

Small-scale barriers mitigate desertification processes and enhance plant recruitment in a degraded semiarid grassland

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Abstract. Anthropogenic desertification is a problem that plagues drylands globally; however, the factors which maintain degraded states are often unclear. In Canyonlands National Park on the Colorado Plateau of southeastern Utah, many degraded grasslands have not recovered structure and function >40 yr after release from livestock grazing pressure, necessitating active restoration. We hypothesized that multiple factors contribute to the persistent degraded state, including lack of seed availability, surficial soil-hydrological properties, and high levels of spatial connectivity (lack of perennial vegetation and other surface structure to retain water, litter, seed, and sediment). In combination with seeding and surface raking treatments, we tested the effect of small barrier structures (“ConMods”) designed to disrupt the loss of litter, seed and sediment in degraded soil patches within the park. Grass establishment was highest when all treatments (structures, seed addition, and soil disturbance) were combined, but only in the second year after installation, following favorable climatic conditions. We suggest that multiple limiting factors were ameliorated by treatments, including seed limitation and microsite availability, seed removal by harvester ants, and stressful abiotic conditions. Higher densities of grass seedlings on the north and east sides of barrier structures following the summer months suggest that structures may have functioned as artificial “nurse-plants”, sheltering seedlings from wind and radiation as well as accumulating wind-blown resources. Barrier structures increased the establishment of both native perennial grasses and exotic annuals, although there were species-specific differences in mortality related to spatial distribution of seedlings within barrier structures. The unique success of all treatments combined, and even then only under favorable climatic conditions and in certain soil patches, highlights that restoration success (and potentially, natural regeneration) often is contingent on many interacting factors.

Key words: aeolian processes; Colorado Plateau; conmods; connectivity; contingency; drylands; ecological filters; feedbacks; invasive species; restoration; *Salsola* spp.; *Sporobolus* spp.

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INTRODUCTION

Many arid and semiarid grasslands globally have undergone transitions from states dominated by perennial grasses to states dominated by shrubs or annual grasses with increased bare ground connectivity (a form of desertification; Okin et al.

2009, Bestelmeyer et al. 2015). These compositional changes may have negative consequences for ecosystem function, including persistent declines in productivity, livestock forage, biodiversity, soil fertility, and regional water availability and air quality (Schlesinger et al. 1990, Masters and Sheley 2001, Turnbull et al. 2008). Often conceptualized

as transitions to “alternative stable states” (Beisner et al. 2003), these changes may be difficult or impossible to reverse without active restoration (Whisenant 1999, Suding et al. 2004, Suding and Hobbs 2009). Identifying and overcoming the mechanisms which maintain these “degraded” states is a central aim of management and restoration in drylands (Bestelmeyer et al. 2009).

Dryland degradation can result from a breakdown in feedbacks between vegetation patches and local resource capture (Schlesinger et al. 1990). Compared to their adjacent un-vegetated matrix, perennial grass patches are associated with higher levels of water infiltration, water-holding capacity, soil nutrients, physical retention of soil, grass propagule density, and reduced microclimatic water stress (Schlesinger et al. 1990, Wainwright et al. 2002, Rotundo and Aguiar 2005), creating improved conditions for grass recruitment and persistence in many cases (but can be scale dependent; Svejcar et al. 2015). Significant fragmentation of these vegetated patches by heavy livestock grazing or drought may generate an alternative set of feedbacks that reverse these conditions and promote a degraded state. Most notably, depletion of soil resources through erosion and alteration of competitive dynamics via invasions of shrubs or annuals are commonly associated with these persistent alternative states (Schlesinger et al. 1990, D’Antonio and Vitousek 1992, Allen 1995, Okin et al. 2009).

In degraded arid grasslands, feedbacks related to erosion and invasion may be operating simultaneously, both hampering the identification of limiting factors by single-factor experiments, and compounding the difficulty of restoration efforts (Allen 1995, Hobbs and Norton 2004). In severely degraded locations, harsh abiotic conditions may effectively “mask” important negative biotic interactions that are only observed once abiotic conditions are ameliorated, such as competition from weeds only becoming apparent following restoration of topsoil (Whisenant 1999). Given the expense and high failure rates of restorations in arid and semiarid contexts (Bainbridge 2012, DeFalco et al. 2012, Duniway et al. 2015), developing restoration methods that have a high probability of success given these contingencies remains a challenge. It is necessary to find techniques that are adaptive to variable and dry conditions, present low risk, and are cost-effective.

Variation in abundance of desired species’ propagules across space and time is one such challenge that is often addressed as a first step in restoration (a “propagule availability” filter in assembly rules parlance, Hobbs and Norton 2004). In severely degraded sites, populations of some species may be so depleted that lack of seed may limit regeneration (DeFalco et al. 2009). In such cases of *seed limitation*, addition of seed results in a (proportional) increase in population size (Turnbull et al. 2000, Clark et al. 2007).

However, availability of seeds alone often is insufficient to initiate recovery—there also must be a simultaneous availability of favorable microsites for seed retention, germination, and establishment (Harper et al. 1965, Sheldon 1974, Chambers 2000). In dryland systems, soil surface properties such as roughness, presence of litter and depth of coarse surficial sediment are particularly important determinants of microsite because of their influence on seed retention and soil hydrology (Hillel 1998, Rotundo and Aguiar 2005). In particular, surface litter and coarse-textured sediment increase infiltration and reduce hydrologic conductivity between subsurface moisture and atmospheric evaporative demand (a “mulching” effect related to the “inverse texture hypothesis”; Noy-Meir 1973). Under degraded conditions soil surfaces are commonly bare, sealed, and lacking sufficient amounts of litter and/or coarse surface sediment, which greatly reduce the chances that arriving seed may be retained, germinate, or survive (Aguiar and Sala 1997, DeFalco et al. 2009, Kinyua et al. 2010). This is a form of *microsite limitation*, wherein recruitment of individuals remains limited in spite of seed availability, often necessitating disturbance of soil surfaces to break physical crusts and facilitate seed burial. Dryland restoration efforts often address this using equipment such as rangeland drills and harrows to increase soil-seed contact. However, these approaches introduce considerable risk of erosion due to broad-scale soil disturbance (Miller et al. 2012, Duniway et al. 2015).

Many of the factors that limit recovery in degraded drylands appear to be related to the extent of interconnected bare patches on the landscape (termed “connectivity” by Okin et al. 2009, 2015). The heightened loss of litter and coarse sediment via aeolian and fluvial transport

in these areas exacerbates microclimatic stress for developing seedlings, as these elements buffer against harsh temperatures and water loss (Evans and Young 1970). In agricultural systems, physical barriers that slow the movement of wind and water across soil surface (e.g., shelterbelts and terracing) have been implemented to reduce the loss of resources (soil, water, seed) and mitigate evaporative stress on crops. Variations of these approaches have been used in non-cultivated dryland systems, with methods such as straw checkerboards for dune stabilization (Li et al. 2006); various forms of “pitting”, “trenching”, or other means to break the surface of sealed soil (Winkel and Roundy 1991, Kinyua et al. 2010, Bainbridge 2012); metal shrub surrogates for seed retention (Turnbull et al. 2008); and piles of woody debris for shading and seed retention (Visser et al. 2004).

One technique that has recently met with success in Chihuahuan Desert shrublands is the implementation of arrays of small wire-mesh barrier structures (termed “connectivity modifiers” or “ConMods”; Okin et al. 2015, Rachal et al. 2015). These structures have been shown to significantly increase the retention of sediment and litter (Okin et al. 2015, Rachal et al. 2015) which is thought to improve soil-hydrologic conditions for seedling germination and survival. These structures are also of practical interest because in contrast with seeding methods such as harrowing, they do not require intensive surface disturbance.

In this study, we examined the effectiveness of similar structures for restoration of degraded grasslands on the Colorado Plateau, in a fully crossed experimental design that also included supplemental seeding and raking (breaking surface soil). In this cold-desert environment, state transitions primarily are characterized by transitions from perennial grass and shrub states to exotic-annual dominated (rather than shrub dominated states as is common in other deserts globally; Bowker et al. 2014) resulting in large canopy gaps between perennial vegetation and low retention rates of litter, surficial sediment and seed. In sites that had previously been identified as having transitioned into these alternative states (Miller et al. 2011), we here demonstrate experimentally that multiple factors in combination limit native grass recruitment in these environments, including unfavorable climate conditions,

lack of favorable seed microsites, and stress related to the microenvironment experienced by seedlings during early growth. We also demonstrate that establishment of barrier structures increased the likelihood of native grass establishment, but also establishment of exotic annuals, and that this increased establishment likely was due to effects of structures on multiple processes.

METHODS

Study area

This study was conducted within the Needles District of Canyonlands National Park, in southeast Utah, USA (38.168 N, 109.759 W; 1490 m elevation). The Park is located in the Colorado Plateau physiographic region, and is composed predominantly of broad, gently sloping valleys surrounded by sandstone outcrops. The climate is cool desert, with a mean annual temperature of 12°C and a mean annual precipitation of 207 mm (Western Regional Climate Center 2015). Approximately 50% of precipitation falls in the cool season (Oct–May) as frontal storms and 50% falls in the warm season as “monsoonal” thunderstorms (June–Sept). Inter-annual variability in precipitation is high, ranging from 119 to 330 mm (CV = 0.25).

Average temperatures range from −1.7°C in the coldest month (Jan) to 26°C in the hottest month (Jul). Vegetation at the study site reflects this seasonality with a mix of native cool-season C3 grasses and forbs (*Stipa hymenoides*, *Cryptantha crassiseppala*) maturing in spring, native warm-season C4 grasses (*Sporobolus airoides*, *S. cryptandrus*, *S. contractus*, *S. flexuosus*, *Hilaria jamesii*) and the invasive annual forbs *Salsola tragus* and *Salsola paulsenii* (both exotic, hereafter *Salsola*) maturing in mid-late summer. The study area was grazed by domestic livestock (cattle) from the late 1880s until 1974, resulting in persistently altered and degraded soil and vegetation properties in settings that were most heavily used by livestock (Neff et al. 2005, Miller et al. 2011).

Specific sites selected for this restoration experiment were located within a 50-ha area in patches with extensive bare ground, a vascular plant community dominated by *Salsola*, and sparse cover of native perennial grasses. Relative to reference conditions found in comparable ungrazed areas (e.g., Kleiner and Harper 1972), these persistently

degraded sites are characterized by low soil stability and surface roughness, large basal and canopy gaps between perennial plants, greater susceptibility to wind erosion, and dominance by annual exotic forbs and grasses rather than biological crust (which confers soil stability and surface roughness, Belnap et al. 2003) and native perennial grasses and shrubs (see Miller et al. 2011 for detailed comparison). Following dry periods, large connected patches of bare ground are exposed on degraded sites, resulting in large fetch-distances for erosive winds and subsequent transport and loss of soil, litter, and seeds. All sites occurred on gentle slopes where overland water-flow is infrequent, occurring only in response to high-intensity precipitation events.

Soils at sites included in this study are characterized as the Begay series (Ustic Haplocambid) and attributed to the Semidesert Sandy Loam Fourwing Saltbush ecological site by the U.S. Department of Agriculture Natural Resources Conservation Service (035XY215UT; USDA NRCS 2009). Although generally within the same soil series and ecological site type, study sites fall within three different soil-geomorphic units identified in a surficial geology map of the area (U.S. Geological Survey, *unpublished data*): (1) “hard-pan”, consisting of very fine textured, sealed, and/or cracked surfaces resulting from recurrent ponding and evaporation in topographic depressions (Qp), (2) “intermediate”, aeolian or alluvial sheet deposits of sand, silt, and clay (Qas and Qes), and (3) “coppice-dune” consisting of fine to coarse grained stabilized aeolian sand dune deposits (Qed).

Experimental design

In a randomized, fully factorial design replicated across 10 blocks representative of these different types of degraded soil patches, we established 0.35×0.35 m plots that received all combinations of three treatments: (1) addition of native *Sporobolus* seed, (2) soil surface disturbance at the time of seeding, and (3) establishment of a wire-mesh barrier structure (ConMod; Fig. 1) prior to seeding. Plots were laid out in a line perpendicular to prevailing winds within each block, to reduce the potential for wind-shading between plots. Prior to treatment application, a $1 \text{ m} \times 1 \text{ m}$ area surrounding each plot was cleared of vegetation and litter by clipping

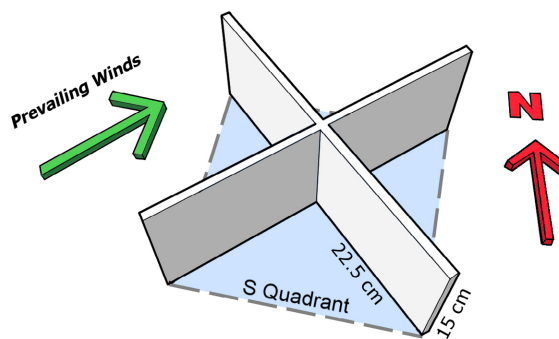


Fig. 1. Schematic of barrier structure (“ConMod”, Okin et al. 2015). Walls constructed of fine galvanized wire-mesh sheeting. Plot area is divided into four quadrants (blue shaded areas) facing the four cardinal directions (N, E, S, W). Prevailing winds come from 220° (<http://esp.cr.usgs.gov/projects/sw/clim-met/needles.html>).

and gentle sweeping to reduce heterogeneity among plots. Cleared areas were pretreated with the broadleaf pre-emergent herbicide Plateau © (Ammonium salt of imazapic (\pm)-2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-5-methyl-3-pyridinecarboxylic acid; BASF, Florham Park, New Jersey), at a rate of 327 liters/ha (35 gal/acre) in an attempt to reduce local densities of *Salsola*. All plots were established in the same manner, including controls (no treatments applied).

Barrier structures consisted of two upright 15×45 cm wire-mesh panels placed perpendicular to each other flush to the ground (see Fig. 1). The corners of each structure were fixed to the ground with 20-cm metal ground-staples. One axis of each structure was oriented parallel to 220 degrees azimuth (relative to true north), the direction of prevailing winds, dividing plot space into four quadrants (hereafter called N, E, S, W).

The “disturbance” treatment was applied immediately prior to seeding and consisted of raking the plot area with a 3-prong hand rake to a depth of ~ 5 cm, such that any surface crust was broken.

Seeding occurred twice: once in late July 2012 and again in late September 2012. The first application consisted of approximately 1.05 g per plot (~ 2000 seeds/ m^2) of a mix of *Sporobolus contractus*, *S. airoides*, and *S. cryptandrus*. The second application consisted of 1.54 g per plot (~ 3000 seeds/ m^2) of a mix containing *S. airoides*, *S. cryptandrus*,

and *S. flexuosus*. During the second application of seed (September), seed was raked gently into plots receiving a seed \times raking treatment, whereas seed was only dropped on the surface of these plots during the first seeding (July).

An additional set of fully crossed, replicate treatments was initiated in late summer which received only the second seeding and no pre-emergent herbicide application. Analyses indicated that for *Sporobolus*, there was no significant difference between these plots and those initiated earlier in the summer (i.e. no effect of "later starting date"). This made for 170 plots in total: two replicates of all treatment combinations per block, plus one additional late season replicate

with all factors (+seed +raking +structure) across 10 blocks.

Data collection

Immediately after seeding in September, the number of harvester ants (*Pogonomyrmex occidentalis*) present at each plot was counted at 24-h intervals for 3 d, following observations of ant-granivory following initial seeding in July.

In April the following year (2013), plots were surveyed for presence of both *Sporobolus* and *Salsola* seedlings. Plots were surveyed again in June 2014 and October 2014, following conditions favorable for plant germination and growth (above average precipitation and cool

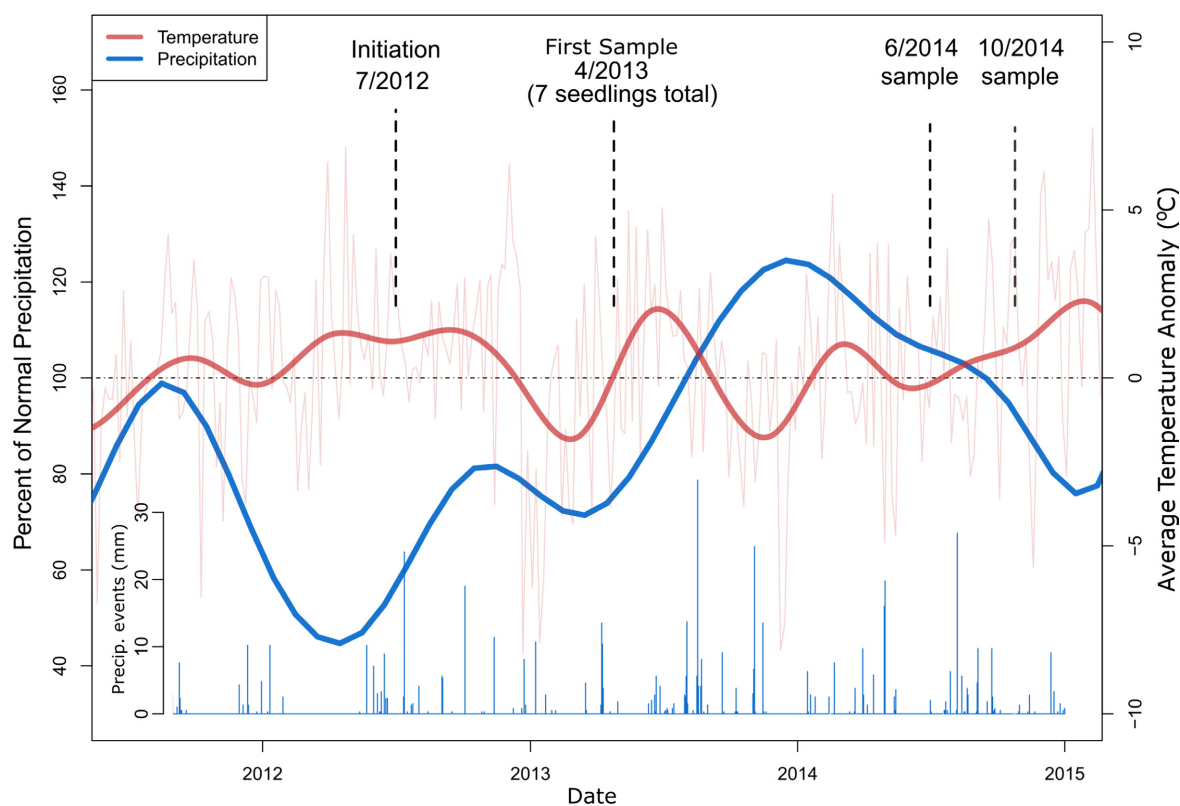


Fig. 2. Timeline and climate characteristics during the study, taken from the Western Regional Climate Center (<http://www.wrcc.dri.edu>). Precipitation events indicated by blue vertical lines along the horizontal axis. Relative precipitation (heavy blue) calculated as the percentage of accumulated precipitation in the three previous months compared to the 50-yr average for that window. Temperature anomaly was calculated as the average daily deviation from the 50-yr average in 5 d increments (light red) and the splined trend (heavy red). Note most germination for this experiment likely occurred during the fall of 2013, with above average precipitation and cool temperatures.

temperatures Fall-Spring; Fig. 2). In each quadrant of each plot, numbers of seedlings of both *Sporobolus* and *Salsola* present were counted. These seedlings were not identified to species. Litter depth was measured at two central points within each quadrant.

Analysis

The probability of a plot containing at least one viable *Sporobolus* seedling at either of the two sampling periods in 2014 was modeled with a Generalized Linear Mixed Model (GLMM) using a log link and binomial error term. To account for non-independence between samples taken from the same plot at different sampling times, plot was added as a random effect, with soil patch (block) as a fixed effect.

Following analysis at the plot level, additional analysis was carried out for counts of *Sporobolus* per quadrant in plots with barrier structures. Counts of *Salsola* were modeled in a similar manner to *Sporobolus*, with the exception that *Salsola* counts rather than presence/absence were modeled on both the plot and quadrant scale. Data for both species were best approximated with a negative binomial distribution, and initial analyses using zero-inflated models with both Poisson and negative-binomial error terms indicated that single-stage GLMMs with negative binomial error terms were superior in terms of fit and AIC-based parsimony. To account for non-independence between quadrants in the same plot and repeat samples within each quadrant, a nested random effect was added for quadrant-within-plot. In addition to relevant experimental treatments, classes of litter depth (“none”, “low”, and “high”, scaled by season) and generalized classes of soil texture (hard-pan, intermediate, coppice-dune) were included as covariates for quadrant-scale analysis. All models were fit with the package glmmADMB in R (Skaug et al. 2011, R Development Core Team 2015) using Maximum Likelihood (ML) Laplace approximation to estimate parameters. Stepwise backward selection using Wald χ^2 tests was used to remove non-significant terms from an initial saturated model with all relevant predictors and interaction terms using the ANOVA function in the R package car (Fox and Weisberg 2011). Negative binomial models were checked for overdispersion by comparing the ratio of sum-of-squared Pearson

residuals divided by residual degrees of freedom to a χ^2 distribution (Venables and Ripley 2002).

RESULTS

Plot occupancy by native *Sporobolus*

In the first sampling date (April 2013), following an extended period of lower than average precipitation (Fig. 2), there were only seven *Sporobolus* seedlings observed across all plots, with no obvious pattern related to treatment. The remainder of the results presented here is based on sampling dates in the summer and fall of 2014, following above-average levels of precipitation (Fig. 2). Overall, the frequency of *Sporobolus* seedlings was low across these seasons, with approximately 75% of plots having no seedlings in summer or fall. There were no *Sporobolus* seedlings observed in any control plot in either season.

By far the highest numbers of seedlings were observed in plots which received all treatments (Fig. 3), and 70% of these plots had at least one seedling across sampling dates. Barrier structures had a strong positive effect on establishment overall (10-fold increase in odds of seedling presence, $P < 0.01$, Table 1). Establishment success was higher when seeding was combined with raking (29-fold increase odds of occupation, $P = 0.04$, Table 1), though neither seeding nor raking had a significant effect individually.

Probability of occupancy declined as the season progressed (19-fold decrease in odds for October sampling date, $P = 0.01$, Table 1). However, presence of a barrier structure offset this mortality, increasing the probability of *Sporobolus* presence in the fall when barriers were present (net 69% increase in odds when barrier present in October, $P = 0.01$, Table 1).

There were significant differences related to site, with lower overall probabilities of seedlings present in areas with the more extreme soil textures in our study area (all $P < 0.025$). Across patches characterized as “hard-pan” or “coppice-dune”, there were no more than two plots containing *Sporobolus* each, whereas the more intermediate-textured patches averaged 30% occupation.

Fine-scale patterns in *Sporobolus* density

The density of *Sporobolus* seedlings in barrier structures differed by quadrant (Fig. 4), but

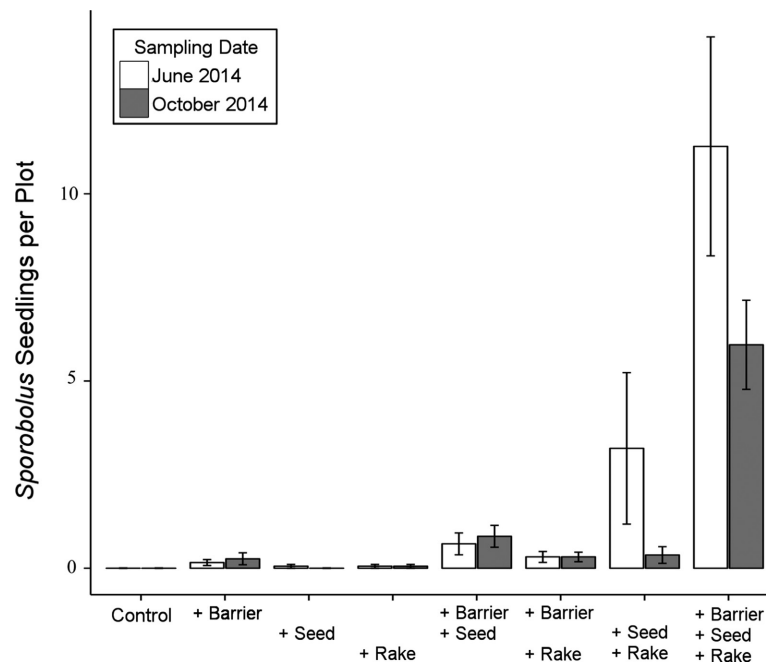


Fig. 3. Mean number of *Sporobolus* seedlings by treatment and sampling date ± 1 standard error. Open bars indicate the June 2014 sampling date and shaded bars represent the October 2014 sampling date. *Sporobolus* density and occupancy (not shown) was highest when all treatments were combined for both sampling dates. The combination of seeding and raking yielded high densities in June, but not in October.

these differences were only significant later in the growing season (quadrant \times sample date interaction, Chi = 14.68, df = 3, $P = 0.03$). In October, north- and east-facing quadrants had twice as many *Sporobolus* seedlings than south- and west-facing quadrants. In contrast, there were no significant differences across quadrants in June (all $P > 0.25$, Table 2), suggesting

quadrant-specific mortality between June and October. The effect of accumulated litter depth was positive and slightly higher at low levels, but not significantly so (Table 2).

Invasive *Salsola* density

At the whole plot level, there was a strong positive effect of the presence of a barrier

Table 1. Factors affecting *Sporobolus* occupancy† at the plot-level.

Factor	Log odds	Standard error	Wald's Z	P-value	Odds ratio	Lower 95% CI	Upper 95% CI
Intercept	-4.85	1.63	-2.97	<0.005	0.01	0	0.19
Barrier	2.31	0.91	2.54	0.01	10.07	1.7	60.01
Raking	1.18	1.09	1.08	0.28	3.25	0.38	27.79
Seeding	1.57	1.09	1.44	0.15	4.81	0.57	40.66
Raking \times Seeding	3.37	1.62	2.08	0.04	29.08	1.22	691.32
Sampling = October	-2.95	1.15	-2.56	0.01	0.05	0.01	0.5
Barrier \times October	3.48	1.32	2.62	0.01	32.46	2.41	433.55
Later start date	0.21	0.67	0.31	0.75	1.23	0.33	4.57
Coppice-dune block	-4.31	1.8	-2.4	0.02	0.01	0	0.46
Hard-pan block	-5.85	2.39	-2.45	0.01	0.00	0	0.31

Note: Coefficients for the eight remaining blocks and non-significant interactions not shown.

† Modeled as log odds of observing at least one *Sporobolus* seedling in a plot using a GLMM with binomial error term.

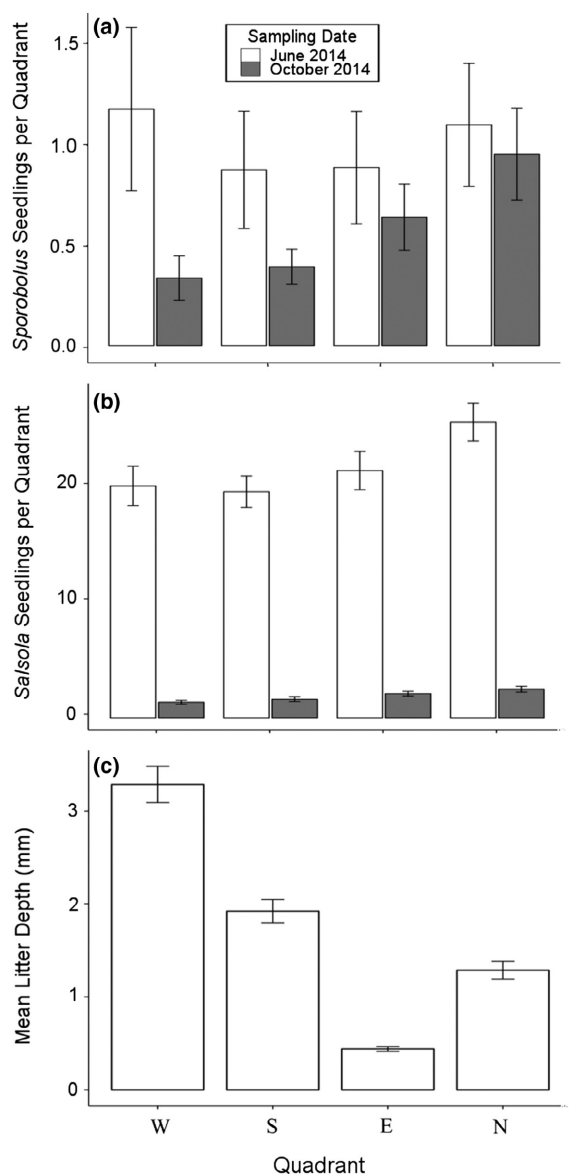


Fig. 4. Fine scale patterns in density of *Sporobolus* (a), *Salsola* (b), and litter depth (c) in barrier structures by quadrant and sampling date. Bar colors are as in Fig. 3. Error bars represent one standard error. Litter estimates are averaged across both sampling dates.

structure on *Salsola* density (15-fold increase, $P < 0.001$, Table 3), and a negative effect of herbicide application (twofold reduction, $P < 0.001$, Table 3). There were no significant effects detected of adding native seed or raking.

As with *Sporobolus*, counts of *Salsola* declined with time (ninefold decline between June and

October, $P < 0.001$, Table 3), however, unlike *Sporobolus*, the effects of barrier structures did not change across seasons. There were also significant differences related to soil patch (although weaker than with *Sporobolus*), with nearly three-times lower *Salsola* density in the fine hard-pan block ($P < 0.001$, Table 3).

At the individual quadrant level, there were differences in *Salsola* density among barrier quadrants, but in contrast with *Sporobolus* densities, these differences were evident in both June and September sampling dates. Again, West-facing quadrants had the lowest seedling densities, significantly lower than East, North, but not South-facing quadrants (Table 4). The presence of litter at both low and high levels was associated with double the *Salsola* density of plots with no or trace amounts of litter ($P < 0.001$, Table 4). The effect of herbicide was not as strong in plots with barrier structures at this scale, (20% reduction in density, $P = 0.09$, Table 4).

Harvester ant density

Average harvester ant density observed in plots following seed addition was dramatically reduced when seeds were buried by raking (Fig. 5). This difference declined over the first 3 d following seeding, likely due to removal of surface seeds in unraked plots by this time.

DISCUSSION

The combination of structure, seed, and raking yielded the highest probability and density of native grass establishment

The fact that native seedling presence was far higher when all restoration treatments were combined than any single treatment or any pair of treatments demonstrates that multiple factors are simultaneously and synergistically inhibiting successful recovery of native perennial vegetation at this study site. Although rates of native grass emergence and survival were low under any one treatment (and non-existent in control plots), and even under most combinations of two treatments, the combination all three restoration treatments (barrier structure, seeding, and raking) yielded the highest probability and density of native grass establishment in both June and October of 2014 (Fig. 3). The combination of treatments in this study directly

Table 2. Factors affecting native *Sporobolus* counts in ConMod barrier structures (quadrant-scale).

Factor	Log number seedlings	Standard error	Wald's Z	P-value	Multiplicative effect	Lower 95% CI	Upper 95% CI
Intercept	-3.27	0.96	-3.41	<0.001	0.04	0.01	0.25
Raking	0.34	0.66	0.52	0.6	1.40	0.39	5.16
Seeding	1.29	0.61	2.12	0.03	3.63	1.1	12.02
Raking × Seeding	2.35	0.79	2.97	<0.001	10.49	2.22	49.28
Sampling = October	-1.11	0.34	-3.23	<0.001	0.33	0.17	0.65
E Quadrant	-0.4	0.37	-1.09	0.28	0.67	0.33	1.37
N Quadrant	-0.01	0.31	-0.04	0.97	0.99	0.54	1.81
S Quadrant	-0.24	0.31	-0.79	0.43	0.79	0.43	1.43
E Quadrant × October	1.23	0.47	2.63	0.01	3.42	1.37	8.54
N Quadrant × October	1.21	0.45	2.69	0.01	3.35	1.39	8.06
S Quadrant × October	0.76	0.48	1.58	0.12	2.14	0.83	5.49
Later start date	-0.13	0.34	-0.39	0.69	0.88	0.45	1.71
Litter = Low	0.33	0.63	0.52	0.6	1.39	0.4	4.83
Litter = High	0.18	0.67	0.28	0.78	1.20	0.33	4.43
Coppice-dune block	-2.94	0.96	-3.07	<0.001	0.05	0.01	0.35
Hard-plan block	-2.18	0.86	-2.54	0.01	0.11	0.02	0.61

Notes: Response modeled as a GLMM with negative-binomial error term with dispersion parameter of 1.064 (SE = 0.204). Coefficients for the eight remaining blocks and non-significant interactions not shown.

overcame multiple limitations related to the availability of seed (seed limitation), the coincident availability of favorable microsites for seed for germination (Harper et al. 1965), and subsequent abiotic stresses limiting emergence and survival, apparently ameliorated by the barrier structures.

The fact that seeding increased likelihood of *Sporobolus* presence in plots that were raked and/or had a barrier structure suggests that seed-limitation plays a role in maintaining the degraded state of the sites selected for this study. It is likely that few native seeds arrive or persist in degraded soils of these sites despite the fact that native seed sources exist within 100 m of most of the study plots. Experimental studies

indicate that arid systems tend to be more seed limited than mesic systems (Turnbull et al. 2000), and studies of seed banks in arid systems frequently reveal that degraded and bare areas have significantly reduced quantities of native seed compared to vegetated patches (Aguilar and Sala 1997, Rotundo and Aguilar 2005, DeFalco et al. 2009). In this study site, where scattered reproductive *Sporobolus* individuals are present, our results suggest that the majority of native seed rain to these patches is conveyed away by wind or seed predators (Aguilar and Sala 1997, Chambers 2000, DeFalco et al. 2012), given the lack of surface features to catch, retain, and obscure seeds in these bare patches which have a high degree of spatial connectivity.

Table 3. Factors affecting exotic *Salsola* counts at the plot-level.

Factor	Log number seedlings	Standard error	Wald's Z	P-value	Multiplicative effect	Lower 95% CI	Upper 95% CI
Intercept	1.72	0.25	6.91	<0.001	5.58	3.44	9.15
Barrier	2.73	0.15	17.89	<0.001	15.33	11.41	20.77
Raking	0.03	0.13	0.25	0.8	1.03	0.8	1.35
Sampling = October	-2.2	0.17	-13.08	<0.001	0.11	0.08	0.15
Barrier × October	-0.28	0.2	-1.42	0.15	0.76	0.52	1.11
Herbicide (early starting date)	-0.66	0.14	-4.63	<0.001	0.52	0.39	0.68
Coppice-dune block	0.1	0.3	0.34	0.73	1.11	0.61	2.01
Hard-pan block	-1.01	0.33	-3.03	<0.001	0.36	0.19	0.7

Notes: Response modeled as a GLMM with negative-binomial error term with dispersion parameter of 2.89 (SE = 0.541). Coefficients for the eight remaining blocks and non-significant interactions not shown.

Table 4. Factors affecting exotic *Salsola* counts in ConMod barrier structures.

Factor	Log number seedlings	Standard error	Wald's Z	P-value	Multiplicative effect	Lower 95% CI	Upper 95% CI
Intercept	1.71	0.3	5.69	<0.001	5.53	3.07	9.94
Sampling = October	-2.62	0.12	-22.03	<0.001	0.07	0.06	0.09
E Quadrant	0.26	0.1	2.55	0.01	1.30	1.06	1.58
N Quadrant	0.38	0.09	4.41	<0.001	1.46	1.23	1.73
S Quadrant	0.03	0.08	0.35	0.73	1.03	0.88	1.2
E Quadrant × October	0.34	0.16	2.16	0.03	1.40	1.03	1.93
N Quadrant × October	0.31	0.16	1.99	0.05	1.36	1	1.85
S Quadrant × October	0.2	0.16	1.19	0.23	1.22	0.88	1.68
Herbicide	-0.19	0.11	-1.69	0.09	0.83	0.66	1.03
Litter = Low	0.9	0.22	4.05	<0.001	2.46	1.59	3.79
Litter = High	1.05	0.24	4.4	<0.001	2.86	1.79	4.56
Coppice-dune block	0.11	0.25	0.45	0.65	1.12	0.69	1.81
Hard-pan block	-0.59	0.25	-2.42	0.02	0.55	0.34	0.89

Notes: Response modeled as a GLMM with negative-binomial error term with dispersion parameter of 4.814 (SE = 0.572). Coefficients for the eight remaining blocks and non-significant interactions not shown.

It also is not surprising that the effectiveness of seed addition in our study strongly depended on whether seeds were raked into the soil (Fig. 3, Table 1). The importance of combining seed additions with some kind of surface disturbance and burial is supported both generally (Turnbull et al. 2000, Clark et al. 2007) and specifically

in the context of arid and semiarid restorations (Snyman 2003, Cox and Anderson 2004, Visser et al. 2004, Kinyua et al. 2010). The combination of surface disturbance and seed burial often improves seed capture and retention, soil-seed contact and imbibition, seed longevity, and seed escape from granivory (Harper et al. 1965, Sheldon 1974). Although fine-scale surface disturbance was found to benefit plant establishment in this study, broad-scale surface disturbance and associated soil destabilization can carry significant risks in semiarid and arid environments where postdisturbance precipitation conditions can be unfavorable for plant establishment for an extended period of time (e.g., Duniway et al. 2015). In addition to postdisturbance climatic conditions, existing soil-surface conditions (e.g., presence and degree of biological crust development), landscape setting, and the spatial extent, connectivity, and alignment of treatment areas are additional factors to consider when weighing the benefits vs. risks of surface-disturbing restoration treatments (Miller et al. 2012).

The positive effects of surface disturbance often are attributed to improved seed retention or surface hydrologic properties (Kinyua et al. 2010), but in our sites protection from granivory by harvester ants also may have been a particularly important consequence of raking treatments. Harvester ants are known to preferentially forage where seed densities are high, and only when seed is available on the soil surface (Reichman 1979). Within minutes of sowing, harvester

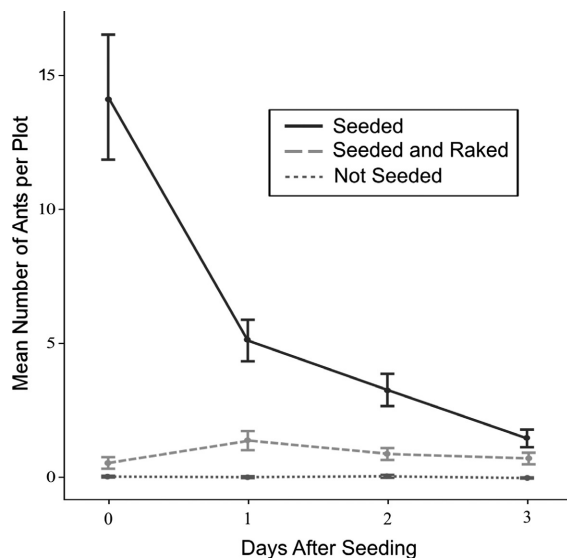


Fig. 5. Mean number of harvester ants (± 1 SE) observed on plots following seed application in early September, 2012. The solid line represents seeded plots, the gray line with long dashes represents plots in which seed was raked into the soil surface, and the line with short dashes represents unseeded plots.

ants were observed removing seeds from the plots. However, when seed was buried (seeding treatment + raking), ant foraging was reduced substantially during the initial days following seeding (see Fig. 5). Although the magnitude of effects of harvester ants on plant populations via granivory are often unclear, in arid systems harvester ants can significantly reduce seed densities and alter plant distributions via selective consumption and transport (Reichman 1979, Mull and MacMahon 1996, MacMahon et al. 2000, DeFalco et al. 2009).

Between sampling dates in June and October there was a large reduction in native grass density, coinciding with elevated temperatures and reduced available soil moisture of summer months (Fig. 2). High mortality between seedling emergence and establishment is a common bottleneck for plant populations, but even more so in arid and semiarid contexts where soil moisture can be extremely limiting (Noy-Meir 1973). In our study, seedling mortality was dramatically reduced when barrier structures were present, (structure \times sampling period interaction, Table 1), suggesting that structures served to ameliorate these harsh abiotic conditions.

Native grass establishment was strongly related to position within structure

The spatial variation in *Sporobolus* abundance observed within barrier structures following the summer months provides some insight into the mechanisms by which structures improved seedling survival. At this site, the North- and East-facing quadrants received the most shade from incident solar radiation and wind, and also had the highest abundance of *Sporobolus* seedlings in the fall. In this way, structures may have been functioning as artificial “nurse-plants” (Niering et al. 1963, Flores and Jurado 2003), serving as physical barriers from water and heat stress during the hot dry summer months. Like nurse plants, the barrier structures also concentrated litter and loose soil (S.E. Fick, *personal observation*), mimicking the “islands of fertility” phenomenon (although without contributing to biogeochemical cycling themselves; Schlesinger and Pilmanis 1998). Buildup of litter was highest on the West- and South-facing quadrants, which did not correlate with fall seedling abundance (Fig. 4a–c). However,

seedling responses to these resources may not be linear (Rotundo and Aguiar 2005), and accumulation of litter and sediment may have been optimal in the leeward side of the structure. In this system, as in other arid systems, fine-scale patterns in soil chemical and textural properties are closely linked with the distribution of plant populations (Bestelmeyer et al. 2006b, Miller et al. 2006, Okin et al. 2015) thus longer term persistence may rely on the accumulating effect of these structures (Rachal et al. 2015). Isolating the mechanisms by which barrier structures affect seedling response may be important for designing optimal structures for large-scale implementations.

Barrier structures also increased the densities of a non-native, invasive species

The invasive annual plant *Salsola* benefitted from barrier structures in a similar way to that of *Sporobolus*, with higher densities overall compared to control. Like *Sporobolus*, the highest densities occurred in the N quadrant, likely due to shading and/or optimal accumulation effects. Unlike *Sporobolus*, this pattern was evident in both June and October 2014, rather than only in October for *Sporobolus*. In the spring and early summer, *Salsola* germinates rapidly and at high densities, with significant mortality (perhaps due to intra-specific competition; Young and Evans 1972). Variation in microsite quality may thus have been equally important for *Salsola* abundance in the spring as the fall. Unlike *Sporobolus*, *Salsola* density also was positively associated with litter, which may have been related to the fact that most litter in these sites was derived from desiccated *Salsola* tissue that may have deposited seed. These differences highlight the fact that seedling responses to microsite may be species-specific and variable through time, even if the broader adult niche is similar (Rotundo and Aguiar 2005, Donohue et al. 2010).

The increased density of *Salsola* seedlings near obstructions highlights the fact that attempts to improve physical conditions for target species during restoration may have unintended positive impacts on undesirable species as well. This phenomenon has also been demonstrated in other degraded arid contexts, where additions of nitrogen (Brooks 2003) or water (Banerjee

et al. 2006) also promote noxious weed growth. Thus, restoration practitioners seeking to ameliorate harsh abiotic conditions at a site must give equal, or even elevated consideration to control of potentially negative biotic components of the system. In this study, the significant reduction in *Salsola* density associated with application of pre-emergent herbicide, with no apparent effect on *Sporobolus* densities, suggests a potential solution to this dilemma.

Effectiveness of treatments were contingent on climatic and local edaphic conditions

The response of *Sporobolus* to treatments in this study was contingent on climate conditions. In the first year after initiation of the experiment, following an extended period of below-average precipitation (Fig. 2), native grass germination was minimal, with only seven *Sporobolus* seedlings observed across all plots, none of which survived to subsequent sampling dates. It was only in the second year (2014), following a cool, moist, fall, and spring, that substantial *Sporobolus* emergence and growth was observed. Strong dependence on yearly climate conditions is a hallmark of plant populations in arid and semiarid environments (Allen 1995, Grantz et al. 1998, Knapp and Smith 2001), often leading to variable success in restoration (Bakker et al. 2003, Cox and Anderson 2004, Bernstein et al. 2014). Even in rare favorable years rates of plant establishment may remain low in desert systems (Bainbridge 2012). Ideally, restoration efforts in arid and semiarid systems will incorporate approaches that are both economically feasible and tolerant of inter-annual climate variations. In this study, native grass establishment was aided by burial of seed, which allowed seeds to persist until conditions became favorable. Structures greatly improved survival once climatic conditions permitted germination and growth.

The fact that *Sporobolus* presence varied greatly among soil patches with subtle differences in texture highlights how the effectiveness of restoration treatments are often strongly contingent on local site conditions (e.g. "site effects", Bakker et al. 2003, Young et al. 2015). At both ends of the texture gradient represented at our site, consisting of either deep sand or a sealed hardpan, probability of *Sporobolus* occupancy was

extremely low, even with all treatment combinations (seed, raking, and structure). In our study area, these textural variations likely produce different constraints to germination and growth, with hydrologically extreme conditions limiting germination in the fine-textured soils and seed burial below optimum depth for germination in the coppice dune soils. Many restoration studies have found important interactions between treatments and sites, as well as interactions between treatments and year of initiation (Cox and Anderson 2004, Vaughn and Young 2010), leading to dramatic differences in restoration outcomes. Quantifying this variation in replicated experiments will help managers identify sites where restoration may be most effective, thus making more efficient use of limited resources.

CONCLUSIONS AND RECOMMENDATIONS

The synergistic effects of treatments demonstrated in this study highlight how multiple factors, both biotic and abiotic, and both more or less tractable to management, may collude to maintain ecological states and govern ecological processes. Native grass response was substantial only when experimental treatments overcame seed and microsite limitation (via seeding and raking) in conjunction with amelioration of harsh abiotic conditions related to erosion and heightened connectivity among bare patches (mitigated via ConMod barrier structures). This response was only apparent under favorable weather conditions and in soil patches with suitable texture and depth. Had this experiment only examined any one treatment (or even combinations of treatments in single years or soil types), we would have concluded they were ineffective, emphasizing the reality that experimental conclusions and management interventions tend to be contingent on the limited conditions under which they are conducted (Vaughn and Young 2010, Young et al. 2015). Study designs with sufficient breadth in scale (especially temporal) that also include factorial interactions among variables will help guide restoration efforts by determining conditions where limited resources may be most effective.

In drylands, finding ways to mitigate multiple contingencies in restoration may be particularly

important since factors limiting system recovery operate (and interact) on dramatically different spatial and temporal scales (e.g., climate vs. seed movement; see Peters et al. 2004, Bestelmeyer et al. 2006a). Spatial connectivity between degraded patches has been proposed as a central concept which integrates many of these factors and underlies desertification worldwide (Okin et al. 2009). Here, we have demonstrated the effectiveness of techniques designed to directly address the negative effects of spatial connectivity (loss of seed, litter, soil, surface structure) in a way that is tolerant of climatic variation. Modification of connectivity for restoration (via Con-Mods) has been successful in other systems (e.g. the Chihuahan Desert; Okin et al. 2015, Rachal et al. 2015), and this study provides further evidence of its usefulness in a cold desert system, with a different set of biophysical characteristics distinguishing degraded vs. intact states (Bowker et al. 2014).

For sites sharing the characteristics of those used in this study, particularly ecological sites with similar climate characteristics (Semi-Desert) and surface textural class (Sandy Loam), which are among the most abundantly distributed ecological site types on the Colorado Plateau, it is recommended that restoration efforts simultaneously address all the specific physical and biological limitations cited in this study (amounting to plots with all treatments combined, at the very least). Efforts should pay particular attention to the biotic elements of the system which may be inhibiting recovery but are often less apparent than or obscured by salient abiotic factors. In particular, the problem of seed predation by harvester ants and strong positive response to barrier structures by exotic weeds are two negative influences which otherwise might not be anticipated given a cursory site examination. Further research should document how plant populations respond to structures in the medium and long-term, and the way in which barrier structure design (e.g., permeability, height, etc.) and scale of arrangement (density) affects native and non-native plant population dynamics.

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LITERATURE CITED

- Aguiar, M. R., and O. E. Sala. 1997. Seed distribution constrains the dynamics of the patagonian steppe. *Ecology* 78:93–100.
- Allen, E. B. 1995. Restoration ecology: limits and possibilities in arid and semiarid lands. Pages 7–15 in B. A. Roundy, and E. D. McArthur, editors. *Proceedings of the Wildland Shrub and Arid Land Restoration Symposium*, Las Vegas, Nevada, October 19–23, 1993. Intermountain Research Station, USDA Forest Service, Ogden, Utah, USA.
- Bainbridge, D. A. 2012. *A guide for desert and dryland restoration: new hope for arid lands*. Island Press, Washington, D.C., USA.
- Bakker, J. D., S. D. Wilson, J. M. Christian, X. Li, L. G. Ambrose, and J. Waddington. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications* 13:137–153.
- Banerjee, M. J., V. J. Gerhart, and E. P. Glenn. 2006. Native plant regeneration on abandoned desert farmland: effects of irrigation, soil preparation, and amendments on seedling establishment. *Restoration Ecology* 14:339–348.
- Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1:376–382.
- Belnap, J., B. Büdel, and O. L. Lange. 2003. Biological soil crusts: characteristics and distribution. Pages 3–30 in P. D. J. Belnap, and O. L. Lange, editors. *Biological soil crusts: structure, function, and management*. Springer, Berlin, Heidelberg, Germany.
- Bernstein, E. J., C. M. Albano, T. D. Sisk, T. E. Crews, and S. Rosenstock. 2014. Establishing cool-season grasses on a degraded arid rangeland of the Colorado Plateau. *Restoration Ecology* 22:57–64.

- Bestelmeyer, B. T., D. A. Trujillo, A. J. Tugel, and K. M. Havstad. 2006a. A multi-scale classification of vegetation dynamics in arid lands: What is the right scale for models, monitoring, and restoration? *Journal of Arid Environments* 65:296–318.
- Bestelmeyer, B. T., J. P. Ward, and K. M. Havstad. 2006b. Soil-geomorphic heterogeneity governs patchy vegetation dynamics at an arid ecotone. *Ecology* 87:963–973.
- Bestelmeyer, B. T., A. J. Tugel, G. L. Peacock, D. G. Robinett, P. L. Shaver, J. R. Brown, J. E. Herrick, H. Sanchez, and K. M. Havstad. 2009. State-and-transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology & Management* 62:1–15.
- Bestelmeyer, B. T., G. S. Okin, M. C. Duniway, S. R. Archer, N. F. Sayre, J. C. Williamson, and J. E. Herrick. 2015. Desertification, land use, and the transformation of global drylands. *Frontiers in Ecology and the Environment* 13:28–36.
- Bowker, M. A., M. E. Miller, S. L. Garman, and T. Belote. 2014. Applying threshold concepts to conservation management of dryland ecosystems: case studies on the Colorado Plateau. Pages 101–130 in G. R. Guntispergen, editor. *Application of threshold concepts in natural resource decision making*. Springer, New York, New York, USA.
- Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* 40:344–353.
- Chambers, J. C. 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. *Ecological Applications* 10:1400–1413.
- Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist* 170:128–142.
- Cox, R. D., and V. J. Anderson. 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *Rangeland Ecology & Management* 57:203–210.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- DeFalco, L. A., T. C. Esque, J. M. Kane, and M. B. Nicklas. 2009. Seed banks in a degraded desert shrubland: influence of soil surface condition and harvester ant activity on seed abundance. *Journal of Arid Environments* 73:885–893.
- DeFalco, L. A., T. C. Esque, M. B. Nicklas, and J. M. Kane. 2012. Supplementing seed banks to rehabilitate disturbed Mojave Desert shrublands: where do all the seeds go? *Restoration Ecology* 20:85–94.
- Donohue, K., R. Rubio de Casas, L. Burghardt, K. Kovach, and C. G. Willis. 2010. Germination, post-germination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics* 41:293–319.
- Duniway, M. C., E. Palmquist, and M. E. Miller. 2015. Evaluating rehabilitation efforts following the Milford Flat Fire: successes, failures, and controlling factors. *Ecosphere* 6:80.
- Evans, R. A., and J. A. Young. 1970. Plant litter and establishment of alien annual weed Species in rangeland communities. *Weed Science* 18:697–703.
- Flores, J., and E. Jurado. 2003. Are nurse-protégé interactions more common among plants from arid environments? *Journal of Vegetation Science* 14:911–916.
- Fox, J., and S. Weisberg. 2011. *An R companion to applied regression*. Second edition. Sage, Thousand Oaks, California, USA.
- Grantz, D. A., D. L. Vaughn, R. Farber, B. Kim, M. Zeldin, T. VanCuren, and R. Campbell. 1998. Seeding native plants to restore desert farmland and mitigate fugitive dust and PM10. *Journal of Environment Quality* 27:1209–1218.
- Harper, J. L., J. T. Williams, and G. R. Sagar. 1965. The behaviour of seeds in soil: I. the heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *Journal of Ecology* 53:273–286.
- Hillel, D. 1998. *Environmental soil physics: fundamentals, applications, and environmental considerations*. Academic Press, San Diego, California, USA.
- Hobbs, R. J., and D. A. Norton. 2004. Ecological filters, thresholds, and gradients in resistance to ecosystem reassembly. Pages 72–95 in V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. *Assembly rules and restoration ecology*. Island Press, Washington, D.C., USA.
- Kinyua, D., L. E. McGeoch, N. Georgiadis, and T. P. Young. 2010. Short-term and long-term effects of soil ripping, seeding, and fertilization on the restoration of a tropical rangeland. *Restoration Ecology* 18:226–233.
- Kleiner, E. F., and K. T. Harper. 1972. Environment and community organization in grasslands of Canyonlands National Park. *Ecology* 53:299–309.
- Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481–484.
- Li, X. R., H. L. Xiao, M. Z. He, and J. G. Zhang. 2006. Sand barriers of straw checkerboards for habitat restoration in extremely arid desert regions. *Ecological Engineering* 28:149–157.
- MacMahon, J. A., J. F. Mull, and T. O. Crist. 2000. Harvester ants (*Pogonomyrmex* spp.): their community

- and ecosystem influences. *Annual Review of Ecology and Systematics* 31:265–291.
- Masters, R. A., and R. L. Sheley. 2001. Principles and practices for managing rangeland invasive plants. *Journal of Range Management* 54:502–517.
- Miller, M. E., J. Belnap, S. W. Beatty, and R. L. Reynolds. 2006. Performance of *Bromus tectorum* L. in relation to soil properties, water additions, and chemical amendments in calcareous soils of south-eastern Utah, USA. *Plant and Soil* 288:1–18.
- Miller, M. E., R. T. Belote, M. A. Bowker, and S. L. Garman. 2011. Alternative states of a semiarid grassland ecosystem: implications for ecosystem services. *Ecosphere* 2:55.
- Miller, M. E., M. A. Bowker, R. L. Reynolds, and H. L. Goldstein. 2012. Post-fire land treatments and wind erosion—lessons from the Milford Flat Fire, UT, USA. *Aeolian Research* 7:29–44.
- Mull, J. F., and J. A. MacMahon. 1996. Factors determining the spatial variability of seed densities in a shrub-steppe ecosystem: the role of harvester ants. *Journal of Arid Environments* 32:181–192.
- Neff, J. C., R. L. Reynolds, J. Belnap, and P. Lamothe. 2005. Multi-decadal impacts of grazing on soil physical and biogeochemical properties in south-east Utah. *Ecological Applications* 15:87–95.
- Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The Saguaro: a population in relation to environment. *Science* 142:15–23.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25–51.
- Okin, G. S., A. J. Parsons, J. Wainwright, J. E. Herrick, B. T. Bestelmeyer, D. C. Peters, and E. L. Fredrickson. 2009. Do changes in connectivity explain desertification? *BioScience* 59:237–244.
- Okin, G. S., M. M. Las Heras, P. M. Saco, H. L. Throop, E. R. Vivoni, A. J. Parsons, J. Wainwright, and D. P. Peters. 2015. Connectivity in dryland landscapes: shifting concepts of spatial interactions. *Frontiers in Ecology and the Environment* 13:20–27.
- Peters, D. P. C., R. A. Pielke, B. T. Bestelmeyer, C. D. Allen, S. Munson-McGee, and K. M. Havstad. 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences USA* 101:15130–15135.
- R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rachal, D. M., G. S. Okin, C. Alexander, J. E. Herrick, and D. P. C. Peters. 2015. Modifying landscape connectivity by reducing wind driven sediment redistribution, Northern Chihuahuan Desert, USA. *Aeolian Research* 17:129–137.
- Reichman, O. J. 1979. Desert granivore foraging and its impact on seed densities and distributions. *Ecology* 60:1086–1092.
- Rotundo, J. L., and M. R. Aguiar. 2005. Litter effects on plant regeneration in arid lands: a complex balance between seed retention, seed longevity and soil-seed contact. *Journal of Ecology* 93:829–838.
- Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant-soil interactions in deserts. *Biogeochemistry* 42:169–187.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. *Science* 247:1043–1048.
- Sheldon, J. C. 1974. The behaviour of seeds in soil: III. the influence of seed morphology and the behaviour of seedlings on the establishment of plants from surface-lying seeds. *Journal of Ecology* 62:47–66.
- Skaug, H., D. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2011. glmmADMB: generalized linear mixed models using AD Model Builder. R package version 0.6.
- 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.
- Suding, K. N., and R. J. Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. *Trends in Ecology & Evolution* 24:271–279.
- Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* 19:46–53.
- Svejcar, L. N., B. T. Bestelmeyer, M. C. Duniway, and D. K. James. 2015. Scale-dependent feedbacks between patch size and plant reproduction in desert grassland. *Ecosystems* 18:146–153.
- Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? a review of seed sowing experiments. *Oikos* 88:225–238.
- Turnbull, L. A., J. Wainwright, and R. E. Brazier. 2008. A conceptual framework for understanding semi-arid land degradation: ecohydrological interactions across multiple-space and time scales. *Ecohydrology* 1:23–34.
- USDA NRCS. 2009. Web soil survey. <http://www.websoilsurvey.ncsc.usda.gov/app/>
- Vaughn, K. J., and T. P. Young. 2010. Contingent conclusions: year of initiation influences ecological field experiments, but temporal replication is rare. *Restoration Ecology* 18:59–64.
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*. Springer-Verlag, New York, New York, USA.

- Visser, N., J. C. Botha, and M. B. Hardy. 2004. Re-establishing vegetation on bare patches in the Nama Karoo, South Africa. *Journal of Arid Environments* 57:155–177.
- Wainwright, J., A. J. Parsons, W. H. Schlesinger, and A. D. Abrahams. 2002. Hydrology–vegetation interactions in areas of discontinuous flow on a semi-arid bajada, Southern New Mexico. *Journal of Arid Environments* 51:319–338.
- Western Regional Climate Center. 2015. Cooperative climatological data summaries. <http://www.wrcc.dri.edu/climatedata/climsum/>
- Whisenant, S. 1999. *Repairing damaged wildlands: a process-orientated, landscape-scale approach*. Cambridge University Press, Cambridge, UK.
- Winkel, V. K., and B. A. Roundy. 1991. Effects of cattle trampling and mechanical seedbed preparation on grass seedling emergence. *Journal of Range Management* 44:176–180.
- Young, J. A., and R. A. Evans. 1972. Germination and establishment of *Salsola* in relation to seedbed environment. I. temperature, afterripening, and moisture relations of *Salsola* seeds as determined by laboratory studies. *Agronomy Journal* 64: 214–218.
- Young, T. P., E. P. Zefferman, K. J. Vaughn, and S. Fick. 2015. Initial success of native grasses is contingent on multiple interactions among exotic grass competition, temporal priority, rainfall and site effects. *AoB Plants* 7:81.