Journal of Arid Environments 73 (2009) 885–893

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Seed banks in a degraded desert shrubland: Influence of soil surface condition and harvester ant activity on seed abundance

L.A. DeFalco*, T.C. Esque, J.M. Kane [1], M.B. Nicklas [2]

US Geological Survey, Western Ecological Research Center, Las Vegas Field Station, 160 North Stephanie Street, Henderson, NV 89074, USA

ARTICLE INFO

Article history:
Received 19 December 2008
Received in revised form
16 April 2009
Accepted 17 April 2009
Available online 22 May 2009

Keywords:
Granivores
Mojave Desert
Restoration
Reseeding
Seed banks

ABSTRACT

We compared seed banks between two contrasting anthropogenic surface disturbances (compacted, trenched) and adjacent undisturbed controls to determine whether site condition influences viable seed densities of perennial and annual Mojave Desert species. Viable seeds of perennials were rare in undisturbed areas (3–4 seeds/m^2) and declined to <1 seed/m^2 within disturbed sites. Annual seed densities were an order of magnitude greater than those of perennials, were one-third the undisturbed seed densities on compacted sites, but doubled on trenched sites relative to controls. On trenched sites, greater litter cover comprising the infructescences of the dominant spring annuals, and low gravel content, enhanced seed densities of both annuals and perennials. Litter cover and surface ruggedness were the best explanations for viable perennial seed densities on compacted sites, but litter cover and the presence of a common harvester ant explained annual seed densities better than any other surface characteristics that were examined. Surface disturbances can have a varied impact on the condition of the soil surface in arid lands. Nevertheless, the consistently positive relationship between ground cover of litter and viable seed density emphasizes the importance of litter as an indicator of site degradation and recovery potential in arid lands.

Published by Elsevier Ltd.

1. Introduction

Viable seed banks of many arid and semi-arid environments are vulnerable to surface disturbances because they occur in the uppermost layers of soils (Reichman, 1984; Gutterman, 1993; Guo et al., 1998; Marone et al., 1998). Land uses, including heavy or prolonged grazing, have reduced soil seed densities in the Negev Desert (Sternberg et al., 2003), southern Ethiopia (Solomon et al., 2006), China's Horqin steppe and Inner Mongolia (Zhao et al., 2001; Zhan et al., 2007), central Australia (Kinloch and Friedel, 2005a,b) and eastern Nama Karoo in South Africa (Jones and Esler, 2004). Heavy recreational use in the Sonoran Desert (Walters, 2004) and trampling of coastal sand dunes in Israel (Sternberg et al., 2004) reduced seed densities and plant abundance. In contrast, seed densities rebounded after grazing pressure was reduced in grasslands of Israel (Osem et al., 2006) and northwestern Patagonia (Ghermandi, 1997). Disturbances that increase soil bulk density through trampling or vehicle activity, as well as those that mix topsoil and subsurface soils, can alter the physical, chemical and biological properties that influence viable seed densities. However, the relationships between soil surface properties and seed densities are poorly understood because soil properties associated with disturbances are rarely characterized at the same time seed banks are quantified.

Soil seed densities vary across a range of soil surfaces in undisturbed arid lands (Reichman, 1984). Understanding how viable seed densities are related to the surface properties that result after disturbance can help to develop indicators for determining the severity of site degradation, whether management action is required, and determine the potential for vegetation recovery. A reduction in organic debris that contains ripening infructescences may diminish inputs into the seed bank and decrease the capture of wind-blown seeds as they disperse across disturbed surfaces. Disturbances often remove shrub canopies where seeds are concentrated after seed rain and where seeds of annual and perennial grasses and forbs accumulate as they disperse from shrub interspaces (Nelson and Chew, 1977; Price and Reichman, 1987; Guo et al., 1998; Marone et al., 1998; Caballero et al., 2003, 2005, 2008; Li, 2008). Large or small soil particle sizes entrap like-sized seeds (Price and Reichman, 1987; Chambers et al., 1991; Chambers, 1995), so disturbance-induced shifts in particle sizes will likely change the abundance and species

* Corresponding author. Tel.: +1 702 564 4507; fax: +1 702 564 4600.
E-mail address: lesley_defalco@usgs.gov (L.A. DeFalco).
[1] Present address: Northern Arizona University, School of Forestry, Flagstaff, AZ 86001, USA.
[2] Permanent address: 244 South Pitkin Road, Craftsbury Common, VT 05827 USA.

0140-1963/$ – see front matter Published by Elsevier Ltd.
doi:10.1016/j.jaridenv.2009.04.017

composition of seeds and the resulting establishment of seedlings. Compaction reduces the number of available microsites that capture drifting seeds and produces a mechanical barrier for root growth of developing seedlings (Sheldon, 1974). By enhancing microslope – the slope associated with a seed bank over a topographic area less than several meters – disturbances can deplete seed densities through greater water run-off during extreme rainfall events (Caballero et al., 2003). Soil micro-relief, or the collective small crevices and peaks due to physical texture or biological crusts, captures seeds and influences the small-scale redistribution of seeds (Boudell et al., 2002; Serpe et al., 2006). Thus, disturbances that reduce soil micro-relief, such as heavy trampling or vehicle use, can reduce seed bank abundance whereas others that roughen the soil surface can increase seed banks.

In addition to the physical properties of soils, seed harvesting activities of granivores influence the regeneration of plant communities in arid lands. In the desert southwest of North America, harvester ants alter plant species abundance and diversity through seed predation (Brown et al., 1979; MacMahon et al., 2000). While seeds from nearby undisturbed areas move onto disturbed areas via wind or water transport, ants and small mammals can be important dispersal agents for plant species with large seeds that are not easily dispersed (Brown et al., 1979; Vander Wall et al., 2006). Seed banks are likely a function of soil properties and granivore activities that are characteristic of the disturbances themselves, yet the influences of numerous physical and biological soil properties have not been simultaneously evaluated for degraded arid lands. Little is known about seed bank dynamics among contrasting disturbances, or whether there are common surface properties that explain seed bank abundance and species composition of disturbed surfaces in general.

This study compares the viable seed densities for two different surface soil disturbances and illustrates how the properties of these disturbances can interact to influence seed banks in an arid shrubland community. The study was conducted at a military training facility in the Mojave Desert of southern California, USA where severely degraded environments provide excellent opportunities for understanding how seed banks respond to changes in the surface properties due to disturbance. The study area has compacted sites with concentrated and heavy vehicle use that results in high soil bulk density, and trenched sites that were excavated and backfilled without regard to original soil structure. Specifically, this study addresses whether the viable seed densities for annual and perennial species differ between compacted sites and backfilled tank trenches and nearby undisturbed areas or by the distance into the disturbance. Secondly, we evaluated whether patterns in viable seed densities are influenced by site properties including soil particle size, soil compaction, shrub canopy cover, ground cover of litter, microslope, micro-relief, and ant harvesting activity. The goal of this study is to provide an assessment of the properties associated with different disturbances and to better understand the processes driving seed retention and movement in disturbed arid landscapes. Evaluating how disturbances impact seed banks contributes to our understanding of the resistance and resilience of degraded arid and semi-arid environments and directs recommendations for the level of human intervention necessary to rehabilitate degraded habitats.

2. Materials and methods

2.1. Study area

The United States Army's Fort Irwin National Training Center (NTC) occurs 37 miles northeast of Barstow, California USA and occupies an area that is greater than 2500 km^2. Long-term mean rainfall ± SD for the hydrologic year (October–September, 1949–2004) is 98 ± 45 mm (Daggett FAA Airport, California; http://www.wrcc.dri.edu). Rainfall during the hydrologic year prior to seed bank collection was 119 mm, which was above the long-term mean. Creosote bush (*Larrea tridentata*) and bur-sage (*Ambrosia dumosa*) are the co-dominant species in undisturbed areas with an understory of native and non-native species. The study was conducted at three compacted and three trenched sites distributed from the northwest to the southeast across the NTC (Fig. 1). Trenches were constructed one to two years prior to the study, and compacted areas received concentrated use during training exercises for several decades (R. Sparks, NTC, Integrated Training Area Management, personnel communication). Compacted sites were broad areas with recurring and concentrated vehicle traffic. These sites were flat with minimal slope and low surface roughness. Litter was minimal, and only scattered individuals of the perennials *Eriogonum fasciculatum*, *L. tridentata*, *Croton californica*, *Stephanomeria pauciflora* and *Hymenoclea salsola* were present. These plants were likely adult plants that endured repeated vehicular impacts and survived by crown-sprouting (Gibson et al., 2004). Annual species observed during the study included *Ambrosia acanthicarpa*, *Cryptantha angustifolia*, *Pectocarya heterocarpa*, *Amsinckia tessellata*, *Astragalus acutirostris*, and *Lupinus humistratus* and the non-native species *Schismus barbatus*, *Salsola tragus*, *Erodium cicutarium*, and *Bromus madritensis* ssp. *rubens*.

In contrast to compacted sites, trenched sites are narrow, linear features where subsoil layers have been mixed with topsoil to a depth of ∼2 m (R. Sparks, NTC, Integrated Training Area Management, personnel communication). Trenched sites have both slightly higher litter cover and surfaces with higher within-plot micro-relief than compacted sites due to the wide tire treads of the mechanized equipment used to replace the soil. Annual and perennial species composition on trenched sites is similar to compacted sites: perennial cover is low (<1%) and both native and non-native annual plant species co-occur.

2.2. Sampling design

Seed bank samples were collected and site characteristics were measured on trenched and compacted sites during October 24–29,

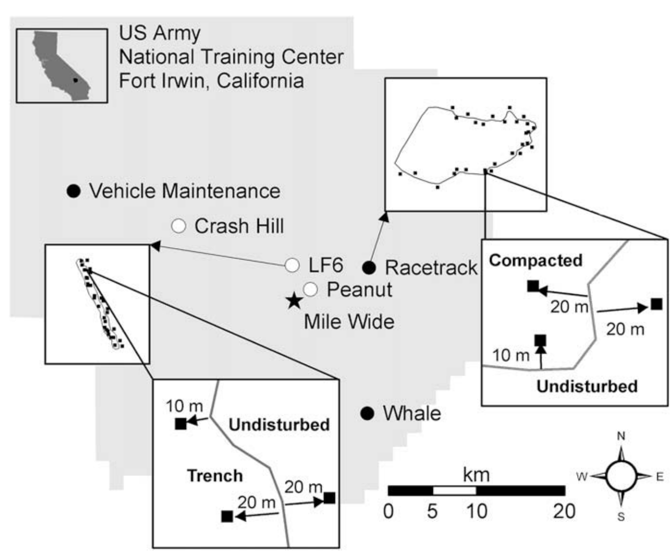

Fig. 1. Compacted and trenched sites located at the US Army NTC, Fort Irwin, California, USA. Three compacted (solid circles) and three trenched sites (clear circles) were selected, and 1 m^2 replicate plots were sampled at 10 m and 20 m into each site as well as 20 m outside the sites (inset). Observations of foraging ants were conducted at the Mile Wide Site (solid star).

2004. Within each of the six disturbed sites, 10 sampling points were randomly selected at each of two distances from the disturbance edge (10 and 20 m) and 10 undisturbed control sampling points were selected on areas outside of the disturbances for a total of 30 sampling points per site ($n = 180$ across the six sites, Fig. 1). The average width of the trenches was 40 m, and this distance was used to assign the two edge distances for sampling within the trenches and compacted sites (i.e., 20 m was the greatest distance from edge and the approximate mid-point of the trenches). The undisturbed control sampling points were randomly placed in adjacent undisturbed areas set 20 m from the edge of each compacted and trenched site.

2.3. Site condition and ant harvesting activity

Site conditions were characterized for each 1 m^2 sampling plot prior to collecting seed bank samples (Fig. 1), and included shrub canopy cover (%), ground cover of litter (%), micro-relief (%), soil penetration depth (cm), and the distance to (m) and diameter of (cm) active harvester ant nests. Shrub canopy and soil litter cover were visually estimated on the 1 m^2 plot to the nearest 0.5%. Micro-relief was calculated as the coefficient of variation using a 9-pin contact profile meter ($0.5 \text{ m} \times 0.5 \text{ m}$) centered within each 1 m^2 plot. A dynamic penetrometer was used by dropping a 2 kg weight 10 times from a height of 40 cm (Herrick and Jones, 2002) and using the penetration depth as an indicator of compaction (i.e., a shallower depth indicates greater compaction). The distance to the closest harvester nest entrance and the nest diameter were measured as indicators for seed harvesting activity, and ant species were identified. We used US Department of Agriculture particle size classification for approximating particle-size limits for soils collected to a depth of 2 cm (Gee, 2002). Cobbles larger than 3 cm were removed and remaining soil passed through four stacked sieves and processed on a shaker table for 10 min. Fractions were weighed and expressed on a percent mass basis. The resulting fractions correspond to fine sand, silt and clay (<0.25 mm), medium sand (0.25–0.50 mm), course sand (>0.50–2.0), fine gravel (>2.0–8.0 mm), course gravel (>8.0 mm to 3 cm) and cobbles (>3 cm).

2.4. Seed bank sampling and greenhouse assay

Seed bank samples were collected by placing 1 m^2 plots at each randomly sampled point and lightly loosening the surface with a steel rake to a depth of 2 cm. Surface soil containing seeds was removed using a gasoline powered leaf vacuum. This method was effective for collecting seeds as well as organic materials and fine soils less than 1 cm diameter.

The greenhouse assay for determining viable seed densities was modified from methods developed for the Great Basin (Young et al., 1969, 1981; Young and Evans, 1975) and specifically used for seed bank studies of Mojave Desert species (Esque, 2004). Each of the soil samples was placed in 15 cm diameter bulb pots lined with weed blocker cloth to reduce soil loss. Each pot contained 118 ml of soil with a layer of vermiculite (59 ml). Samples with more than 118 ml of sieved soil were divided among multiple pots, each with a layer of vermiculite to ensure that the same soil depth within each pot was maintained. All pots were placed on a bench in the greenhouse and subjected to four wetting cycles known to promote germination of seeds (Mayer and Poljakoff-Mayber, 1989; Baskin and Baskin, 1998) alternating with approximately 3 wk intervals when soils were not watered and allowed to air dry. In the first and second wetting phases, pots were watered with tap water using a hand-held sprayer, and water was applied until it drained from the bottom of the pots, but no standing water remained. In the third and fourth wetting phases, 50 ml of a 0.01 M solution of potassium nitrate and 50 ml of a 6.5×10^{-4} M solution of gibberellic acid, respectively, were added followed by daily watering with tap water. These chemical treatments are known to germinate seeds that have physiological dormancy (Mayer and Poljakoff-Mayber, 1989). During each wetting phase, seedlings were counted and harvested as soon as they could be identified. Unknown seedlings were transplanted to pots and given time to develop so they could be identified to species.

2.5. Observations of foraging harvester ants

At the Mile Wide site (Fig. 1), we quantified the net transport of materials associated with ant nests to understand the impact that the harvester ants, predominantly *Messor pergandei*, had on the local seed bank. The Mile Wide site is a compacted roadside approximately 40 m in width that was decompacted with a tractor and then hand seeded on February 3 with native perennials species (*A. dumosa*, *L. tridentata*, *Isomeris arborea*, *Ephedra californica*, *Atriplex canescens*, *Encelia farinosa*, *H. salsola*, *Abronia villosa*, *Baileya multiradiata*, *Sphaeralcea ambigua* and *Eschscholtzia californica*). Five ant nests were selected at each of 0 m, 10 m, and 20 m distance from the disturbed edge in the adjacent undisturbed area ($n = 15$) and observed on February 3, February 10, March 3, and March 10, 2005. Five observers were each assigned three different nests that they monitored rotationally throughout each day. Observations began between 0845 and 1000 h and ended between 1600 and 1700 h. A total of five 20 min observations were made for each nest at equal intervals on each date. During each observation period, observers identified and counted ant mandible loads (i.e., single items clasped in the mandibles and transported to and away from the nest entrance). Identification was based on a sample of the seed mix that was applied and on a seed library of extant Mojave Desert species maintained at USGS, Las Vegas Field Station. Mandible loads for plant tissues transported to the nest were summed by plant species across all observations and dates.

2.6. Statistical analyses

Viable seed densities of annuals and perennials associated with compacted sites and trenched sites were analyzed using SAS statistical software (version 9.1, Cary, NC). First, a split-plot ANOVA using the MIXED procedure determined whether seed density and species richness of annual species were influenced by disturbance type (compacted vs. trenched) and distance to the undisturbed edge (10 m, 20 m, and undisturbed). Disturbance type was designated as the whole plot factor, and distance from edge was the split-plot factor. The random effect site within disturbance type was used as the error term to test differences between disturbance types, and the mean square error was used to test the distance from edge effect and the interaction. Viable seed density of annual forbs and grasses was $\log_{10} + 1$ – transformed before analysis to satisfy the assumption of equal variance. The abundance of viable perennial seeds was patchy (i.e., many plots contained zero seeds). Thus, a log-linear analysis fitting a Poisson distribution and adjusting for overdispersion using the GENMOD procedure evaluated whether seeds of perennials were more likely to occur in trenched vs. compacted sites and in undisturbed areas vs. 10 m and 20 m within the disturbances. Means and standard errors were calculated for disturbance and distance factorial combinations for annuals and perennials for graphical representation.

We used an information-theoretic approach to determine the most plausible model explaining viable annual and perennial seed densities on compacted and trenched sites. The use of Akaike's Information Criterion corrected for small sample size (AICc) is favored over traditional methods such as stepwise, backward or forward selection because it considers existing knowledge about the biology or ecology of the system when developing the set of candidate models (Burnham and Anderson, 2002). The possible explanations for the viable seed densities of herbaceous annuals and shrubs were developed into separate linear regression models based on three guidelines: 1) we expected that processes controlling annual and perennial seed densities would differ between the disturbances, so compacted and trenched sites were analyzed separately; 2) litter was expected to provide the source of seeds for annuals and perennials, so this term was included or excluded in combination with the other variables; 3) we expected that the relationships between seed densities and some of the site variables might be curvilinear or have interactive effects between indicators, so variables representing soil condition and seed harvesting activity by ants (soil texture, soil compaction, shrub cover, litter cover, slope, micro-relief, distance to closest ant nest and ant nest diameter) were screened before model selection to determine whether they were best represented as linear or quadratic relationships or with or without interactions. For example, the model for litter on compacted sites includes the linear term Lit, and the model for trenched sites includes the quadratic $\mathrm{Lit}+\mathrm{Lit}^2$. Based on these guidelines, we developed separate sets of candidate models for undisturbed, compacted and trenched sites that examined the influence of site condition and ant activity on viable seed densities. These models were based on seed bank literature and on expert opinion of the authors (Table 1). The plots located at 10 m and 20 m within each disturbance comprised the observations to analyze the trenched and compacted treatments separately, and observations in the undisturbed areas for trenches and compacted sites were pooled to analyze the undisturbed treatment ($n=60$ for each treatment). Two observations on compacted sites were omitted because nest diameters were not measured.

Multicollinearity did not occur among variables based on Pearson correlation coefficients <0.75 and variation inflation factors <10 (Neter et al., 1996). A correction for small sample size (AICc) was calculated for each annual seed density model using the MIXED procedure and for each perennial seed density model in GENMOD in SAS and maximum likelihood as the model estimate method. The lowest AICc value denotes the "best" model, or most plausible explanation, out of the set of models that were considered. The models were ranked by rescaling AICc values so that the model with the minimum AICc had a value of 0. The difference calculated from this best model, ΔAIC, allows comparisons with the remaining models: $\Delta\mathrm{AIC}<2$ suggests substantial support for the model, ΔAIC between 4 and 7 suggests considerably less support, and $\Delta\mathrm{AIC}>10$ suggests essentially no support for the model (Burnham and Anderson, 2002). The importance of each plot attribute (a value ranging between 0 and 1 for least and most important, respectively) was derived from all the candidate models by summing the Akaike weights (w_is) across all the models where the attribute occurred (Burnham and Anderson, 2002).

Table 1
Models explored in the analyses describe viable seed densities as a function of site condition (Lit; Can; Slope; MR; Fs; Ms, Cs; Fg, Cg; Cob; Depth; and Dist, Diam). Rationale for models was based on expert opinion and published literature (referenced by superscripted letters). The simplest models included an intercept model (1 model) and a litter only model (1 model). Complex models had site condition without litter (9 models) and combinations of litter and site condition with or without their interaction (9 models). These complex models are denoted by "(Lit)". Linear or quadratic relationships were also pre-screened for the better-fitted models that comprised the final sets of candidate models tested separately for undisturbed, compacted and trenched sites.

Model combinations	Rationale
Intercept	No model terms included
Lit	Litter (organic debris) consists of infructescences and/or traps drifting seeds
(Lit), Can	Shrub seeds fall beneath canopy close to parent plant [a,b,c,e,f]
(Lit), Slope	Greater incline reduces seed density through horizontal transport [a]
(Lit), MR	Litter and micro-relief (soil surface roughness) capture drifting seeds [e,g,h]
(Lit,) Fs	Fine soil increases water holding capacity and enhances seed production or traps seeds with gelatinous seed coats [d]
(Lit), Ms, Cs	Sand particles trap seeds with like dimensions (i.e., annual species) [d]
(Lit), Fg, Cg	Large soil particle sizes enhance vertical transport of seeds [d]
(Lit), Cob	Cobble enhances percolation below seed germination zone
(Lit), Depth	Compacted surfaces reduce seed capture and/or water holding capacity
(Lit), Dist, Diam	Greater seed collection and removal by ants are associated with large, nearby ant nests

Lit (% ground cover of litter), Can (% canopy cover of shrubs), Depth (soil penetration depth, cm), Slope (% slope of plot), MR (micro-relief of soil surface as % coefficient of variation), Fs (% fine sand, silt and clay <0.25 mm), Ms (% medium sand, 0.25–0.50 mm), Cs (% coarse sand, >0.5–2 mm), Fg (% fine gravel, >2–8 mm), Cg (% coarse gravel, >8 mm to 3 cm), Cob (% cobble, >3 cm), Diam and Dist (diameter (cm) and distance (m), respectively, of closest ant nest).

[a] Caballero et al., 2003, 2005.
[b] Cabin and Marshall, 2000.
[c] Guo et al., 1998.
[d] Chambers et al., 1991.
[e] Reichman, 1984.
[f] Nelson and Chew, 1977.
[g] Burrows, 1986.
[h] Johnson and Fryer, 1992.

3. Results

3.1. Viable seed densities

More than 11 000 seeds germinated from soils collected at undisturbed, trenched and compacted sites during the course of four wetting and drying cycles. Less than 3% of the total number of seedlings that germinated from the seed bank (likely annuals) could not be identified to species because they died prematurely. However, of the species that could be identified, native and non-native annual forbs and grasses were the most numerous and diverse compared with native perennials (Fig. 2). Seedlings represented 18 native annual species (including an unidentified annual of the Family Boraginaceae and *Cryptantha* sp. that was not identified to species but likely *C. angustifolia*), 6 non-native annual species and 6 native perennial species.

The distribution of viable seeds for annual and perennial species differed between compacted and trenched sites. Compared with the undisturbed controls, annual seeds occurred at lower densities inside the compacted sites but at higher densities inside the trenched sites (Disturbance × Distance; $F_{2,170}=9.35$, $P<0.01$; Fig. 3). The mean (±SE) number of annual species reflected the same pattern as seed density with the fewest species at 20 m within the compacted sites (1.9 ± 0.3 species/m^2) and the most found at 10 m inside the trenched sites (4.5 ± 0.5 species/m^2). Seed densities of perennials, while more variable than annuals, were equally likely to occur in compacted and trenched areas ($\chi^2=0.40$, df $=1$, $P=0.53$) but were less likely to occur 10 and 20 m inside the disturbances than the undisturbed controls ($\chi^2=13.73$, df $=2$, $P<0.01$; Fig. 3).

3.2. Influence of site condition on viable annual and perennial seed densities

Whereas both disturbance types decreased canopy cover of shrubs, compacted sites had comparably less litter cover, greater soil compaction (as inferred from greater soil penetration depth),

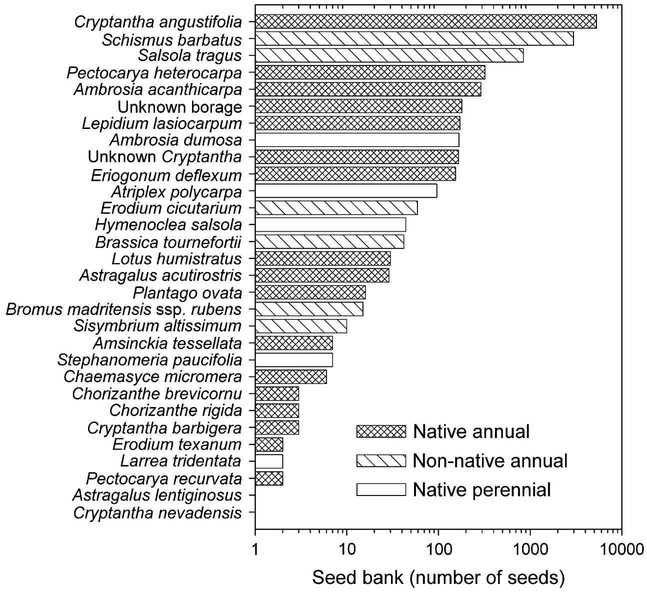

Fig. 2. Total viable seeds of annual and perennial species identified in the seed banks (0–2 cm) at compacted, trenched and undisturbed sites. Some viable seeds could only be identified as from the Family Boraginaceae (Unknown borage) or as a *Cryptantha* species. (Unknown *Cryptantha*.) Note that the x-axis is on the $\log_{10}$-scale, and thus only 1 seed for the native perennial *Astragalus lentiginosus* and the native annual *Cryptantha nevadensis*.

and soil particle sizes shifted toward less sand and fine gravel and more cobble content than the undisturbed control (Table 2). Trenched sites had greater litter cover, slope and micro-relief, and lower soil compaction compared with undisturbed sites. The diameter of the nearest ant nest and the distance from the sampling plots to the nearest ant nest were not significantly different among undisturbed, compacted or trenched sites.

Viable seed densities of annual species were related to different site characteristics for the undisturbed, compacted and trenched sites (Table 3). In undisturbed sites, annual seed densities were positively related to accumulated litter and large nearby ant nests ($\log_{10}+1$[Annual density (seeds/m^2)] $= 0.4979 + 0.1389 \times \text{Lit} - 0.0041 \times \text{Lit}^2 + 0.0295 \times \text{Diam} - 0.0002 \times \text{Diam}^2 - 0.0152 \times \text{Dist}$). Other plausible models explained annual seed densities, but these models had considerably less support ($\Delta\text{AIC} = 2$–7). Litter was common to all of these models (sum of model w_is for those that included litter was 0.9984) suggesting its high importance in explaining annual seed densities at undisturbed sites. Ant nest size (Diam) and proximity (Dist) each had moderate importance (0.4775), but all other variables had summed w_is that were ≤ 0.1100 and therefore did not adequately explain annual seed densities. Similar to undisturbed sites, seed densities on compacted sites were positively related to accumulated litter but also to large distant ant nests ($\log_{10}+1$[Annual density (seeds/m^2)] $= -0.0658 + 0.1589 \times \text{Lit} + 0.0077 \times \text{Diam} + 0.0164 \times \text{Dist}$). This compacted model had a very large weight of 0.9995. Annual densities on trenched sites were related more to litter and soil texture than to ant nests: greater densities of annuals occurred with litter accumulation and lower composition of fine (>2–8 mm) and coarse gravels (>8 mm to 3 cm): $\log_{10}+1$[Annual density (seeds/m^2)] $= 1.8162 + 0.7735 \times \text{Lit} - 0.0015 \times \text{Lit}^2 - 0.0129 \times \text{Fg} - 0.0384 \times \text{Cg}$. This model had a very large weight of 0.9976. For both compacted and trenched sites, no other plausible models occurred with $\Delta\text{AIC} < 7$.

The models that best explained viable perennial seed densities varied among the undisturbed, compacted and trenched sites (Table 4). Undisturbed sites with more litter and greater shrub canopy cover were likely to have more perennial seeds: Perennial

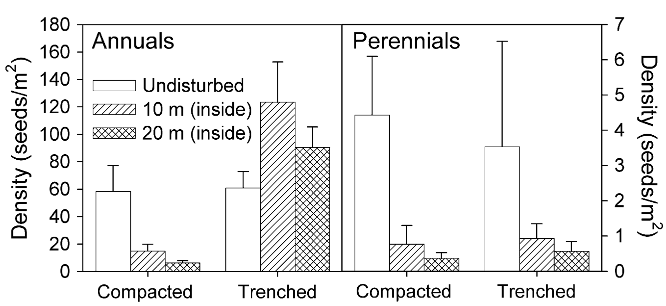

Fig. 3. Viable seed densities of annuals (left graph) and perennials (right graph) associated with compacted and trenched sites. Bars represent means ± SE. Note different y-axis scales on each graph.

Table 2
Plot variables used for estimating viable seed densities of annual and perennial plants on undisturbed, compacted and trenched sites. Different letters following means among sites denote statistical significance at $P < 0.05$ based on Tukey's HSD.

Plot variables	Undisturbed (n = 60)		Compacted (n = 58)		Trenched (n = 60)	
	Mean	95% CI	Mean	95% CI	Mean	95% CI
Lit (%)	4.4a	2.8–6.0	1.41b	0.8–2.0	8.0c	5.7–10.3
Can (%)	1.0a	0.08–2.00	0.01b	0.00–0.03	0.04b	0.00–0.09
Slope (%)	5.5a	4.2–6.7	3.3a	2.8–3.8	15.4b	12.7–18.1
MR (%)	4.4a	3.4–5.5	3.8a	2.8–4.8	9.10b	7.5–10.7
Fs (%)	15.7a	14.1–17.3	10.9b	9.3–12.4	19.4a	16.3–22.5
Ms (%)	10.8a	9.6–12.1	7.2b	6.1–8.4	12.9a	11.6–14.2
Cs (%)	36.2a	32.5–40.0	26.7b	22.6–30.7	35.4a	32.6–38.2
Fg (%)	28.6a	24.9–32.4	37.9b	31.9–43.9	25.9a	23.4–28.3
Cg (%)	6.9ab	4.8–9.0	9.8a	7.6–12.1	6.2b	4.6–7.8
Cob (%)	1.7a	0.2–3.2	7.6b	4.1–11.1	0.2a	0.0–0.4
Depth (cm)	16.4a	15.2–17.6	12.7b	11.3–14.0	24.2c	22.2–26.2
Dist (m)	9.3a	7.3–11.3	11.9a	10.0–13.7	9.4a	7.5–11.3
Diam (cm)	36.9a	30.3–43.6	39.6a	31.7–47.4	44.1a	33.2–55.1

Lit (litter), Can (canopy cover of shrubs), Depth (soil penetration depth), Slope (slope of plot), MR (micro-relief of soil surface), Fs (fine sand, silt and clay < 0.25 mm), Ms (medium sand, 0.25–0.50 mm), Cs (coarse sand, >0.5–2 mm), Fg (fine gravel, >2–8 mm), Cg (coarse gravel, >8 mm to 3 cm), Cob (cobble, >3 cm), Diam and Dist (diameter and distance, respectively, of closest ant nest).

Table 3
Separate model comparisons using surface condition for estimating viable seed densities of annuals for undisturbed, compacted and trenched sites. Only models with reasonable support ($\Delta\text{AIC} < 7$) were included. Akaike's weights (w_is) were calculated based on the entire candidate set of models; variables that were omitted had negligible summed w_is (<0.0010).

	Model	AICc	ΔAIC	w_i
Undisturbed	Lit[a], Diam[a], Dist	105.6	0.0	0.4766
	Lit[a], Fg, Cg	108.7	3.1	0.1011
	Lit[a]	108.9	3.3	0.0915
	Lit[a], Cob	108.9	3.3	0.0915
	Lit[a], Can	109.5	3.9	0.0678
	Lit[a], MR	110.0	4.4	0.0528
	Lit[a], Depth	110.8	5.2	0.0354
	Lit[a], Slope	111.0	5.4	0.0320
	Lit[a], Fs	111.0	5.4	0.0320
	Lit[a], Ms, Cs	112.2	6.6	0.0176
Compacted	Lit, Diam, Dist	61.8	0.0	0.9995
Trenched	Lit[a], Fg, Cg	76.6	0.0	0.9976

Lit (% ground cover of litter), Can (% canopy cover of shrubs), Depth (soil penetration depth, cm), Slope (% slope of plot), MR (micro-relief of soil surface as % coefficient of variation), Fs (% fine sand, silt and clay < 0.25 mm), Ms (% medium sand, 0.25–0.50 mm), Cs (% coarse sand, >0.5–2 mm), Fg (% fine gravel, >2–8 mm), Cg (% coarse gravel, >8 mm to 3 cm), Cob (% cobble, >3 cm), Diam and Dist (diameter (cm) and distance (m), respectively, of closest ant nest).

[a] Includes both linear and quadratic terms in model.

Table 4
Separate model comparisons using surface condition for estimating viable seed densities of perennials for undisturbed, compacted and trenched sites. Only models with reasonable support (ΔAIC < 7) were included. Akaike's weights (w_is) were calculated based on the entire candidate set of models; variables that were omitted had negligible summed w_is (<0.0010).

	Model	AICc	ΔAIC	w_i
Undisturbed	Lit, Can	−451.5	0.0	0.9999
Compacted	Lit, Slope	30.1	0.0	0.4034
	Lit, MR	30.7	0.6	0.2959
	Lit	33.3	3.2	0.0795
	Lit, Diam, Dist	34.5	4.5	0.0432
	Lit, Cob	34.8	4.7	0.0376
	Lit, Fs	34.9	4.9	0.0357
	Lit, Can	35.1	5.0	0.0330
	Lit, Depth	35.4	5.3	0.0280
	Lit, Fg, Cg	35.8	5.7	0.0231
	Lit, Ms, Cs	36.0	5.9	0.0206
Trenched	Lit, Fg, Cg	57.2	0.0	0.9497
	Fg, Cg	63.0	5.9	0.0503

Lit (% ground cover of litter), Can (% canopy cover of shrubs), Depth (soil penetration depth, cm), Slope (% slope of plot), MR (micro-relief of soil surface as % coefficient of variation), Fs (% fine sand, silt and clay < 0.25 mm), Ms (% medium sand, 0.25–0.50 mm), Cs (% coarse sand, >0.5–2 mm), Fg (% fine gravel, >2–8 mm), Cg (% coarse gravel, >8 mm to 3 cm), Cob (% cobble, >3 cm), Diam and Dist (diameter (cm) and distance (m), respectively, of closest ant nest).

density (seeds/m^2) = 0.7318 + 0.0518 × Lit + 0.0926 × Cov. Litter and canopy cover had the greatest importance values (1.0000 and 0.9999, respectively) and all other variables had negligible importance (≤0.0001). Compacted sites had a number of plausible models all of which included litter (importance value = 1.0000). Compacted sites that had accumulated litter and greater slope were likely to have more perennial seeds (Perennial density (seeds/m^2) = 0.4075 + 0.0774 × Lit + 0.0602 × Slope). Also likely for compacted sites, ΔAIC < 2, was the model with accumulated litter and greater micro-relief (Perennial density (seeds/m^2) = 0.5382 + 0.0926 × Lit + 0.0369 × MR). The best model that explained perennial seed densities on trenched sites included litter and soil texture: accumulated litter and low gravel content were likely to have more perennial seeds (Perennial seed density (seed/m^2) = 1.5333 − 0.0391 × Fg − 0.3522 × Cg).

3.3. Foraging activity of harvester ants

The harvester ant species that was common at the Mile Wide site (*M. pergandei*) collected a broad range of items including mineral soil, organic debris, invertebrate body parts, and fecal pellets of small mammals, but plant tissues comprised more than three-quarters of the mandible loads transported to the nests. Most of the plant tissues were infructescences (59% of mandible loads), which comprised two species, *C. angustifolia* and *S. barbatus* (Fig. 4). Seeds (13% of total mandible loads), leaves (25%) and stems (3%) represented species found either in the seed mixture applied prior to observations (*A. canescens*, *S. ambigua*, *E. farinosa*), those from the immediate area (*S. barbatus*, *C. angustifolia*, *S. tragus*, *A. acanthicarpa*, and *B. madritensis* spp. *rubens*) or those that were in the mixture and locally available (*A. dumosa*, *L. tridentata*, *P. heterocarpa*, *A. villosa*, and *H. salsola*).

4. Discussion

Even though some desert shrubs resprout after light injury (Gibson et al., 2004), moderate to heavy surface disturbances remove reproductive adults and erode topsoil, thereby reducing seed inputs and promoting seed bank depletion. Disturbances that compact soil surfaces or mix topsoil with deeper soil layers alter the surface characteristics that control seed dispersal and seed bank

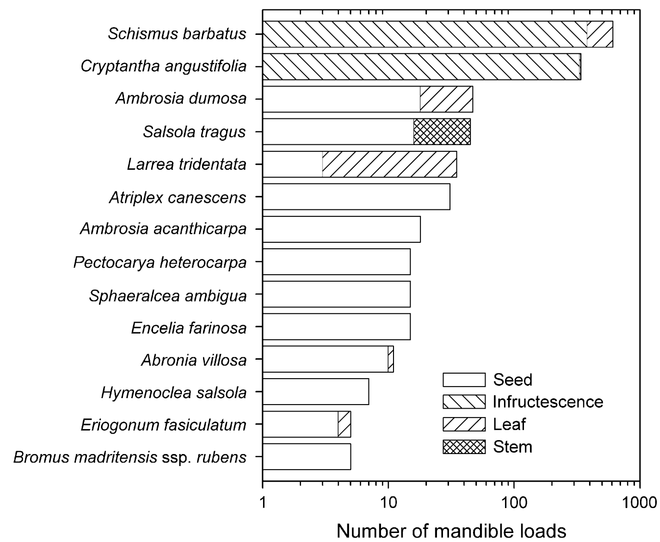

Fig. 4. Net nest intake of plant material collected by the harvester ants, predominantly *Messor pergandei*, at the Mile Wide site. Note $\log_{10}$-scale on x-axis.

composition. Recurring and concentrated military activity that increased soil bulk density on compacted sites decreased viable seed densities of annual grasses and forbs to less than one-third those in the adjacent undisturbed sites. Viable perennial seed densities – scarce compared to annuals, and generally rare even in relatively undisturbed North American deserts (Guo et al., 1999) – were also diminished at compacted sites. The small boundary across which annual and perennial seeds must disperse into compacted areas relative to the large disturbance area (i.e., low perimeter-to-area ratio) makes recovery on large disturbed sites challenging through natural seed dispersal. Trenched sites were excavated and backfilled one to two years prior to the study, and the two-fold higher annual seed densities close to the undisturbed edge implies that these ruderal species access a relatively greater proportion of this high perimeter-to-area ratio disturbance compared with compacted sites. However, as with the compacted sites, the almost undetectable densities of perennial seeds within trenched sites, regardless of the distance beyond the undisturbed edge, emphasize the difficulty of shrub recruitment in the absence of active reseeding efforts in heavily disturbed desert landscapes (Bertiller and Aloia, 1997; De Villiers et al., 2003).

Seed bank densities were not compared with subsequent plant establishment in this study, yet we recognize that an abundant seed bank, such as for the annual species on trenched sites relative to compacted sites, may not always translate into immediate plant establishment. Surface soils in arid lands store the prior years' seed production and receive pronounced inputs during periods of high rainfall (Gutierrez et al., 2000; Gutierrez and Meserve, 2003; Esque, 2004). Dispersing seeds that enter the seed bank are vulnerable to seed harvesting animals (Ireland and Andrew, 1995; Espigares and Lopez-Pintor, 2005) and fungal decomposition (Crist and Friese, 1993). Those seeds that persist will germinate and establish only when adequate rainfall is synchronized with suitable germination temperatures (Baskin and Baskin, 1998). Developing seedlings are subject to other sources of mortality including herbivory and suppression by other plants competing for limited soil resources (Milton, 1995). Winter and spring rainfall following our assessment of soil seed densities were more than two times the long-term average and resulted in almost three times greater annual plant canopy cover in trenched areas compared with compacted sites (L. DeFalco, unpublished data). While abundant seed densities associated with some disturbances do not guarantee the immediate recruitment of plants in many arid lands, seed banks signify the potential for site recovery and are expressed when climate conditions become suitable.

Surface conditions for compacted and trenched sites differed, but litter cover was consistently important in explaining viable seed densities for annual and perennial species. Litter comprised decomposing organic matter and plant debris including much of the previous spring's annuals – the most abundant being *S. barbatus* and *C. angustifolia* – so it is not surprising that these two species comprised almost three-quarters of the total viable seeds identified in the seed bank. Litter cover has also been shown to influence soil seed densities in the Patagonian steppe (Aguiar and Sala, 1997). Compacted sites differed from undisturbed sites due to lower litter cover and a shift toward large soil particle sizes. Coarse particle sizes in surface soils can enhance vertical movement to soil depths where germination conditions are unfavorable (Chambers et al., 1991; Chambers, 1995). Similar to undisturbed sites, and despite this shift toward coarser particle sizes at compacted sites, litter accumulation and ant activity continued to dominate as the site properties that best explained viable annual seed densities. Shrub canopy enhanced perennial seed densities on undisturbed sites as observed in numerous other seed bank studies (Nelson and Chew, 1977; Reichman, 1984; Guo et al., 1998; Cabin and Marshall, 2000; Caballero et al., 2003, 2005, 2008). Shrub canopies in arid lands are seed traps (Zhao et al., 2007; Caballero et al., 2008; Li, 2008) and improve the local environment for plants to establish, reproduce and concentrate their own seeds (Facelli and Temby, 2002; Holzapfel et al., 2006). However, once military training diminished shrub cover on compacted sites, litter accumulation and greater slope or micro-relief enhanced the likelihood of viable perennial seeds. Even though slope and micro-relief were low and less variable on compacted sites compared with undisturbed sites, these indicators of surface roughness were more important than the change in soil particle size, namely the increase in coarse gravel and cobble components. Accumulated litter was also influential in annual and perennial seed densities on trenched sites, yet perennial seed densities were more likely to occur where gravel content was low even though particle size distribution did not differ from undisturbed sites.

Vegetation change has been attributed to the foraging activities of harvester ants (MacMahon et al., 2000; Anderson and MacMahon, 2001), and in undisturbed and compacted areas, large ant populations in combination with accumulated litter had the greatest impact on annual seed densities in our study. The most common harvester ant species, *M. pergandei*, appears to be adept at inhabiting compacted sites such as unpaved road beds (Todd C. Esque, personnel observation), and coarse textured soils may encourage *M. pergandei* nesting and foraging activity (Johnson, 1992). Areas with active nests provide favorable growth and reproductive conditions for some prolific annual plant species (Rissing, 1986; Esque, 2004), and we did observe enhanced growth of *C. angustifolia*, *S. barbatus* and *E. cicutarium* on inactive or abandoned ant nests during this study. Depletion of seeds commonly occurs on or within 1 m of ant nests (Anderson and MacMahon, 2001). Yet the positive relationship between annual seed densities and ant nests is not solely explained by seed deposition at the nest because the nests occurred on average >7 m from our seed bank sampling plots. Our observations of ant foraging at the Mile Wide site documented infructescences of *S. barbatus* and *C. angustifolia* as the majority of items that ants returned to their nests. The seeds of these two species are the smallest of those collected (<1 mm diameter measured on any seed axis). These observations suggest that harvester ants carry seeds inside the infructescences for later processing at the nest, which may incur a lower energetic cost than carrying seeds individually, but likely increases the risk of losing seeds from infructescences during transport. Greater seed densities of annuals associated with litter and large ant nests at undisturbed sites reflect the loss of seeds from infructescences being carried by ants along the ant trails – a process called dyszoochory (Buckley, 1982) – and have been documented for *M. (Veromessor) pergandei* (Tevis, 1958) as well as for other harvester ant species of the genus *Pogonomyrmex* (Gordon, 1980; Kelrick et al., 1986; Mull, 2003). Ants will often collect the most common species (Davidson, 1993), yet they may also select seeds based on nutrient content. In one study, *C. angustifolia* and *S. barbatus* had the highest protein and carbohydrate contents, respectively, of the 12 most preferred species in California's Sonoran Desert (Gordon, 1980). While seed harvesting by ants can reduce seed densities in other arid systems (Espigares and Lopez-Pintor, 2005), our study maintains that ants can also augment local seed densities. Seed predation, dyszoochory and enhanced seed production for plants located near nests (Wagner and Jones, 2006) likely occur simultaneously in arid systems, and understanding their net effects on seed banks in disturbed landscapes will require further study.

In disturbed arid lands invaded by non-native species, harvester ants may indirectly influence plant community composition as they transport seeds to their nests. In our study, over half of the ant mandible loads we observed were seeds and infructescences of the non-native annual species *S. barbatus*, *S. tragus* and *B. madritensis* ssp. *rubens*. During a year with above-average rainfall in the northeast Mojave Desert, granivorous ants and small mammals increased the local seed bank by more than 50%, which was primarily comprised of non-native *Schismus* spp. (Esque, 2004). Some non-native annuals in the Mojave Desert use soil resources more rapidly than their native counterparts and decrease native annual plant abundance (Brooks, 2000; DeFalco et al., 2003). Thus, seed transport of non-native annual species by harvester ants may have consequences for rehabilitation of degraded sites if ants alter competitive interactions between non-native and native species through their seed harvesting activities (Inouye et al., 1980; Davidson et al., 1984).

While not measured in this study, seed harvesting rodents also influence the abundance and composition of soil seed banks in arid lands (Howe and Brown, 2000). In particular, Mojave Desert perennials generally have large seeds (Guo et al., 1999) and are differentially depleted by rodents compared with smaller seeded species (Price and Joyner, 1997). Compacted sites in this study were largely devoid of rodent burrows (DeFalco et al., unpublished data) and likely deterred fossorial rodent activity due to the low shrub canopy cover and high soil bulk density. The friability of soils and small surface-to-perimeter ratio of the trenches provided greater opportunity for access by rodents, and seed predation by rodents may have played a role in the seed movements of perennial species as demonstrated in a companion study on trenched sites (DeFalco et al., unpublished data).

This study demonstrates that soil seed densities are influenced by changes in soil conditions due to surface disturbance and by the direct losses of seed-bearing plants (Kinloch and Friedel, 2005b). Even though disturbance changed surface conditions – such as the shift toward coarse textured soils on compacted sites and the increase in surface topography on trench sites – litter had a dominant influence on viable seed densities. Litter is also known to promote nutrient cycling (Hooker and Stark, 2008), lower sediment yield and run-off (Fuchs et al., 2003; Neave and Rayburg, 2007), and reduce wind erosion (Li et al., 2005). Litter can be rapidly and easily estimated, which makes it a prospective indicator of site condition in degraded arid lands (de Soyza et al., 1998). Although we examined only compacted and trenched sites associated with military training activities, results from this study may be applicable to other compacted sites in the Mojave Desert such as abandoned town sites (Webb and Newman, 1982) or to excavated sites similar to trenches such as aqueduct, power line and pipeline developments (Vasek et al., 1975a,b; Lathrop and Archbold, 1980a,b). Rehabilitation of these degraded sites may benefit from litter additions to facilitate the development of seed banks and accelerate the recovery of degraded lands, and this approach warrants further investigation. Whereas we cannot directly ascribe cause and effect to the relationships between seed densities and site conditions in this study, these results emphasize the need to more thoroughly understand the influence of altered surface characteristics on seed banks in arid lands. Previously thought to have been detrimental to seed banks in arid systems, harvester ants and other granivores can enhance seed movements and must be considered in relation to the goals of passive or active rehabilitation.

Acknowledgments

We are grateful to many individuals that assisted in the field, laboratory and greenhouse on this project including K. Coulson, T. Draper, M. Garnett, I. Jacobs, R. Kipp, J. Lissow, A. Nilsson, G. Reese, S. Scoles-Sciulla, K. Smith, B. Waitman, and U. Wijayratne. J. Draper and E. Orling generously provided assistance in the greenhouse, and P. Griffiths provided guidance on soil particle size analyses. We especially thank R. Sparks, M. Hamilton, M. "Sharky" Hopkins, P. Dolan and G. Morrissette at US Army Integrated Training Area Management for their support and logistical assistance on site. J. Cassel of Johnson Controls helped us maximize our time in the field in conjunction with the military training schedule. We also thank J. Belnap, K. Thomas, J. Yee, D. Housman, K. Phillips and two anonymous reviewers for helpful comments that improved this manuscript. Funding for this research was provided by US Army, Integrated Training Area Management, United States Department of Interior Landscape Science Initiative (Mojave), Invasive Species Program, and Recoverability and Vulnerability of Desert Ecosystems. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US government.

References

Aguiar, M.R., Sala, A.E., 1997. Seed distribution constrains the dynamics of the Patagonian steppe. Ecology 78, 93–100.
Anderson, C.J., MacMahon, J.A., 2001. Granivores, exclosures, and seed banks: harvester ants and rodents in sagebrush-steppe. Journal of Arid Environments 49, 343–355.
Baskin, C.C., Baskin, J.M., 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego.
Bertiller, M.B., Aloia, D.A., 1997. Seed bank strategies in Patagonian semi-arid grasslands in relation to their management. Biodiversity and Conservation 6, 639–650.
Boudell, J.A., Link, S.O., Johansen, J.R., 2002. Effect of soil microtopography on seed bank distribution in the shrub-steppe. Western North American Naturalist 62, 14–24.
Brooks, M.L., 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. The American Midland Naturalist 144, 92–108.
Brown, J.H., Davidson, D.W., Reichman, O.J., 1979. An experimental study of competition between seed-eating desert rodents and ants. American Zoologist 19, 1129–1143.
Buckley, R.C., 1982. Ant–plant interactions: a world review. In: Buckley, R.C. (Ed.), Ant–Plant Interactions in Australia. Dr. W Junk, The Hague, pp. 111–141.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second ed. Springer-Verlag, New York, 488 pp.
Burrows, F.M., 1986. The aerial motion of seeds, fruits, spores and pollen. In: Murray, D.R. (Ed.), Seed Dispersal. Academic Press, Sydney, pp. 2–46.
Caballero, I., Olano, J.M., Loidi, J., Escudero, A., 2003. Seed bank structure along a semi-arid gypsum gradient in Central Spain. Journal of Arid Environments 55, 287–299.
Caballero, I., Olano, J.M., Luzuriaga, A.L., Escudero, A., 2005. Spatial coherence between seasonal seed banks in a semi-arid gypsum community: density changes but structure does not. Seed Science Research 15, 153–160.
Caballero, I., Olano, J.M., Escudero, A., Loidi, J., 2008. Seed bank spatial structure in semi-arid environments: beyond the patch-bare area dichotomy. Plant Ecology 195, 215–223.
Cabin, R.J., Marshall, D.L., 2000. The demographic role of soil seed banks. I. Spatial and temporal comparisons of below- and above-ground populations of the desert mustard *Lesquerella fendleri*. Journal of Ecology 88, 283–292.
Chambers, J.C., MacMahon, J.A., Haefner, J.H., 1991. Seed entrapment in alpine ecosystems: effects of soil particle size and diaspore morphology. Ecology 72, 1668–1677.
Chambers, J.C., 1995. Relationships between seed fates and seedling establishment in an alpine ecosystem. Ecology 76, 2124–2133.
Crist, T.O., Friese, C.F., 1993. The impact of fungi on soil seeds: implications for plants and granivores in a semiarid shrub-steppe. Ecology 74, 2231–2239.
Davidson, D.W., Inouye, R.S., Brown, J.H., 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. Ecology 65, 1780–1786.
Davidson, D.W., 1993. The effects of herbivory and granivory on terrestrial plant succession. Oikos 68, 25–35.
DeFalco, L.A., Bryla, D.R., Smith-Longozo, V., Nowak, R.S., 2003. Are Mojave Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* subsp. *rubens* (Poaceae) and two native species. American Journal of Botany 90, 1045–1053.
de Soyza, A.G., Whitford, W.G., Herrick, J.E., Van Zee, J.W., Havstad, K.M., 1998. Early warning indicators of desertification: examples of tests in the Chihuahuan Desert. Journal of Arid Environments 39, 101–112.
De Villiers, A.J., Van Rooyen, M.W., Theron, G.K., 2003. Similarity between the soil seed bank and the standing vegetation in the Strandveld Succulent Karoo, South Africa. Land Degradation and Development 14, 527–540.
Espigares, T., Lopez-Pintor, A., 2005. Seed predation in a Mediterranean pasture: can ants modify the floristic composition of soil seed banks? Revista Chilena de Historia Natural 778, 615–622.
Esque, T.C., 2004. The role of fire, rodents and ants in changing plant communities in the Mojave Desert. Dissertation, University of Nevada, Reno, Nevada, 168 pp.
Facelli, J.M., Temby, A.M., 2002. Multiple effects of shrubs on annual plant communities in arid lands of South Australia. Austral Ecology 27, 422–432.
Fuchs, E.H., Wood, M.K., Jones, T.L., Racher, B., 2003. Impacts of tracked vehicles on sediment from a desert soil. Journal of Range Management 56, 342–352.
Gee, G.W., 2002. Particle-size analysis. In: Dane, J.H., Topp, G.C. (Eds.), Methods of Soil Analysis: Part 4, Physical Methods. Soil Science Society of America, Inc., Madison, pp. 255–293.
Ghermandi, L., 1997. Seasonal patterns in the seed bank of a grassland in north-western Patagonia. Journal of Arid Environments 35, 215–224.
Gibson, A.C., Sharifi, M.R., Rundel, P.W., 2004. Resprout characteristics of creosote bush (*Larrea tridentata*) when subjected to repeated vehicle damage. Journal of Arid Environments 57, 411–429.
Gordon, S.A., 1980. Analysis of twelve Sonoran Desert seed species preferred by the desert harvester ant. Madroño 27, 68–78.
Guo, Q., Rundel, P.W., Goodall, D.W., 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. Journal of Arid Environments 38, 465–478.
Guo, Q., Rundel, P.W., Goodall, D.W., 1999. Structure of desert seed banks: comparisons across four North American desert sites. Journal of Arid Environments 42, 1–14.
Gutierrez, J.R., Arancio, G., Jaksic, F.M., 2000. Variation in vegetation and seed bank in a Chilean semi-arid community affected by ENSO 1997. Journal of Vegetation Science 11, 641–648.
Gutierrez, J.R., Meserve, P.L., 2003. El Niño effects on soil seed bank dynamics in north-central Chile. Oecologia 134, 511–517.
Gutterman, Y., 1993. Seed Germination in Desert Plants. Springer-Verlag, Berlin. 253 pp.
Herrick, J.E., Jones, T.L., 2002. A dynamic cone penetrometer for measuring soil penetration resistance. Soil Science Society of America Journal 66, 1320–1324.
Holzapfel, C., Tielbörger, K., Parag, H.A., Kigel, J., Sternberg, M., 2006. Annual plant–shrub interactions along an aridity gradient. Basic and Applied Ecology 7, 268–279.
Hooker, T.D., Stark, J.M., 2008. Soil C and N cycling in three semiarid vegetation types: response to an in situ pulse of plant detritus. Soil Biology and Biochemistry 40, 2678–2685.
Howe, H.F., Brown, J.S., 2000. Early effects of rodent granivory on experimental forb communities. Ecological Applications 10, 917–924.
Inouye, R.S., Byers, G.S., Brown, J.H., 1980. Effects of predation and competition on survivorship, fecundity, and community structure on desert annuals. Ecology 61, 1344–1351.
Ireland, C., Andrew, M.H., 1995. Ants remove virtually all western myall (*Acacia papyrocarpa* Benth) seeds at Middleback, South Australia. Australian Journal of Ecology 20, 565–570.
Johnson, E.A., Fryer, G.I., 1992. Physical characterization of seed microsites – movement on the ground. Journal of Ecology 80, 823–836.
Johnson, R.A., 1992. Soil texture as an influence on the distribution of the desert seed-harvester ants *Pogonomyrmex rugosus* and *Messor pergandei*. Oecologia 89, 118–124.
Jones, F.E., Esler, K.J., 2004. Relationship between soil-stored seed banks and degradation in eastern Nama Karoo rangelands (South Africa). Biodiversity and Conservation 13, 2027–2053.

Kelrick, M.I., MacMahon, J.A., Parmenter, R.R., Sisson, D.V., 1986. Native seed preferences of shrub-steppe rodents, birds and ants: the relationships of seed attributes and seed use. Oecologia 68, 327–337.
Kinloch, J.E., Friedel, M.H., 2005a. Soil seed reserves in arid grazing lands of central Australia. Part 1: seed bank and vegetation dynamics. Journal of Arid Environments 60, 133–161.
Kinloch, J.E., Friedel, M.H., 2005b. Soil seed reserves in arid grazing lands of central Australia. Part 2: availability of 'safe sites'. Journal of Arid Environments 60, 163–185.
Lathrop, E.W., Archbold, E.F., 1980a. Plant response to Los Angeles aqueduct construction in the Mojave Desert. Environmental Management 4, 137–148.
Lathrop, E.W., Archbold, E.F., 1980b. Plant response to utility right of way construction in the Mojave Desert. Environmental Management 4, 215–226.
Li, F.R., Kang, L.F., Zhang, H., Zhao, L.Y., Shirato, Y., Taniyama, I., 2005. Changes in intensity of wind erosion at different stages of degradation development in grasslands of Inner Mongolia, China. Journal of Arid Environments 62, 567–585.
Li, F.R., 2008. Presence of shrubs influences the spatial pattern of soil seed banks in desert herbaceous vegetation. Journal of Vegetation Science 19, 537–548.
MacMahon, J.A., Mull, J.F., Crist, T.O., 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. Annual Review of Ecology and Systematics 31, 265–291.
Marone, L., Rossi, B.E., Horno, M.E., 1998. Timing and spatial patterning of seed dispersal and redistribution in a South American warm desert. Plant Ecology 137, 143–150.
Mayer, A.M., Poljakoff-Mayber, A., 1989. The Germination of Seeds, fourth ed. Pergamon Press, New York, 96 pp.
Milton, S.J., 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. Journal of Applied Ecology 1, 145–156.
Mull, J.F., 2003. Dispersal of sagebrush-steppe seeds by the western harvester ant (*Pogonomyrmex occidentalis*). Western North American Naturalist, 358–362.
Neave, M., Rayburg, S., 2007. A field investigation into the effects of progressive rainfall-induced soil seal and crust development on runoff and erosion rates: the impact of surface cover. Geomorphology 87, 378–390.
Nelson, J.F., Chew, R.M., 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. The American Midland Naturalist 97, 300–320.
Neter, J., Juter, M.H., Nachtsheim, C.J., Wasserman, W., 1996. Applied Linear Statistical Models: Regression, Analysis of Variance, and Experimental Designs, fourth ed. Irwin, Chicago, USA.
Osem, Y., Perevolotsky, A., Kigel, J., 2006. Size traits and site conditions determine changes in seed bank structure caused by grazing exclusion in semiarid annual plant communities. Ecography 29, 11–20.
Price, M.V., Joyner, J.W., 1997. What resources are available to desert granivores: seed rain or soil seed bank? Ecology 78, 764–773.
Price, M.V., Reichman, O.J., 1987. Distribution of seeds in Sonoran Desert soils: implications for heteromyid rodent foraging. Ecology 68, 1797–1811.
Reichman, J., 1984. Spatial and temporal variation of seed distributions in Sonoran Desert soils. Journal of Biogeography 11, 1–11.
Rissing, S.W., 1986. Indirect effects of granivory by harvester ants: plant species composition and reproductive increase near ant nests. Oecologia 68, 231–234.
Serpe, M.D., Orm, J.M., Barkes, T., Rosentreter, R., 2006. Germination and seed water status of four grasses on moss-dominated biological crusts from arid lands. Plant Ecology 185, 163–178.
Sheldon, J.C., 1974. The behaviour of seeds in soil: III. The influence of seed morphology and the behaviour of seedlings on the establishment of plants from surface-lying seeds. Journal of Ecology 62, 47–66.
Solomon, T.B., Snyman, H.A., Smit, G.N., 2006. Soil seed bank characteristics in relation to land use systems and distance from water in a semi-arid rangeland of southern Ethiopia. South African Journal of Botany 72, 263–271.
Sternberg, M., Gutman, M., Perevolotsky, A., Kigel, J., 2003. Effects of grazing on soil seed bank dynamics: an approach with functional groups. Journal of Vegetation Science 14, 375–386.
Sternberg, M., Yu, S.L., Bar, P., 2004. Soil seed banks, habitat heterogeneity, and regeneration strategies in a Mediterranean coastal sand dune. Israel Journal of Plant Sciences 52, 213–221.
Tevis, L., 1958. Interrelations between the harvester ant *Veromessor pergandei* (Mayr) and some desert ephemerals. Ecology 39, 695–704.
Vander Wall, S.B., Esque, T.C., Waitman, B.A., Haines, D.F., Garnett, M.G., 2006. Joshua tree (*Yucca brevifolia*) seeds are dispersed by seed-caching rodents. Ecoscience 13, 539–543.
Vasek, F.C., Johnson, H.B., Eslinger, D.H., 1975a. Effects of pipeline construction on creosote bush scrub vegetation of the Mojave Desert. Madroño 23, 1–13.
Vasek, F.C., Johnson, H.B., Brum, G.D., 1975b. Effects of power transmission lines on vegetation of the Mojave Desert. Madroño 23, 114–131.
Wagner, D., Jones, J.B., 2006. The impact of harvester ants on decomposition, N mineralization, litter quality, and the availability of N to plants in the Mojave Desert. Soil Biology and Biochemistry 9, 2593–2601.
Walters, G.M., 2004. Perennial plants and ephemeral seed banks in Papago Park, Phoenix, Arizona. Natural Areas Journal 24, 36–43.
Webb, R.H., Newman, E.B., 1982. Recovery of soil and vegetation in ghost-towns in the Mojave Desert, southwestern United States. Environmental Conservation 9, 245–248.
Young, J.A., Evans, R.A., Eckert Jr., R.E., 1969. Population dynamics of downy brome. Weed Science 17, 20–26.
Young, J.A., Evans, R.A., 1975. Germinability of seed reserves in a big sagebrush community. Weed Science 23, 358–364.
Young, J.A., Evans, R.A., Kay, B.L., Owen, R.E., Budy, J., 1981. Collecting, processing, and germinating seeds of western wildland plants. US Department of Agriculture, Science and Education Administration, Agricultural Reviews and Manuals. ARM-W-3.
Zhan, X., Li, L., Cheng, W., 2007. Restoration of *Stipa kryloviisteppes* in Inner Mongolia of China: assessment of seed banks and vegetation composition. Journal of Arid Environments 68, 298–307.
Zhao, H.L., Zhou, R.L., Su, Y.Z., Zhang, H., Zhao, L.Y., Drake, S., 2007. Shrub facilitation of desert land restoration in the Horqin Sand Land of Inner Mongolia. Ecological Engineering 31, 1–8.
Zhao, W.Z., Liu, Z.M., Chang, X.L., 2001. Influence of grazing intensity on seed bank of a sandy grassland in Horqin Steppe of China. Annals of Arid Zone 40, 397–404.