

## Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie

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### Abstract

A prairie dog (*Cynomys ludovicianus*) colony with a known history of habitation was studied to quantify the effects of herbivory on plant species composition, dominance, stature and diversity in a North American mixed-grass prairie. Gradient analysis was used to quantify the relationship between plant community structure, prairie dog density, burrow density and habitation history and to document community-level responses of plants subjected to heavy grazing pressure. The results quantify the type, rate and extent of change which plant populations and communities may undergo in response to the differential grazing of plants variously tolerant of defoliation.

Detrended correspondence analysis indicated that 69% of the between-sample floristic variance on the site was attributable to prairie dog habitation. Perennial grasses were rapidly displaced from the site within 3 yr of colonization and were replaced by annual forbs. The net result was an increase in species richness and diversity on the prairie dog colony. Within the colony, however, the number of species was more a function of stand size than colonization history.

Significant decreases in canopy stature after 2 yr of habitation resulted from replacement of mid-height grass species by shortgrass species and forbs. In addition, there was a shift from tall growth forms of off-colony species to dwarf growth forms of the same species on the colony. Decreases in litter and increases in bare soil cover were substantial during the first 2 yr of habitation but changed little thereafter.

**Abbreviations:** WCC – Wind Cave Canyon, DCA – Detrended Correspondence Analysis

### Introduction

Herbivores in some grassland systems consume more than half of the annual aboveground net primary production and in so doing may become primary agents of ecosystem change (McNaughton,

1983). Because forage preferences vary among herbivores and because plant life forms, growth forms and species are differentially tolerant of defoliation (Archer & Tieszen, 1980), grazing-induced changes in plant community organization typically involves an alteration of interference interactions among

plants. The preferential utilization of one set of plants may give less preferred or more grazing-resistant plants a competitive advantage and an opportunity to replace stressed plants (Archer & Detling, 1984). Over time, plant population dynamics (Jones & Mott, 1980) and distribution patterns (Jaksic & Fuentes, 1980) are altered and a grazing-induced retrogressive succession results (Bakker, 1985).

To determine the rate and extent of changes in plant community structure under conditions of continuous, high-intensity grazing, vegetation on a black-tailed prairie dog (*Cynomys ludovicianus*) colony with a known history was examined. Most analyses of plant assemblages on prairie dog colonies have simply compared vegetation on the colony with that of nearby uncolonized areas (e.g., Bonham & Lerwick, 1976; Hansen & Gold, 1977) without regard to patterning of vegetation. In this study, native prairie stands with known prairie dog habitation histories were sampled to (1) examine the relationship between plant community structure, prairie dog density, burrow density, and colonization history; and (2) evaluate the community-level response of grassland plants subjected to heavy grazing pressure from a native herbivore once widely distributed throughout North American grasslands.

### Study site

The Wind Cave Canyon (WCC) prairie dog colony selected for this study was one of 11 colonies in Wind Cave National Park (37°30'N, 103°17'E) in the Black Hills of South Dakota. The 11 355 ha park is about 25% *Pinus ponderosa* forest and 75% mixed-grass prairie. Free-ranging ungulate populations within the fenced park boundaries include approximately 350 bison (*Bison bison*), 420 elk (*Cervus canadensis*), 125 pronghorn (*Antilocapra americana*) and 125 mule deer (*Odocoileus hemionus*). See Coppock *et al.* (1983a) for additional description of vegetation, climate and soils of the area.

The WCC colony was located on a level 3.6 ha floodplain of an ephemeral water course at an elevation of ca. 1300 m. Soils were deep, dark silty loams. The site had been burned in the spring of 1976. We

assumed that vegetation was similar across the site before colonization. Prairie dogs were first noted at the site in the autumn of 1976. In May 1979, 32 individuals occupied a 0.47 ha area on the floodplain. By October 1980 there were ca. 85 individuals, colony area had expanded to 1.57 ha and 206 burrow entrances had been excavated. The data presented here were collected in July 1982, at which time the colony covered 1.86 ha, had 535 burrows and a population of 146 prairie dogs. See Garrett *et al.* (1982) for a detailed account of colony development and prairie dog demography. Growing-season precipitation in Wind Cave National Park ranged from 83% to 154% of the long-term average (320 mm) during the 1976 to 1982 period.

### Methods

A system of 15 by 15 m grids was constructed on the site in May 1979 to quantify colony development. The grid encompassed the area inhabited by prairie dogs at that time plus an additional 30 m boundary of uncolonized prairie. Expansion of the colony into previously uninhabited portions of the gridded site was mapped at three-month intervals. In July 1982 vegetation on the site was sampled after partitioning the area into 13 stands based upon our knowledge of colonization history and prairie dog family-unit territories (Table 1). Five contiguous stands, each inhabited 4–6 yr, occupied the center portion of the colony. Two stands colonized for three years each were spatially distinct from each other and occurred

Table 1. Summary of colonization history and prairie dog and burrow densities (mean  $\pm$  SE) for 13 stands sampled on a North American mixed-grass prairie site in July 1982. Animal densities represent a weighted family-unit average computed over a period from June 1979 to May 1982.

Stand age (yr)	N of stands	Burrows per ha	Prairie dogs/ha
0	2	0 $\pm$ 0	0 $\pm$ 0
2	4	123 $\pm$ 17	53 $\pm$ 5
3	2	239 $\pm$ 66	54 $\pm$ 3
4–6	5	271 $\pm$ 26	52 $\pm$ 5

around the periphery of the 4- to 6-yr old stands. Four stands colonized for two years were located on the colony extremities bordering two uncolonized areas. Where stands with the same colonization history interfaced, boundaries were set to coincide with prairie dog family-unit territorial boundaries, as determined by Garrett *et al.* (1982). Because territorial boundaries and colonization history dictated boundaries, stand sizes ranged from 0.04 to 0.39 ha.

In each stand, 20 × 50 cm plots were systematically located at 5 m intervals along parallel transects. Aerial cover of all vascular plant species rooted in the plot, height of the tallest ungrazed ramet of each species, and amounts of bare soil and litter were estimated for each plot. Our objective was to examine community changes resulting from grazing, thus, bison wallows and mounds associated with prairie dog burrows were not sampled. A total of 151 plots (10 to 20 per stand) were sampled among the 13 stands. Species-area curves for each stand were used

as an index of sample adequacy.

Species cover estimates, which ranged from a trace to 60%, were transformed to an octave scale logarithmic to the base 2. A total of 60 vascular plant species were encountered. Two grasses, *Bouteloua gracilis* and *Buchlōe dactyloides*, were grouped under the latter name because of difficulties with field identification of vegetative plant parts on the most heavily grazed site. *B. dactyloides* was the more abundant of the two on stands colonized ≤ 3 yr. The resulting 151 plots by 59 species matrix of transformed cover values was analyzed by DCA (Hill, 1979).

Cover values for each species were averaged across stands with similar colonization histories and diversity was calculated as  $\exp(H')$ , where  $H' = -\sum p_i \ln p_i$ ;  $p_i$  was the relative cover of species  $i$  (Peet, 1974). Burrow densities were computed for each stand in May 1982. Prairie dog densities were weighted territorial group densities averaged over the peri-

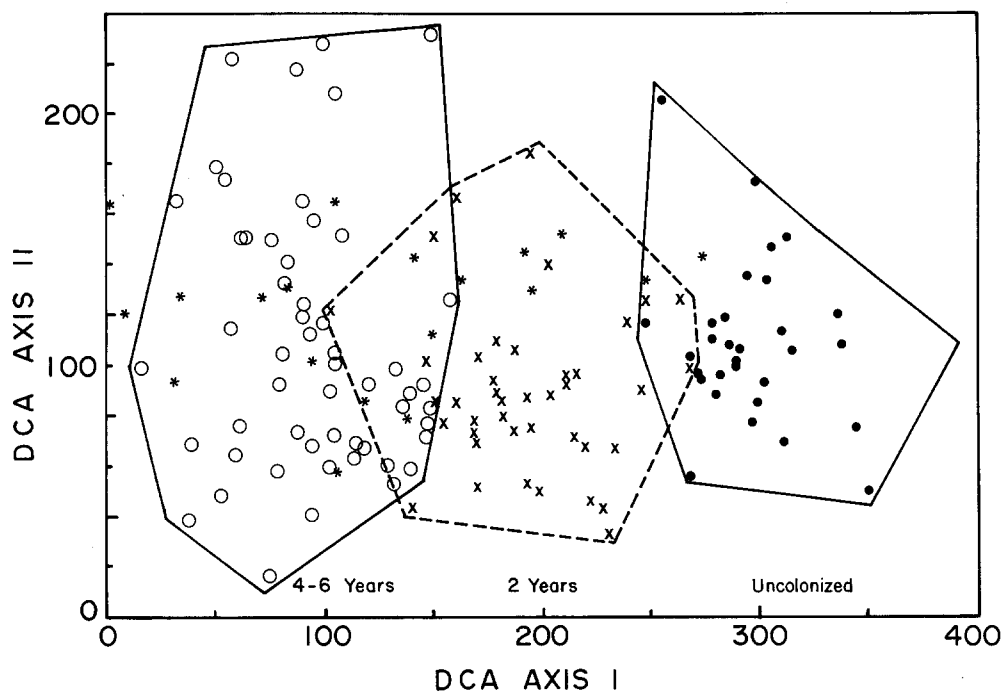


Fig. 1. Convex polygons in the plane of the first two axes of detrended correspondence analysis encompassing sample scores from stands with varying prairie dog habitation histories. The uncolonized polygon encompassed 31 samples from two stands (●). Four stands (45 samples) were contained in the second year polygon (X). Twenty samples from two stands (\*) represent the three-year-old portion of the colony (polygon omitted for clarity). Five stands (55 samples) were contained within the 4- to 6-year polygon (○). A linear regression of DCA Axis I scores with habitation history yielded an  $R^2 = 0.69$ .

od from May 1979 to May 1982 for each stand (Garrett, 1982). Analysis of variance (Nie *et al.*, 1975) and Tukey's *Q* procedure (Kirk, 1968) were used to test for significant ( $P < 0.05$ ) differences among means.

## Results

The distribution of sample scores in the plane defined by the first two axes of DCA indicated the first axis was a colonization history gradient (Fig. 1). Samples from off-colony stands were clustered at one extreme while samples from stands colonized 4–6 yr characterized the other extreme. Samples from stands colonized for 2 to 3 yr occupied intermediate, overlapping positions. A linear regression of colonization history and DCA Axis I sample scores generated an  $R^2 = 0.69$  ( $P < 0.001$ ).

Perennial mid-grasses characterized samples from uncolonized stands and forbs dominated samples from portions of the prairie dog town colonized longest. Generally, annual forbs increased and perennial graminoid lifeforms decreased with time of habitation. Uncolonized areas were dominated by the perennial grasses *Buchlœe dactyloides*/*Bouteloua gracilis*, *Stipa comata*, and *Poa pratensis* (Table 2). Stands inhabited for 2 yr were dominated by *Buchlœe/Bouteloua*. *Agropyron smithii* assumed more

Table 2. Mean percent absolute cover (C) and frequency of occurrence (F) of species dominating portions of a prairie dog town having a known colonization history.

Colony age (yr)	Dominant species	Traits <sup>1</sup>	C (%)	F (%)
0	<i>Buchlœe dactyloides</i> <sup>2</sup>	PGS	26	77
	<i>Stipa comata</i>	PGM	17	97
	<i>Poa pratensis</i>	PGM	16	81
2	<i>Buchlœe dactyloides</i>	PGS	18	87
	<i>Agropyron smithii</i>	PGM	8	91
3	<i>Buchlœe dactyloides</i>	PGS	12	50
	<i>Dyssodia papposa</i>	AF	12	90
4–6	<i>Tridactantia bracteata</i>	PF	7	80
	<i>Dyssodia papposa</i>	AF	31	100
	<i>Tridactantia bracteata</i>	PF	8	89

<sup>1</sup> Traits: A = annual, P = perennial, G = graminoid; F = forb, W = woody. For grasses: M = mid-grass; S = short-grass.

<sup>2</sup> Includes *Bouteloua gracilis*.

importance in these stands which also had a greater forb component than uncolonized stands. Stands inhabited for 3 yr were co-dominated by *Buchlœe/Bouteloua* and *Dyssodia papposa*, an annual dicot, and displayed a great deal of floristic heterogeneity (Fig. 1). Stands colonized 4–6 yr were clearly dominated by *Dyssodia papposa*.

Perennial mid-grass cover and frequency declined after prairie dog colonization (Fig. 2). Forb taxa absent or of little importance on off-colony stands as-

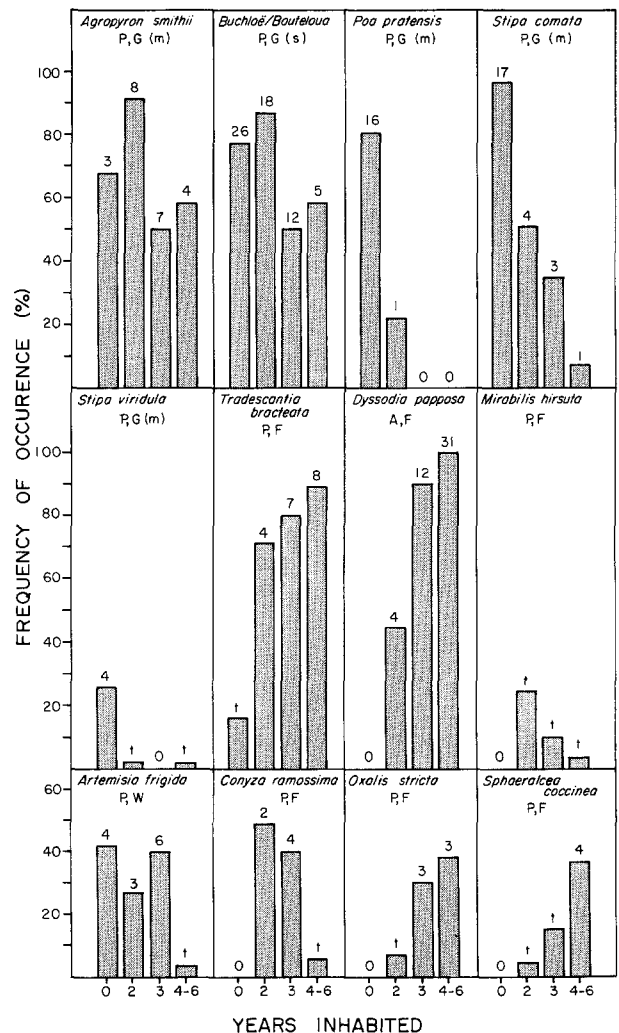


Fig. 2. Frequency of occurrence of selected growth forms (see Table 2 for key; *A. frigida* is a suffrutescent shrub) on a North American mixed-grass prairie dog colony as a function of colonization history. *Bouteloua gracilis* plants were included with *Buchlœe dactyloides* because of identification problems on heavily grazed sites. Numbers above bars are mean absolute cover (%) values (t = trace = <1%).

sumed greater abundance with prairie dog habitation. Most notable of these were *Dyssodia papposa* and *Tradescantia bracteata*. Rapid decreases in graminoid and litter cover during the first 2 yr of habitation resulted in a threefold increase in bare ground (Fig. 3). After a short time lag, forb cover rapidly increased to offset continued decreases in graminoid cover, thus stabilizing percent bare ground at 35% by the third year of habitation.

Mean canopy stature, as defined by measuring height of ungrazed plants, decreased 62% during the first 2 yr of habitation but changed little thereafter (Fig. 4f). Some differences in stature resulted from the replacement of taller mid-height grass species with shorter grass and forb taxa (Fig. 2). However, much of the difference reflected a shift from taller growth forms of off-colony species to shorter growth forms of the same species on the colony (Fig. 4a–e).

Three perennial grasses (*B. dactyloides*/*B. gracilis*, *Stipa comata*, and *Poa pratensis*) accounted for over 70% of the total cover on uncolonized stands. In contrast, 70% relative coverage in stands colonized 2 and 3 yr was contributed by seven and eight species, respectively, while five species accounted for 70% of the coverage in stands colonized 4–6 yr.

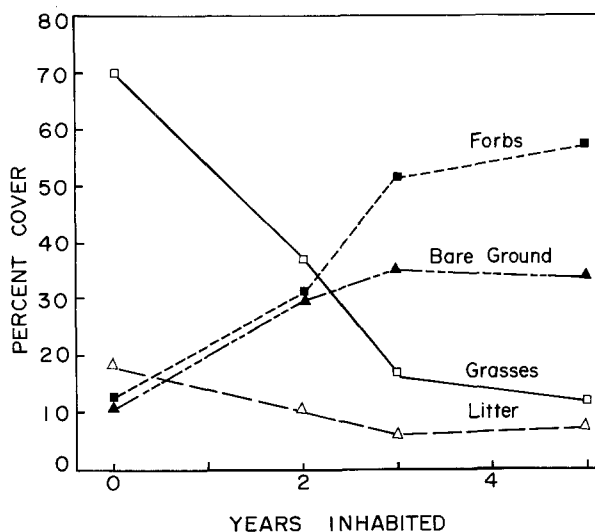


Fig. 3. Changes in cover (%) of graminoids, forbs, bare ground and litter with colonization history. Points are means of samples from stands with similar colonization histories.

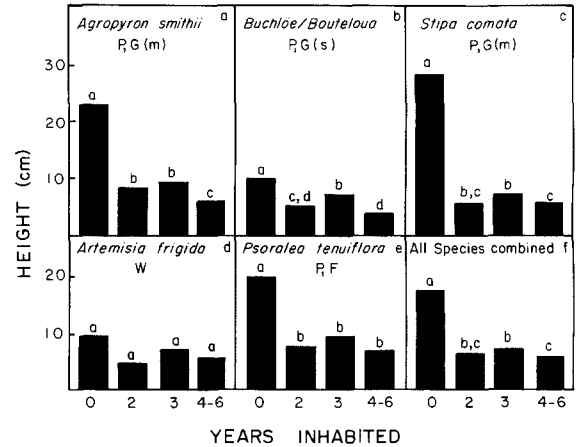


Fig. 4. Mean height (cm) of ungrazed perennial growth forms (see Table 2 legend; *A. frigida* is a suffrutescent shrub) occurring in stands inhabited by prairie dogs for different lengths of time. An AOV of height versus colonization history was significant at  $P = 0.04$  for *A. frigida* and  $P \leq 0.01$  for all other taxa, including the 'all species combined' group. Columns headed by the same letter were not significantly different at  $P \leq 0.05$ . *B. dactyloides* includes *Bouteloua gracilis* plants because of identification problems on heavily grazed sites.

Diversity increased during the first 3 yr of habitation (Table 3), resulting from the influx of forbs which offset the decline in graminoid species cover (Fig. 3) and numbers. After 4–6 yr of habitation exp ( $H'$ ) dropped to values comparable to that of uncolonized stands while species richness remained high. The decline in exp ( $H'$ ) was mainly a result of the pervasive influence of *Dyssodia papposa*, an annual forb (Fig. 2). Generally, the number of graminoid species decreased with time since colonization while the number of forb species increased. The result was a 67% increase in species richness during the first 2 yr of habitation. However, when related to stand area, it became apparent that differences in

Table 3. Vascular plant species diversity [exp ( $H'$ )] and species richness (in parentheses) on a North American mixed-grass prairie site as a function of prairie dog colonization history.

Colony age (yr)	Graminoids	Forbs	Total vegetation
0	1.6 (9)	2.0 (18)	2.1 (27)
2	1.4 (9)	2.8 (36)	2.7 (45)
3	1.3 (4)	2.6 (28)	2.8 (32)
4–6	1.3 (6)	1.9 (34)	2.2 (40)

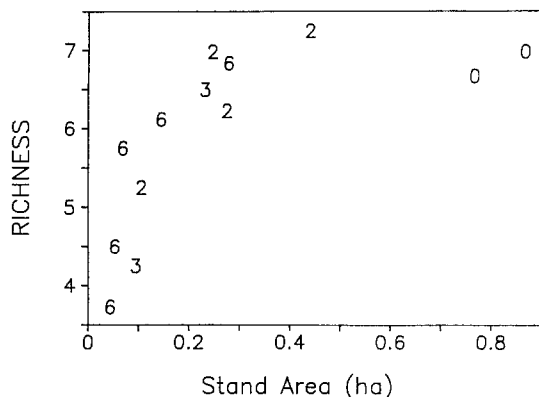


Fig. 5. Species-area curve illustrating the relationship between stand area (ha) and species richness on the prairie dog colony. Numbers represent years of habitation by prairie dogs for each stand. Note that richness increased with increasing stand area, regardless of grazing history. Because stands were unequally sampled ( $N = 10$  to 20 plots) richness was standardized by dividing by the log of the area sampled (Whittaker, 1970).

species richness on the colony may have been more a consequence of stand size than grazing history (Fig. 5).

There was no correlation ( $R^2 = 0.04$ ) between colonization history and prairie dog density (Table 1). However, a regression of colonization history ( $CH$ ) and burrow density ( $BD$ ) yielded an  $R^2 = 0.82$ :  $BD = 20.7 + 52.7 CH$ .

## Discussion

Prairie dogs preferentially consume graminoids (Hansen & Gold, 1977), but also utilize forbs and shrubs (Fagerstone *et al.*, 1981). However, the proportion of plant tissue ingested is often small relative to the amount of vegetation felled, since many plants are not eaten, but are cut down to facilitate communication and predator avoidance (King, 1955). Thus, defoliation pressure on colonies is high in terms of intensity (percent of tissue removed) and frequency, across most species. The result was the creation of distinct patches of vegetation on the landscape whose structure varied with colonization history. Because prairie dogs abandon large portions of colonies after graminoids are reduced, burrow densities were a better indicator of colony age than prairie dog densities (King, 1955).

Results of DCA suggested that 69% of the floristic variation was attributable to time since colonization. However, prairie dogs themselves cannot be considered solely responsible for vegetation changes among stands, since their activities are known to modify the grazing patterns of other herbivores. For example, a variety of ungulates, small mammals, insects and root-feeding nematodes preferentially utilize vegetation on prairie dog colonies (Hansen & Gold, 1977; O'Meillia *et al.*, 1982; Coppock *et al.*, 1983b; Ingham & Detling, 1984). In addition, decreases in litter and increases in bare soil during the first 2 yr of habitation (Fig. 3) might have resulted in warmer, drier micro-environments which could have accelerated changes indirectly. However, these potentially adverse indirect effects of grazing may be offset by a variety of factors (see Archer & Detling, 1986).

The shift from taller to shorter morphs, which occurred during the first 2 yr of habitation (Fig. 4), may have prolonged the survival of preferred graminoids by making them less accessible to herbivores. The rapid expression of such morphs on this heavily grazed site may represent either the plastic response of existing genotypes (Quinn & Miller, 1967) or the differentiation of grazing ecotypes (Detling & Painter, 1983; McNeilly, 1984). Thus, populations in these communities may be comprised of genotypes variously adapted to cope with tradeoffs between enhanced competitive ability (tall, upright growth habit) under conditions of light grazing and enhanced survival (short, decumbent growth habit) under conditions of heavy grazing pressure (e.g., McNaughton, 1984).

An examination of the persistence of species in the context of heavy, uniform and continuous grazing pressure also provided some quantitative perspectives on plant response to grazing at the community level of organization. As seen in Fig. 2, responses varied greatly among species and growthforms on the site. The mid-height grasses (*Poa pratensis*, *Stipa viridula* and *S. comata*) decreased most rapidly with the onset of prairie dog habitation, either because they were less tolerant to defoliation or were more preferred and thus grazed more heavily than others on the site. Two years after prairie dog habitation *Poa pratensis* was locally extinct. Short-grasses such

as *Buchlœ dactyloides/Bouteloua gracilis* maintained dominance for three yr of heavy grazing and were still well-represented in the oldest portion of the colony. Each of these species is known to be very tolerant of defoliation. Other graminoids which were important but subordinate components of off-colony stands (*Agropyron smithii*, a mid-grass, and *Carex heliophila*, a short sedge) assumed greater relative importance with grazing pressure up to two and three yr. Both of these graminoids are utilized by prairie dogs (Fagerstone *et al.*, 1981), indicating their increase in abundance with the advent of heavy grazing was the combined result of their ability to tolerate defoliation and the decreased abundance of mid-grass competitors. The principal dicots on the uncolonized site contributed little cover and are not preferred food items for prairie dogs (Hansen & Gold, 1977; Fagerstone *et al.*, 1981). These species maintained their abundance during the first three yr of habitation, thus, the increase in unvegetated soil observed within the first two yr (Fig. 3) was primarily the result of the loss of perennial grasses.

*Tradescantia bracteata* was the first forb to exploit the gaps left by grasses (Fig. 2). It was joined by *Dyssodia papposa*, *Conyza ramosissima*, *Oxalis stricta* and *Sphaeralcea coccinea*, none of which were encountered in uncolonized stands. Both *Dyssodia* and *Tradescantia* continued to increase in abundance, dominating the site after 4–6 yr. Little is known of the autecology of *Dyssodia papposa*. It is an odoriferous and apparently very unpalatable composite (Asteraceae) frequent in disturbed areas (van Bruggen, 1976) and on other prairie dog colonies in the region.

Patterns of species diversity and richness varied with colonization history (Table 3). Our results illustrate that herbivory enhanced overall plant diversity, apparently by decreasing the capacity of the competitive dominants (mid-grasses) to exclude other species (e.g. forbs) (Huston, 1979) and by creating unoccupied gaps (Fig. 3) (Gross & Werner, 1982). Floristic richness was consistently higher on the colony, even though we underestimated this parameter by not sampling other disturbances such as bison wallows and mounds of prairie dog burrows (e.g. Collins & Barber, 1985). However, generalizations regarding grazing-enhancement of diversity (e.g. Ta-

ble 3; Harper, 1969; Coppock *et al.*, 1983a) may be difficult to evaluate unless species-area relationships have been taken into account (Fig. 5).

In terrestrial plant communities much of the theory of community organization has stressed the role of competitive interactions among key species. Although plant species may occupy distinct niches in terms of their resource use (Chapin & Shaver, 1985), herbivores can mediate community organization through the differential utilization of plants variously tolerant to grazing. While prairie dogs represent an extreme example of herbivory, their activities serve to illustrate the type, magnitude, rate and extent of change which plant populations and communities may undergo in response to grazing.

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