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Restoring Perennial Grasses in Medusahead Habitat: Role of Tilling, Fire, Herbicides, and Seeding Rate☆

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ABSTRACT

Restoring arid regions degraded by invasive annual grasses to native perennial grasses is a critical conservation goal. Targeting site availability, species availability, and species performance is a key strategy for reducing invasive annual grass cover while simultaneously increasing the abundance of seeded native perennial grasses. However, the potential for establishing successful seedings is still highly variable in rangeland ecosystems, likely because of variable year-to-year weather. In this study, we evaluated the independent and combined inputs of tilling, burning, applying imazapic herbicide, and varying seeding rates on existing species and seeded native perennial grass performance from 2008 to 2012 in a southwestern Idaho rangeland ecosystem. We found that combining tilling, fire, and herbicides produced the lowest annual grass cover. The combination of fire and herbicides yielded the highest seeded species density in the hydrologic year (HY) (October—September) 2010, especially at higher than minimum recommended seeding rates. Although the independent and combined effects of fire and herbicides directly affected the growth of resident species, they failed to affect seeded species cover except in HY 2010, when weather was favorable for seedling growth. Specifically, low winter temperature variability (few freeze-thaw cycles) followed by high growing season precipitation in HY 2010 yielded 14× more seeded perennial grasses than any other seeding year, even though total annual precipitation amounts did not greatly vary between 2009 and 2012. Collectively, these findings suggest that tilling, applying prescribed fire, and herbicides before seeding at least 5× the minimum recommended seeding rate should directly reduce resident annual grass abundance and likely yield high densities of seeded species in annual grass—dominated ecosystems, but only during years of stable winter conditions followed by wet springs.

Introduction

Invasive annual grasses like medusahead (*Taeniatherum caput-medusae* [L.] Nevski) and cheatgrass (*Bromus tectorum* L.) threaten the ecological integrity of arid lands across the western United States (Brooks et al., 2016). Frequent wildfires reduce native perennial bunchgrass abundance (Davies et al., 2012; Boyd et al., 2015), while the compounding effects of high neighboring invasive annual grass cover (Balch et al., 2013) and increasingly dry summers (Barbero et al., 2015) increase the spread of invasive annual grasses (D'Antonio and Vitousek, 1992; Brooks et al., 2004). Annual grasses sustain dominance by beginning growth earlier than most native perennial grasses (Abraham et al., 2009) and preempting available soil resources (Coleman and Levine, 2007). Furthermore, annual grasses produce up to 5 000× more seeds than native perennial grasses (Humphrey and Schupp, 2001; Hempy-Mayer and Pyke, 2008) with first-yr emergence rates averaging 95% (Smith et al., 2008). Because of these conditions, areas invaded by invasive annual grasses will not transition back to any acceptable level of compositional or functional plant diversity without active and persistent management intervention (Morris and Leger, 2016).

Successful revegetation and restoration strategies in annual grass invaded ecosystems must mitigate the underlying ecological processes responsible for invasive plant success while augmenting processes that restore desirable perennial species (Holmes et al., 2010). Ecologically based invasive plant management strategies facilitate desirable species recovery in regions currently dominated by annual grasses by addressing the underlying causes of invasion including site availability, species availability, and species performance (Sheley et al., 2010). Site availability refers to both how disturbance cycles sustain annual grasses and the appropriate disturbance inputs that may be necessary to break the annual grass feedback cycle (Yelenik and D'Antonio, 2013). For example, while wildfires can facilitate annual grass dominance, prescribed fire can also improve site availability for seeded species by reducing litter

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accumulation (Alba et al., 2015). Species availability depicts how dispersal and reproduction dynamics of existing and seeded species affect plant community structure, which includes both increasing the number of desirable propagules and limiting the presence of undesirable weedy species (Knutson et al., 2014; Barr et al., 2017). Finally, species performance classifies management impacts on resource acquisition, response to the environment, life strategy, stress, and interference of both existing and seeded species (Sheley et al., 2010).

Improving site availability for seeded species may require direct disturbance inputs to create safe sites for successful establishment (Gornish and James, 2016). Tilling or raking reduces existing plant species and litter abundance through direct soil disturbances and thereby opens safe sites for seeded species development (Ott et al., 2016). However, soil disturbance, like raking and tilling, may also open safe sites for greater annual grass invasion and impede restoration attempts when seedings are unsuccessful (Diamond et al., 2009; Ott et al., 2017). Prescribed fire and herbicides also reduce invasive annual grasses but leave the soil intact, which may reduce the risk of increased annual grass abundance and interference with seeded species (Brummer et al., 2016). Prescribed fire also directly reduces existing annual grass litter and seedbank abundance (Brisbin et al., 2013), while herbicides increase site availability and species performance by targeting annual grass seed banks, preventing germination and any future interference with perennial grass species (Morris et al., 2009). However, burning is not always feasible depending on the area or annual weather (Gundale et al., 2008) and herbicide performance can be limited under conditions of high surface litter, which prevents adequate seed-to-soil contact (Monaco et al., 2005).

Strategically preparing sites by first tilling and then applying prescribed fire before herbicides can increase herbicide efficacy by reducing herbicide's binding with existing litter (Holmes, 2008; Ott et al., 2017). Hirsch-Schantz et al. (2015) found that combining prescribed fire with herbicides improved site availability and thereby seeded species cover and density more than the independent effects of either of these management inputs. Furthermore, Davies (2010) suggests that imazapic herbicide was only effective at reducing medusahead cover when prescribed fire was first applied to reduce litter cover. However, nontarget effects of preemergent herbicides can reduce seed viability when seeding occurs shortly after herbicide applications (Orloff et al., 2015).

Increasing seeding rates can improve seeded species recovery (Barr et al., 2017) by facilitating desirable species availability, but higher seeding rates will only produce more seeded species to the point of safe site saturation (Luzuriaga and Escudero, 2008). The seeding rate necessary to reach this point, however, likely occurs at a higher rate than typically used in rangeland field plantings (Hardegree et al., 2016). For example, Schantz et al. (2016) found that increased seeding rate was only effective when competing annual grass seed densities were < 1 500 seeds m^{-2} and only effective up to a perennial grass seeding rate of 2 500 seeds m^{-2}.

The objectives of this study were to evaluate existing annual grass and desirable seeded species performance under the independent and combined effects of tilling, burning, applying imazapic herbicide (preemergence), and varying seeding rates. We hypothesized that 1) seeded species would have higher initial establishment in years with more favorable temperature and precipitation; 2) the combination of tilling, burning, and applying herbicides would yield the lowest annual grass density across all sites and years while the combination of burning and applying herbicides would produce the highest seeded-species densities across all sites and years; and 3) the highest seeding rates would produce the highest seedling densities, especially where fire and herbicide treatments were combined.

Methods

Site Description

The Warm Springs experimental study area is in a natural basin in the foothills approximately 2 miles northeast of Boise, Idaho (43E 35′ 51′′N, 116E 07′ 21′′W). Soils in the study area are a McHandy silty clay loam (fine smectitic mesic Chromic Haploxererts) that have undergone significant historical disturbance by tillage. The historical plant community on this site was Wyoming big sagebrush (*Artemisia tridentata* Nuttall ssp. *wyomingensis* Beetle and Young) with a predominantly bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) understory that may have also included Sandberg bluegrass (*Poa secunda* J. Presl), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), basin wildrye (*Leymus cinereus* [Scribn. and Merr.] A. Löve), and rabbitbrush (*Chrysothamnus viscidiflorus* [Hoot.] Nutt.). The current vegetation in the basin is dominated by medusahead, which produces a dense thatch layer and a variety of annual and perennial weedy species such as: cheatgrass, annual sunflower (*Helianthus annuus* L.), prickly lettuce (*Lactuca serriola* L.), field bindweed (*Convolvulus arvensis* L.), bulbous bluegrass (*Poa bulbosa* L.), storks bill (*Erodium ciconium* [L.] L'Hér. ex Aiton), fiddleneck (*Amsinckia menziesii* [Lehm.] A. Nelson & J.F. Macbr. var. intermedia [Fisch. & C.A. Mey.] Ganders), skeletonweed (*Chondrilla juncea* L.), goats beard (*Tragopogon dubius* Scop.), buckwheat (*Eriogonum* Michx. ssp.), mountain brome (*Bromus marginatus* Nees ex Steud.), moth mullein (*Verbascum blattaria* L.), 6-wk fescue (*Vulpia octoflora* [Walter] Rydb.), Sandberg bluegrass, and soft brome (*Bromus hordeaceus* L.).

Weather variables were estimated for the study site from the gridMet database (Abatzoglou 2011; http://climate.nkn.uidaho.edu/METDATA/). GridMet contains daily weather variable estimates for the continuous United States from 1979 to present at a spatial resolution of ≈4 km and is updated daily. The parameters estimated for our study included precipitation (mm) and air temperature (minimum, maximum; °C) and were evaluated by hydrologic year (HY), October − September, to conform to the annual planting (fall) and monitoring period (spring/summer). HYs are as follows: HY 2009 refers to October 2008 − September 2009, HY 2010 denotes October 2009 − September 2010, HY 2011 denotes October 2010 − September 2011, and HY 2012 refers to October 2011 − September 2012.

Study Design

A randomized complete block design with 8 blocks and 250 plots/block was used to evaluate the individual and combined effects of year, fire, herbicide, site preparation, and seeding rate treatments on seeded species and major functional plant group cover and densities. Each block measured 200 m × 200 m, and experimental plots within each block measured 2 m × 2 m. Blocks represented regions seeded with either native or non-native species, while each experimental plot was randomly assigned to treatment yr (HY2009 − HY2012) and treatment application: fire (fire/no-fire), herbicide (0, 4, 6, or 8 oz/ac); site preparation (tilling/no-preparation); seeding rate (0, 1×, 2×, 3×, 5×, and 10×); and their interactions (Table 1, Fig. S1 Each individually applied treatment or treatment combination was replicated in six locations per block. However, because not all treatments were applied in each year of the study (e.g., seeding did not occur in HY 2011 because of environmental constraints), the number of treatments/treatment combinations changed depending on the treatment year (see Table 1). This design yielded 1 184 treatment plots and 7 104 sampling sites.

Management Treatments

Seedbeds were either not prepared (control) or prepared by hand raking or tilling. In HY 2009 and HY 2010 all seeded plots were hand raked, while all seeded plots were hand tilled before seeding in HY 2012. Seedbeds were prepared following fire application but before herbicide application in autumn. Where no seeding occurred, seedbeds were not prepared (control) in HY 2009 and HY 2010, while in HY 2011 and HY 2012, seedbeds were either not prepared (control) or hand tilled.

Table 1
Management treatment inputs and year of application.

Treatments (autumn application)	HY 2009	HY 2010	HY 2011	HY 2012
Seedbed Preparation (no-preparation, rototilled)			X	X
Fire (no-fire, fire)	X	X	X	X
Plateau herbicide (0, 4, 6, 8 oz/ac)	X	X	X	X
Low seeding rates—HY 2009 (0×, 1×, 2×, 3×)	X			
High seeding rates—HY 2010-2012 (0×, 2×, 5×, 10×)		X		X
Number of tested treatments/treatment combinations	32	32	16	68

HY indicates hydrologic yr.

Fire treatments were implemented in October of a given treatment year and consisted of incinerating all aboveground vegetation, thatch, and ground litter with a propane torch. The fire treatment was contained by placing a square aluminum frame along the plot boundary to restrict flames to the within-plot area. Herbicide treatments consisted of application of 0, 4, 6, or 8 oz/ac^{-1} (0, 292, 438, 584 mL-ha^{-1}, respectively) of Plateau (imazapic) using a backpack sprayer (see Table 1).

Seeding occurred using a simulated rangeland drill seeding pattern where columns measured 0.203 m wide to simulate a common spacing interval (8 in. for planting rows in field seeding equipment (see Fig. S1). Row spacing was 0.33 m to allow for a minimum 0.33-m buffer strip around the microplot area. Each plot was further subdivided into microplots with a perimeter buffer zone and an interior treatment area (122 × 133.3 cm) to ensure accurate species monitoring within the treatment area (see Fig. S1).

To evaluate the effects of the seeding rate treatment, plots were seeded with one of four seeding rates. A baseline seeding rate of 240 m^{-2} was designated the 1× rate on the basis of historical recommendations for rangeland seeding under favorable conditions, at optimal seeding depth, and without significant weed competition (Hardegree et al., 2011). Seeding rate treatments included a nonseeded control, 1× (240 seeds/m^{-2}), 2× (480 seeds/m^{-2}), 3× (720 seeds/m^{-2}), 5× (1 200 seeds/m^{-2}), and 10× (2 400 seeds/m^{-2}) seeding rates.

Seed mixes and rates changed in different years of the experiment. Seeding treatments in HY 2009 compared 3 seed mixes (native mix, non-native mix, native/non-native mix) and 4 seeding rates (0×, 1×, 2×, 3×). The native seed mix consisted of Anatone bluebunch wheatgrass, Mountain Home Sandberg bluegrass, Fish Creek bottlebrush squirreltail, Eagle western Yarrow (*Achillia millefolium* L. var. alpicola [Rydb.] Garrett), and nineleaf biscuitroot (*Lomatium triternatum* [Pursh] J.M. Coult. & Rose). Introduced species included Vavilov2 Siberian Wheatgrass (*Agropyron fragile* [Roth] P. Candargy), Luna pubescent wheatgrass (*Thinopyrum intermedium* [Host] Barkworth & D.R. Dewey), Sherman big bluegrass (*Poa ampla* Merr.), Delar small burnet (*Sanguisorba minor* Scop.), and Appar blue flax (*Linum perenne* L.). All native and non-native plots also included the native shrubs antelope bitterbrush (*Purshia tridentata* [Pursh] DC.) and Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young). Larger grass and shrub seeds (Siberian and bluebunch wheatgrass, pubescent wheatgrass, bottlebrush squirreltail, bitterbrush, biscuitroot) were planted in alternating columns in drill rows simulated with a narrow hoe and raked. The surface was compressed with a plot-scale rubber-tire soil compactor. Smaller grass, forb, and shrub seeds (Sandberg and big bluegrass, sagebrush, flax, small burnet) were broadcast, raked, and compressed.

As there was 100% failure of all planted species in HY 2009, a wider range of seeding rates were tested (0×, 2×, 5×, 10×). Species were also pooled into native and introduced grass groupings for the HY 2010 — HY 2012 seeding treatments as compared with seeding by species. Seeded species included the native species, Anatone bluebunch wheatgrass, Fish Creek bottlebrush squirreltail, Mountain Home Sandberg bluegrass, and the non-native species, Vavilov2 Siberian wheatgrass, Luna Pubescent wheatgrass, Sherman big bluegrass.

Environmental conditions in HY 2011 did not allow for small plot seeding as the ground froze early that year and did not thaw out until early spring. Even though we were unable to seed, fire and herbicide effects were tested against unseeded control treatments on weed establishment during HY 2011. Plateau application in the HY 2011 treatment yr was delayed until early March when environmental conditions allowed for the treatment application.

Monitoring occurred in late May in the year following any seeding treatment. One microplot per column in any treatment plot was randomly selected for ocular estimation of percent cover of the principal weed species; cheatgrass and medusahead-wildrye, and ground litter. All other species including native and non-native annual forbs, perennial forbs, and seeded species were counted for density in the entire plot area (plants/m^{-2}).

Statistical Analyses

Individual effects and interactions among management treatments and the hydrologic year on seeded and resident species cover and densities were evaluated using mixed-model analyses of variance in JMP (Version 13; SAS Institute Inc., Cary, NC). The lack of replication in seedbed preparation among and within years only allowed us to test the differences between the control and tilling seedbed preparation treatments where seeding did not occur in HY 2011 and HY 2012. This model tested the individual effects and interactions among fire, herbicide application, hydrologic year, and seedbed preparation on the density of annual forbs and perennial forbs, and the cover of litter, cheatgrass, and medusahead (Table 2A). Furthermore, because of the complete seeding failure in HY 2009 and lack of seeding in HY 2011 precluded including a fourth-order analysis, we were unable to test a four-way interaction among year, fire, herbicide, and seeding rate. Consequently, we used two models, the first of which tested the individual effects and interactions among fire, herbicide application, and HY on the density of seeded species, annual forbs, and perennial forbs and the cover of litter, cheatgrass, and medusahead (Table 2B) while the second model tested the individual effects and interactions among fire, herbicide, and seeding rates on the density of seeded species, annual forbs and perennial forbs, and the cover of litter, cheatgrass, and medusahead (Table 2C).

For all models, the annual grasses medusahead and cheatgrass were tested by species while annual forbs and perennial forbs were pooled into functional groups. Initial tests showed no difference in the number of emerged native versus emerged introduced seeded species. Consequently, all seeded species were pooled into one group (seedlings). All species and functional groups required a square-root transformation to meet the minimum standards of linear parametric models before analysis. Tukey's honest significance difference was then used to determine differences in all models, and these treatments were considered significant when $\alpha \leq 0.05$.

Results

Climate Variability

Air temperature and precipitation magnitude varied both between and within treatment years (Fig. 1). Precipitation was lower than average during HY 2009 and from May — December in 2012 and higher than average in HY 2010, October — December 2011, and from January to

Table 2

Analysis of variance summaries of treatments and treatment interactions on species and functional groups. *A* refers to Yr, Fire, Herbicide, and Seed Preparation interaction. *B* refers to Yr, Fire, and Herbicide interaction. *C* refers to Fire, Herbicide, and Seed Rate interaction.

A	TACA	BRTE	Litter	Seedlings	Perennial forbs	Annual forbs
Treatment	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)
Yr	NS	NS	411.97 ($P<0.0001$)	N/A	10.44 ($P=0.0013$)	483.52 ($P<0.0001$)
Fire	86.00 ($P<0.0001$)	NS	260.51 ($P<0.0001$)	N/A	NS	91.52 ($P<0.0001$)
Herbicide	102.21 ($P<0.0001$)	7.72 ($P<0.0001$)	5.06 ($P=0.0009$)	N/A	7.59 ($P<0.0001$)	43.59 ($P<0.0001$)
Site preparation	83.14 ($P<0.0001$)	NS	454.62 ($P<0.0001$)	N/A	NS	251.43 ($P<0.0001$)
Yr ● Fire	14.93 ($P<0.0001$)	NS	NS	N/A	NS	56.27 ($P<0.0001$)
Yr ● Herbicide	NS	NS	3.76 ($P=0.0104$)	N/A	NS	22.66 ($P<0.0001$)
Yr ● Site preparation	5.41 ($P=0.0201$)	5.33 ($P=0.0210$)	6.37 ($P=0.0116$)	N/A	NS	203.79 ($P<0.0001$)
Fire ● Herbicide	28.08 ($P<0.0001$)	2.34 ($P=0.0707$)	3.94 ($P=0.0081$)	N/A	NS	3.28 ($P=0.0201$)
Fire ● Site preparation	19.57 ($P<0.0001$)	NS	17.12 ($P<0.0001$)	N/A	NS	47.55 ($P<0.0001$)
Herbicide ● Site preparation	25.00 ($P<0.0001$)	NS	4.14 ($P=0.0062$)	N/A	NS	10.06 ($P<0.0001$)
Yr ● Fire ● Herbicide	3.27 ($P=0.0204$)	NS	NS	N/A	NS	3.34 ($P=0.0185$)
Yr ● Fire ● Site preparation	12.25 ($P<0.0005$)	NS	10.91 ($P=0.0010$)	N/A	NS	46.32 ($P<0.0001$)
Yr ● Herbicide ● Site preparation	4.05 ($P=0.0070$)	3.30 ($P=0.0195$)	NS	N/A	NS	6.52 ($P=0.0002$)
Fire ● Herbicide ● Site preparation	3.92 ($P=0.0084$)	NS	3.85 ($P=0.0092$)	N/A	NS	2.72 (P=0.0433)
Yr ● Fire ● Herbicide ● Site preparation	3.56 ($P=0.0137$)	NS	NS	N/A	NS	3.75 ($P=0.0106$)

B	TACA	BRTE	Litter	Seedlings	Perennial forbs	Annual forbs
Treatment	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)
Yr	336.57 ($P<0.0001$)	121.32 ($P<0.0001$)	512.55 ($P<0.0001$)	130.94 ($P<0.0001$)	6.61 ($P=0.0002$)	386.89 ($P<0.0001$)
Fire	275.01 ($P<0.0001$)	8.44 ($P=0.0037$)	871.74 ($P<0.0001$)	NS	5.75 ($P=0.0165$)	62.94 ($P<0.0001$)
Herbicide	384.34 ($P<0.0001$)	84.93 ($P<0.0001$)	NS	4.50 ($P=0.0037$)	6.61 ($P<0.0001$)	39.06 ($P<0.0001$)
Yr ● Fire	11.81 ($P<0.0001$)	5.23 ($P=0.0013$)	35.22 ($P<0.0001$)	NS	3.03 ($P=0.0283$)	19.46 ($P<0.0001$)
Yr ● Herbicide	37.42 ($P<0.0001$)	17.29 ($P<0.0001$)	3.93 ($P<0.0001$)	4.31 ($P<0.0001$)	NS	22.18 ($P<0.0001$)
Fire ● Herbicide	15.21 ($P<0.0001$)	NS	NS	4.85 ($P=0.0023$)	NS	NS
Yr ● Fire ● Herbicide	4.96 ($P<0.0001$)	3.64 ($P=0.0001$)	1.83 ($P=0.0271$)	3.70 ($P=0.0001$)	2.12 ($P=0.0246$)	3.13 ($P=0.0009$)

C	TACA	BRTE	Litter	Seedlings	Perennial forbs	Annual forbs
Treatment	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)	F ratio (*P* value)
Fire	263.89 ($P<0.0001$)	17.62 ($P<0.0001$)	618.29 ($P<0.0001$)	NS	NS	12.36 ($P=0.0004$)
Herbicide	300.05 ($P<0.0001$)	82.00 ($P<0.0001$)	NS	3.03 ($P=0.0280$)	25.06 ($P<0.0001$)	10.88 ($P<0.0001$)
Seed rate	33.99 ($P<0.0001$)	26.27 ($P<0.0001$)	29.30 ($P<0.0001$)	27.05 ($P<0.0001$)	3.69 ($P=0.0025$)	79.12 ($P<0.0001$)
Fire ● Herbicide	5.55 ($P=0.0008$)	NS	NS	5.45 ($P=0.0010$)	NS	1.43 ($P=0.2321$)
Fire ● Seed rate	5.48 ($P<0.0001$)	3.02 ($P=0.0100$)	4.56 ($P=0.0004$)	NS	2.77 ($P=0.0167$)	4.23 ($P=0.0008$)
Herbicide ● Seed rate	9.85 ($P<0.0001$)	5.23 ($P<0.0001$)	NS	2.06 ($P=0.0089$)	2.32 ($P=0.0027$)	3.65 ($P<0.0001$)
Fire ● Herbicide ● Seed Rate	2.07 ($P=0.0087$)	1.78 ($P=0.0321$)	NS	4.21 ($P<0.0001$)	4.56 ($P<0.0001$)	3.27 ($P<0.0001$)

NS indicates a nonsignificant interaction; N/A, not applicable.

May 2012 (see Fig. 1A). In both HY 2010 and HY 2011, precipitation was 1.5× higher than average during the primary growing season, March – May. Monthly temperature was generally average throughout this study (Fig. 1B and C). However, temperature was below average for much of the HY 2009 growing season and had a thaw-freeze interval in late January (Fig. 2A). Alternatively, temperature increased above normal before dropping well below normal in December 2009 but was normal to above average for the rest of HY 2009 (Fig. 2B). In HY 2010, temperature followed a similar above-normal to below-normal pattern in November, before seeding, but fluctuated from above to below normal again in early January, early February, and late February (Fig. 2C). During HY 2011, there was a cold stretch from mid-November to late-December 2011, where temperatures were below normal but rose to above normal by late January and again followed a freeze-thaw interval in late February 2012 (Fig. 2D).

Nonseeded Site Treatment Effects

Where tilling occurred, medusahead cover was > 3× lower than where sites were not prepared (Fig. 3A and B; $P < 0.05$). Medusahead cover was also lower where tilling, fire, and herbicides were applied compared with regions that were not tilled, not burned, nor applied with any herbicides in both HY 2011 and HY 2012 (see Fig. 3A and B; $P < 0.05$). Regardless of site preparation in both HY 2011 and HY 2012, at the 0 oz/ac herbicide rates, medusahead cover was higher where burning did not occur compared with where fire was applied (Fig. 3A; $P < 0.05$).

Cheatgrass cover was not directly affected by tilling (Table 2A; $P =$ 7328). However, cheatgrass cover was higher in HY 2011 at the 0 oz/ac herbicide rates where fire was applied and tilling did not occur compared with the 0 oz/ac herbicide rate treatment at both the no-tilling and no-burning and the rototilled and no-fire applied sites (Fig. 3C and D; $P < 0.05$).

In the absence of site preparation, litter cover was > 2× lower than where sites were prepared by tilling (see Table 2A; $P < 0.05$). The combination of burning and tilling yielded lower litter cover compared with where neither tilling nor herbicides were applied at all herbicide rates in both HY 2011 and HY 2012 (Figure 3E and F; $P < 0.05$). In HY 2012 at the 0-, 6-, and 8 oz/ac herbicide rates, litter cover was also lower where tilling and fire were applied compared with all other fire and site preparation treatments (Fig. 3F; $P < 0.05$).

Annual forb densities were highest where neither tilling nor burning occurred across 0, 6, and 8 oz/ac herbicide rates in HY 2011 (Fig. 3G; $P <$ 0.05). Where tilling occurred, annual forb density was > 2× lower than where sites were not prepared in HY 2011 (Fig. 3G; $P < 0.05$). The combination of tilling and adding at least 4 oz/ac imazapic herbicide produced lower annual forb density compared with where neither tilling nor fire was applied in HY 2011 (Fig. 3G; $P < 0.05$). Furthermore, in HY 2011, the combination of no-tilling and burning produced more annual forbs at 4 oz/ac herbicide rates compared with this same treatment combination at 6 or 8 oz/ac herbicide rates (Fig. 3G; $P < 0.05$). Alternatively, there were no differences in annual forb density across the fire, herbicide, or site preparation treatments in HY 2012 (Fig. 3H; $P > 0.05$).

Although site preparation did not significantly affect perennial forb density in HY 2011, perennial forb density was higher in HY 2012 where sites were both rototilled and burned in the absence of herbicide application compared with tilling and burning at both 6 and 8 oz/ac herbicide application rates (Fig. 3I and J; $P < 0.05$).

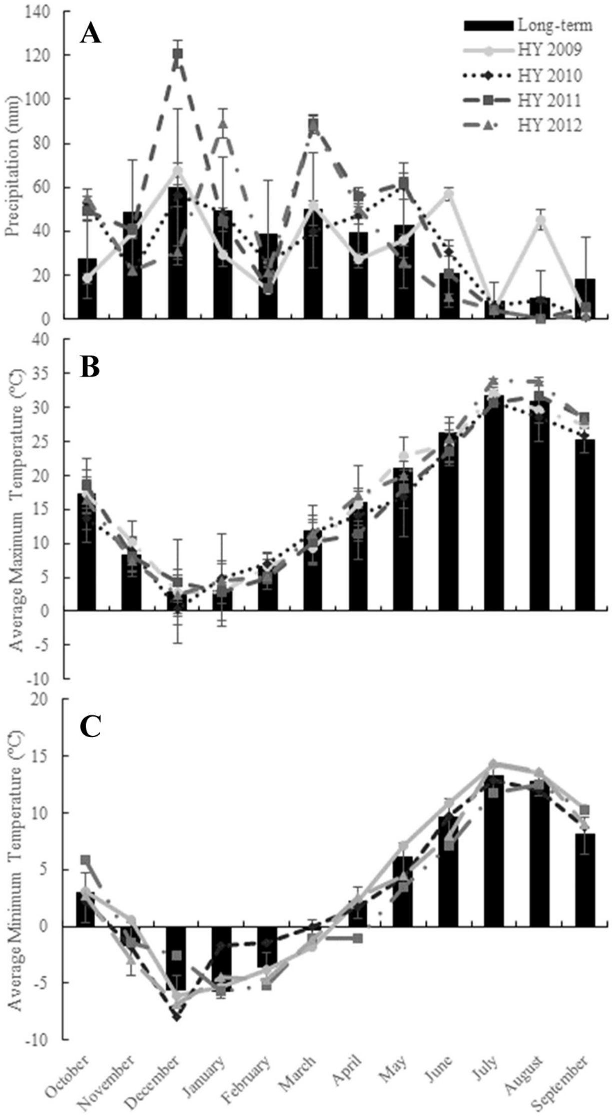


Figure 1. Long-term climate and weather during the study period. **A,** The 40-yr long-term average precipitation and average monthly precipitation for the hydrologic years (September — October) 2009 — 2012 (mm). **B**, The 40-yr long-term average maximum temperature and average monthly maximum temperature for the hydrologic yr 2009 — 2012 (°C). **C,** The 40-yr long-term average minimum temperature and average monthly minimum temperature for the hydrologic yr 2009 — 2012 (°C).

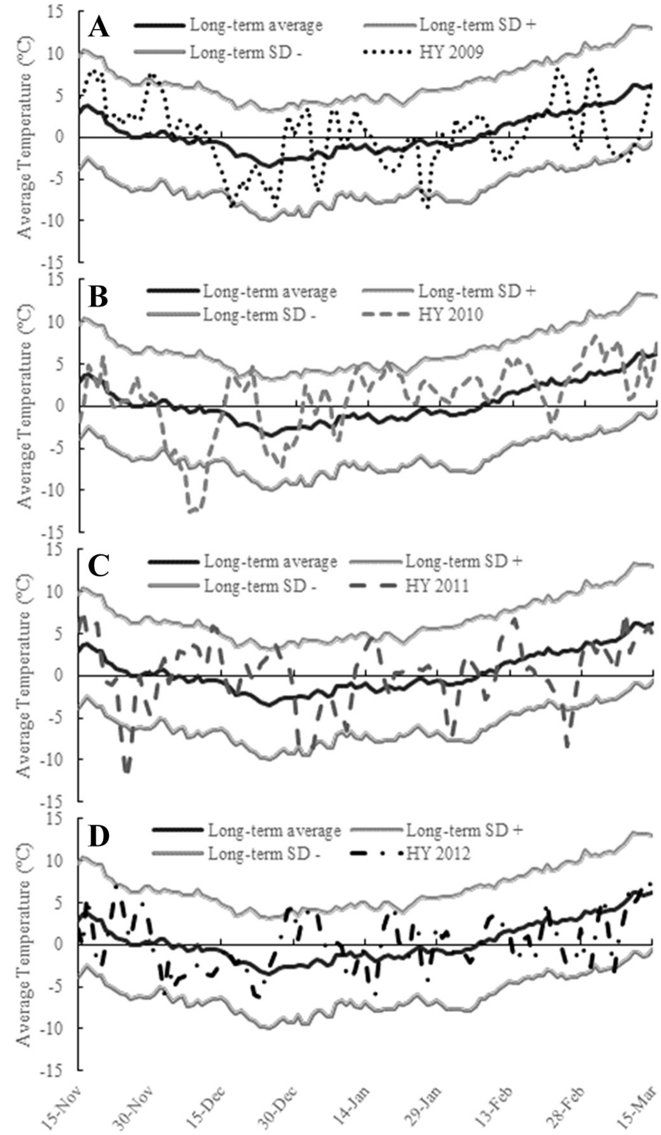


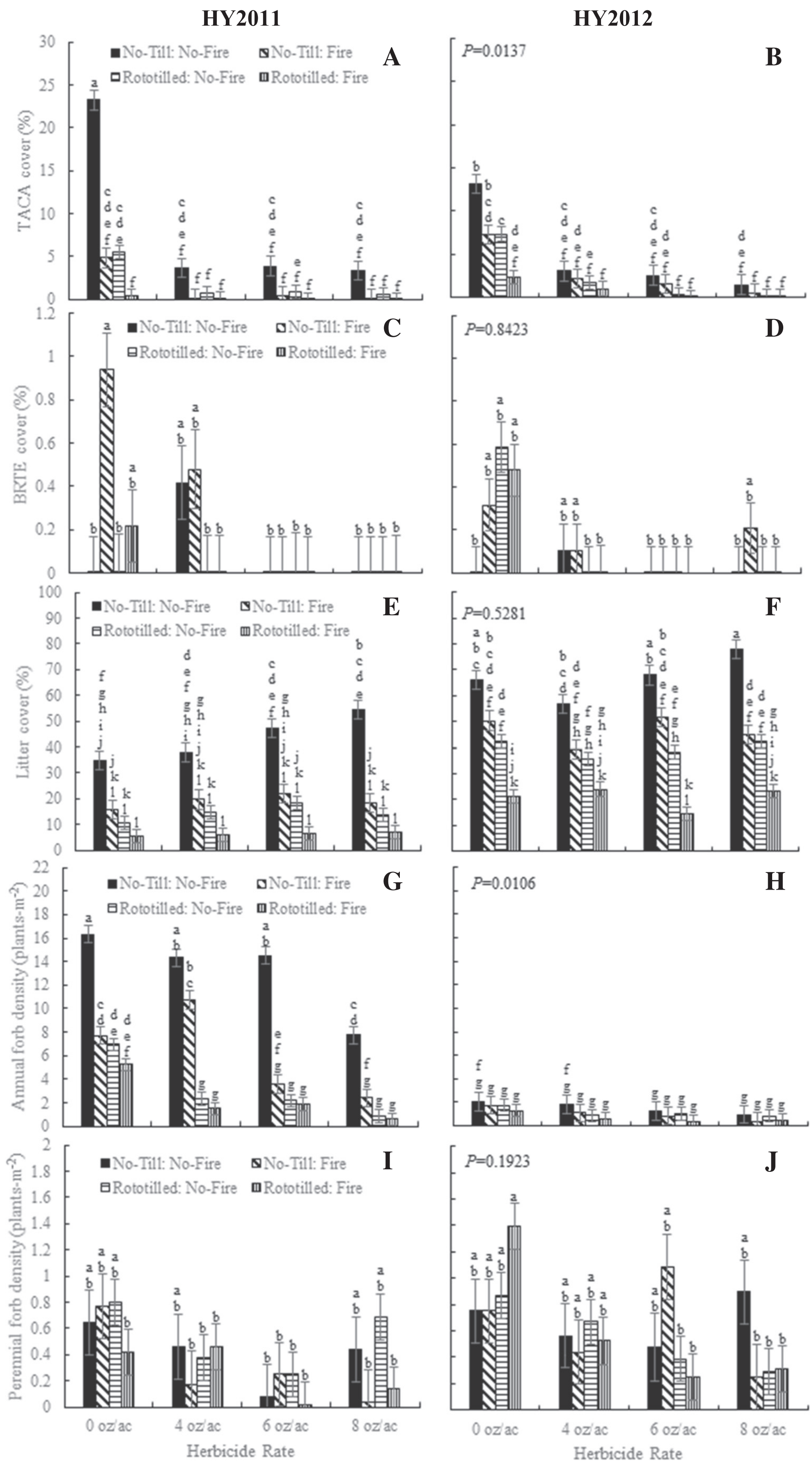
Figure 2. Average daily temperature (°C) over the winter months (15 November–15 March) for the hydrologic yr (HYs) (October — September. **A,** HY 2009. **B,** HY 2010. **C,** HY 2011. **D,** HY 2012. Each figure also includes the 40-yr long-term average temperature (long-term average), the positive (long-term standard deviation [SD] +) and negative (long-term SD −) standard deviation of the long-term average temperature, and the average temperature during the study yr (2008 — 2012).

Seeded Site Treatment Effects

In general, both medusahead and cheatgrass responded similarly to years and management treatment. For example, the cover of both medusahead and cheatgrass was higher in HY 2009 and HY 2010 compared with HY 2011 and HY 2012 (Fig. 4A; $P < 0.05$). Burning yielded lower annual grass cover compared with nonburned regions (Fig. 4B; $P < 0.05$). Similarly, applying herbicides produced lower medusahead and cheatgrass cover compared with control plots (Fig. 4C; $P < 0.05$). For example, where herbicides were applied, medusahead cover was lowest and only yielded 2.15% ± 0.93% at the highest (8 oz/ac) herbicide rates compared with 10.31% ± 0.93% in control plots (Table 3; $P < 0.05$). Medusahead cover was highest in HY 2009 where fire and herbicide application did not occur and was lowest in HY 2012 when fire was combined with the highest herbicide rate (8 oz/ac) (see Table 3; $P < 0.05$). Similarly, cheatgrass had the highest cover in HY 2009 where neither fire nor herbicides were applied (see Table 3; $P < 0.05$). Moderate seeding rates produced higher medusahead and cheatgrass cover compared with control and 10× seeding rates (Fig. 4D; $P < 0.05$). Furthermore, annual grass cover was highest where neither fire nor herbicides were applied and at moderate seeding rates (Table 4B; $P < 0.05$).

Litter cover was over 2× higher in HY 2009 and HY 2012 compared with HY 2010 and HY 2011 (Fig. 4A; $P < 0.05$). Similarly, litter was 2× lower where burning occurred compared with control plots (Fig. 4B; $P < 0.05$). Alternatively, litter cover was not affected by herbicide application (Fig. 4C; $P < 0.05$), nor was litter cover affected by the interaction of fire, herbicide, and year (see Table 2; $P = 0.06$). Seeding at 1× seeding rates yielded the highest litter cover (Fig. 4D; $P < 0.05$). Litter cover was also highest where burning was not applied and seeding rates were 1× (see Table 4; $P < 0.05$).

Seeding in HY 2010 produced > 13× higher density compared with all other years of this study (Fig. 5A; $P < 0.05$). While burning did not affect seeded species density (Fig. 5B; $P = 0.56$), seeded species densities were almost 2× higher where herbicides were applied at 6 oz/ac compared with control plots (Fig. 5C; $P < 0.05$). The combined effects of burning and no-herbicides produced lower seeded species density compared with where fire was applied with moderate rates; i.e., 6 oz/ac herbicide


HY2011
HY2012
No-Till: No-Fire
No-Till: Fire
Rototilled: No-Fire
Rototilled: Fire
A
B
C
D
E
F
G
H
I
J
P=0.0137
P=0.8423
P=0.5281
P=0.0106
P=0.1923
TACA cover (%)
BRTE cover (%)
Litter cover (%)
Annual forb density (plants-m-2)
Perennial forb density (plants-m-2)
0 oz/ac
4 oz/ac
6 oz/ac
8 oz/ac
Herbicide Rate

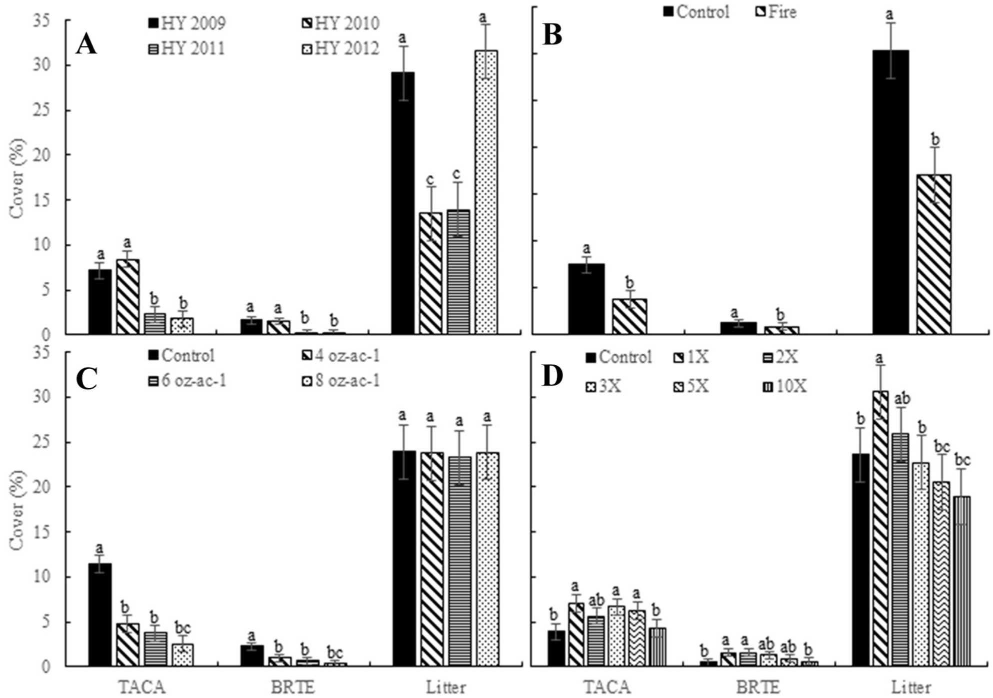


Figure 4. Annual grasses TACA (medusahead) and BRTE (cheatgrass) and litter cover in response to differing years and treatments. **A,** Differing years. **B,** Response to fire. **C,** Differences in imazapic herbicide rates. **D,** Differences in seeding rates. Different letters above bars signify differences within the annual grass species or litter. Specific F ratios and *P* values of individual effects are identified in Table 2.

rates (see Table 2B and C; $P < 0.05$). For example, seeded species densities were highest in HY 2010 where fire was combined with 6 oz/ac herbicide rates at 0.30 ± 0.02 plants/m^{-2} (see Table 3; $P < 0.05$). Seeded species density was 6.5× higher at the highest seeding rate (10×) compared with the lowest seeding rate (1×) (see Fig. 5D; $P < 0.05$). Furthermore, the interaction of fire and high herbicide rates produced the highest seeded species density where 6 oz/ac yielded 0.11 ± 0.01 plants/m^{-2} and 8 oz/ac produced 0.07 ± 0.01 plants/m^{-2}, compared with only 0.04 ± 0.01 plants/m^{-2} in control plots (see Table 3; $P < 0.05$).

Nonseeded annual forb density was highest in HY 2011 at 4.22 ± 0.22 plants/m^{-2} and lowest in HY 2009, where density only averaged 0.81 ± 0.21 plants/m^{-2} (see Fig. 5A; $P < 0.05$). Burning yielded lower annual forb density compared with no-fire plots (see Fig. 5B; $P < 0.05$), and annual forb density was also lower where herbicides were applied compared with no-herbicide plots (Fig. 5C; $P < 0.05$). However, the interaction of fire and herbicides did not affect annual forb density in this study (see Table 2B and C; $P = 0.06$). Across all years, fire treatments, and herbicide rates, annual forb density was highest in HY 2011 where neither fire nor herbicides were applied and lowest in HY 2009 where plots were burned, and herbicides were applied at 6 oz/ac (see Tables 2B and 3; $P < 0.05$). Annual forb densities were highest where seeding did not occur followed by the three highest seeding rates (Fig. 5D; $P < 0.05$). The combination of burning, no-herbicides, and no-seeding produced the highest annual forb densities (see Table 4; $P < 0.05$).

Nonseeded perennial forb density increased from HY 2009 to HY 2012 where density was only 0.39 ± 0.16 plants/m^{-2} in HY 2009, 0.45 ± 0.16 plants/m^{-2} in HY 2010, 0.46 ± 0.16 plants/m^{-2} in HY 2011, and 0.60 ± 0.16 plants/m^{-2} in HY 2012 (Fig. 5A; $P < 0.05$). Burning produced lower perennial forb densities compared with areas not applied with fire (Fig. 5B; $P < 0.05$). Similarly, no-herbicide plots yielded over 2× higher perennial forb densities compared with plots applied with the highest herbicide application rates, 8 oz/ac (see Fig. 5C; $P < 0.05$). Alternatively, the interaction of fire and herbicide application did not significantly affect the density of perennial forbs (see Table 2B; $P = 0.19$). Across years, perennial forb density was lowest in HY 2009 at 0.15 ± 0.18 plants/m^{-2} where fire did not occur and herbicide rates were highest at 8 oz/ac and highest at 0.99 ± 0.19 plants/m^{-2} in HY 2010 where neither fire nor herbicides were applied (see Tables 2B and 4; $P < 0.05$). Perennial forb density was 1.34× higher at the two highest seeding rates compared with the three lowest seeding rates (Fig. 5D; $P < 0.05$). The combination of the highest seeding rates with no-fire and no-herbicides also produced the highest perennial forb density (see Table 4; $P < 0.05$).

Discussion

Management inputs that modify the ecological processes associated with site availability, species availability, and species performance can aid in restoring desirable structure and function to annual grass−invaded ecosystems (Sheley et al., 2010). However, seedling establishment depends on the interactions of management inputs with annual weather patterns, particularly during stages of initial growth and development (Hardegree et al., 2016). To produce self-sustaining stands, it is critical that desirable seedlings begin establishing within the first growing season because annual grasses recover quickly following disturbance events and can double in cover within 2 yr (Rew and Johnson, 2010; Bansal and Sheley, 2016). Therefore, quantifying the effects of varying management inputs on seedling and resident species establishment following restoration should further our understanding of the management strategies that yield the highest seedling recruitment.

In support of our first hypothesis, seeded species had higher cover in years with more favorable temperature and precipitation (see Figs. 1 and 5). Freeze-thaw cycles are common in the Intermountain west and can significantly reduce seedling emergence by promoting

Figure 3. Plant functional group density in response to differing years, site preparation, fire, and herbicide management treatments. Left-hand figures represent HY 2011 while right-hand figures represent HY 2012. **A** and **B**, Medusahead (TACA) cover. **C** and **D,** Cheatgrass (BRTE) cover. **E** and **F,** Litter cover. **G** and **H,** Annual forb density. **I** and **J**, Perennial forb density. Different letters represent significant differences among treatments. Specific F ratios and *P* values for each individual effect are identified in Table 2.

Table 3
Least squared means ± standard error of the fire by herbicide-by-yr interaction. Columns represent species or functional groups, and the fire treatment and rows indicate the hydrologic yr and herbicide rate. Seedlings, forbs, and perennial grasses are represented by their density in plants/m^{-2}, while the annual grasses TACA (medusahead) and BRTE (cheatgrass) and litter are represented by their percent (%) cover.

		Seedlings		Annual forbs		Perennial forbs		TACA		BRTE		Litter	
		No fire	Fire	No fire	Fire	No fire	Fire	No fire	Fire	No fire	Fire	No fire	Fire
Hydrologic yr	Herbicide rate	Plants/m^{-2}	Plants/m^{-2}	Plants/m^{-2}	Plants/m^{-2}	Plants/m^{-2}	Plants/m^{-2}	% cover	% cover	% cover	% cover	% cover	% cover
2009	Control	NS	NS	0.88 ± 0.30	1.01 ± 0.30	0.85 ± 0.19	0.45 ± 0.19	19.77 ± 1.02	13.78 ± 1.02	3.57 ± 0.44	3.88 ± 0.44	38.26 ± 3.15	20.08 ± 3.15
	4 oz/ac	NS	NS	3.53 ± 0.32	3.50 ± 0.32	0.72 ± 0.18	0.26 ± 0.18	7.19 ± 1.01	4.40 ± 1.01	2.17 ± 0.43	0.70 ± 0.43	37.29 ± 3.14	21.84 ± 3.14
	6 oz/ac	NS	NS	8.21 ± 0.37	5.10 ± 0.37	0.34 ± 0.18	0.17 ± 0.18	5.73 ± 1.01	1.85 ± 1.01	1.25 ± 0.43	0.56 ± 0.43	37.43 ± 3.13	20.74 ± 3.13
	8 oz/ac	NS	NS	1.85 ± 0.31	1.78 ± 0.31	0.15 ± 0.18	0.18 ± 0.18	3.29 ± 1.01	1.07 ± 1.01	0.86 ± 0.43	0.23 ± 0.43	36.71 ± 3.13	20.81 ± 3.13
2010	Control	0.17 ± 0.02	0.06 ± 0.02	1.36 ± 0.29	0.73 ± 0.29	0.99 ± 0.19	0.52 ± 0.19	14.94 ± 1.05	11.23 ± 1.05	3.47 ± 0.45	2.76 ± 0.45	20.55 ± 3.21	10.98 ± 3.21
	4 oz/ac	0.10 ± 0.02	0.17 ± 0.02	3.63 ± 0.32	4.07 ± 0.32	0.37 ± 0.19	0.37 ± 0.19	9.44 ± 1.05	6.67 ± 1.05	1.01 ± 0.45	1.32 ± 0.45	16.37 ± 3.21	10.92 ± 3.21
	6 oz/ac	0.15 ± 0.02	0.30 ± 0.02	5.06 ± 0.37	3.90 ± 0.37	0.26 ± 0.19	0.34 ± 0.19	9.95 ± 1.05	3.89 ± 1.05	1.56 ± 0.45	0.40 ± 0.45	15.40 ± 3.21	9.19 ± 3.21
	8 oz/ac	0.22 ± 0.02	0.22 ± 0.02	1.29 ± 0.31	0.75 ± 0.31	0.21 ± 0.19	0.52 ± 0.19	7.87 ± 1.05	3.35 ± 1.05	0.84 ± 0.45	0.70 ± 0.45	14.57 ± 3.21	9.77 ± 3.21
2011	Control	NS	NS	0.54 ± 0.29	0.45 ± 0.29	0.74 ± 0.21	0.64 ± 0.21	10.79 ± 1.12	2.72 ± 1.12	0.13 ± 0.48	0.84 ± 0.48	17.66 ± 3.32	7.75 ± 3.32
	4 oz/ac	NS	NS	4.49 ± 0.32	3.22 ± 0.32	0.51 ± 0.21	0.45 ± 0.21	1.46 ± 1.12	0.05 ± 1.12	0.16 ± 0.48	0.13 ± 0.48	18.32 ± 3.32	8.30 ± 3.32
	6 oz/ac	NS	NS	5.12 ± 0.37	2.45 ± 0.37	0.24 ± 0.21	0.19 ± 0.21	1.64 ± 1.12	0.16 ± 1.12	0.00 ± 0.48	0.00 ± 0.48	21.57 ± 3.32	8.92 ± 3.32
	8 oz/ac	NS	NS	1.03 ± 0.31	0.57 ± 0.31	0.61 ± 0.21	0.33 ± 0.21	1.10 ± 1.12	0.00 ± 1.12	0.00 ± 0.48	0.11 ± 0.48	20.64 ± 3.32	8.11 ± 3.32
2012	Control	0.00 ± 0.02	0.01 ± 0.02	0.62 ± 0.29	0.91 ± 0.29	0.94 ± 0.19	0.97 ± 0.19	6.26 ± 1.03	3.00 ± 1.03	0.56 ± 0.44	0.28 ± 0.44	38.55 ± 3.18	23.68 ± 3.18
	4 oz/ac	0.01 ± 0.02	0.01 ± 0.02	4.58 ± 0.32	3.80 ± 0.32	0.58 ± 0.19	0.76 ± 0.19	2.77 ± 1.03	0.72 ± 1.03	0.00 ± 0.45	0.00 ± 0.45	36.94 ± 3.18	23.98 ± 3.18
	6 oz/ac	0.02 ± 0.02	0.01 ± 0.02	2.66 ± 0.37	1.26 ± 0.37	0.42 ± 0.19	0.39 ± 0.19	0.55 ± 1.03	0.30 ± 1.03	0.00 ± 0.45	0.00 ± 0.45	38.99 ± 3.18	20.84 ± 3.18
	8 oz/ac	0.02 ± 0.02	0.01 ± 0.02	0.80 ± 0.31	0.46 ± 0.31	0.43 ± 0.19	0.32 ± 0.19	0.47 ± 1.03	0.09 ± 1.03	0.00 ± 0.44	0.00 ± 0.44	45.35 ± 3.18	24.37 ± 3.18

germination during warming periods followed by mortality from a freezing event (James et al., 2011). Stable winter conditions, like HY 2010, may have increased seedling recruitment because few to no freeze-thaw intervals reduced seedling mortality during the critical postgermination/pre-emergence life stage (see Fig. 2) (James et al., 2012). High precipitation during the HY 2010 growing season likely further facilitated seeded species density. Higher precipitation during the growing season is especially important for native perennial grass seedlings in the Intermountain west because much of the available water results from winter precipitation (Roundy et al., 2007). Winter precipitation generally facilitates the growth of annual grasses, which begin growth earlier than native perennial grasses (Abraham et al., 2009). The earlier growth of annual grasses uses much of the existing soil water before seeded native perennial grass species begin developing (Trowbridge et al., 2013). Thus, stable winter temperatures followed by above-normal precipitation will likely yield the highest seeded species recruitment.

Preparing sites by tilling, burning, and applying herbicides in combination with increasing seeding rates of native perennial grasses should decrease existing species interference and increase safe site availability for seeded species establishment (Ott et al., 2017). Tilling can be an effective site preparation treatment because it directly reduces existing plant species and litter abundance and can limit the seed bank of resident plant species (Bakker et al., 1997). In support of the first part of our second hypothesis, we found that tilling reduced annual grass cover and the densities of existing resident species, especially when combined with fire and herbicides in HY 2011 and HY 2012 (see Fig. 3). However, we were only able to test the effects of tilling in nonseeded plots in HY 2011 and HY 2012. Alternatively, combining burning and herbicides can limit the production of annual grasses, while simultaneously facilitating seeded species (Davies and Sheley, 2011; Hirsch-Schantz et al., 2014). In support of the second part of our second hypothesis, we found that the interaction of burning and herbicides produced higher seeding densities across all 4 yr of this study. Using fire and herbicides to decrease annual grass cover can benefit seeded species production by reducing the mat of litter produced by annual grasses (Kessler et al., 2015) and thereby increase safe site abundance, or areas with conditions favorable for seedling production (Duncan et al., 2009). Burning can also reduce current annual grass growth (Munson et al., 2015) and annual-seedbank abundance (Brisbin et al., 2013), which increases resource availability for seeded species production (Gundale et al., 2008). In this study, however, seeded species only responded to fire or herbicides in HY 2010 (see Tables 2 and 3). This is likely because precipitation occurring during the growing season facilitated seeded species production, whereas in all other years, precipitation primarily occurred in winter before seeded species began growth and instead facilitated earlier growing species, like annual grasses (Larson et al., 2015).

Seeding higher rates of native perennial grasses should yield greater seeded species development (Barr et al., 2017), but only to a point of safe-site saturation (Aicher et al., 2011). Schantz et al. (2016) found that seeding 3 500 seeds m^{-2} did not produce more seed species than seeding 2 500 seeds m^{-2}. Similarly, we found that adding more species yielded higher seedling densities to the point of 5× the recommended seeding rates. Adding > 5× the recommended seeding rate did not produce more seeded species than seeding 10× the recommended seeding rate in this study. This is likely due to the law of diminishing returns, with increased seeds over a certain density having a lower likelihood of developing into a viable seedling because of limited resource and safe site availability (Crowley et al., 2005). Alternatively, our finding that higher perennial grass seeding rates yielded lower annual grass densities suggests that increased seeding rates can improve the likelihood that seeded species locate, occupy, and develop in safe sites across the area (Kulpa et al., 2012). Conversely, Reid and Holl (2013) suggest that regardless of native perennial grass seed input, species will develop on the basis of their demographic characteristics. The lower annual grass densities at

Table 4

Least squared means ± standard error of the fire by herbicide by seeding rate interaction. Columns represent species or functional groups, and the fire treatment, and rows indicate the herbicide rate and seeding rate. Seedlings, forbs, and perennial grasses are represented by their density in plants/m^{-2}, while the annual grasses TACA (medusahead) and BRTE (cheatgrass) and litter are represented by their percent (%) cover.

		Seedlings		Annual forbs		Perennial forbs		TACA		BRTE		Litter	
		No fire	Fire	No fire	Fire	No fire	Fire	No fire	Fire	No fire	Fire	No fire	Fire
Herbicide rate	Seeding rate	Plants/m^{-2}	Plants/m^{-2}	Plants/m^{-2}	Plants/m^{-2}	Plants/m^{-2}	Plants/m^{-2}	% cover	% cover	% cover	% cover	% cover	% cover
Control	0	0.01 ± 0.02	0.01 ± 0.02	4.84 ± 0.28	3.52 ± 0.28	0.73 ± 0.18	0.68 ± 0.18	11.38 ± 1.00	5.80 ± 1.00	1.42 ± 0.43	1.14 ± 0.43	30.48 ± 3.14	16.68 ± 3.14
	1×	0.00 ± 0.04	0.00 ± 0.04	0.47 ± 0.51	1.01 ± 0.51	0.46 ± 0.25	0.49 ± 0.25	20.94 ± 1.32	12.39 ± 1.32	3.44 ± 0.56	2.50 ± 0.56	40.72 ± 3.73	20.21 ± 3.73
	2×	0.02 ± 0.03	0.01 ± 0.03	1.68 ± 0.38	1.56 ± 0.38	0.67 ± 0.21	0.64 ± 0.21	14.09 ± 1.13	10.81 ± 1.13	3.03 ± 0.48	3.65 ± 0.48	31.75 ± 3.38	18.84 ± 3.38
	3×	0.05 ± 0.02	0.03 ± 0.02	2.02 ± 0.35	1.81 ± 0.35	1.39 ± 0.20	0.38 ± 0.20	16.04 ± 1.09	11.71 ± 1.09	2.84 ± 0.46	3.25 ± 0.46	30.63 ± 3.30	16.26 ± 3.30
	5×	0.02 ± 0.04	0.08 ± 0.04	1.64 ± 0.51	2.59 ± 0.51	1.10 ± 0.25	0.90 ± 0.25	13.08 ± 1.32	7.03 ± 1.32	2.09 ± 0.56	2.14 ± 0.56	26.83 ± 3.73	17.30 ± 3.73
	10×	0.31 ± 0.04	0.04 ± 0.04	2.33 ± 0.51	2.03 ± 0.51	1.11 ± 0.25	1.02 ± 0.25	8.19 ± 1.32	5.38 ± 1.32	1.15 ± 0.56	0.61 ± 0.56	24.89 ± 3.73	12.14 ± 3.73
4 oz/ac	0	0.02 ± 0.02	0.03 ± 0.02	3.46 ± 0.28	2.99 ± 0.28	0.51 ± 0.18	0.45 ± 0.18	3.54 ± 1.00	3.33 ± 1.00	0.34 ± 0.43	0.25 ± 0.43	28.11 ± 3.14	17.41 ± 3.14
	1×	0.00 ± 0.04	0.00 ± 0.04	2.97 ± 0.52	0.78 ± 0.52	0.02 ± 0.25	0.28 ± 0.25	9.15 ± 1.34	3.54 ± 1.34	2.72 ± 0.56	0.94 ± 0.56	40.18 ± 3.78	23.88 ± 3.78
	2×	0.03 ± 0.02	0.04 ± 0.02	0.94 ± 0.36	1.00 ± 0.36	1.39 ± 0.20	0.22 ± 0.20	6.22 ± 1.10	2.54 ± 1.10	2.12 ± 0.47	0.71 ± 0.47	34.75 ± 3.32	18.38 ± 3.32
	3×	0.04 ± 0.02	0.13 ± 0.02	1.85 ± 0.35	1.69 ± 0.35	0.28 ± 0.20	0.54 ± 0.20	7.59 ± 1.09	4.67 ± 1.09	0.96 ± 0.46	0.63 ± 0.46	26.67 ± 3.30	18.71 ± 3.30
	5×	0.10 ± 0.04	0.09 ± 0.04	2.65 ± 0.51	1.16 ± 0.51	0.40 ± 0.25	0.81 ± 0.25	6.17 ± 1.32	2.30 ± 1.32	0.73 ± 0.56	1.25 ± 0.56	22.30 ± 3.73	15.33 ± 3.73
	10×	0.06 ± 0.04	0.09 ± 0.04	1.79 ± 0.51	2.33 ± 0.51	0.30 ± 0.25	0.53 ± 0.25	6.05 ± 1.32	2.51 ± 1.32	0.42 ± 0.56	0.63 ± 0.56	26.15 ± 3.73	13.29 ± 3.73
6 oz/ac	0	0.02 ± 0.02	0.02 ± 0.02	4.09 ± 0.29	2.40 ± 0.29	0.32 ± 0.18	0.28 ± 0.18	3.02 ± 1.00	0.99 ± 1.00	0.38 ± 0.43	0.22 ± 0.43	29.74 ± 3.14	16.65 ± 3.14
	1×	0.00 ± 0.04	0.00 ± 0.04	0.07 ± 0.51	0.10 ± 0.51	0.41 ± 0.25	0.18 ± 0.25	6.46 ± 1.32	0.84 ± 1.32	1.46 ± 0.56	0.73 ± 0.56	40.63 ± 3.73	19.38 ± 3.73
	2×	0.04 ± 0.02	0.07 ± 0.02	0.91 ± 0.36	0.65 ± 0.36	0.29 ± 0.20	0.16 ± 0.20	4.79 ± 1.09	2.36 ± 1.09	0.94 ± 0.47	0.29 ± 0.47	33.09 ± 3.31	17.07 ± 3.31
	3×	0.07 ± 0.02	0.13 ± 0.02	1.57 ± 0.35	1.16 ± 0.35	0.35 ± 0.20	0.15 ± 0.20	5.19 ± 1.09	2.05 ± 1.09	1.14 ± 0.46	0.33 ± 0.46	28.20 ± 3.29	15.59 ± 3.29
	5×	0.09 ± 0.04	0.18 ± 0.04	1.50 ± 0.51	0.85 ± 0.51	0.18 ± 0.25	0.59 ± 0.25	8.23 ± 1.32	3.86 ± 1.32	0.52 ± 0.56	0.21 ± 0.56	23.97 ± 3.73	15.11 ± 3.73
	10×	0.10 ± 0.04	0.24 ± 0.04	1.69 ± 0.51	1.03 ± 0.51	0.49 ± 0.25	0.63 ± 0.25	6.25 ± 1.32	0.73 ± 1.32	1.25 ± 0.56	1.04 ± 0.56	27.45 ± 3.73	12.31 ± 3.73
8 oz/ac	0	0.04 ± 0.02	0.02 ± 0.02	2.56 ± 0.28	2.03 ± 0.28	0.44 ± 0.18	0.39 ± 0.18	2.16 ± 1.00	0.83 ± 1.00	0.19 ± 0.43	0.15 ± 0.43	32.77 ± 3.14	16.97 ± 3.14
	1×	0.00 ± 0.04	0.00 ± 0.04	0.22 ± 0.51	2.68 ± 0.51	0.27 ± 0.25	0.03 ± 0.25	2.61 ± 1.32	0.52 ± 1.32	0.64 ± 0.56	0.00 ± 0.56	36.88 ± 3.73	22.60 ± 3.73
	2×	0.03 ± 0.02	0.05 ± 0.02	0.77 ± 0.35	1.02 ± 0.35	0.14 ± 0.20	0.30 ± 0.20	3.46 ± 1.09	0.79 ± 1.09	1.25 ± 0.46	0.29 ± 0.46	35.16 ± 3.30	18.09 ± 3.30
	3×	0.19 ± 0.02	0.09 ± 0.02	2.12 ± 0.35	1.03 ± 0.35	0.19 ± 0.20	0.21 ± 0.20	3.73 ± 1.09	2.09 ± 1.09	0.38 ± 0.46	0.75 ± 0.46	28.88 ± 3.30	16.45 ± 3.30
	5×	0.10 ± 0.04	0.10 ± 0.04	2.29 ± 0.51	0.85 ± 0.51	0.31 ± 0.25	0.27 ± 0.25	7.50 ± 1.32	1.67 ± 1.32	0.00 ± 0.56	0.00 ± 0.56	28.44 ± 3.73	15.48 ± 3.73
	10×	0.02 ± 0.04	0.20 ± 0.04	2.09 ± 0.51	0.86 ± 0.51	0.44 ± 0.24	0.61 ± 0.24	3.34 ± 1.32	1.67 ± 1.32	0.73 ± 0.56	0.00 ± 0.56	19.64 ± 3.73	15.16 ± 3.73

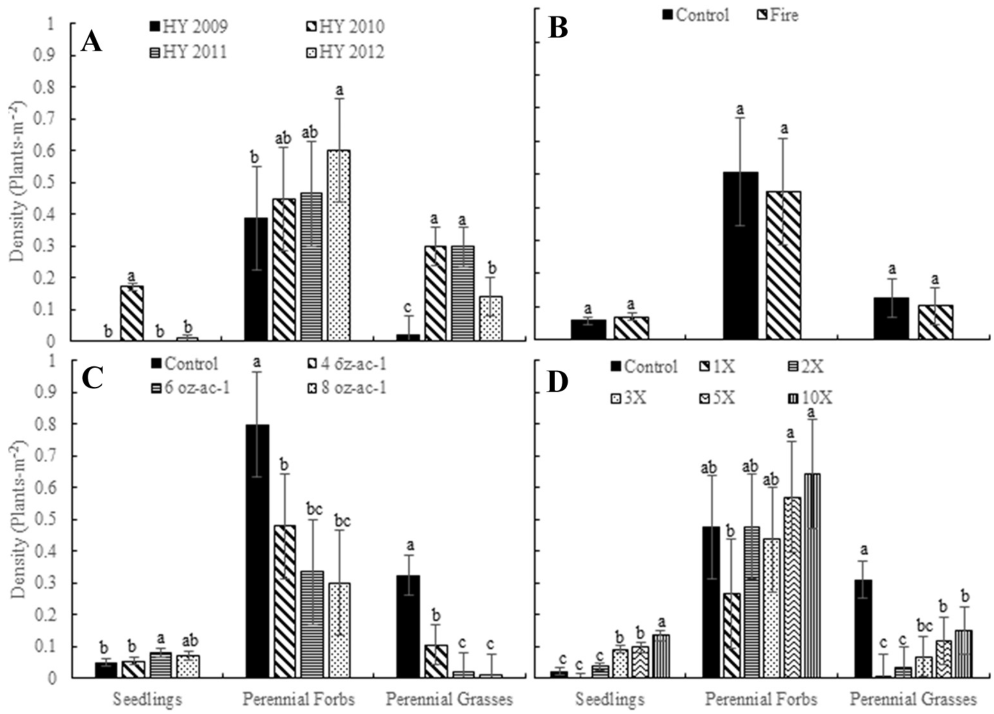


Figure 5. Plant functional group density in response to differing years and treatments. **A,** Differing years. **B,** Response to fire. **C,** Differences in imazapic herbicide rates. **D**, Differences in seeding rates. Different letters above bars represent differences within that plant functional group (i.e., seedlings, forbs, or perennial grasses). Specific F ratios and *P* values for each individual effect are identified in Table 2.

higher seeding rates may instead be because of increased competition for available soil resources (Jones et al., 2015), especially when fire and herbicides are first applied to reduce annual grass seed banks.

In support of our third hypothesis, we found that seeded species had higher density where fire and herbicides were combined and at the three highest seeding rates (see Table 4). Burning before applying imazapic has been shown to be an effective management treatment for reducing annual grass interference with seeded species establishment (Davies and Sheley, 2011), especially when seeding introduced species (Davies et al., 2015). However, when fire was not applied, increasing the seeding rate only produced more seeded species cover when herbicides were not applied and at the highest seeding rates (see Table 4). Many soil-active herbicides, like imazapic, can have nontarget effects on seeded species, especially in sagebrush steppe soils and when seeding occurs within short time frames of herbicide application (Hirsch et al., 2012). It may be possible that when herbicides were applied without fire, instead of binding with the litter (Monaco et al., 2005), the applied herbicides directly targeted seeded species.

Collecting seedling recruitment data across multiple sites and seeding years is important to fully interpret the impacts of ecologically based management treatments (James et al., 2010). Unfortunately, many research studies only include 1 or 2 seeding yr that are monitored over short durations (≤ 5 yr), which is insufficient to adequately survey potential variability in seedbed microclimate at a given field site (Hardegree et al., 2012). While we were able to quantify how differing years affected seeded species in HY 2010 and HY 2012, no seeded species emerged during the HY 2009 growing season and we were unable to seed in autumn 2010 (i.e., HY 2011) because of early winter conditions. However, our finding that fire and herbicide treatments significantly reduced the cover annual grasses and density of annual and perennial forbs during HY 2009 and HY 2011 suggests that there may be opportunities to delay seeding until 1 yr after management treatment inputs. Weather variability significantly affects seedling establishment (Hardegree et al., 2016). In this study alone, we found that weather variation had as much or greater impacts on seedling recruitment compared with management treatment inputs. Thus, if weather forecasts predict poor winter and spring conditions, but time or funding limitations require management to be input during the current year, delaying seeding until the following spring or autumn could be a good option to increase seedling recruitment on degraded rangelands.

Conclusions

Successful native perennial grass seedling recruitment into annual grass — invaded sage-steppe ecosystems may be possible when using strategically planned process-based management tools like tilling, prescribed fire, herbicides, and modified seeding rates. Throughout this study, we found that modifying site and species availability through the combination of tilling, prescribed fire, and imazapic herbicide applications produced the lowest cover of annual grasses and existing resident species. Furthermore, increasing seeding to at least 5× the minimum recommended seeding rates yielded the highest seeded species cover. However, we also found that seeding yr and, specifically, low winter weather variability followed by high precipitation during the growing season yielded the highest seedling recruitment. These findings suggest that although modifying seeding practices can improve seeded species cover, seeding year weather variation will likely have the greatest impact on seeding success in most years.

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