Plant Compositional Change in a Colony of Black-Tailed Prairie Dogs in South Dakota[1]

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Abstract.--Peak season multi-species cover of vegetation and burrow mound density were estimated for 3 years along a transect that ran from the geometric center of a black-tailed prairie dog (Cynomys ludovicianus) colony, to its edge. The forb dominated core of the colony expanded 25 m in radius during the study, while plant composition changed dramatically in a small (<0.3 ha) zone midway between the edge and the core. We determined that year to year functional increases in multi-species canopy cover, described by the natural growth function (R^2=0.72, P<0.001), occurred only after shortgrasses were reduced below 75% cover. The density of burrow mounds was positively correlated to compositional change (r=0.58; P<0.01). We observed that burrow mounds provided early sites for the eatablishment of forbs. However, after the canopy cover of shortgrasses receded below 75% (in this location, probably from 4 to 7 years after initial inhabitancy by prairie dogs), extensive compositional changes occurred between burrow mounds.

INTRODUCTION

Largely because of the influence that the black-tailed prairie dog (Cynomys ludovicianus Ord) exerts on trend in rangeland vegetation, the species has been a target of extermination or intensive control since the early 1900's (Merriam 1902, Schenbeck 1982, Uresk 1987). Plant succession within colonies has been described as consisting of the initial disappearance of perennial grass cover, followed by an increase in shortgrasses (Bonham and Lerwick 1976), and an eventual increase and dominance by annual forbs and dwarf shrubs (Koford 1958, Garrett et al. 1982, Coppock et al. 1983, Archer et al. 1987). The pattern of plant composition appears to recapitulate colony expansion, i.e. as prairie dog colonies expand outward, a forb-dominated community follows. The objective of our study was to determine the extent, rate, and pattern of prairie dog induced changes in plant composition within a colony on mixed-grass prairie habitat.

MATERIALS AND METHODS

Study Area

The study was conducted in Badlands National Park, in southwestern South Dakota, in a colony of black-tailed prairie dogs situated in mixed-grass prairie, north of the edge of the White River Badlands. Vegetation of the area is wheatgrass-grama-buffalo grass type described by Kuchler (1975). Occurrence of flora and fauna in the area is described by Agnew et al. (1986). Descriptions of soils, topography and climate are available in Cincotta et al. (1987), and Uresk and Schenbeck (1987). The prairie dog colony selected was <10 years old at the beginning of the research. It was located approximately 1 km north of the valley ridge, or "wall", that marks the northern extent of

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the White River Badlands, about 16 km. south from Wall, South Dakota. When prairie dogs first became established, the location was a privately owned horse pasture. Livestock Bison (Bison bison) grazed on the colony, during the study, however livestock did not utilize the area.

Changes in Plant Composition

The colony was sampled once annually, from 1981 to 1983, during the peak period for biomass of ungrazed vegetation (the last week in July and first week in August). In order to intersect the full range of vegetation, the canopy cover of individual plant species was evaluated along three parallel center-to-edge transects, which we have collectively termed a profile. Five meters apart, the three replicates traced straight lines from the origin of the colony (the oldest burrows, pinpointed by the former property owner) near the geometric center of the colony, to points (525 m away) on the western edge of the colony.

Along the profile, we chose an interval of 25 m to separate sampling sites, S (S=0,1,2,..., 21), inside the colony (on-colony). At each S, we established three sampling transects, one on each replicate of the profile. To quantify local plant composition without prairie dogs, we extended the profile 50, 75, and 100 m beyond the colony, thus establishing a site, S', of nine sampling transects outside the colony (off-colony). Each transect was 29 m long, along which thirty (50 cm by 20 cm; 0.1 m^2) quadrats were placed, 1 m apart. Canopy cover per species was estimated by recording the appropriate class, from six possible cover classes (Daubenmire 1957), for each plant species present in the quadrat.

We defined plant composition as the canopy cover of plant species encountered, i.e. multi-species cover. To compare multi-dimensional data (on-colony vs off-colony) with a computer algorithm for the multi-response permutation procedure (MRPP; Berry and Mielke 1983), we reduced the data to 20 plant species (from 75 encountered) by selecting the twenty species with the highest maximum cover among pooled sites. These species (common and scientific names according to Van Bruggen 1985) were: western wheatgrass (Agropyron smithii Rydb.), red threeawn (Aristida purpurea Steud.), dwarf sagebrush (Artemisia cana Pursh), Aster falcatus Lindl., Japanese chess (Bromus japonicus Thunb.), cheat grass (B. tectorum L.), buffalo grass (Buchloe dactyloides (Nutt.) Engelm.), Carex eleocharis Bailey, Chenopodium strictum Roth, horseweed (Conyza canadensis (L.) Cronq.), six-weeks fescue (Festuca octoflora Walt.), summer cypress (Kochia scoparia (L.) Schrad.), poverty weed (Monolepis nuttalliana (Schultes) Greene), buckhorn (Plantago patagonica Jacq.), Russian thistle (Salsola iberica Sennen & Pau), tumblegrass (Schedonnardus panniculatus (Nutt.) Trel.), cut leaf nightshade (Solanum triflorum Nutt.), scarlet mallow (Sphaeralcea coccinea (Pursh) Rydb.), sand dropseed (Sporobolus cryptandrus (Torr.) A.Gray), and prostrate vervain (Verbena bracteata Lag. & Rodr.). All species with a cover value greater than 2.0% were retained, including nearly all local major forage species for livestock (Uresk 1986) and prairie dogs (Uresk 1984, Fagerstone et al. 1981). The absence of blue grama (Bouteloua gracilis (H.B.K.) Griffiths) from this list is due both to its paucity on this site and our inability to distinguish it from buffalo grass when the grasses were in a clipped condition.

The difference in cover between S and S', was calculated as the euclidean distance measure between multi-species means:

$$D_s=\left(\sum_{i-1}^{20} (C_{is}-C_{is'})^2\right)^{0.5}$$

where C_i is the cover of a species.

To test the null hypothesis, $H_0: D_s=0$ ($n_s=3$, $n_{s'}=9$), we used a permutation technique, MRPP (Mielke 1986, Mielke et al. 1981, Mielke et al. 1976). MRPP utilizes the sum of the euclidean distances (weighted for group size; Berry et al. 1983), d, between all possible within-group pairs to express concentration within a particular mutually exclusive, exhaustive grouping with group sizes $g_1, g_2, \ldots, g_m$ (Berry et al. 1983; for detailed example, see Zimmerman et al. 1985). The null hypothesis actually proposed with MRPP, that all permutations of $g_1, g_2, \ldots, g_m$ are equally likely, is tested by: (1) ordering the computed values of d, (2) locating the relative position of the statistic on the list and (3) determining the P-value as the proportion of all values of d less than or equal to the observed value of the a priori grouping. We assumed that the group mean at each S was different from S' when the P of more extreme distances was ≤ 0.05. The full set of species encountered in sampling was used in this computation.

Plant composition was further described by calculating the ratio of forb to grass cover at sampling sites. Forbs included all broad-leaved plants. Grasses included species from the taxonomic families of Poaceae and Cyperaceae (sedges). All species encountered during sampling were included in this computation.

Rate of Compositional Changes

Since we did not know the exact time of prairie dog establishment on all points along the profile, we calculated a growth rate relative to the previous year's state (Green 1979). Thus, we assumed that D[t+ t] was a function of D[t], where t equaled 1 year, and t was peak season during each of the first two study years. Since D has a finite upper limit (the maximum possible difference between compared cover samples), we fit a simple asymptotic growth curve, the natural growth function [$f(x)=a(1-e^{-bx})$], to this data. Parameters (a,b) were estimated by least squares estimate using a non-linear regression algorithm (Marquardt 1963).

Effects of Burrowing

During the same period, the number of burrow mounds were counted within a 25 m x 25 m square (0.0625 ha) of which the sampling site was the center. We determined the relationship between the density (ha^{-1}) of burrow mounds (independent variable, random effect) and D (dependent variable) by regression. For calculations of r, significance ($P \leq 0.05$) was evaluated using the F-statistic (Cacoullos 1965).

RESULTS

Changes in Plant Composition

The off-colony site was dominated almost completely by buffalo grass, western wheatgrass, Japanese brome (Table 1), while sand dropseed and six-week fescue were minor community constituents (<5% cover). Other species present (<2.0% cover), though not among the 20 species use to calculate multi-species cover, were green needlegrass (Stipa viridula Trin.) and needle-and-thread (S. comata Trin. & Rupr.). On-colony sites near the edge had low forb:grass ratios (Fig. 1a) though most perennial mid-grasses, e.g. sand dropseed, green needlegrass and needle-and-thread were virtually absent (<0.5% cover). Forb: grass ratios were highest (1.73:1 in 1981, 1.62:1 in 1982, and 8.59:1 in 1983) in the core of the colony (from 0 to 50 m from the center). A taxonomically diverse array of annual forbs were dominant at the core, including prostrate vervain, buckhorn, cut leaf nightshade, rough pigweed (Amaranthus retroflexus L.), tumble- tumbleweed (A. albus L.), poverty weed and Russian thistle. Tumblegrass, a perennial graminoid that frequents disturbed soils, was also an important constituent of this community. Unexpectedly, forb: grass ratio increased from 0.08:1 (1981) to 1.21:1, two years later, in a small (<0.3 ha) mid-colony zone (MCZ) about 350 m from the colony center. This zone was completely surrounded by grass dominated communities. The dominant constituents of MCZ were prostrate vervain, horseweed, and red threeawn (a perennial grass).

TABLE 1. Canopy cover of plant species (>2.0% cover) in the off-colony site.

	Canopy cover (± SD) off-colony		
Species	1981 n=9	1982 n=9	1983 n=9
	%		
Buffalo grass	80 (6)	79 (12)	86 (8)
Western wheatgrass	5 (4)	6 (2)	5 (3)
Sand dropseed	2 (2)	2 (<1)	2 (<1)
Six-week fescue	3 (1)	4 (1)	2 (2)
Japanese brome	5 (1)	4 (3)	9 (5)

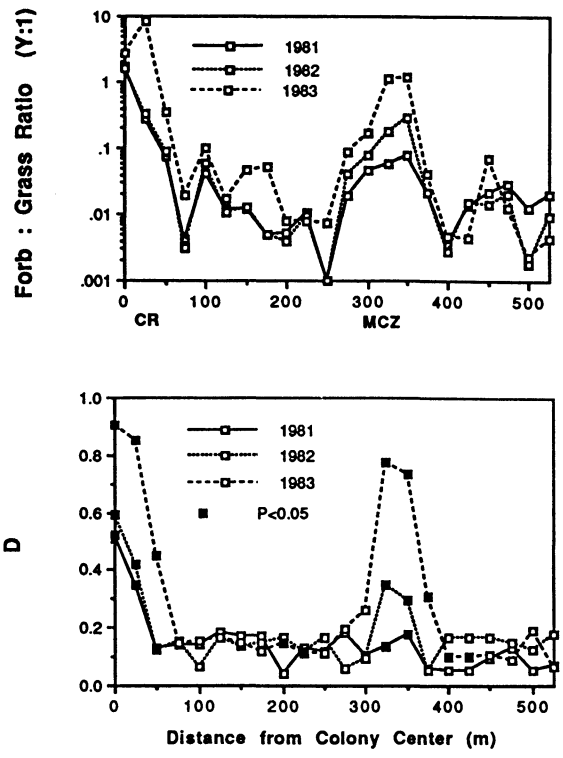

Figure 1.--Three year comparisons of: (a) the ratios of forb to grass cover along the colony profile; (b) the differences in multi-species (20 species) cover, D, between on-colony and off-colony sites along the profile. Locations of zones of extensive compositional change, the core (CR) and mid-colony zone (MCZ), are indicated.

During the study, D increased mainly in the core and surrounding MCZ (Fig. 1b). Also, D increased on sites adjacent to the original core, thus enlarging its radius by about 25 m in two years. Although there was a positive correlation between forb:grass ratio and D (r=0.72, F=6.14, 64 df, P<0.001), forb:grass ratio was not always a true indicator of change; some compositional changes involved the replacement of perennial grass species by other grasses (e.g., buffalo grass was sometimes replaced by red threeawn or tumblegrass).

Rate of Compositional Change

Upon plotting D[t+1] as a function of D[t], we noted a difference between points representing "highly disturbed" zones of the colony (the core and MCZ), and those from the remaining locations along the profile. Highly disturbed zones showed a high positive correlation between yearly states (r=0.84, F=11.5, 12 df, P<0.001). Application of the the natural growth function to these data (Fig. 2) yielded a good fit (R^2=0.72, P<0.001). The remaining points, where grasses dominated, were clumped near the origin. On these sites, yearly states were negatively correlated (r=-0.53, F=3.32, 28 df, P<0.01).

Effect of Burrowing

The density of burrow mounds and D (Fig. 3) were positively correlated (r=0.58; F=3.76, 64 df, P<0.01). However, linear, exponential, and polynomial regressions of these variables yielded poor fits (R^2<0.38). Burrow mounds, and disturbed soil directly adjacent to mounds were observed to be sites for initial establishment of annual forbs. In highly disturbed zones, annual forbs, dwarf shrubs (e.g., pasture sagebrush [Artemisia frigida Willd.]) and some "pioneer" perennial grasses (e.g., red threeawn and tumblegrass) occupied the ground surface between mounds.

Discussion

The differential extinction, replacement and resilience of plant species during prairie dog inhabitancy create the observed pattern of community change. Knowing the long-term response of similarly behaving plant species (Harper 1977; rather than taxonomic affinities) may help range and wildlife managers understand prairie dog induced succession. We considered species on the prairie dog colony to fall roughly into four categories: (1) perennials that quickly disappeared after initial prairie dog inhabitancy; primarily mid-grasses, e.g. sand dropseed, green needlegrass, and needle-and-thread; (2) shortgrasses that were initially resistant to the impacts of prairie dog grazing, e.g. buffalo grass (Fig. 4); (3) annuals that became established on recently disturbed soil associated with burrow mounds, e.g. buckhorn, prostrate vervain, and scarlet mallow; (4) annuals and perennials that only became established on the most disturbed sites, e.g. poverty weed. Although the

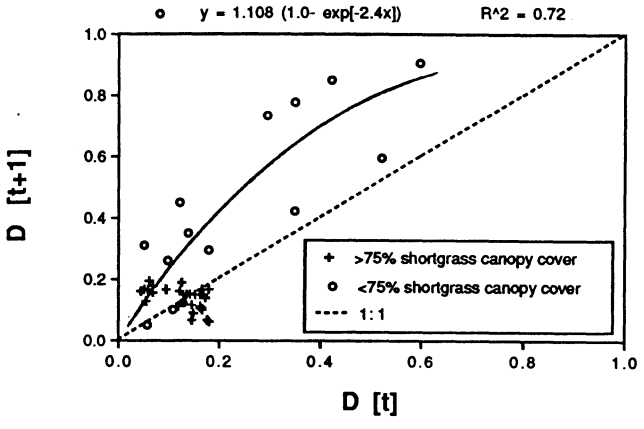

Figure 2.--Year to year changes in the difference between multi-species cover, D, between on-colony and off-colony sites. The natural growth function was fit to points (n=14) that went below 75% shortgrass canopy cover during the study. A year to year increase in D was not observed for points (n=30) above this threshold.

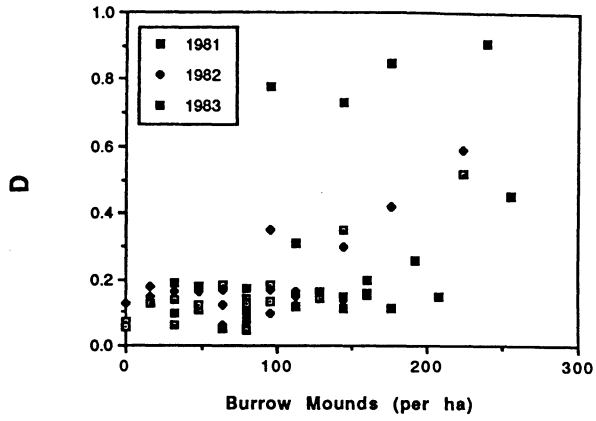

Figure 3.--The relationshp between the difference in multi-species cover between on-colony and off-colony sites, D, and the density of prairie dog burrow mounds.

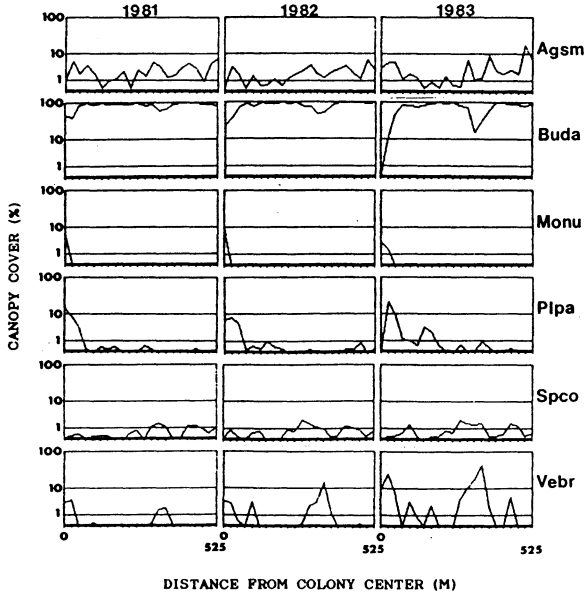

Figure 4. Mean canopy cover for six plant species along the colony profile for three consecutive years. The species are western wheatgrass (Agsm), buffalo grass (Buda), poverty weed (Monu), Patagonia Indianwheat (Plpa), scarlet mallow (Spco), and prostrate verfain (Vebr). The Y-axis is transformed using $Log_{10}(Y+1)$. Distance from the colony center to an edge 525 m distant was measured in 25 m intervals.

cover of western wheatgrass initially decreased with prairie dog inhabitancy, the species was not displaced entirely as were all other mid-grasses. The ability of this species to maintain a presence under intense prairie dog grazing may be due to the survival of decumbent "grazing" ecotypes that are known to occur in some prairie dog colonies (Detling and Painter 1983).

At the colony edge, plant composition was not radically affected by the loss of mid-grasses. Reduction of mid-grass cover, resulting from prairie dogs clipping tall plants for predator avoidance rather than for forage (King 1955), may have a greater consequence on more mesic grasslands (Archer et al. 1987). The initial 2 yr period of soil disturbance, resulting from building burrow mounds and allowing the introduction of some annual forbs, had a minor impact on the plant community. However, long-term inhabitancy of prairie dogs on mixed-grass prairie vegetation in our location (we estimate from 11 to 13 yrs) can cause the complete disappearance of perennial shortgrasses between mounds.

The nature of soil disturbance and plant community structure varied markedly between the two characteristic types of burrow mounds (King 1955, Sheets et al. 1971), (1) dome mounds and (2) crater mounds. Whereas these structures may reach 1 m in height and 2.5 m in diameter in an old colony (King 1955), all were less than half these dimensions in our colony. Dome mounds were composed of loosely packed subterranean soil spread widely over the ground surrounding the entrance. These mounds became sites for the establishment of a variety of forbs that assumed a prostrate habit, either as a consequence of their natural growth form (Warwick and Briggs 1980) or because they were heavily clipped by prairie dogs. Prostrate vervain, tumbling mustard, buffalo bur (Solanum rostratum Dunal), and cut leaf nightshade were frequent occupants of dome mound sites in our study colony.

"Crater mounds" were narrow, roughly cone-shaped structures that prairie dogs constructed from uprooted vegetation, displaced litter, humus, and mineral soil which they scraped from a patch adjacent to the burrow entrance. After a rain, prairie dogs packed the material tightly with their noses. Thus, surfaces of the crater mounds made poor sites for seedling establishment. However, adjacent "quarried" patches were invaded by annual forbs, most frequently buckhorn, during the following spring.

On our colony, the buffalo grass dominated community experienced a resilient period (probably from 4 to 7 yrs) during which little change occurred. This may be a period during which root carbohydrate reserves were being depleted (Santos and Trlica 1978), both to supply above ground regrowth and from increased microbial grazers below ground (Ingham and Detling 1984). A decisive shift in composition was experienced when shortgrass was replaced by a mixture of armed and/or sprawling grasses and forbs, aromatic dicots, and bare ground. The shortgrass "threshold" at our location was 75% cover; sites that went below this level experienced abrupt changes in composition during the following year. Thus, sites below threshold slipped from temporary stability into the asymptotic increase in D that we have described.

Although compositional changes in colonies are likely to be most evident in an expanding core, irregular patches closer to the periphery may undergo change, as well. Archer et al. (1987) concluded that the formation of forb dominated communities in prairie dog colonies could be attributed mostly to the length of time of sustained prairie dog activity. The initial amount of shortgrass cover may also affect the rate of prairie dog induced succession. Since prairie dog colonies are aggregates of highly territorial family groups (coteries) rather than a cooperating colonial entity (King 1955, Hoogland 1981), population and activity of prairie dogs is non-uniformly distributed across the colony. Whereas territories at the core are contiguous, those at the edge of expanding colonies are often spread spaciously amongst relatively undisturbed vegetation. Thus, compositional changes outside the core are likely to be patchy. In our study site, compositional changes outside the core area (in MCZ) appeared to result from sustained inhabitancy of a single coterie on a site with below average shortgrass cover.

In many colonies in the Badlands area, the presence of a shortgrass understory imparts resiliency to the plant community, delaying the eventual shift to annual forbs that is usually incompatible with range livestock management objectives. It should be noted, however, that prairie dog colonies provide valuable forage resources for native ruminants; pronghorns (Antilocapra americana) prefer the high quality herbage in colony cores (Krueger 1986), while bison are attracted to the highly nitrogenous, low fiber regrowth of grasses at the edges of colonies (Coppock et al. 1983). Extrapolation of results from this study to other prairie dog colonies should be done cautiously. In fact, where plant composition and herbivore use is much different from the single colony studied, extreme care should be used in extrapolating these results to other areas.

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