SEED MOVEMENTS AND SEEDLING FATES IN DISTURBED SAGEBRUSH STEPPE ECOSYSTEMS: IMPLICATIONS FOR RESTORATION

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Abstract. Understanding species establishment patterns and community structure following disturbance, and developing effective restoration methods requires knowledge of both the movements and fates of seeds. I used a restoration experiment in a severely disturbed sagebrush steppe ecosystem near Kemmerer, Wyoming to examine the effects of soil surface characteristics and seed morphology on seed entrapment and retention, and the effects of soil surface characteristics on soil water potential and seedling emergence and survival. Seeds of native species with awns, mucilaginous seedcoats, wings, hairy pappi, or no appendages were sown over soil surface treatments consisting of silty loam soil, sand, gravel, surface mulch, shrub mimics, and large and small holes. Seeds that lacked appendages and that had small surface areas did not exhibit significant horizontal movement or redistribution. Seeds with appendages that resulted in exposure of a large surface area to the wind did exhibit significant redistribution, despite apparent adaptations for seed burial or retention. When the entire seed population was considered, the effectiveness of the treatments for trapping and retaining seeds was large holes > small holes ≥ gravel ≥ shrub mimics > soil ≥ sand. Surface mulch neither gained nor lost seeds. The most effective treatments for seedling emergence had among the least negative soil water potentials and included large holes, surface mulch, and sand. Gravel provided an inadequate growing medium, and both shrub mimics and small holes accumulated fine-textured soils resulting in highly negative water potentials and low seedling emergence. Once a seedling emerged, the probability of survival was reasonably high (56.3% over 2 yr) regardless of treatment. This study indicates that soil surfaces that trap and retain high densities of seeds with large surface areas may have little or no effect on seeds with small surface areas, and may or may not result in high seedling emergence and survival. Restoring diverse native ecosystems requires creating soil surface features that can trap and retain seeds with varying morphologies as well as provide favorable conditions for seedling establishment.

Key words: depressions; disturbance; litter mulch; restoration; seed attributes; seed dispersal; seed entrapment; seed retention; seedling emergence and establishment; semiarid ecosystems; shrubs; soil particle size; surface.

INTRODUCTION

Knowledge of the movements and fates of seeds is essential for understanding species establishment patterns and community structure and, consequently, for restoring disturbed ecosystems. In arid and semi-arid ecosystems the movement of seeds once they have arrived on the soil surface, or Phase II dispersal, is as or more important in determining seed fates than is the movement of seeds from the parent plant to the soil surface, or Phase I dispersal (Chambers and MacMahon 1994). When these ecosystems are severely disturbed, Phase II dispersal is often even more important. The seed bank can be lost or reduced if the topsoils and vegetation are removed (Dickie and Gajjar 1988, Johnson and West 1989). Ecosystem recovery then depends on seeds that are naturally dispersed to the site or placed on the site during restoration. Because wind is a dominant feature of the environment in arid and semi-arid ecosystems, significant horizontal and vertical movement of both naturally and human-dispersed seeds can occur before they arrive at their final resting spot.

Despite the critical consequences of abiotic Phase II seed dispersal for seedling establishment in arid and semi-arid ecosystems, relatively few studies have focused in this area and most have been on single or related species (Peart and Clifford 1987, Stamp 1989a, b, Kelrick 1991, Russel and Schupp 1998). At the community level, we know very little about the effects of soil surface characteristics on seed entrapment and retention (but see Reichman 1984) or the influence of seed morphology on patterns of seed entrapment. Also, we have little information about the combined effects of Phase II seed dispersal processes and seedling establishment requirements on plant establishment patterns (but see Peart and Clifford 1987). Determining how soil surface characteristics and seed morphology affect seed entrapment and seedling establishment patterns is difficult because it requires evaluating several different surface characteristics and multiple species simultaneously. Restoration experiments permit a high
degree of manipulation and, thus, are conducive to examining the requisite number of surfaces and species.

In arid and semi-arid ecosystems, several common soil surface characteristics potentially influence seed dispersal and seedling establishment and can be manipulated both experimentally and during restoration. Soil particle size varies across the landscape depending on the geologic material, topography, and erosional processes, and has been shown to affect seed entrapment and seedling establishment in other ecosystems (Chambers et al. 1991, Chambers 1995). Surface litter can prevent movement of seeds arriving on the surface or trap wind-blown seeds (Fowler 1986, Stamp 1989b). Surface mulches used during restoration can hold both seeds and soils in place in windy environments (Chambers et al. 1990), and can increase soil water availability during critical seedling establishment periods (Cochran 1969, Munshower 1994). Crevices and both large and small holes from soil cracking, animal digging, or burrowing can trap seeds (Reichman 1981, 1984, Eckert et al. 1986), and often provide favorable soil water relations for establishment (Eckert et al. 1986, Evans and Young 1987). These characteristics are mimicked during restoration by soil gouging in which holes are scooped into the soil to concentrate soil water (Dollhopf et al. 1985). Wind barriers such as shrubs, rocks, or woody debris trap wind-transported seeds, soil fines, and litter on the downwind side of the shrub or barrier (Fuentes et al. 1984, Reichman 1984, Mull and MacMahon 1996, Russel and Schupp 1998), and influence soil water relations by accumulating snow and channeling water to their bases.

Seed morphology influences seed entrapment, seed retention, and seedling establishment, and is another important consideration in restoration. Seed size determines the soil depth from which seedlings can emerge; seedlings from large seeds emerge from deeper in the soil than those from small seeds (Evans and Young 1987, Munshower 1994). Consequently, larger seeds can be drilled into the soil, but smaller seeds must be placed on or near the soil surface where they are subject to movement by wind and less favorable soil water conditions. Because of this requirement, and also the limited information available on native species establishment, restoration efforts have often included large-seeded, broadly adapted, introduced species and either excluded or used only small quantities of native species (Richards et al. 1998). Many native sagebrush steppe species have seeds with morphological attributes that could potentially increase seed entrapment or burial, and that could be used to facilitate restoration of native ecosystems. For example, several grass species have passive awns or barbed calluses that can serve to orient and anchor the seeds in a standing position that is favorable for seed germination, or hygroscopic awns that can auger seeds into the soil surface (Peart 1979, 1981, 1984).

Restoring diverse native communities requires creating soil surfaces that are effective in both trapping and retaining seeds with varying morphologies and in providing favorable conditions for seedling establishment. Previous research has shown that relationships between the soil surface characteristics and seed morphological attributes determine the rate and distance of movement, and the likelihood of being captured and retained in particular microsites (Stamp 1989b, Chambers et al. 1991, Johnson and Fryer 1992). The environmental characteristics of the microsites in which seeds ultimately come to rest determine the likelihood of seedling establishment (e.g., Harper et al. 1965, Stamp 1989b, Chambers 1995). It has been suggested that the effectiveness of animal dispersers be evaluated as “the contribution a disperser makes to the future reproduction of a plant” population (Schupp 1993). Effectiveness has a quantitative component (number of seeds dispersed), and a qualitative component (likelihood that a dispersed seed will survive to produce a new plant in the population). These concepts apply equally well to abiotic Phase II dispersal. The effectiveness of soil surface characteristics can be evaluated in terms of their ability to trap and retain seeds (quantity) and provide suitable microsites for establishment (quality). The total number of seedlings that establish result from both the quantitative and qualitative components.

Restoration experiments can increase our understanding of both basic processes and their ecological applications. In this study, I use a restoration experiment in a severely disturbed (mined) semi-arid ecosystem to examine the effectiveness of different soil surface characteristics on seed entrapment and retention, on seedling emergence, and on the survival of species with varying seed morphological characteristics. Because of the importance of soil water availability in determining the qualitative effectiveness of soil surface characteristics for seedling establishment in this ecosystem, I also examine the effects of the soil surface characteristics on soil water potential. The implications of the results for restoring sagebrush steppe ecosystems are discussed.

**Methods**

The study site is on the Pittsburgh and Midway Company coal mine in southwestern Wyoming (41°43' N, 110°37' W; elevation 2240 m). This area is typical of the semi-arid sagebrush steppe that occurs at higher elevations in this region (West 1983). Mean monthly temperature ranges from −8°C in January to 17°C in July, and most of the annual mean precipitation of 226 mm arrives as winter snow. Wind is a persistent feature of this landscape. Soils are primarily coarse-loamy, mixed-frigid, typic Ustiluvents. Dominant native plant species in the original communities include the shrubs *Artemisia tridentata xericensis*, *A. arbuscula,* and *Chrysothamnus viscidiflorus,* and the grasses *Elymus elymoides,* *Achnatherum hymenoides,* and *Heterostipa*...
comata (grass nomenclature follows Barkworth and Dewey 1985; M. Barkworth, personal communication; other nomenclature follows Hickman 1993).

The study site had been mined, the overburden material replaced, and the area shaped to a slope of \(5\%\). In August 1991, topsoil that had been removed from the preexisting native community and stockpiled for 12 mo was spread over a study area \(30 \times 65\) m to a depth of \(30\) cm. The study treatments were applied in October after most of the native species in the area had dispersed seed. The study design was a randomized, complete block with four replications (blocks). Eight different soil surface treatments were randomly located within each block. Circular treatment plots (10 m\(^2\)) were used to minimize boundary area, and plot spacing was \(3\) m so that the primary interchange of seeds for any given plot was with the adjacent interspace. The treatment plots were divided into four equal sections, with the principal axis of each plot parallel to the prevailing wind direction (west).

The treatments examined the effects that varying soil particle sizes, surface mulches or litter, small and large holes, and shrub mimics had on soil water potential, seed entrapment and retention, seedling emergence, and survival of species with varying seed morphology. The soil treatments were applied to the plots after the topsoil had been leveled by raking and included: (1) smooth, bare topsoil; (2) a 2-cm layer of coarse sand (0.5 to 4 mm diameter); (3) a 2-cm layer of gravel (4–16 mm diameter); (4 and 5) a commercially prepared straw mulch “blanket” (1–2 cm deep) applied (a) before or (b) after the site was seeded; (6) small holes uniformly spaced 20 cm apart (8 cm wide \(\times\) 3 cm deep, \(\sim 130\) holes per treatment plot); (7) single large holes (50 cm wide \(\times\) 10 cm deep, one in each plot subsection, \(n = 4\) per plot); and (8) two-dimensional shrub mimics (one in each plot subsection, \(n = 4\) per treatment plot). The purpose of the shrub mimics was to duplicate the wind barrier effect of shrubs. They consisted of rectangular pieces of thin sheet-metal (20 cm high \(\times\) 78.5 cm long) that were stood upright and bent into a half-circle with a 0.5 m diameter. The exterior of the half-circle was pointed into the prevailing wind (west), and staked down with rebar. The height and diameter of the shrub mimics were determined by measuring low-growing native shrubs (A. arbuscula and C. viscidiflorus) in an adjacent undisturbed community.

Following application of the soil treatments, the entire area (excluding one set of mulched plots) was broadcast seeded by hand. The set of mulched plots that was seeded after the mulch blanket was applied (mulch + seed) was used to examine the effects of seed entrapment, while plots that were seeded before mulch application (seed + mulch) evaluated seed retention. The seeded species were native perennial grasses, forbs, and shrubs with different seed morphological characteristics including awns, mucilaginous seed-coats, wings, hairy pappi, and no appendages (Table 1). Species with different seed masses were included to evaluate the effects of seed size and seed appendages independently. Commercially purchased seeds that were adapted to local conditions and that had intact appendages were used. The seeding level was 60 viable seeds of each of the 11 species/m\(^2\). Seed viability was tested with standard tetrazolium tests (Copeland 1981).

To ensure uniform seed application, four parts rice hulls were mixed with one part seeds prior to seeding, and each replicate was seeded separately. Rice hulls facilitate uniform broadcast seeding by keeping the different seed types evenly dispersed, providing a larger volume of material, and serving as a visual marker. The study plots were located within a large area that had been mined and not yet revegetated. Thus, it is likely that seed predation by animals was minimal. The only potential seed predators observed during the 2-yr study were horned larks (Eremophila alpestris).

### Table 1. Seed morphological attributes of species used in the experiment.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean mass (mg)</th>
<th>Length with appendage (mm)</th>
<th>Length without appendage (mm)</th>
<th>Maximum width (mm)</th>
<th>Special attribute</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Achnatherum hymenoides</em></td>
<td>3.7</td>
<td>4.2 ± 0.04</td>
<td>1.5 ± 0.02</td>
<td>basal hairs</td>
<td></td>
</tr>
<tr>
<td><em>Pascopyrum smithii</em></td>
<td>4.1</td>
<td>9.4 ± 0.2</td>
<td>1.5 ± 0.04</td>
<td>awn-tipped</td>
<td></td>
</tr>
<tr>
<td><em>Elymus elymoides</em></td>
<td>1.6</td>
<td>28.1 ± 1.1</td>
<td>7.1 ± 1.1</td>
<td></td>
<td>bent awn</td>
</tr>
<tr>
<td><em>Heterostipa comata</em></td>
<td>6.9</td>
<td>150.0 ± 7.3</td>
<td>9.8 ± 0.3</td>
<td>0.9 ± 0.03</td>
<td>hygroscopic awn</td>
</tr>
</tbody>
</table>

Forbs

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean mass (mg)</th>
<th>Length with appendage (mm)</th>
<th>Length without appendage (mm)</th>
<th>Maximum width (mm)</th>
<th>Special attribute</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sphaeralcea munroana</em></td>
<td>0.7</td>
<td>1.6 ± 0.03</td>
<td>1.3 ± 0.03</td>
<td>none</td>
<td></td>
</tr>
<tr>
<td><em>Penstemon palmerii</em></td>
<td>1.1</td>
<td>1.8 ± 0.04</td>
<td>1.3 ± 0.03</td>
<td>none</td>
<td></td>
</tr>
<tr>
<td><em>Linum lewisii</em></td>
<td>1.6</td>
<td>3.5 ± 0.04</td>
<td>2.1 ± 0.03</td>
<td>mucilaginous seed coat</td>
<td></td>
</tr>
</tbody>
</table>

Shrubs

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean mass (mg)</th>
<th>Length with appendage (mm)</th>
<th>Length without appendage (mm)</th>
<th>Maximum width (mm)</th>
<th>Special attribute</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Artemisia tridentata</em></td>
<td>0.5</td>
<td>2.1 ± 0.05</td>
<td>1.0 ± 0.02</td>
<td>none</td>
<td></td>
</tr>
<tr>
<td><em>Artemisia nova</em></td>
<td>0.5</td>
<td>5.2 ± 0.16</td>
<td>3.7 ± 0.21</td>
<td>4-wings</td>
<td></td>
</tr>
<tr>
<td><em>Chrysothamnus viscidiflorus</em></td>
<td>0.5</td>
<td>3.6 ± 0.12</td>
<td>0.6 ± 0.01</td>
<td>hairy pappus</td>
<td></td>
</tr>
</tbody>
</table>

Note: Individual seed masses were obtained from a composite sample of \(n = 100\); individual lengths and widths are means ± se; \(n = 20\).
Destructive sampling (seed entrapment and retention, and soil water potential) was conducted in two diagonally opposite sections of the treatment plots, while nondestructive sampling (seedling emergence and survival) was performed in the other two sections. To determine the total number of seeds retained in or dispersed to the different soil surface treatments, eight soil seed samples were collected from each of the four treatment replications just prior to seed germination in March 1992. Individual soil samples were collected from small blocks (10 cm × 10 cm) stratified by depth. Past work indicated that it was unlikely that seeds would move beyond the 6 cm depth in the fine-textured (silty clay loam) topsoils on the study area (Chambers et al. 1991). Thus, for all treatments, soils were collected from the 0–1 cm and the 1–6 cm depths (8 samples × 4 replicates × 2 depths [n = 64 per treatment]). Also, for the sand, gravel, and straw surface treatments, the treatment layer (sand, gravel, or straw) was collected (8 samples × 4 replicates [n = 32 per treatment]). Soil blocks from the large-hole treatment were taken from the bottoms of the holes, while blocks from the small-hole treatment encompassed entire 8-cm holes. Samples collected from shrub mimics were located on the downwind side of the artificial shrub. In the laboratory, seeds were extracted from the soils with a high-density salt solution, identified to species, and counted (Malone 1967). This procedure has been shown to retrieve ~99% of the seeds (Chambers et al. 1991). For mulched plots, seeds were highly visible, and so were picked from the straw and then identified and counted. The seed counts determined filled seeds, that were then converted to numbers of viable seeds, based on the original viability tests. A random sample (n = 10) of the soil seed bank collected prior to seeding revealed none of the study species, indicating that seeds from the topsoil had a minimal effect on the study results.

Seedling emergence and survival were monitored at 2–5 wk intervals throughout the 1992 and 1993 growing seasons (April through August) in the two nondestructive portions of each treatment plot (2 samples × 4 replicates [n = 8 per treatment]). Standard mapping table techniques (Chambers and Brown 1988, Chambers et al. 1990) were used with a plot size of 0.5 m. For the treatment with large holes, one large hole was monitored. For the shrub mimic treatment, seedling emergence and survival were monitored on the downwind side of the barrier.

Because of the importance of water for seedling establishment in these arid ecosystems, near-surface (0–2 and 2–10 cm depths) soil water potentials were determined for the same sample dates as seedling emergence and survival. The same sample locations were used as for seedling survival, except that the samples were collected from the destructive portions of the plots. For the mulch and gravel treatments, soils were collected from beneath the treatment layer. Soil samples were extracted using a small soil corer (3 cm in diameter), placed in sealed containers, and transported to the lab. Soil water potentials of samples with values of >−8.0 MPa were determined using screen-caged, single-junction, Peltier thermocouple psychrometers under isothermal conditions; those with values of <−8.0 MPa were analyzed with a Decagon DC-10 thermocouple psychrometer (Decagon Devices Incorporated, Pullman, Washington), again under isothermal conditions (Brown and Bartos 1982).

A general linear model (ANOVA) for analyzing randomized, complete block designs was used to examine overall differences among treatments, species, and depths for the seed entrapment and retention data, and to evaluate differences among treatments and species for the seedling emergence data using Proc GLM in SAS (SAS Institute, Incorporated 1993). Both species and depths were treated as split-plot factors. Separate analyses were performed on both data sets to evaluate differences among treatments for individual species, and on the seed entrapment and retention data to examine differences among species and depths within individual treatments. Because it was not possible to distinguish seeds of the two Artemisia species from one another after extraction from the soil, these species were combined in the seed entrapment and retention analyses. The soil water potential data were analyzed with repeated measures ANOVA to examine differences among treatments, depths, and dates, with dates as the repeated measure. Depths were again treated as a split-plot factor. Mean comparisons were conducted using t test comparisons of least square means (LSM: least squares estimates of marginal means) (SAS Institute, Incorporated 1993).

Logistic regression was used to examine differences in seedling survival among treatments and years in SAS (SAS Institute, Incorporated 1993). The likelihood ratio test and binomial response distribution were used. Seedling emergence of several seeded species was low, and both the emergence and survival analyses were performed only for mean seedling numbers of all species combined, and for A. hymenoides, E. elymoides, Pascopyrum smithii, and Linum lewisii. Because of a high proportion of zeros in the survival data, only the total numbers of individuals that survived to the ends of the first and second growing seasons were included in the analyses.

**Results**

*Seed entrapment and retention*

Distinct differences existed in the total number of seeds that were either retained in or dispersed to the various soil surface treatments (Fig. 1). In this windy shrub steppe environment, the highest total number of seeds was located in large holes, followed by small holes. Soil particle size was an important factor in determining seed entrapment and retention, and gravel
had the third-highest number of seeds. The bare soil and sand treatments had the lowest numbers of seeds, although these did not differ significantly from the seed + mulch treatment. The shrub mimic had higher seed numbers than the bare soil and sand treatments. Both the seed + mulch and mulch + seed treatments had approximately the same numbers of seeds as were originally broadcast onto the site (i.e., 60 seeds $\times$ 11 species or 660 seeds/m²).

Significant differences existed among species in overall numbers of seeds trapped ($F_{7,144} = 31.1$, $P \leq 0.0001$), and in their responses to the different soil surface treatments (species $\times$ treatment interaction; $F_{63,144} = 1.1$, $P = 0.011$). The species with seeds lacking specialized morphological features exhibited no or slight differences among surface treatments (A. hymenoides, P. palmerii, S. munroana, and Artemisia sp.) (Fig. 2). Achnatherum hymenoides, a species with heavy seeds and basal hairs, had similar seed numbers among treatments, and seed numbers were only slightly higher than the original seeding level. In contrast, the lightweight seeds of the Artemisia species had similar numbers among treatments, but occurred at lower numbers than were originally seeded and than any of the other species. Both Penstemon palmerii and Sphaeralcea munroana had intermediate seed numbers and appeared to exhibit some seed redistribution, but high variability, especially for S. munroana, may have obscured real differences.

Species that exhibited significant differences among treatments generally had seeds with large surface areas, and many had specialized appendages for seed retention or burial (Fig. 3). The awned grasses, E. elymoides and Heterostipa comata, and the large-seeded awntipped grass, P. smithii, exhibited strong treatment differences and also had among the highest seed entrapment and retention. Species with winged seeds (Atriplex canescens) or seeds with pappi (C. viscidaflorus) had highly significant treatment differences, but had low seed entrapment and retention, indicating high mobility. A species with a mucilaginous seedcoat, Linum lewisii, exhibited differences among treatments, but had intermediate seed entrapment and retention.

The vertical movement of seeds varied among surface treatments for those treatments with only two sample depths (treatment $\times$ depth interaction, $F_{3,16} = 8.3$, $P = 0.008$; Fig. 1). Bare soil exhibited no differences in seed numbers between the 0–1 and 1–6 cm soil depths. In contrast, the shrub mimics, small holes, and large holes all had higher numbers of seeds in the 0–1 cm depth than in the 1–6 cm depth ($P = 0.01$, $P = 0.0003$, and $P = 0.0002$, respectively). Differences in the vertical movement of seeds also existed among the sand, gravel, and mulch treatments (treatment $\times$ depth interaction, $F_{5,16} = 8.0$, $P = 0.0004$). The gravel treatment had higher numbers of seeds in the surface layer than in the 1–6 cm depth ($P = 0.026$), but the surface and 0–1 cm depth had similar seed numbers. The sand treatment had higher numbers of seeds in the sand layer than the 0–1 cm soil depth ($P = 0.052$). For the treatment that was seeded and then mulched, no seeds were found in the mulch layer and the 0–1 cm depth had higher numbers of seeds than the 1–6 cm depth ($P \leq 0.0001$). In contrast, for plots that were mulched and then seeded, similar numbers of seeds were found in the surface mulch and two soil depths.

In general, the vertical movement of seeds resulting from the different surface treatments was consistent among species. An exception was the mulch + seed treatment. Seeds of all species were found in the surface mulch, but only the awned seeds of H. comata and E. elymoides, and the mucilaginous seeds of L. lewisii occurred in higher densities in the straw mulch than in the 0–1 or 1–6 cm depths ($P \leq 0.05$).

**Seedling emergence**

Overall seedling emergence was low, and the number of seedlings that emerged for all species combined varied significantly among treatments (Fig. 4). Higher numbers of seedlings emerged from the treatment with large depressions than from most other treatments. The sand and mulch treatments had the next highest emergence values. Shrub mimics and small depressions had slightly lower emergence, but did not differ from the sand or seed + mulch treatments. The lowest emergence was from the soil and gravel treatments. Individual species analyses revealed differences among treatments only for P. smithii and L. lewisii, despite
somewhat similar patterns for *E. elymoides* and *A. hymenoides* (Fig. 4).

To provide an assessment of the overall environmental quality of the different soil surfaces for seedling emergence, independent of seed densities (quantity), differences among treatments for all species combined were examined, with seedling emergence calculated as a proportion of the seeds that were trapped and retained in the individual treatments. The data were arcsine-transformed and analyzed with the same ANOVA model used for the nonproportional data. When the data were examined in this manner, significant differences still existed among treatments ($F_{7,14} = 3.3, P = 0.026$), however, the highest proportional emergence was in the sand treatment ($P = 0.05$), followed by the mulch treatments. Large holes had only intermediate proportional emergence, while shrub mimics, small holes, bare soil, and gravel had low proportional emergence. The difference in the results for the proportional vs. nonproportional data indicate that overall seedling emergence was a function of both the numbers of seeds trapped (quantity) and microsite conditions (quality).

### Seedling survival

Once a seedling emerged, the probability of survival to the end of the study was relatively high (53.6%). Logistic regression indicated that overall species survival was dependent upon both treatments ($\chi^2 = 15.7, df = 7, P = 0.03$) and years ($\chi^2 = 14.7, df = 1, P \leq 0.0001$) (Fig. 5). At the end of the 2-yr study, sand had the highest overall survival, followed by the large holes, mulch treatments, shrub mimics and small holes. Bare soil and gravel had the lowest 2-year survival. In this arid environment, survival decreased from 64% the first year to 43% the second year. Low seedling emergence and the failure of several of the species to emerge within all of the treatments made comparisons between species and between treatments within species

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**Fig. 2.** The mean numbers of seeds trapped or retained in the sand, gravel, or mulch layer and in 0–1 cm depth or 1–6 cm depth of soils with different surface treatments in a disturbed sagebrush steppe ecosystem, for species with seeds lacking appendages. Vertical bars represent ± 1 SE and are for the means of all surface layers and soil depths combined. The $P$ values shown are for ANOVA results comparing treatment differences. Treatments with different letters differ statistically (LSM; $P < 0.05$).
Fig. 3. The mean numbers of seeds trapped or retained in the sand, gravel, or mulch layer and in 0–1 cm depth or 1–6 cm depth of soils with different surface treatments in a disturbed sagebrush steppe ecosystem, for species with seeds that have appendages. Vertical bars represent ±1 SE and are for the means of all surface layers and soil depths combined. The P values shown are for ANOVA results comparing treatment differences. Treatments with different letters differ statistically (LSM; P < 0.05).
FIG. 4. The mean numbers of seedlings (+1 se; \( n = 8 \)) that emerged from soils with different surface treatments in a disturbed sagebrush steppe ecosystem. Data are for all seeded species combined and for the four seeded species with the highest emergence. The \( P \) values shown are for ANOVA results comparing treatment differences. Treatments with different letters differ statistically (LSM; \( P < 0.05 \)).
difficult. In general, *E. elymoides* and *P. smithii* had the highest survival for those treatments with emergence. *Achnatherum hymenoides* had intermediate survival, while *L. lewisii* had low survival. Individual species analyses showed that differences existed only for *E. elymoides*.

**Soil water potential**

On this arid site, soil water potentials differed significantly among surface treatments ($F_{7,21} = 15.4, P \leq 0.0001$), depths ($F_{1,24} = 561.7, P \leq 0.0001$), and dates ($F_{6,288} = 147.5, P \leq 0.0001$). The least significant means procedure ordered the treatments as follows:
soils beneath gravel < soils beneath mulch < large holes = sand < shrub mimic = bare soil = small holes (P ≤ 0.05). In general, the soils beneath the gravel and straw mulch consistently had the least negative water potentials, while the bare soil, shrub mimic, and small holes were the most negative (Fig. 6). Sand and large holes had intermediate soil water potentials. The soils at the 2–10 cm depth were less negative than those at the 0–2 cm depth for almost all dates (P ≤ 0.05). The highly negative values for the 0–2 cm depths for most of the sampling dates (>1.5 MPa) indicate that only a short time period existed in which germination and initial root elongation could occur for seeds within that depth interval. The higher water potentials for the 2–10 cm depth indicate a higher potential for growth and survival of species with seeds that can germinate and emerge from greater depths or that exhibit rapid root elongation.

**Discussion**

*Seed entrapment and retention*

This study illustrates that the movement of seeds after they have arrived on the soil surface, or Phase II dispersal, is clearly important in determining the quantity of seeds dispersed to different microsites in disturbed sagebrush steppe environments. The quantity of seeds trapped and retained in the different soil surfaces depended on relationships between the soil surface characteristics and seed morphologies of the individual species. When the entire seed population was considered, most seeds were blown off the bare soil and sand, and accumulated in the large-hole, gravel, shrub mimic, and small-hole treatments. Higher total seed densities relative to bare soil have been observed in large and small surface depressions (Reichman 1981, 1984), in soil crevices (Evans and Young 1987), and under shrubs (Mull and MacMahon 1996) in other arid ecosystems. However, when individual species were examined, distinct differences in seed entrapment patterns existed that were directly attributable to seed morphology. Small or heavy seeds that lacked specialized morphological attributes exhibited little redistribution regardless of soil surface characteristics (see Chambers et al. 1991, Thompson et al. 1993). The relatively heavy mass and small size of *A. hymenoides* seeds and the low mass and small size of *Artemisia* seeds resulted in little or no horizontal movement of these species. Although the heavy seeds of *P. palmeri* exhibited some redistribution, they appeared to be near or at the threshold for seed retention. For these seed types, different soil surface characteristics appear to have little effect on horizontal seed movement and, consequently, seed dispersion patterns.

Seeds that exhibited significant redistribution had morphological features that resulted in the exposure of a large surface area to the wind, and generally exhibited similar patterns. The large, winged seeds of *A. canescens* were obviously adapted for movement over the soil surface, but many of the other species exhibited significant redistribution despite having seeds with specialized attributes for soil burial or retention (mucilaginous seed coats, hygroscopic awns, and collapsing pappi). The seed coats of *L. lewissii* are characterized by the mucilage that adheres to the soil surface when hydrated, resulting in seed retention (see Gutterman et al. 1967, Chambers et al. 1991). *Heterostipa comata* has a mucilage, hygroscopic awns, *E. elymoides* has awned rachis segments, and *C. viscidiflorus* has pappi that all respond to humidity by moving the diaspores over the soil surface and pushing them into the soil under the right conditions (see Sheldon and Burrows 1973, Peart 1979, 1984). Under dry, windy conditions, the primary effect of these appendages appeared to be tossing and moving the seed about, an effect observed for awned grasses in other arid ecosystems (Fowler 1986, Peart and Clifford 1987). This indicates that in arid and wind-driven environments, seed attributes for soil burial or retention that require high humidity are often ineffective, and that surface area is relatively more important in determining seed dispersion patterns.

*Seedling establishment*

While relationships between soil surface characteristics and seed morphological attributes determined the quantity of seeds trapped and retained in the different soil surfaces, environmental characteristics determined the quality of the soil surfaces for seedling emergence and survival. Differences among both treatments and species were most evident during the seed germination and seedling emergence stages. Seedling emergence in sagebrush steppe is often low (e.g., Pyke 1990), and was <2% for all species combined in the current study. Overall low seedling emergence was due largely to the highly negative soil water potentials of surface soils and the short time frames in which there was adequate soil water available for germination and establishment. Most of the study species exhibit seed dormancy (e.g., Meyer et al. 1990, Meyer and Kitchen 1994, and Meyer et al. 1995), and the combined soil water and temperature requirements for germination were probably not met for several of the species. Also, seedling death shortly after germination undoubtedly contributed to the low emergence. Soil surfaces with the highest seedling emergence had among the least negative water potentials, specifically large holes, mulch, and sand. Once a seedling had emerged, the probability of survival to the end of the study was relatively high (53.6%) regardless of treatment.

*Soil surface effectiveness*

A summary of the relative effectiveness of the different soil surfaces for trapping and retaining seeds (quantity), and for providing favorable conditions for emergence and survival (quality) is shown in Table 2. In this experiment, relatively few surface treatments
Fig. 6. Soil water potentials (MPa) of the eight different soil treatments for the 0–2 cm and 2–10 cm depths. Values are means ± 1 SE (N = 8). Within each treatment, dates with different letters are statistically significant (LSM; P < 0.05).
were both quantitatively and qualitatively effective for all seed types.

Larger soil particle sizes typically have higher seed entrapment and retention than do smaller particle sizes (Chambers et al. 1991). Both bare soil and sand had lower numbers of seeds than were originally sown onto the site as indicated by net seed losses, while the gravel had net seed gains. Soils with different particle sizes can also provide different environmental conditions for seedling emergence and survival (Chambers 1995). Sand and gravel can function as surface mulches when applied over finer-textured soils (Cochran 1969) and these treatments exhibited less negative soil water potentials than did the bare soil. However, the sand treatment exhibited relatively high seedling emergence and survival, while the gravel did not. Gravel consisting of the particle sizes used here has been shown to provide an inadequate medium for seedling growth and survival (Chambers 1995), and even the shallow gravel layer (2 cm) used here may have resulted in low emergence and survival of seedlings germinating within or below the gravel layer. Overall, the gravel trapped and retained high numbers of seeds and was thus quantitatively effective, but it did not provide the conditions required for emergence and establishment and was thus qualitatively ineffective. The sand was qualitatively but not quantitatively effective (Table 2). Bare soil was neither qualitatively nor quantitatively effective.

The mulch treatments were highly effective in retaining seeds that were sown before or after the mulch was applied, but exhibited little or no seed accumulation after sowing. Although litter often has a positive effect on seed entrapment and retention (e.g., Stamp 1989a), the highest seed densities and greatest species richness in arid woodlands and shrublands are found at the interface between the interspaces and the dense litter under shrubs or trees (Koniak and Everett 1983).

It is likely that the primary effects of uniform surface mulches applied during restoration are to increase the entrapment of any seeds moving across the soil surface at the interface between the mulch and the surrounding soils, and of seeds dispersed aerially over long distances or produced on site during the first few years after restoration. Not all seeds trapped in mulch or litter reach the soil surface (Facelli and Pickett 1991). In a similar environment, litter was found to retard the burial of awned grass seeds such as Aristida longiseta (Fowler 1986). Surface mulch used during restoration may impede the burial not only of awned seeds, but also of mucilaginous seeds if the mucilage becomes hydrated before the seeds reach the soil surface. In the mulch + seed treatment, the awned seeds of E. elymoides and H. comata, and mucilaginous seeds of L. lewisii were all found in higher densities in the straw mulch than in the soil underneath. This treatment trapped and retained most of the seeds sown onto the area, but was quantitatively less effective than many of the other treatments (Table 2). Litter has been shown to increase soil water availability for establishing seedlings (Williams et al. 1990), and mulch exhibited among the least negative soil water potentials in the current study. The mulch treatment had high seedling emergence and survival, and was qualitatively very effective (Table 2), explaining its widespread use in restoration (Munshower 1994).

The shrub mimic exhibited only a moderate accumulation of seeds and had relatively low seedling emergence and survival. In arid shrublands, wind velocities are as much as four times greater in interspaces than under shrubs (Parmenter and MacMahon 1983) and, consequently, wind-blown soil, litter, and seeds tend to accumulate under the shrub canopies (Nelson and Chew 1977, Reichman 1984, Mull and MacMahon 1996, Russell and Schupp 1998). Deposition of snow also occurs on the downwind sides of shrubs and other barriers, often resulting in higher soil moisture early in the growing season and improved seedling establishment (Fowler 1986). In undisturbed ecosystems, the accumulation of litter under shrubs over time further increases seed entrapment and retention (Koniak and Everett 1983, Kelrick 1991) and may result in higher numbers of seeds adjacent to shrubs than was observed for the shrub mimics. Also, fine, powdery soils accumulated behind the shrub mimics on my severely disturbed study site, resulting in highly negative soil water potentials, and low seedling emergence and survival. The shrub mimics were both quantitatively and qualitatively less effectiveness for seedling establishment than were many of the other treatments (Table 2).

Depressions or crevices in the soil frequently serve as seed accumulation or seedling establishment sites in arid ecosystems (Reichman 1984, Eckert et al. 1986). For artificially created depressions in Sonoran Desert soils, depression size, including perimeter, volume, depth, and surface area were highly correlated with the density of trapped seeds (Reichman 1981). Soil depressions in arid environments often have higher soil water availability because they trap snow and accumulate precipitation (Eckert et al. 1986, Evans and Young 1987). In this study, the small holes trapped a
relatively high number of seeds, but rapidly filled with wind-blown topsoil. Consequently, large holes were more effective in trapping and retaining seeds and persisted longer (>2 yr). Also, large holes had less negative soil water potentials, and higher emergence and survival than did small holes. Although the large holes had the highest absolute seedling emergence, emergence within large holes was lower than for the sand or mulch treatments, when the data were adjusted for initial seed density. Also, survival within the large holes was lower than in the sand treatment and similar to the mulch treatments. This may have resulted partly from competition, because emergence of annual species was high in large holes. Natural depressions or soil gouging during restoration may be both quantitatively and qualitatively effective for seed types that exhibit significant horizontal movement and redistribution (Table 2). They may be quantitatively ineffective for small seeds that exhibit little redistribution, and qualitatively ineffective for species adversely affected by competition.

Synthesis

The surface characteristics of the soil in arid and semi-arid environments clearly form the template for both species establishment patterns and plant community structure following disturbances in which the surface vegetation is removed. The array of microsites present determines both the quantity of seeds trapped and retained in the different microsites, and the quality of the microsites for seed germination and seedling emergence and survival. Sites that are quantitatively effective in trapping and retaining seeds are not necessarily those that are qualitatively effective for seedling establishment, a dichotomy that occurs in other systems and that has been described as seed and seedling conflicts (Schupp 1995). In addition, this study indicates that the quantitative effectiveness of microsites varies among species. Soil treatments that increase roughness, provide a wind barrier, or prevent seed movement trap or retain the highest numbers of seeds when the entire seed population is considered. However, for individual species, the quantity of seeds trapped in the different soil surfaces depends on seed type. Small or heavy seeds exhibit little horizontal movement (Chambers et al. 1991, Thompson et al. 1993) and few differences in seed numbers among soil surfaces, while seeds with large surface areas exhibit significant horizontal movement and large differences among surfaces. This indicates that in relatively undisturbed environments, the seed dispersion patterns of small-seeded species should reflect those of the parent plant, while the dispersion patterns of large-seeded species should reflect the surface characteristics of the surrounding soil. In artificially seeded, restored ecosystems, seed dispersion patterns of small-seeded species should be relatively uniform, while those of large-seeded species should again reflect the surface characteristics of the surrounding soil. Regardless of seed type, seedling emergence depends on soil water availability in these environments, and surfaces that result in less negative soil water potentials, such as those covered with litter or mulch, are the most effective qualitatively. Seeds that arrive or are placed in these microsites have the highest probability of emergence, although higher seed densities and emergence probabilities that cause competitive interactions among species may significantly influence establishment outcomes. Knowledge of seed movements and seedling fates is critical for both understanding species establishment patterns following disturbance, and designing effective methods for restoring diverse native ecosystems.

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