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Cover of Spring Annuals on Nitrogen-rich Kangaroo Rat Mounds in a Chihuahuan Desert Grassland

ABSTRACT.—Species composition and cover of spring annual plant communities on banner-tailed kangaroo rat (*Dipodomys spectabilis*) mounds in a northern Chihuahuan Desert grassland differed from those on intermound areas. After seasons of adequate precipitation, cover of annual plants was greater on mounds than on adjacent areas; dominant species on mounds were those known to increase with nitrogen fertilization. Soil nitrogen content was consistently higher in mound soils than in intermound soils; however, plant cover on mounds was not different from intermound areas following periods of limited precipitation despite differences in nitrogen levels. Patterns of species composition and cover of annual plants on kangaroo rat mounds are attributed to differential species responses to water and nutrient availabilities.

INTRODUCTION

Patterns of primary productivity and plant community structure in arid and semiarid regions have traditionally been viewed as functions of moisture availability (Noy-Meir, 1973). However, recent studies have shown that soil nutrients, especially nitrogen (N), may also be important regulators in these ecosystems (Gutierrez and Whitford, 1987, 1988; Fisher *et al.,* 1988; Romney *et al.,* 1978). An additional factor affecting composition and productivity of grassland communities is surface soil disturbance by burrowing animals (Laycock, 1958; Mielke, 1977; Tilman, 1983). Animal disturbances can affect vegetation by modifying infiltration, water storage and nutrient concentration and distribution (Grant *et al.,* 1980; Spencer *et al.,* 1985; Carlson and White, 1987).

Banner-tailed kangaroo rat (*Dipodomys spectabilis*) mounds are a characteristic feature of Chihuahuan Desert grasslands (Moroka *et al.,* 1982). They are large mounds (1–2-m diam and average height of 30 cm above the surrounding area) consisting of numerous tunnels and chambers to depths of 1 m and contain large quantities of stored seeds (Kay and Whitford, 1978; Reichman *et al.,* 1985). Moroka *et al.* (1982) reported there are between 7 and 10 mounds ha^{-1} occupying up to 2% of the land area in good habitat. They further reported that plant cover is generally higher off mounds than on mounds and that vegetation composition differs as well, but offered no explanation for these differences.

In early May 1985, we observed that banner-tailed kangaroo rat mounds had a dense cover of annual plant species similar to nearby N-fertilized plots (Ludwig *et al.,* 1988). We hypothesized that mounds would have different species composition and higher production of annual plants, available N, and N mineralization potential than intermound areas.

METHODS

Study site.—This study was conducted on the Jornada Long Term Ecological Research (LTER) area on the New Mexico State University Ranch, 40 km NNE of Las Cruces, New Mexico. The midslope portion of the area was formerly a black grama (*Bouteloua eriopoda*) grassland that now is a mixture of widely separated shrubs, perennial herbs and annual plants. This portion of the area is characterized by numerous (mean = 15.6 mounds ha^{-1}) active and abandoned mounds of banner-tailed kangaroo rat (*Dipodomys spectabilis*).

Precipitation and air temperature at the study site are recorded continuously as part of the LTER program. Mean annual precipitation of the area is ca. 213 mm, with 55% falling during July through September during convectional thundershowers. April has the lowest mean precipitation. Temperatures exceed 40 C in summer and regularly drop below freezing in December–February.

Vegetation sampling.—In early May 1985 and late April 1986, the vegetation cover on 10 kangaroo rat mounds and 10 intermound sites was sampled by the line intercept method. Four, 2-m line transects were extended (N, S, E and W) from the center of each mound and a randomly located intermound point. Relative ground cover of each species was estimated as the percent of the total transect line intersected by the plant canopy.

Soil sampling.—Soil samples were collected on the same days the vegetation was sampled. Soil cores of 2.5-cm diam and 10-cm depth were taken from each mound and intermound site and immediately analyzed. Soil moisture content was determined by oven-drying (40 C) to constant weight. NH_4 and NO_3+NO_2 nitrogen were extracted in 2.0 M KCl and quantities determined colorimetrically using an Orion Scientific continuous flow analyzer (Fisher *et al.,* 1987). Total N content of the 1985 samples was determined by a semimicro Kjeldahl technique (Nelson and Sommers, 1980). Soil particle size analysis was performed on the 1985 samples using the hydrometer method (Day, 1965).

Both total N and KCl extractable inorganic N have important weaknesses as indicators of N availability. The majority of total N consists of stable compounds that contribute little to available N (Black, 1968). Therefore, total N values are unlikely to differ from 1985 to 1986 and may not accurately represent biologically important differences between mound and intermound sites. On the other hand, KCl extractable inorganic N measures only part of the N available to plants because it fails to account for N mineralized from soil organic matter and taken up by plants over time. One of the simplest ways to get an improved estimate of N availability is to incubate soils in the absence of plants and follow the net mineralization of N over time (Keeney, 1982).

N mineralization incubations were performed using soil samples collected in April 1986. Subsamples (25 g) were incubated aerobically for 8 wk at 35 C in 50-ml plastic vials covered with polyethylene film (Fisher *et al.,* 1987). Moisture content was adjusted to field capacity weekly during the incubation.

Data analyses.—Plant cover (percent) and sand, silt and clay content of soil (percent) data were arcsine-transformed and analysis of variance performed to test for significant differences between dates and sites (SAS, 1982). Soil N concentrations (mg kg^{-1} soil) and soil moisture content (fraction dry soil weight) data were log-transformed for similar analyses.

RESULTS

Vegetation.—Total annual plant cover was significantly higher on mound sites than on intermound sites in 1985, while in 1986 total annual plant cover on the mounds was about half that of intermound sites, but the difference was not statistically significant (Table 1). In 1985, covers of *Cryptantha crassisepala, Escholtzia mexicana* and *Lepidium lasiocarpum* were significantly higher on the mounds. In the following year, *E. mexicana* and *L. lasiocarpum* appeared only on the mounds while *C. crassisepala* was not present on either site. In contrast, the cover of *Eriastrum diffusum* was significantly greater on intermound areas in both years.

Total annual plant cover was lower in 1986 than 1985 on both the mound and intermound sites although the reduction on intermound areas was smaller (Table 1). Some species present in 1985 were absent the following year (*cf. Cryptantha* spp., and *Descurainia pinnata*) while others had significantly lower cover where present (*e.g., Escholtzia mexicana, Lepidium lasiocarpum,* and *Lesquerella gordoni*). A few species (such as *E. diffusum* and *Eriogonum abertianum*) had similar cover between years; however, none showed an increase from 1985 to 1986.

Soil characteristics and precipitation.—Soil N was higher on mound sites than on intermound sites for all measured parameters in both years (Table 2). The N mineralization potential of mound soils in 1986 was nearly three times higher than intermound soils. In addition, ammonium concentrations were higher on both sites in 1986 than in 1985. Nitrate was also higher in mound soils in 1986, but

TABLE 1.—Spring annual plant cover on banner-tailed kangaroo rat mounds and in intermound (Inter) areas (untransformed means, n = 10)

	Year							
	1985			1986			Year diff. (P<)[b]	
Plant species	Mound	P<[a]	Inter	Mound	P<[a]	Inter	Mound	Inter
Baileya multiradiata	0.03	—[c]	0.34	0	ns[d]	0.72	—	ns
Chaenactis stevioides	2.27	ns	1.43	0.59	ns	2.66	0.05	ns
Cryptantha angustifolia	0.99	ns	0.33	0	—	0	—	—
C. crassisepala	2.70	0.05	0.04	0	—	0	—	—
Descurainia pinnata	9.00	—	0	0	—	0	—	—
Eriastrum diffusum	0.60	0.01	3.91	0.23	0.05	3.44	ns	ns
Eriogonum abertianum	0.36	ns	0.51	0.68	ns	0.76	ns	ns
Escholtzia mexicana	25.95	0.01	3.46	0.49	—	0	0.01	—
Lepidium lasiocarpum	4.38	0.01	0.20	0.25	—	0	0.05	—
Lesquerella gordoni	10.80	ns	7.21	0.34	ns	0.47	0.01	0.01
Malacothorix fendleri	0.04	—	0.13	0	—	0.17	—	ns
Total annual plant cover	56.51	0.05	13.64	2.34	ns	4.80	0.01	0.01

[a] Significance level of differences between sites (mounds and intermounds) within years

[b] Significance level of differences between years within sites

[c] No statistical tests performed

[d] Not significant

not on intermound sites (Table 2). Soil moisture was higher in intermound areas in both years but differences were greater in 1986 (Table 2). Soil moisture contents were lower in 1986 than in 1985.

Sand, silt and clay composition of the mound and intermound soils was virtually identical: 82.2% sand, 9.7% silt and 8.0% clay. However, the soil structure was quite different since mound soils were more loosely aggregated.

Precipitation from November 1984 until sampling in May 1985 was 143.4 mm, while precipitation from November 1985 until sampling in late April 1986 was much lower, totalling 28.4 mm.

DISCUSSION

The results indicate banner-tailed kangaroo rat mounds are N-rich, relatively dry patches in this desert grassland. Higher N concentrations in mound soils suggest N accumulation in the upper layers, possibly originating from the decomposition of seeds stored in the mounds (Reichman *et al.,* 1985) as well as the urine and feces of the rodents. The N mineralization potentials of mound soils were nearly three times higher than intermound soils, suggesting that total N values underestimate the difference in N availability between sites. Lower moisture content of mound soils may result from looser soil aggregation, which could decrease water-holding capacity and lead to greater moisture losses by evaporation or infiltration.

Data from wet and dry winters illustrate how variation in precipitation interacts with soil characteristics to influence vegetation. Following the wet winter of 1985, total plant cover was much higher on the mounds than off the mounds. At the same time, total plant cover was increased on N-fertilized plots adjacent to the study area (Ludwig *et al.,* 1988). Species occurrences were similar on mounds and N-fertilized plots, strongly suggesting N levels of the mounds caused the increased plant cover. Following the dry winter of 1986, annual plant cover both on and off the mounds was lower than following the wet winter of 1985. These data suggest that moisture availability had a more important influence on annual plants than did N availability in 1986.

Patterns of species occurrence and cover indicate differential sensitivities to resource availability, a conclusion also reached by Gutierrez and Whitford (1987, 1988) and Kemp (1983). Many species had higher cover in 1985 than 1986 (suggesting a positive response to precipitation) and others had

TABLE 2.—Soil nitrogen (mg kg^{-1}) and soil moisture (%) on banner-tailed kangaroo rat mounds and in intermound (Inter) areas (untransformed means, n = 20)

Soil characteristic	Year						Year diff. (P<)[b]	
	1985			1986				
	Mound	P<[a]	Inter	Mound	P<[a]	Inter	Mound	Inter
Nitrate-N	3.1	0.001	0.7	11.0	0.001	0.3	0.001	ns[c]
Ammonium-N	0.7	0.01	0.4	6.0	0.05	4.0	0.001	0.001
Total N	458	0.01	411	—	—	—		
N mineralization	—	—	—	43.4	0.001	15.2		
Soil moisture	1.85	0.01	2.18	0.93	0.001	1.42	0.001	0.001

[a] Significance level of differences between sites (mounds and intermounds) within years

[b] Significance level of differences between years within sites

[c] Not significant

higher cover on mounds than intermounds (suggesting a positive response to N), especially evident when soil moisture was high (1985). For example, *Escholtzia mexicana* had higher cover on mounds than off mounds in 1985, and very low cover on both sites in 1986 (Table 1). In contrast, *Eriastrum diffusum* did not differ in cover between years and had significantly higher cover off mounds than on mounds in both years, suggesting no response to water availability and a negative relationship to N concentration. This latter pattern may have occurred in response to soil N content or competition with other species. Only *Eriogonum abertianum* showed no response to either factor, with comparable cover values for both sites in both years.

These results suggest the traditional view of water as the main factor controlling plant productivity in arid environments (Noy-Meir, 1973) is an oversimplification. Here we observed spatial patchiness in the availability of another resource (nitrogen) produced by animal disturbance significantly influenced plant cover. This is consistent with mechanisms proposed by Fisher *et al.* (1987) to explain how vegetation in a single patch may have different responses to moisture availability at different times. It is apparent the factors controlling plant cover of desert annuals can vary both seasonally and spatially.

Previous studies suggest this ecosystem has limited ability to respond to increased moisture availability; 5 years of irrigation produced virtually no increase in production of the perennial creosotebush (Fisher *et al.*, 1988) and 3 years of irrigation had variable effects on annual plant production (Gutierrez and Whitford, 1987, 1988). This lack of response to irrigation probably resulted from depletion of available soil N (Fisher *et al.*, 1987). It is significant that neither irrigation study included kangaroo rat mounds since these nitrogen-rich patches could be important in the response of the ecosystem to increased moisture availability.

Kangaroo rat mounds are sites of high N availability where plants such as *Escholtzia mexicana* respond to increased moisture availability with greatly increased cover. The importance of these patches to overall ecosystem production during wet years is greater than their relative area would suggest (2% of the land surface). For example, the total cover values from this study indicate kangaroo rat mounds contributed 8% of total ecosystem aboveground cover in the spring of 1985.

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