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Mesquite (*Prosopis glandulosa*) germination and survival in black-grama (*Bouteloua eriopoda*) grassland: relations between microsite and heteromyid rodent (*Dipodomys* spp.) impact

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Abstract

We conducted experiments to examine microsite and rodent influence on mesquite (*Prosopis glandulosa*) germination and survival in Chihuahuan Desert black-grama (*Bouteloua eriopoda*) grassland. Simulated caches with mesquite seeds were placed in undisturbed grassland, burned grassland patches with reduced grass cover, and on the periphery of kangaroo rat mounds. Rodent access to cached seeds was controlled by covering half of the caches with mesh domes. Kangaroo rats destroyed dung pats containing scarified mesquite seeds and excavated all seeds in simulated caches during a year in which no grasses or forbs set seed. Germination was the highest in unburned grassland, but over-winter survival was only observed across experiments in burned grassland microsites. A large proportion of seed caches were excavated (1.1–5.5% of the rodent-excluded caches and between 15.6% and 21.1% of the control caches). There were seasonal differences in numbers of emergent seedlings, with a peak in September 2002 following late summer rains. There were no significant differences in numbers of germinants in burned and unburned grassland microsites, but significantly fewer mesquite seeds germinated on banner-tail kangaroo rat mounds. Caches excavated by rodents yielded 46.6% of

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germinants. This study suggests that scarification of mesquite seeds is not necessary for germination and heteromyid rodents may be responsible for increased mesquite density in grasslands with some mature mesquite plants. The data also suggest that competition between mesquite seedlings and grasses in black-grama grassland is weak because of the physical characteristics of this system.

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Keywords: Banner-tail kangaroo rats; Black-grama grassland; *Bouteloua eriopoda*; Fire; Germination; Heteromyid rodents; Mesquite; *Prosopis glandulosa*

1. Introduction

The once expansive arid grasslands of North America's Chihuahuan Desert have largely been converted to shrub savannas, honey mesquite (*Prosopis glandulosa*) coppice dunes, and creosotebush (*Larrea tridentata*) shrublands during the past 150 years (Buffington and Herbel, 1965; Grover and Musick, 1990; Archer, 1989). Mesquite is thought to have spread from drainages and riparian zones into upland desert grasslands (Johnston, 1963; Archer et al., 1988).

Van Auken and Bush (1987, 1988, 1989, 1990) reported that mesquite is a poor competitor with grasses, including buffalo grass (*Buchloe dactyloides*), little bluestem (*Schizachyrium scoparium*) and side oats grama (*Bouteloua curtipendula*). However, these grass species are minor components of Chihuahuan desert grassland communities (Dick-Peddie, 1993). Historically, black-grama (*Bouteloua eriopoda*) is the dominant grass species in much of the upland Chihuahuan desert grassland of southern New Mexico, southeastern Arizona, northeastern Mexico and west Texas. There is generally less perennial grass cover in black-grama systems than in the south Texas grasslands studied by Van Auken and Bush, and that difference may affect the competitive interactions between mesquite and grasses in Chihuahuan Desert grasslands.

Large mesquite shrubs in former black-grama grasslands are frequently associated with burrow mounds of banner-tail kangaroo rats (*Dipodomys spectabilis*). Anecdotal evidence from ranchers suggests that mesquite on or around mounds had been "planted" by kangaroo rats. Banner-tail kangaroo rat mound soils are characterized by higher infiltration rates, greater concentrations of nitrogen, higher nitrogen mineralization rates, accelerated microbial activity and greater plant biomass than surrounding soils (Moorhead et al., 1988; Mun and Whitford, 1990; Ayarbe and Kieft, 2000). These characteristics of banner-tail kangaroo rat mound soils may enhance germination and growth of mesquite seeds cached near or on the margins of the mounds.

The dispersal of mesquite from ephemeral stream and ephemeral lake margins has been attributed to the consumption of mesquite fruit pods and seeds by livestock. When domestic animals consume mesquite seeds, they pass through the animal's digestive tract, a process that enhances the germinability of mesquite, and the seeds are then often deposited in areas distant from the parent plants (Brown and Archer, 1989; Kramp et al., 1998).

Rodents in the family Heteromyidae (*Dipodomys* spp., *Perognathus* spp., and *Chaetodipus* spp.) scatter hoard seeds in shallow caches (Price et al., 2000). While livestock may be the primary long-distance dispersal vector of mesquite seeds, Merriam's kangaroo rats (*Dipodomys merriami*) are documented short-distance dispersers of mesquite (Reynolds and Glendening, 1949; Reynolds, 1950; Reynolds, 1954). Reynolds and Glendening (1949) reported that mesquite seeds were a preferred food item of Merriam's kangaroo rats, and rats buried mesquite seeds in shallow caches where germinants were subsequently observed. Most investigators have concluded that mesquite seeds must be scarified by mechanical abrasion or passage through an herbivore digestive system in order to germinate (Kramp et al., 1998) and have dismissed rodent scatter hoard caches as a means of increasing mesquite density in desert grassland.

We designed field experiments to address questions about mesquite germination and survival in Chihuahuan desert black-grama grasslands in relation to microsite location and heteromyid impact. Our experiments evaluated (1) the germination success of scarified and unscarified mesquite seeds in cattle dung pats and simulated rodent caches, (2) relative germination and establishment of mesquite on banner-tail kangaroo rat mounds, disturbed (burned) grassland, and intact black-grama grassland, and (3) the impact of heteromyid rodents on germination of mesquite seeds in simulated caches and seedling survival.

2. Methods

2.1. Study area

Research was conducted at the Armendaris Ranch, approximately 30 km east of Truth or Consequences, New Mexico. The Armendaris is an operational bison (*Bison bison*) ranch. The study site is Chihuahuan Desert grassland, dominated by black-grama grass, scattered soap tree yucca (*Yucca elata*), Torrey ephedra (*Ephedra torreyana*) and honey mesquite (*P. glandulosa*). The soils of the study area are characterized as sandy loam aridisols. We conducted our experiments within a 32 ha plot enclosed by an electric fence to exclude bison.

The rodent community in this area in 2000 and 2001 was dominated by Ord's kangaroo rats (*Dipodomys ordii*) (3.4 per 100 trap nights) and Silky pocket mice (*Perognathus flavus*) (1.8 per 100 trap nights). Other rodents that occurred at less than 1 per 100 trap nights included dusky wood rat (*Neotoma micropus*), banner-tail kangaroo rat (*D. spectabilis*), spotted ground squirrel (*Spermophilus spilosoma*) and southern grasshopper mouse (*Onychomys torridus*).

2.2. Cattle versus rodent influences on germination

In August 2000, mesquite seeds were scarified in 1.0N sulfuric acid to simulate passage through an herbivore digestive tract. Five scarified seeds were placed in cattle dung and five unscarified seeds were placed in simulated heteromyid seed

caches. Twenty-four dung pats and 24 caches were placed on banner-tail kangaroo rat mounds. Twenty-four dung pats and cache pits were placed along a transect, 10 m from each other, in bare soil between black-grama grass tussocks.

2.3. *Mesquite response to microsite and rodent impact*

On 7 July 2001, a controlled burn was initiated on approximately 20 ha of the bison-excluded plot. The post-burn study area was a mosaic of burned and unburned patches, ranging in size from a fraction of a hectare to 1.5 ha. The grass cover in burned patches was 50.0% lower than unburned patches 1 year after the fire. Between 70.0% and 100% of the shrubs in the burn plot were killed by the fire (Killgore et al., 2005). The burned patches provided cache sites that were more than 50 cm from the nearest live grass tussock.

Within the enclosure plot, we planted simulated heteromyid seed caches in three microsites: unburned grassland, burned grassland, and on banner-tail kangaroo rat mounds. It has been established that black-grama systems are not fire adapted (McPherson, 1995), and we used burn microsites to compare mesquite germination and survival in areas with and without live black-grama tussocks. The mound microsites were selected to examine the influence of soil modification by banner-tail kangaroo rats on the germination and survivorship of mesquite.

We dug simulated caches that were 3–5 cm deep, and 3–5 cm in diameter, the mean size of natural heteromyid caches on the Armendaris (Killgore et al., 2005). In unburned and burned grassland, caches were installed between grass tussock interspaces. Seed caches on banner-tail kangaroo rat mounds were placed in bare soil at the periphery of mounds. At each microsite, four caches were dug approximately 15–20 cm from each other. One pair of caches was covered with a 30 cm diameter chicken wire dome to exclude small mammals, and the other two were left uncaged as a control. One cache in each pair contained five seeds with their pod covering intact and the other contained five cleaned seeds. There were 15 replicates (burned grassland, unburned grassland, and banner-tail kangaroo rat mound) with rodent enclosure and uncovered caches at each microsite, and each replicate set of caches was flagged for subsequent census.

2.4. *Mesquite response to precipitation patterns*

Mesquite flowers and sets fruit between late May and early June irrespective of winter rainfall, and may flower and set fruit again in late summer–early autumn in response to summer monsoon rains. These monsoons occur between July and September and account for more than half of the precipitation in the Chihuahuan Desert. Seeds set between May and June are likely cached by rodents in July and August. These cached seeds may germinate in response to summer monsoons, and therefore exhibit higher germination rates and over-winter survival than seeds produced in August and September. We implemented two experiments to evaluate potential differences in germination and over-winter survival of seeds cached before and after the summer monsoons.

Experiment I (pre-monsoon mesquite seed set) was initiated on 14 September 2001. The field plot was monitored on six dates ($n = 540$ total cache-observations) in the spring and autumn of 2001 and 2002 to examine differences in germination, survivorship, and animal-related disturbances on the seeds and germinants in the dry spring and following late summer rains. On 17 November 2002, we initiated Experiment II (post-monsoon mesquite seed set) by discarding remaining seeds and germinants from the previous experiment, and planting fresh seeds in the aforementioned configuration. Three census dates were recorded during Experiment II ($n = 270$ total cache-observations). Field plots were monitored for presence of new germinants, evidence of herbivory and excavation of planted seeds in respective microsite and exclosure plots. Only new germinants and excavations were recorded to avoid pseudo-replication of observations (Hurlbert, 1984).

2.5. Statistical analysis

Data were tested for normality using the Shapiro–Wilk Test. Seedling emergence and the number of seeds excavated by small mammals were not normally distributed data sets for either Experiment I or II. Mean germinants and excavations per cache, the experimental unit, per census date were tested for differences across microsite and exclosure treatments. Mean germination was analysed separately for Experiment I and II as different cohorts of seeds were being observed.

One-way ANOVA was used to test differences in mean number of germinants among treatments separately for Experiment I and II when assumptions of variance equality were met. Kruskal–Wallis Test was used to make comparisons between treatments when variance equality could not be ensured. Data from each experiment were analysed with two-factor ANOVA to determine significant interactions between microsite and exclosure treatment on mean germination. We also used two-factor ANOVA to test interactions between microsite location and observation date on occurrence of cache excavations. When ANOVA was employed, p -values from Type III sums of squares were utilized to eliminate the effect of position of treatment in the model on the results. Correlation analysis was utilized to compare the relationship between mean germinants and number of excavations, as well as mean seedling emergence and precipitation. All test are two-tailed and evaluated at the significance level of $\alpha = 0.05$.

3. Results

3.1. Cattle versus rodent influences on germination

In October 2000, we found no mesquite germinants in the experimental dung pats or cache pits. All simulated caches had been excavated in a manner consistent with rodent disturbance, and all seeds removed. Dung pats were broken into small fragments, and all seeds removed. Tail drag marks and kangaroo rat footprints around disturbed dung pats and excavated caches provided presumptive evidence

that Ord’s kangaroo rats were responsible for harvesting the mesquite seeds. On eight of the banner-tail mounds (33.3%), we recorded that pits had been excavated under the dung pats. This suggests that rodents harvested our planted mesquite seeds or that some germination had occurred and rodents excavated and removed the seedlings.

3.2. Mesquite response to microsite and rodent impact

In both Experiment I and II, we recorded more new mesquite germinants in caches within unburned and burned grassland microsites (Fig. 1) than on banner-tail kangaroo rat mounds (Experiment I: Kruskal–Wallis, $\chi^2 = 23.22$, d.f. = 2, $p < 0.0001$; Experiment II: $\chi^2 = 15.10$, d.f. = 2, $p < 0.001$). More germinants were recorded under rodent exclosures than open caches, but the differences were not statistically significant for Experiment I or II, respectively (ANOVA, $F_{1,538} = 1.34$, $p = 0.25$; $F_{1,268} = 0.89$, $p = 0.35$). The highest overall germination rate per cache was observed in the rodent-excluded grassland microsites (20.0%), while rodent-excluded banner-tail mound sites yielded the lowest germination rate (7.33%) (Table 1).

We recorded no significant differences in the mean number of caches excavated by rodents between microsites in Experiment I (ANOVA, $F_{2,537} = 0.53$, $p = 0.59$), but more excavations occurred in burned grassland microsites during Experiment II (Kruskal–Wallis, $\chi^2 = 7.13$, d.f. = 2, $p < 0.03$). Significantly more control caches were excavated than rodent-excluded caches in Experiment I (Kruskal–Wallis, $\chi^2 = 28.89$, d.f. = 2, $p < 0.001$) but not in Experiment II (ANOVA, $F_{1,268} = 2.73$, $p = 0.10$) (Fig. 3).

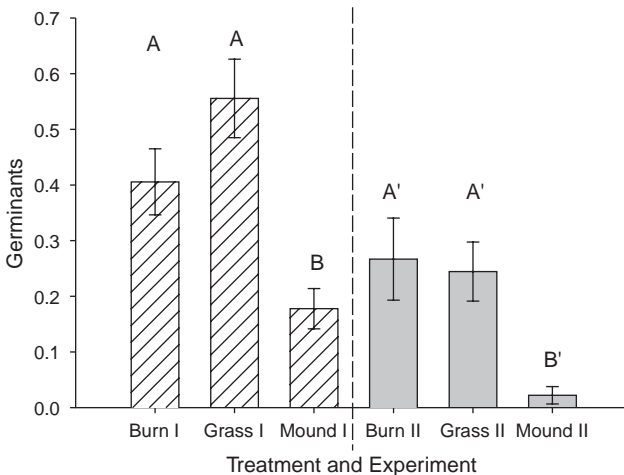


Fig. 1. Mean number of mesquite germinants per simulated cache ± SE, in vegetation microsites burned grassland, unburned grassland and kangaroo rat mound, on the Armendaris Ranch between 11 October 2001 and 24 May 2004. Experiment I (striped bars) represents a simulated pre-monsoon seed set, and Experiment II (solid bars) represents a simulated mesquite seed set in response to adequate monsoon rain. Bars with the same letter are statistically equal.

Table 1

Percent of mesquite seeds that germinated from simulated heteromyid caches in burned grassland (Burn), unburned grassland (Grass) and kangaroo rat mound (Mound) microsites on the Armendaris Ranch, New Mexico

Treatment	Experiment I germination (%)	Experiment II germination (%)
Burn no cage	12.67	4.67
Burn cage	17.33	7.33
Grass no cage	16.67	4.67
Grass cage	20.0	5.33
Mound no cage	8.67	0.00
Mound cage	7.33	1.33
Total	13.78	3.89

Experiment I was designed to simulate mesquite seeds set and cached before summer monsoon rains, and Experiment II was designed to simulate mesquite seeds set and cached after summer monsoon rains.

Correlation analyses between mean rodent excavations and mean new seedlings per date were performed separately for each microsite. Caged microsites were excluded from analyses as excavations recorded under cages are most parsimoniously attributed to invertebrates or lizards, and not relevant for evaluating rodent impact on mesquite germination and survivorship. Across microsites, excavation and mean mesquite germinants were not correlated, and only burned grassland microsites displayed a negative relationship with mesquite germination (Spearman's Rank Correlation, $r_s = 0.63$, $r^2 = 0.27$, $p = 0.07$). Furthermore, control (uncaged) caches had post-excavation germination rates of 36.8%, 50.0%, and 53.8%, respectively, for the burn, grass, and mound microsites.

Angular cuts on the stem bases of mesquite seedlings provided evidence that heteromyid rodents browsed seedlings between the 3-leaf and 9-leaf stages. The proportion of mesquite seedlings killed by rodent browsing was between 12.5% and 15.4% of the germinants in the unburned grassland and burned grassland microsites in October 2002.

We performed two-factor ANOVAs to ascertain potential interactions between microsite and enclosure on germination, and microsite and date influence on cache excavation. Germination was significantly impacted by the combination of microsite and enclosure treatment in both Experiment I and II, respectively (ANOVA, $F_{5,534} = 4.77$, $p = 0.0003$, $F_{5,264} = 2.67$, $p = 0.02$). Mean excavations were not significantly related to interactions between microsite location and date for Experiment I (ANOVA, $F_{17,522} = 1.21$, $p = 0.25$) but were for Experiment II (ANOVA, $F_{8,261} = 4.66$, $p < 0.0001$).

3.3. Mesquite and rodent response to season/precipitation

Mesquite seeds planted in Experiment I germinated at a higher rate per cache than seeds planted for Experiment II across microsite and enclosure treatments (Table 1). However, only seeds planted in caged, burned grassland microsites survived over-winter during Experiment I, and only mesquite seeds cached in the caged, burned

grassland sites and control grassland sites survived over-winter during Experiment II (Table 2).

We recorded more new germinants and precipitation in September 2002 than any other month of the study (Fig. 2). However, there was no correlation between the mean number of germinants and precipitation per observation date (Spearman’s Rank Correlation, $r_s = 0.24$, $r^2 = 0.28$, $p = 0.54$), and new germinants were recorded on every census date (Fig. 2).

Table 2
Percent over-winter survival of mesquite seeds planted in simulated heteromyid caches in burned grassland (Burn), unburned grassland (Grass) and kangaroo rat mound (Mound) microsites and rodent exclosures (Cage, No Cage) on the Armendaris Ranch, New Mexico

Treatment	Survival Experiment I (%)	Survival Experiment II (%)
Burn no cage	0.0	0.0
Burn cage	50.0	28.6
Grass no cage	0.0	50.0
Grass cage	0.0	0.0
Mound no cage	0.0	*
Mound cage	0.0	0.0
Total	8.0	13.64

Experiment I was designed to simulate mesquite seeds set and cached before summer monsoon rains, and Experiment II was designed to simulate mesquite seeds set and cached after summer monsoon rains. An asterisk denotes that no seedlings were alive in the fall, and therefore over-winter survival is an invalid measurement.

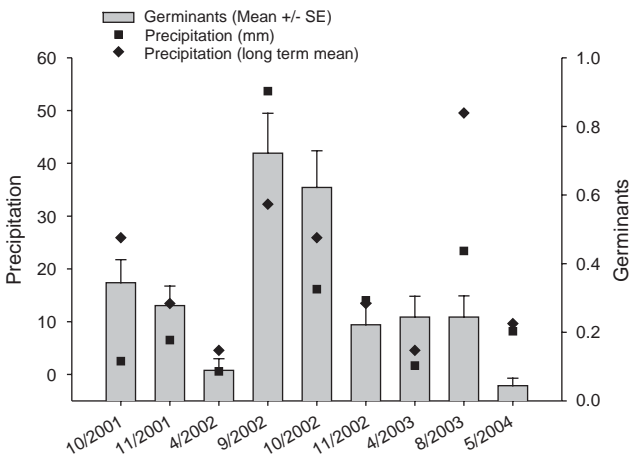


Fig. 2. Comparison of new mesquite germinants per simulated cache (bars) ±SE, mean precipitation (mm) at Armendaris Ranch during the study, and mean rainfall for Truth or Consequences, New Mexico per sampling date. Y-axes are scaled to highlight relationship between emergent seedlings and peaks in rainfall.

4. Discussion

4.1. Cattle versus rodent influences on mesquite germination

Kangaroo rats forage extensively on the flowering tillers of grasses and seeds (Brown and Davidson, 1977; Parmenter et al., 1984; Brown and Heske, 1990; Kerley et al., 1997). During the growing season of the dung pat experiment, no grasses or annual herbaceous plants flowered, and the only plants that set fruit or seed were mesquite. The dry conditions and lack of other food resources likely account for the complete destruction of the dung pats and excavation of all of the caches.

4.2. Mesquite response to microsite and rodent impact

Contrary to anecdotal reports, more mesquite seeds germinated in unburned and burned grassland microsites than on banner-tail kangaroo rat mounds. Mesquite is a poor competitor with several grass species (Van Auken and Bush, 1987, 1988, 1989, 1990), but our results demonstrate that mesquite germinates readily in undisturbed Chihuahuan Desert black-grama grasslands. Black-grama grassland is characterized by sparse grass cover and relatively large bare soil patches between grass tussocks. Mesquite seeds scatter-hoarded by heteromyid rodents in black-grama grassland are frequently cached in these bare patches (Killgore, 2004). Larger patches of bare ground in black-grama habitats enable more solar radiation to contact soil, a condition favorable for mesquite growth and survival (Van Auken and Bush, 1990). Bare patches between grass tussocks have lower concentrations of nutrients than soils under tussocks (Killgore, 2004), possibly conferring an additional competitive advantage to mesquite over neighboring vegetation (Van Auken and Bush, 1989). (Fig. 3)

More mesquite germinants were recorded in unburned grass microsites than the other vegetation microsites. This observation does not dismiss competitive interactions between mesquite and black-grama. Establishment is dependent on survivorship, and the only treatment in which seedlings survived over-winter in both Experiments I and II were the caged, burned microsite. Mesquite has difficulty competing with grasses in the early stages of its life history (Van Auken and Bush, 1990) and the higher survival observed for burned grassland may be related to the >50.0% reduction in basal cover in these patches compared to unburned grassland (Killgore et al., 2005). The physical structure of black-grama systems may reduce competition between grasses and mesquite compared to landscapes in southern Texas, but competition with black-grama is further decreased when a perturbation such as fire reduces vegetation cover and produces larger unvegetated patches favoring mesquite germination and survival (Fig. 4).

4.3. Rodent impact on seeds

The lack of differences in caches excavated across microsites is perhaps not surprising because all caches were uniform in area and depth, factors influencing seed detectability for heteromyid rodents (Cox et al., 1993). Moreover, the study area

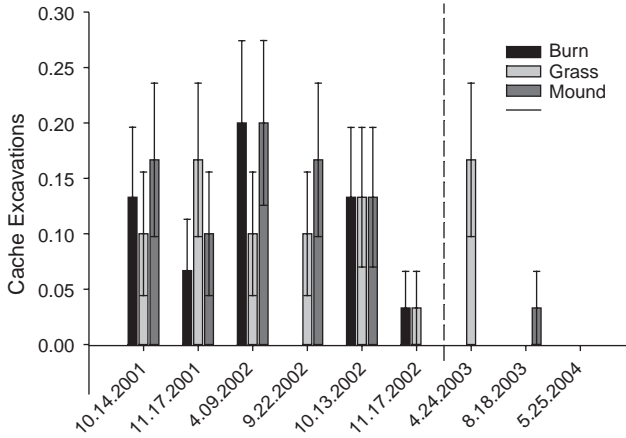


Fig. 3. Mean number of experimental caches excavated by small mammals \pm SE within burned grassland (black bars), unburned grassland (light gray bars) and kangaroo rat mound (dark gray) microsites. Experiment I (pre-monsoon seed set) results are displayed left of the dashed line, Experiment II (post-monsoon seed set) to the right of the dashed line.

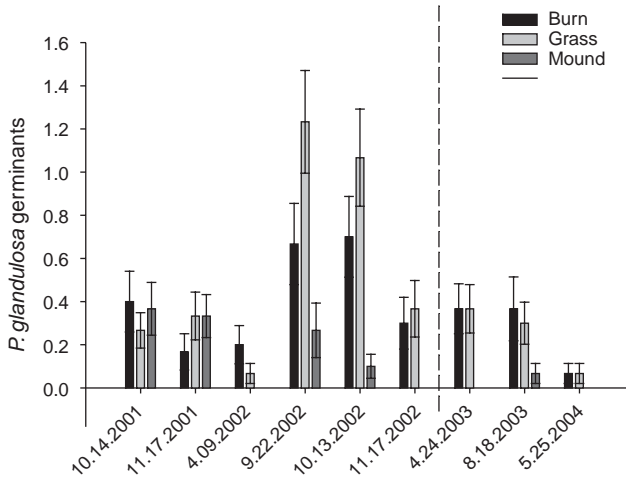


Fig. 4. Mean number of mesquite germinants \pm SE in experimental caches for burned grassland (black bars), unburned grassland (light gray bars) and kangaroo rat mound microsites (dark gray bars), shown per observation date, Armendaris Ranch, Engle, New Mexico. Dates to the left of dashed line are observations from Experiment I (pre-monsoon mesquite seed set); dates to the right represent number of germinants observed during Experiment II (post-monsoon seed set).

was relatively small (32 ha), and the microsites were close to one another in terms of kangaroo rat dispersal distances (Whitford, 1976). Thus, all simulated caches had roughly an equal chance of being detected and pilfered by heteromyids. However, germination rate was significantly related to the interaction between microsite

location and exclosure treatment, and excavations were related to the interaction between microsite and census date in Experiment II. These results suggest that the spatial and seasonal location of mesquite seed caches, and rodent access to them, may be interrelated factors modulating the importance of heteromyids in the establishment of mesquite.

The relationship between mesquite germination rate and number of excavated caches is more complex than we originally believed. We assumed that rodents would harvest all seeds from excavated caches. This proves erroneous as 46.6% of all seedlings from the uncaged microsites germinated from excavated caches. Why rodents leave seeds in excavated caches could be related to idiosyncrasies in their foraging behavior such as predator vigilance or handling time per seed. Relevant to this study is that seeds remaining in pilfered caches profit from increases in water infiltration and nutrient enrichment from decomposing litter characteristic of these depressions (Killgore, 2004). Furthermore, a reduction in the number of seeds within a cache may relax competition between remaining seeds, an important factor in a water- and nutrient-limited system such as the Chihuahuan Desert.

Regarding the fate of seeds removed from excavated caches, it is reasonable to assume that some seeds were consumed by heteromyids. It is also likely that many seeds were re-cached away from the original microsites from which they were excavated. However, our lack of certainty regarding the fate of seeds after their excavation does not contravene the hypothesis that heteromyids enhance the establishment of mesquite.

Mesquite seeds in intact and excavated caches readily germinate. Pilfered, re-cached seeds that eventually germinate cause us to underestimate the actual number of seeds from simulated caches that germinated. Thus, results reported in this study should be viewed as conservative, as the inclusion of pilfered, re-cached seeds in our data set would likely reinforce that heteromyid biopedoturbation and seed dispersal behavior positively influence mesquite germination in black-grama grasslands.

4.4. Mesquite and rodent response to precipitation patterns

Differences in germination of mesquite across census dates are partially related to Chihuahuan desert precipitation regimes. Approximately 60% of the annual precipitation occurs between July and September. Therefore, it is not surprising that we recorded the most new germinants in September 2002, coincident with the highest amount of precipitation recorded during the study. However, new germinants were recorded for every sampling date in the study and there was no correlation between the number of germinants and amount of precipitation. If mesquite can germinate during dry periods when neighboring forbs and grasses are dormant or senescent, it is expected that the shrub seedling would experience a competitive advantage over these plants (Van Auken and Bush, 1990).

Differences in the frequency of caches excavated by rodents per observation date are possibly a function of rainfall patterns. A dearth of green vegetation in the spring months of the study likely accounts for the spikes in cache excavations in April 2002 and 2003.

Our study demonstrates that the role of kangaroo rats in the spread of mesquite in Chihuahuan Desert grasslands is not limited to caching seeds but also includes cutting the stems of small seedlings thereby eliminating those plants. However, a sufficient number of seedlings escaped herbivory to account for the establishment of mesquite shrubs in grasslands with sparse mesquite cover. It is also apparent that successful germination of mesquite seeds can occur without scarification by passage through the digestive tract of large herbivores.

Because the home ranges of kangaroo rats in the Chihuahuan Desert are less than 1 ha (Whitford, 1976), these rodents contribute to short-distance dispersal of mesquite in areas where mature seed producing shrubs are already present. The low germination and establishment of mesquite from simulated caches at the margins of banner-tail kangaroo rat mounds suggests that banner-tail kangaroo rats select mature mesquite shrubs as locations for the construction of new nest mounds.

On the Jornada Experimental Range, a research station within the same desert basin as the Armendaris Ranch, mesquite density increased within livestock (but not rodent) exclosures in the same amount as areas grazed by livestock (Hennessy et al., 1983). Our study suggests that the caching of mesquite seeds by heteromyid rodents could explain the historical increase in mesquite within those livestock exclosures. The germination and establishment success of mesquite from simulated caches in undisturbed Chihuahuan Desert grassland suggests that the lower grass cover in desert grasslands reduces the competition between the grasses and mesquite germinants and that allows these shrubs to establish in this system. We conclude that heteromyid rodents contribute to the increase in shrub density in Chihuahuan Desert grasslands but are unlikely to have contributed to the initial widespread dispersal of mesquite from historic, pre-livestock industry habitats.

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