Assessment of Seed Banks Associated with Disturbances at Fort Irwin National Training Center, California

Prepared for:

Integrated Training Area Management
US Army National Training Center
Fort Irwin, California
Contact: Ruth Sparks; voice: 760-380-3169

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

WESTERN ECOLOGICAL RESEARCH CENTER

USGS
science for a changing world

Assessment of Seed Banks Associated with Disturbances at Fort Irwin National Training Center, California

Prepared by
Lesley DeFalco, Jeffrey Kane, Melissa Nicklas and Todd Esque

United States Geological Survey
Western Ecological Research Center, Las Vegas Field Station
160 N. Stephanie St., Henderson, Nevada 89074
voice: 702-564-4507; fax: 702-564-4600; email: Lesley_Defalco@usgs.gov

Final Report Prepared for
Integrated Training Area Management
U. S. Army National Training Center
Fort Irwin, California
Contact: Ruth Sparks; voice: 760-380-3169

September 22, 2005

U.S. DEPARTMENT OF THE INTERIOR
GALE A. NORTON, SECRETARY

U.S. GEOLOGICAL SURVEY
P. Patrick Leahy, Acting Director

The use of firm, trade, or brand names in this report is for identification purposes only and does not constitute endorsement by the U.S. Geological Survey.

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, CA 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. Large-scale military operations at the NTC modify vegetation and soils, reducing the re-establishment of vegetation. The Integrated Training Area Management (ITAM) program at NTC monitors and quantifies the impact that training has on the condition of the land. In an effort to rehabilitate areas that have been degraded, ITAM uses a variety of techniques including supplementing the natural seed banks through broadcast seeding. Although climatic variation is thought to be largely responsible for variability in reseeding success, there are no quantitative explanations for successes or failures.

This report summarizes results from experiments conducted on two types of disturbances commonly found at the NTC: compacted sites where concentrated and heavy vehicular use has compacted soils and removed vegetation, and tank trenches where soil has been excavated to a depth of ~ 6 feet for tank deterrence maneuvers and subsequently backfilled. In the first study, we examined the distribution of the existing seed bank at locations 10 and 20 m inside the compacted and trenched sites and at nearby undisturbed desert shrub habitat. In the second study, we tracked the movement of seeds of six perennial species commonly used in rehabilitation efforts and determined whether tackifier and surface ripping retain seeds on the soil surface and assist re-establishment.

More than 11,000 seeds were germinated from trenched and compacted sites and identified during a four-cycle seed bank assay. Seedlings represented 18 native annuals (including one that could only be identified to the Family Boraginaceae and another to the genus *Cryptantha*), 6 non-native annual and 6 native perennial species. Compared with nearby undisturbed sites, annual seed densities and species richness were lower inside the compacted sites but higher inside the trenches. Seed densities of perennials, while more variable than annuals, declined inside the compacted and trenched sites to < 1 seed/m^2. The densities of annual and perennial seeds at compacted sites were positively related to litter cover and the size of the nearest ant nest but negatively related to micro-relief. Annual seed densities on trenched sites were positively related to litter and the percent fine sand-silt-clay fraction, but perennial seed densities on trenched sites were not related to any of the variables measured. The combination of litter that was largely comprised of stems and inflorescences of the spring's dominant annual, *Cryptantha angustifolia* and the foraging activities of a common black harvester ant (*Messor pergandei*) likely contributed to the abundance of annuals in the seed bank.

Ten weeks after six species of perennial seeds (*Larrea tridentata*, *Ambrosia dumosa*, *Hymenoclea salsola*, *Encelia farinosa*, *Atriplex canescens* and *Isomeris arborea*) were broadcast on 4 m^2 plots in trenched and compacted sites, 26,731 seeds were recovered from seed traps. Seeds were lost from plots rapidly in the first 3 weeks after seeding and then losses diminished after 4 to 6 weeks. Losses of perennial seeds broadcast on plots were reduced by surface roughness of soil, whether created by ripping with a tractor or characteristic of the trenches themselves. Among the species with the greatest losses on compacted sites, *Larrea*, *Ambrosia* and *Encelia* retained more seeds when tackifier was sprayed after seeds were broadcast, but *Larrea* and *Ambrosia* had even fewer losses when the soil surface was ripped prior to seeding. Seed losses of other species were either marginally lower (*Atriplex*) or not significantly diminished (*Hymenoclea* and *Isomeris*) on compacted sites with either tackifier or ripping. Tackifier reduced losses of *Larrea* on compacted sites but had little effect on trenched sites because trenches without tackifier already had low losses. We observed emptied seed caryopses of *Encelia* and *Atriplex* on nearby ant nest disks, discarded husks of *Isomeris* seeds close to seed traps and *Isomeris* seedlings emerging from nearby small mammal caches. *Messor pergandei* were observed collecting all six species of seeds that were broadcast. In general, the role of granivores in the movement and removal of seeds used for rehabilitation deserves further investigation.

Following above-average winter rainfall, establishment of perennial seedlings for all six species was highest on ripped, compacted sites by late March. The highest establishment was for *Encelia* followed in decreasing order by *Hymenoclea*, *Larrea*, *Atriplex*, *Ambrosia* and *Isomeris*. By early May, seedling numbers declined uniformly across all species to < 5 seedlings/plot as increasing daytime ambient temperatures likely reduced soil moisture and increased water stress. This level of establishment was achieved as a "best case scenario" during one of the highest rainfall years on record for many regions of the Mojave Desert. The remaining seeds swept from plots at the end of the experiment will be counted in the future to shed light on whether the sites and treatments with low seed losses (compacted sites with tackifier and trenched sites in general) retained seeds for germination in following years or whether granivores removed significant numbers of seeds from plots.

Introduction

Disturbances to soil surfaces can have enduring effects on the diverse vegetation communities in the Mojave Desert. Estimated recovery rates of desert lands that have been disturbed by motorized vehicle use range from decades to centuries (Lovich and Bainbridge 1999). Because the upper portion of desert soils contains the majority of the seed bank and a large percentage of the organisms that are associated with nutrient cycling (Foth and Turk 1972, Childs and Goodall 1973, Reichman 1984), surface disturbance can have a profound impact on the regeneration of degraded desert plant communities.

Large-scale military operations at the National Training Center (NTC) in Fort Irwin, California adversely impact both vegetation and soil characteristics, potentially reducing re-establishment of vegetation. The Integrated Training Area Management (ITAM) program at Fort Irwin monitors and quantifies the impact that training has on the condition of the land and seeks methods to rehabilitate areas of the NTC that have been degraded. Some of this rehabilitation is done through supplementing natural seed banks by broadcast seeding using perennial plant species. However, monitoring at rehabilitated sites indicates that reseeding has had variable results, and although climatic variation is thought to be largely responsible for the variability, there have been no quantitative explanations for successes or failures.

When vegetation is lost through soil surface disturbance, seed banks are not readily replenished. Consequently, seeds from nearby undisturbed areas must be moved onto the disturbed site by wind or, for some plant species with large seeds that are not easily dispersed, by ants and small mammals (Brown *et al*. 1979). ITAM regularly reseeds areas disturbed by military training to accelerate the establishment of vegetation. These reseeding efforts can be improved through a better understanding of how military training sites–such as heavily compacted, high use areas and tank trenches–impact the natural seed bank. Furthermore, little is known about the dispersal of seeds across the disturbed-undisturbed boundary, or whether the shapes of some disturbances (*e.g*., linear vs. broad disturbances) have different seed dispersal dynamics, thereby requiring less intervention from ITAM land managers. Results of this study will help the ITAM office prioritize the disturbed sites to reseed, and determine which combination of plant species and surface treatments can be used most effectively in re-vegetation efforts. Assessing how surface disturbances impact native seed banks and determining the efficacy of methods for re-vegetating disturbed areas are essential to minimizing the impact of future disturbances and for directing rehabilitation efforts.

This study was conducted at field sites representing two types of disturbances: sites compacted by heavy vehicle use and sites trenched to create tank obstacles which were subsequently refilled. For both types of disturbances, this study examined the distribution of the seed bank by comparing the seed densities at the edge of the disturbance with those inside the disturbance. Whereas the role of "seed rain" in regenerating plant communities has been determined using seed traps (Jensen 1998), the application of such traps to monitor the movements of seeds has not been widely used in desert rehabilitation projects. Seed trap arrays can help determine the identity and quantity of seeds in the community as well as the timing of seed arrival (Page *et al*. 2002). We modified this approach to examine the movement of seeds following reseeding and to determine which surface treatments reduce seed losses. Specifically, this study addresses the following questions: 1) Are the natural density and species richness of seeds impacted by disturbance type (*i.e*., compacted sites vs. tank trenches) or by the dispersal distance into the disturbance?, 2) Are patterns in natural density and species richness influenced by soil texture, soil compaction, shrub cover, litter cover and/or micro-relief?, 3) What is the fate of seeds that are broadcast on compacted and trenched sites?, and 4) Does ripping the soil surface or applying tackifier reduce seed losses on disturbed sites?

Methods

Study sites

Study areas consist of three compacted sites and three trenched sites (Figure 1, Table 1). Compacted sites are expansive areas which were heavily compacted by recurring vehicular traffic (Figure 1 A-C). The compacted sites are flat with slopes ranging from 2-3% (Whale and Vehicle Maintenance sites) to 7% (Racetrack Site) and low micro-relief as defined as the roughness of the soil surface that is detected within 1 m^2 plots (Table 1). While cobbles are prevalent at the Vehicle Maintenance Site, the Whale and Racetrack sites have greater proportions of coarse sand and fine gravel, respectively. Litter is minimal with only scattered perennial individuals including *Eriogonum fasciculatum*, *Larrea tridentata*, *Croton californica*, *Stephanomeria pauciflora* and *Hymenoclea salsola*, which were likely adult plants that endured repeated vehicular impacts and survived by crown-sprouting. Annual species observed during the study included *Ambrosia acanthicarpa*, *Cryptantha angustifolia*, *Pectocarya heterocarpa*, *Amsinckia tessellata*, *Astragalus acutirostris*, *Lupinus humistratus* and the non-native species *Schismus barbatus*, *Salsola tragus*, *Erodium cicutarium*, and *Bromus madritensis* ssp. *rubens*.

In contrast to the compacted sites, the trenched sites are narrow, linear features where subsoil layers have been mixed with topsoil to a depth of ~6 feet (R. Sparks, pers. comm.). Trenched sites have slopes ranging from 9-10% (LF6 and Peanut) to 17% (Crash Hill), but with consistently higher within-plot micro-relief of 9% compared with compacted sites. Soil compaction in trenches is generally lower than compacted sites (*i.e.*, greater penetration depth) and litter cover is slightly higher. Course sand and fine gravel predominate with a general absence of cobbles. Annual and perennial species composition is similar to compacted sites, perennial cover is low (< 1%) and both native and non-native annual species co-occur.

Part I — Impact of disturbance type and distance from edge on natural seed banks

Baseline seed bank samples were collected on trenched and compacted sites on October 24-29, 2004. Within each of the six disturbed sites, 10 sampling points were randomly selected at each of two distances from the disturbance edge (10 and 20 m) plus 10 control sampling points on nearby less disturbed areas for a total of 30 sampling points/site (N = 180 across the six sites). The average width of the trenches was 40 m, and this distance was used as the standard to determine the two edge distances to sample in the trenches and compacted sites (*i.e.*, 20 m was the greatest distance from either edge and the approximate mid-point of the trenches). The control sampling points were randomly placed in adjacent undisturbed areas set 20 m from the edge of each compacted and trenched site.

Prior to collecting seed bank samples, shrub cover (%), litter cover (%), micro-relief (%), soil penetration (cm), and the distance to and size of active harvester ant nest disks were measured for each 1 m^2 sampling plot (Table 1). Shrub and litter cover were determined by ocular estimate. Micro-relief was quantified with a modified contact profile meter, and the coefficient of variation (standard deviation ÷ mean × 100%) was calculated for 9 points within each plot.

Figure 1. Replicated compacted and trenched sites selected to understand seed bank dynamics associated with disturbances at Fort Irwin NTC. Compacted sites include A) Vehicle Maintenance (0547472 E 3913594 N), B) Whale (0514034 E 3922508 N), and C) Racetrack (0547389 E 3897189 N). Trenched sites are D) Crash Hill (0525939 E 3918707 N), E) LF6 (0538935 E 3914573 N) and F) Peanut (0540884 E 3911366 N).

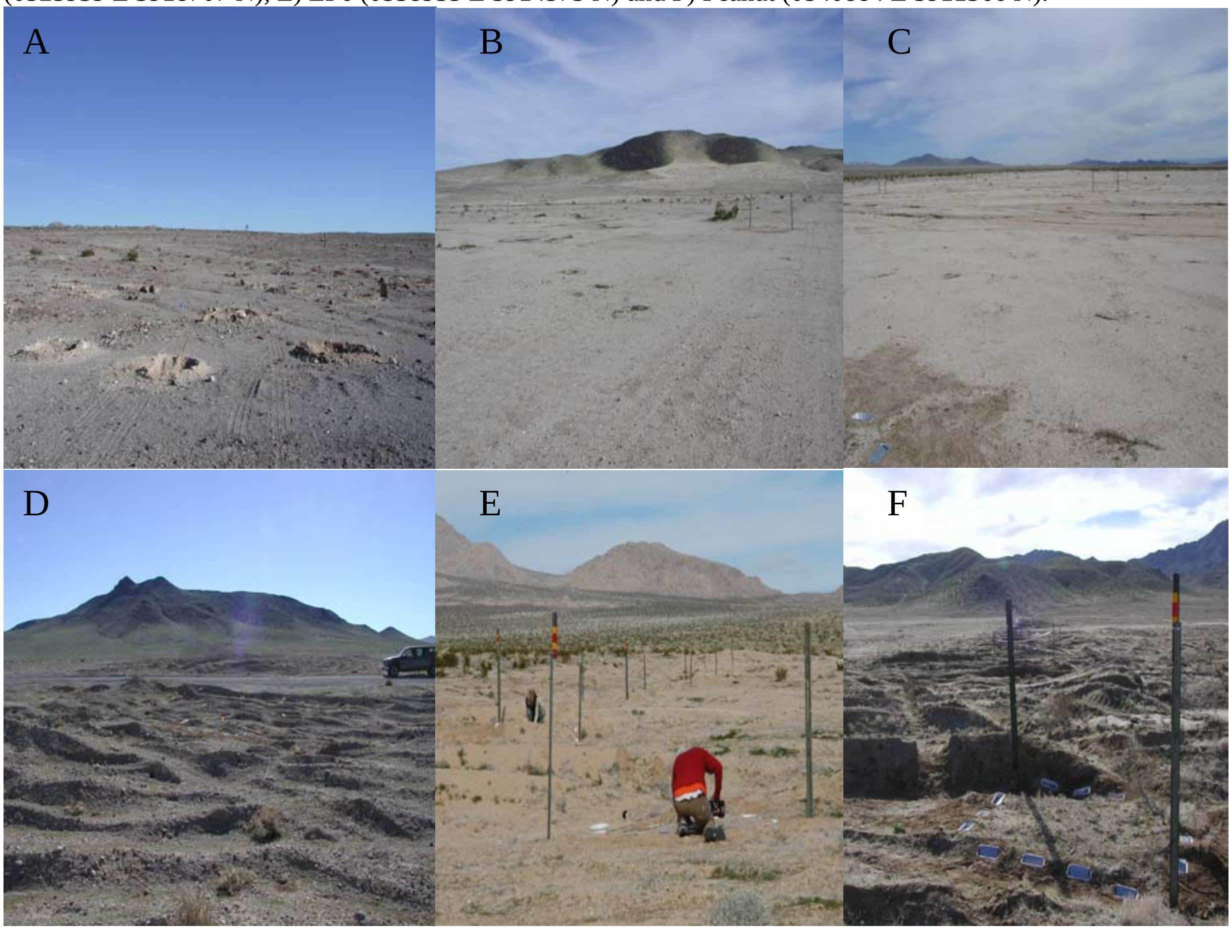

Table 1. Plot-level characteristics for compacted (RT=Racetrack, VM=Vehicle Maintenance, Wh=Whale) and trenched sites (CH=Crash Hill, LF=LF6, PN=Peanut) at US Army NTC measured during fall 2004 (see description of measurements under "Part I"). Values are means for $1\ m^2$ plots averaged over 10 and 20 m distances from edge into the disturbances. Significantly different sites are represented with different superscripted, lowercase letters.

					Particle size distribution (%)						Ant disk	
	Micro (%)	Lit (%)	Slope (%)	PeneD (cm)	fine sand, silt, clay	med sand	course sand	fine gravel	course gravel	cobble	Diam (cm)	Dist (m)
Compacted												
RT	2^{b}	3^{c}	3^{c}	10^{b}	7^{c}	3^{a}	23^{b}	60^{a}	6^{b}	$<1^{a}$	57^{b}	12^{ac}
VM	6^{ac}	4^{cd}	7^{b}	13^{b}	14^{b}	12^{c}	21^{b}	17^{d}	19^{a}	22^{b}	35^{abc}	16^{a}
Wh	3^{bc}	1^{d}	2^{c}	17^{cd}	15^{b}	9^{ab}	46^{a}	27^{bc}	3^{c}	$<1^{a}$	23^{a}	8^{bc}
Trenched												
CH	9^{a}	3^{c}	17^{a}	20^{ad}	14^{b}	10^{ac}	28^{b}	34^{b}	14^{a}	$<1^{a}$	33^{c}	17^{a}
LF	9^{a}	9^{bc}	9^{b}	19^{cd}	14^{b}	11^{ac}	48^{a}	25^{c}	1^{d}	$<1^{a}$	46^{b}	7^{bc}
PN	9^{a}	11^{a}	10^{b}	26^{a}	29^{a}	18^{d}	30^{b}	20^{cd}	3^{c}	$<1^{a}$	47^{b}	6^{b}

Micro = micro-relief (coefficient of variation), Lit = litter, PeneD = penetration depth, Diam = diameter of closest ant nest disk, Dist = distance to closest ant nest disk.

A dynamic penetrometer was used by dropping a 2 kg weight 10 times from a height of 40 cm (Herrick and Jones 2002) and measuring the resulting depth of penetration into the soil as an indicator of compaction. The distance to the closest harvester ant nest disk, the disk diameter and ant species were identified. A soil sample collected adjacent to the sampling plot was analyzed for particle size distribution (= soil texture). Soils were dried in a convection oven at 50° C for 24 hr. We used USDA particle size classification for approximating particle-size limits (Gee 2002). Cobbles larger than 3 cm were removed and remaining soil passed through four stacked sieves and shaken on a shaker table for 10 min. Fractions were weighed and expressed on a percent mass basis. The resulting fractions correspond to fine sand, silt and clay (< 0.25 mm), medium sand (0.25 - 0.50 mm), course sand (> 0.50 - 2.0), fine gravel (> 2.0 - 8.0 mm), course gravel (> 8.0 mm – 3 cm) and cobbles (> 3 cm).

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

The seed bank assay was modified from methods developed for the Great Basin (Young et al. 1969, Young and Evans 1975, Young et al. 1981). Each of the collected soil/seed/litter samples was placed in one or more 6" bulb pots lined with weed blocker cloth to reduce soil loss. Each pot contained 118 ml (½ cup) of soil/litter sample with 59 ml (¼ cup) of vermiculite. Multiple pots were used if the volume of a sample was greater than 118 ml. All pots were placed on a bench in the greenhouse (Figure 2) and subjected to four alternating wet-dry cycles known to promote germination of seeds (Meyer and Poljakoff-Mayber 1982, Baskin and Baskin 1998), including those of desert species (Esque 2004). The first wetting phase began with tap water (November 1- December 14, 2004). Pots were watered with a hand-held sprayer to maintain pot capacity (*i.e.*, water was applied until it drained from the bottom, but no standing water was present). Watering occurred daily, but when evaporative demand decreased due to cooler temperatures and heavy cloud cover, watering frequency was adjusted accordingly. The second wetting phase began on January 4, 2005 and extended until March 11, 2005 as we did not want to prematurely begin dry- down when cotyledons of perennials continued to emerge. A third wetting phase (March 28 – May 4, 2005) occurred with the initial addition of 50 mL of a 0.01 M solution of potassium nitrate followed by daily watering with tap water. Similarly, the fourth and final wetting phase (May 23 – June 28, 2005) occurred with the addition of 50 mL of a 6.5×10^{-4} M solution of gibberellic acid. All pots were air dried between wetting phases. During each wetting phase, seedlings were counted and harvested as soon as they could be identified. Seedlings of unknown identity were transplanted to pots and given time to develop so they could be identified to species.

Figure 2. Seed bank assay in the greenhouse. Soils collected from the field were subjected to four wetting cycles, and the seedlings that germinated were counted and identified before they were removed. Seed bank samples reflected numerous annual plants and few perennials. Cotyledons of plants that were too small to determine species were transplanted to grow-out pots for later identification.

Part II — Fate of perennial plant seeds following reseeding

After baseline seed bank data were collected, we established study plots on January 19-21, 2005 within the same compacted and trenched sites to determine whether ripping and tackifier treatments reduced seed loss of perennial species. At each of the three compacted sites, 15 sampling plots (2 m × 2 m each with a minimum distance apart of 25 m) were randomly selected and assigned a treatment of tackifier + seed, ripping + seed or seed only control (N = 5 per treatment, Figure 3). In contrast, within the three trenched sites, 10 sampling plots of the same size and distance apart as the compacted sampling plots were selected, with two treatment levels of either tackifier + seed or seed only assigned. Surface ripping 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 the inherent ruggedness of these sites.

The seed traps were constructed using a standard aluminum bread pan (20.3 cm × 9.5 cm × 6.4 cm) and a piece of aluminum flashing affixed to one side at the top and angled down at approximately 45° (Figure 3). A space of 1-2 cm was allotted along the remaining three sides to allow the seeds to fall in. The piece of flashing aids in preventing seeds from blowing out once captured and also prohibits rodents from gaining access to the captured seeds. The seed trap array was composed of 16 seed traps evenly spaced along all four sides of the sampling plot (4 traps/side), covering 40% of the plot perimeter. Installation of the 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.

Surface ripping was administered by ITAM personnel using a harrow dragged behind a small tractor prior to seeding. The harrow passed once across each plot in one direction and then again, perpendicular to the first pass. Each tine of the harrow left a furrow that was approximately 3 cm wide and 5 cm deep, with the exception of the Vehicle Maintenance

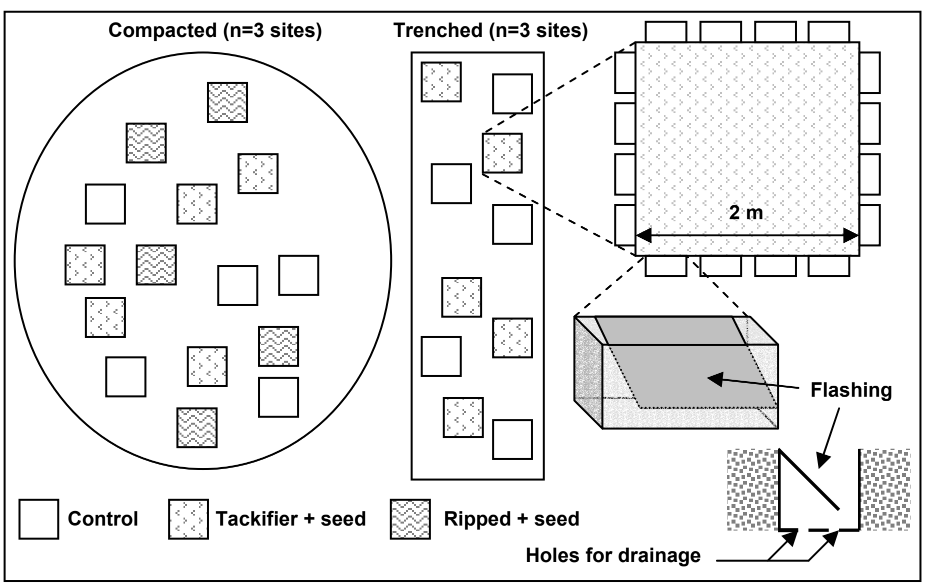

Figure 3. Experimental design and plot layout with seed trap array. Experimental treatments were randomly assigned among the 2 m × 2 m plots located within the replicated compacted and trenched sites. Tank trenches received only control and tackifier treatments while compacted sites received controls, tackifier and ripping treatments. Traps were established along the perimeter of the plots to catch seeds that were not retained on the surface by the treatments. Note: diagram is not to scale.

Site, which was slightly shallower in depth. The ripping treatments were designed to completely cover the treatment plots in a checkerboard pattern (Figure 4). Soil Sement®, a latex polymer emulsion, was administered as the tackifier treatment in a 1:8 tackifier-to-water solution. Tackifier was applied in a series of two or three coats across the entire 2 m × 2 m surface after seed was broadcast.

Figure 4. Completed seed trap array at the compacted Racetrack Site. Seed traps were installed along the perimeter of the 2 m × 2 m sampling plots. This plot was ripped before traps were installed and seed was applied.

Seeds were applied to plots to attain a target of 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 (Figure 5). The number of live seeds per unit weight of bulk seed (*i.e*., % pure live seed) was estimated for each species using standard methods at qualified seed testing laboratories. Due to large differences in the purity and viability among species that were commercially available, total seeds sown (live + unviable) for each 4 m^2 plot were approximately 3,890 bur-sage (*Ambrosia dumosa*, 10.29% pure live seed), 1,684 creosote bush (*Larrea tridentata*, 21.95%), 1,038 fourwing saltbush (*Atriplex canescens*, 38.56%), 710 brittlebush (*Encelia farinosa*, 59.12%), 682 cheesebush (*Hymenoclea salsola*, 60.50%), and 509 bladderpod (*Isomeris arborea*, 78.66%). As a result, the total number of seeds (live + unviable) was approximately 8,513 seeds/plot or 2,128 seeds/m^2. All species of seed were combined with mulch (1:1 seed-to-mulch ratio by volume) to aid in even distribution of seed across the plots and to duplicate ITAM seeding procedures. Seeds were hand broadcast across the surface of each plot using a cardboard barrier along the edge to prevent seeds from prematurely falling into traps.

Seeds (and trapped arthropods) were removed from the seed traps beginning 1 week after plots were seeded (January 26-28, 2005). Removal of trap contents continued each subsequent week (February 1-3, February 9-10, February 16-17) until seed capture decreased significantly, after which time seed trap contents were collected every two to three weeks (March 1-2,

Figure 5. Seeds of Mojave Desert perennials. The establishment of perennial seeds on the soil surface was expected to vary depending on the mass, shape and textures of the seeds and as a function of the soil surface treatments – ripping vs. tackifier. Scale is in mm.

March16-17, March 29-31, April 27-May 3 and May 9-11). All seeds and arthropods were removed from the seed traps using a Ryobi Tuff Sucker wet/dry vacuum (battery driven) with a modified nozzle. All seeds from the 16 seed traps per plot were combined to obtain one representative sample of the loss of seed per plot per time period. Seeds were separated by species and counted. Seedlings of perennial plants were counted on each plot on March 30-31 and May 9 to determine the seed species and density that germinated. During the week of May 9, 2005 the surfaces of the plots were swept with a hand broom and collected in paper grocery bags. These samples are being stored at USGS for future analysis to determine how many seeds remained on the plots with the potential to germinate in following years.

Statistical Analyses

All analyses were conducted using SAS statistical software (version 9.0, Cary, NC). Because annual species were more abundant than perennials, the natural occurrences of annuals and perennials associated with compacted sites and trenched sites were analyzed differently (Part I). First, a split-plot ANOVA was used to determine whether seed density and species richness of annual species were impacted by disturbance type and distance from edge. Disturbance type was designated as the whole plot factor, and distance from edge was the split plot factor. Seed density was $\log_{10}$+1-transformed before analysis to satisfy the assumption of equal variance. Because the abundance of perennial seeds was patchy (*i.e*., many plots contained zero seeds), a log-linear analysis was used to determine whether seeds were more likely to occur in trenched vs. compacted sites and in undisturbed areas vs. 10 m and 20 m within the disturbances. Means and standard errors were calculated for disturbance and distance factorial combinations for annuals and perennials for graphical representation. Including only plots with annual and perennial seeds present, multiple linear regressions were tested separately for each level of disturbance (compacted, trenched and control) to determine which plot factors (soil texture, soil compaction, shrub cover, litter cover, slope, micro-relief, distance to closest ant nest disk and disk diameter) influenced seed abundance and species richness (Fernandez 2003). Observations at 10 and 20 m were pooled to analyze the trenched and compacted treatments separately, and observations in the undisturbed areas for trenches and compacted sites were pooled for analysis of the undisturbed treatment. Soil texture included pooled soil fractions to represent “Sand” (includes fine sand, silt and clay < 2 mm), “Gravel” (2 mm – 3 cm), and “Cobble” (> 3 cm).

For the seed fate experiment (Part II), we analyzed data in two ways because the design was an incomplete factorial experiment (*i.e*., trenched sites were not ripped). To determine whether seed loss varied among tackifier ripped 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 loss between compacted and trenched sites, the ripped treatment was omitted, and data were analyzed in a split plot design with disturbance type as the whole plot factor and surface treatment as the split plot factor. All tests were conducted at 0.05 significance level, and multiple comparisons were conducted using Tukey’s HSD.

Results

Part I — Impact of disturbance type and distance from edge on natural seed banks

More than 11,000 seedlings germinated during the course of four wetting and drying cycles. Less than 3% of the seedlings (likely annuals) could not be identified to species because they died prematurely; however, of the majority of seedlings that could be identified, annual species were the most numerous and diverse compared with perennial species (Table 2). Seedlings

Table 2. Natural abundance of species represented in the seed bank at compacted and trenched sites at US Army NTC during fall 2004.

Annual species			Annual species (cont.)		
Scientific name	Habit	#	Scientific name	Habit	#
Cryptantha angustifolia	N	5,305	*Amsinkia tessellata*	N	7
Schismus barbatus	NN	2,978	*Chaemasyce micromera*	N	6
Salsola tragus	NN	843	*Cryptantha barbigera*	N	3
Pectocarya heterocarpa	N	322	*Chorizanthe rigida*	N	3
Ambrosia acanthicarpa	N	291	*Chorizanthe brevicornu*	N	3
Unidentified borage	N	180	*Pectocarya recurvata*	N	2
Lepidium lasiocarpum	N	171	*Erodium texanum*	N	1
Cryptantha sp.	N	166	*Cryptantha nevadensis*	N	1
Eriogonum deflexum	N	154	***Annuals subtotal***		10,638
Erodium cicutarium	NN	59	Perennial species		
Brassica tournefortii	NN	42	*Ambrosia dumosa*	N	168
Lotus humistratus	N	30	*Atriplex polycarpa*	N	96
Astragalus acutirostris	N	29	*Hymenoclea salsola*	N	44
Plantago ovata	N	16	*Stephanomeria paucifolia*	N	7
Bromus madritensis	NN	15	*Larrea tridentata*	N	2
Sisymbrium altissimum	NN	10	*Astragalus lentiginosus*	N	1
			Perennials subtotal		318
			Unidentified Seeds subtotal		310
N=native, NN=non-native			**Grand total**		11,266

represented 18 native annual species (including an unidentified annual of the Family Boraginaceae, and *Cryptantha* sp. that was not identified to species but likely *C. angustifolia*), 6 non-native annual species and 6 native perennial species.

The distribution of seeds that naturally occurred within the compacted and trenched sites differed between annual and perennial species. Compared with the undisturbed controls, annual seeds occurred at lower densities inside the compacted sites but at higher densities inside the trenched sites (Figure 6). The number of annual species reflected the same pattern as seed density with the fewest species 20 m within the compacted sites (1.9 ± 0.3 species/m^2) and the most found 10 m inside the trenched sites (4.5 ± 0.5 species/m^2). Seed densities of perennials, while more variable than annuals, declined inside the compacted and trenched sites to < 1 seed/m^2 (Figure 6).

Annual and perennial seed densities were associated with different site characteristics (Table 3). In the undisturbed controls, greater annual seed densities were associated with greater litter cover and slope, lower gravel and cobble fractions, and shorter distance to and greater diameter of the closest ant nest disk. Perennial seed densities in the undisturbed controls were higher on plots with greater slopes and shrub cover only. Compacted sites had greater annual and perennial densities associated with greater litter cover, larger ant nest disks but negatively related to micro-relief. While annual densities on trenched sites were positively related to litter and the percent sand-silt-clay fraction, perennial densities were not significantly related to any of the variables measured.

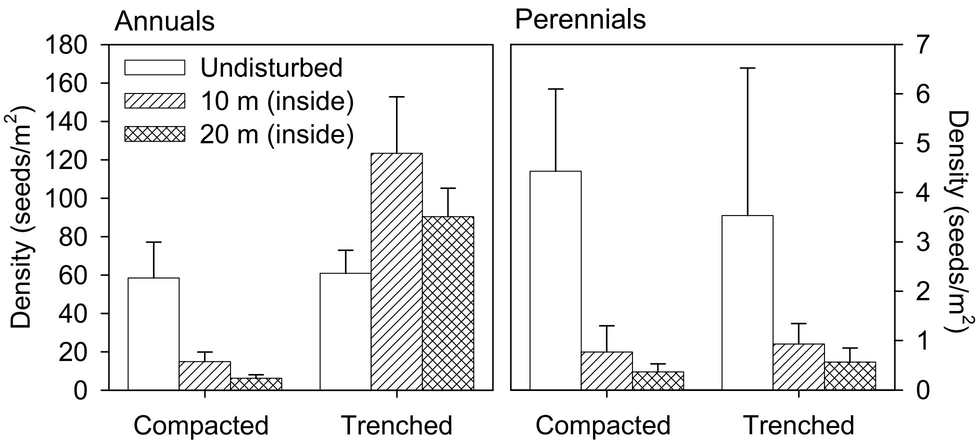

Figure 6. Natural densities of annuals (left graph) and perennials (right graph) associated with compacted and trenched sites at US Army NTC. Bars represent means (± SE). The pattern of annual seed densities associated with the distance from the disturbance edge varied between the compacted and trenched sites (Disturbance × Distance; $F_{2,170} = 9.35$, $P < 0.01$). Conversely, seeds of perennials were equally likely to occur in compacted and trenched areas ($\chi^2 = 0.40$, df = 1, $P = 0.53$) but were less likely to occur 10 and 20 m inside the disturbances than the controls ($\chi^2 = 13.73$, df = 2, $P < 0.01$).

Table 3. Significant site variables ($P < 0.05$) that explain the greatest variation in annual and perennial seed densities determined from multiple linear regressions. "+" and "-" refer to positive and negative relationships between seed densities and site variables.

	Parameter estimates†									Overall model			
	Lit	Slope	Diam	Dist	Micro	Cov	Sand	Grav	Cob	F	df	P	R^2
Annuals													
Undist	+#	+	+#	-				-	-	7.78	8, 47	< 0.01	0.50
Compact	+		+		-					15.72	3, 45	< 0.01	0.48
Trench	+						+			37.30	2, 55	< 0.01	0.56
Perennials													
Undist		+				+#				8.49	3, 27	< 0.01	0.43
Compact	+		+		-					5.72	3, 9	0.02	0.54
Trench				No significant variables						-	-	-	-

†Lit = % litter, Slope = % slope of plot, Diam = diameter of closest ant nest disk (cm), Dist = distance to closest ant nest (cm), Micro = soil micro-relief (%), Cov = % shrub cover, Sand = % fine sand, silt and clay (< 2 mm), Grav = % gravel (2 mm – 3 cm) and Cob = % cobble (> 3 cm).
#Quadratic term included in overall model.

Part II — Fate of perennial plant seeds following reseeding

Seed losses for the six species, as determined by the number of seeds that fell into traps, were determined at 1, 2, 3, 4, 6, 8 and 10 weeks after seeding (Figure 7). Seeds were rapidly lost from plots in the first 3 weeks and losses generally declined after 4 to 6 weeks. A total of 26,731 seeds were collected by 10 weeks after seeding, but due to diminished losses by this time, seed trap contents collected between 10 and 15 weeks were not separated and counted.

Surface roughness of soil, whether created by ripping with a tractor or characteristic of the trenches themselves, reduced the losses of perennial seeds broadcast on plots. Seed loss on compacted sites was reduced by spraying tackifier after seeds were broadcast (32% reduction in

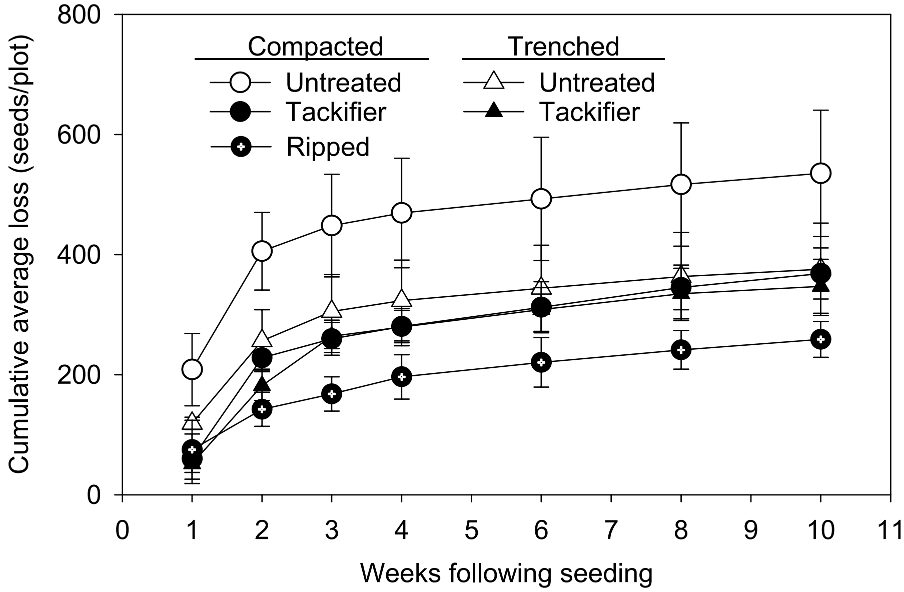

Figure 7. Cumulative loss of perennial seeds 10 weeks after they were broadcast on 4 m^2 plots.

seed loss compared with untreated mean) but even more by ripping the soil surface prior to seeding (55% reduction in seed loss, Figure 8). The impact of using tackifier to reduce seed loss in trenched sites was not as dramatic as it was for compacted sites (Figure 8) because trenches already had lower seed losses before tackifier was applied.

Expressed as a percent of the total seeds (live + unviable), seed loss was greatest for creosote bush (*Larrea tridentata*) and lowest for bladderpod (*Isomeris arborea*). The large effect of tackifier or ripping on reducing total seed loss in compacted areas as seen in Figure 8 was primarily driven by *Larrea*, *Ambrosia* and *Encelia* (Figure 9). The effect that tackifier had on total seed loss for both disturbance types was reflected in a large reduction in seed loss for *Larrea* using tackifier on compacted sites but little change in loss on trenched sites regardless of tackifier treatment (Figure 10). Tackifier also significantly decreased seed loss for *Encelia* and marginally decreased seed loss for *Atriplex* regardless of disturbance type.

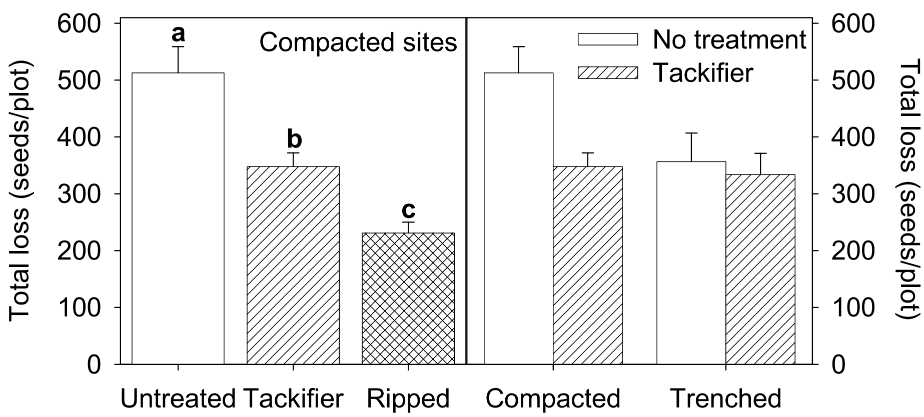

Figure 8. Loss of perennial seeds (live + unviable) 10 wks after they were broadcast on 4 m^2 plots. For compacted sites only (left graph), seed loss was reduced by the tackifier and ripping treatments (Treatment, $F_{2, 40} = 30.65$, $P < 0.01$; treatment means with different letters are statistically different based on Tukey's HSD). The reduction in seed loss using tackifier (right graph) was much greater for compacted sites compared with trenched sites (Disturbance × Treatment, $F_{1,52} = 4.26$, $P = 0.04$).

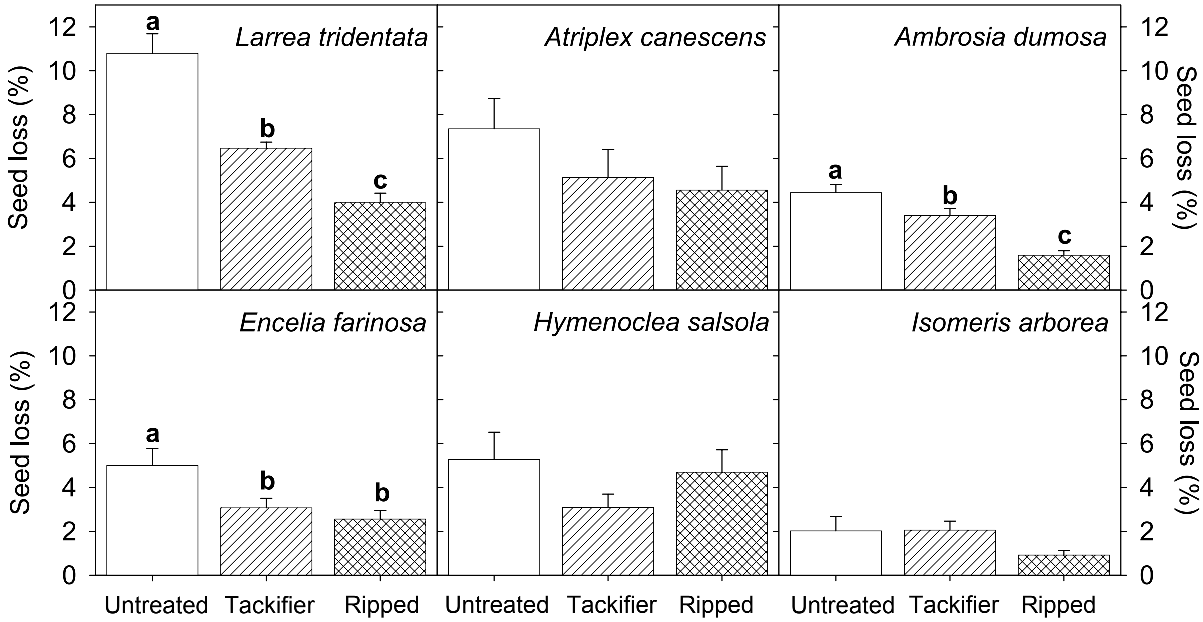

Figure 9. Percent loss of seeds for each species (live + unviable) at compacted sites only. Seed losses were significantly different among treatments for *Larrea* ($F_{2, 40} = 36.21$, $P < 0.01$), *Ambrosia* ($F_{2, 40} = 24.49$, $P < 0.01$) and *Encelia* ($F_{2, 40} = 6.22$, $P < 0.01$) but not for *Hymenoclea* ($F_{2, 40} = 1.59$, $P = 0.22$) or *Isomeris* ($F_{2, 40} = 2.10$, $P = 0.14$). Whereas seed loss for *Atriplex* was marginally significant ($F_{2, 40} = 3.17$, $P = 0.05$), Tukey's HSD did not detect statistical differences when means were compared. Treatments with different letters are statistically different.

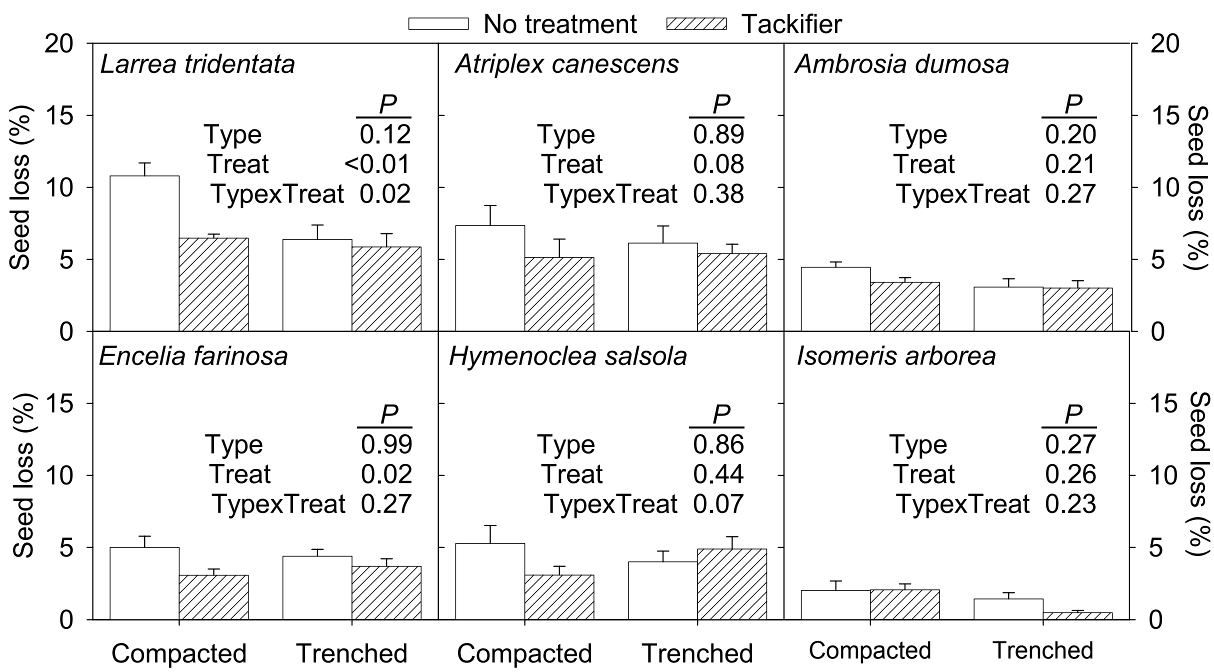

Figure 10. Percent loss of seeds for each species (live + unviable) associated with type of disturbance and surface treatments. *P*-values are inset for testing the difference between compacted and trenched sites (Type effect), the difference between tackifier and untreated treatments (Treat effect) and the interaction (Type × Treat).

Seedlings representing all six species established in the treatment plots by late March, but by early May seedling numbers declined. Establishment was greatest for compacted sites that were ripped before seeding (mean total = 70.6 ± 11.8 seedlings/plot or 17.7 ± 2.9 seedlings/m^2). *Encelia* seedlings were most abundant followed in decreasing order by *Hymenoclea*, *Larrea*, *Atriplex*, *Ambrosia* and *Isomeris* (Figure 11). Two months later, when high daytime ambient temperatures typically reduce soil moisture and increase plant water stress in spring, compacted sites still supported the most seedlings (mean total = 20.3 ± 3.6 seedlings/plot or 5.1 ± 0.9 seedlings/m^2) with fewer than 5 seedlings/plot for each species including those that initially showed higher seedling germination (Figure 11).

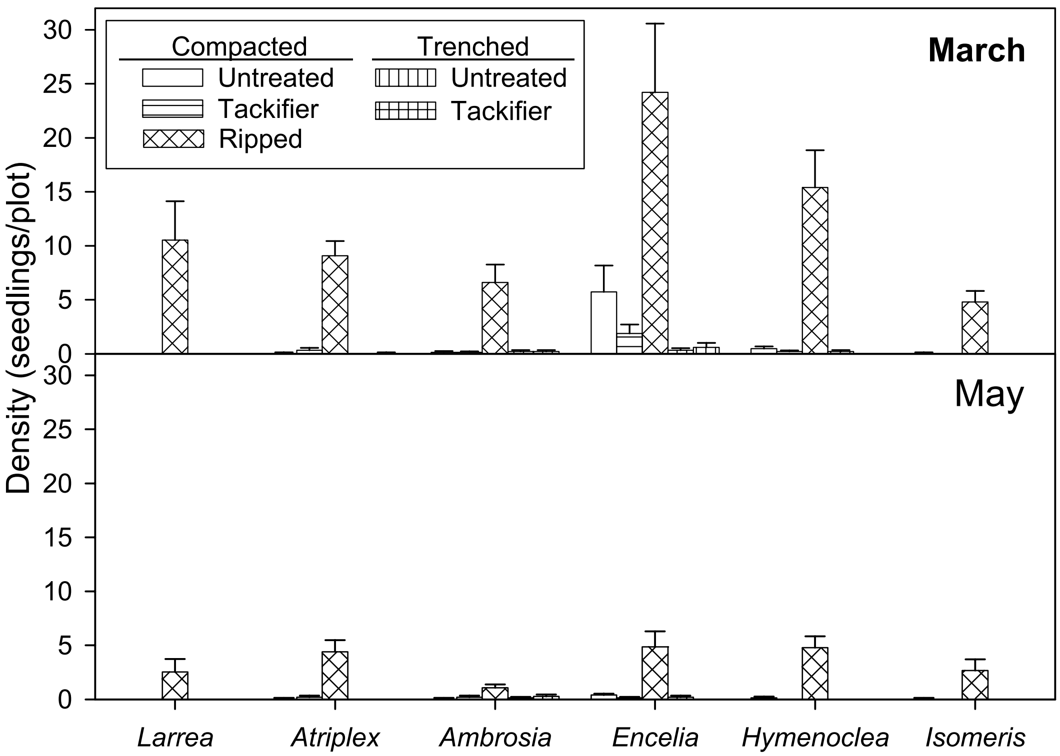

Figure 11. Density of seedlings that germinated as a result of seeding plots with 2,400 live seeds/plot across six perennial species. Pooled across all species, the most seedlings encountered in late March occurred in the ripped-compacted sites followed by untreated-compacted and tackifier-compacted and then the trench-tackifier and trench-untreated sites, ($F = 46.32$, $P < 0.01$). By early May, more surviving seedlings occurred in the ripped-compacted sites compared with any other disturbance type-treatment combinations ($F = 39.48$, $P < 0.01$).

Conclusions

The densities of seed found in undisturbed soil samples in this study occur at the lower end of published studies in the Mojave Desert. Guo et al. (1999) measured seed densities as low as 427 seeds/m^2 while Nelson and Chew (1977) found densities of up to 7,682 seeds/m^2. Both of these studies, however, did not discriminate between live and dead or unviable seeds, likely inflating the live seed densities they measured. Early seed bank research has documented highly variable seed densities over time and space (Brenchley and Warington 1930). During one study in Mojave Desert scrub (using similar methods as the present study), live seed densities ranged from less than 100 seeds/m^2 following a year of below average precipitation, to over 2,000 seeds/m^2 during a subsequent year with above average precipitation (Esque 2004). The relatively low seed densities that we observed were likely due to 4 consecutive years of below average winter precipitation in this region of the Mojave Desert and perhaps due to the widespread heavy surface impacts at the NTC. When seed densities were compared among plots where the presence of ants, rodents and fire were manipulated, Esque (2004) found the amount of winter precipitation to have an overriding effect on seed bank densities. Reichman (1984) also noted that climate had a significant effect on seed bank densities and that granivores (*i.e.*, harvester ants and rodents) had more of an influence in years of high seed density than years of low density.

The number of annual species that we detected in seed bank samples was relatively low with less than 2 species/m^2 at compacted sites and more than 4 species/m^2 at trenched sites. Seed bank assays typically provide data on the most abundant species of plants (Juhren, *et al*. 1956) while under representing rare species because the amount of work to analyze one sample is so great that only relatively small portions of the landscape can be sampled (Nelson and Chew 1977, Reichman 1984).

The natural abundances of seeds of annual and perennial species varied between trenched and compacted sites as well as location along the disturbed-undisturbed boundary. Perennial seed densities, while comparatively scarce, diminished dramatically inside both trenched and compacted sites. The almost undetectable densities of perennials within disturbances, regardless of the distance beyond the disturbed-undisturbed boundary, emphasizes the challenge of allowing natural recovery of perennial vegetation without active reseeding efforts in this heavily disturbed landscape. Likewise, annual seed densities 10 m inside compacted sites declined rapidly to less than one-third of the control sites, and even greater losses were observed at a further distance of 20 m. However, annual seed densities on trenched sites doubled at 10 m and then decreased slightly at 20 m from the edge of the disturbance. Hence, not only were the annual densities different between trenched and compacted sites, but the abundance of seeds in the disturbances were fundamentally different. The pattern in annuals supports the hypothesis that annual seed densities inside trenched sites are augmented from seed sources dispersing into the trench from two directions, but dispersal into the expansive compacted areas we studied is likely unidirectional. In addition, we speculate that trench construction more completely eliminates established shrubs and herbaceous plants compared with compacted sites, thus providing a competitive release of resources for recolonizing annual plants.

We initially thought that the patterns in annual and perennial seed abundance would be related to greater soil micro-relief, abundant shrub and litter cover and surface rocks. Troughs and depressions resulting from variable surface characteristics create sites where turbulence from localized air currents form eddies and slow the movement of seeds or facilitate the trapping of seeds altogether (Burrows 1986). In relatively undisturbed sites in the Sonoran Desert, micro-relief was found to be more important than distance to seed sources such as shrubs (Reichman 1984). However, we found that seeds did not always follow these predicted patterns. Undisturbed sites with higher percentages of gravel and cobble (> 8 mm) had low annual seed densities. This relationship between fewer seeds on plots with large soil particle sizes was driven in particular by the samples collected from the Vehicle Maintenance site where we also observed fine sediment movement (and often the dislodging and transport of our seed traps!) during rainfall and high wind events. We speculate that during such events, annual seeds are transported away from the site with smaller soil sediments and debris leaving behind heavier gravels and cobbles. Likewise, lower seed densities associated with greater micro-relief within the compacted area at Vehicle Maintenance may reflect the influence of larger sized soil particles on enhancing micro-relief, as measured at the plot level with the contact profile meter. Whereas we cannot ascribe cause and effect to the relationships between low seed densities and particle size or micro-relief in this study, these results emphasize the need to understand more thoroughly the influence of soil surface characteristics on seed transport.

Other relationships between seed densities and site characteristics are more logical, albeit unexpected. The amount of litter was associated with greater annual seed densities at all sites and greater perennial seed densities on compacted sites. Interestingly, the diameter of the closest ant nest disk was also positively related to seed densities. We attribute these patterns to the activities of the most prevalent harvester ants in the area, *Messor pergandei*. Litter cover during this study was comprised of detached plant debris and other decomposing organic matter and included much of the previous spring's annual plants– the most abundant, *Cryptantha angustifolia*. Litter of this species consisted predominantly of stem and inflorescence segments that frequently piled up to several centimeters deep on the soil surface, particularly in the trenched sites. During observations of ant foraging behavior in spring 2005, we documented ants carrying these segments to their nests, as well as florets of *Schismus barbatus* and seeds of annual and perennials species. Therefore, we speculate that greater seed densities (annuals in particular) associated with litter and large ant nest disks reflect the harvest and transport of *Cryptantha* by ants, during which time the nutlets fall from inflorescences and enter the seed bank. Furthermore, areas with active nests are known to provide favorable growth and reproductive conditions for the most prolific annual plant species (Rissing 1986; Esque 2004). We observed enhanced growth of annuals on ant nest disks in trenched sites during this study for *Cryptantha angustifolia* in 2004, and *Schismus barbatus* and *Erodium cicutarium* in 2005.

This study demonstrates that perennial seeds are exceedingly rare in disturbed areas as demonstrated at the six sites examined. Consequently, we recommend that 1) broadcast seeding of perennial species should continue as a means to re-vegetate heavily disturbed areas at NTC, and 2) consideration should be made for creating surface roughness to reduce seed loss and increase seed-soil contact. Among the species that had the greatest seed losses, *Larrea* and *Ambrosia* benefited the most from surface treatments. Retention of seeds on trenched sites (predominantly *Larrea*) was enhanced by tackifier until heavy rains that fell shortly after application resulted in rapid seed losses up to control levels at 10 weeks. Tackifier use on compacted sites minimized loss of *Larrea*, *Ambrosia* and *Encelia* seeds throughout the 10 week period, although ripping of compacted sites prior to seeding further reduced seed losses for *Larrea* and *Ambrosia*. In contrast, tackifier and ripping in compacted areas only marginally reduced losses of *Atriplex* seeds but did not significantly reduce losses of *Hymenoclea* and *Isomeris* seeds. During this study we observed emptied seed caryopses of *Encelia* and *Atriplex* on nearby ant nest disks, discarded seed coats of *Isomeris* close to seed traps likely by small mammals as well as clusters of *Isomeris* seedlings emerging from small mammal caches several meters away from plots in spring. Quantification of the remaining seeds swept from plots at the end of the experiment will shed light on whether granivores removed significant numbers of seeds from plots (Figure 12), thus underestimating the tackifier's ability to reduce seed losses for these species.

Figure 12. Harvester ants (*Messor pergandei*) were observed carrying seeds of all six species that were broadcast on 4 m^2 plots. Species names of seeds follow in the order they are presented in Figure 5.

When evaluating the success of shrub re-establishment after broadcast seeding, the number of plants that become established long after seed is placed on the soil surface is rarely quantified. We initially assumed the treatments that minimized wind-induced losses of seeds would also ensure that intact seeds would germinate and develop into seedlings, especially in this year of exceptionally high rainfall for the Mojave Desert (Figure 13). Compacted sites where the soil surface was ripped had the lowest loss of seed and the highest establishment success by May resulting in approximately 20.3 seedlings/plot (5 seedlings/m^2) and representing all six perennial species. Successful plant establishment has been observed in related studies where soils were ripped in years with abundant rainfall (Snyman 2003, ven den Berg and Kellner 2005). Ripping of the compacted sites retained seeds in the furrows left by the harrow. In addition, ripping likely influenced soil physical and hydrological properties such as by decreasing bulk density, increasing soil porosity, reducing rainfall run-off and enhancing infiltration (Osunbitan *et al*. 2005), and thereby encouraged seedling establishment. However, this year does not typify rainfall patterns and amounts characteristic of the Mojave Desert in most years. Thus, it remains to be seen how plant establishment would change for the soil surface treatments tested – and those commonly used but not tested in this study – on compacted and trenched sites when climate conditions are different than those in 2004/2005.

Reduced loss of seeds from plots, as inferred from lower numbers of seeds collected in traps, was not always associated with enhanced seedling establishment. While trenched sites in general also had low seed losses compared with ripped compacted sites, the resulting establishment of seedlings was comparably low. This failure for seedlings to establish at trenched sites may be due to the removal or consumption of seeds by granivores (Roth and Vander Wall 2005), competitive exclusion of seedlings by non-native annuals (Stylinski and Allen 1999), or poor conditions for germination and development of the seedling, which may include low root mycorrhizal infection associated with soil disruption (Moorman and Reeves 1979, Caravaca *et al*. 2003, Kabir 2005). While not all these sources of establishment failure were quantified in this study, enumeration of the seeds from plots collected at the end of the experiment will determine whether granivores use trenched sites more than compacted sites and thus influenced the abundance and viability of the remaining seeds.

Acknowledgments

We are grateful to many individuals that assisted in the field, laboratory and greenhouse on this project including Kathleen Coulson, Trent Draper, Megan Garnett, Isaac Jacobs, Becky Kipp, Jessica Lissow, Adam Nilsson, Gary Reese, Sara Scoles, Karissa Smith, Ben Waitman, and Upekala Wijayratne. Julie Draper and Emily Orling generously provided assistance in the greenhouse, and Peter Griffiths provided guidance on soil texture analyses. We especially thank Ruth Sparks, Matt Hamilton, Mark "Sharky" Hopkins, Pete Dolan and Gary Morrissette at ITAM for their support and logistical assistance on site. Jeff Cassel of Johnson Controls helped us maximize our time in the field in conjunction with the military training schedule.

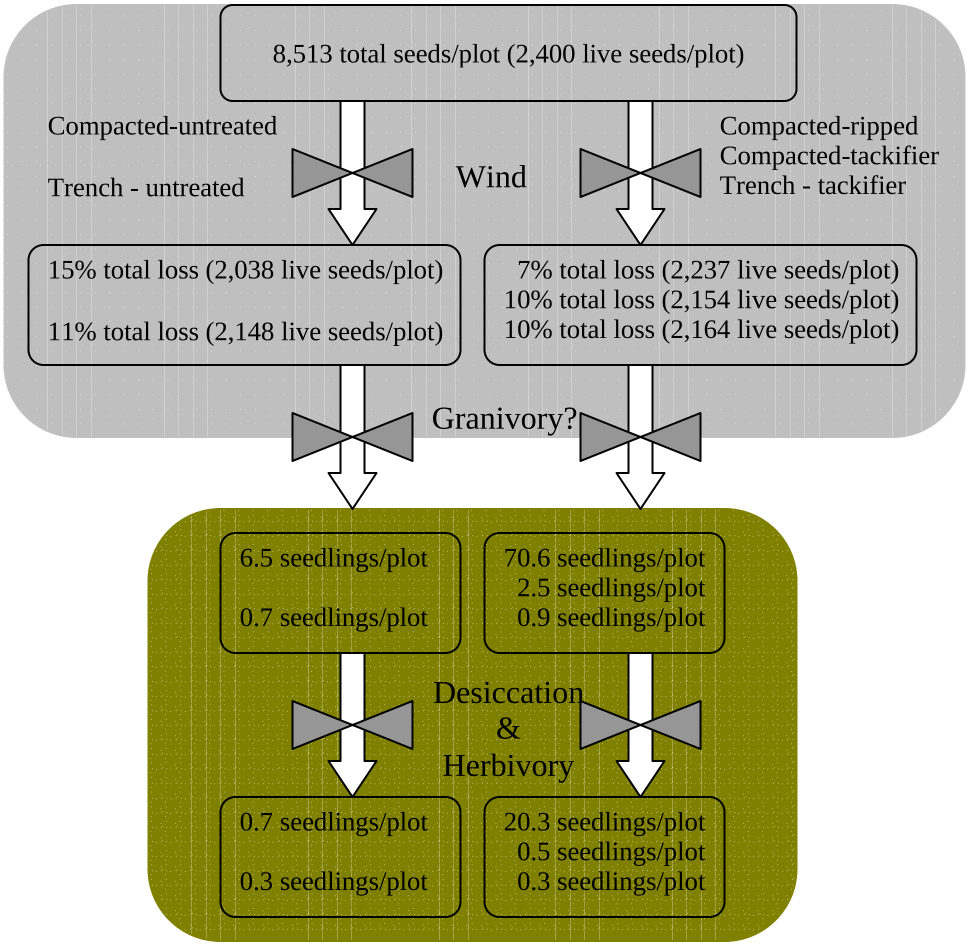

Figure 13. The fate of live perennial seeds in winter/spring 2005 depended on the type of disturbance and the surface treatments measured in this study. Approximately 2,400 live seeds/plot pooled across six perennial species comprised the initial seed bank (grey box). The percent loss of total seed (live + unviable) as measured by trap contents represents a normalized estimate to the entire plot given that seed traps covered 40% of the plot perimeter. In the absence of any surface treatments, more seeds were blown from the soil surface of compacted than trenched sites (left). However, ripping in compacted sites reduced losses below those for tackified trenched or tackified compacted sites (right). While generally more seeds germinated into seedlings (green box) in the untreated compacted than untreated trenched sites (left), ripping of compacted sites enhanced germination ten-fold (right). Fewer granivores and herbivores or enhanced microsite conditions into mid to late spring likely contributed to greater seedling survival on the ripped compacted areas.

References

Baskin, C. C., and J. M. Baskin. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press. San Diego, CA. 666 pp.

Brenchley, W. E., and K. Warington. 1930. The weed seed population of arable soil. 1. Numerical estimation of viable seeds and observations on their natural dormancy. *Journal of Ecology* 18: 235-272.

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.

Burrows, F. M. 1986. The aerial motion of seeds, fruits, spores and pollen. *In* Murray, D.R., (ed.), Seed Dispersal, Academic Press. Sydney, Australia, pp. 2-46.

Caravaca, F., M. M. Alguacil, D. Figueroa, J. M. Barea and A. Roldán. 2003. Re-establishment of *Retama sphaerocarpa* as a target species for reclamation of soil physical and biological properties in a semi-arid Mediterranean area. *Forest Ecology and Management* 182:49-58.

Childs, S. and D. W. Goodall. 1973. Seed Reserves of Desert Soils. US/IBP Desert Biome Research Memorandum 73-5. Utah State University, Logan. 23 pp.

Esque, T. C. 2004. The role of fire, rodents and ants in changing plant communities in the Mojave Desert. Dissertation. University of Nevada. Reno, Nevada. 168 pp.

Fernandez, G. 2003. Data Mining Using SAS Applications. Chapman and Hall/CRC. Boca Raton, FL. 367 pp.

Foth, H. D. and L. M. Turk. 1972. Fundamentals of Soil Science. John Wiley and Sons, Inc. New York.

Gee, G. W. 2002. Particle-size analysis. *In* Dane, J. H. and G. C. Topp, (eds.), Methods of Soil Analysis: Part 4, Physical Methods. Soil Science Society of America, Inc. Madison, WI, pp. 255-293.

Guo, Q., P. W. Rundel and D. W. Goodall. 1999. Structure of desert seed banks: comparisons across four North American desert sites. *Journal of Arid Environments* 42:1-14.

Herrick, J. E. and T. L. Jones. A dynamic cone penetrometer for measuring soil penetration resistance. *Soil Science of America Journal* 66:1320-1324.

Jensen, K. 1998. Species composition of soil seed bank and seed-rain of abandoned meadows and their relation to aboveground vegetation. *Flora* 193:345-359.

Juhren, M., F. W. Went, and E. Phillips. 1956. Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. *Ecology* 37:318-330.

Kabir, Z. 2005. Tillage or no-tillage: impact on mycorrhizae. *Canadian Journal of Plant Science* 85:23-29.

Lovich, J. E. and D. Bainbridge. 1999. Anthropogenic degradation of the California desert ecosystem and prospects for natural recovery and restoration. *Environmental Management* 24:309-326.

Meyer, A. M., and A. Poljakoff-Mayber. 1982. The Germination of Seeds. Pergamon Press. 4th Edition. New York, NY. 96 pp.

Moorman, T. and F. B. Reeves. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. *American Journal of Botany* 66:14-18.

Nelson, J. F., and R. M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. *American Midland Naturalist* 97:300-320.

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.

Page, M. J., L. Newlands, and J. Eales. 2002. Effectiveness of three seed-trap designs. *Australian Journal of Botany* 50:587-594.

Reichman, J. 1984. Spatial and temporal variation of seed distributions in Sonoran Desert soils. *Journal of Biogeography* 11:1-11.

Rissing, S.W. 1986. Indirect effects of granivory by harvester ants: Plant species composition and reproductive increase near ant nests. *Oecologia* 68: 231-234.

Roth, J. K. and S. B. Vander Wall. 2005. Primary and secondary seed dispersal of bush chinquapin (Fagaceae) by scatterhoarding rodents. *Ecology* 86:2428-2439.

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.

Stylinski, C. D. and E. B. Allen. 1999. Lack of native species recovery following severe exotic disturbance in southern California shrublands. *Journal of Applied Ecology* 36:544-554.

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.

Young, J. A., R. A. Evans, and R. E. Eckert, Jr. 1969. Population dynamics of downy brome. *Weed Science* 17:20-26.

Young, J. A., and R. A. Evans. 1975. Germinability of seed reserves in a big sagebrush community. *Weed Science* 23: 358-364.

Young, J. A., R. A. Evans, B. L. Kay, R. E. Owen, and J. Budy. 1981. Collecting, processing, and germinating seeds of western wildland plants. U.S. Department of Agriculture, Science and Education Administration, Agricultural Reviews and Manuals. ARM-W-3.