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# Restoring Abandoned Agricultural Lands in Cold Desert Shrublands: Tradeoffs between Water Availability and Invasive Species

Jeanne C. Chambers, Eric P. Eldredge, Keirith A. Snyder, David I. Board, Tara Forbis de Queiroz, and Vada Hubbard*

Restoration of abandoned agricultural lands to create resilient ecosystems in arid and semi-arid ecosystems typically requires seeding or transplanting native species, improving plant–soil–water relations, and controlling invasive species. We asked if improving water relations via irrigation or surface mulch would result in negative tradeoffs between native species establishment and invasive species competition. We examined the effects of sprinkler irrigation and straw mulch on native seed mixtures planted in two consecutive years in an abandoned agricultural field in a cold desert shrubland in southwestern Nevada, USA. Restoration effects differed among years because of contingency effects of growing season conditions. Precipitation was low during the first year and seeded plant density and biomass increased in response to irrigation. Precipitation was relatively high during the second year, seeded plant densities and biomass were generally high, and irrigation had inconsistent effects. Mulch increased native plant cover in the absence of irrigation during the dry year. Invasive plant biomass and cover also were influenced by year, but irrigation increased invasive plants regardless of precipitation. Positive effects of irrigation on seeded plant density, cover, and biomass outweighed negative tradeoffs of increases in invasive plants. In ecosystems with highly variable precipitation, the most effective restoration strategies will most likely be adaptive ones, requiring determination of timing and amount of irrigation based on precipitation, native plant establishment, and invasive species composition and abundance.

**Nomenclature:** 2, 4-D; dimethylamine salt of 2,4-dichlorophenoxyacetic acid.

**Key words:** Competition, irrigation, mulch, native plant establishment, revegetation, sagebrush ecosystems, weed species.

The area of abandoned agricultural land is growing on a global basis and these lands are becoming increasingly important from conservation, restoration, and social perspectives (Cramer et al. 2008; Navarro and Pereira 2012). Modification of the environment for agriculture can alter ecosystem processes and result in loss of the biotic and abiotic legacies necessary for recovery (Cramer et al. 2008). Abandoned agricultural lands that lack the capacity for recovery to the original condition can exhibit decreased structural heterogeneity and loss of biological diversity, increased vegetation homogeneity and soil erosion, and loss of cultural and aesthetic values (Benayas et al. 2007). These lands can persist for decades in a degraded state dominated by invasive plant species (Cramer and Hobbs 2007). Active restoration that includes controlling invasive species, seeding or transplanting, and improving plant–soil–water relations is often necessary to return these lands to a desired condition (Bainbridge 2007; Whisenant 1999). However, the ultimate objective of such restoration efforts is typically to create ecosystems that are resilient to disturbance and resistance to invasive species and that require minimal subsequent input (Chambers et al. 2013).

Cold desert shrublands are characterized by low and highly variable precipitation and water availability is arguably the most important constraint to plant establishment during restoration (Allen 1995; Bainbridge 2007; Call and Roundy 1991; Hardegree and Van Vactor 2004; Hardegree et al. 2011). Most precipitation falls during

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## Management Implications

Restoration of abandoned agricultural land to native plant communities can increase soil stability, reduce the spread of invasive species, and enhance the conservation value of the land. In cold desert shrublands where irrigation systems are still in place, irrigation can promote native species establishment despite also increasing invasive species. Irrigation must be sufficiently frequent during initial establishment of the seeded species to maintain the soil drying front above the depth of active root growth. Periodic watering may be required through the second year to allow plants to survive the generally low precipitation and highly variable weather conditions that characterize cold desert shrublands. In cases where irrigation systems are not available, mulch may be a viable alternative for improving water relations and increasing plant cover, especially during dry years. Larger seeded species, such as the grasses Indian ricegrass, squirreltail and needle and thread are likely to establish at higher rates than smaller seeded species like sagebrush and many native forbs. Flexible restoration strategies that adapt the timing and amount of irrigation to soil water availability are most likely to succeed.

winter as snow, and seed germination and seedling emergence typically occur in late fall to spring during periods with favorable soil temperatures and soil water availability. Subsequent plant growth and survival depend on growing season conditions and water availability over the next 2 to 3 yrs (Chambers 2001; Chambers and Linnerooth 2001; Goergen and Chambers 2011). Restoration methods for increasing water availability on abandoned agricultural lands during plant establishment include irrigation and application of surface mulches among other techniques (Bainbridge 2007). In those areas where functional irrigation systems exist, supplemental water during the critical establishment period can increase seedling emergence, growth, and short-term survival of both native and introduced species (Roundy et al. 2001). However, high plant mortality can occur after irrigation is stopped (Cox and Madrigal 1988; Padgett et al. 2000). Developing effective irrigation schemes requires considering the prevailing climatic regime, timing and duration of seedling establishment, and characteristics of the restoration species.

Mulches may provide an alternative to supplemental watering in those cases where irrigation systems no longer exist. Although mulch will not increase water availability as much as irrigation, the effects on invasive species' populations should be less and mulch may have other positive effects on the establishment of seeded species. Organic mulch, like litter accumulation, can increase soil water availability because of decreased evaporation resulting from an increase in the resistance of water vapor diffusion from the soil surface to the atmosphere and a reduction in soil temperature (Facelli and Pickett 1991). Litter or mulch also can reduce runoff and erosion by intercepting rain and snow and increasing infiltration and water retention (Facelli and Pickett 1991). Mulch can increase seedling establishment of both native and invasive species by preventing movement of surface soils and seeds, providing shade and insulation, and moderating soil temperatures (Chambers 2000; Chambers and MacMahon 1994; Wolkovich et al. 2009).

Increasing water availability through irrigation or mulching may result in tradeoffs between providing conditions conducive to native plant establishment and increasing competition with invasive species. Because abandoned agricultural lands often have established populations of invasive species and high densities of their seeds in the soil seed bank (Cramer and Hobbs 2007), irrigation during restoration can increase the abundance of these species (Padgett et al. 2000). Invasive species often are highly competitive with seedlings of native species (Humphrey and Schupp 2004; Mangla et al. 2011) and limit restoration success in a wide variety of ecosystem types (D'Antonio and Meyerson 2002). Invasive species control after seeding can be difficult in large fields, but selective herbicides can be applied depending on the life forms, phenology, and growth rates of the seeded species versus the invasive species (Marushia and Allen 2011).

In this study, we evaluated the effects of irrigation, and mulch on the density, biomass and cover of seeded restoration species and on the biomass and cover of invasive species in an abandoned agricultural field in a cold desert shrubland. We asked two questions. (1) Does higher water availability from irrigation increase seeded species density and biomass sufficiently to outweigh the negative effects of increased biomass and cover of invasive species? (2) Does mulch increase seeded species density and biomass and provide an alternative to irrigation? We discuss the implications of our results for the restoration of these and other abandoned agricultural lands.

## Materials and Methods

**Study Area.** The study area is an upland field located on the Humboldt-Toiyabe National Forest in west-central Nevada, USA (38.4375°N, 119.1258°W; 1,804 m [5,919 ft] elevation). Historically, the area was a pasture within a large ranch complex that was irrigated on a regular basis. In 1995, the U.S. Forest Service (USFS) acquired the ranch from a private owner and stopped irrigating the pasture. Several attempts were made to restore the field to native upland vegetation, but these attempts failed and over time the vegetation converted to invasive annuals. Restoration of the former agricultural land is of considerable interest to the USFS, its partner agencies, and members of the public. The upland field is adjacent to a "blue-ribbon" trout (*Oncorhyncus* spp.) fishing stream, and a riparian corridor that serves as habitat for the distinct Bi-State population of greater sage-grouse (*Centrocercus urophasianus*) that was listed 25 Oct 2013 under the U.S. Endangered Species Act.

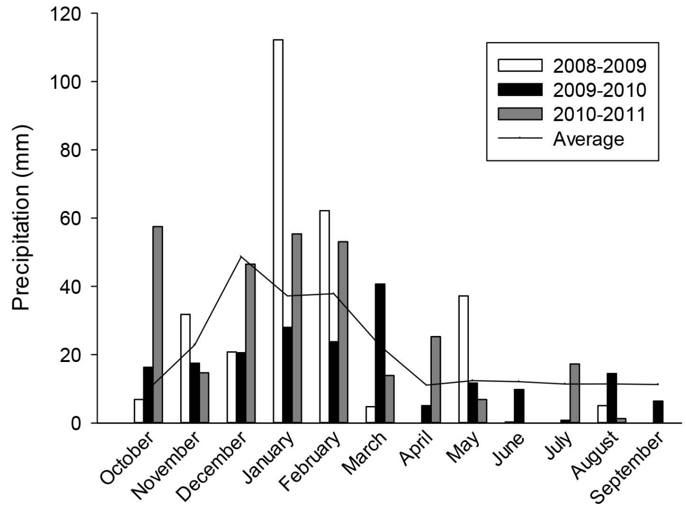


Figure 1. Average monthly precipitation of Bridgeport, California, USA for 2008, 2009, and 2010 and for the historic average monthly precipitation from 1948 through 2012 (National Oceanic and Atmospheric Adminstration 2013).

The upland field occurs in a 200 to 250 mm (7.9 to 9.8 in) precipitation zone and is characterized by a cold, dry climate. Precipitation occurs primarily during the winter months (November through March) in the form of snow and was highly variable during the study period ( Figure 1). Soils are characterized as sandy loams and the upland field has a 4% to 8% slope (USDA Natural Resources Conservation Service 2011). The fields are dominated largely by invasive species including downy brome (*Bromus tectorum* L.), tansy mustard [*Descurainia sophia* (L.) Webb ex Prantl], Russian-thistle (*Salsola tragus* L.), and redstem filaree [*Erodium cicutarium* (L.) L'Hér. ex Aiton]. Adjacent vegetation communities are characterized by: shrubs including Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young), black sagebrush (*Artemisia nova* A. Nelson), green rabbitbrush [*Chrysothamnus viscidiflorus* (Hook.) Nutt.], and fourwing saltbush [*Atriplex canescens* (Pursh) Nutt.]; grasses including James' galleta (*Pleuraphis jamesii* Torr.), western wheatgrass [*Pascopyrum smithii* (Rydb.) Á. Löve], Indian ricegrass [*Achnatherum hymenoides* (Roem. & Schult.) Barkworth], and squirreltail [*Elymus elymoides* (Raf.) Swezey]; and forbs like woolypod milkvetch (*Astragalus purshii* Douglas ex Hook) and scabland penstemon (*Penstemon deustus* Douglas ex Lindl.). Occasional individuals or patches of species like Wyoming big sagebrush, western wheatgrass and Palmer's penstemon (*P. palmeri* A. Gray) occur in the abandoned fields.

**Experimental Design.** We used a factorial design in which irrigation and seeding year were treated as main factors. Seed mix and mulching were treated as replicated split–split-plots and herbicide application was treated as an unreplicated split plot within the irrigation treatment. Each treatment had two levels: irrigated for the first growing season and not irrigated; grass seed mix and diverse seed mix; mulched and not mulched; and herbicide and no herbicide. The experiment was repeated in 2 yr (seeded on November 4, 2008 and seeded on October 20, 2009), and there were five replications of each seeding year and water treatment combination for a total of 20 main plots. Plots were 44 by 44 m and were separated by 50 m buffers. In each seeding year, plots were randomly assigned as irrigated the first year or not irrigated. One half of each plot was randomly designated to receive the mulch treatment while the other half was not mulched, and one half of each mulch treatment was randomly designated to be seeded with the grass seed mix while the other half was seeded with the diverse seed mix. Thus, each plot contained four subplots (11 by 44 m): diverse seed mix/mulch; diverse seed mix/no mulch; grass seed mix/mulch; and grass seed mix/no mulch. Half of each subplot was treated with a selective herbicide in 2010. Herbicide was not applied in 2009 because the dominant invasive species that year was *S. tragus*, which is low growing and has a phenology similar to the seeded species. In 2010, the dominant invasive species was the invasive mustard, *D. sophia*, which is taller and matures earlier than the seeded species during favorable years.

**Treatments.** We selected restoration species that occurred in adjacent native communities or that had established on restored sites near the study area. The grass seed mix was comprised only of grasses and the diverse mix of grasses, forbs, and shrubs. The grasses seeded were *E. elymoides*, *A. hymenoides*, needle and thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth], basin wildrye [*Leymus cinereus* (Scribn. & Merr.) Á. Löve], and thickspike wheatgrass [*Elymus lanceolatus* (Scribn. & J.G. Sm.) Gould ssp. *lanceolatus*]. The forbs were *P. palmeri*, and gooseberryleaf globemallow [*Sphaeralcea grossulariifolia* (Hook. & Arn.) Rydb.], and the shrubs were *A. tridentata* ssp. *wyomingensis* and *A. canescens*. The target seed rate for each mix was 538 seeds PLS (pure live seed) $m^{-2}$, or 103 seeds PLS $m^{-2}$ for each of the five species in the grass mix and 54 seeds PLS $m^{-2}$ for each species in the diverse mix. We purchased seed of seed sources believed to be adapted to the site (Comstock Seed, Gardnerville, Nevada, USA). Strong ecotypic differences exist in species germination and establishment requirements for many cold desert shrub species, and long term plant survival requires obtaining species and seed sources adapted to the climatic regime (Hardegree et al. 2011).

Seeding was conducted using a no-till drill (model 3P605NT, Great Plains Mfg., Salina, KS, USA) which had separate seed boxes for different types of seed. Grasses and dewinged fourwing saltbrush were seeded from a grain box

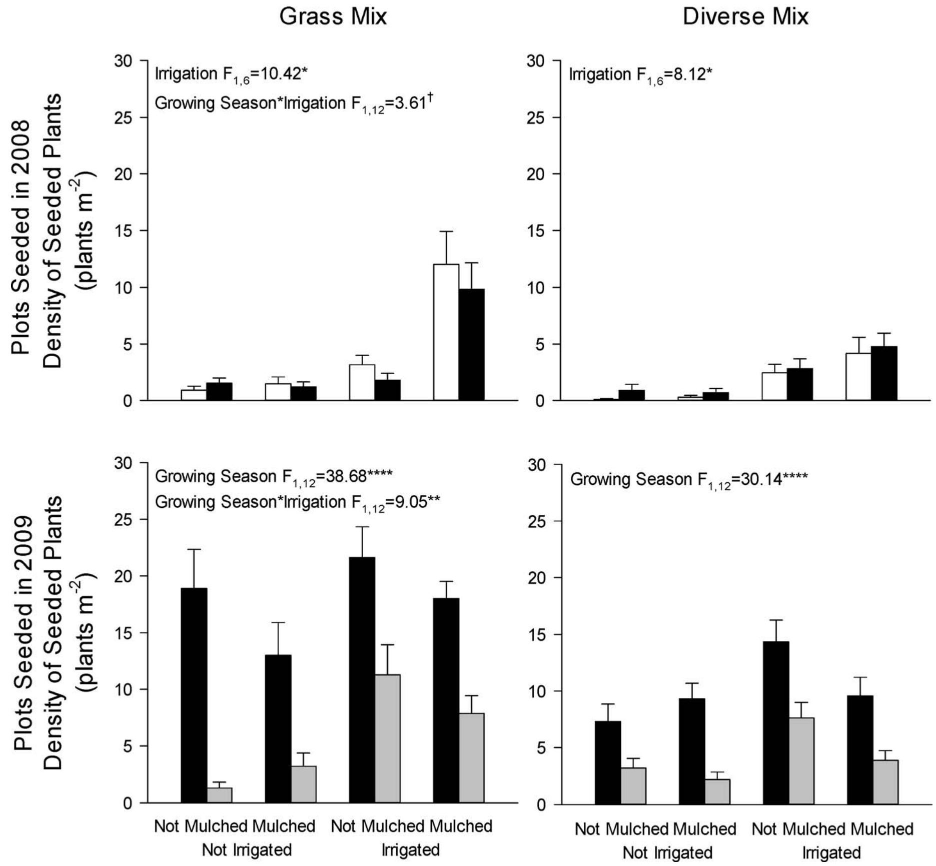


Figure 2. Plant density (mean ± SE ) of all seeded species combined in the grass and diverse seed mixes for the irrigation and mulch treatments. Treatments seeded in 2008 were sampled during the 2009 and 2010 growing season; treatments seeded in 2009 were sampled during the 2010 and 2011 growing season. Open bars = 2009 growing season; black bars = 2010 growing season; gray bars = 2011 growing season. †$P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

to a depth of about 20 mm. Sagebrush and the forbs were seeded from a separate box onto the soil surface, and then pressed into the soil with the drill's press wheels. Rice hulls were used to facilitate flow of seeds. Because of problems with drill performance, seeding rates of needle and thread and fourwing saltbush in the separate seed box were 60% of the target rate in 2008. To maintain constant seeding rates between years, 2009 seeding rates were adjusted to 2008 rates. Following seeding with the appropriate mixture, half of the plot was mulched with weed-free wheat (*Triticum aestivum* L.) straw at a rate of 2242 kg ha$^{-1}$ (2000 lbs ac$^{-1}$)using a Bowie Aero Mulcher (Bowie Ind., Bowie, TX, USA). The straw was then crimped into the soil to an approximate depth of 25 mm using a roller crimper.

Irrigation was applied with a big-gun sprinkler (Nelson Irrigation, Walla Walla, WA, USA) centered in each irrigated plot and operated at sufficient pressure to cover the plot. Water applied during the duration of each irrigation was measured with a totalizing flow meter (McCrometer, Inc., Hemet, CA, USA) installed in the aluminum pipe mainline (254 mm). Water was distributed from riser valves on the mainline through 76.2 mm aluminum pipes. In 2009, irrigation began on 16-Apr and ended on 18-Aug. Irrigation was conducted as water and personnel were available, and dates between irrigations ranged from 5 to 23 d (April 16, April 21, May 14, May 20, May 26, June 4, June 16, June 25, June 30, July 7, July 14, July 28, August 12, and August 22). A total of 510 mm of irrigation water was applied. In 2010, which had a wetter spring, irrigation began on May 14 and ended on September 14. Dates between irrigation ranged from 6 to 27 d with infrequent irrigation in spring because of rain (May 14, May 20, June 17, June 23, July 9, July 15, July 21, July 19, August 6, August 20, September 1, and September 14). A total of 480 mm of irrigation water was applied. On average, the amount of irrigation water was more than double the mean annual precipitation for the site (see Figure 1).

In 2010 when there was high cover of *D. sophia*, half of each subplot was treated with 33% 2,4-D using a weed wiper before the seeded species grew to the height of the wiper (75 cm). The area surrounding the plots was boom sprayed with dimethylamine salt of 2,4-D at 863 g ai ha$^{-1}$ (13 oz ai ac$^{-1}$) in all years to minimize seed production of invasive species outside the plots area.

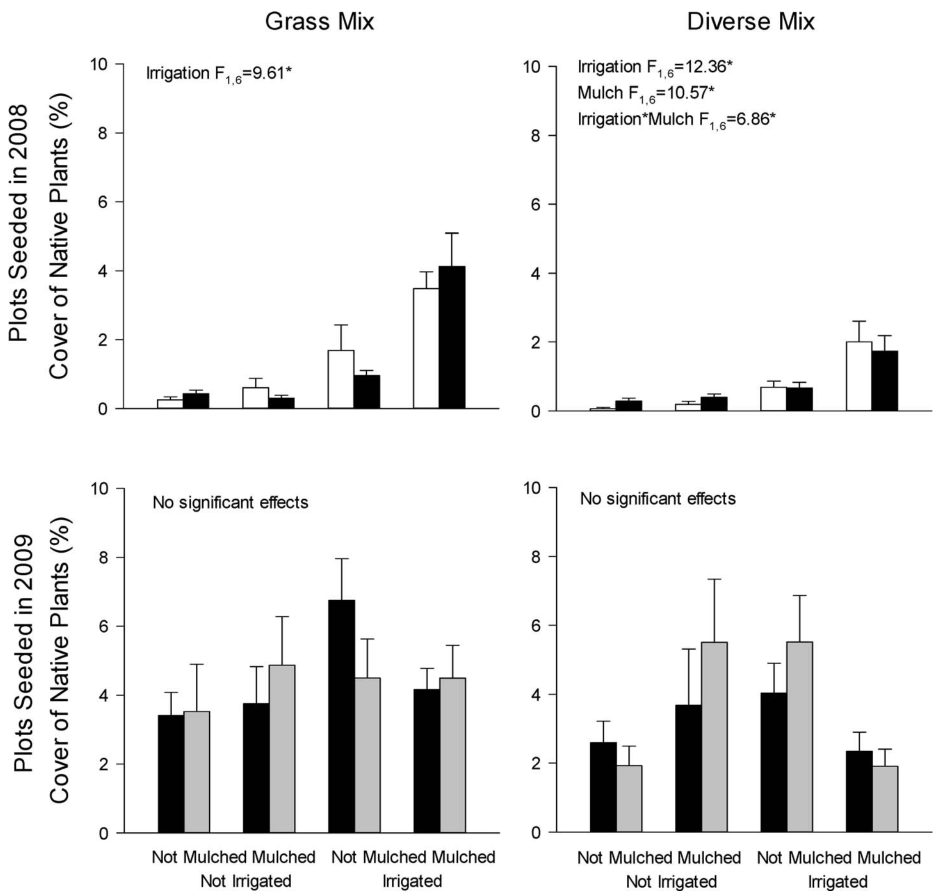


Figure 3. Percentage cover (mean ± SE ) of seeded species in the grass and diverse seed mixes for the irrigation and mulch treatments. Treatments seeded in 2008 were sampled during the 2009 and 2010 growing season; treatments seeded in 2009 were sampled during the 2010 and 2011 growing season. Open bars = 2009 growing season; black bars = 2010 growing season; gray bars = 2011 growing season. * $P < 0.05$.

**Sampling Protocol.** Data were collected during peak plant growth in early July 2009, 2010 and 2011 from 16, 0.25 $m^2$ quadrats located within each subplot using a stratified random approach ($n = 1{,}280$ quadrats $yr^{-1}$). Plant establishment was evaluated by counting the density of each seeded species within the quadrats. Community response was evaluated by estimating the aerial cover of each species, and then harvesting the aboveground biomass of each functional group within each quadrat. Functional groups were: (1) annual, native grasses and forbs, (2) annual, nonnative grasses and forbs, (3) native perennial grasses, (4) native perennial forbs, and (5) nonnative, perennial grasses and forbs. Aboveground biomass was returned to the lab, dried at 60 C until a constant weight was obtained, and then weighed.

**Statistical Analyses.** Analyses were done in two steps. First, mixed effects ANOVAs were performed using generalized linear models to examine overall effects of seeding year, irrigation, mulch, seed mix and herbicide on total seeded plant density, native plant biomass and cover, and invasive plant biomass and cover. Seeding year, irrigation, mulch, and herbicide were treated as fixed factors. Seeding year and irrigation were main plot factors. Mulch and herbicide were split-plots within seeding year and irrigation, and seed mix was a split–split-plot within seeding year, irrigation, and mulch. Because herbicide had no effect on invasive plant cover and had only marginal effects on invasive plant biomass (irrigation × mulch × seeding mix × herbicide; $P = 0.073$), it was dropped from subsequent analyses and discussion.

A second set of mixed effects ANOVAs was run for each seeding year and seed mix combination to examine the effects of growing season (the year in which the data were collected) and to better understand the effects of irrigation and mulch (the two treatments of primary interest). In this case, irrigation, mulch, and growing season were treated as fixed effects. Mulch was a split-plot within irrigation, and growing season was a split-plot within irrigation and mulch. Variables included in these models were total

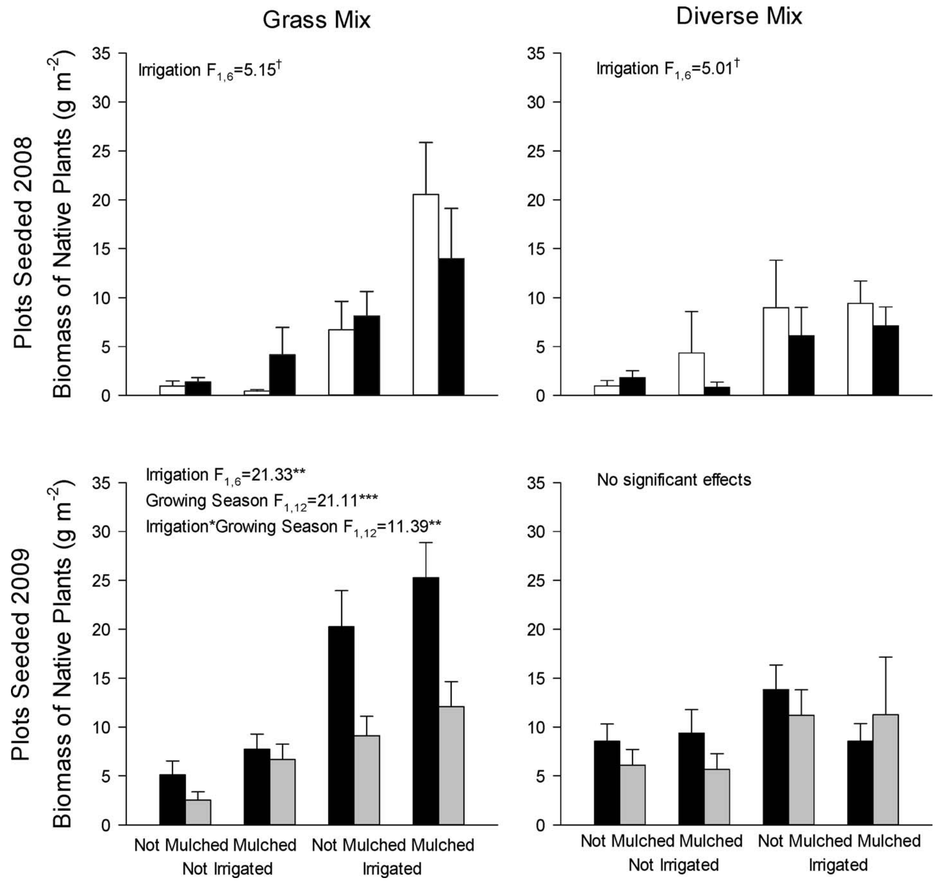


Figure 4. Biomass (mean ± SE ) of seeded species in the grass and diverse seed mixes for the irrigation and mulch treatments. Treatments seeded in 2008 were sampled during the 2009 and 2010 growing season; treatments seeded in 2009 were sampled during the 2010 and 2011 growing season. Open bars = 2009 growing season; black bars = 2010 growing season; gray bars = 2011 growing season. †$P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

seeded plant density, native plant biomass and cover, invasive plant biomass and cover, and also seeded plant density and invasive plant cover of native and invasive species with values that were large enough for analyses.

For plant density measures in all ANOVA models, we used a negative binomial distribution with a log link, and an offset of the log of the number of quadrats sampled to adjust for differences in quadrats sampled among years. For all other plant measures in the ANOVA models, we used a Gaussian distribution with an identity link. Residuals were checked for deviation from model assumptions and found to be within standard tolerances. All analyses were performed with SAS Version 9.2 software (SAS Institute 2010). Mean comparisons were conducted using the least significant means comparison in SAS software. We considered P values < 0.1 to be statistically significant.

## Results

**Native Plant Response.** In the ANOVA model that examined overall effects, seeding year and seed mix differed significantly because of large differences in climatic conditions among years and effects of different seeding rates. Seeded plant densities were lower for plots seeded the first year (2008) than those seeded the second year (2009) ($F = 3.88_{1,16}$, $P = 0.067$) likely reflecting relatively low precipitation during the 2009 growing season and relatively high precipitation in the 2010 and 2011 growing seasons (Figures 1 and 2). Similarly, plots seeded in 2008 had lower native plant biomass ($F = 6.94_{1,16}$, $P = 0.022$) and native plant cover ($F = 9.18_{1,16}$, $P = 0.011$) than those seeded in 2009 (Figures 3 and 4). Plant densities were lower in the diverse mix than in the grass seed mix ($F = 6.14_{1,64}$, $P = 0.015$) because of low establishment of shrubs and forbs and lower seeding rates for the grasses in the diverse mix (Figure 2). Native plant biomass was also lower in the diverse mix than grass mix ($F = 3.99_{1,64}$, $P = 0.051$) (Figure 4). If only the grasses are considered, the effective seeding rate was 515 seeds PLS $m^{-2}$ in the grass mix and 270 seeds PLS $m^{-2}$ in the diverse mix. The largest treatment effects were caused by irrigation which resulted in increased native plant density ($F = 10.26_{1,16}$, $P = 0.0055$) and biomass ($F = 16.05_{1,16}$, $P = 0.0017$) (Figures 2 and 4).

Table 1. Mean density of seeded species (plants $m^{-2}$) in the grass seed mix in irrigated and mulched treatments seeded in 2008 and sampled during the 2009 and 2010 growing seasons, and seeded in 2009 and sampled during the 2010 and 2011 growing seasons.

| Seeded 2008 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Not irrigated | | | | Irrigated | | | |
| | Not mulched | | Mulched | | Not mulched | | Mulched | |
| Species | 2009 | 2010 | 2009 | 2010 | 2009 | 2010 | 2009 | 2010 |
| *A. hymenoides* | 0.85±0.47 | 0.05±0.05 | 1.98±0.71 | 0.29±0.18 | 2.75±0.60 | 0.17±0.17 | 5.50±1.35 | 0.33±0.20 |
| *E. elymoides* | 0.20±0.12 | 0.10±0.07 | 0.19±0.12 | 0 | 0.08±0.08 | 0.08±0.08 | 2.08±0.76 | 0.83±0.31 |
| *E. lanceolatus* | 0.05±0.05 | 0 | 0 | 0 | 0.67±0.32 | 0 | 0.08±0.08 | 0 |
| *H. comata* | 1.35±0.33 | 1.00±0.25 | 1.93±0.55 | 1.83±0.44 | 0 | 2.50±0.53 | 0.33±0.26 | 6.83±1.44 |
| *L. cinereus* | 0.20±0.10 | 0 | 0.29±0.20 | 0 | 0 | 0 | 1.83±0.73 | 0 |
| Seeded 2009 | | | | | | | | |
| | Not irrigated | | | | Irrigated | | | |
| | Not mulched | | Mulched | | Not mulched | | Mulched | |
| Species | 2010 | 2011 | 2010 | 2011 | 2010 | 2011 | 2010 | 2011 |
| *A. hymenoides* | 3.05±0.57 | 0 | 2.65±0.44 | 0.35±0.13 | 3.17±0.66 | 6.75±1.95 | 2.42±0.54 | 0.75±0.28 |
| *E. elymoides* | 3.80±0.65 | 0.05±0.05 | 3.15±0.67 | 0.35±0.18 | 6.42±0.90 | 1.67±0.59 | 6.92±0.90 | 0.83±0.31 |
| *E. lanceolatus* | 1.75±0.53 | 1.00±0.31 | 0.65±0.31 | 2.00±0.62 | 2.33±0.79 | 4.25±0.83 | 0.33±0.20 | 6.75±1.28 |
| *H. comata* | 4.75±0.87 | 0.45±0.16 | 3.35±0.60 | 0.70±0.23 | 1.58±0.57 | 1.17±0.44 | 0.83±0.38 | 1.17±0.34 |
| *L. cinereus* | 6.05±0.92 | 0 | 1.55±0.50 | 0 | 7.67±1.11 | 0.17±0.17 | 6.50±1.04 | 0 |

In the second set of models, which examined treatment and growing season effects for each seeding year and seed mix combination, effects of irrigation, mulch, and growing season depended on seeding year (Figures 2–4). In plots seeded in 2008, the irrigation treatment had higher native plant density, cover, and biomass than the not irrigated treatment for both the grass and diverse mix. Also, native plant cover was higher in the mulch treatment for the diverse mix. After irrigation was stopped there was low mortality for all treatment combinations as indicated by a growing season by irrigation interaction for the grass mix.

In plots seeded in 2009, plant density did not differ between irrigated and not irrigated treatments in the 2010 growing season, but was higher in the irrigated than the not irrigated treatment in the 2011 growing season in both the grass and diverse mix because of low plant mortality (Figure 2). Native plant biomass in the grass mix also was higher in irrigated than nonirrigated plots in 2011 (Figure 4). Unlike plots seeded in 2008, plant density declined significantly from 2010 to 2011.

Individual seeded species differed in plant densities and in treatment response. All seeded grass species established in some seeding year and treatment combination (Table 1), but the only forb or shrub species that established was *A. tridentata,* which occurred in low densities in plots seeded in 2008 (data not shown). *Achnatherum hymenoides*, *E. lanceolatus* ssp. *lanceolatus*, *E. elymoides*, and *H. comata* all had sufficient individuals to examine treatment and growing season effects for most seeding year and seed mix combinations (Table 2). For plots seeded in 2008, irrigation resulted in higher plant densities of *A. hymenoides*, *E. lanceolatus* ssp. *lanceolatus*, and *E. elymoides* in the 2009 growing season, but few plants survived until the 2010 sampling, resulting in irrigation by growing season interactions in either the grass or diverse seed mix. In contrast, *H. comata* was not affected by irrigation in the 2009 growing season, and exhibited a significant increase in plant densities in 2010, perhaps because of delayed germination. Again, irrigation by growing season interactions existed for plots seeded with the grass and diverse seed mix. *Leymus cinereus* had low plant densities in the dry 2009 growing season and no individuals were recorded in 2010.

For plots seeded in 2009, *E. elymoides* and *L. cinereus* had higher plant densities in irrigated than not irrigated plots in 2010, but few plants survived until the 2011 sample, resulting in strong growing season effects in the grass and diverse seed mixes (Tables 2, 3). *Elymus lanceolatus* ssp. *lanceolatus* plant densities were higher on irrigated plots and in 2011, resulting in a growing season effect for this species in the diverse mix. Plant densities of this species were also higher on mulched plots in 2011 for the diverse mix. *Achnatherum hymenoides* had similar and

Table 2. Results of ANOVAs examining effects of treatment and growing season on native plant densities for each seeding year and seed mix combination. Missing treatment combinations had insufficient data for analyses. Numbers in bold have a P-value < 0.10; those in italicized bold are P < 0.05.

| | | Seeded 2008 | | | | Seeded 2009 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Grass mix | | Diverse mix | | Grass mix | | Diverse mix | |
| | df | F | P-value | F | P-value | F | P-value | F | P-value |
| *Achnatherum hymenoides* | | | | | | | | | |
| Irrigation | 1,6 | 6.83 | ***0.0399*** | 14.85 | ***0.0084*** | 1.63 | 0.2494 | 0.15 | 0.7151 |
| Mulch | 1,6 | 2.44 | 0.1693 | 1.91 | 0.2160 | 1.74 | 0.2356 | 0.22 | 0.6560 |
| Irrigation × Mulch | 1,6 | 1.52 | 0.2636 | 1.50 | 0.2661 | 2.55 | 0.1615 | 0.34 | 0.5820 |
| Growing Season | 1,12 | 10.21 | ***0.0077*** | 0.22 | 0.6458 | 2.16 | 0.1676 | 5.57 | ***0.0361*** |
| GS × I | 1,12 | 7.86 | ***0.0160*** | 0.32 | 0.5841 | 0.98 | 0.3425 | 3.39 | **0.0904** |
| GS × M | 1,12 | 2.50 | 0.1395 | 0.02 | 0.8773 | 0.32 | 0.5800 | 0.00 | 0.9469 |
| GS × I × M | 1,12 | 1.42 | 0.2570 | 0.00 | 0.9993 | 0.66 | 0.4330 | 0.00 | 0.9495 |
| *Elymus elymoides* | | | | | | | | | |
| Irrigation | 1,6 | | | | | 2.34 | 0.1773 | 6.34 | ***0.0454*** |
| Mulch | 1,6 | | | | | 0.37 | 0.5631 | 0.04 | 0.8492 |
| Irrigation × Mulch | 1,6 | | | | | 0.10 | 0.7622 | 3.70 | 0.1026 |
| Growing Season | 1,12 | | | | | 18.28 | ***0.0011*** | 56.92 | <***0.0001*** |
| GS × I | 1,12 | | | | | 1.33 | 0.2708 | 9.08 | 0.***0108*** |
| GS × M | 1,12 | | | | | 0.20 | 0.6602 | 1.34 | 0.2690 |
| GS × I × M | 1,12 | | | | | 0.33 | 0.5764 | 3.01 | 0.1085 |
| *Elymus lanceolatus* | | | | | | | | | |
| Irrigation | 1,6 | | | 1.07 | 0.3401 | 4.11 | **0.0890** | 0.84 | 0.3952 |
| Mulch | 1,6 | | | 0.27 | 0.6242 | 0.00 | 0.9586 | 0.06 | 0.8083 |
| Irrigation × Mulch | 1,6 | | | 0.11 | 0.7544 | 0.12 | 0.7380 | 0.98 | 0.3601 |
| Growing Season | 1,12 | | | 4.04 | **0.0676** | 3.68 | **0.0792** | 19.53 | ***0.0008*** |
| GS × I | 1,12 | | | 1.36 | 0.2666 | 3.46 | **0.0874** | 2.24 | 0.1602 |
| GS × M | 1,12 | | | 0.26 | 0.6201 | 0.60 | 0.4544 | 4.98 | ***0.0454*** |
| GS × I × M | 1,12 | | | 0.11 | 0.7435 | 0.53 | 0.4804 | 1.91 | 0.1917 |
| *Hesperostipa comata* | | | | | | | | | |
| Irrigation | 1,6 | 1.40 | 0.2810 | 4.55 | 0.**0768** | 0.08 | 0.7865 | 2.78 | 0.1466 |
| Mulch | 1,6 | 1.27 | 0.3031 | 0.15 | 0.7159 | 2.46 | 0.1678 | 0.26 | 0.6269 |
| Irrigation × Mulch | 1,6 | 1.75 | 0.2341 | 1.06 | 0.3435 | 0.01 | 0.9357 | 0.00 | 0.9947 |
| Growing Season | 1,12 | 6.63 | 0.***0243*** | 19.01 | 0.***0009*** | 0.81 | 0.3868 | 12.68 | ***0.0039*** |
| GS × I | 1,12 | 5.07 | 0.***0439*** | 9.45 | 0.0096 | 0.12 | 0.7398 | 7.12 | 0.***0205*** |
| GS × M | 1,12 | 2.44 | 0.1442 | 0.97 | 0.3436 | 0.64 | 0.4388 | 0.28 | 0.6065 |
| GS × I × M | 1,12 | 1.75 | 0.2101 | 2.61 | 0.1319 | 0.10 | 0.7631 | 0.02 | 0.8873 |

relatively high plant densities for all treatment combinations, except in not irrigated plots in 2011, which had low densities resulting in a growing season effect in the diverse mix. *Hesperostipa comata* had higher plant densities in not irrigated plots in 2010, but had low densities in 2011 as indicated by an irrigation by growing season interaction in the grass mix.

**Invasive Plant Response.** In the overall model, plots seeded in 2008 had lower invasive plant cover than those seeded in 2009 ($F = 12.49_{1,16}$, $P = 0.0041$) reflecting relatively low precipitation during the 2009 growing season and relatively high precipitation in the 2010 growing season (Figures 1 and 5). Invasive plant cover was higher in irrigated plots that were seeded with the diverse mix in 2008, and in irrigated plots seeded with the grass mix in 2009 ($P < 0.05$), as indicated by interactions between seeding year and seed mix ($F = 7.87_{1,64}$, $P = 0.0072$) and among seeding year, seed mix, and irrigation ($F = 6.28_{1,64}$, $P = 0.016$). Invasive plant biomass responded strongly to irrigation and was greater in irrigated than not irrigated plots ($F = 17.31_{1,16}$, $P = 0.0013$) (Figure 6).

Table 3. The percentage cover (mean ± SE ) of invasive species in the irrigation treatment in the plots that were seeded in 2008 and sampled during the 2009 and 2010 growing season, and in the plots that were seeded in 2009 and sampled during the 2010 and 2011 growing season. Data were averaged across mulching and seeding treatments.

| | Seeded 2008 | | | | Seeded 2009 | | | |
|---|---|---|---|---|---|---|---|---|
| | Not irrigated | | Irrigated | | Not irrigated | | Irrigated | |
| Species | 2009 | 2010 | 2009 | 2010 | 2010 | 2011 | 2010 | 2011 |
| Forbs | | | | | | | | |
| *Amaranthus albus* | 0±0 | 0±0 | 0.05±0.04 | 0±0 | 0±0 | 0±0 | 1.88±0.65 | 0±0 |
| *Amaranthus deflexus* | 0.01±0.01 | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 |
| *Chenopodium album* | 0.03±0.01 | 0±0 | 0.34±0.11 | 0±0 | 0.01±0.01 | 0.05±0.05 | 0.54±0.24 | 4.48±1.08 |
| *Chorispora tenella* | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 | 0.01±0.01 |
| *Convolvulus arvensis* | 0.53±0.14 | 0.2±0.03 | 0.09±0.06 | 0.03±0.02 | 0.32±0.07 | 0.35±0.09 | 0.18±0.08 | 0.29±0.17 |
| *Descurainia sophia* | 0±0 | 17.4±1.21 | 0.13±0.11 | 9.11±0.93 | 14.39±1.16 | 0.01±0.01 | 9.94±0.98 | 0±0 |
| *Erodium cicutarium* | 0±0 | 0±0 | 0.23±0.11 | 0.06±0.05 | 0.35±0.16 | 2.66±0.62 | 0.05±0.04 | 1.98±0.67 |
| *Lactuca serriola* | 0±0 | 0±0 | 0.02±0.02 | 0±0 | 0±0 | 0±0 | 0.01±0.01 | 0.02±0.02 |
| *Lepidium latifolium* | 0±0 | 0±0 | 0.05±0.05 | 0±0 | 0±0 | 0±0 | 0.01±0.01 | 0±0 |
| *Portulaca oleracea* | 0±0 | 0.01±0.01 | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 |
| *Salsola tragus* | 4.43±0.52 | 1.9±0.45 | 21.68±2.3 | 1.79±0.46 | 4.66±0.62 | 17.51±1.58 | 17.43±1.48 | 14.54±1.66 |
| *Sisymbrium altissimum* | 0.05±0.03 | 0.04±0.02 | 0.03±0.02 | 0.05±0.04 | 0.01±0.01 | 0±0 | 0±0 | 0±0 |
| *Solanum physalifolium* | 0±0 | 0±0 | 0.01±0.01 | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 |
| Grasses | | | | | | | | |
| *Bromus tectorum* | 0±0 | 0.36±0.12 | 1.58±0.71 | 7.02±1.57 | 7.13±1.25 | 21.03±1.91 | 5.85±1.23 | 27.59±2.82 |
| *Elymus repens* | 0±0 | 0±0 | 0.01±0.01 | 0.06±0.03 | 0±0 | 0±0 | 0.06±0.02 | 0±0 |
| *Setaria viridis* | 0±0 | 0±0 | 0.01±0.01 | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 |
| *Triticum aestivum* | 0±0 | 0±0 | 0±0 | 0±0 | 0.01±0.01 | 0±0 | 0.05±0.02 | 0±0 |

In the second set of models, which examined treatment and growing season effects for each seeding year and seed mix combination, effects of irrigation and growing season depended on seeding year and the variable measured. In plots seeded in 2008, strong interactions existed between irrigation and growing season for invasive plant cover and biomass in both the grass and diverse mixes (Figures 5 and 6). Invasive plant cover and biomass were both higher in irrigated than not irrigated plots in 2009, but did not differ among treatments in 2010 after irrigation was stopped. In contrast, for plots seeded in 2009, invasive plant cover did not differ among treatments, and was higher in 2011 after irrigation was stopped than during 2010 when irrigation was occurring in both the grass and diverse seed mix. However, a strong interaction existed between irrigation and growing season for invasive biomass in the grass and diverse seed mix. Invasive biomass was higher in irrigated plots in the 2010 growing season, but did not differ among treatments in 2011.

Seventeen invasive species occurred in the plots, but only six species comprised more than 1% of the cover in any given treatment combination or growing season, including: the annual forbs tumble pigweed (*Amaranthus albus* L.), common lambsquarters (*Chenopodium album* L.), *D. sophia*, *E. cicutarium*, *S. tragus*, and the annual grass *B. tectorum* (Table 3). Individual species responses were specific to growing season conditions and were strongly influenced by irrigation. Only *D. sophia*, *B. tectorum* and *S. tragus* had sufficient data for analyses. The ANOVA models for the individual species generally showed significant differences between growing seasons for both diverse and grass plots seeded in 2008 and 2009 and sampled in 2009 and 2010 (Table 4). *Descurainia sophia* had consistently high cover (9.1% to 17.4%) in 2010 regardless of treatment, but had low cover (< 1%) in all other growing seasons. *Salsola tragus* had generally higher cover on irrigated than not irrigated plots seeded in 2008 and 2009 and during 2011 resulting in an irrigation by growing season interaction for all treatment combinations. *Bromus tectorum* cover was not affected by irrigation treatment, but was lower in the 2010 growing season (6% to 7%) than in 2011 (21% to 28%) resulting in growing season effects for plots seeded in 2009 with the diverse and grass seed mixes.

## Discussion

**Native Plant Establishment and Growth.** Few studies exist on the effects of increasing water availability using

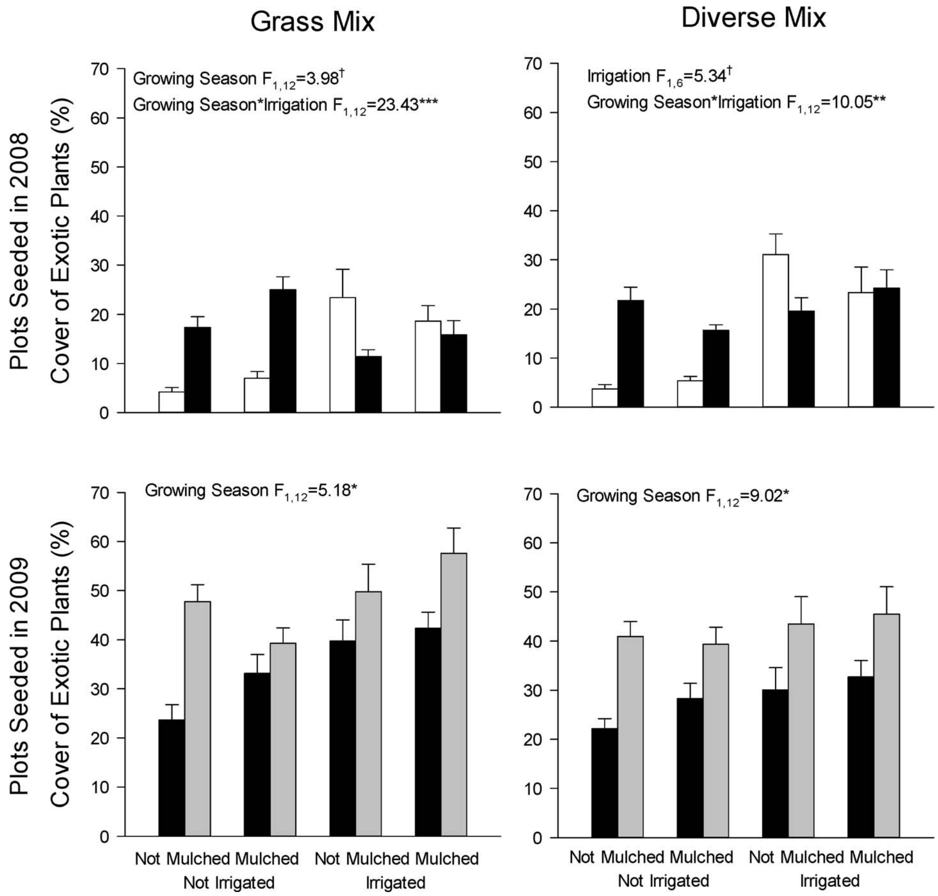


Figure 5. Percentage cover (mean ± SE ) of invasive species in the grass and diverse seed mixes for the irrigation and mulch treatments. Treatments seeded in 2008 were sampled during the 2009 and 2010 growing season; treatments seeded in 2009 were sampled during the 2010 and 2011 growing season. †P < 0.10; * P < 0.05; ** P < 0.01; *** P < 0.001; **** P < 0.0001.

irrigation on native plant establishment and growth in semi-arid shrublands. We showed that seeded plant establishment and growth increased in response to irrigation but, as in other ecosystems, contingency effects existed because of growing season conditions and competition from invasive plants (Bakker et al. 2003; Hendrickson and Lund 2010). In our study, irrigation generally resulted in higher establishment and growth during the drier 2009 growing season for plots seeded the previous fall. However, irrigation had a lesser effect during the wetter 2010 growing season when seeded plant establishment, growth, and biomass were generally high in all treatment plots. Increased water availability caused by irrigation during the 2010 growing season had carryover effects — plots that were seeded in fall 2009 and irrigated in 2010 had higher second year survival than plots that were not irrigated. Native plant establishment has been linked to wet periods or years in other arid and semiarid ecosystems, and seedling survival has been related to water availability and its effects on root length, leaf habit and plant size (Leon et al. 2011). Mature or larger plants are often stronger competitors with invasive annuals in cold desert ecosystems (Blank and Morgan 2012; Booth and Caldwell 2003; Chambers et al. 2007), and seeded species that established during the wetter growing season and in irrigated plots likely had increased abilities to tolerate competition from the abundant invasive annuals.

Mulch has been found to have generally positive effects on plant establishment in cold desert shrublands and other semi-arid ecosystems (Fehmi and Kong 2012; Hardegree et al. 2011). Beneficial effects of mulch can include decreased seedling heat and water stress because of more moderate soil temperatures and increased soil water availability as a result of increased infiltration and water retention and decreased evaporation (Chambers 2000; Facelli and Pickett 1991; Winkel et al. 1991). In this study, mulch increased native plant cover or plant density for certain treatment combinations and species during relatively dry growing seasons such as 2009. This indicates that in cold desert shrublands, the effects of mulch on water availability are likely to be greater during relatively dry growing seasons.

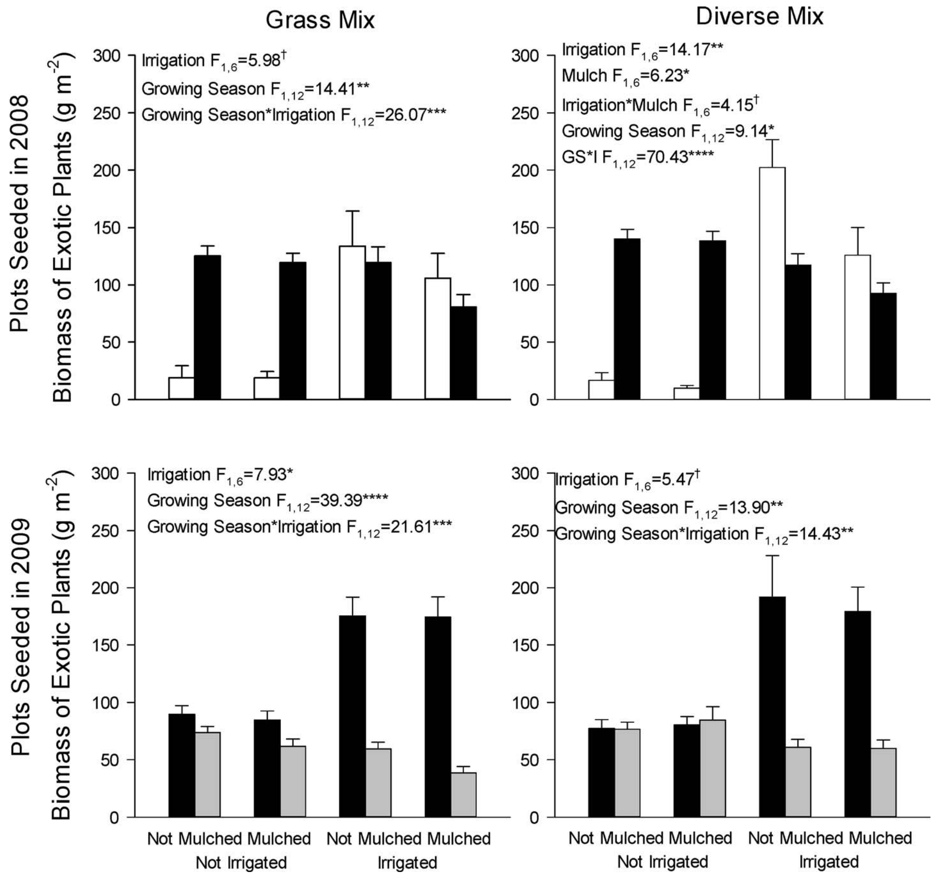


Figure 6. Biomass (mean $\pm$ SE ) of invasive species in the grass and diverse seed mixes for the irrigation and mulch treatments. Treatments seeded in 2008 were sampled during the 2009 and 2010 growing season; treatments seeded in 2009 were sampled during the 2010 and 2011 growing season. Open bars = 2009 growing season; black bars = 2010 growing season; gray bars = 2011 growing season. †$P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

Seedling establishment following active restoration is often low in cold desert shrublands (Call and Roundy 1991, Hardegree et al. 2011). In this study, plant densities ranged from about 10 to 20 plants $m^{-2}$ in favorable treatments and years, which is sufficient for site restoration. Larger seeded grasses, including *A. hymenoides*, *E. elymoides*, and *H. comata*, had higher establishment than the small seeded shrub, *A. tridentata* spp. *tridentata*, and the forbs, *P. palmeri* and *S. grossulariifolia*. Although most large-seeded species germinate and emerge when buried or planted in soil, small-seeded species with low carbohydrate reserves and species with specific physiological requirements (e.g., light for phytochrome transformation, fluctuating temperatures) germinate and emerge only when located or planted at or near the soil surface (Chambers 2000; Chambers and MacMahon 1994). We planted larger seeded grasses to a depth of 20 mm, but the smaller seeded species were spread on the soil surface in the furrow and then pressed into the soil with the drill's press wheels to facilitate germination and establishment. Species with small seeds generally tend to establish at lower rates than species with large seeds as water stress increases (Leishman and Westoby 1994), and the effects of water stress and invasive species can be additive (Matansanz et al. 2008).

Our irrigation schedule may not have provided sufficient water availability in near surface soils during seedling emergence and initial root elongation to ensure survival of the seeded species, especially the small seeded species. Also, increased abundance of invasive species because of precipitation or irrigation may have rapidly depleted available soil water reserves during the critical establishment period. The importance of pulsed precipitation for establishment and persistence of aridland species is well documented (Reynolds et al. 2004; Sher et al. 2004), and frequent irrigation during periods of low precipitation early in the growing season is necessary to promote establishment. Irrigation can be less frequent once emergence has occurred, but plant survival depends on maintaining the soil drying front above the depth of active root growth (Roundy et al. 2001). Acclimating plants to the level of soil

Table 4. Results of ANOVAs examining effects of treatment and growing season on invasive plant densities for each seeding year and seed mix combination. Numbers in bold have a P-value < 0.10; those in italicized bold are P < 0.05.

| | | Seeded 2008 | | | | Seeded 2009 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Grass mix | | Diverse mix | | Grass mix | | Diverse mix | |
| | df | F | P-value | F | P-value | F | P-value | F | P-value |
| *Bromus tectorum* | | | | | | | | | |
| Irrigation | 1,6 | 2.42 | 0.1711 | 3.87 | **0.0966** | 0.00 | 0.9677 | 0.25 | 0.6329 |
| Mulch | 1,6 | 2.25 | 0.1840 | 3.38 | 0.1156 | 0.02 | 0.8983 | 1.26 | 0.3049 |
| Irrigation × Mulch | 1,6 | 3.12 | 0.1279 | 3.29 | 0.1198 | 0.21 | 0.6635 | 0.05 | 0.833 |
| Growing Season | 1,12 | 3.28 | **0.0953** | 3.79 | **0.0754** | 12.04 | ***0.0046*** | 15.45 | ***0.002*** |
| GS × I | 1,12 | 1.04 | 0.3281 | 3.55 | **0.0838** | 0.88 | 0.3659 | 0.92 | 0.3556 |
| GS × M | 1,12 | 0.91 | 0.3589 | 3.40 | **0.0898** | 0.00 | 0.9464 | 0.00 | 0.9616 |
| GS × I × M | 1,12 | 2.12 | 0.1708 | 3.31 | **0.0938** | 0.33 | 0.5747 | 0.02 | 0.9 |
| *Descurainia sophia* | | | | | | | | | |
| Irrigation | 1,6 | 2.90 | 0.1397 | 1.35 | 0.2893 | 0.13 | 0.7314 | 0.27 | 0.6249 |
| Mulch | 1,6 | 0.71 | 0.4304 | 1.04 | 0.3476 | 0.11 | 0.75 | 0.34 | 0.5822 |
| Irrigation × Mulch | 1,6 | 2.33 | 0.1780 | 0.00 | 0.9522 | 0.49 | 0.5091 | 0.04 | 0.8538 |
| Growing Season | 1,12 | 27.54 | ***0.0002*** | 28.24 | ***0.0002*** | 17.46 | ***0.0013*** | 22.51 | ***0.0005*** |
| GS × I | 1,12 | 6.00 | ***0.0306*** | 1.73 | 0.2124 | 0.27 | 0.6115 | 0.49 | 0.498 |
| GS × M | 1,12 | 0.88 | 0.3669 | 1.03 | 0.3294 | 0.11 | 0.7447 | 0.34 | 0.5692 |
| GS × I × M | 1,12 | 2.06 | 0.1768 | 0.00 | 0.9524 | 0.50 | 0.4942 | 0.04 | 0.8524 |
| *Salsola tragus* | | | | | | | | | |
| Irrigation | 1,6 | 11.46 | ***0.0147*** | 3.82 | **0.0985** | 1.38 | 0.2843 | 0.05 | 0.8334 |
| Mulch | 1,6 | 2.81 | 0.1449 | 2.30 | 0.1803 | 0.04 | 0.8569 | 0.68 | 0.4415 |
| Irrigation × Mulch | 1,6 | 2.90 | 0.1397 | 1.50 | 0.2666 | 1.19 | 0.3172 | 0.05 | 0.8362 |
| Growing Season | 1,12 | 45.38 | ***<0.0001*** | 19.45 | ***0.0008*** | 0.33 | 0.5789 | 4.12 | **0.0652** |
| GS × I | 1,12 | 29.04 | ***0.0002*** | 9.47 | ***0.0096*** | 4.87 | ***0.0476*** | 3.44 | **0.0885** |
| GS × M | 1,12 | 2.13 | 0.1699 | 0.00 | 0.9676 | 0.20 | 0.6602 | 1.34 | 0.2690 |
| GS × I × M | 1,12 | 1.70 | 0.2168 | 3.86 | 0.0731 | 0.33 | 0.5764 | 3.01 | 0.1085 |

water naturally available on the site by progressively decreasing the amount of water may be necessary to reduce mortality after initial irrigation is stopped (Padgett et al. 2000). Thus, periodic watering during the second growing season may be necessary to ensure establishment, especially during low precipitation years.

**Treatment Effects on Invasive Species.** Similar to the seeded native species, growing season precipitation strongly mediated the effects of irrigation on the invasive annuals. Irrigation resulted in an increase in invasive annual cover and especially biomass regardless of growing season. However, in the absence of irrigation, growing season conditions, especially precipitation, determined invasive species abundance. Because the seeded native species and invasive annuals responded similarly to increased water availability, competition with the invasive annuals may have decreased overall establishment of the seeded species. Invasive annual grasses such as *B. tectorum* are often strong competitors with seedlings of cold desert species because of earlier germination and more rapid growth than native perennials (James et al. 2011; Knapp 1996). Although less well studied, many annual invasive forbs also are strong competitors with seedling of native species because of rapid growth and resource use. Mature plants of native, perennial grasses and forbs, especially those with growth forms and phenology similar to annual invasive plants, can be highly effective competitors with annual invaders (Blank and Morgan 2012; Booth et al. 2003; Chambers et al. 2007). Previous research on restored mine lands in cold desert shrublands indicates that abundance of invasive annuals can decrease over time as perennials grow and reproduce (Allen and Knight 1984; McLendon and Redente 1990). Because cover of native perennials, and especially invasive annuals, closely tracks annual precipitation (West and Yorks 2002), it is likely that precipitation will interact with treatment effects and continue to influence both native perennial and annual exotic cover.

Year-to-year variability in establishment and productivity of invasive species in arid and semi-arid ecosystems is widely recognized, but in cold desert ecosystems the mechanisms have been determined for only a few widespread invaders like *B. tectorum* (e.g., Chambers et al. 2007; Newingham et al. 2007). In this study, invasive annuals had large differences in species life histories and growth forms and differed in their responses to growing season conditions and irrigation. For example, *D. sophia* is a cool-season species that matures early in the growing season (USFS Fire Effects Information System, 2012) and had high cover only in 2010, while *S. tragus* is a warm-season species that matures later and had high cover only in irrigated plots and during the 2011 growing season (Table 2). Previous research in arid systems indicates that one of the major factors influencing year-to-year variability in relative abundance of annual plants is species-specific sensitivity of germination to environmental factors coupled with year-to-year variation in these factors (Facelli et al. 2006; Guo and Brown 1996). Once germination and emergence has occurred, factors that influence growth and reproduction include growing season precipitation and competitive interactions with other annual species (DeFalco et al. 2003) and native species (Booth et al. 2003). Little to no information exists on the effects of growing season conditions (temperature and seasonal distribution and timing of precipitation) and competitive interaction on establishment and growth of invasive annual forbs in cold desert shrublands. In order to develop effective control and restoration strategies for these invasive annuals, additional information is needed on their establishment, growth responses, and competitive interactions with native species and other invasive annuals.

Overall, we found that the positive effects of irrigation on seeded plant density, cover, and biomass outweighed the negative tradeoffs of increased biomass and cover of invasive plant species. However, growing season precipitation strongly mediated the effects of the irrigation and mulch treatments. Individual seeded species differed in plant densities and treatment response. Relatively large seeded grasses including *A. hymenoides*, *E. elymoides*, and *H. comata* which were planted to a depth of 20 mm established in most treatment combinations. However, the small seeded shrub, *A. tridentata*, and forbs, *P. palmeri* and *S. grossulariifolia*, which were planted near the soil surface had little to no establishment, likely because soil water pulses from irrigation and precipitation were not frequent enough. Invasive annuals and seeded native species responded similarly to irrigation and growing season precipitation, and competitive interactions likely decreased overall establishment of the seeded species. In ecosystems with high precipitation variability among years, the most effective irrigation strategy for establishing a diversity of seeded species is likely an adaptive one where timing and amount of irrigation is determined by precipitation, the seed characteristics of the native species and planting method, and the composition and abundance of invasive species.

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