The composition of seed banks on kangaroo rat (Dipodomys spectabilis) mounds in a Chihuahuan Desert grassland

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ABSTRACT

Disturbance is a major factor determining the plant community structure of ecological systems. In particular, small-scale disturbances from animals can increase heterogeneity and species diversity in plant communities. Kangaroo rat (Dipodomys spectabilis) mounds are small-scale disturbances that support unique plant communities compared to surrounding habitats. The seed bank, which is usually an overlooked part of plant communities, is an important trait of some plant species that allows for their persistence in unpredictable environments. To further understand how small-scale disturbances by kangaroo rats affect the plant community in Chihuahuan Desert grassland, we studied the composition of the seed bank for eight forb taxa on and off kangaroo rat mounds. Kangaroo rat mounds accumulated more seeds and supported different seed compositions than the adjacent grassland. Also, kangaroo rat mounds had different microhabitats than areas away from the mound. This suggests that kangaroo rat mounds facilitate some plant species by providing microhabitats that contain ‘safe sites’ for seeds to accumulate where adult plant populations can establish and colonize thus increasing plant diversity and altering plant structure in communities.

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1. Introduction

Seed banks rarely correlate with the above ground vegetation (Kinucan and Smeins, 1992; Lopez-Marino et al., 2000; Major and Pyott, 1966; Robinowitz, 1981; Thompson and Grime, 1979). This is in part because perennial species often have transient short-lived seed banks (Thompson et al., 1998) or no seed bank, which means the long-lived adult populations are maintained above ground rather than below. Annual plants, however, often produce long-lived, persistent seed banks (Guo et al., 1999; Meissner and Facelli, 1999; Milberg and Hansson, 1993; Thompson and Grime, 1979); so, that if environmental cues are not met for seed germination, then the population is maintained primarily below ground. This is particularly important in unpredictable environments like the deserts of southwestern North America where seed banks maintain plant species diversity below ground during periods of drought (Thompson, 2000).

Moore (1980) theorized that frequently and unpredictably disturbed areas have plant compositions of early successional species that rely on a large persistent seed bank rather than late successional species that establish from invasion (Thompson and Grime, 1979). As an area becomes available, early successional species become established. Then through facilitation, tolerance, or inhibition, communities can reach a climax when early successional species become less suitable for the new environment. Disturbance destroys this climax stage and returns the system to early colonization. Specifically, regular unpredictable tidal fluctuations in a New Jersey freshwater marshland had seed banks with similar plant compositions as the above ground plant community (Leck and Graveline, 1979). Grassland in central New Mexico, which is prone to drought, had similar seed and above ground plant populations (Henderson et al., 1988). The composition of above and below ground plant populations on frequently and unpredictably disturbed areas are exceptions to the generalized pattern where the seed bank rarely correlates with the above ground vegetation.

Soil disturbance resulting from biotic factors can affect the composition of the plant community both above and below ground. In particular, biotic small-scale disturbances can create unique species combinations in plant communities (Bullock, 2000; King, 1977; Peart, 1989; Platt, 1975). For example, porcupine digs, which are soil pockets containing both litter and seeds (Alkon, 1999), contributed to maintaining a high diversity of annual plants (Boeken et al., 1995); gopher disturbances increased legumes while decreasing perennial grass species (Hobbs et al., 2007); and
seed densities were either higher or lower around ant mounds than in adjacent habitats depending on ant species and disturbance location. Specifically, mounds constructed by the ant *Formica exsecta* in sub-alpine grassland had fifteen times more total seeds and slightly higher species richness than the surrounding grassland (Schutz et al., 2008). In contrast, Dostal (2005) found half the number of seeds on ant mounds of *Tetratomorium caespitum* compared to control plots in Slovakian mountain grassland. Given that many biotic small-scale disturbances can impact the number and types of plants and their seeds in an area, it is not surprising that disturbances caused by kangaroo rats also influence plant communities.

Banner tail kangaroo rat (*Dipodomys spectabilis*) mounds are noticeable features of many arid landscapes, creating a mosaic of disturbed patches with distinct environmental conditions (Guo, 1996; Schroder and Gelsoso, 1975). In the Chihuahuan Desert, soil on kangaroo rat mounds had higher concentrations of nitrogen and lower water availability after rainfall than non-mound soil (Greene and Reynard, 1932; Moorhead et al., 1988; Mun and Whiftd, 1990). The extent to which these disturbances affect the vegetation is so profound that *D. spectabilis* is considered a keystone species (Heske et al., 1993). Many studies have addressed vegetation succession and plant species composition on and off kangaroo rat mounds (Davidson and Lightfoot, 2006, 2008; Fields et al., 1999; Guo, 1996, 1998; Moorhead et al., 1988; Moroka et al., 1982; Mun and Whiftd, 1990). They have found that annual plant cover is generally higher on mounds than off (*Davidson and Lightfoot, 2008; Moorhead et al., 1988; Moroka et al., 1982*). Furthermore, kangaroo rat mounds create an ecotone where one habitat type, the mound area, shifts to another, the inter-mound, with the highest plant species diversity occurring where the two habitats meet (Guo, 1996). Even though there has been extensive research on the vegetation associated with mounds, no research has examined the composition of the seed bank on kangaroo rat mounds.

Kangaroo rat activity (mound building and herbivory) may affect the seed bank in a plant community in several ways. First, the plant community on mounds typically consists of a wide variety of annual plant species (Davidson and Lightfoot, 2008; Guo, 1996, 1998). Many plants disperse their seeds via the seed rain close to the parent plant (Willson and Travest, 2000). As a consequence, these annuals may directly deposit a large proportion of their seeds into the seed bank on the mound. Second, kangaroo rat seed caching and selective foraging can change seed distributions and densities in plant communities (Davidson et al., 1980; Reichman, 1979). Banner tail kangaroo rats are larder hoarders that cache seeds in mounds at depths near or below 30 cm of the soil surface (Reichman et al., 1985), making them unavailable for germination (Kemp, 1989). Selective foraging by a kangaroo rat guild (*Dipodomys merriami, Dipodomys ordii, and D. spectabilis*) in the Chihuahuan Desert in Arizona changed the plant community by decreasing above ground populations of large seeded winter annuals (Brown and Heske, 1990; Samson et al., 1992). Therefore, to more fully understand plant populations and the effects of kangaroo rat activity on plant populations, an investigation of the seed bank is important.

We surveyed part of the seed bank in Chihuahuan Desert grassland to understand the impact of banner tail kangaroo rat mounds on plant communities. Regarding eight dominant forb taxa in the area, we asked the following questions: 1) Do mounds compared to off mounds have more seeds in the seed bank? 2) Does the species composition of the seed bank differ between mounds and off mounds? We predict that the eight plant taxa will have seed banks that differ between mounds and off mounds and that mounds will have high seed numbers of early successional plant species.

2. Materials and methods

2.1. Study site

We collected data at Sevilleta National Wildlife Refuge Long-term Ecological Research (LTER) site in Socorro County in central New Mexico, latitude 34°18′50″N, longitude 106°42′36″W. The Sevilleta is located along a transition zone among several biomes: Great Plains Grassland, Colorado Plateau Shrub Steppe, Conifer Woodland and Chihuahuan Desert. The Chihuahuan Desert grassland is dominated by black grama (*Bouteloua eriopoda*) with associated species consisting of creosote bush (*Larrea tridentata*), yucca (*Yucca glauca*), snakeweed (*Gutierrezia sarothrae*) and several annual and perennial forbs. Long-term total precipitation from September 2000 to August 2001 was 293.9 mm where the mean annual precipitation for 2000 and 2001 in the area was 249.9 mm. Most of this precipitation in 2001 occurred during the summer in August. Long-term monthly mean temperatures for 2001 were 0.5 °C and 23.8 °C in January and August, respectively. We used meteorological data obtained from the Sevilleta LTER website, http://sev.lternet.edu/project_details.php?id=SEV001, for precipitation and temperature assessments.

2.2. Collecting soil samples

We randomly selected 10 active kangaroo rat mounds over an area of 1.1 km². We collected soil on the kangaroo rat mound at the base of the mound (B, termed ‘base’), 1 m away from the base to capture the disturbed area surrounding the mound (S, termed ‘surrounding’), and approximately 5 m from the surrounding sample to represent off mound locations (Fig. 1). Off mound locations were at the edge of the nearest black grama clump (E, termed ‘edge’) and in an open undisturbed area between black grama clumps (I, termed ‘inter-space’). We sampled the edge and inter-space of black grama since this is the dominant grass species in the Chihuahuan Desert and should represent a large proportion of the microhabitats that are off the mound. We collected subsamples in the four cardinal directions resulting in a total of 16 subsamples per mound (4 subsamples by 4 mound locations). Some subsamples for some mounds were destroyed. To ensure that the data for mounds with missing samples were orthogonal, we used a lesser number of samples so that the number of samples was the same for each mound location.

We collected samples using a soil auger with 10 cm diameter and 2 cm depth during the last week of August 2001 when most spring annuals would have already dispersed their seeds. We recorded percent cover of undisturbed and disturbed soil, gravel, litter and vegetation within a 30 cm × 30 cm area at each subsample location to understand the potential effects of these physical variables on seed accumulation. We calculated the percentage of undisturbed soil by subtracting the sum of the other physical variable percentages from 100%. We then described microhabitats using the combination of these five physical variables. This should not be confused with Harper’s (1961) term of a ‘safe site’, which is an area at a much smaller scale where a seed can successfully germinate and a species can establish.

2.3. Processing samples

We dried soil samples in an oven for 48 h at 50 °C and sieved them using the finest possible sieve to capture small seeds and a larger sieve to exclude large particles. To further separate seeds from remaining soil we floated samples in a salt solution (sodium bicarbonate (5 g), sodium hexametaphosphate (10 g), and magnesium sulphate (25 g) in 200 ml of tap water) and dried them.
From this organic material, a subsample was taken to represent the sample. We counted and tested seeds from these subsamples for viability. We identified eight target taxa based on their high occurrences in the above ground vegetation at an adjacent study site (T. Koontz and H. Simpson, personal observation). Four of the taxa (Cryptantha crassisepala, Descurainia pinnata, Phacelia integrifolia, and Plantago patagonica) are spring annuals, three (Astragalus missouriensis, Lesquerella fendleri, and Oenothera spp.) are perennial forbs that flower in the spring, and one (Sphaeralcea spp.) is a perennial forb that flowers in the fall. Since we could not distinguish species for the seeds of Sphaeralcea and Oenothera taxa at our site, we analyzed these seeds at the genus level. We assumed that spring annuals are early successional species and perennial species are not. We made identifications under a dissecting microscope using a reference collection compiled by Sevilleta biologists along with seeds that we had collected. We tested for viability using the pressure method (see Meissner and Facelli, 1999 and Roberts and Ricketts, 1979 for details on the pressure method). Due to time constraint we only counted the number of viable seeds from the eight taxa.

2.4. Statistical analysis

We used an analysis of variance (ANOVA) to assess differences in total number of seeds among the four different kangaroo rat mound locations. We added seed counts from the subsamples for each of the four mound locations (base, surrounding, edge, and inter-space) on each mound to calculate the total number of seeds. Since neither total number of seeds nor any transformations of the data had normal distributions, we used the GLIMMIX procedure in SAS that does not require normal distributions of populations. For the model, the total seed number was the dependent variable and mound location (mound: base and surrounding; off mound: edge and inter-space) was the independent variable. We did not pool the data together for mound and off mound samples since the ANOVA indicated that the four mound locations were significantly different from each other for total seed numbers. To determine whether the seed composition differed among mound locations, we used a multivariate analysis of variance (MANOVA) where ranks of total seed numbers for the eight target taxa were dependent variables and the independent variable was mound location. We also tested whether five physical variables (disturbed and undisturbed soil, gravel, litter, and vegetation) differed among mound locations. Again, a MANOVA was used for this analysis where ranks of percent cover for the physical variables were the dependent variables and mound locations were the independent variables.
location was the independent variable. Statistical analyses were performed in SAS version 9.2 (SAS Institute Inc., Cary, North Carolina).

3. Results

Average total seed numbers differed significantly among mound locations \((F_{3,36} = 31.30, P < 0.0001)\). We extracted 10,658 seeds of the eight target taxa: 9,269 from mounds and 1,389 seeds off mounds (see Fig. 1 to reference mound locations). The base had significantly more seeds \((n = 6,662)\) than all other mound locations, and surrounding mound areas had significantly more seeds \((n = 2,607)\) than both off mound locations (edge and inter-space). The inter-space had the lowest number of seeds \((n = 377)\), but this was not significantly different from the number of seeds \((n = 1,012)\) at the edge.

Seeds of all eight taxa were found at each mound location (Fig. 2) and seed composition of the eight taxa differed significantly among mound locations (MANOVA, \(P < 0.0001\)). The first canonical axis (CAN1), which accounted for 93% of total variation, indicated that mound locations supported a different seed assemblage than off mound locations. The second canonical axis (CAN2, 5% total variation) indicated differences in seed bank composition between the two off mound locations (Fig. 3A). *D. pinnata* accounted for 77% of seeds extracted and explained most of the variation in seed composition among mound locations since it had the highest loading on the first canonical axis. When we compared the number of *D. pinnata* seeds extracted among locations, base locations had

![Diagram](image_url)

**Fig. 3.** Canonical coefficients for (A) the seed composition for the eight plant taxa during summer 2001 (MANOVA: \(F_{8,31} = 24.05, P < 0.0001\)) and (B) the five physical variables that were used to describe the mound microhabitats where soil samples were collected (MANOVA: \(F_{5,34} = 42.67, P < 0.0001\)). Ellipses represent two standard deviations from the mean for both CAN1 and CAN2. Note that CAN1 groups different seed compositions and microhabitats between on mound locations and off mound locations and CAN2 groups different microhabitats between the off mound locations. CAN2 for seed composition shows only a slight grouping for seed composition between off mound samples. Roy’s greatest root statistics are reported for MANOVAs.
over three-times more seeds than surrounding locations, 29.7 times more than edge locations and 67.3 times more than inter-
space locations (Fig. 2).

The five physical variables also differed significantly among
mound locations (MANOVA, \( P < 0.0001 \)), demonstrating that
mound locations contained different microhabitats. The first
canonical axis (71% of total variation) indicated different
microhabitats between mound (base and surrounding) and off
mound (edge and inter-space). The second canonical axis (28% of total
variation) indicated different microhabitats among mound, edge
and inter-space (Fig. 3B). Gravel, litter and disturbed soil had the
highest loadings on the first canonical axis. Mound microhabitats
had higher percent cover of these three attributes than off mound
microhabitats (Fig. 4). Most of the variation between edge and
inter-space microhabitats was explained by vegetation cover, with
four-fold greater vegetation cover in edge microhabitats compared
with inter-space microhabitats (Fig. 4).

4. Discussion

We found that kangaroo rat mounds influenced the size and
composition of a subset of the seed bank in this arid grassland.
Mounds had nearly seven-times more seeds than the adjacent
grassland. The base of kangaroo rat mounds had 64% of total seeds,
surrounding areas of mounds had 25% of total seeds, and off mound
locations had only 12% of total seeds. Mounds contained larger seed
banks of four taxa (C. crassisepala, D. pinnata, Oenothera spp. and
Sphaeralcea spp.) compared to off mounds. Of these four taxa, only
the two annuals (C. crassisepala and D. pinnata) had significantly
larger seed banks on the mound where D. pinnata had six-times
more seeds on the mound than any of the other seven taxa (Fig. 2).

The mechanism of seed dispersal is an important factor in
determining the number of seeds in the seed bank and their spatial
distribution. D. pinnata is a small seeded, weedy annual that can
produce copious amounts of seeds. In 2001, we observed that above
ground plant populations on kangaroo rat mounds were dominated
by D. pinnata. Other studies support this observation, indicating
that above ground populations of D. pinnata are more prevalent on
disturbed, nitrogen rich kangaroo rat mounds (Davidson and
Lightfoot, 2008; Guo, 1996, 1998). Our results show that D. pin-
Vata seeds were highest on the mound where most parental plants
exist. The size of D. pinnata’s seed pools decreased farther away
from parental plants and the mound area. This pattern is typical of
gravity dispersed seeds where the majority of seeds are deposited
near the parent plant.

The remaining plant taxa that we looked at did not show
a similar pattern of seed distribution. Many taxa had low seed
populations with more homogeneous distributions. Of these taxa
there was no obvious mode of dispersal. None of the other seven
plant taxa had seeds small enough or had appendages for wind
dispersal (T. Koontz and H Simpson, personal observation). Since
water is a limiting resource in this arid grassland, it is unlikely that
any of our plant taxa rely on water as their primary mode for
dispersal. While some plants rely on more than one mode of
dispersal (Willson and Traveset, 2000), it is likely that most of the
seeds that we extracted from the soil are dispersed by animals.

The main function of dispersal is to move a seed to an area that
optimizes the survival of the seed and its seedling (Willson and
Traveset, 2000). This leads to many plant species having seed banks
with patchy or heterogeneous distributions on the landscape
(Thompson, 1986). Many of our plant taxa, however, had low seed
populations with homogeneous distributions. Six of the taxa (C.
crassisepala, D. pinnata, Oenothera spp., Phacelia integrifolia, P.
patagonica, and Sphaeralcea spp.) that we assessed are known prey
items of the consumers that exist in this grassland (Andrew Edel-
mann, personal observation: Hope and Parmenter, 2007); and
selective foraging can actually decrease the spatial patchiness of
seed populations (Reichman, 1979). If the seeds we extracted from
the soil were selectively foraged on, this could explain why some
taxa had seed banks with low seed numbers and homogeneous
distributions. Animal dispersal and consumption both probably
contributed to the seed bank sizes and distributions that we found
in this grassland.

Different microhabitats that occupy these small-scale disturbed
areas can also explain the size and distribution of seed populations
on kangaroo rat mounds compared to the adjacent grassland. Both
the base and surrounding mound microhabitats had more
disturbed soil, gravel, and litter than the microhabitats of off
mound locations. One of these physical variables or a combination
of these physical variables could have provided ‘safe sites’ where
these species not only can germinate and establish in this grassland
on kangaroo rat mounds, but also can accumulate seeds. The
increased disturbed soil and gravel could provide depressions and
cracks where dispersed seeds can accumulate. The disturbance
and litter that are common on the mound probably increased nitrogen
levels; and other studies have indicated that kangaroo rat mounds
do have higher nitrogen content than adjacent habitats that they
occur in (Greene and Reynard, 1932; Moorhead et al., 1988; Mun
and Whitford, 1990). This increase in nitrogen can promote the
growth of seedlings that have germinated from captured seeds; so,
species that have dispersed and accumulated seeds on the mound
can persist in a community. An evaluation of all seed bank populations and the above ground
vegetation on kangaroo rat mounds at different stages of a mound’s
disturbance would help to determine which species are functioning
as early successional species in this arid grassland. Kangaroo rat
mounds are known to have unique plant assemblages compared to their
surrounding environments (Davidson and Lightfoot, 2008; Moorhead et al., 1988; Moroka et al., 1982). Which of these species
are early successional species is uncertain. For our study we evalu-
ated a subset of the grassland community rather than what is
considered dominant species on kangaroo rat mounds. All of the
plant taxa that we evaluated, except one, had small seed bank
populations, suggesting that they are not early successional species.

‘Snap shots’ are what most seed bank studies report. Under-
standing the spatial and temporal dynamics of the seed bank

community can elucidate how plant communities function. In desert ecosystems this is especially important, because certain plants in the desert are only represented in the community by their seed bank (Kemp, 1989). Our study, even though it was only a ‘snap shot’, increased the knowledge of how some desert species respond to small-scale disturbance in a desert grassland community. In particular, we demonstrated that not only do kangaroo rat mounds contain unique plant assemblages above ground, but they also support different plant communities below ground compared to the surrounding area. More seed bank studies like ours are essential to understand how consumers and specifically how their disturbances facilitate particular plant populations and communities.

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References