



# Arid old-field restoration: Native perennial grasses suppress weeds and erosion, but also suppress native shrubs



Lauren M. Porensky<sup>a,\*</sup>, Elizabeth A. Leger<sup>a</sup>, Jay Davison<sup>b</sup>, W. Wally Miller<sup>a</sup>,  
Erin M. Goergen<sup>a,1</sup>, Erin K. Espeland<sup>a,2</sup>, Erin M. Carroll-Moore<sup>a</sup>

<sup>a</sup> Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV 89557, USA

<sup>b</sup> University of Nevada Cooperative Extension, Fallon, NV 89406, USA

## ARTICLE INFO

### Article history:

Received 11 July 2013

Received in revised form

12 November 2013

Accepted 21 November 2013

Available online 20 December 2013

### Keywords:

Cropland abandonment

Irrigation

Native shrub facilitation

US arid Great Basin

Walker Basin

Weed control

## ABSTRACT

Rates of cropland abandonment in arid regions are increasing, and abandoned fields in such regions can have low levels of ecosystem function and biodiversity. Long-lived, drought-tolerant shrubs are dominant components of many arid ecosystems, providing multiple ecosystem services such as soil stabilization, herbaceous plant facilitation, carbon storage and wildlife habitat. On abandoned agricultural fields, shrub restoration is hindered by multiple challenges, including erosion, water stress and invasive species. We hypothesized that applying short-term irrigation and seeding native perennial grasses would facilitate native shrub establishment by reducing erosion and weed abundance. Using a blocked split-plot design, we evaluated the separate and combined impacts of short-term irrigation and perennial grass seeding on five-year restoration outcomes (including direct measurements of wind erosion) at two former agricultural fields in North America's arid Great Basin. **After two years, irrigation had increased the density and biomass of seeded grasses by more than ten-fold.** The combination of irrigation and seeded grasses was associated with significantly lower wind erosion, weed density and weed biomass. **Three years after irrigation ended, seeded grasses remained significantly more abundant in formerly irrigated than non-irrigated plots. Formerly irrigated plots also had significantly less bare ground, annual plant cover and weed biomass than non-irrigated plots.** Large plant-canopy gaps were fewer in irrigated and seeded plots. Although seeded grasses reduced erosion and invasion, they failed to facilitate native shrub establishment. Shrub cover and density were highest in plots that had been drill-seeded and irrigated, but lacked perennial grasses. **Our results indicate that short-term irrigation has persistent restoration benefits, and that a tradeoff exists between the benefits and costs of seeding perennial grasses into degraded arid shrubland sites.**

Published by Elsevier B.V.

## 1. Introduction

Shrub establishment is often a central goal of restoration in arid regions. Long-lived, drought-tolerant shrubs dominate the plant communities of many arid ecosystems (e.g., Ackerly, 2004; Miller et al., 2011; Wang et al., 2012), and these shrubs provide important functional benefits. For example, shrubs can stabilize soils, facilitate

the establishment of other plants, store carbon, and provide critical wildlife habitat (Garcia-Estringana et al., 2013; Fonseca et al., 2012; Miller et al., 2011; Stavi et al., 2011; van Zonneveld et al., 2012). Shrubs can also increase ecosystem-level biodiversity, both by increasing the abundance and diversity of understory plants (van Zonneveld et al., 2012) and by providing resident and transient wildlife with habitat and forage (Miller et al., 2011).

On denuded sites, native shrub restoration is hindered by both abiotic and biotic challenges. Abiotic challenges include wind erosion and water stress, which can reduce seedling survival and growth (Maestre et al., 2001; Okin et al., 2006). Climate change will likely exacerbate abiotic challenges by increasing drought frequency and intensity (IPCC, 2012). Shrubs can also be difficult to restore due to the presence of mature grasses, which can limit or reduce shrub establishment (Boyd and Svejcar, 2011; reviewed by Meyer, 1992; but see Williams et al., 2002). To improve shrub restoration in degraded drylands, it may be necessary to actively mitigate these restoration barriers.

\* Corresponding author at: USDA ARS, Rangeland Resources Research Unit, Fort Collins, CO 80526, USA. Tel.: +1 408 621 0804.

E-mail addresses: [lauren.porensky@ars.usda.gov](mailto:lauren.porensky@ars.usda.gov) (L.M. Porensky), [elager@cabnr.unr.edu](mailto:elager@cabnr.unr.edu) (E.A. Leger), [davisonj@UNCE.unr.edu](mailto:davisonj@UNCE.unr.edu) (J. Davison), [wilymalr@cabnr.unr.edu](mailto:wilymalr@cabnr.unr.edu) (W.W. Miller), [erin.goergen@gmail.com](mailto:erin.goergen@gmail.com) (E.M. Goergen), [erin.espeland@ars.usda.gov](mailto:erin.espeland@ars.usda.gov) (E.K. Espeland), [ecarrollmoore@gmail.com](mailto:ecarrollmoore@gmail.com) (E.M. Carroll-Moore).

<sup>1</sup> Present address: St. Petersburg College, Clearwater, FL 33733, USA.

<sup>2</sup> Present address: USDA ARS, Pest Management Research Unit, Sidney, MT 59270, USA.

**Table 1**  
Seeded species and management methods for different subplots.

Common Name	Scientific name and authority	Season; variety	kg/km <sup>2</sup> Sown	Planting date	Seed preparation and planting	Code
–	–	–	0	–	Only cultipacker	Control
Inland saltgrass	<i>Distichlis spicata</i> (L.) Greene	Warm; Wildland collection	1.57	Jul 2008	Scarified for 2 mo. before seeding (40 °C & 20 °C, each 12 h); only drill	Disp
Indian ricegrass	<i>Achnatherum hymenoides</i> (Roem. & Schult.) Barkworth	Cool; Nezpar, Rimrock	0.896	Dec 2007	Drill + cultipacker	Achy
Basin wildrye	<i>Leymus cinereus</i> (Scribn. & Merr.) Á. Löve	Cool; Trailhead	1.12	Dec 2007	Drill + cultipacker	Leci
Western wheatgrass	<i>Pascopyrum smithii</i> (Rydb.) Á. Löve	Cool; Arriba, Rosana	1.34	Dec 2007	Drill + cultipacker	Pasm
Beardless wheatgrass	<i>Pseudoroegneria spicata</i> (Pursh) Á. Löve	Cool; Whitmar	0.896	Dec 2007	Drill + cultipacker	Pssp

We studied shrub restoration on abandoned agricultural fields in a cold desert ecosystem. Globally, cropland abandonment has increased exponentially since the mid-1800s (Cramer et al., 2008), and abandoned agricultural fields represent an emerging focus of restoration ecology in arid regions. In Nevada, at the heart of North America's arid Great Basin ecoregion, the amount of actively farmed land declined by 34% between 1992 and 2011 (USDA National Agricultural Statistics Service, 2012). Although passive restoration of arid agricultural fields may be possible in some circumstances (e.g., Scott and Morgan, 2012), a passive approach usually leads to slow or incomplete recovery (Otto et al., 2006; Munson et al., 2012), or further degradation (Jackson and Comus, 1999).

The long-term ecological legacies of agricultural abandonment in arid regions can include altered soil properties (e.g., less organic matter, less soil carbon, nitrogen and phosphorous, higher bulk density), altered plant communities (e.g., lower plant diversity, lower native plant abundance, lower total plant cover, lower cover of dominant shrubs, less forb cover) and reduced ecological stability (e.g., larger temporal fluctuations in plant cover, density and diversity, higher probability of conversion to a degraded state) (Burke et al., 1995; Elmore et al., 2006; Kawada et al., 2011; Morris et al., 2011; Munson et al., 2012; Xu et al., 2010). Agricultural abandonment without active restoration often leads to substantial wind erosion (Kawada et al., 2011; Okin et al., 2006), and the combination of soil disturbance, loss of vegetation, reduced native propagule pressure, increased nutrient availability, and dense weed seed-banks makes abandoned fields highly susceptible to exotic plant invasion (Cramer et al., 2008; Elmore et al., 2006; Milton and Dean, 2010; Török et al., 2012). Thus, on arid old-fields, active restoration (e.g., soil remediation, herbicide application, or planting) is often necessary to improve ecosystem stability and function (Jackson and Comus, 1999; Otto et al., 2006; Munson et al., 2012).

Planting native perennial grasses in abandoned fields can prevent or reduce weed invasion (Bugg et al., 1997; Blumenthal et al., 2005; Török et al., 2012) and reduce wind erosion (Okin et al., 2006), mitigating some of the barriers hindering shrub establishment (Maestre et al., 2001). At the same time, co-occurring grasses and shrubs will likely compete for limited resources (Maestre and Cortina, 2004). Impacts of grasses on shrub success may vary depending on grass or shrub species identity (Maestre et al., 2001; Meyer, 1992) or resource availability (Maestre and Cortina, 2004). According to the stress-gradient hypothesis, positive interspecific interactions should be more common when stress is high (Bertness and Callaway, 1994), and several studies in dryland ecosystems have found evidence for greater plant–plant facilitation at more stressful sites (e.g., Arredondo-Núñez et al., 2009; Forey et al., 2009) or at more stressful times (e.g., Veblen, 2008). In contrast, other studies suggest that stress can lead to increased competition for

scarce resources (e.g., Bowker et al., 2010; Holmgren and Scheffer, 2010; Odadi et al., 2011).

Irrigation infrastructure is still present on many abandoned agricultural fields in arid regions, and this allows restoration practitioners to modify stress by irrigating seedlings during the establishment phase. However, it remains unclear whether short-term irrigation translates into longer-term restoration success (Josa et al., 2012; Roundy et al., 2001). It is also unclear whether short-term irrigation will increase or decrease the likelihood of grass–shrub facilitation (Forey et al., 2009; Jankju, 2013; Maestre and Cortina, 2004; Maestre et al., 2001).

We used a broad-scale manipulative experiment to determine the separate and combined impacts of seeded perennial grasses and short-term irrigation on 5-year restoration outcomes at abandoned agricultural sites in the Great Basin, where little previous work exists. Our study addressed three specific research questions:

- (1) Does short-term irrigation increase the establishment and long-term survival of shrubs or grasses, and do the impacts of irrigation depend on grass species identity?
- (2) Do grasses mitigate potential shrub restoration barriers by suppressing weeds or reducing erosion, and do grass impacts depend on irrigation status or grass species identity?
- (3) Do grasses facilitate shrubs, and does facilitation depend on irrigation status or grass species identity?

Our results provide information about the likely outcomes of passive vs. active restoration on former agricultural fields in arid shrublands, as well as what specific restoration methods succeed best in arid ecosystems.

## 2. Materials and methods

### 2.1. Study sites and species descriptions

Two study sites were located along the lower reaches of the Walker River, 11.5 km south of Mason, Nevada USA. The Valley Vista Ranch (VV) site (38°50'58"N, 119°11'04"W) was used for alfalfa production until the start of the experiment, while the 5 C's Cottonwood Ranch (5C) site (38°50'45"N, 119°11'02"W) was a denuded pasture formerly used for burro and llama grazing. Both sites are located on Malpais (loamy-skeletal, mixed, superactive, mesic Typic Haplocambids) complex soils (dominated by Malpais gravelly sandy loam and Malpais stony sandy loam) (USDA Soil Conservation Service, 1984). Soil testing indicated that the sites have a moderately alkaline pH and low salinity (saturated soil paste, Bower and Wilcox, 1965), relatively high concentrations of water extractable nitrate (saturation extract, Bower and Wilcox, 1965),

and relatively low concentrations of water extractable phosphate and most cations (Appendix A). Annual precipitation averages 127 mm but is highly variable across years. For 2008–2011, water year precipitation (October 1–September 30) ranged from 66 to 177 mm. Natural vegetation near the sites is dominated by long-lived desert shrub species such as *Atriplex canescens* (Pursh) Nutt., *Atriplex confertifolia* (Torr. & Frém.) S. Watson, *Sarcobatus vermiculatus* (Hook.) Torr., *Artemisia tridentata* subsp. *wyomingensis* Beetle & A.M. Young, and *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird.

We planted five native grass species at each site: four cool-season perennial bunchgrasses known to survive in Great Basin regions receiving <300 mm of annual precipitation, and one warm-season, perennial rhizomatous grass with high drought- and salt-tolerance (Table 1) (USDA NRCS, 2013). We planted four native shrub species (*A. canescens*, *A. confertifolia*, *S. vermiculatus*, and *A. tridentata* subsp. *wyomingensis*) grown from wildland seed collections.

## 2.2. Experimental design

The experiment had a blocked split-plot design with three 56 × 54 m blocks at each site. Each block was split into two 56 × 27 m plots, with one plot assigned to the “Irrigation” treatment and the other to the “No Irrigation” treatment. Within each plot, six 9.3 × 27 m subplots were assigned to different seeding treatments, which included one unseeded control (intended to represent a field receiving no active restoration planting) and five grass monocultures (one per species). Though restoration practitioners typically plant species mixtures, here we planted grasses in monocultures so that we could compare the effects of different grass species on erosion, weed invasion and shrub establishment. For *Achnatherum hymenoides* and *Pascopyrum smithii* we planted a different variety in each half of each subplot. As commercial variety did not affect long-term performance for either species, data were pooled at the species level for final analysis. In one block per site, the same subplot treatment randomization was inadvertently applied to both irrigation plots. In the other blocks, subplot treatments were randomized separately within each irrigation plot. Seven shrubs (one per species, plus three others randomly assigned with respect to species) were transplanted into each subplot planted with perennial grasses.

## 2.3. Management and planting

To prepare sites for planting, we applied herbicides (glyphosate and dicamba to kill alfalfa on the VV site in June and August 2007) and mechanical treatments (ripping, disking and floating on both sites in September 2007). To reduce annual weed pressure during the first growing season, we applied 2,4-D on all plots in May 2008 (56 kg/km<sup>2</sup> 2,4-D ester in 18.7 × 10<sup>3</sup> L/km<sup>2</sup> of water) and mowed all plots biweekly until the end of the first growing season. For *Distichlis spicata* subplots, we also applied glyphosate (85 kg/km<sup>2</sup>, 5.69 g/L concentration, ±0.025% NIS) in late June 2008, prior to planting. No weed control efforts were undertaken in future years.

Cool-season grasses were planted in December 2007, and warm-season *D. spicata* was planted in July 2008. All species were sown at recommended seeding rates (Table 1) using a Truax drill with seeds placed 1.3 cm deep and followed by press wheels. All fall-planted subplots were also rolled with a cultipacker to form a firm seed bed, but *D. spicata* subplots were drilled-seeded only; in July the soil was sufficiently firm for planting without the cultipacker treatment. Shrubs were grown in 1.9 L plastic pots for two years in an outdoor location in Reno, NV. Individually-marked shrubs were hand-transplanted approximately 5 m apart into subplots (excluding Control subplots) in December 2008. In total, 118 *A.*

*canescens*, 77 *A. confertifolia*, 93 *S. vermiculatus*, and 132 *A. tridentata* were planted across both sites.

Irrigation was applied using sprinklers (set on a 9.1 × 9.1 m pattern) that delivered approximately 7.6 L/min/sprinkler. Plots assigned to the irrigation treatment were watered approximately once per week from late spring (April–May) to mid-summer (July–August). Irrigation was discontinued when approximately 85 and 30 cm of water had been applied to each irrigation plot in 2008 (year 1) and 2009 (year 2), respectively. Irrigation plots only received natural precipitation after 2009.

Cattle grazing occurred during plant dormancy at the VV site in 2009, 2010, and 2011. This unplanned treatment was the result of animals from nearby alfalfa fields entering our restoration treatments during cold winter months in spite of electric fencing. Livestock grazing did not occur at the 5C site. To account for potential effects of grazing on restoration outcomes, “site” was included as a factor in all models (see Section 2.5).

## 2.4. Data collection

### 2.4.1. Vegetation and bare ground

In August 2009 (year 2) and late July 2011 (year 4), we monitored seeded grass density (no. of individuals/m<sup>2</sup>) and wet biomass (g/m<sup>2</sup>) using 25 × 25 cm quadrats. On each sampling date, five quadrats were randomly placed in each *Leymus cinereus*, *Pseudoroegneria spicata*, *D. spicata* and Control subplot. Subplots planted with *A. hymenoides* and *P. smithii* were sampled using 6 quadrats (three randomly-placed quadrats within each of the two varieties). We sampled weeds (non-native plants, which were primarily annual forbs) in years 2 and 4 using methods identical to those used for seeded grasses. We monitored the survival and height of transplanted shrubs in year 2 and year 4. To estimate cover of transplanted shrubs, we also measured the length and width of each shrub, then used the formula for the area of an ellipse ( $\pi \times \text{length}/2 \times \text{width}/2$ ) to calculate area in m<sup>2</sup>.

In year 4, plants were large enough to contribute substantially to ground cover, and we quantified percent cover of perennial grasses, shrubs, annual plants, litter, and bare ground using point-intercept sampling, in addition to the density and biomass measurements described above. Ten evenly-spaced points were sampled along each of three 9.3 m-long, randomly located and non-overlapping transects per subplot. To quantify longer-term effects of treatments on vegetation cover, erosion potential and shrub density, we took additional measurements in December 2012 (year 5) at the 5C site; the VV site transitioned to other land uses after year 4. We determined percent bare ground and percent cover of perennial grasses, shrubs, and annual plants using line-intercept sampling. Two randomly located and non-overlapping 9.3 m-long transects were sampled in each subplot. We used line-intercept data to calculate the frequency of large canopy gaps (>2 m) within each subplot. Shrub density was measured along each transect by counting all individuals found in a 9.3 × 4 m belt.

### 2.4.2. Wind erosion

Dust collector nests (Appendix A, Fryrear, 1986) were used to monitor the effects of restoration treatments on wind erosion. At each site, groups of four nests were placed on one non-irrigated plot and one irrigated plot. Nests were also installed at two ‘natural’ sites (covered by less-disturbed natural vegetation) located <400 m from the experimental sites, resulting in a total of six groups of four nests. Although different sized particles may move by different mechanisms, the larger sizes typically move at lower elevations relative to the soil surface, and movement occurs further from the ground when particle sizes are smaller or erosive force (shear velocity) is greater (Okin et al., 2006). Hence, each dust collector nest was equipped with four traps set at heights of 7, 35, 60 and

100 cm above the soil surface (Appendix A) to account for potential treatment-induced differences in particulate load distribution (i.e. larger particles closer to the surface or finer particles at greater heights).

Dust data were collected from year 2 (January 2009 for 5C and June 2009 for VV) through year 4 (December 2011). Initially, the four nests in each treatment plot were arranged in a diamond formation with each nest located 1 m from the midpoint of a different plot edge (Appendix A). Nests were moved toward the center of each plot in April 2010 to minimize edge effects. After this adjustment, each diamond-shaped group of nests had a diameter of 20 m. One of the 'natural' groups had a diameter of 30 m throughout the experiment. Dust collection traps were emptied following major wind events (gusts >30 mph) or when there was a substantial break in wind activity, and samples were weighed in the laboratory.

For each wind event, prevailing wind direction (based on data from an on-site weather station) was used to determine which collector nests within each nest group would be designated as incoming and outgoing (Appendix A). For each trap height, we subtracted incoming nest sediment weights from outgoing nest sediment weights to estimate overall dust generation (+) or deposition (−) amounts. Totals were divided by the distance between incoming and outgoing nests to obtain milligrams of dust generated or deposited per meter traveled (Appendix A, Fryrear et al., 1998). Multiple nest heights allowed us to characterize changes in the sediment load distribution relative to the soil surface.

## 2.5. Data analysis

Data were analyzed using generalized linear mixed models. Response variables included planted grass density and biomass, weed density and biomass, and dust (years 2 and 4), percent cover of different plant types and bare ground (years 4 and 5), frequency of large canopy gaps and total shrub density (year 5), and transplanted shrub survival and size (years 2 and 4). If multiple measurements were taken per subplot, data were pooled at the subplot level (one value per subplot for analysis). Variance-weighting was used when variances were not homogenous, and response values were transformed when necessary.

For vegetation and cover data from years 2 and 4, random factors included site, block nested within site, and irrigation plot nested within block and site. For year 5 data (which were only collected at one site), random factors included block and irrigation plot nested within block. In dust models, random factors included site and dust collector group nested within site.

For vegetation and cover data, fixed factors included irrigation treatment, planted species treatment, and the irrigation × species interaction. Fixed factors in dust models included irrigation treatment, trap height, and the irrigation × height interaction. If interaction terms were significant ( $P < 0.05$ ), simple effects tests were performed. Interaction terms were removed from models in which they had  $P$ -values  $> 0.10$ . In all cases, Tukey's Honestly Significant Difference tests ( $\alpha = 0.05$ ) were used for post-hoc means comparisons. Analyses were completed in R (package nlme, Pinheiro et al., 2013; R Development Core Team, 2011). Results are reported as means  $\pm$  1 standard error.

## 3. Results

### 3.1. Planted grasses

In year 2, planted grass density and biomass were 0 in all Control and *D. spicata* subplots. To avoid heteroscedasticity,

these subplots were excluded from further analysis. Cool season grass densities varied based on species identity and irrigation treatments (Fig. 1a; Table 2). In non-irrigated plots, all species occurred at similar (and low) densities (Fig. 1a; simple effects  $F_{3,15} = 1.1$ ,  $P = 0.4$ ). In irrigated plots, *P. smithii* density was over twice as high as densities of the other three grass species (Fig. 1a; simple effects  $F_{3,15} = 8.8$ ,  $P = 0.001$ ). For all four cool-season species, densities were significantly higher in irrigated than in non-irrigated plots (Fig. 1a; all simple effects  $P$ -values  $< 0.004$ ). Planted grass biomass was similar across cool-season grass species and was 200 times higher in irrigated than non-irrigated plots (Fig. 1c; Table 2).

By year 4, two years after irrigation ceased, planted grass density and biomass had declined to 48% and 38% of year 2 levels, respectively (Fig. 1b and d). All values remained 0 in Control subplots, suggesting that planted grasses had not spread beyond their subplot boundaries. Control subplots were excluded from further analysis to meet model assumptions. Planted grass density and biomass values in *D. spicata* subplots were  $< 5\%$  of values in subplots seeded with other grass species (Fig. 1b and d; Table 2). Across species, irrigated plots had at least 3 times more planted grass than non-irrigated plots (Fig. 1b and d; Table 2).

### 3.2. Weeds

In year 2, the density and biomass of weeds (i.e. non-native plants, which were primarily annual forbs) were 14 and 7 times higher in irrigated than non-irrigated plots, respectively (Fig. 2a and c; Table 2). Weed density was 3.5 times higher in *D. spicata* subplots (where perennial grasses were absent) than in *A. hymenoides* and *P. smithii* subplots (Fig. 2a; Table 2). Weed biomass was almost 7 times higher in Control and *D. spicata* subplots than in *L. cinereus* and *P. smithii* subplots, and 4 times higher in *D. spicata* subplots than *A. hymenoides* subplots (Fig. 2c; Table 2). By year 4, weed densities had increased in non-irrigated plots and weed biomass had declined across all plots (Fig. 2b and d). Irrigation and planted species had no significant effects on weed density or biomass in year 4 (Fig. 2b and d;  $P$ -values  $> 0.10$ ).

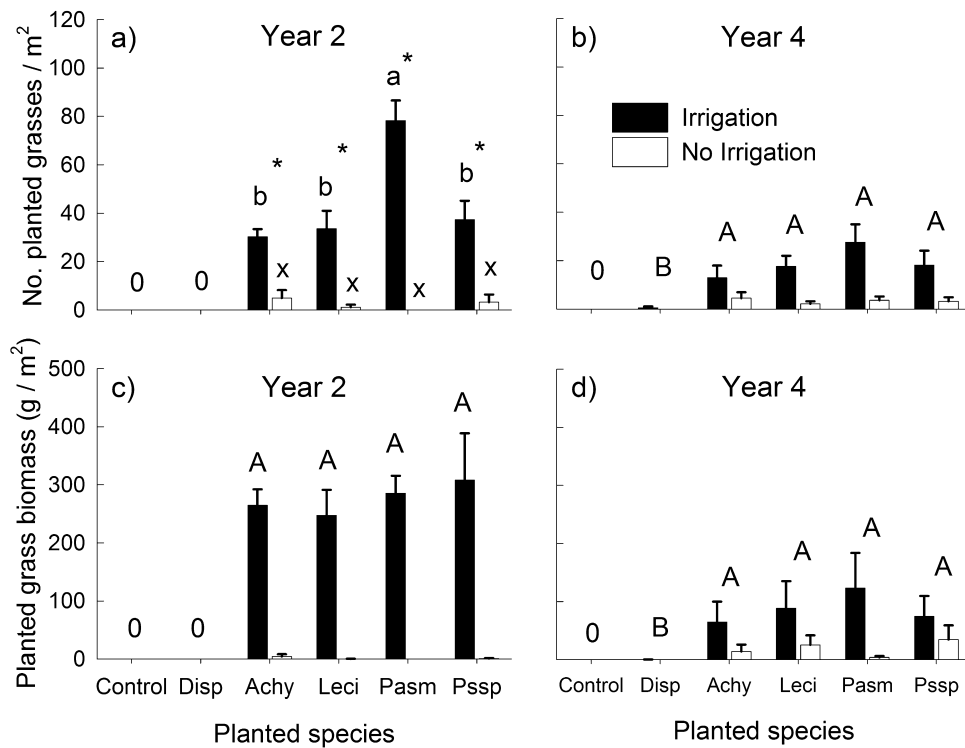
### 3.3. Long-term differences in understory plant cover, bare ground and canopy gaps

In year 4, perennial grass cover was 6.7 times higher in irrigated than in non-irrigated plots (Fig. 3a; Table 2). Subplots planted with *D. spicata* had significantly lower cover than subplots planted with *A. hymenoides*, *L. cinereus*, or *P. spicata*, while Control and *P. smithii* subplots had intermediate cover (Fig. 3a; Table 2). Note that this analysis included both seeded perennial grasses ( $11 \pm 4\%$  cover) and unseeded (volunteer) perennial grasses ( $3 \pm 1\%$  cover). Volunteer grasses were dominated by *Sporobolus airoides*.

Percent cover of annual plants (mostly forbs) was 37% higher in non-irrigated than irrigated plots (Fig. 3b; Table 2). Annual cover included both non-native species (e.g., *Erodium cicutarium*, *Salsola iberica*, *Sisymbrium altissimum*) and native species (mostly *Amsinckia tessellata*). Native and non-native annuals responded similarly to treatments. Bare ground was 76% more abundant in non-irrigated than irrigated plots (Fig. 3c; Table 2). Annual plant cover and bare ground did not differ significantly based on planted species (Fig. 3b and c; Table 2). Irrigation and planted species treatments did not significantly affect litter cover ( $P$ -values  $> 0.07$ ). In year 5, sampling at the 5C site revealed that treatment effects on plant cover and bare ground had not changed substantially since year 4 (Appendix B).

In year 5 at the 5C site, the effects of planted species treatments on the frequency of large ( $> 2$  m) gaps between plant canopies varied based on irrigation treatment (Fig. 3d; Table 2). In non-irrigated plots, gap frequency was similar across planted species and the





**Fig. 1.** Impacts of irrigation and seeded species on planted grass density ((a) and (b)) and biomass ((c) and (d)) in year 2 ((a) and (c)) and year 4 ((b) and (d)). Large letters indicate significant differences among seeded species across irrigation treatments (Tukey post-hoc means comparisons for main effects). Asterisks indicate significant differences among irrigation treatments within a given seeded species treatment, and small letters indicate significant differences among seeded species within a given irrigation treatment (Tukey post-hoc means comparisons for simple effects; letters a–c are used for irrigated plots and letters x–z for non-irrigated plots). “0” indicates that no plants were observed in a given treatment, and this treatment was excluded from analysis. In all cases, treatments sharing a letter are not significantly different. Disp = *Distichlis spicata*, Achy = *Achnatherum hymenoides*, Leci = *Leymus cinereus*, Pasm = *Pascopyrum smithii*, and Pssp = *Pseudoroegneria spicata* subsp. *inermis*.

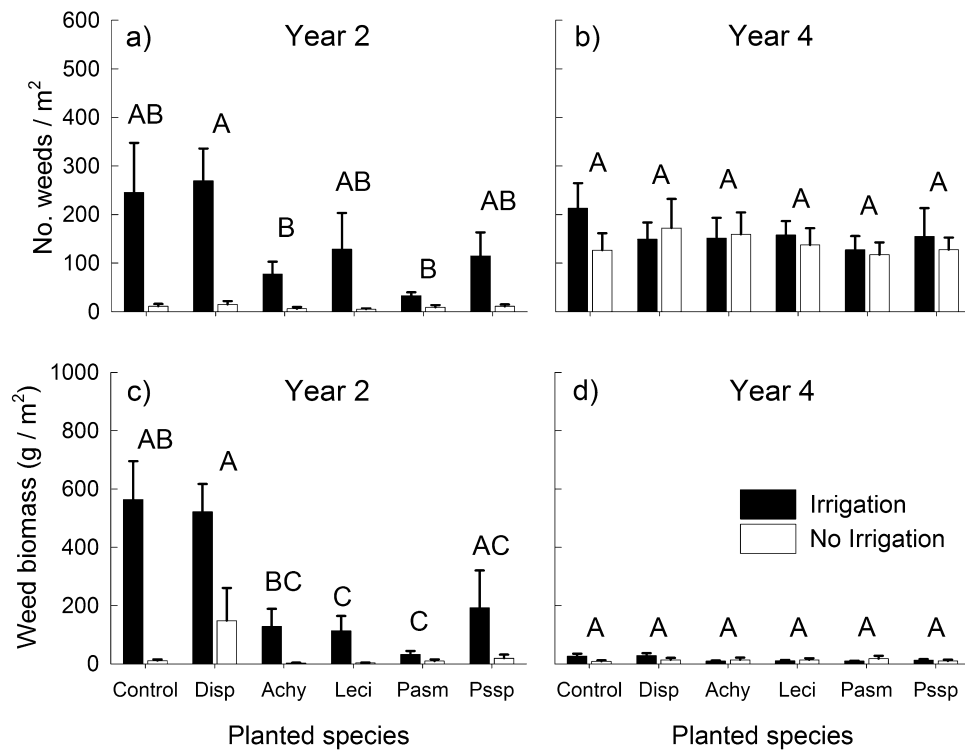
**Table 2**

Summary of statistical results for vegetation, bare ground and canopy gaps. Significant main effects or interactions of grass species and irrigation treatment are presented for all response variables.

Response variable	Treatment effects		
	Grass species identity	Irrigation	Brief description of result
Seeded grasses			
Seeded grass density, year 2 <sup>a</sup>	Species × irrigation: $F_{3,30} = 8.03$ , $P = 0.0004$		Higher density in irrigated plots; within irrigated plots, higher in <i>P. smithii</i> subplots
Seeded grass biomass, year 2 <sup>a</sup>	$F_{3,33} = 0.76$ , $P = 0.5$	$F_{1,5} = 510$ , $P < 0.0001$	More biomass in irrigated plots
Seeded grass density, year 4 <sup>b</sup>	$F_{4,44} = 8.4$ , $P < 0.0001$	$F_{1,5} = 29$ , $P = 0.003$	More biomass in irrigated plots; less in <i>D. spicata</i> subplots
Seeded grass biomass, year 4 <sup>b</sup>	$F_{4,44} = 7.3$ , $P = 0.0001$	$F_{1,5} = 18$ , $P = 0.008$	More biomass in irrigated plots; less in <i>D. spicata</i> subplots
Weeds			
Weed density, year 2	$F_{5,55} = 3.4$ , $P = 0.0009$	$F_{1,5} = 26$ , $P = 0.004$	Higher weed density in irrigated plots; higher in Control and <i>D. spicata</i> subplots
Weed biomass, year 2	$F_{5,55} = 6.9$ , $P < 0.0001$	$F_{1,5} = 31$ , $P = 0.003$	More weed biomass in irrigated plots; more in Control and <i>D. spicata</i> subplots
Understory cover, bare ground, gaps			
Perennial grass cover, year 4	$F_{5,55} = 4.0$ , $P = 0.004$	$F_{1,5} = 78$ , $P = 0.0003$	Higher cover in irrigated plots; lower in <i>D. spicata</i> subplots
Annual cover, year 4	$F_{5,55} = 1.7$ , $P = 0.2$	$F_{1,5} = 8.7$ , $P = 0.03$	Lower annual cover in irrigated plots
Bare ground, year 4	$F_{5,55} = 1.5$ , $P = 0.2$	$F_{1,5} = 8.1$ , $P = 0.03$	Less bare ground in irrigated plots
Canopy gaps, year 5	Species × irrigation: $F_{5,20} = 2.8$ , $P = 0.04$		Within irrigated plots, fewest canopy gaps in <i>L. cinereus</i> and <i>P. smithii</i> subplots
Shrubs			
Transplanted shrub survival, year 4	$F_{4,44} = 3.6$ , $P = 0.01$	$F_{1,5} = 3.2$ , $P = 0.13$	Greater survival in <i>D. spicata</i> subplots
Shrub cover, year 4	$F_{5,55} = 5.3$ , $P = 0.0005$	$F_{1,5} = 7.3$ , $P = 0.04$	Higher shrub cover in irrigated plots; higher in <i>D. spicata</i> subplots
Shrub density, year 5	$F_{5,25} = 5.9$ , $P = 0.001$	$F_{1,2} = 12$ , $P = 0.07$	Higher shrub density in <i>D. spicata</i> subplots

<sup>a</sup> No seeded grasses in Control or *D. spicata* subplots, these subplots excluded from analysis to meet model assumptions.

<sup>b</sup> No seeded grasses in Control subplots, these subplots excluded from analysis to meet model assumptions.

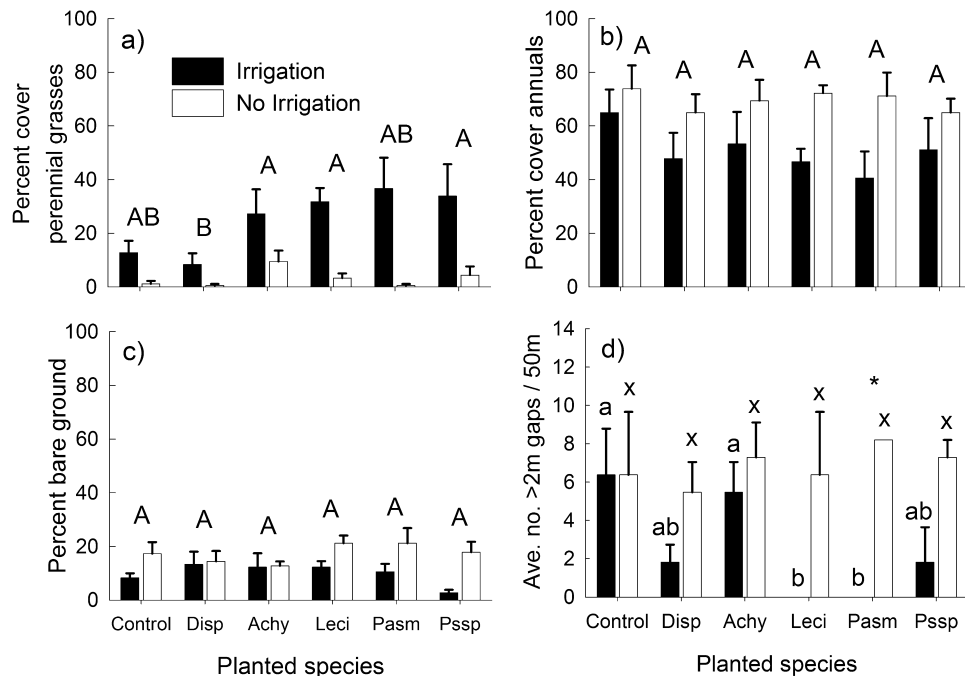


**Fig. 2.** Impacts of irrigation and seeded species on weed density ((a) and (b)) and biomass ((c) and (d)) in year 2 ((a) and (c)) and year 4 ((b) and (d)). Refer to Fig. 1 for explanation of letters and codes.

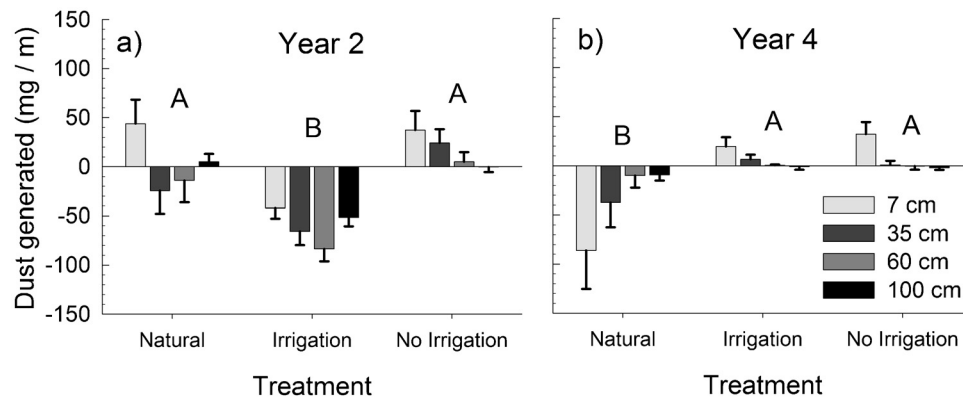
Control treatment (Fig. 3d; simple effects  $F_{5,10} = 0.39$ ,  $P = 0.8$ ). In irrigated plots, Control and *A. hymenoides* subplots had >5 large gaps per 50 m segment, while *L. cinereus* and *P. smithii* subplots had no large gaps (Fig. 3d; simple effects  $F_{5,10} = 6.6$ ,  $P = 0.006$ ). For *P. smithii*, gaps were significantly more abundant in non-irrigated than irrigated plots (Fig. 3d; simple effects  $P < 0.0001$ ).

### 3.4. Wind erosion

In year 2, natural sites and non-irrigated plots produced dust, while irrigated plots collected dust (Fig. 4a;  $F_{2,6} = 20$ ,  $P = 0.002$ ). Dust production tended to be highest at low trap heights (i.e. close to the ground; Fig. 4a;  $F_{1,35} = 4.1$ ,  $P = 0.052$ ). In year 4, dust production at



**Fig. 3.** Impacts of irrigation and seeded species on perennial grass cover (a), annual plant cover (b) and bare ground (c) in year 4 and the frequency of large gaps between plant canopies in year 5 (d). Refer to Fig. 1 for explanation of letters and codes.



**Fig. 4.** Impacts of irrigation and trap height (cm above soil surface) on dust generation in year 2 (a) and year 4 (b). 'Natural' sites covered by less-disturbed natural vegetation were located <400 m from the experimental sites. Refer to Fig. 1 for explanation of letters.

natural sites was highest at high trap heights, but dust production in irrigated and non-irrigated plots was highest at low trap heights (Fig. 4b; treatment  $\times$  height  $F_{2,33} = 16$ ,  $P < 0.0001$ ). Across heights, irrigated and non-irrigated plots generated significantly more dust than natural sites in year 4 (Fig. 4b).

### 3.5. Shrubs

In August of year 2 (nine months after transplanting), roughly 25% of transplanted shrubs were still alive (1–3 per subplot). These included 71 *A. tridentata*, 29 *A. canescens*, 6 *S. vermiculatus* and 0 *A. confertifolia* (54%, 25%, 6% and 0% survival, respectively). Neither irrigation nor planted species significantly affected the percent survival of transplanted shrubs (Fig. 5a; species:  $F_{4,40} = 1.3$ ,  $P = 0.3$ ; irrigation:  $F_{1,5} = 0.44$ ,  $P = 0.5$ ; species  $\times$  irrigation:  $F_{4,40} = 2.3$ ,  $P = 0.07$ ).

By year 4, two years after irrigation was discontinued, overall shrub survival rates had dropped to about 10%. Survivors included 22 *A. tridentata*, 14 *A. canescens*, 3 *S. vermiculatus*, and 0 *A. confertifolia* (17%, 12%, 3% and 0% survival, respectively). Survival rates in *D. spicata* subplots were more than twice as high as survival rates in plots planted with *L. cinereus*, *P. smithii*, or *P. spicata* (Fig. 5b; Table 2). Irrigation did not significantly impact survival in year 4 (Table 2). Neither irrigation nor planted species significantly affected shrub height or the average area covered by a surviving transplanted shrub ( $m^2$  per shrub) in year 2 or year 4 ( $P$ -values  $> 0.10$ ).

In year 4, shrub cover (including both planted and volunteer shrubs) was 1.4 times higher in irrigated than non-irrigated plots (Fig. 5c; Table 2). Shrub cover in *D. spicata* subplots was 13 times higher than cover in other subplots (Fig. 5c; Table 2). To determine whether these results were driven by perennial grasses, we included perennial grass cover as a predictor in a modified model. We found that both perennial grass cover and species identity were significant drivers of shrub cover (grass cover:  $F_{1,53} = 46$ ,  $P < 0.0001$ ; (grass cover) $^2$ :  $F_{1,53} = 25$ ,  $P < 0.0001$ ; planted species:  $F_{5,53} = 5.3$ ,  $P = 0.0005$ ). After accounting for grass cover and grass species identity, shrub cover no longer differed in response to irrigation treatments ( $F_{1,5} = 0.4$ ,  $P = 0.5$ ). In year 5, sampling at the 5C site revealed that treatment effects on shrub cover had not changed substantially since year 4 (Appendix B).

In year 5 at the 5C site, shrub density (including both planted and volunteer shrubs) was almost 7 times higher in *D. spicata* subplots than in other subplots (Fig. 5d; Table 2). Shrub density was 1.3 times higher in irrigated than in non-irrigated plots (Fig. 5d; Table 2). Across irrigation and species treatments, 98% (178) of the 181 shrubs encountered in our belt transects were volunteers

rather than transplants. Volunteer shrubs included 104 *A. canescens* (58.4%), 72 *E. nauseosa* (40.4%) and 2 *A. tridentata* (1.1%).

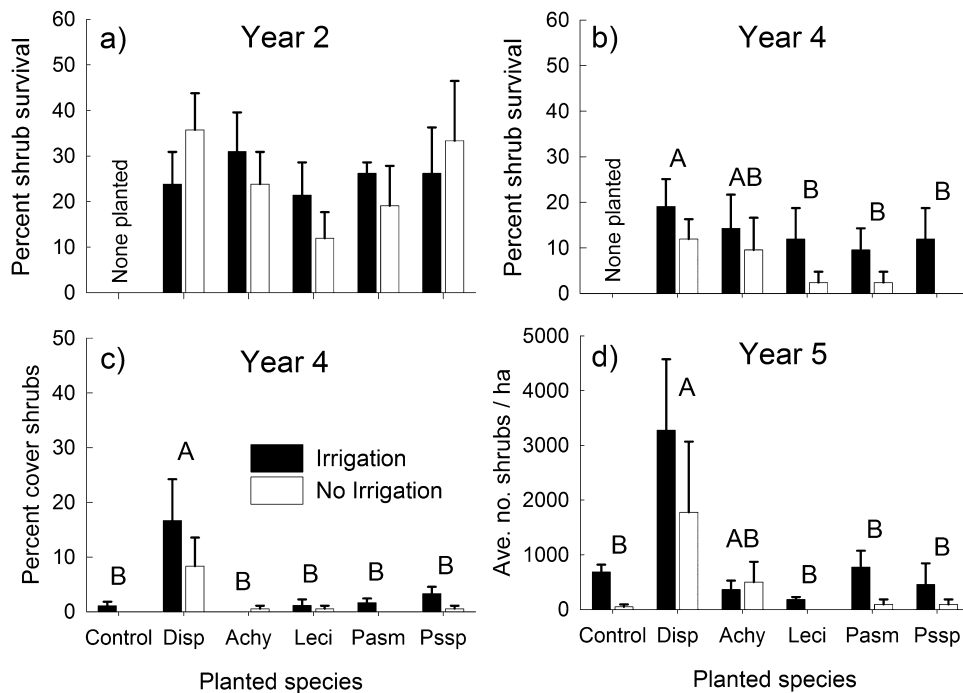
## 4. Discussion

Restoration of former agricultural areas can be challenging due to altered soil chemistry and soil structure as well as extensive weed seed banks (Elmore et al., 2006; Kawada et al., 2011; Török et al., 2012), but irrigation infrastructure provides opportunities for restoration establishment that are rarely available on more natural sites (Roundy et al., 2001). In arid systems, shrubs may be the ultimate restoration goal, but planting grasses in the first year of a restoration provides a more rapid ground cover which may suppress weeds and reduce erosion (Okin et al., 2006; Török et al., 2012), and allows the use of broadleaf herbicides to suppress common agricultural weeds. Our results support previous studies suggesting that active approaches which include herbicide and irrigation can improve restoration success and reduce further degradation (e.g., wind erosion and weed invasion) in arid old fields (Jackson and Comus, 1999; Munson et al., 2012; Otto et al., 2006).

At our sites, short-term irrigation had long-term restoration benefits. Irrigating for two years improved the long-term abundance of perennial grasses and irrigated plots had fewer large vegetation gaps, even three years after irrigation ceased. Impacts of irrigation on initial grass establishment varied based on grass species identity, with *P. smithii* gaining the most establishment benefit from additional water (Fig. 1). However, this species-level effect was short-lived; two years after irrigation ended, grass densities were similar across all cool-season species (Fig. 1). Irrigation marginally improved the long-term cover and density of shrubs, but did not significantly affect the survival of transplanted shrubs.

Irrigation and seeding of cool-season grasses provided substantial short-term reductions in weed invasion and wind erosion (Figs. 2 and 4). The magnitude of these functional benefits was generally similar across all of the cool-season grass species, suggesting a minor role for species identity within this guild. However, species identity did affect the ability of grasses to provide long-term benefits such as reduction in canopy gaps. Large gaps between plants are an important indicator of wind and water erosion potential (Herrick et al., 2005; Okin et al., 2009). By 2012, perennial grass cover in most subplots was below 20% (Appendix B). However, irrigated subplots planted with *L. cinereus* or *P. smithii* maintained  $> 20\%$  cover and had fewer canopy gaps than other subplots (Fig. 3d). These results suggest that *L. cinereus* and *P. smithii* may be worthy of attention by restoration practitioners seeking long-term reductions in erosion potential.

Although seeded grasses ameliorated several potential restoration barriers during the period of shrub establishment, seeded



**Fig. 5.** Impacts of irrigation and seeded species on transplanted shrub survival in year 2 (a) and year 4 (b), shrub cover in year 4 (c), and shrub density in year 5 (d). Refer to Fig. 1 for explanation of letters and codes.

grasses did not facilitate shrubs. In years 4–5, shrub cover, density and survival were highest in plots that were drilled and irrigated but lacked seeded grasses (*D. spicata* subplots), and shrub outcomes did not differ among different seeded cool-season grasses (Fig. 5). Thus, any benefits shrubs received from seeded grasses (e.g., reduced weed pressure and reduced erosion) may have been offset by the costs of competing directly with grasses. Our work supports previous studies suggesting that facilitation can give way to competition under extreme resource stress (Holmgren and Scheffer, 2010; Maestre and Cortina, 2004; Maestre et al., 2009; Odadi et al., 2011).

If grasses hinder shrub establishment, should they be included in arid old-field restoration? Our results suggest that grasses do provide important functional benefits such as reduced erosion and invasion, especially in the short-term, despite their negative effects on shrubs. Thus, restoration practitioners may want to focus on how to improve shrub establishment without losing the functional benefits produced by perennial grasses. It may be possible to improve shrub success using temporal priority (i.e. planting shrubs before grasses) (Young et al., 2005) or spatial segregation (Porensky et al., 2012). Under the latter scenario, managers would plant grasses and shrubs in separate patches or strips. Fine-scale spatial segregation would reduce grass-shrub competition, allowing grasses to accrue weed and erosion reduction benefits in the short-term while shrub establishment proceeds for long-term site stability. An added benefit of a spatial approach is that it would allow for targeted shrub- or grass-specific weed control within different patches/strips.

While transplanted shrubs exhibited low success (survival rates of ~10%; Fig. 5), many shrubs established from seeds that were either present in the seedbank or dispersed into our sites. This was especially true in the *D. spicata* subplots (discussed in detail below). For arid sites where appropriate root development is critical, shrubs that grow from seeds may have higher success than shrub transplants. Natural shrub populations were present near our sites and could easily have served as a seed source, especially for wind-dispersed species. Volunteer shrubs were dominated by *A. canescens* and *E. nauseosa*, both of which are wind-dispersed and set seed in the fall. Elmore et al. (2006) also noted high abundances

of these two species on previously cultivated fields, suggesting that *A. canescens* and *E. nauseosa* may be good candidates for future restoration work at similar sites. Short-lived and early successional shrubs such as *E. nauseosa* are not usually included as target species for restoration, but these species may be able to effectively stabilize restoration sites and facilitate the establishment of later successional shrub species (e.g., Meyer and Monsen, 1990). More generally, our results point to the importance of landscape context, and particularly proximity to local seed sources, in determining restoration outcomes. Future research could further explore how to use remnant local plant populations to improve arid old-field restoration success. For example, it may be worthwhile to gather seed from remnant shrub populations and actively plant this seed on adjacent old-fields. As many species show evidence of adaptation to local climates (Leimu and Fischer, 2008), locally-sourced seeds may have higher per-plant establishment success than non-local seeds or transplants. Compared to non-local transplants, locally gathered seeds may also be lower cost (e.g., Palmerlee and Young, 2010).

We observed a remarkable difference in shrub performance between Control subplots (neither drilled nor seeded), where shrub performance was comparable to cool-season grass subplots, and *D. spicata* subplots (drilled, but lacking perennial grass), where both volunteer and transplanted shrubs were the most successful (Fig. 5). This suggests that drilling itself may help facilitate shrub establishment. The furrows created by our seed drill could have increased shrub performance by capturing wind-dispersed seeds, serving as favorable microsites, or improving water infiltration and soil moisture storage (van der Merwe and Kellner, 1999). Drilling may also have helped expose shrub seeds buried deeper in the soil column. Alternatively, other management factors unique to the *D. spicata* subplots (e.g., the fact that *D. spicata* was planted in July or the fact that *D. spicata* subplots were sprayed with glyphosate just prior to planting) could have facilitated shrub establishment. Further studies investigating the importance of summer or early-fall furrowing, combined with seeding of native shrubs, would be valuable in these systems.



Cool-season grass density and biomass were high during the first two years of the experiment, and densities were especially high in irrigated *P. smithii* subplots (Fig. 1). After irrigation was terminated, however, the density and biomass of seeded grasses in irrigated plots declined precipitously, and initial differences among seeded species disappeared. To some degree, declines in grass abundance probably reflected normal self-thinning processes. However, it is also possible that commercial grasses experienced unusually high mortality because they were poorly adapted to the climate of our study sites (Leimu and Fischer, 2008). All of the commercial varieties we used were grown from seeds collected at sites experiencing at least twice as much annual precipitation as Mason Valley, Nevada, and at our very stressful sites, locally-adapted grass seeds may perform better than the commercial varieties (e.g., Rowe and Leger, 2012). We did observe some colonization of our plots by perennial grass volunteers, though these did not dominate the plots. Perennial grass volunteers were most abundant in irrigated Control and *D. spicata* subplots, suggesting competition between seeded grasses and volunteer grasses.

## 5. Conclusions

Future monitoring will be critical in determining whether grasses and shrubs continue to survive at our sites. Long-term monitoring is especially important in dryland ecosystems where results can be strongly influenced by year effects (e.g., Cox and Anderson, 2004; Visser et al., 2004) and initial restoration successes can fade over longer time periods (e.g., Rinella et al., 2012). Nevertheless, our results point to several concrete management actions that may improve 5-year restoration outcomes in arid old fields:

- (1) Short-term irrigation can increase long-term grass establishment and reduce erosion, and has minor positive effects on shrub establishment.
- (2) Seeded, non-local perennial grasses can suppress weeds and reduce erosion, especially while the grasses are being irrigated. In general, these results are not dependent on grass species identity.
- (3) Restoration projects located near remnant shrub populations may be able to take advantage of volunteer shrubs, which were quite successful in our plots.
- (4) Drilling appears to improve shrub establishment, but seeded grasses may compete with rather than facilitate shrubs in arid ecosystems.
- (5) Restoration treatments that seed grasses and shrubs in separate strips or islands may be most effective for achieving the combined goals of reducing short-term erosion, suppressing weeds and increasing long-term shrub establishment.

As agricultural abandonment continues to accelerate, the restoration of abandoned agricultural fields in drought-prone, arid shrubland ecosystems will become increasingly relevant. In order to restore ecosystem function at such sites, ecologists and practitioners must seek innovative strategies for simultaneously suppressing weeds, reducing erosion, and facilitating shrub establishment. Successful restoration of arid old-fields may represent an opportunity to mitigate ongoing habitat fragmentation and land degradation.

## Acknowledgments

We thank Kevin Badik, Earl Creech, Cynthia Downs, Taraneh Emam, Akiko Endo, Sandra Li, Anthony Regalia, Cub Wolfe, and Hiro Zamma for field assistance and guidance. We are grateful to Michael Collopy for coordinating this project. We thank the VV and 5C's

Ranches for the opportunity to conduct research on their properties. This project was funded by a grant under Public Law 109-103, Section 208(a), through the US Bureau of Reclamation (Cooperative Agreement 06FC204044).

## Appendices A and B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.11.026>.

## References

- Ackerly, D., 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecol. Monogr.* 74, 25–44.
- Arredondo-Núñez, A., Badano, E.I., Bustamante, R.O., 2009. How beneficial are nurse plants? A meta-analysis of the effects of cushion plants on high-Andean plant communities. *Community Ecol.* 10, 1–6.
- Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193.
- Blumenthal, D.M., Jordan, N.R., Svenson, E.L., 2005. Effects of prairie restoration on weed invasions. *Agric. Ecosyst. Environ.* 107, 221–230.
- Bower, C.A., Wilcox, L.V., 1965. Soluble salts. In: Black, C.A. (Ed.), *Methods of Soil Analysis*. American Society of Agronomy, Madison, pp. 933–951.
- Bowker, M.A., Soliveres, S., Maestre, F.T., 2010. Competition increases with abiotic stress and regulates the diversity of biological soil crusts. *J. Ecol.* 98, 551–560.
- Boyd, C.S., Svejcar, T.J., 2011. The influence of plant removal on succession in Wyoming big sagebrush. *J. Arid. Environ.* 75, 734–741.
- Bugg, R.L., Brown, C.S., Anderson, J.H., 1997. Restoring native perennial grasses to rural roadsides in the Sacramento Valley of California: establishment and evaluation. *Restor. Ecol.* 5, 214–228.
- Burke, I.C., Lauenroth, W.K., Coffin, D.P., 1995. Soil organic matter recovery in semi-arid grasslands: implications for the Conservation Reserve Program. *Ecol. Appl.* 5, 793–801.
- Cox, R.D., Anderson, V.J., 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *J. Range Manage.* 57, 203–210.
- Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land abandonment and ecosystem assembly. *Trends Ecol. Evol.* 23, 104–112.
- Elmore, A.J., Mustard, J.F., Hamburg, S.P., Manning, S.J., 2006. Agricultural legacies in the great basin alter vegetation cover, composition, and response to precipitation. *Ecosystems* 9, 1231–1241.
- Fonseca, F., de Figueiredo, T., Ramos, M.A.B., 2012. Carbon storage in the Mediterranean upland shrub communities of Montesinho Natural Park, northeast of Portugal. *Agrofor. Syst.* 86, 463–475.
- Forey, E., Lortie, C.J., Michalet, R., 2009. Spatial patterns of association at local and regional scales in coastal sand dune communities. *J. Veg. Sci.* 20, 916–925.
- Fryrear, D.W., 1986. A field dust sampler. *J. Soil Water Conserv.* 41, 117–120.
- Fryrear, D.W., Saleh, A., Bilbro, J.D., 1998. A single event wind erosion model. *Trans. ASAE* 41, 1369–1374.
- García-Estrigana, P., Alonso-Blázquez, N., Marques, M.J., Bienes, R., González-Andrés, F., Alegre, J., 2013. Use of Mediterranean legume shrubs to control soil erosion and runoff in central Spain. A large-plot assessment under natural rainfall conducted during the stages of shrub establishment and subsequent colonisation. *CATENA* 102, 3–12.
- Herrick, J.E., Zee, J.W.V., Havstad, K.M., Whitford, W.G., 2005. *Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems, Volume 1: Quick Start*. University of Arizona Press, Tucson, AZ.
- Holmgren, M., Scheffer, M., 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. *J. Ecol.* 98, 1269–1275.
- IPCC, 2012. Managing the risks of extreme events and disasters to advance climate change adaptation. In: Field, C.B., Barros, V., Stocker, T.F., Qin, D., Dokken, D.J., Ebi, K.L., Mastrandrea, M.D., Mach, K.J., Plattner, G.-K., Allen, S.K., Tignor, M., Midgley, P.M. (Eds.), *A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge and New York.
- Jackson, L.L., Comus, P.W., 1999. Ecological consequences of agricultural development in a Sonoran desert valley. In: Robichaux, R.H. (Ed.), *Ecology of Sonoran Desert Plants and Plant Communities*. University of Arizona Press, Tucson, AZ, pp. 215–254.
- Jankju, M., 2013. Role of nurse shrubs in restoration of an arid rangeland: effects of microclimate on grass establishment. *J. Arid. Environ.* 89, 103–109.
- Josa, R., Jorba, M., Vallejo, V.R., 2012. Opencast mine restoration in a Mediterranean semi-arid environment: failure of some common practices. *Ecol. Eng.* 42, 183–191.
- Kawada, K., Wuyunna, Nakamura, T., 2011. Land degradation of abandoned croplands in the Xilingol steppe region Inner Mongolia, China. *Grassl. Sci.* 57, 58–64.
- Leimu, R., Fischer, M., 2008. A meta-analysis of local adaptation in plants. *PLoS One* 3, e4010, <http://dx.doi.org/10.1371/journal.pone.0004010>.
- Maestre, F.T., Bautista, S., Cortina, J., Bellot, J., 2001. Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecol. Appl.* 11, 1641–1655.
- Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* 97, 199–205.

- Maestre, F.T., Cortina, J., 2004. Do positive interactions increase with abiotic stress?—A test from a semi-arid steppe. *Proc. R. Soc. London, Ser. B* 271, S331–S333.
- Meyer, S.E., 1992. Germination and establishment ecology of big sagebrush: implications for community restoration. In: *Proceedings—Ecology and Management of Annual Rangelands*, Gen. Tech. Rep. INT-313. US Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, pp. 244–251.
- Meyer, S.E., Monsen, S.B., 1990. Seed source differences in initial establishment for big sagebrush and rubber rabbitbrush. In: McArthur, E.D., Romney, E.M., Smith, S.D., Tueller, P.T. (Eds.), *Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management*, Gen. Tech. Rep. INT-276. U.S. Department of Agriculture Forest Service, Intermountain Research Station, Ogden, pp. 200–208.
- Miller, R.F., Knick, S.T., Pyke, D.A., Meinke, C.W., Hanser, S.E., Wisdom, M.J., Hild, A.L., 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In: Knick, S.T., Connelly, J.W. (Eds.), *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats*, Stud. Avian Biol., 38. University of California Press, Berkeley, CA, p. 145.
- Milton, S.J., Dean, W.R.J., 2010. Plant invasions in arid areas: special problems and solutions: a South African perspective. *Biol. Invasions* 12, 3935–3948.
- Morris, L.R., Monaco, T.A., Sheley, R.L., 2011. Land-use legacies and vegetation recovery 90 years after cultivation in Great Basin sagebrush ecosystems. *Rangel. Ecol. Manage.* 64, 488–497.
- Munson, S.M., Lauenroth, W.K., Burke, I.C., 2012. Soil carbon and nitrogen recovery on semiarid Conservation Reserve Program lands. *J. Arid. Environ.* 79, 25–31.
- Odadi, W.O., Karachi, M.K., Abdulrazak, S.A., Young, T.P., 2011. African wild ungulates compete with or facilitate cattle depending on season. *Science* 333, 1753–1755.
- Okin, G.S., Gillette, D.A., Herrick, J.E., 2006. Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semi-arid environments. *J. Arid. Environ.* 65, 253–275.
- Okin, G.S., Parsons, A.J., Wainwright, J., Herrick, J.E., Bestelmeyer, B.T., Peters, D.C., Fredrickson, E.L., 2009. Do changes in connectivity explain desertification? *BioScience* 59, 237–244.
- Otto, R., Krusi, B.O., Burga, C.A., Fernandez-Palacios, J.M., 2006. Old-field succession along a precipitation gradient in the semi-arid coastal region of Tenerife. *J. Arid. Environ.* 65, 156–178.
- Palmerlee, A.P., Young, T.P., 2010. Direct seeding is more cost-effective than planting container stock across ten woody species in California. *Native Plants J.* 11, 89–102.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Package Version 2013. R Development Core Team, nlme: Linear and Nonlinear Mixed Effects Models., pp. 3.
- Porensky, L.M., Vaughn, K.J., Young, T.P., 2012. Can initial intraspecific spatial aggregation increase multi-year coexistence by creating temporal priority? *Ecol. Appl.* 22, 927–936.
- R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, <http://www.R-project.org/>
- Rinella, M.J., Mangold, J.M., Espeland, E.K., Sheley, R.L., Jacobs, J.S., 2012. Long-term population dynamics of seeded plants in invaded grasslands. *Ecol. Appl.* 22, 1320–1329.
- Roundy, B.A., Heydari, H., Watson, C., Smith, S.E., Munda, B., Pater, M., 2001. Summer establishment of Sonoran desert species for revegetation of abandoned farmland using line source sprinkler irrigation. *Arid. Land Res. Manage.* 15, 23–39.
- Rowe, C.L., Leger, E.A., 2012. Seed source affects establishment of *Elymus multisetus* in postfire revegetation in the Great Basin. *West. N. Am. Nat.* 72, 543–553.
- Scott, A.J., Morgan, J.W., 2012. Recovery of soil and vegetation in semi-arid Australian old fields. *J. Arid. Environ.* 76, 61–71.
- Stavi, I., Ungar, E.D., Lavee, H., Sarah, P., 2011. Soil aggregate fraction 1–5 mm: an indicator for soil quality in rangelands. *J. Arid. Environ.* 75, 1050–1055.
- Török, P., Migléc, T., Valkó, O., Kelemen, A., Deák, B., Lengyel, S., Tóthmérész, B., 2012. Recovery of native grass biodiversity by sowing on former croplands: is weed suppression a feasible goal for grassland restoration? *J. Nat. Conserv.* 20, 41–48.
- USDA, 2012. National agricultural statistics service. In: *Nevada Agricultural Statistics Bulletin*. USDA, NV.
- USDA NRCS, 2013. The PLANTS Database. National Plant Data Team, Greensboro, NC, <http://plants.usda.gov> (accessed 12 April 2013).
- USDA, 1984. Soil conservation service. In: *Soil Survey of Lyon County Area*. USDA, Nevada.
- van der Merwe, J.P.A., Kellner, K., 1999. Soil disturbance and increase in species diversity during rehabilitation of degraded arid rangelands. *J. Arid. Environ.* 41, 323–333.
- van Zonneveld, M.J., Gutierrez, J.R., Holmgren, M., 2012. Shrub facilitation increases plant diversity along an arid scrubland-temperate rain forest boundary in South America. *J. Veg. Sci.* 23, 541–551.
- Veblen, K.E., 2008. Season- and herbivore-dependent competition and facilitation in a semiarid savanna. *Ecology* 89, 1532–1540.
- Visser, N., Botha, J.C., Hardy, M.B., 2004. Re-establishing vegetation on bare patches in the Nama Karoo, South Africa. *J. Arid. Environ.* 57, 155–177.
- Wang, X.P., Zhang, Y.F., Hu, R., Pan, Y.X., Berndtsson, R., 2012. Canopy storage capacity of xerophytic shrubs in Northwestern China. *J. Hydrol.* 454, 152–159.
- Williams, M.I., Schuman, G.E., Hild, A.L., Vicklund, L.E., 2002. Wyoming big sagebrush density: effects of seeding rates and grass competition. *Restor. Ecol.* 10, 385–391.
- Xu, Z.W., Wan, S.Q., Zhu, G.L., Ren, H.Y., Han, X.G., 2010. The influence of historical land use and water availability on grassland restoration. *Restor. Ecol.* 18, 217–225.
- Young, T.P., Petersen, D.A., Clary, J.J., 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecol. Lett.* 8, 662–673.