The Fate of Perennial Seeds Used in Rehabilitating Disturbed Sites at Fort Irwin National Training Center, California

Administrative Report

Prepared for:

Integrated Training Area Management
U.S. Army National Training Center
Fort Irwin, California
Contact: David Housman: voice: 760-380-5202

U.S. DEPARTMENT OF THE INTERIOR
U.S. GEOLOGICAL SURVEY
WESTERN ECOLOGICAL RESEARCH CENTER

This Page Intentionally Left Blank

WESTERN ECOLOGICAL RESEARCH CENTER

The Fate of Perennial Seeds Used in Rehabilitating Disturbed Sites at Fort Irwin National Training Center, California

Prepared by
Lesley A. DeFalco and Todd C. Esque

U.S. Geological Survey
Western Ecological Research Center, Las Vegas Field Station
160 N. Stephanie St., Henderson, Nevada 89074
phone: 702-564-4507; fax: 702-564-4600; email: lesley_defalco@usgs.gov

Final Administrative Report Prepared for
Integrated Training Area Management
U.S. Army National Training Center
Fort Irwin, California
Contact: David Housman: 760-380-5202

October 1, 2008

This Page Intentionally Left Blank

U.S. DEPARTMENT OF THE INTERIOR
DIRK KEMPTHORN, SECRETARY

U.S. GEOLOGICAL SURVEY
Mark D. Myers, Director

For additional information, contact:

Steven E. Schwarzbach, Center Director
Western Ecological Research Center
US Geological Survey
3020 State University Drive East
Modoc Hall Floor 3, Room 3006
Sacramento, California 95819

Executive Summary

The mission of the US Army National Training Center (NTC) at Fort Irwin, California is to provide tough, realistic training for Army brigade combat teams under full battle conditions. The Integrated Training Area Management (ITAM) program at NTC monitors the effect that training has on the condition of the land and quantifies the effectiveness of rehabilitation treatments in revegetating disturbed shrubland communities. ITAM implements a variety of techniques including supplementing the natural seed banks through broadcast seeding in combination with treating the soil surface with tackifier or surface harrowing to maintain adequate seed-soil contact. Although climatic variation is thought to be largely responsible for variability in reseeding success, there have been no quantitative explanations for successes or failures of these activities.

We report on the second of two phases of an investigation that focuses on the fate of native seeds applied to experimental plots at the NTC in 2005. In the first phase, we tracked seeds of six perennial species commonly used in rehabilitation efforts and determined whether tackifier and surface harrowing enhanced seed retention and seedling establishment on two disturbance types. Seeds were broadcast on 2 m × 2 m plots in January, and movement of seed away from plots (referred to as "seed loss") was estimated during the following 10 weeks using seed traps installed around the periphery of each plot. Seedling establishment of each species also was determined in March and May. In a previous report about Phase I, we concluded that compacted sites that were harrowed and trenched sites in general had the lowest seed losses after seed was broadcast, but seedling establishment was enhanced only on harrowed compacted sites. Totaling seed losses and germination across all species, we accounted for less than 20% of the total seed that initially was distributed across the experimental plots. Our observations of ant and rodent activity during the experiment—including emptied seed caryopses of *Encelia* and *Atriplex* on nearby ant nest disks, discarded seed coats of *Isomeris* seeds close to seed traps, and *Isomeris* seedlings emerging from nearby small mammal caches—suggested that granivore activity may account for additional seed losses from plots. In addition, the abundance of competitive non-native annual plants was high on many of the trenched sites. This report examines whether plots established on compacted and trenched sites in January retained seeds in May (a period of 16 weeks after the seeds were broadcast) and explores the impacts that ant and rodent activities, non-native plant competition, and the interaction with surface treatments may have on seed fates in rehabilitation efforts.

The total seed that remained on the plots in Phase II mirrored our previous findings of seed movements associated with the surface treatments: compacted sites that were harrowed and trenched sites in general retained the most seeds 16 weeks after seed was applied. Enhanced seed retention on harrowed compacted sites was driven by *Larrea*, *Ambrosia,* and *Hymenoclea* and on trenched sites by *Larrea* and *Ambrosia.* The average unrecovered seeds per plot– that is, after accounting for seeds collected in traps, seeds that germinated, and seeds retained on plots – ranged from 68% to 74% in compacted areas and 55% to 68% on trenched sites. These large percentages of unrecovered seeds were unlikely a result of our soil collection or processing: we used soil sieves that trapped seeds of all six species (between 1 mm and 8 mm), and no seeds remained in soil samples after the final step of elutriation.

We explored the potential influence of granivore activity and non-native annual plant competition by relating the number of ant nests and rodent burrow entrances within a 12.5 m radius and the annual plant cover of each plot to the percent of unrecovered seed. The surface treatments—harrowing, tackifier, and no treatment—were also considered separately for compacted and trenched sites. We expected that if granivores were removing seeds from plots, then the unrecovered seed would be positively related to the number of ant mounds or to the number of rodent burrow entrances. Similarly, if seeds that germinated into seedlings died due to competition with non-native annuals, then we expected that unrecovered seeds would be positively related to non-native plant cover. Plots on compacted sites that had more harvester ant nests nearby generally had a greater percentage of unrecovered seeds, and plots on harrowed sites had a lower percentage of unrecovered seeds than did tackified and untreated plots when the number of ant nests was low. In contrast, plots on trenched sites with more nearby rodent burrow entrances generally had a high percentage of unrecovered seed. Although these metrics were crude measures for understanding the removal of seeds from experimental plots, they do imply that large numbers of seeds that are broadcast during rehabilitation efforts may be removed by granivores, and seed removal by ants versus rodents can vary among different disturbances. While it is expected that ants and rodents consume many of the seeds they removed, other seeds are buried in shallow caches by rodents and can germinate during favorable soil moisture and temperature conditions.

The timing of seeding and harrowing, just prior to the return of winter rainfall, is important in compacted areas so that soil temperatures are low enough to diminish ant activity and so seeds of species that require cooler temperatures can take advantage of winter storms for germination. For compacted sites where intense management

is permissible, alternative seeding prescriptions, such as drill seeding or disking, may be necessary to ensure that good seed-soil contact is made and seeds are buried and inaccessible to ants. Seedling establishment on trenched sites may be more challenging. Although seed retention is greater compared with compacted sites, soil chemistry and microbiota that are conducive to seedling establishment may have been altered during trench development and removal, thus trenched sites may require additional remediation before seeds are applied. Re-establishment of vegetation on degraded lands at the NTC requires the use of appropriate surface treatments for different disturbances while appreciating the impacts of seed harvesting animals and plant species-specific germination requirements.

Introduction

When vegetation is lost through soil surface disturbance, seed banks are not readily replenished. Consequently, natural recovery requires that seeds from nearby undisturbed areas be moved onto the disturbed site by wind or water. Alternatively, for some plant species with large seeds that are not easily dispersed, ants and small mammals may be dispersal agents (Brown *et al*. 1979, Vander Wall *et al*. 2006). The Integrated Training Area Management (ITAM) program regularly reseeds areas disturbed by military training to accelerate the establishment of vegetation. Little is known about the dispersal of seeds across the disturbed-undisturbed boundary, how surface treatments affect supplemented seeds, or whether different disturbances (*e.g*., linear vs. broad disturbances) have different seed dispersal dynamics, thereby requiring more or less intervention from ITAM land managers.

We conducted a two-phase study to understand the fate of perennial seed species broadcast on experimental plots on heavily compacted and trenched sites at the US Army National Training Center (NTC). The goal of the study was to determine the fate of seeds for six Mojave Desert perennial species commonly acquired from commercial seed suppliers and broadcast by ITAM in areas heavily impacted by military training. In Phase I, we learned that harrowing the soil surface on compacted sites resulted in the greatest establishment of seedlings for all species and treatments. This enhanced establishment on harrowed plots was accompanied by relatively low losses of seeds, measured as the amount of seeds captured in seed traps, compared with control and tackifier treatments. In contrast, trenched sites had low seed losses relative to harrowed compacted sites, but the establishment of seedlings was unexpectedly low.

During Phase I of the study we also observed emptied seed caryopses of *Encelia* and *Atriplex* at the entrances of nearby ant nests, discarded seed coats of *Isomeris* seeds close to seed traps, and established *Isomeris* seedlings emerging from nearby small mammal caches at one compacted site. The dominant harvester ant *Messor pergandei* was observed collecting all six species of seeds that were broadcast (Fig. 1). Multiple rodent burrow entrances were observed near plots at trenched sites. In addition, annual plant cover, predominantly of the invasive

Figure 1. Harvester ants (*Messor pergandei*) were observed carrying seeds of all six species that were broadcast on 4 m^2 plots during Phase I of a two-phase study to understand the fate of perennial seeds used in rehabilitating disturbed sites at the U.S. Army National Training Center. Species names of seeds are, from left to right: *Hymenoclea salsola, Encelia farinosa, Atriplex canescens, Ambrosia dumosa, Larrea tridentata,* and *Isomeris arborea.*

annuals *Erodium cicutarium* and *Schismus barbatus*, varied considerably among sites but often was higher on trenched sites. We speculated that the failure of seedlings to establish at trenched sites may be due to seed predation by ants and rodents, competitive exclusion of seedlings by non-native annuals, or inadequate soil conditions for germination and seedling development related to the trench disturbance itself. By the end of Phase I our observations led us to speculate on the importance of granivores in the movement and removal of seeds and the potential competitive effect of non-native invasive annuals on native seedling establishment.

To learn more about the fates of seeds used in vegetation rehabilitation treatments at NTC, we initiated a second phase of this study. In Phase II we determined if seeds remained on the experimental treatment plots or were lost from those plots during the first 16 wks after they were applied. We also explored the potential for competition with annual plants, seed removal by granivorous animals and distance to the nearest undisturbed edge to explain unrecovered seed. Phase II addressed three questions: (1) How much of the seed mix initially broadcast on plots remained on compacted and trenched sites; (2) Are tackifier and harrowing effective at retaining seeds on the soil surface; and (3) Are granivore activity, competition with non-native annuals, or distance of the 2 m × 2 m seeded plots from the undisturbed edge plausible explanations for the fates of seeds that were not recovered in Phase I? We expected that if ants and small mammals were removing seeds from plots, or if non-native annuals were suppressing seedlings that germinated from the seeds, then unrecovered seeds would be positively related to the number of ant mounds and rodent burrow entrances and to annual plant cover. Because granivores foraging along disturbed-undisturbed edge habitat would intercept seeded plots located closer to the edge, we also expected more unrecovered seeds on 2 m × 2 m seed plots that occur closer to the undisturbed edge.

Methods

Study Sites and Surface Treatments

The study area consists of three compacted and three trenched sites. Compacted sites are expansive areas that were run over by recurring vehicular traffic and include the Whale (0514034 E 3922508 N), Vehicle Maintenance (0547472 E 3913594 N), and Racetrack (0547389 E 3897189 N) sites. The trenched sites are narrow (approximately 40 m) linear features where subsoil layers were mixed with topsoil to a depth of ~2 m (R. Sparks, oral. comm., 2004) and include the LF6 (0538935 E 3914573 N), Peanut (0540884 E 3911366 N), and Crash Hill sites (0525939 E 3918707 N). At each of the three compacted sites, 15 sampling plots (2 m × 2 m each with a minimum distance apart of 25 m) were selected and randomly assigned one of three treatments of tackifier + seed, harrowing + seed, or seed only control (N = 5 per treatment). Tackifier is a water soluble, latex polymer emulsion typically used to reduce dust emissions but may be effective for adhering seeds to the soil surface. The tackifier Soil-Sement was administered in a 1:8 tackifier-to-water solution and applied in a series of two or three coats across each plot after seeds were broadcast (Fig. 2). Harrowing (previously called "ripping" in Phase I report – DeFalco *et al*. 2005) left furrows of approximately 3 cm wide and 5 cm deep by dragging rigid metal tines behind a tractor (Fig. 2). In contrast, 10 sampling plots of the same size and distance apart as the compacted sampling plots were selected within the three trenched sites, with two treatment levels of either tackifier + seed or seed only assigned (N = 5 per treatment). Surface harrowing was excluded as a treatment for the trenched sites because of the difficulty of applying the treatment, and ITAM does not expect to use this treatment because of

Figure 2. Tackifier and surface harrowing treatments applied to plots where seeds of six Mojave Desert perennials were broadcast on compacted and trenched sites at the U.S. Army National Training Center. Tackifier was applied to compacted and trenched plots using a backpack sprayer (A, inset; LF6 trench site) after seed traps were installed and seed was applied. Harrowing occurred on compacted sites (B, inset; Racetrack compacted site) prior to trap installation and seeding. Scale for the seeds of six perennial species is in mm.

the inherent ruggedness of these sites. Details of soil attributes, extant seed quantities prior to seeding, and vegetation composition at the sites are described in DeFalco *et al.* (2005).

Seed traps constructed of standard aluminum bread pans were spaced along the perimeter of each 2 m × 2 m plot to capture seeds moved by wind and rain (see DeFalco *et al.* 2005). A total of 16 seed traps were evenly spaced along all four sides of the sampling plot (4 traps per side), covering 40% of the plot perimeter. Installation of each seed trap was done so that one side abutted the sampling plot and the top was flush with the ground surface. In the event of plot micro-topography, the trap followed the predominant slope of its location.

Bulk Weight vs. Count Estimates of Seeds Applied to Experimental Plots

At the onset of the experiment, we weighed seed for each species separately and mixed seeds together for each plot to attain a target of approximately 600 live seeds/m^2 (2,400 live seeds/plot) with approximately 100 live seeds/m^2 (400 live seeds/plot) for each of six perennial species. The number of live seeds per unit weight of bulk seed (*i.e.*, the percentage of pure live seed) was estimated for each species using standard methods at qualified seed testing laboratories (*Ambrosia*, 10.29%; *Larrea*, 21.95%; *Atriplex*, 38.56%; *Encelia*, 59.12%; *Hymenoclea*, 60.50%; and *Isomeris*, 78.66%). As a result, the total estimated number of seeds (live and unviable) was

Table 1. Comparison of estimated numbers of seeds initially sown on experimental plots at the Fort Irwin National Training Center in January 2005. The weight estimate is based on the number of seeds per bulk pound of seed mix calculated by the commercial supplier. The count estimate is based on three samples prepared for plots using bulk pounds, sorted by hand and counted individually. Estimated total seeds sown (live and unviable) is the product of the estimate and the percentage of pure live seed calculated by the commercial supplier.

	Estimated total seeds per plot		Estimated live seeds per plot	
	By weight	By count (± 95% CI)	By weight	By count (± 95% CI)
Ambrosia dumosa	3,890	2,378 ± 209	400	245 ± 22
Larrea tridentata	1,684	1,512 ± 44	370	332 ± 10
Atriplex canescens	1,038	997 ± 49	400	384 ± 19
Encelia farinosa	710	589 ± 41	420	348 ± 24
Hymenoclea salsola	682	695 ± 37	413	420 ± 22
Isomeris arborea	509	498 ± 28	400	392 ± 22
Total	8,513	6,669 ± 350	2,403	2,121 ± 111

approximately 8,513 seeds/plot or 2,128 seeds/m^2. Three samples of the same seed mix prepared for the 4 m^2 plots were saved and sorted so we could directly count seed numbers applied for each species (Table 1). Total seed numbers from our counts were 22% lower than bulk estimates; however, estimates for three of the species, *Atriplex, Hymenoclea, and Isomeris* were within the 95% confidence interval of their bulk estimates.

Ant Nests, Rodent Burrows, Non-Native Annuals and Disturbance Edge

The number of ant nests and rodent burrow entrances were counted within a 12.5 m radius of the center of each treatment plot in April when we observed peak activity. Nests of harvester ants (predominantly *Messor pergandei)* were conspicuous, relatively large and easy to identify. Nests of other ants were noted and counted, but they occurred at lower numbers compared with those of *Messor*. Rodent burrow entrances similarly were quantified within the 12.5 m radius. Annual plant cover was ocularly estimated for each 2 m × 2 m plot; the majority of cover was comprised of the non-native annual species *Erodium cicutarium* and *Schismus barbatus*. The distance of the plots in the compacted and trenched sites from the closest undisturbed edge was estimated from the plot locations overlaid on an aerial photo of the NTC where the disturbance edges were distinct. Edge distances on trenches that were developed after aerial imagery were derived from relative distances among plots with known edge distances (DeFalco *et al.* 2005).

Recovery of Seed from Soil Collected on Experimental Plots

We began Phase II by collecting surface soils of each plot 16 weeks after they initially were seeded. Surface soils with the remaining seeds were collected to a depth of 2 cm to 5 cm at the end of the experiment in May 2005 (Fig. 3) and stored at U.S. Geological Survey, Las Vegas

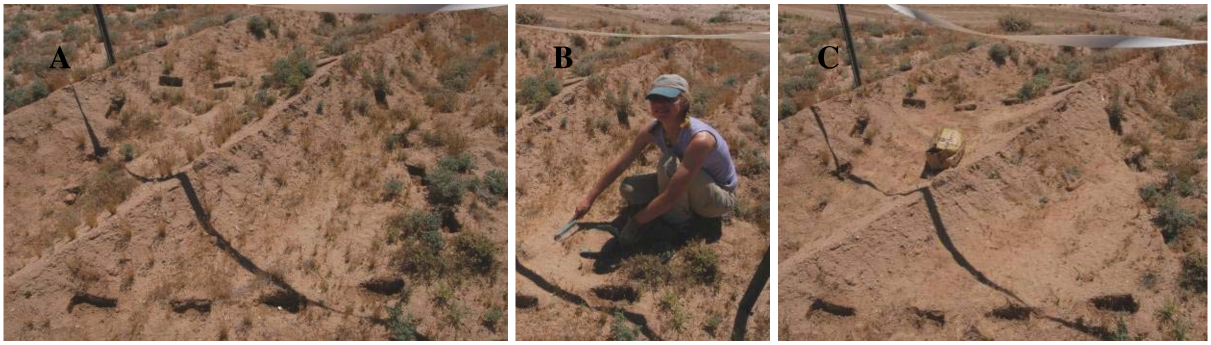

Figure 3. Recovery of seeds at Peanut Trench at the U.S. Army National Training Center**.** After seed traps were vacuumed for the last time on May 29, 2005 they were removed from each plot (A). Using stiff-bristled hand brooms and dust pans (B), soil was swept from each plot and collected in paper grocery bags (C). Paper bags were placed within puncture-resistant plastic trash bags and transported to the laboratory where they awaited sieving and elutriation in fall 2007.

Field Station. One plot was not recovered from a harrowed, compacted site (Whale plot #273) for unknown reasons but not as a result of training activities.

We conducted several trials using soil sieves with various mesh sizes to determine the best method to separate the seeds from the bulk soils collected in the field. The method we established allowed us to attain complete seed recovery while minimizing the processing time per sample (*i.e.*, the soils that remained after processing were re-sorted by hand and no seeds were found). All soil samples were subjected to two phases of processing to recover seeds of the six perennial species: dry sieving and elutriation. The bulk dry soil sample first was processed by passing ~ 472 ml (2 cups) of soil at a time through three stacked sieves of 8 mm, 2 mm, and 1 mm, and shaking back-and-forth by hand for 15 s to 30 s. No seeds passed through the 1-mm sieve, but a considerable amount of fine soil was removed. Small *Encelia* and *Ambrosia* seeds, soil and organic litter were captured between the 1-mm and 2-mm sieves; this fraction was set aside for elutriation. Larger seeds of *Encelia* and *Ambrosia*, all seeds of the other species, soil, and litter were captured between the 2-mm and 8-mm sieves; this fraction also was set aside for elutriation. A considerable amount of cobble and gravel, but no seeds, were removed on the 8-mm sieve.

The elutriation phase consisted of separately rinsing the fractions that passed between the 1-mm and 2-mm sieves and the 2-mm and 8-mm sieves with water. Subsamples of approximately 472 ml (2 cups) of sieved sample at a time were placed in a small dish tub with twice the volume of tap water. The soil-water mixture was vigorously stirred or agitated, and at the same time, organic material that floated to the surface or remained in suspension was rapidly collected using a cloth aquarium net until all organic material was recovered. Collected organic material was immediately spread on aluminum oven liners, secured with wire mesh, and placed in a convection oven to dry for 4 h at 50 °C. Seeds did not appear to imbibe water during the elutriation phase due in part to the hydrophobic nature of the organic material and to the very short time that seeds were in suspension.

Dried samples were hand sorted and seeds were removed. Seeds were sorted from organic litter, and the status of each seed was classified as intact (*i.e.*, seed coat, endosperm, and embryo were not broken) or impaired (*i.e.*, seed coats were cut or fragmented and often there was damage to the endosperm and/or embryo). Finally, recovered seeds for each plot were counted by species and status. We attempted to use a tetrazolium test to stain the embryo and endosperm of a subset of seeds for determining viability. All species of seeds except *Isomeris* were difficult to dissect for evaluating viability, and the variability between observers in determining a positive stain was so large that we could not confidently use this method to indicate live seeds.

Statistical Analyses

Analyses were conducted using SAS statistical software (version 9.0, Cary, North Carolina). We analyzed seed retention (total number of seeds and the percent of seeds for each species) using Analysis of Variance in two ways because the design was an incomplete factorial experiment (*i.e.*, trenched sites were not harrowed). To determine whether seed loss varied among tackifier, harrowed, and control treatments, only the compacted sites were used and analyzed in a random complete block design with site as the blocking factor. To compare seed retention between compacted and trenched sites, the harrowed treatment was omitted, and data were analyzed in a split plot with disturbance type as the whole plot factor and surface treatment as the split plot factor. The harrowed compacted plot that was not recovered from the field was omitted from all analyses. All tests were conducted at $\alpha = 0.05$ significance level and multiple comparisons were conducted using Tukey's studentized range (HSD) test.

We used an information-theoretic approach to determine the most plausible model explaining the fate of unrecovered seeds 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 (Burnham and Anderson 2002) because it considers only a set of models we developed based on existing knowledge about the biology or ecology of the system. We hypothesized that granivory by ants and rodents, competition by non-native annuals, and proximity to the undisturbed edge were possible explanations for the unrecovered seeds. These possible explanations were developed into separate linear regression models based on several guidelines: (1) Compacted and trenched sites would have different explanations for the unrecovered seeds, based on our observations of site differences in ant and rodent activity and in the cover of annual plants during the study. Also, compacted and trenched sites had different surface treatments (*i.e.*, no harrowing occurred at trench sites). Therefore compacted and trenched sites were analyzed separately; (2) The relationships between unrecovered seeds and some of the indicators might be curvilinear. Therefore, the terms representing total ants, *Messor pergandei*, rodents, annuals and distance to the edge were screened before model selection to determine whether they were best represented as linear or quadratic relationships. For example, a model for harvester ants on trenched sites includes a linear term (Ant), and a model for compacted sites includes a quadratic term ($\text{Ant} + \text{Ant}^2$); and (3) Surface treatment could be important in explaining unrecovered seeds, so we developed models with and without surface treatment for model comparison. Based on these guidelines, we developed separate sets of candidate models for compacted and trenched sites to examine the fate of unrecovered seeds.

The percent of unrecovered seeds was transformed before AIC analysis using arcsine-square root transformation. 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 model using the MIXED procedure 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, Δ_i, allows comparisons with the remaining models: $\Delta_i < 2$ suggests substantial support for the model, Δ_i between 4 and 7 suggests considerably less support for the model, and $\Delta_i > 10$ 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 rather than on just the highest ranked model by summing the Akaike weights (w_i) across all the models where the attribute occurred (Burnham and Anderson 2002).

Results

Seed Retention for Six Perennial Species 16 Weeks after Seeding

Out of 493,506 seeds estimated to have been broadcast on study plots, 109,567 (22%) were recovered using our sieving and elutriation methods in Phase II of the study (excluding plot #273). A portion of the seeds were impaired (9,172 seeds), but species still could be identified. The harrowed treatment, which increased surface roughness, doubled retention of all seeds in compacted areas. Trenches retained almost three times the number of seeds after 16 wks compared with compacted sites irrespective of the use of tackifier (Fig. 4).

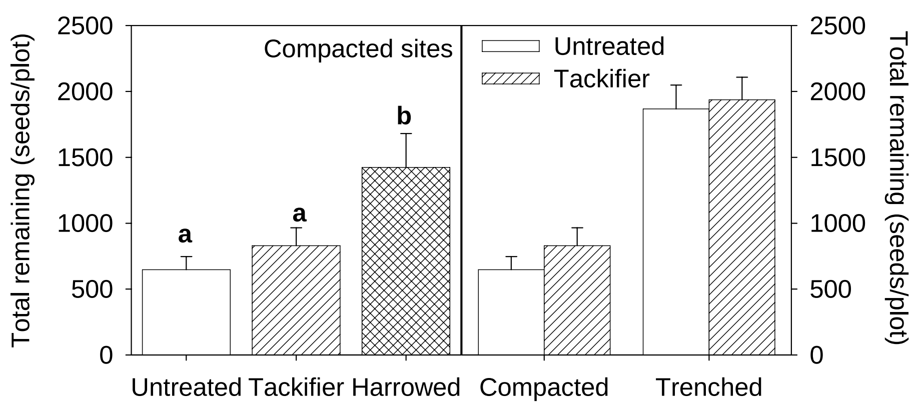

Figure 4. Number of seeds that remained on the experimental plots 16 wks after application on compacted and trenched sites at Fort Irwin National Training Center. For compacted sites (left), seed retention was increased by harrowing (Treatment effect, $F_{2, 39} = 9.93$, $P < 0.01$; means (± SE) with different letters are statistically different based on Tukey’s HSD). Tackifier did not enhance seed retention (right), but retention was greater on trenched sites than on compacted sites (Disturbance effect, $F_{1,52} = 10.75$, $P = 0.03$).

Expressed as the percentage of total seeds initially added to plots, *Atriplex* and *Isomeris* generally had the greatest seed retention on compacted sites. The large effect that harrowing had on total seed retention in compacted areas shown in Figure 4 primarily was driven by *Larrea, Ambrosia,* and *Hymenoclea* (Fig. 5). Similarly, the effect that trenched sites had on total seed retention compared with compacted sites—irrespective of the tackifier treatment— also was reflected in a large increase of *Larrea* and *Ambrosia* seeds (Fig. 6).

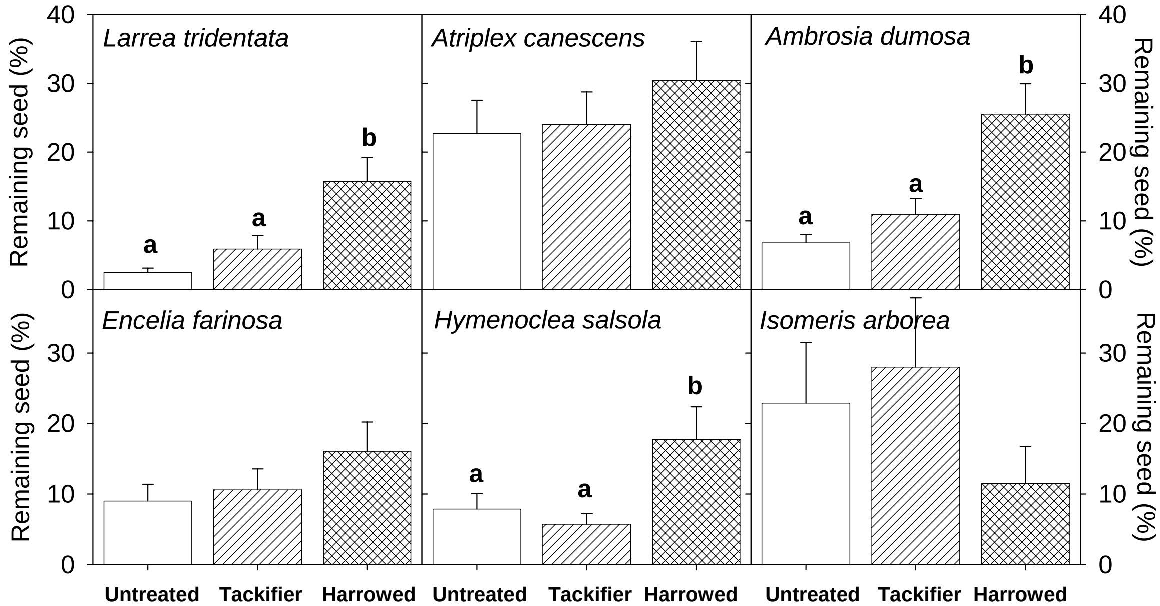

Figure 5. Percent of total intact seeds remaining after 16 wks for each species at compacted sites only (untransformed means ± SE) at the U.S Army National Training Center. Seed losses were significantly different among treatments for *Larrea* ($F_{2, 39}$ = 12.89, $P < 0.01$), *Ambrosia* ($F_{2, 39}$ = 8.28, $P < 0.01$), and *Hymenoclea* ($F_{2, 39}$ = 5.42, $P = 0.01$) but not for *Atriplex* ($F_{2, 39}$ = 1.45, $P = 0.25$), *Encelia* ($F_{2, 39}$ = 1.63, $P = 0.21$), or *Isomeris* ($F_{2, 39}$ = 1.58, $P = 0.22$). Bars with different letters are statistically different based on Tukey's HSD of arcsine-square root transformed data.

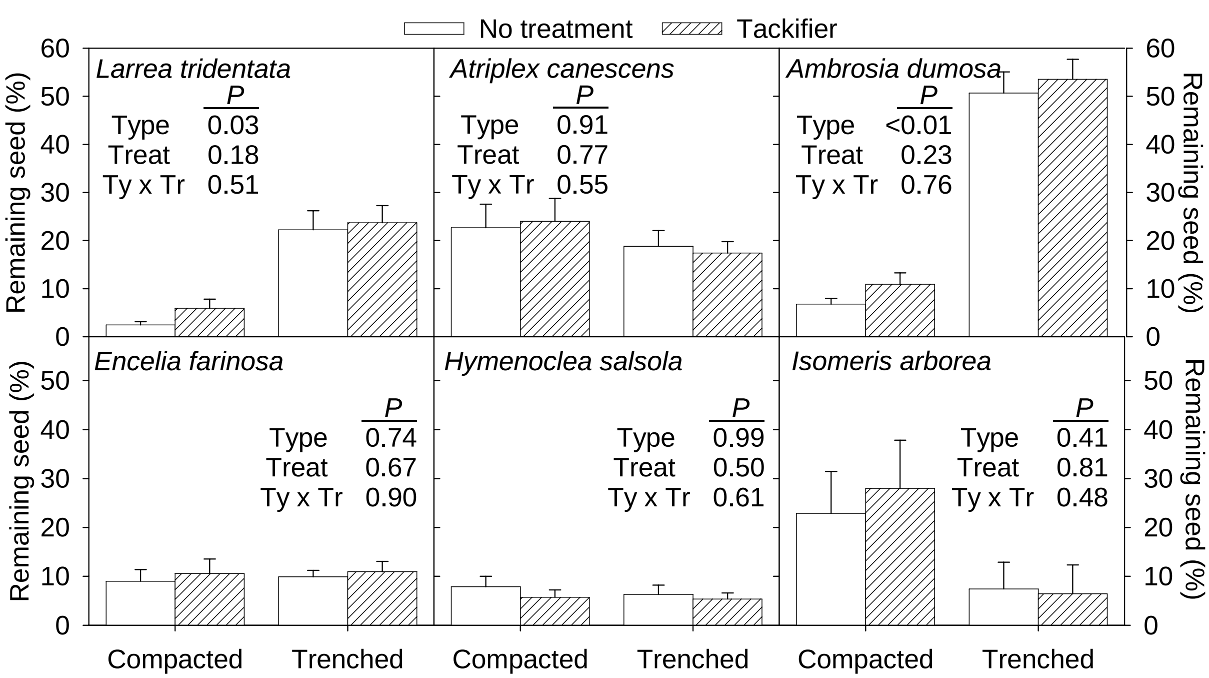

Figure 6. Percent of total intact seeds remaining after 16 wks for each species associated with trenched and compacted sites treated with tackifier (untransformed means ± SE) at the U.S Army National Training Center. Inset *P*-values test the difference between compacted and trenched sites (Type effect), the difference between tackifier and untreated treatments (Treat effect), and the interaction of Type and Treat (Ty × Tr) based on arcsine-square root transformed data.

Fates of Seeds

Seeds succumbed to a variety of fates, depending on the disturbance type, as well as the surface treatment. After totaling the number of seeds collected in traps, the seeds that established as seedlings (DeFalco *et al.* 2005) and the seeds that remained on plots after 16 wks, a large portion of the initial seeds broadcast were still unrecovered, ranging from an average of 68% to 74% in compacted areas and 55% to 68% on trenches (Table 2). Based on the estimated 6,669 seeds initially broadcast on each plot, we examined whether ant and rodent granivory, non-native plant competition and proximity to the undisturbed edge explained the fate of unrecovered seed. We expected that plots with a greater percentage of unrecovered seeds would have more nearby ant nests and/or rodent burrow entrances, more cover of annual plants (as a correlate of plant competition), and/or would be closer to the undisturbed edge. Distance to the edge was expected to be a better explanation than the ant or rodent models if the 12.5 m diameter distance that we used in the latter models did not adequately characterize ant and rodent activity.

Using the information–theoretic approach to determine the best model, we found that ants or rodents were the most plausible models explaining unrecovered seed, although the granivore models differed between compacted and trenched sites (Fig. 7). The best model on compacted sites included a quadratic relationship between unrecovered seeds and ant nests and the interaction between surface treatment and ant nests (Table 3). By summing w_i for each variable across all candidate models in which they occurred on compacted sites, we found the relative importance of surface treatment (0.9972) and number of ant nests (0.9336) were greater compared with *Messor pergandei* nests (0.0590) or rodent burrow entrances (0.0055). In contrast to compacted sites, trenched plots that had more rodent burrow entrances nearby generally had more unrecovered seed (Fig. 7, Table 3). Relative importance of rodent burrow entrances (0.9534) was greater than surface treatment (0.3969), ant nests (0.0484), or *Messor* nests (0.0138) on trenched sites. The cover of annual plants and distance to undisturbed edge had the

Table 2. The fates of seeds for six Mojave Desert species combined for surface treatments at compacted and trenched sites. Shown are means and percent of total seeds (in parentheses).

	Compacted			Trench	
	Untreated	Tackifier	Harrowed	Untreated	Tackifier
Total seeds broadcast	**6,669 (100)**	**6,669 (100)**	**6,669 (100)**	**6,669 (100)**	**6,669 (100)**
Trapped after 10 wks:*					
Intact	1,198 (18)	819 (12)	534 (8)	770 (12)	746 (11)
Impaired	33 (<1)	20 (<1)	17 (<1)	48 (<1)	36 (<1)
Established as seedlings	6 (<1)	3 (<1)	71 (1)	1 (<1)	1 (<1)
Remained on plots:					
Intact	646 (10)	828 (12)	1,422 (21)	1,867 (28)	1,937 (29)
Impaired	28 (<1)	38 (<1)	71 (1)	195 (3)	285 (4)
Total seeds unrecovered	**4,758 (71)**	**4,961 (74)**	**4,554 (68)**	**4,558 (68)**	**3,664 (55)**

*Values are seeds trapped after 10 wks reported in DeFalco *et al.* (2005) multiplied by 2.5 because traps covered 40% plot perimeter; thus, values estimate plot loss if traps covered 100% of plot perimeter.

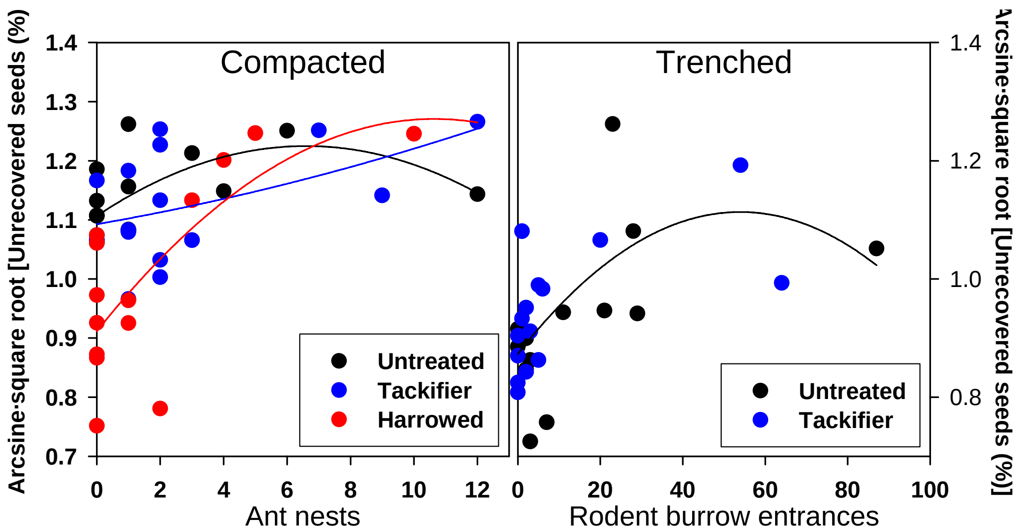

Figure 7. Percent of unrecovered seeds (arcsine-square root transformed) after 16 wks on compacted and trenched sites at U.S. Army National Training Center. Regressions represent harrowed (arcsine-square root [% seeds] = 0.9113+0.0676*Ant-0.0032*Ant^2; r^2 = 0.53), tackifier (arcsine-square root [% seeds] = 1.0927+0.0094*Ant+0.0003*Ant^2; r^2 = 0.24), and untreated treatments (arcsine-square root [% seeds] = 1.1066+0.0359*Ant-0.0027*Ant^2; r^2 = 0.36) on compacted sites (left). Treatments were combined on trenched sites (arcsine-square root [% seeds] = 0.8726+0.0089*Rodnt-0.0001*Rodnt^2; r^2 = 0.42; right).

Table 3. Analysis of unrecovered seeds on compacted and trenched sites as a function of plot attributes. Unrecovered seed was arcsine-square root transformed before analysis. Models are ranked by Δ_i. Only models with some level of support (Δ_i < 10) are presented. Akaike weights (w_i) were included for comparing the relative importance of the plot attributes. *Plot attributes: Trt = surface treatment; Ant = total ant nests; Mepe =*M. pergandei* nests; Rodnt = rodent burrow entrances.

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

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 models that had some support ($\Delta_i < 10$). Separate species analyses (not shown) reflected the results for the combined species analysis: the unrecovered seeds of *Ambrosia, Atriplex, Encelia, Hymenoclea,* and *Larrea* were positively related to the number of nearby ant nests on compacted sites, and unrecovered seeds of *Ambrosia, Atriplex, Hymenoclea, Isomeris,* and *Larrea* were positively related to the number of nearby rodent burrow entrances on trenched sites.

Conclusions

Consistent with the results of DeFalco *et al.* (2005), the compacted sites that were harrowed and the trenched sites in general retained the most seeds 16 weeks after seeds were broadcast in January 2005. Seeds were trapped in the furrows made on the harrowed compacted sites. Consequently, successful plant establishment occurred on those sites, despite heavy rains that otherwise may have washed away seeds after they were broadcast (DeFalco *et al.* 2005). Rainfall during the period January–May for the Barstow NE, California climate station [622 m (2,040 ft) elevation] was 123 mm, which was 273% of the long-term average for this station (http://www.wrcc.dri.edu/). Favorable plant establishment has been found in related studies where soils were harrowed in years with abundant rainfall (Snyman 2003, van den Berg and Kellner 2005). In addition, harrowing likely influenced the physical and hydrological properties of the soil by decreasing bulk density, increasing soil porosity, reducing rainfall run-off and enhancing infiltration (Osunbitan *et al*. 2005) and, thereby, encouraged seedling establishment. It remains to be seen whether ungerminated seeds would remain in place and survive long enough on harrowed compacted sites to take advantage of rainfall in subsequent seasons or years. It should be noted that while non-native annual plant abundance was generally low during this study, irrespective of harrowing on compacted sites (mean ± SD = 10.9 ± 9.9%), harrowing can increase the abundance of competitive non-native Mojave Desert annuals and potentially reduce the establishment of seedlings from the seed mix (S. Scoles *et al*, USGS, written communication). Therefore, invasibility of compacted sites should be evaluated before soil surface manipulation and seeding of compacted sites.

Seeds in the surface furrows that remained beyond the spring period of favorable temperature and soil moisture are vulnerable to desiccation, UV degradation, microbial decomposition, and seed predation, dispersal, or caching. Indeed, a large percentage of the seed that was unrecovered at the end of this study was positively related to the abundance of nearby ant nests supporting the assertion that ants may remove many seeds before conditions for germination are optimal (Anderson and Ostler 2002). When we made daily observations of ant foraging behavior in February and March 2005, we observed lower ant activity when ground surface temperatures dropped below 20 °C (L. DeFalco, unpubl. data, 2005). Thus, in severely degraded compacted sites where intense management is permissible, we suggest that harrowing and seeding on compacted sites start as early as October when average soil temperatures begin to drop below 20 °C (based on temperatures at the Barstow NE, California station) and when winter frontal storms provide adequate soil moisture necessary for germination. It is important to note that while the harrowing performed in this study was a light surface treatment, the practice of surface ripping that is sometimes prescribed to alleviate compaction often mixes soil layers and can negatively alter soil hydrologic properties that may challenge plant establishment (Caldwell *et al.* 2006).

Although successful at reducing seed losses after 10 weeks on compacted sites (DeFalco *et al.* 2005), tackifier did not enhance seed retention on compacted sites 16 weeks after application. The tackifier we applied (Soil-Sement) typically is used for reducing dust emissions from dirt roadways, but ITAM was interested in its potential to hold seeds in place on the soil surface until climate conditions were favorable for germination. Tackifier was applied prior to the exceptional rainfall period during this study. The tackifier's effect was diminished on compacted sites before heavy rains fell in the third week, but tackifier is water soluble and continued to be mobilized off of the plots with the seeds during subsequent rain events. Seasonality of rainfall should be considered when using tackifier in future seed applications on compacted sites because its effectiveness likely will be reduced during high intensity summer storms of short duration (*e.g.*, July through September). In addition, tackifier may be more successful if used only to retain seeds for short time intervals during periods of low rainfall (*e.g.,* May through June). Additional studies may be needed to understand whether a greater concentration of tackifier or higher rates of application would yield greater success, given the variability in climate and soils at the NTC.

In contrast to compacted sites, tackifier was largely ineffective on trenched sites, likely due to the surface roughness inherent at these sites. Trenches, in general, had more seed retention and a lower percentage of unrecovered seeds compared with compacted sites. Yet the percentage of unrecovered seeds was positively related to the presence of rodents, thereby illustrating the impact these seed predators have on the seeds that are broadcast during rehabilitation efforts. It is important to note that some portion of seeds that were not recovered during this study were cached by rodents and potentially will germinate within or adjacent to trenched sites when germination conditions are optimal (Vander Wall 1990). However, the vast failure of seedling establishment on trenched sites (DeFalco *et al*. 2005) suggests either that rodents were redistributing considerably more seeds than our experimental manipulations could account for, or that factors other than granivore activity that we did not measure may hinder the rehabilitation at trenched sites. The mixing of soil layers during trench development and removal may be similar to the process of topsoil collection and reapplication during reclamation in that soil organic matter, nutrient availability and chemistry are altered and potentially beneficial mycorrhizae and microbial biomass are reduced (Abdul-Kareem and McRae 1984; Visser *et al.* 1984*a,b*; Johnson *et al.* 1991; Harris *et al.* 1993; Stahl *et al.* 2002). Remediation of soils (*e.g*., addition of fertilizers, mycorrhizae, or other soil amendments) may be necessary to enhance soil conditions and accelerate seedling establishment in areas disturbed by trenching activity.

Although germination requirements among the six species were not evaluated directly in this study, differences in seedling establishment among the species on harrowed sites (DeFalco *et al.* 2005) suggest that seed mixes prepared for rehabilitation should not only consider the type of disturbance being seeded, but also the timing of application (Table 4). For seed species that potentially will remain ungerminated on the re-seeded site for many months after application, alternative seeding prescriptions, such as drill seeding or imprinting, may be necessary to ensure good seed-soil contact (Montalvo *et al.* 2002, Snyman 2003, van den Berg and Kellner 2005), and seeds are buried so they are inaccessible to ants. If it is undesirable to mechanically incorporate seeds into the soil to make them inaccessible to granivores [*e.g*., in habitat for sensitive species such as the desert tortoise (*Gopherus agassizii*)], surface seeding should occur as close as possible to the time when conditions are optimal for germination. According to the

Table 4. Potential seeding periods and/or optimal air temperatures for the six species based on available literature (referenced by superscripted letters). Optimal planting depth for all species typically is 1 cm deep[e,f,h,o].

Species	Optimal period and/or air temp (°C)
*Larrea tridentata**	Mid-June to late-Sept [a,c,n] (21–29 [b,d,i,j])
Ambrosia dumosa‡	August to September[a,c] (15–30 [e,j])
Hymenoclea salsola	15–30 [f,i,,j]
Atriplex canescens	Winter or summer[k] (5-15, 2–40 [g,i ,j,l ,p])
Isomeris arborea	5 – 15 [h,j]
Encelia farinosa†	15[q]

‡ Unfavorable germination when temperature[e] = 2 °C or 5 °C.

*Unfavorable germination in summer[m,o] when T_{min}>30 °C or in winter[o, n] when T_{min}<8–10 °C.

† Unfavorable germination when air temperature [q] < 5 °C or > 25 °C.

[a]Ackerman et al 1979; [b]Barbour 1968; [c]Beatley 1974a; [d]Kay et al. 1977a; [e]Kay et al. 1977b; [f]Kay et al. 1977c; [g]Kay et al. 1977d; [h]Kay et al 1977e; [i]Kay et al. 1984; [j]Kay et al 1988; [k]Meyer and Carlson 2007; [l]Mikhiel *et al.* 1992; [m]Sheps 1973; [n]Went 1948; [o]Went and Westergaard 1949; [p]Springfield 1969; [q]Szarek et al 1996.

Barstow NE climate station, large rainfall events occurred on February 11 (12.7 mm), February 18–19 (15.75 mm), February 22–23 (14.23 mm) and March 4–5 (33.78 mm) during this study. Average soil temperatures for the 7 days following these early spring storms ranged between 10 °C and 15 °C. The greatest establishment of *Encelia* seedlings in March (DeFalco *et al.* 2005) reflects the cooler germination temperature for this early colonizing species (Szarek *et al.* 1996). *Atriplex* has been found to have broad and potentially highly variable germination requirements (Kay *et al.* 1977*d*) which may make it a suitable species in seed mixes applied during winter or summer (Meyer and Carlson 2007). Other research has shown that *Isomeris* should be planted for winter germination (Kay *et al*. 1977*e*).

Not surprisingly, *Larrea* and *Ambrosia* either did not germinate or had low germination during the late winter/early spring period of this study. According to seed testing results for the seeds used in this study, the viability of *Ambrosia* and *Larrea* were 10.29% and 21.95%, respectively. Seeding recommendations for these and other species may require higher application rates to overcome lower seed fill or germination percentages (Kay *et al* 1984, 1988). These species also are known to germinate primarily in July through September when monsoonal storms deliver sufficient rainfall to maintain soil moisture while overcoming the high evaporation demand associated with elevated summer air temperatures (Barbour 1968, Kay *et al*. 1977*a,b,c*). Germination trials at the NTC in 2001 (Ostler and Anderson 2003) demonstrated that when seeds of *Larrea* and *Ambrosia* were distributed and irrigated in March, germination was enhanced beneath a plastic mulch cover that increased soil temperatures by 10 °C over the 15 °C average for the site. Germination for *Larrea* and *Ambrosia* was even higher in similar trials performed in April where plastic mulch increased soil temperatures by 8 °C to 10 °C over the 22 °C average for the sites studied (Ostler and Anderson 2003). Application of these species' seeds in winter increases their risk of removal during the subsequent winter months (for example, by wind or water redistribution, granivores, decay, desiccation, and aging) and decreases their likelihood of germination. In contrast, if species with higher germination temperature requirements were delivered to sites in June and early July—just prior to the optimal germination and establishment conditions—predation could be minimized and success optimized. Multiple applications of different seed mixes, each with their specific germination temperatures matched with the timing of application, may be more successful than a single seed application of species representing a diversity of germination requirements; however, these contrasting approaches need further evaluation. In conclusion, careful consideration of the species-specific requirements for germination of Mojave Desert perennials as well as the constraints placed on seed densities by granivores and the unique characteristics of disturbances themselves will help develop future compositions of seed mixes and the timing of their application at the NTC.

Acknowledgments

We are grateful to many individuals that assisted during Phase II of this project including Kyla Bauer, Jeff Kane, Martin Kang, Melissa Nicklas, Jessica Ramirez, Bryant Reynolds, Sara Scoles–Sciulla, Justin Sharick, Anine Smith, Karissa Smith, and Amy Trexler. We especially thank Ruth Sparks and Matt Hamilton at Integrated Training Area Management for their support and logistical assistance on site. Comments on earlier drafts by David Housman, Ruth Sparks, Karen Phillips, Jan van Wagtendonk, Kathy Longshore, and Julie Yee improved the final report.

References Cited

Abdul-Kareem, A.W. and S.G. McRae. 1984. The effects on topsoil of long-term storage in stockpiles. *Plant and Soil* 76:357-363.

Ackerman, T.L. 1979. Germination and survival of perennial plant species in the Mojave Desert. *The Southwestern Naturalist* 24:399-408.

Anderson, D.C. and W.K. Ostler. 2002. Revegetation of degraded lands at U.S. Department of Energy and U.S. Department of Defense installation: strategies and successes. *Arid Land Research and Management* 16:197-212.

Barbour, M.B. 1968. Germination requirements of the desert shrub *Larrea divaricata*. *Ecology* 50: 679-685.

Beatley, J.C. 1974. Phenological triggers and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55:856-863.

Brown, J.H., D.W. Davidson, and O.J. Reichman. 1979. An experimental study of competition between seed-eating desert rodents and ants. *American Zoologist* 19:1129-1143.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel Inference: A Practical Information-Theoretic Approach, 2nd Edition. Springer-Verlag, New York, NY. 488 p.

Caldwell, T.G., E.V. McDonald, and M.H. Young. 2006. Soil disturbance and hydrologic response at the National Training Center, Ft. Irwin, California. *Journal of Arid Environments* 67:456-472.

DeFalco, L., J. Kane, M. Nicklas, and T. Esque. 2005. Assessment of seed banks associated with disturbances at Ft. Irwin National Training Center, California. Final report presented to

U.S. Army National Training Center, September 22, 2005: Integrated Training Area Management, 23 pp.

Harris, J.A., P. Birch, and K.C. Short. 1993. The impact of storage of soil during opencast mining on the microbial community: A strategist theory interpretation. *Restoration Ecology* 1:88-100

Johnson, D.B., J.C. Williamson, and A.J. Bailey. 1991. Microbiology of soils at opencast coal sites. I. Short- and long-term transformations in stockpiled soils. *Journal of Soil Science* 42:1-8.

Kay, B.L., C.M. Ross, and W.L. Graves. 1977a. Creosotebush. UC Davis, Agronomy and Range Science. *Mojave Restoration Notes* 9:1-10.

Kay, B.L., C.M. Ross, and W.L. Graves. 1977b. Burrobrush. UC Davis, Agronomy and Range Science. *Mojave Restoration Notes* 1:1-6.

Kay, B.L., C.M. Ross, and W.L. Graves. 1977c. White Burrobush. UC Davis, Agronomy and Range Science. *Mojave Restoration Notes* 7:1-5.

Kay, B.L., C.R. Brown, and W.L. Graves. 1977d. Fourwing Saltbush. UC Davis, Agronomy and Range Science. *Mojave Restoration Notes* 17:1-12.

Kay, B.L., C.R. Brown, and W.L. Graves. 1977e. Bladderpod. UC Davis, Agronomy and Range Science. *Mojave Restoration Notes* 8:1-4.

Kay, B.L., C.C. Pergler, and W.L. Graves. 1984. Storage of seed of Mojave Desert shrubs. *Journal of Seed Technology* 9:20-28.

Kay, B.L, W.L. Graves, and J.A. Young. 1988. Long-term storage of desert shrub seed. *Mojave Restoration Notes* 23:1-22

Meyer, S.E., and S.L. Carlson. 2007. Seed germination biology of Intermountain populations of fourwing saltbush (*Atriplex canescens*: Chenopodiaceae). *In* Sosebee, R.E.; D.B. Wester, C.M. Britton, D.E. McArthur, S.G. Kitchen. Proceedings: Shrubland dynamics – fire and water, Lubbock, TX, August 10–12, 2004.. RMRS-P-47. Fort Collins, CO: U.S. Forest Service, Rocky Mountain Research Station. p. 153-162.

Mikhiel, G.S., S.E. Meyer, and R.L. Pendleton. 1992. Variation in germination response to temperature and salinity in shrubby *Atriplex* species. *Journal of Arid Environments* 22:39-49.

Montalvo, A.M., P.A. McMillan, and E.B. Allen. 2002. The relative importance of seeding method, soil ripping, and soil variables on seeding success. *Restoration Ecology* 10:52-67.

Neter, J., M.H. Kutner, C.J. Nachtsheim, and W. Wasserman. 1996. Applied linear regression models. Third edition: Chicago, IL, USA. Richard D. Irwin, Inc., 720 p.

Ostler, W.K. and D.J. Anderson. 2003. Diagnostic tools and reclamation technologies for mitigating impacts of DOD/DOE activities in arid areas. Final report delivered to SERDP Project No. CS-1131. URL, http://www.osti.gov/bridge/.

Osunbitan, J.A., D.J. Oyedele, and K.O. Adekalu. 2005. Tillage effects on bulk density, hydraulic conductivity and strength of a loamy sand soil in southwestern Nigeria. *Soil & Tillage Research* 82:57-64.

Sheps, L.O. 1973. Survival of *Larrea tridentata* S. & M. seedlings in Death Valley National Monument, California. *Israel Journal of Botany*:8-17.

Snyman, H.A. 2003. Revegetation of bare patches in a semi-arid rangeland of South Africa: an evaluation of various techniques. *Journal of Arid Environments* 55:417-432.

Springfield, H.W. 1969. Temperatures for germination of fourwing saltbush. *Journal of Range Management* 22:49-50.

Stahl, P.D., B.L. Perryman, S. Sharmasarkar, and L.C. Munn. 2002. Topsoil stockpiling versus exposure to traffic: a case study on *in situ* uranium well fields. *Restoration Ecology* 10:129-137.

Szarek, S.R., S. Cole, G. Ortiz, and S. Kaufman. 1996. Factors influencing the germination of the desert shrub Brittlebush (*Encelia farinosa,* Asteraceae). *American Journal of Botany* 83 (Suppl.): 88.

van den Berg, L. and K. Kellner. 2005. Restoring degraded patches in a semi-arid rangeland of South Africa. *Journal of Arid Environments* 61:497-511.

Vander Wall, S.B. 1990. Food hoarding in animals: Chicago, IL, USA, University of Chicago Press, 445 p.

Vander Wall, S.B., T.C. Esque, B.A. Waitman, D.F. Haines, and M.G. Garnett. 2006. Joshua tree (*Yucca brevifolia*) seeds are dispersed by seed-caching rodents. *Ecoscience* 13(4): 593-543.

Visser, S., J. Fujikawa, C.L. Griffiths, and D. Parkinson. 1984a. Effect of topsoil storage on microbial activity, primary production and decomposition potential. *Plant and Soil* 82:41-50.

Visser, S., C.L. Griffiths, and D.Parkinson. 1984b. Topsoil storage effects on primary production and rates of vesicular-arbuscular mycorrhizal development in *Agropyron trachycaulum. Plant and Soil* 82:51-60.