RESEARCH ARTICLE

Supplementing Seed Banks to Rehabilitate Disturbed Mojave Desert Shrublands: Where Do All the Seeds Go?

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Abstract

Revegetation of degraded arid lands often involves supplementing impoverished seed banks and improving the seedbed, yet these approaches frequently fail. To understand these failures, we tracked the fates of seeds for six shrub species that were broadcast across two contrasting surface disturbances common to the Mojave Desert—sites compacted by concentrated vehicle use and trenched sites where topsoil and subsurface soils were mixed. We evaluated seedbed treatments that enhance soil-seed contact (tackifier) and create surface roughness while reducing soil bulk density (harrowing). We also explored whether seed harvesting by granivores and seedling suppression by non-native annuals influence the success of broadcast seeding in revegetating degraded shrublands. Ten weeks after treatments, seeds readily moved off of experimental plots in untreated compacted sites, but seed movements were reduced 32% by tackifier and 55% through harrowing.

Harrowing promoted seedling emergence in compacted sites, particularly for the early-colonizing species *Encelia farinosa*, but tackifier was largely ineffective. The inherent surface roughness of trenched sites retained three times the number of seeds than compacted sites, but soil mixing during trench development likely altered the suitability of the seedbed thus resulting in poor seedling emergence. Non-native annuals had little influence on seed fates during our study. In contrast, the prevalence of harvester ants increased seed removal on compacted sites, whereas rodent activity influenced removal on trenched sites. Future success of broadcast seeding in arid lands depends on evaluating disturbance characteristics prior to seeding and selecting appropriate species and seasons for application.

Key words: arid land restoration, germination requirements, harvester ants, *Messor pergandei*, plant competition, rodents.

Introduction

Vascular plants in arid- and semiarid environments spend a portion of their life cycle as seeds in the soil seed bank where they are vulnerable to surface disturbances such as wildfire (Esque 2004), grazing by domestic and feral animals (Zhao et al. 2001; Kinloch & Friedel 2005; Eldridge et al. 2006; Kassahun et al. 2009), trampling, and vehicle impacts (Sternberg et al. 2004; DeFalco et al. 2009). Removal of disturbances does not always ensure the recovery of seed numbers or species composition in the short term (Kassahun et al. 2009). Natural replenishment of the seed bank depends on seeds drifting from nearby intact areas assisted by wind or surface flow during rainfall events. In addition, for shrubs and perennial grasses with large seeds that do not easily disperse, granivores can move seeds to favorable sites for germination but also consume and store large quantities of seeds, thereby removing them from the soil-seed bank (Brown et al. 1979; Barberá et al. 2006; Vander Wall et al. 2006). In general, disturbances left to naturally recover often lack persistent seed banks or late successional species in the flora, thus requiring replenishment by other means (Bakker et al. 1996; DeFalco et al. 2009).

Natural recovery of surface disturbances in the Mojave Desert is typically slow (Webb 2002), and active revegetation efforts in recent decades have sought to restore low-elevation *Larrea tridentata* and *Ambrosia dumosa* and mid-elevation *Yucca brevifolia* and *Coleogyne ramossisima* communities to their pre-disturbance conditions. Restoration of broad disturbed areas has included replenishing depleted desert seed banks through broadcast seeding in combination with preparing the seedbed (Kay & Graves 1983). Broadcast seeding may be a more viable option for revegetating large disturbances in arid environments compared to more intensive treatments such as transplanting greenhouse-raised seedlings, but the costs and benefits of seeding and other treatments are rarely assessed

(Abella & Newton 2009). Seeding success in the Mojave Desert has been variable during past decades with densities of young plants in seeded areas typically lower than those found in adjacent undisturbed areas (Kay & Graves 1983; Walker & Powell 1999). Mixtures of seeds are often applied with little consideration for granivorous animals (Anderson & Ostler 2002), availability of safe sites (Kinloch & Friedel 2005), or suitability of climate for germination (Kay et al. 1988; Baskin & Baskin 1998). Processes that ultimately impact seed rain—such as suppression of establishing plants by invasive species—can also impede replenishment of seed banks (Assaeed & Al-Doss 2002). Surface treatments that roughen the soil are intended to capture seeds, but can instead increase the abundance of these competitive non-native annuals (Banerjee et al. 2006). Seed attributes that influence seed dispersal and eventual plant establishment are rarely considered when developing seed mixes for seeding disturbed areas, but are nevertheless important (Chambers & MacMahon 1994). Seeding failure is likely a consequence of multiple interacting abiotic and biotic factors; however, studies that examine the relative influences of these factors are lacking in many arid regions including the Mojave Desert.

Understanding the fates of seeds from dispersal through plant establishment will guide revegetation efforts in degraded arid lands (Chambers & MacMahon 1994) and identify strategies for maximizing seeding success while minimizing costs. We supplemented soil-seed densities of native Mojave Desert shrubs on two types of disturbance in combination with surface treatments. We tracked seeds as they were transported by wind and surface water flow, established as seedlings, and those that remained entrapped on the soil surface. We also quantified the number of seeds that disappeared from disturbances once seedlings were established and explored possible explanations for their absence.

We addressed two questions about arid land seeding: (1) How do different types of disturbances and methods to treat the soil seedbed vary in their ability to retain seeds and promote seedling establishment? and (2) Do factors other than disturbance type and surface treatment have a role in the fate of seeds used in revegetating disturbed shrublands? We expected seed harvesting by ants and rodents or the suppressive effects of non-native annuals on emerging seedlings to explain seed losses that can occur during restoration efforts (MacMahon et al. 2000; Susana & Miriti 2009). Intact shrub cover in undisturbed areas adjacent to disturbances likely provides lower predation risk for foraging granivores (Kotler 1984). Thus, we also expected that the placement of reseeding treatments closer to undisturbed areas would result in the loss of supplemented seeds due to greater rodent access in particular.

Methods

Site Description

Military training under full battle conditions creates a diversity of surface disturbances at the U.S. Army's Fort Irwin National Training Center (NTC). Located 60 km northeast of Barstow, CA, United States (35°22′36″N, 116°37′23″W), the greater than 2,500 km² NTC provides ample opportunities for studying restoration of degraded desert shrublands. We concentrated on two types of disturbances because of their prevalence at the NTC, their historically variable revegetation success, and their potential applicability to functionally similar disturbances in arid environments including utility corridors, livestock watering holes, off-road vehicle staging areas, and military encampments (Vasek et al. 1975; Lathrop & Archbold 1980; Webb & Newman 1982). Expansive compacted sites at the NTC have been trampled by troops and their military vehicles. Trenched sites are narrow linear features where subsoil layers were removed to a depth of approximately 2 m to produce vehicle barriers and replaced without regard to mixing subsoil with topsoil layers (R. Sparks 2004, NTC Integrated Training Area Management, Barstow, CA, personal communication). Creosote bush (*Larrea tridentata*) and bur-sage (*Ambrosia dumosa*) are the codominant species in undisturbed areas adjacent to the study sites with an understory of native and non-native annual species. 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).

Experimental Design

We selected three replicate compacted and trenched sites. Fifteen plots were located within each compacted site (2 m × 2 m, spaced at ≥25 m apart) and randomly assigned a surface treatment of tackifier, harrowed, or untreated control ($n = 5$ per treatment). Ten plots occurred within each trenched site where only tackifier or untreated controls were assigned ($n = 5$). Trenches are rarely harrowed by restoration specialists due to their inherent surface roughness, so we did not test harrowing of trenches. In total, 75 plots were included for the study (45 compacted + 30 trenched plots).

Seeds and Surface Treatments

Disturbed sites had <1 live perennial seed/m² prior to the experiment (DeFalco et al. 2009), and we supplemented each plot with a commercial seed mixture (Stover Seed Company, Los Angeles, CA, U.S.A.). Species selected for the mixture included the codominants creosote bush (*L. tridentata* (D.C.) Coville) and white bur-sage (*A. dumosa* (A. Gray) Payne) and early-colonizing species that are found within the adjacent undisturbed plant community (four-wing saltbush *Atriplex canescens* (Pursh) Nutt., brittlebush (*Encelia farinosa* A. Gray ex Torr.), cheesebush (*Hymenoclea salsola* A. Gray), and bladderpod (*Isomeris arborea* Nutt.). We developed the seed mixture based on the estimated number of live seeds per bulk pound of seed (i.e. percentage of pure live seed) determined through germination and tetrazolium tests performed by qualified seed testing laboratories. The percentages of germination and dormant seeds, respectively, were the following for each

species: 2 and 23% for *A. dumosa*; 18 and 13% for *L. tridentata*; 34 and 7% for *A. canescens*; 81 and 0% for *E. farinosa*; 56 and 15% for *H. salsola*; and 30 and 50% for *I. arborea*. These species vary in mass, sphericity, surface morphology, and their temperature requirements for germination, which we expected would influence their seed movements and establishment on different disturbances as well as their interaction with surface treatments (Fig. 1). Actual live seeds were estimated by multiplying the combined germination and dormant percentages by the total number of seeds that were hand-sorted from three replicate plot mixes (mean ± 95% CI): *A. dumosa*, 149 ± 13; *L. tridentata*, 117 ± 3; *E. farinosa*, 119 ± 8; *A. canescens*, 102 ± 5; *I. arborea*, 100 ± 6; and *H. salsola*, 123 ± 6 live seeds/m². Thus, the estimated density of live seeds applied was approximately 710 ± 32 seeds/m² (2,841 ± 129 seeds/plot), and the total number of seeds (live + unviable) was 1,667 ± 88 seeds/m² (6,669 ± 352 seeds/plot).

We established experimental plots on 19–21 January 2005. Harrowing was implemented before seeding by dragging rigid metal tines behind a tractor to produce 3-cm wide and 5-cm deep furrows in perpendicular directions (Fig. 1). Harrowing breaks up compacted soil structure, produces surface roughness to increase safe sites for seeds, and concentrates moisture and nutrients for developing seedlings. Harrowing was light in comparison with surface ripping that is prescribed to alleviate highly compacted soils, yet can alter soil hydrologic properties (Caldwell et al. 2006). We combined weed-free organic mulch with seeds (1:1 ratio by volume) for even distribution of seeds across plots. For the tackifier treatment, we sprayed a 1:8 tackifier-to-water solution (Soil-Sement®, Midwest Industrial Supply, Canton, OH, U.S.A.) in two to three coats following seed application. Tackifier is a water-soluble, latex polymer emulsion typically used to reduce dust emissions, but we tested its effectiveness in maintaining soil-seed contact and enhancing seedling establishment (Fig. 1).

We positioned 16 traps along the perimeter of each plot and flush to the ground surface to estimate the horizontal movement of seeds (Fig. 1). Traps were constructed of aluminum bread pans (20 cm × 10 cm × 6 cm) with aluminum flashing affixed to one side and angled down at approximately 45°. The flashing prevented trapped seeds from escaping, prohibited rodent access, and trapped ants that tried to remove seeds. Holes in the bottom of traps that were smaller than the narrowest seeds allowed drainage.

Influence of Ants, Rodents, Non-native Annuals, and Disturbance Edge

In April, we counted ant nests and rodent burrow entrances as indicators of granivore activity within a 12.5 m radius from the plot center. Active nests of harvester ants, predominantly *Messor pergandei* (Mayr) (Formicidae), were conspicuous, relatively large and easy to identify. Nests of unidentified harvester ants occurred at lower numbers than *M. pergandei* (mean ± SD for untreated compacted sites was 34 ± 63 *M. pergandei* nests/ha and 5 ± 21 nests/ha for others; trenched sites had 66 ± 58 *M. pergandei* nests/ha and 8 ± 18 ant nests/ha for others). The density of rodent burrow entrances was markedly lower at compacted sites (1 ± 5 entrances/ha) than trenches (336 ± 485 entrances/ha).

We estimated annual plant cover within each plot in April during peak plant production. Cover was estimated to the nearest 1% by counting the number of 20 cm × 20 cm grid cells occupied by vegetation within each 2 m × 2 m plot. The
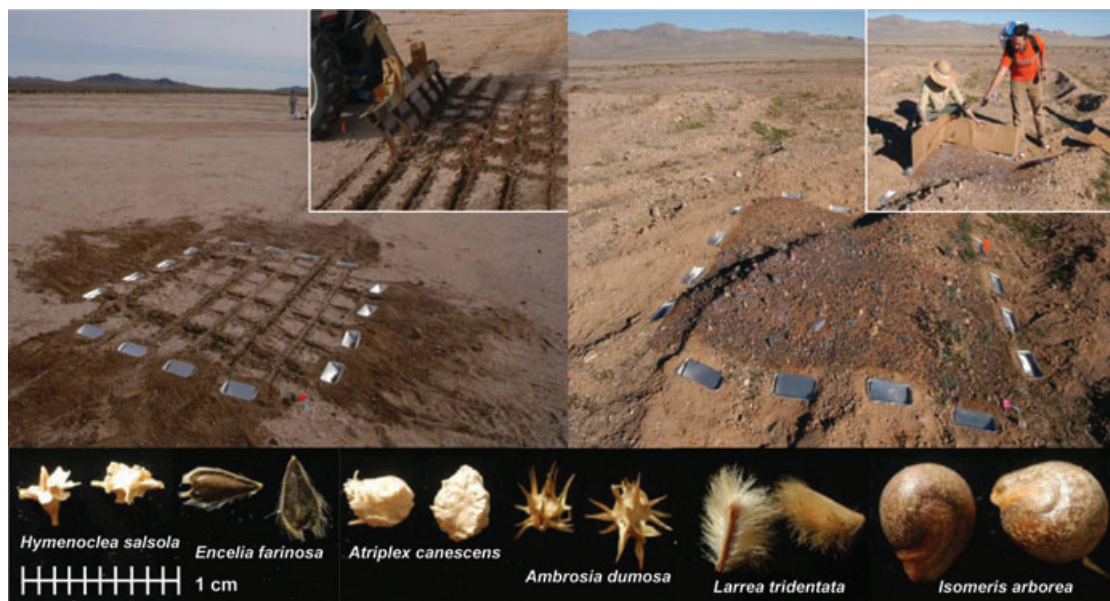

Figure 1. Compacted sites were harrowed and seeded prior to trap installation (upper left). Tackifier was applied to compacted and trenched plots using a backpack sprayer after seed traps were installed and seed was applied (upper right). Seeds of six Mojave Desert perennials (lower) were broadcast on plots, and their fates were monitored for 16 weeks.

majority of cover was comprised of the non-native annual species red-stemmed filaree (*Erodium cicutarium* (L.) L'Her Aiton) and Mediterranean grass (*Schismus* spp. P. Beauv)."

For compacted sites, we estimated the distance of plots to the closest undisturbed edge by overlaying plot locations on an aerial photo where the disturbance edge was distinguishable. Trenches were constructed after aerial photographs were taken; thus, we derived disturbance edge distances for the trenched plots by triangulating among plots within these sites that were used in a companion study and had known edge distances (DeFalco et al. 2009).

Seed Movement, Establishment, and Retention

We emptied traps beginning 1 week after seeding (26–28 January) and each week thereafter (1–3 February, 9–10 February, 16–17 February) until seed capture declined significantly, after which time we collected contents at 2–3 week intervals (1–2 March, 16–17 March, 29–31 March, 27 April to 3 May, and 9–11 May). We modified the nozzle on a battery-operated Ryobi Tuff Sucker™ wet/dry vacuum (Ryobi Technologies, Inc., Anderson, SC, U.S.A.) to facilitate removing contents from traps. We combined contents of the 16 seed traps per plot for one representative sample at each time period. Seeds were separated by species and counted in the laboratory.

Seedlings were counted to determine initial emergence (30–31 March) and subsequent seedling survival (9 May). Cotyledons were often intact on seedlings, and seedlings typically developed beyond the primary leaf stage.

During the week of 9 May (16 weeks after plots were initially seeded), the entire surface of each plot was collected to 5 cm depth, which we expected to contain the majority of the soil-seed bank (Guo et al. 1998). These surface soils were transported to the laboratory to recover seeds of the six species. Soil samples were passed through 8, 2, and 1 mm sieves to remove seedless soil fractions and then stirred with equal volumes of water while removing organic material using a cloth aquarium net. Organic material was spread on aluminum oven liners, secured with wire mesh, and dried in a convection oven for 4 hours at $50°C$. Seeds were sorted from debris, identified, and counted. We hand-sorted a subset of washed plot samples and did not recover any additional seeds.

Statistical Analyses

We analyzed seed fates using analysis of variance in two ways because of the incomplete factorial design (i.e. trenched sites were not harrowed). To compare seed fates among tackifier, harrowing, and controls, we analyzed compacted sites in a random complete block design with site as the blocking factor. To compare fates between compacted and trenched sites, we omitted the harrowing treatment and analyzed the data with disturbance type as a whole plot factor and surface treatment as a split-plot factor. One harrow, compacted plot that was not recovered from the field was omitted from analyses. All tests were conducted at $\alpha = 0.05$; means were compared using

Tukey's HSD (SAS statistical software, version 9.0, Cary, NC, U.S.A.).

We used Akaike's Information Criterion to evaluate plausible explanations for seeds that were missing after all other fates were considered at the end of 16 weeks. We used this over traditional selection methods because it selects from a candidate set of models developed from existing knowledge about the system (Burnham & Anderson 2002). We compared the same number of linear regression models with parallel combinations of site variables for both disturbances. The terms representing nests of all harvester ants (Ant) and *M. pergandei* (Mepe), burrows of rodents (Rodent), non-native annual plant cover (Anncov), and distance to edge (Edge) were screened separately for compacted and trenched sites to determine linear or quadratic relationships before model selection. For example, the model for harvester ants on trenched sites included a linear term (Ant), and the parallel model for compacted sites included a quadratic ($Ant + Ant^2$). We also expected that surface treatment would be important in explaining missing seeds, so we included models with and without surface treatment (Trt) and with and without the interaction between Trt and the site variables for model comparison (Table 1).

A correction for small sample size (AICc) was calculated for each model using the MIXED procedure and maximum likelihood as the model estimation method. The lowest AICc value denoted the "best" model out of the set of models, and the other models were subtracted after rescaling the lowest AICc to 0: models with $\Delta AIC < 2$ had substantial support,

Table 1. Models explored in the analyses describe missing seeds as a function of site variables.

Models	Rationale
Intercept	No model terms explain missing seeds
Trt	Surface treatments retain seeds on the soil surface
(Trt), Mepe	*Messor pergandei* foraging from nearby nests deplete seeds
(Trt), Ant[a]	All harvester ants foraging from nearby nests deplete seeds
(Trt), Rodent[b]	Rodents that reside in nearby burrows deplete seeds
(Trt,) Ant[a], Rodent[b]	Both harvester ants and rodents deplete seeds
(Trt), Anncov	Annual plants (predominantly non-natives) suppress germinating seeds
(Trt), Edge	Distance from the undisturbed–disturbed edge protects seeds from granivores

Trt, harrowing, tackifier, and control surface treatments; Mepe, number of *Messor pergandei* ant nests; Ant, number of nests for all harvester ant species; Rodent, number of rodent burrow entrances; Anncov, annual plant cover (%); Edge, distance to disturbed–undisturbed boundary (m).
The simplest models included an intercept only (1 model) and a Trt only model (1 model). More complex models include each site variable separately (6 models), combinations of site variables with Trt (6 models), and their interaction with Trt (6 models). These complex models with and without Trt and their interactions are denoted by "(Trt)." Linear and quadratic relationships were also pre-screened for the better-fitted models that comprised the final sets of candidate models for compacted and trenched sites.
[a] Quadratic term included for compacted site analysis.
[b] Quadratic term included for trench site analysis.

those between 4 and 7 have considerably less support, and those >10 had essentially no support (Burnham & Anderson 2002). The importance value of each plot attribute, ranging between 0 and 1, was derived by summing the Akaike weights (w_i) across all the models where the attribute occurred.

Results

Seed Movements and Seedling Establishment

A large proportion of the total seeds moved off plots during the first 3 weeks, and seed movements declined considerably after 4–6 weeks. Seed capture was negligible by 10 weeks; thus, trap contents collected beyond this time were not separated. Tackifier reduced seed movements off compacted sites by 32% compared with untreated sites, but harrowing was even more effective with 55% reduction ($F_{2,40} = 30.65$, $p < 0.01$). Tackifer was less effective in reducing seed movements off trenched sites compared with the larger reduction on compacted sites (Disturbance × Treatment, $F_{1,52} = 4.26$, $p = 0.04$).

Surface treatments applied to compacted sites reduced seed movements for *Larrea tridentata* ($F_{2,40} = 36.21$, $p < 0.01$), *Ambrosia dumosa* ($F_{2,40} = 24.49$, $p < 0.01$), and *Encelia farinosa* ($F_{2,40} = 6.22$, $p < 0.01$; Fig. 2). Reduced movement of *Atriplex canescens* seeds was marginally significant ($F_{2,40} = 3.17$, $p = 0.05$), but due to large variation, Tukey's HSD did not discriminate among treatment means. Tackifier reduced *L. tridentata* seed movements on compacted sites but had little effect on trenched sites (Type × Treat, $F_{1,52} = 5.94$, $p = 0.02$; Fig. 2). Tackifier also decreased movements for *E. farinosa* averaged across disturbances ($F_{1,52} = 5.71$, $p = 0.02$).

Total seedling emergence by late March was greatest for harrowed, compacted sites ($F_{4,66} = 46.32$, $p < 0.01$). *Encelia farinosa* seedlings were most abundant followed in decreasing order by *Hymenoclea salsola*, *L. tridentata*, *A. canescens*, *A. dumosa* and *Isomeris arborea* (Fig. 3). Accounting for seeds that were trapped through mid-March, the percent of estimated live seeds available that germinated in late March
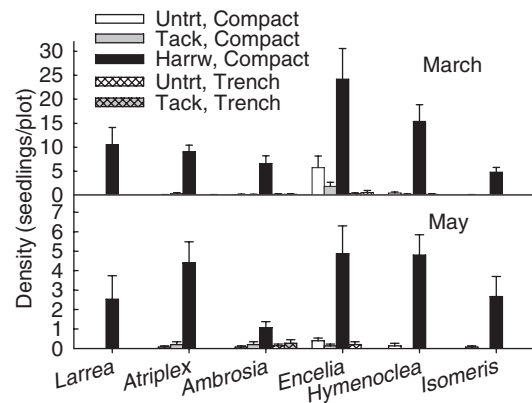

Figure 3. Density of seedlings (mean ± SE) for six perennial species that resulted from 2,841 ± 129 live seeds applied to plots. Plot area = 4 m². Note different *y*-axis scales for March and May.

on harrowed, compacted sites was highest for *E. farinosa* (6%), and markedly lower for *H. salsola* (3%), *L. tridentata* (2%), *A. dumosa* (2%), *A. canescens* (1%), and *I. arborea* (1%). By early May, harrowed, compacted sites still supported the most total seedlings with 20 ± 4 seedlings/plot ($F_{4,66} = 39.48$, $p < 0.01$; Fig. 3), but seedling densities declined across all species.

Remaining Seed Bank

Of the total seeds broadcast on study plots, only 22% remained on the plots after 16 weeks. Harrowing more than doubled retention of total seeds in compacted areas ($F_{2,39} = 10.14$, $p < 0.01$), and specifically enhanced *L. tridentata* ($F_{2,39} = 12.89$, $p < 0.01$), *A. dumosa* ($F_{2,39} = 8.28$, $p < 0.01$), and *H. salsola* ($F_{2,39} = 5.42$, $p = 0.01$; Fig. 4). Trenched sites retained approximately three times the number of seeds as compacted sites irrespective of the use of tackifier ($F_{1,52} = 16.14$, $p = 0.02$) due to the species *L. tridentata* ($F_{1,4} = 12.63$, $p = 0.02$) and *A. dumosa* seeds ($F_{1,4} = 64.82$, $p < 0.01$; Fig. 4).
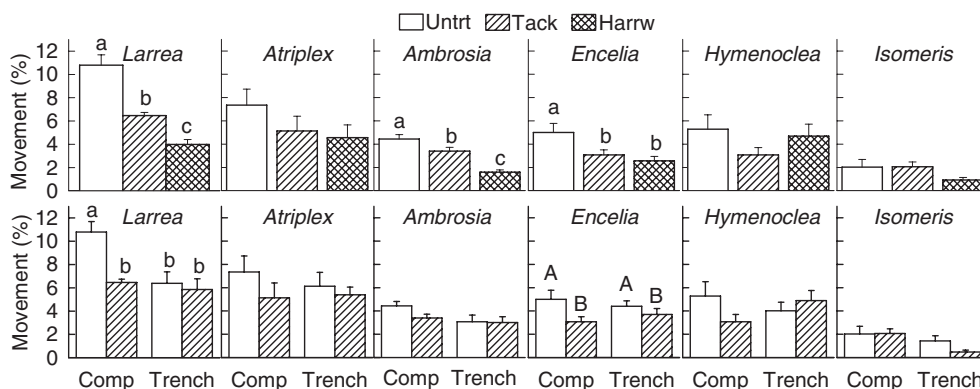

Figure 2. Percent of total seeds (live + unviable) that moved off plots after 10 weeks (mean ± SE). Treatments were compared for compacted sites only (upper figures) and untreated and tackified treatments were compared between compacted and trenched sites (lower). Different lowercase letters denote differences among treatment levels; uppercase letters denote differences between treatments averaged over disturbance type.
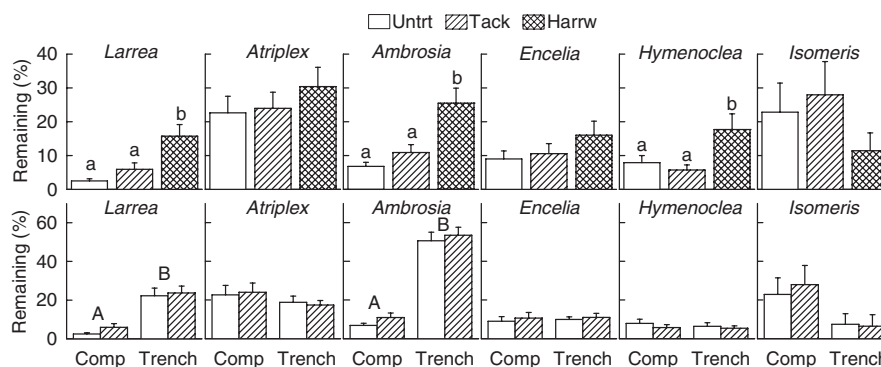
Figure 4. Percent of total seeds associated with surface treatments remaining after 16 weeks (untransformed mean ± SE). Treatments were compared for compacted sites only (upper figures), and untreated and tackified treatments were compared between compacted and trenched sites (lower). Different lowercase letters denote differences among treatment levels; uppercase letters denote differences between disturbance types averaged over surface treatments.

Missing Seeds

Even after accounting for seeds that collected in traps, established as seedlings, and remained on plots, a large proportion of the original seeds was absent after 16 weeks (from about 4,233–5,478 seeds in the different treatments out of about 6,669 seeds originally applied per plot). Granivore presence was the most plausible explanation for these missing seeds, yet ants and rodents were implicated on different disturbance types. The best model for compacted plots included a quadratic relationship between missing seeds and ant nests and the interaction between surface treatment and ant nests (Fig. 5; Table 2). Summing w_i for each variable across all candidate models in which they occurred on compacted sites, we found that surface treatment (0.9972) and total ant nests (0.9336) explained missing seeds better than *Messor pergandei* nests (0.0590) or rodent burrow entrances (0.0055). In contrast, trenched plots with more rodent burrow entrances nearby

Table 2. Analysis of missing seeds on compacted and trenched sites. Missing seed was arcsine square root transformed before analysis.

Model*	k	AICc	Δ_i	w_i
Compacted sites				
Trt, Ant, Ant^2, Trt*Ant	6	−73.3	0.0	0.6013
Trt, Ant, Ant^2	5	−72.1	1.2	0.3300
Trt, Mepe, Trt*Mepe	5	−67.8	5.5	0.0384
Trt, Mepe	4	−66.5	6.8	0.0201
Trt, Rodent	4	−63.7	9.6	0.0049
Trenched sites				
Rodent, Rodent^2	4	−45.4	0.0	0.5399
Trt, Rodent, Rodent^2	5	−44.0	1.4	0.2681
Trt Rodent Rodent^2 Trt*Rodent	6	−42.3	3.1	0.1146
Ant Rodent Rodent^2 Ant*Rodent Ant* Rodent^2	7	−39.3	6.1	0.0257
Ant	3	−38.4	7.0	0.0164
Mepe	3	−37.5	7.9	0.0105
Trt, Ant	4	−35.7	9.7	0.0042

* Plot attributes: Trt, surface treatment; Ant, total ant nests; Mepe, *Messor pergandei* nests; Rodent, rodent burrow entrances.
Missing seed was arcsine square root transformed before analysis. Models are ranked by Δ_i. Only models with some level of support ($\Delta_i < 10$) are presented. Akaike weights (w_i) were included for comparing the relative importance of the plot attributes.

generally had more missing seeds (Fig. 5; Table 2). Rodent burrow entrances (0.9534) explained missing seeds better than surface treatment (0.3969), ant nests (0.0484), or *M. pergandei* nests (0.0138) on trenched sites. The mean (± SD) cover of annual plants was 11.1 ± 9.9% for compacted and 31.5 ± 18.8% for trenched sites. Cover of annual plants and distance to undisturbed edge had the lowest relative importance values for compacted (0.0003 and 0.0008) and trenched sites (0.0013 and 0.0042, respectively) and did not occur in the set of plausible models (i.e. ΔAIC for these models were >10).

Discussion

Abundant rainfall during the period of our study was atypical of most years in the Mojave Desert, yet such pulses are
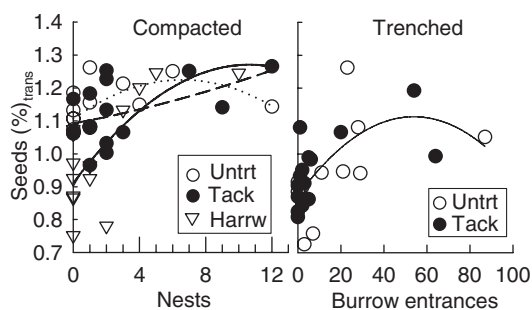

Figure 5. Percent missing seeds (arcsine square root transformed) associated with ant nests and rodent burrow entrances after 16 weeks on compacted and trenched sites. Regressions on compacted sites represent untreated (arcsine square root [% seeds] = 1.1066 + 0.0359*Ant − 0.0027*Ant^2; $r^2 = 0.36$; dotted line), tackifier (arcsine square root [% seeds] = 1.0927 + 0.0094*Ant + 0.0003*Ant^2; $r^2 = 0.24$; dashed line), and harrowed treatments (arcsine square root [% seeds] = 0.9113 + 0.0676*Ant − 0.0032*Ant^2; $r^2 = 0.53$; solid line). Treatments were combined on trenched sites (arcsine square root [% seeds] = 0.8726 + 0.0089*Rodent − 0.0001*Rodent^2; $r^2 = 0.42$).

known to have a vital role in revegetating surface disturbances in many arid lands (Webb 2002; Squeo et al. 2007; Grigg et al. 2010). January through May rainfall was 123 mm (Barstow NE, California climate station, 622 m [2,040 ft] elevation)—273% of the long-term average—and followed a pronounced drought lasting several years for the region (Cook et al. 2004). Such a pulse in spring rainfall represents an opportunity for shrub recruitment, especially in the absence of strong non-native annual plant pressure during our study (Hardegree & Van Vactor 2005). However, a large proportion of the seeds initially broadcast were missing after 16 weeks (63–82%, depending on treatment), and overall seedling emergence was ≤3% even with this favorable rainfall. These results emphasize that revegetation of disturbed desert shrublands through supplementing seed banks is more complex than previously thought.

We expected that surface treatments such as tackifier and harrowing would minimize seed transport associated with extreme rain and wind events and increase seedling recruitment. Harrowing of the compacted sites decreased seed movements and increased seedling establishment above all other treatments, as observed for degraded semiarid rangelands in South Africa (Snyman 2003; van den Berg & Kellner 2005) and grassland steppe in China (Liu et al. 2008). Furrows retained seeds despite heavy rain events, and likely improved soil physical and hydrological properties such as bulk density, porosity, run-off, and infiltration (Osunbitan et al. 2005), thereby enhancing establishment.

Despite the success of harrowed compacted sites, seeds that remained on the soil surface were vulnerable to seed predation. Rodents had little impact on seeds at compacted sites, likely a consequence of the low soil penetration found there (DeFalco et al. 2009) and thus the rare incidence of burrows compared with trenched sites. The number of seeds missing on compacted sites by 16 weeks was positively related to the abundance of nearby ant nests supporting the assertion that ants remove many seeds distributed during seeding efforts in arid environments (Anderson & Ostler 2002). At a nearby site where ant foraging was monitored in February and March, harvester ants ceased collecting and transporting seeds to their nests and moved belowground when diurnal ground surface temperatures dropped below 20°C (DeFalco, USGS, unpublished data). Diminished ant activity associated with declining ground temperatures has also been observed for *M. pergandei* (Tevis 1958; MacMahon et al. 2000) and *Pogonomyrmex* spp. (Pol & de Casanave 2004) (Formicidae) in North and South America, respectively. In severely compacted sites in the Mojave Desert where seeding in combination with surface harrowing is desirable, seed harvesting by ants may be avoided by broadcasting seeds as early as October when average soil temperatures are typically below 20°C and winter frontal storms provide soil moisture necessary for germination of many desert species (Beatley 1974).

Desert shrub species germinate within temperature ranges that generally reflect the spring, winter or summer/autumn seasons (Baskin & Baskin 1998). We seeded our plots several months after natural dispersal typically occurs for many

perennial species but during the time that seeds could take advantage of late winter/early spring rainfall. After seeding occurred in January, rainfall events >10 mm occurred on 11 February (12.7 mm), 18–19 February (15.75 mm), 22–23 February (14.23 mm), and 4–5 March (33.78 mm). Average soil temperatures for the 7 days following these early spring storms ranged between 10 and 15°C. The greatest establishment of *Encelia farinosa* seedlings by March reflects the cooler germination temperature for this early-colonizing species (Brum et al. 1983; Bowers 1994). *Atriplex canescens* has broad and potentially high variable germination requirements (Kay et al. 1988), which make it a suitable species in seed mixes applied during winter or summer (Brum et al. 1983). *Isomeris arborea* germinates well under winter conditions and at temperatures of 5–15°C, whereas *Hymenoclea salsola* germinates at late spring or early fall temperatures of 15–25°C (Kay et al. 1988; Brum et al. 1983). Thus, in addition to consideration for ant harvesting activity, seasonal applications of different seed mixes, each with their specific germination temperatures matched with the timing of application, may be a more successful strategy for maximizing establishment than single applications of species mixes with a range of germination requirements.

Some Mojave Desert shrub species require the warmer summer and fall temperatures to germinate, which coincides with aboveground activities of many harvester ant species. *Larrea tridentata* and *A. dumosa* germinate primarily in July through September when monsoonal storms deliver sufficient rainfall to maintain soil moisture and soil temperatures are above 15°C (Barbour 1968; Kay et al. 1988). Seeding disturbed areas in winter with *L. tridentata* and *A. dumosa* or similar species with higher temperature requirements increase their vulnerability to redistribution, decay, and predation. Seeding in late summer or early fall—immediately prior to the season when favorable germination and establishment conditions prevail—minimizes the window of opportunity for seed predators to deplete reserves. Ant activity will be high during this time, and as suggested for semiarid environments of coastal California (Montalvo et al. 2002) and South Africa (Snyman 2003; van den Berg & Kellner 2005), drill seeding or imprinting ensure suitable seed-soil contact and bury seeds so that they are inaccessible to granivores. However, these are among the more intensive alternatives to broadcast seeding and should be considered in the context of other management goals, such as protecting habitat for sensitive species (e.g. desert tortoise and Mohave ground squirrel).

In contrast to compacted sites, seed removal was associated with rodent activity on trenched sites. The large failure of seedling emergence on trenched sites suggests in part that rodents had full access to these linear features and were redistributing considerably more seeds than we could account for on our experimental plots. Granivores remove and consume many seeds of perennial species in arid and semiarid environments (Roth & Vander Wall 2005; Barberá et al. 2006), yet the number of seeds buried in shallow caches that result in seedling recruitment can be much greater than seeds collected by ants (Longland et al. 2001). Indeed, seeds

that were not recovered during our study were observed as multiple seedlings sprouting from rodent caches within several meters of seeded plots. Application of native seed mixtures that include "decoy" species for rodents to cache and consume while leaving native "target" species to establish is a promising approach for arid land seeding efforts (Longland & Bateman 1998), but remains largely untested. Rodent-caching behavior is known to be beneficial to regenerating arid land plant communities (Vander Wall 1990) and deserves further attention in the context of revegetating disturbances in arid environments including the Mojave Desert.

Factors other than germination temperatures and granivore activity at trenched sites that were not measured during our study likely also hindered seedling establishment. For some germinating seeds, the emerging radicle may have simply failed to penetrate the disturbed soil surface and anchor the seedling. Alternatively, emerging seedlings may have been consumed by herbivores; thus, seeded areas or individual plants may require protection until seedlings are no longer vulnerable to tissue damage (Koch et al. 2004). Similar to the process of topsoil collection and reapplication during reclamation, the mixing of soil layers during trench development may have altered soil organic matter, nutrient availability, and chemistry (Abdul-Kareem & McRae 1984; Stahl et al. 2002). Remediation of soils (e.g. addition of fertilizers or other soil amendments) may be necessary to enhance soil conditions and accelerate seedling establishment in areas disturbed by trenching activity (Bainbridge 2007; Liu et al. 2008).

Although successful at reducing seed losses after 10 weeks on compacted sites, tackifier did not enhance seed retention on compacted sites or have any influence on trenched sites 16 weeks after implementation. Tackifier was applied prior to the exceptional rainfall period during the study. Its effect was diminished on compacted sites before heavy rains occurred in the third week, and because tackifier is water-soluble, seeds continued to be mobilized off the plots with the tackifier when it rained.

Although we have discussed the factors affecting seed fates on disturbed sites following broadcast seeding, pre-seeding conditions should also be considered when maximizing establishment success. For example, according to seed testing results, the germination of *A. dumosa* and *L. tridentata* were 2 and 18%, respectively. Seeding recommendations for these and other low viability species planned for revegetation of degraded arid lands (Brum et al. 1983; van den Berg & Kellner 2005) may require higher application rates to overcome lower seed fill or germination percentages (Kay et al. 1984, 1988). Seeds of desert species are often in short supply for rehabilitation efforts, and as in our study, commercially available seeds were used. The genetic source of commercially available seeds as well as the size and degree of disturbance are rarely considered when selecting seed material, but are nevertheless important for the success of revegetation efforts (Lesica & Allendorf 1999; McKay et al. 2005).

This is the first study to consider multiple sources of immediate seed losses related to seeding efforts in degraded Mojave Desert shrublands, and we have considered how complex interactions among factors including inter-annual precipitation, seasonality of seed application, temperature requirements of seeded species, seed viability, seed predation, disturbance type, surface treatment, and invasive plant competition affect the outcome of vegetation reestablishment. We recognize that fates of seeds were followed for a short time period following seeding (16 weeks) and during a year when rainfall was above-average. Longer duration studies are especially important for evaluating seedling survival during periods of low rainfall or extended drought. Careful consideration for the unique characteristics of disturbances, the species' requirements for germination of Mojave Desert perennials as well as the constraints placed on seed densities by granivores themselves will aid in developing future compositions of seed mixes and determining the timing of their application on disturbed arid lands, especially in light of expected changes in regional climate (Seager et al. 2007).

Implications for Practice

- Light surface harrowing can accelerate seeding success on compacted soils in arid lands, but widespread application of this treatment may conflict with the protection of vulnerable habitats and cultural sites. By restricting harrowing to highly compacted areas and monitoring the movement of harrowing equipment across the landscape, resource specialists can minimize spatial conflicts with sensitive resources and seed large areas compacted by recreation, military activity, or utility corridor development.

- Site assessment of granivore activity prior to seeding—such as by counting densities of active harvester ant nests and rodent burrow entrances—may indicate whether methods that partially bury or conceal seeds are necessary, especially when favorable seeding periods for selected seed species coincide with high granivore activity.

- Supplementing seed banks during the season when favorable germination temperatures for seeded species coincide with effective rainfall will maximize seedling emergence, thus limiting ant and rodent access to seeds.

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 U.S. government.

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