

Factors affecting annual plants assemblages on banner-tailed kangaroo rat mounds

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We studied patterns of annual plants assemblages and soil properties of banner-tailed kangaroo rat (*Dipodomys spectabilis*) mounds. The spring annual flora on mounds was dominated by *Descurainia pinnata* and *Eschscholzia mexicana*; intermound areas were dominated by *Eriastrum diffusum*. The peak above-ground standing biomass of spring annuals on mounds and intermounds respectively was $133.3 \pm 5.9 \text{ g m}^{-2}$ and $25.6 \pm 6.3 \text{ g m}^{-2}$. In summer, the mounds had a high density and biomass of *Tidestromia lanuginosa*. Intermound areas were dominated by *Haplopappus gracilis* and *Eriogonum abertianum*. The peak above-ground standing biomass of summer annuals on mounds and intermounds respectively, was $172.7 \pm 7.3 \text{ g m}^{-2}$ and $98.4 \pm 2.3 \text{ g m}^{-2}$. The above-ground standing biomass of annual plants on irrigated mounds in spring and summer was greater than on non-irrigated mounds. Bulk density was lower on mounds; nitrate and total nitrogen contents of the mound soils were higher than those of intermound soils. Available nitrate measured by absorption on ion exchange resins was consistently higher in mound soils than in intermound soils except for the period from March to April. Mound soils dried faster than intermound soils. Soil water potentials on mounds and intermounds at depths of 20 and 30 cm decreased continuously from January until mid-May, and then fluctuated in response to individual rainstorms. Irrigation of 6 mm of water per week had little effect on the soil water potentials except at the 10-cm soil depth of intermound areas. Differences in species composition and biomass production of annual plants between kangaroo rat mounds and intermound areas are attributed to the differences in both soil physical properties and nitrogen availability.

Introduction

Some species of small mammals are agents of soil disturbance in ecosystems as a result of digging burrows and feeding tunnels and creating seed caches (Grant *et al.*, 1980; Reichman *et al.*, 1985). Soil disturbance by mammals such as pocket gophers, prairie dogs and badgers produce mounds of friable soil that differ from surrounding soils in bulk density (Agnew *et al.*, 1986; Grant *et al.*, 1980; Laycock & Richardson, 1975; Platt, 1975; Spencer *et al.*, 1985). In most cases, soils disturbed by small mammals are temporary and dynamic features on the landscape. Mounds constructed by banner-tailed kangaroo rats (*Dipodomys spectabilis*) are a labyrinth of runways extending to depths greater than 1 m, and are occupied by successive generations of rodents. Because the mounds are long-term features, the soil properties probably differ significantly from short-term disturbances or undisturbed sites.

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Banner-tailed kangaroo rat dens are common in the arid grasslands of New Mexico, Arizona and Mexico (Best, 1972; Reichman *et al.*, 1985). The vegetation on *D. spectabilis* mounds differs from that of surrounding areas (Moroka *et al.*, 1982), and it has been suggested that the mounds are nitrogen-rich sites (Moorhead *et al.*, 1988). The lower bulk density of mound soils should affect water distribution in the soil, thereby affecting nitrogen mineralization processes (Fisher *et al.*, 1987). Are differences in species composition and productivity of vegetation on mounds and intermounds due primarily to differences in nitrogen availability or to differences in water? We designed an experiment using irrigation and ion exchange to answer this question.

Study area and methods

The studies were conducted from November 1986 to September 1987, on the Jornada Long Term Ecological Research site, about 40 km north of Las Cruces, New Mexico. The long-term average precipitation is 225 mm yr⁻¹, mostly from summer convective rainfall. The vegetation is dominated by sub-shrubs, numerous perennial and annual herbaceous plants, and scattered clumps of perennial grasses.

Ten banner-tailed kangaroo rat mounds were selected (average diam. 4.0 m; average height, 0.3 m) in November 1986, one half of which were randomly assigned to irrigation at 6 mm wk⁻¹ from January to September 1987. To estimate annual plant density, frequency and biomass, we established four 40 × 40-cm quadrats on each mound and on each intermound at random in November 1986 before the spring annuals germinated. Each mound was divided into four quadrants and one quadrat was located at random in each quadrant. The spring annuals and summer annuals were harvested in April and September 1987, respectively, at peak biomass, and weighed after oven-drying at 50°C. Roots were harvested with a steel corer, 10 cm diam. and 15 cm high, from another five mounds and adjacent intermounds in April and September 1987. Roots from three cores in each mound and from three cores in each intermound area were separated, dried and weighed. All plant samples were ground in a laboratory mill equipped with a 1-mm screen for nitrogen analysis.

Soil water potential was measured at soil depths of 10 and 30 cm at 3-day intervals with Wescor Thermocouple Psychrometers in two mounds and two intermounds from January to September 1987. To estimate soil water potential, polyvinyl tubes containing two thermocouple hygrometer sensors (Wescor #PCT-55-30-SF), one for 10-cm soil depth and the other for 30 cm, were installed on the mounds and intermounds. Before burial, the psychrometers were calibrated with 0.05, 0.5 and 1.0 mol l⁻¹ solution of NaCl. Hygrometer sensors were installed horizontally to minimize diurnal variations in microvolt output. Field measurements with the microvoltmeter were converted to water potential values utilizing the hygrometer-specific linear regressions (Fonteyn *et al.*, 1987).

Seventeen soil cores (7.8 cm diam. and 10 cm deep), were obtained both on mounds and intermounds in May, oven dried at 105°C and weighed to measure soil bulk density. Thirty-two soil samples from 16 mounds and 32 from intermounds were collected on 2 April for soil nitrate, ammonium and total nitrogen analysis. Ten grams of fresh soil samples were placed into 100 ml of 2N KCl, shaken thoroughly, and allowed to equilibrate for about 24 h. After filtration, the filtrate was analyzed for NH₄-N and NO₃-N using an automated salicylate procedure (Fisher *et al.*, 1987). To analyze total nitrogen, soil samples were air-dried and then ground with a motorized mortar and pestle to pass through a 0.15-mm sieve before micro-Kjeldahl digestion using an aluminum block digester. By using an automated salicylate procedure, NH₄-N in the digest was measured (Fisher *et al.*, 1987). All automated procedures were performed with a Scientific Instruments Continuous Flow Analyzer.

Ion exchange resin bags were used to estimate soil nitrogen availability on mound and intermound areas (Binkley, 1984; Binkley & Matson, 1983). Resin bags were prepared by

placing cation (DOWEX 50W-X8) and anion (DOWEX 1-X8) resin separately in white nylon stockings. Each 60 cm² bag contained 10.0 g moist resin. Cation and anion resin bags were saturated with 0.5N HCl and 0.5N NaHCO₃, respectively, and rinsed several times with deionized water to remove excess HCl and NaHCO₃. After the last rinse, most of the water (98–99%) was removed from the resin bags by centrifuging them in a salad spinner. Ten resin bags were incubated in mounds and 10 in intermound areas at 10-, 20- and 30-cm soil depth, and replaced every 2 months. After 2 months incubation, resin bags were retrieved and washed with deionized water. After removing most of the water from the resin bags by centrifuging them in a salad spinner, they were placed into 100 ml of 2N KCl, shaken thoroughly, and allowed to equilibrate for about 24 h. The solution was then filtered, and the filtrate was analyzed for ammonium- and nitrate-nitrogen using an automated salicylate procedure (Fisher *et al.*, 1987).

Results

The spring annual flora on mounds was dominated by *Descurainia pinnata* and *Eschscholtzia mexicana* (Table 1) which occurred at significantly higher frequencies than in intermound areas (*t*-test, $p < 0.001$). *Eriastrum diffusum* was a dominant species in intermound areas. The most abundant summer annuals on the mound were *Tidestromia lanuginosa* and *Boerhaavia spicata*. *Haploppappus gracilis* and *Eriogonum abertianum* were dominant species on intermound areas (Table 2). The above-ground standing biomass of spring annuals on mounds and intermounds, respectively, was $133.3 \pm 5.9 \text{ g m}^{-2}$ and $25.6 \pm 6.3 \text{ g m}^{-2}$ (mean + S.E.) in April (Table 3, $t_{18} = 4.347$, $t_{18,0.001} = 3.992$, $p < 0.001$). The above-ground biomass of summer annuals on mounds and intermounds, respectively, was $172.7 \pm 7.3 \text{ g m}^{-2}$ and $98.4 \pm 2.3 \text{ g m}^{-2}$ in September ($t_{18} = 4.012$, $p < 0.001$). The roots of annual plants on mounds penetrated more deeply than in intermound soils (Fig. 1). The below-ground biomass of spring annuals on mounds and intermounds at the time of peak above-ground biomass was $106.6 \pm 6.7 \text{ g m}^{-2}$ and $33.0 \pm 3.5 \text{ g m}^{-2}$, respectively (Table 3, $t_8 = 5.472$, $t_{8,0.001} = 5.041$, $p < 0.001$). The below-ground biomass of summer annuals on mounds and intermounds, respectively, was $112.7 \pm 7.7 \text{ g m}^{-2}$ and $47.9 \pm 5.4 \text{ g m}^{-2}$, ($t_8 = 5.315$, $p < 0.001$). The above-ground

Table 1. Comparison of floristic composition and average above ground biomass of spring annuals on mounds and intermounds

Species	Relative frequency (%)		Relative density (%)		Above ground biomass (g/m ²)	
	Mound	Intermound	Mound	Intermound	Mound	Intermound
<i>Descurainia pinnata</i>	16.8**	5.9	46.0**	4.0	54.4**	1.0
<i>Lesquerella gordonii</i>	16.1	12.1	20.0	14.5	45.7*	12.0
<i>Eschscholtzia mexicana</i>	17.9***	6.5	13.3**	2.0	16.8**	0.4
<i>Cryptantha angustifolia</i>	11.6	11.1	7.4	7.7	4.8	2.1
<i>Lepidium lasiocarpum</i>	5.5	3.8	1.5	0.8	2.0	0.6
<i>Eriastrum diffusum</i>	4.9***	14.4	1.1***	38.6	0.1*	3.9
<i>Chaenactis stevioides</i>	3.8	5.0	0.6	2.9	0.4	0.8
<i>Malacothrix fendleri</i>	3.0**	7.9	0.5**	2.3	0.1	0.4
<i>Microsteris lineatis</i>	2.2	2.9	0.3	0.8	0.3	0.1
<i>Lupinus concinnus</i>	1.9**	8.8	0.8*	6.3	0.1**	2.8

t-test, $n = 20$; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 2. Comparison of floristic composition and average above ground biomass of summer annuals on mounds and intermounds

Species	Relative frequency (%)		Relative density (%)		Above ground biomass (g/m ²)	
	Mound	Inter-mound	Mound	Inter-mound	Mound	Inter-mound
<i>Tidestromia lanuginosa</i>	33.6***	2.1	71.7***	0.7	129.4***	1.8
<i>Eriogonum abertianum</i>	11.6**	27.6	6.9**	45.7	25.2*	44.6
<i>Haplopappus gracilis</i>	1.7***	22.1	0.3***	31.2	0.4***	34.5
<i>Aristida adscensionis</i>	13.4	12.4	5.5	9.4	1.2	1.2
<i>Boerhaavia spicata</i>	14.3**	3.4	6.9*	0.7	10.2**	0.9
<i>Bouteloua aristidoides</i>	8.4	5.5	4.1	3.6	0.4	0.5
<i>Bouteloua barbata</i>	1.7	—	2.1	—	1.6	—
<i>Baileya multiradiata</i>	—	11.7	—	2.9	—	7.0
<i>Machaeranthera tanacetifolia</i>	—	4.8	—	2.2	—	2.8
<i>Salsola kali</i>	5.0	—	0.7	—	3.9	—

t-test, *n* = 20, * *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001.

biomass on irrigated mounds was significantly higher than on non-irrigated mounds in spring; ($t_{18} = 2.237$, $t_{18,0.05} = 2.101$, $p <$) and in summer ($t_{18} = 2.215$, $p < 0.05$). On intermounds, however, there were no significant differences in above-ground biomass between irrigated and non-irrigated plots (Table 3).

Mound soils dried faster than intermound soils. Seasonal patterns of soil water potential at soil depths of 10 and 30 cm were similar between irrigated and non-irrigated mounds (Fig. 2). Patterns of soil water potential were also similar between irrigated and non-irrigated intermound soils. However, unlike the mound soils, soil water potential in irrigated intermound soils at a depth of 10 cm was consistently higher than that in non-irrigated intermound soils until a natural rain event in early June (Fig. 3). At this time, the

Table 3. Comparisons of mean peak biomass between banner-tailed kangaroo rat mounds and intermounds and between irrigated and non-irrigated mounds (mean + S.E.)

	Mound	Intermound
<i>Standing biomass of</i>		
Spring annual (g m ⁻²)		
above-ground	133.3 + 5.9***	25.6 + 6.3
below-ground	106.6 + 6.7***	33.0 + 3.5
Summer annual (g m ⁻²)		
above-ground	172.7 + 7.3***	98.4 + 2.3
below-ground	112.7 + 7.7***	47.9 + 5.4
<i>Above-ground biomass of</i>		
Mounds (g m ⁻²)		
spring annual	154.4 + 3.6*	109.1 + 2.5
summer annual	210.0 + 9.7*	138.5 + 7.3
Intermounds (g m ⁻²)		
spring annual	24.4 + 3.5 NS	28.8 + 4.3
summer annual	94.4 + 7.5 NS	103.1 + 6.2

* *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001; NS, not significant.

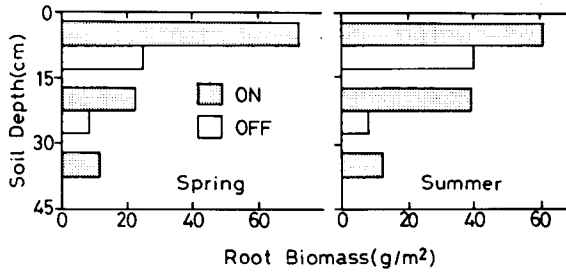


Figure 1. The variation of root biomass with depth on mound and intermound soils.

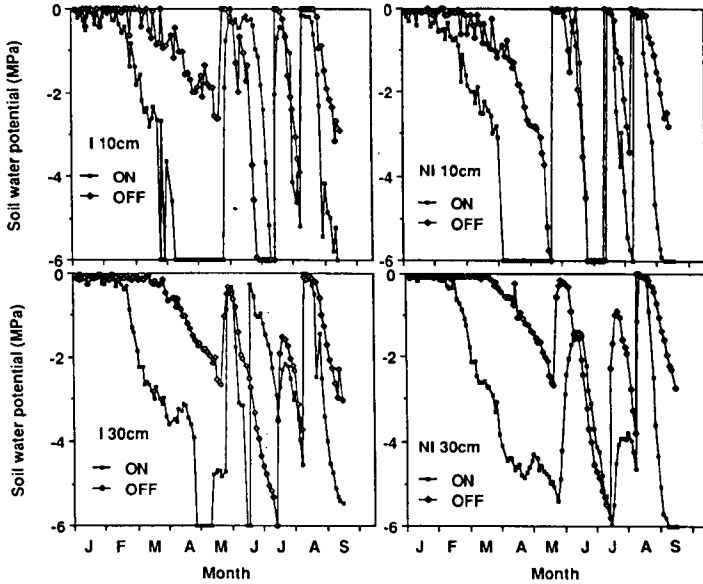


Figure 2. Seasonal changes of soil water potential at soil depths of 10 and 30 cm on mound and intermound areas. I, irrigated; NI, non-irrigated.

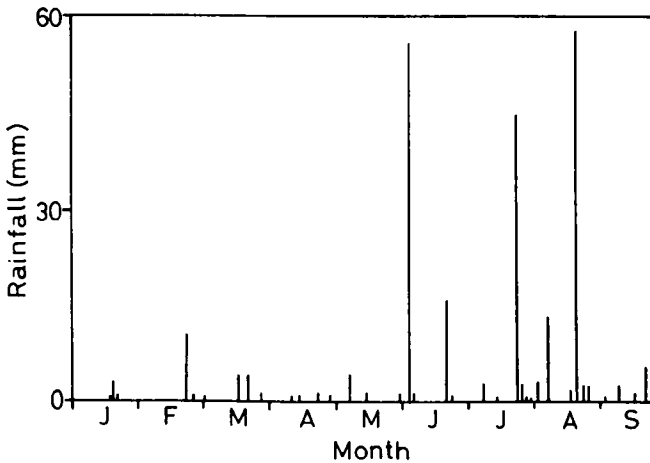


Figure 3. Rainfall at the Jornata LTER site during the study period.

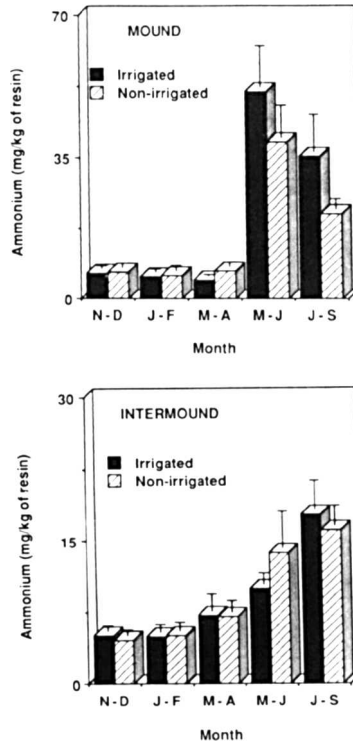


Figure 4. Seasonal patterns of ammonia adsorbed on cation exchange resins in soils on irrigated and non-irrigated kangaroo rat mound and intermound areas.

soil water potential in irrigated intermound soil was -2.26 MPa while that in non-irrigated intermound soil was below -6.0 MPa.

Bulk density of mound soils ($1.6 + 0.02$ g cc⁻¹) was significantly lower than intermound soils ($t_{32,0.001} = 3.646$, $p < 0.001$). Total nitrogen and soil nitrate on mounds were significantly higher than intermounds ($t_{62} = 3.570$, $t_{62,0.001} = 3.460$, $p < 0.001$ for total nitrogen and $t_{62} = 3.462$, $p < 0.001$ for nitrate-nitrogen). However, soil ammonium nitrogen did not differ between mounds and intermound areas (Table 4, Fig. 4).

Seasonal patterns of nitrate availability on mounds and intermounds were similar but the quantities were different (Fig. 5). During the winter the nitrate-nitrogen accumulated on resins in mound soils was 97 mg/kg of resin. However, it decreased sharply until May (3.6 mg/kg of resin), and then increased (27.2 mg/kg of resin in September). Nitrate-nitrogen accumulated on resins in both mound and intermound soils. Ammonium- and

Table 4. Comparison of soil bulk density, and nitrate, ammonium and total nitrogen contents in soils on mound and intermound areas (mean + S.E.)

	Mound	Intermound
Bulk density (g cc ⁻¹)	1.58 + 0.02***	1.74 + 0.03
Nitrate (mg kg ⁻¹)	1.68 + 0.17***	0.62 + 0.04
Ammonium (mg kg ⁻¹)	0.25 + 0.09 NS	0.13 + 0.06
Total nitrogen (g kg ⁻¹)	0.56 + 0.02***	0.43 + 0.01

*** $p < 0.001$.

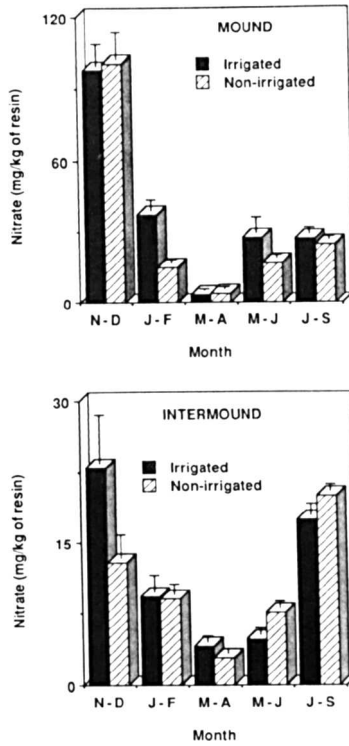


Figure 5. Seasonal patterns of nitrate adsorbed on anion exchange resins in soils on irrigated and non-irrigated kangaroo rat mounds and intermound areas.

nitrate–nitrogen accumulated on resins in mound and intermound soils increased after a large June rainfall event (Fig. 4). There were no significant differences in ammonium– and nitrate–nitrogen accumulated on resins between irrigated and non-irrigated plots (Figs 4 and 5), probably because the amount of nitrogen taken up by plants on irrigated mounds was greater than on non-irrigated mounds.

Discussion

There are many kinds of animal-produced soil disturbances in the desert area where this study was conducted. These disturbances include badger excavations, pocket gopher mounds, rodent cache pits, rabbit forms, ant nests and kangaroo rat burrows. Most are transient features that have no apparent effect on the vegetation. Of these, only the banner-tailed kangaroo rat mounds and nests of the large harvest ant, *Pogonomyrmex rugosus* (Whitford, 1988) have noticeable effects on the vegetation. The mounds created by banner-tailed kangaroo rats have more friable soil than undisturbed areas and have many tunnels and chambers (Moroka *et al.*, 1982).

The soil water potential of mound soils were consistently lower than intermound soils. The former results from high evaporation and high rates of infiltration from the top soil because of the physical and structural characteristics of mound soils. An additional factor is water loss by plant transpiration. Schlesinger *et al.* (1987) reported that 72% of incident rainfall is removed by transpiration annually in this desert. In spring, the above-ground

biomass on mounds was five times greater than that on intermound areas, and the root biomass on mounds was about three times greater than in intermound areas. This greater root mass on mounds apparently removes water and nutrients from the soil more efficiently than the root mass of intermound soils.

Harmsen & van Schreven (1955) reported that nitrogen mineralization can only proceed when there is sufficient moisture in the soil. A pronounced stimulation of nitrogen mineralization by irrigation was reported in work done in the arid region (Harmsen & Kilenbrander, 1965). Binkley (1984) reported that resin ammonium values were strongly affected by soil water regime. During the winter, the soil water potentials at soil depths of 10 and 30 cm on mounds were high, nearly at field capacity, and also the amount of nitrate-nitrogen accumulated on resins in mound soils was quite high. As the soil dried from March to May, microbial activities, mineralization and subsequent nitrification, were probably suppressed by water stress. Therefore, the amount of nitrate-nitrogen accumulated on resins decreased during this period. Another factor contributing to this decrease was the rapid uptake by spring annual plants. Binkley (1984) reported that resin bags were extremely poor competitors for nitrogen in pots containing grass. The spring annuals began to appear from October to December. However, they began to grow actively from February to early April, and ceased their growth at the end of April or early May. The amount of nitrogen taken up by spring annuals during this period on mound and intermound areas was 5.7 gN/m and 0.16 gN/m, respectively. Soil organisms including bacteria, protozoa, and nematodes become inactive as the soil dries (Whitford, 1989). A large rain storm in early June increased soil water potential to nearly zero. This recharge of soil moisture would have restored the microbial activity, which permitted active mineralization of nitrogen. The organic nitrogen sources for this rapid mineralization would have been dead spring annual plant roots and dead micro-organisms. We observed a large concentration of very fine roots which were too fine to be included in root biomass determination in the mound soils. These fine roots probably contributed to increased nitrogen mineralization on mound soils.

The frequent heavy rainstorms from June to September should have maintained soil nitrogen at a higher level. However, the nitrate-nitrogen accumulated on resins on mound soils did not increase significantly. Moreover, ammonium-nitrogen accumulated on resins in mound soils decreased during August and September. This can also be explained by the competition with summer annuals. Most of the summer annuals began to grow actively from July to mid-September and ceased their growth at the end of September or early October. During this period, the amount of nitrogen taken up by plants on mounds and intermounds was 7.3 gN/m and 1.6 gN/m, respectively.

Although irrigation increased water availability in both mound and intermound soils, annual plant biomass increased only on the mounds. This suggests that water was limiting plant growth on the mounds but not on the intermounds. The low levels of available nitrogen in the intermound soils apparently limited the growth of desert annuals (Gutierrez & Whitford, 1987), even with high water availability. The high nitrate levels in mound soils eliminate the nitrogen limitation, and annual plant biomass production is a function of water availability. The data from this study suggest that the greater biomass production on mounds is attributable to higher available nitrogen levels.

Banner-tailed kangaroo rat mounds represent nitrogen-rich patches in a generally low nitrogen environment. The soil characteristics produced by the burrow construction activities of the rodents results in increased nitrogen availability which influences the productivity and species composition of annual plant assemblages on mounds.

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