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Seed Reserves Diluted During Surface Soil Reclamation in Eastern Mojave Desert

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Surface soil reclamation is used to increase the re-establishment of native vegetation following disturbance through preservation and eventual replacement of the indigenous seed reserves. Employed widely in the mining industry, soil reclamation has had variable success in re-establishing native vegetation in arid and semi-arid regions. We tested whether variable success could be due in part to a decrease of seed reserves during the reclamation process by measuring the change in abundance of germinable seed when surface soil was mechanically collected, stored in a soil pile for 4 months, and reapplied upon completion of a roadway. Overall seed reserve declines amounted to 86% of the original germinable seed in the soil. The greatest decrease in seed reserves occurred during soil collection (79% of original reserves), compared to the storage and reapplication stages. At nearby sites where stored surface soil had been reapplied, no perennial plant cover occurred from 0.5 to 5 years after application and <1% cover after 7 years compared to 5% cover in nearby undisturbed areas. The reduction in abundance of germinable seed during reclamation was primarily due to dilution of seed reserves when deeper soil fractions without seed were mixed with the surface soil during collection. Unless more precise techniques of surface soil collection are utilized, soil reclamation alone as a means for preserving native seed reserves is a method ill-suited for revegetating disturbed soils with a shallow seed bank, such as those found in the Mojave Desert.

Keywords lake mead, restoration, revegetation, seed bank

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Introduction

Resource managers often borrow rehabilitation practices from industry to revegetate disturbed lands, but the suitability of such methods in the North American deserts has received little attention. Specifically, surface disturbances are often mitigated by soil reclamation, the removal and storage of surface soil (0–5 cm depth) before construction or mining activities, and the subsequent replacement of soil and associated seed reserves to enhance re-establishment of vegetation. In this study, we measured whether seed reserves are lost during the reclamation process, thus impacting the success of revegetation. Surface soil replacement, in combination with moisture-conservation techniques, has been shown to increase growth of seeded or planted vegetation in some arid lands (Norem and Day, 1985; Cotts, Redente, and Schiller, 1991; Sharma, Kumar, Gough, and Sanfilipo, 2004). Soil salvage alone, however, has had variable effects on vegetation re-establishment in the Mojave Desert (Alice Newton, National Park Service, personal communication), but has not been rigorously examined in an experimental framework.

Anthropogenic disturbance to surface soils can have enduring effects on soil and vegetation communities in desert environments. The upper portion of desert soils contains the majority of seed reserves and a large percentage of the organisms associated with nutrient cycling (Foth and Turk, 1972; Childs and Goodall, 1973; Pake and Venable, 1996; Guo, Rundel, and Goodall, 1998). This productive top few centimeters of soil is easily disturbed or destroyed and is therefore a primary concern for rehabilitation and reclamation efforts. Revegetation of disturbed areas in arid regions can be highly variable due to scant and infrequent rainfall during the initial phases of plant establishment (Grantz et al., 1998). Estimated natural recovery rates for desert plant communities in North America following anthropogenic disturbances range from decades to centuries (Lovich and Bainbridge, 1999). Therefore, an assessment of methods for actively revegetating disturbed desert areas is vital to minimizing impacts from future disturbances and for directing rehabiliation efforts.

With strong physical and physiological dormancy mechanisms (Baskin and Baskin, 1998), desert seeds seem particularly well-suited to the soil stockpiling concept. Many desert species display a very narrow germination tolerance with regard to temperature, day length, and moisture (Baskin and Baskin, 1998), making seeds unlikely to experience false germination within the soil storage pile.

While the process of removing surface soil, storing the soil in piles, and replacing it after several months may enhance germination of some vascular plant seeds (e.g., through seed scarification or break in physiological dormancy), it may cause mortality of others (e.g., through false germination, deep burial, or fungal activity). Compared to direct-returned surface soil, natural seedling recruitment declined 46% in surface soil stockpiled for 1 year and 66% in soil stockpiled for 3 years in western Australia (Rokich, Dixon, Sivasithamparam, and Meney, 2000). Furthermore, the same study found that viability and germinability of all 12 native species tested decreased significantly when the seeds were exposed to the stockpiling process (Rokich et al., 2000). Only one grass species displayed increased recruitment with increasing length of stockpile storage (Rokich et al., 2000). Mojave Desert species have not been studied in this regard, however, and the effects of soil stockpile storage are unknown.

In addition to seed injury and burial, reclamation has the potential to diminish structural and hydrological properties of soil (Stolt et al., 2001), which can reduce seedling establishment and impede root penetration and growth (Bainbridge and Virginia, 1990). Mechanical resistance data from stockpiled and respread soil suggest that both soil structure and aggregation are destroyed, leading to resistance values considered too high for root penetration (Stolt et al., 2001). In spite of these concerns, surface soil removal, storage, and replacement have become standard practice, particularly in the mining industry, for promoting soil genesis (Allen, 1995).

We established a study to determine the effect of surface soil manipulation on seed reserve densities and examine short-term vegetation recovery following surface soil salvage and subsequent reapplication in the northeast Mojave Desert. We anticipated that surface soil collection, storage in stockpiles, and reapplication would reduce germinable seed reserves and that short-term vegetation recovery following reapplication would be adversely impacted. Considering the shallow distribution of seeds in Mojave Desert soils, we predicted the greatest decrease in germinable seed reserves during initial soil collection, when the surface soil layer was inadvertently mixed with deeper soil fractions lacking seed reserves.

Methods

Study Location

We conducted this study in summer and fall 2001 along Lakeshore Scenic Drive (36°05′ N, 114°50′ W) in the Boulder Beach District of Lake Mead National Recreation Area (LMNRA), northeast of Boulder City, NV. Located in the eastern Mojave Desert at an elevation of 400 m, this area receives an average 96.5 mm (3.8″) of precipitation during the hydrologic year, October through September. From 1993 to 2002, the National Park Service contracted to have the 22.5 km Lakeshore Scenic Drive completely reconstructed, partially over existing roadbed, partially through undisturbed desert. Five separate phases of road construction were completed along Lakeshore Scenic Drive in 1995 (Phases 1 and 2), 1998 (Phase 3), 2000 (Phase 4), and 2002 (Phase 5). During each phase of road construction, excluding Phase 1, surface soil was collected using bulldozers in spring, placed nearby in soil piles during the spring and summer months, and then reapplied using a backhoe once construction was completed in autumn. Road construction passed through alluvial benches separated by dry water channels incised to a depth of 5–10 m. The soils are aridisols within the suborder calcid (Soil Survey Staff, 1999). The alluvial bench tops are covered by desert pavement and sparse perennial plant cover dominated by creosote bush (*Larrea tridentata* (D.C.) Cov.), white bur-sage (*Ambrosia dumosa* (A. Gray) Payne), and beavertail cactus (*Opuntia basilaris* Engelm. & J. Bigelow). A 0.5-m thick petrocalcic layer is located one meter or less below the soil surface of the benches, limiting plant rooting depth.

Seed Reserves of Stored Soil

During summer and fall of 2001, we determined whether declines of germinable seed reserves occurred during the collection, storage, and reapplication stages of surface soil reclamation. Ideally, the top 5–20 cm of soil was mechanically scraped and placed in circular soil piles 2–3 m tall during road construction on Lakeshore Scenic Drive. However, the soil depth that was collected regularly averaged between 25–31 cm when large rocks or the petrocalcic layer were encountered (Dona LeNoue, U.S. Park Service, personal communication). The same surface soil collection and storage technique was used during all phases of road construction. Subsequent to pile construction, 24 StowAway temperature data loggers (Onset Computer Corp., Pocasset, MA) were placed within one of the storage piles at 20, 50, and 70 cm depths (eight per depth). Two soil cores were extracted from each depth at the time of instrumentation. Although seeds were undoubtedly present below 70 cm deep, loggers could not be safely placed beyond this depth due to the instability of the storage pile. Two data loggers were also placed just under the soil surface in an adjacent undisturbed control area to monitor control temperatures. The shallow placement of dataloggers in the undisturbed controls was chosen rather than 20, 50, or 70 cm because seeds in North American deserts generally do not occur below 2 cm depth (Childs and Goodall, 1973, Guo et al., 1998, Pake and Venable, 1996). At the same time, 12 soil cores were collected from the soil surface in undisturbed control positions located randomly alongside the length of the bladed road bed (July 5 and 6).

Subsequently, two soil cores at each depth in the stockpile along with their associated dataloggers were collected at 2-week intervals on July 20, August 3, August 17, and August 24. During stockpile storage, 12 undisturbed control cores were collected at random undisturbed locations along the length of the roadbed on August 17.

Twelve surface soil cores were collected from both soil reapplication and undisturbed areas after stockpiled soil was reapplied to a depth of 5–20 cm (October 25). Surface depth was chosen as representative of the effective soil seed reserves because seedlings of many desert plants rarely emerge from soil depths greater than 3 cm (Bowers, 1996; Grant, Bell, Koch, and Loneragan, 1996; Bond, Honig, and Maze, 1999; Rokich et al., 2000; Zhang, Shu, Lan, and Wong, 2001). Post-application soil samples and undisturbed control samples were both collected randomly along the entire length of the reapplication area.

All soil cores were collected using 4-cm deep sampling tins (each tin volume = 113 cm^3) and placed in labeled plastic bags. Soil cores were analyzed for bulk density (Rundel and Jarrell, 1989) and gravimetric soil water content (Gardner, 1986) before seed germinability tests were conducted. We concluded that drying soil samples slowly at 40°C to analyze soil water content would not have an adverse impact on Mojave Desert seed species, as this temperature was well within the limits experienced by seeds in the field (see results).

Soil samples collected in the field were transported to a glasshouse, where each was thoroughly mixed and 1/2 cup spread to a depth of 1 cm in a 6″ diameter plastic bulb pot. The soil samples were covered with a thin layer of Vermiculite to reduce water loss during germination. All pots were randomized on a bench in the glasshouse and subjected to a series of treatments used to assay Mojave Desert species in the seed reserves (Todd Esque, USGS, personal communication): water for 2 weeks, air dry for 1 month, treat with 0.01 M NH_4NO_3, then water for 2 weeks, air dry for 1 month, treat with 6.5×10^{-4} M gibberellic acid, then water for 2 weeks. Seedlings were counted upon emergence, identified to species and removed from the pots. The total number of seedlings for each species was combined across all wetting cycles. Natural germination in the field was not expected during sample collection because the stockpiles were constructed in July, and germination usually depends on winter or early spring rainfall in the Mojave Desert (Beatley, 1974). We carefully searched for seedlings on the surface of the stockpile and in the undisturbed control areas each time soil cores were collected but did not encounter any.

Vegetation Recovery

In addition to collecting soil for understanding the dynamics of seed reserves on recently stored soils, we measured perennial plant establishment along roadside areas where surface soil was stored for 4 months and then reapplied 0.5, 2.5, 4.5, or 7 years previously. Cover and density of perennial plants were measured at each of the construction phases along Lakeshore Scenic Drive, excluding Phase 1 where stockpiled surface soil was not applied consistently. During Phases 2–5 of construction, surface soil was collected and stockpiled as previously described in the spring just prior to construction and reapplied in the fall following completion of construction activities. All respread soil had therefore been stockpiled for 4–6 months before reapplication. For each construction phase, nine permanent belt transects (20 m × 2 m) were established in the soil reapplication area and nine in adjacent undisturbed control areas in March 2002 (72 total transects grouped into three replicates per construction phase). Perennial plant cover and density were recorded by species. Cover was measured using the line intercept method on 20-m long transects, and density was determined on adjoining 2-m wide belt transects (Elzinga, Salzer, and Willoughby, 1998). We searched carefully for annual plants during perennial plant measurements, but none were found.

Statistical Analyses

All statistical analyses were conducted using SAS statistical software (Version 9.1, SAS, Inc., Cary, NC). Decrease in seed reserves was calculated as the percentage difference between the number of germinable seeds in each sample ($n = 6$ for the collection phase, $n = 24$ for the storage phase, and $n = 12$ for the reapplication phase) and the average number of germinable seeds in the undisturbed controls ($n = 12$ for each phase). We then compared germinable seed decline among the different stages of surface soil reclamation in a single-factor ANOVA. We used Tukey's HSD comparisons of means at $\alpha = 0.05$ to examine the difference among the stages. Many of the soil pile samples collected during the storage phase contained no germinable seeds. Therefore, an F-test approximation to Friedman's nonparametric test was used to analyze differences in germinable seed reserves for one factor (storage depth or duration) while blocking by the other (Ipe 1987). To compare conditions (soil moisture and bulk density) among depths during storage, we used mixed model procedures for repeated measures. The most accurate covariance structure for each response variable was selected based on Akaike's Information Corrected Criterion (AICC) comparisons, and type-3 tests of fixed effects were conducted. A two-factor ANOVA with interaction (year × soil treatment) was used to assess short-term perennial plant recovery (density and cover) after surface soil reapplication. In order to compare the species composition between reapplication and undisturbed areas, a Bray-Curtis similarity index was calculated for each replicate within the construction phases. The indices were compared using a single-factor ANOVA to determine if reapplication sites had become more similar to the undisturbed controls over time.

Results

By the time stored surface soil was reapplied along the shoulder of Lakeshore Scenic Drive, 86% of the effective germinable seed had been lost relative to the undisturbed

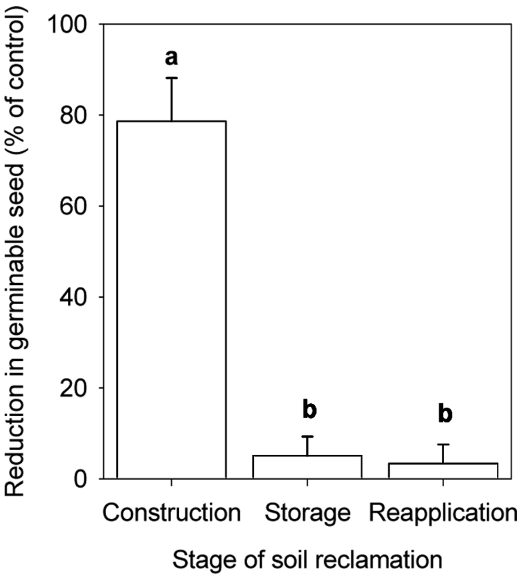

Figure 1. Mean reduction in germinable seed (±SE) compared to undisturbed control sites during the soil reclamation process in the Mojave Desert at LMNRA. Stages of soil reclamation are: Construction of a storage pile by mechanically collecting surface soil from the construction site before work begins, Storage in the soil pile over 4 months, and reapplication of the stored soil onto the road shoulder after construction. Significantly different stages are denoted with different lowercase letters using Tukey's HSD comparisons of means ($\alpha = 0.05$).

control. The undisturbed control had an average germinable seed density of 752 ± 62 seeds m^{-2} (mean ± SE) in the top 4 cm of soil, while the average for reapplied surface soil was 97 ± 55 seeds m^{-2}. The greatest reduction in germinable seed occurred during the process of soil collection ($F_{2,39} = 25.13$, $P < 0.01$), where densities decreased 79% compared to the undisturbed control (Figure 1). Declines in germinable seed also occurred during the 4-month storage of surface soil (7%) and following soil

Table 1. Least-square means for the ranks of the frequency of soil cores where seed was present or absent. A high rank indicates a greater likelihood of a soil core containing seed. Ranks were analyzed separately for soil depth and storage duration using an F-approximation to Friedman's test

Weeks of storage	Rank	Soil depth	Rank
3	3.17^{a}	20 cm	4.38^{a}
5	5.17^{ab}	50 cm	2.88^{b}
7	3.83^{ab}	70 cm	3.25^{ab}
8	5.83^{b}		

The significance of the rank sum multiple comparisons are based on a Bonferroni's adjustment of $\alpha = 0.05$. Ranks that do not share the same lowercase superscripts are significantly different from each other.

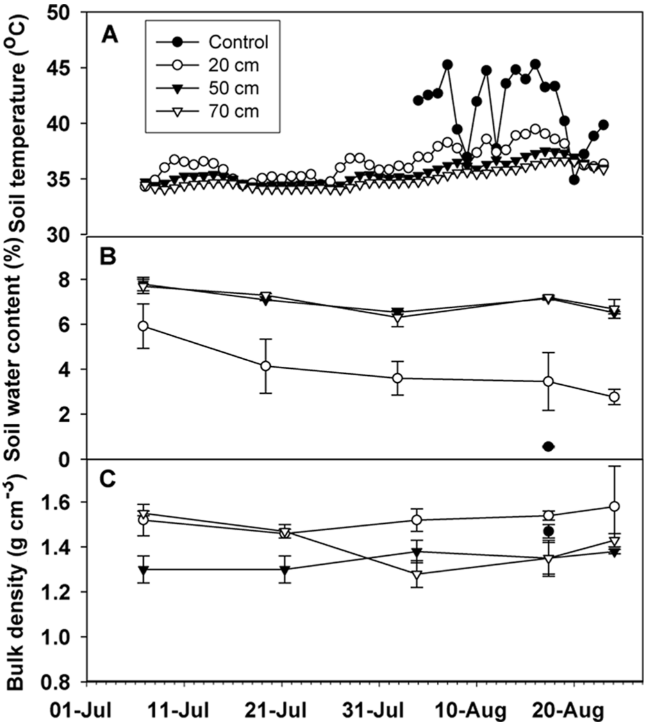

Figure 2. Soil stockpile conditions during storage (±SE), including daily average soil temperature (A), soil gravimetric soil moisture content (B), and soil bulk density (C). Sharp decreases in average soil temperature of the undisturbed control correspond with summer rainfall events on August 9, 13, and 20.

replacement (4%), but these additional reductions were negligible (Figure 1). During stockpile storage, germinable seeds were more likely to be found after 8 weeks of storage compared with 3 weeks of storage ($F_{2,18} = 3.77$, $P = 0.04$). Germinable seeds were also more likely to be present at 20 cm depth than at 50 cm ($F_{3,18} = 3.87$, $P = 0.03$; Table 1). However, these results are based on low numbers of germinating seeds per sample, with more than 50% of the samples having no germinating seeds. The majority of germinable seed species in both reapplied soil and undisturbed control soil were identified as annuals.

Although there were differences in the abiotic conditions within the soil pile (Figure 2), the low number of germinable seeds in all samples during storage precluded us from statistically relating soil pile conditions to germinable seed decline. Within the stockpile, the average soil temperature from July 7 to August 24 was 35.7 ± 0.15°C, lower than the average undisturbed surface temperature of 41.4 ± 0.04°C. The soil pile also dampened day-to-day variation in temperature compared to the undisturbed control (Figure 2A). Soil in the stockpile, pooled across sampling depths, had 12 times more soil moisture ($F_{1,16} = 80.12$, $P < 0.01$), but bulk density was not different ($F_{1,16} = 1.22$, $P = 0.29$) compared to undisturbed control soils by August 17. Soil moisture content was higher at 50 and 70 cm depths than at 20 cm throughout the storage period ($F_{2,23} = 51.83$, $P < 0.01$, Figure 2B). Soil bulk density was greater at 20 cm than at 50 cm across all dates ($F_{2,23} = 8.33$, $P < 0.01$,

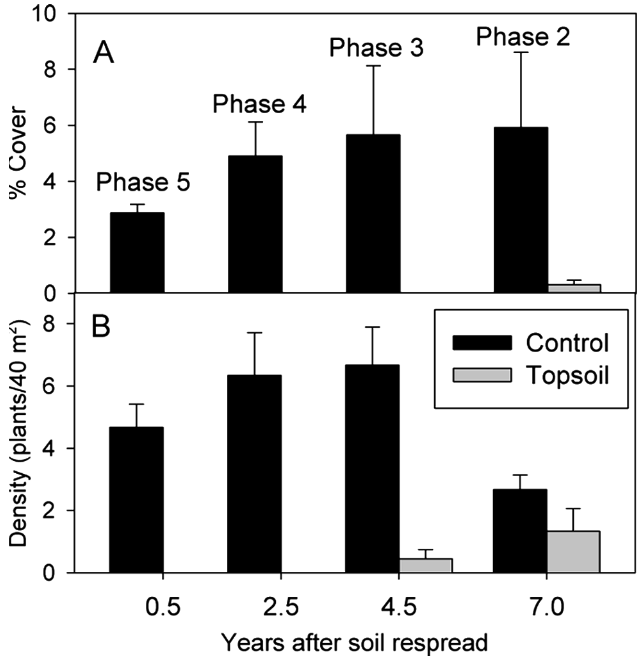

Figure 3. Recovery of perennial cover (A) and density (B) measured in spring 2002 at sites varying in age from 0.5 to 7 years after stockpiled soil was reapplied along roadsides. Soil was reapplied in 1995, 1998, 2000, and 2002 during construction of Lakeshore Scenic Drive.

Figure 2C). After being respread, the reapplied soil had more than six times greater soil moisture than undisturbed control areas ($F_{1,22} = 11.76$, $P < 0.01$, data not shown). The reapplied soil had a bulk density of $1.58 \pm 0.02\,\mathrm{g\,cm^{-3}}$ while the bulk density of undisturbed soil was $1.45 \pm 0.02\,\mathrm{g\,cm^{-3}}$ ($F_{1,23} = 17.61$, $P < 0.01$).

Perennial plant cover was lower at soil reapplication sites than undisturbed controls, regardless of the amount of time since surface soil was reapplied ($F_{1,64} = 53.91$, $P < 0.01$). Undisturbed control areas averaged 5% perennial cover, while reapplication sites averaged <1% (Figure 3A). When compared to the undisturbed control, perennial plant density was also lower at all sites where soil was reapplied, regardless of time ($F_{1,64} = 177.43$, $P < 0.01$, Figure 3B). A significant interaction for density was found ($F_{3,64} = 5.75$, $P < 0.01$) due to the lowest density values for the undisturbed control and the highest values for the surface soil reapplication treatment found at the oldest application site (Phase 2 at 7 years). Several individuals of creosote bush planted by LMNRA staff increased perennial plant density and cover in the reapplication area at this site.

Perennial plant species richness along Lakeshore Scenic Drive was low, with a total of eight species encountered in both undisturbed control and soil reapplication areas. Comparing surface soil reapplication areas with undisturbed controls, the Bray-Curtis similarity index did not change across time since soil was reapplied ($F_{3,8} = 2.86$, $P = 0.10$). The average similarity index (±SE) between the reapplication and control areas was 0.12 (±0.08), in contrast to 0.52 (±0.06) when the undisturbed controls were compared to one another. Species found in undisturbed control areas were creosote bush (*Larrea tridentata* (D.C.) Cov., 67% of cover), white bur-sage

(*Ambrosia dumosa* (A. Gray) Payne, 15%), beavertail cactus (*Opuntia basilaris* Engelm. & J. Bigelow, 9%), sunray (*Enceliopsis argophylla* (D.C. Eaton) A. Nelson, 4%), spurge (*Euphorbia* spp., 4%), cheesebush (*Hymenoclea salsola* A. Gray, < 1%), and desert alyssum (*Lepidium fremontii* S. Watson, < 1%). Surface soil reapplication areas contained creosote bush (38% of cover, mostly planted individuals), desert holly (*Atriplex hymenelytra* (Torrey) S. Watson, 34%), white bur-sage (16%), and sunray (13%).

Precipitation at the Lakeshore Scenic Drive area was above average in 1994/1995 and 1997/1998, when the first three phases of construction were completed. However, the site received 13% of average precipitation during the winter and spring of 2001/2002 when this study was conducted, marking the fourth consecutive year of below-average precipitation at LMNRA.

Discussion

Surface soil salvage has been widely adopted in restoration and reclamation for promoting soil genesis (Allen, 1995). Soil transplantation from nearby undisturbed locations has proven successful in such diverse locations as wetlands (Brown and Bedford, 1997) and the jarrah forest of western Australia (Koch and Ward, 1994). In combination with moisture-conservation techniques, surface soil replacement has been shown to increase growth of seeded or planted vegetation in arid lands, including the Sonoran Desert (Norem and Day, 1985), the Thar Desert in India (Sharma et al., 2004), and sagebrush habitat in Wyoming (Cotts et al., 1991). The process of soil salvage and its influence on seed reserves, however, has been studied little, especially in systems with a shallow seed reserve profile.

We found that surface soil collection alone as carried out during road construction at LMNRA decreased effective seed reserves by 79% likely because deeper, seedless fractions of the soil profile became mixed with the top few centimeters. In the Mojave Desert, 88% of seed reserves have been found to reside within the top 2 cm of soil (Guo et al., 1998). Such shallow distribution of seed reserves has also been measured in the other desert systems of North America (Pake and Venable, 1996; Childs and Goodall, 1973). Given the tremendous dilution of seed reserves we measured, it would be beneficial to explore methods of surface soil collection such as double stripping (Tacey and Glossop, 1980) in arid systems to reduce mixing of soil fractions by concentrating collection efforts in the top few centimeters of soil.

While the fate of seed reserves is not well known in the desert southwest of North America, seed loss associated with soil reclamation has been studied extensively in western Australia. Several studies have shown that single-stripping of the top 10–30 cm of soil and stockpiling is a less effective revegetation technique than double-stripping and direct return (Tacey and Glossop, 1980; Bellairs and Bell, 1993; Ward, Koch, and Ainsworth, 1996; Koch, Ward, Grant, and Ainsworth, 1996; Rokich et al., 2000). Double-stripping keeps the top 5 cm of soil separate from the overburden (5–40 cm), while direct return refers to this top 5 cm being returned to an adjacent reclamation area immediately upon collection without stockpiling.

The slow recovery of perennial plant cover, density, and species composition at LMNRA 7 years after surface soil reapplication is consistent with natural recovery of desert plant communities. Even 51 years after the abandonment of a town site in the northern Mojave Desert, the cover, density, and composition of perennial vegetation differed markedly compared with an undisturbed control site (Webb and

Wilshire, 1980). In the 7 years since surface soil was first reapplied along Lakeshore Scenic Drive, there have been 3 years with less than 50% of average precipitation and only 1 year above the average. These dry conditions are not conducive to rapid perennial plant establishment and growth, and are undoubtedly an important factor influencing revegetation in the Mojave Desert. The marked increase in the bulk density of respread soil also has the potential to reduce seedling emergence, establishment, and growth.

Germinable seed reserves in stockpiled soil have been found to decrease as storage time increases, with the largest reduction in perennial plant species (Bellairs and Bell, 1993; Rokich et al., 2000). At a bauxite mining site in Australia, seed reserve reductions occurred both when surface soil was collected and during 10 months of storage (Koch et al., 1996). Conversely, another study at a bauxite mine attributed seed reserve reduction mainly to the soil collection phase because seed-rich soil from 0–2 cm in depth mixed with deeper seedless soils, thereby burying seeds at depths unfavorable for emergence upon respreading (Tacey and Glossop, 1980). Despite seed reserve declines, soil that was either stockpiled or returned directly after collection has been found to make a significant contribution to species richness in reapplication areas (Koch and Ward, 1994).

In our study, conditions within the soil pile were cooler and moister than those experienced by seeds at the undisturbed control site, but the relationship between these conditions and germinable seed reductions could not be adequately determined. The effect of these conditions on stored Mojave Desert seeds needs to be explored in detail, as has been done with 12 important Australian woodland species (Rokich et al., 2000). Cool, moist conditions increase fungal activity and false germination of seeds, both potentially detrimental to seed reserves (Baskin and Baskin, 1998). Impacts on the native mycorrhizal community should also be considered because a reduction could impair establishment of many desert plant species in surface soil reapplication areas. In desert soils, mycorrhizal spore reserves are likely diluted during the soil salvage process, just as seed reserves are. As many mycorrhizal spores are susceptible to infection, increased fungal activity within the cool, moist storage pile could also negatively impact the mycorrhizal community (Morton, 2002). A study conducted 7 years after reapplication found fewer mycorrhizal spores in stockpiled soil than in undisturbed control areas (Stahl, Perryman, Sharmasarkar, and Munn, 2002). This decline corresponded to reduced herbaceous plant cover.

Despite low seed numbers, our data suggest that germinable seed numbers increased between weeks 3 and 8 of stockpile storage and were higher near the stockpile surface than at 50 cm. This finding indicates that seeds colonized the soil pile during the time surface soil was stored, adding to the seed reserves. Previous studies have found only one species that increased with surface soil storage, possibly due to the soil stockpiles trapping wind-blown seed (Rokich et al., 2000). Alternatively, the germinability of seeds already in the soil pile may have increased during storage under relatively cool, moist conditions (Baskin and Baskin, 1998). Due to the small number of samples containing seeds in this study, the effects of storage depth and duration on Mojave Desert species require more detailed examination.

The density of germinable seed we found in undisturbed control soil samples at LMNRA (752 seeds m^{-2}) falls at the lower end of values found by other studies in the Mojave Desert. Seed densities from 427 seeds m^{-2} (Guo, Rundel, and Goodall, 1999) up to 7,682 seeds m^{-2} (Nelson and Chew, 1977) have been measured in the Mojave Desert. Most seed reserve studies, however, have not discriminated between germinable and dead or inviable seeds, likely inflating the densities of seeds measured. Mojave Desert seed reserves also display seasonal variation, increasing from February through June, as winter annual plants shed seed, and subsequently decreasing until October, when the seed-harvesting activities of ants and rodents diminish (Nelson and Chew, 1977). Collection of surface soils in early summer, as in this study, should therefore coincide with maximum seed reserve densities.

Annual plant species dominated the germinable seed reserves. Perennial seeds in the Mojave Desert are most often located in litter and on the soil surface under shrubs (Guo et al., 1998). The low abundance of perennial plants in the Lakeshore Scenic Drive area likely makes perennial seed distribution highly variable and the seeds therefore less likely to be sampled than annual species in the area. Perennial seed also occurs at naturally lower densities than annual seeds in the Mojave Desert, often an order of magnitude lower in abundance (DeFalco et al., unpublished data). We expect that perennial plant seed, even though poorly represented in our samples, would experience the same magnitude decrease in abundance because they occupy the same shallow soil layers as annual seeds and would be as indiscriminately collected using heavy machinery.

Conclusions

The reduction in seed reserves during surface soil reclamation in this study was 86%, mostly occurring when topsoil was collected with bulldozers. Handling of the surface layer separate from other topsoil layers, such as is done in double-stripping, may reduce dilution of seed reserves and enhance plant re-establishment on disturbances in soils with shallow seed banks.

Seedlings of many species emerge most successfully from soil depths less than 2 cm in nondesert systems (Grant et al., 1996; Rokich et al., 2000; Zhang et al., 2001). Using an equation developed by Bond et al. (1999) to predict maximum emergence depth based on seed mass, we expect the heaviest seed we found in LMNRA soil samples (red brome, 2.5 mg per seed) to emerge from a 3.7 cm depth. In the Sonoran Desert, seedling emergence of three common perennial species was reduced by 50–100% at soil depths of 3 cm compared to 1 cm burial (Bowers, 1996). Although this relationship has not been explored for Mojave Desert species, shallow emergence is expected when the majority of natural seed reserves are found in the top 2.5 cm of soil. For this reason, it is important to reapply stored soil to as shallow a depth as possible to allow for effective germination by all seeds present (Grant et al., 1996; Rokich et al., 2000; Zhang et al., 2001).

If low densities of re-establishing perennials reflect the dilution of seed reserves we measured during the reclamation process, consideration should also be given to reseeding disturbed areas with seed mixtures representing the extant plant species. Litter and plant material collected before construction activities and spread over reapplied surface soil has proven effective at replacing some seed species lost during soil collection and storage (Koch and Ward, 1994; Bellairs and Bell, 1993). When surface soil cannot be collected and respread at very shallow depths (≤ 5 cm), off-site seed collection from shrubs and distribution after disturbance may be the most feasible way of returning native seed to the landscape.

Even when salvaged surface soil does not constitute a significant source of seed, as in this study, it can provide a superior growth medium for plants compared to subsurface soils (Norem and Day, 1985; Zhang et al., 2001). The salvage of surface soils with their associated seed reserves is an important technique with the potential to accelerate restoration and reclamation efforts. Most importantly, alternative methods of surface soil collection should be explored in environments with shallow seed reserves and designed to minimize seed reserve dilution.

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