rangelands are often conducted in small areas (1 ha or less), but management practices are typically implemented over much larger areas (100 ha or more). To extrapolate the rangeland effects of animal disturbances over broader areas, therefore, measurements of the size and frequency of disturbance as well as plant responses to disturbance should be taken across various topographic positions and grazing regimes. Finally, our study points to the need for future studies on the spatial relationships among cattle grazing, prickly pear cactus, and pocket-gopher disturbances in semiarid grasslands.

Literature Cited

Aguilera, M. O. and W. K. Lauenroth. 1993. Neighborhood interactions in a natural population of the perennial bunchgrass *Bouteloua gracilis*. Oecologia 94: 595–602.

Andersen, D. C. 1996. A spatially explicit model of search path and soil disturbance by a fossorial herbivore. Ecol. Model. 89: 99–108.

Andersen, D. C. and J. A. MacMahon. 1981. Population dynamics and bioenergetics of a fossorial herbivore, *Thomomys talpoides* (Rodentia: Geomyidae), in a spruce-fir sere. Ecol. Monogr. 51: 179–202.

Andersen, D. C. and J. A. MacMahon. 1985. The effects of catastrophic ecosystem disturbance: the residual mammals at Mount St. Helens. J. Mammal. 66: 581–589.

Benedix, Jr., J. H. 1993. Area-restricted search by the plains pocket gopher (*Geomys bursarius*) in tallgrass prairie habitat. Behav. Ecol. 4: 318-324.

Coffin, D. P. and W. K. Lauenroth. 1988. The effects of disturbance size and frequency on a shortgrass plant community. Ecol. 69:1609–1617.

Coffin, D. P. and W. K. Lauenroth. 1994. Successional dynamics of a semiarid grassland: effects of soil texture and disturbance size. Vegetatio 110:67–82.

Collins, S. L. 1987. Interactions of disturbances in tallgrass prairie: a field experiment. Ecol. 68: 1243–1250.

Cortinas, M. R. and T. R. Seastedt. 1996. Short- and long-term effects of gophers (*Thomomys talpoides*) on soil organic matter dynamics in alpine tundra. Pedobiologia 40:162–170.

Crist, T. O. and J. A. Wiens. 1996. The spatial distribution of ant colonies in a semiarid landscape: implications for community and ecosystem processes. Oikos 76: 301–311.

Foster, M. A. and J. Stubbendieck. 1980. Effects of the plains pocket gopher (*Geomys bursarius*) on rangeland. J. Range Manage. 33:74–78.

Grant, W. E., N. R. French, and L. J. Folse, Jr. 1980. Effects of pocket gopher mounds on plant production in shortgrass prairie ecosystems. Southwest. Nat. 25: 215–224.

Guo, Q. 1996. Effects of bannertail kangaroo rat mounds on small-scale plant community structure. Oecologia 106:247–256.

Hobbs, R. J. and H. A. Mooney. 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. Oecologia 67: 342-351.

Hunt, J. 1993. Feeding ecology of valley pocket gophers (*Thomomys bottae sanctidiegi*) on a California coastal grassland. Amer. Midl. Natur. 127:41–51.

Huntly, N. J. and R. S. Inouye. 1988. Pocket gophers in ecosystems: patterns and mechanisms. BioSci. 38: 786–793.

Inouye, R. S., N. J. Huntly, D. Tilman, and J. R. Tester. 1987. Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesota. Oecologia 72:178–184.

Lauenroth, W. K. and D. G. Milchunas. 1992. Short-grass steppe. p. 183–226. *In:* R.T. Coupland (ed.) Ecosystems of the World 8a, Natural Grasslands: Introduction and Western Hemisphere. Elsevier, Amsterdam.

Lauenroth, W. K., D. G. Milchunas, J. L. Dodd, R. H. Hart, R. K. Heitschmidt, and L. R. Rittenhouse. 1994. Effects of grazing on ecosystems of the great plains. p. 69–100. *In:* M. Vavra, W. A. Laycock, and R. D. Pieper (eds.), Ecological implications of livestock herbivory in the West. Society for Range Management, Denver, Colo.

Martinsen, G. D., J. H. Cushman, and T. G. Whitham. 1990. Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community. Oecologia 83:132–138.

McCune, B. and M. J. Mefford. 1995. PC-ORD, Multivariate analysis of ecological data, ver. 2.0. MjM Software Design, Gleneden Beach, Ore.

Mielke, H. W. 1977. Mound building by pocket gophers (*Geomyidae*): their impact on soils and vegetation in North America. J. Biogeogr. 4:171–180.

Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. Vegetatio 80:11–23.

Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1990. Community attributes along a perturbation gradient in a shortgrass steppe. J. Veg. Sci. 1:175–184.

Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models, 3rd edition. Irwin, Homewood, Ill.

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecol. 74: 2215–2230.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tallgrass prairie. Ecol. Monogr. 45:285–305.

Reichman, O. J., T. G. Whitham, and G. A. Ruffner. 1982. Adaptive geometry of burrow spacing in two pocket gopher populations. Ecol. 63: 687–695.

Rogers, L. E. and R. J. Lavigne. 1974. Environmental effects of western harvester ants on the shortgrass plains ecosystem. Environ. Entomol. 3: 994–997.

Samuel, M. J. and R. H. Hart. 1995. Observations on spread and fragmentation of blue grama clones in disturbed rangeland. J. Range Manage. 48: 508–510.

Steuter, A. A., E. M. Steinauer, G. L. Hill, P. A. Bowers, and L. L. Tieszen. 1995. Distribution and diet of bison and pocket gophers in a sandhills prairie. Ecol. Appl. 5:756–766.

ter Braak, C. J. F. 1987. Ordination. p. 91-173. *In:* R. H. G. Jongman, C. F. J. ter Braak, and O. F. R. van Tongeren (eds.), Data analysis in community and landscape ecology. Pudoc, Wageningen, The Netherlands.

Vaughan, T. A. 1967. Food habits of the northern pocket gopher on shortgrass prairie. Amer. Midl. Natur. 77: 176–189.

Whicker, A. D. and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. BioSci. 38: 778–785.

Williams, L. R., G. N. Cameron, S. R. Spencer, B. D. Eshelman, and M. J. Gregory. 1986. Experimental analysis of the effects of pocket gopher mounds on Texas coastal prairie. J. Mammal. 67:672–679.