

RESEARCH ARTICLE



Postfire restoration seeding success increases with early fall seeding and simulated precipitation in the Great Basin Desert of North America

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Climate forecasts and disturbance mapping increasingly inform strategies for ecological restoration practices. Our study objectives were to understand how a postfire rehabilitation seed mix responds to fire, seeding timing, and changes in fall precipitation timing due to climate change. We planted seeds commonly used in the Great Basin Desert of North America on soil cores in a randomized block design. We imposed two experimental treatments, experimental fire (burned seedbeds or unburned seedbeds) and timing of seeding with simulated precipitation (early September vs. mid-October) in a two-way factorial design. We measured seedling emergence (1 month posttreatment), plant density, biomass, and seed production. Early seeding and precipitation reduced seedling emergence over 2-fold but increased total plant density (3-fold), biomass (13-fold), and seed production (140-fold) compared to delayed seeding and precipitation applications. Antelope bitterbrush was the only species with a negative response to early seeding and precipitation, with a decrease in both density and biomass (over 2-fold) by the end of the study. Burned seedbeds overall had little effect on measured outcomes for the total plant community. Burned seedbeds decreased forb seedling emergence 2-fold and alfalfa and Lewis blue flax density almost 3-fold but increased overall forb seed production 7-fold while other species and functional groups had minimal responses. Earlier seeding and precipitation interacted with the effects of burned seedbeds to increase biomass of Wyoming big sagebrush and western yarrow. The positive response of species to earlier fall seeding and precipitation underscores the importance of adapting our restoration practices for changing climate conditions.

Key words: climate change, fire, forbs, Great Basin, seed mix, seedling emergence

Implications for Practice

- The positive effect of earlier seeding timing with simulated earlier rainfall on biomass and reproduction underscores the importance of utilizing projected changes in climate in developing restoration strategies in a changing world. Climate change may provide new opportunities for adaptive restoration management in terms of planting windows.
- Faster maturation of some native perennial grass species related to earlier planting dates could increase their competitive advantage against invasive annual grass species and should be emphasized in rehabilitation seeding.
- Burned seedbeds differentially affected individual species. Species-specific responses could be used to potentially restructure seed mix proportions to favor the species that responded well to the burn treatment for post-fire rehabilitation.

Introduction

Ecological restoration efforts focus on reestablishing ecosystem function and services following degradation, often related to human activities (Harris et al. 2006). Predisturbance or precolonization composition and structure of native plant communities

typically provide a reference for restoration or rehabilitation goals. However, historical references may become obsolete as climate change and novel disturbance regimes emerge (Turner 2010). Predicted changes in climate and altered disturbance regimes may shift abiotic threshold points beyond species' historic distribution ranges (Harris et al. 2006). Emerging practices are encouraging innovative approaches to restoration such as incorporating predicted future environmental conditions into historical data (Butterfield et al. 2017; Matzek et al. 2017). The Great Basin is an ecosystem undergoing dramatic changes in vegetation structure due to human activities

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including increased fire frequency and severity, non-native plant species invasion, land-use change, and climate change (Chambers & Pellant 2008; Snyder et al. 2019). Here, we explore how the timing of seeding in postfire environments and shifts in precipitation related to climate change may influence postfire rehabilitation success in the Great Basin Desert of North America.

Precipitation patterns strongly influence plant productivity in arid and semiarid regions (Huxman et al. 2004) including the Great Basin (Tang et al. 2015; Pilliod et al. 2017). The majority of precipitation in the Great Basin occurs during winter and early spring, which supports native foundational plant species such as sagebrush (*Artemisia tridentata* Nutt.) into the hot, dry summers by percolating into deeper soil profiles (Caldwell 1985; Smith et al. 1997). Climate change forecasts predict earlier fall precipitation in the Great Basin and more winter precipitation occurring as rain rather than snow (Abatzoglou & Kolden 2011; Easterling et al. 2017). Precipitation patterns in the Great Basin are trending toward increased extreme rain events and rain days during fall and winter, particularly in the eastern region (Gillies et al. 2012; Xue et al. 2017). Research suggests that earlier fall precipitation and more rain than snow tend to increase plant species invasion potential (e.g. Prevéy & Seastedt 2015; Horn et al. 2017; Pilliod et al. 2017; Gill et al. 2018; Bishop et al. 2020). Variability in climate increases the need to understand how seeding timing responds to projected increases in early fall precipitation and warmer temperatures. A better understanding of the responses of species included in stabilization and restoration seed mixes to fall application timing could increase restoration success as the growing season changes with time (Tang et al. 2015).

Changes in precipitation timing due to climate change are likely to affect plant species differently based on life-history strategies (Harris et al. 2006; Wilsey 2021). For example, grass and forb species exhibit rapid early growth, vegetative dormancy during stressful conditions, and variable seed dormancy (Kitchen 1994). In contrast, shrub species, such as sagebrush, are broadly characterized by slow germination rates linked to light requirements and cold stratification followed by relatively slow growth rates (Bonner & Karrfalt 2008). Research also shows that invasive annual grasses can take advantage of earlier fall precipitation timing in ways that reinforce invasion success (Horn et al. 2015; Horn et al. 2017; Bishop et al. 2020). This highlights the need to better define optimal planting windows for stabilization and restoration seed mixes in response to changing climates. Some studies have found higher success with seeded plant establishment when sowing based on life-cycle characteristics and life-history traits (Frischie & Rowe 2012). Additionally, modeling efforts and network infrastructures have been used to identify ideal planting windows and show promise in predicting plant growth responses to soil moisture and temperature conditions (Hardegree et al. 2017, 2018; Richardson et al. 2018; Havrilla et al. 2020). However, these models may be limited for continued application as they commonly use historic data to make conclusions and predictions. Successful restoration efforts, therefore, depend on identifying optimal seeding windows for establishment success based on changing climate conditions. Matching fall seeding dates to earlier precipitation timing has the potential to improve restoration outcomes

(e.g. Boyd & James 2013; Boyd & Lemos 2015; Bishop et al. 2020; Harvey et al. 2020). Unfortunately, there is limited understanding of how plant species used in restoration efforts respond to changing climate conditions and how modifying the timing of seeding may influence establishment success.

The wildfire season has lengthened, and fire frequency and severity have increased in recent decades in desert ecosystems of North America (Jolly et al. 2015; Abatzoglou & Williams 2016). This is largely related to the establishment and spread of invasive annual grasses such as cheatgrass (*Bromus tectorum* L.) that drive invasive grass-fire cycles (reviewed in Germino et al. 2016; Bradley et al. 2018; Fusco et al. 2019). The emergence of novel fire regimes highlights the need for perennial plant restoration because of their varying tolerances to changing postfire conditions (Germino et al. 2018; Shriver et al. 2019; St. Clair & Bishop 2019). Semiarid and arid native plant communities typically have long recovery times after fire (Belnap & Eldridge 2001; Chambers & Wisdom 2009; Condon et al. 2011). Fire also alters the physical and chemical properties of seedbed environments, including shifts in soil crust structure and function and soil resource availability that can affect seed germination and seedling establishment (Neary et al. 1999; Allen et al. 2011; Abella & Engel 2013; Aanderud et al. 2019). For example, soil mineral nitrogen is documented to have a sharp increase immediately following a wildfire in shrublands (Rau et al. 2007; Esque et al. 2010) from biomass combustion that can provide a nutrient pulse for newly emerging plants. One possible approach to increasing the success of native vegetation in postfire environments is to understand their responses to modified seedbed environments following a fire (McGill et al. 2006; Leger & Baughman 2015). Desirable traits for target species in restoration may therefore include early germination, rapid growth rate, high resource use efficiency, adaptability, and high propagule pressure to compete with invasive annual grasses that tend to dominate in postfire environments (Funk & Vitousek 2007; Blank & Morgan 2012; Uselman et al. 2015).

The objective of this study was to test the effects of burned soil environments and the timing of fall seeding and simulated precipitation on the establishment, growth, and reproductive success of a postfire rehabilitation seed mix. We tested the following hypotheses: (1) earlier seeding in the fall period and simulated rainfall will increase plant density and reproduction by triggering germination and growth during more mild abiotic conditions in the early fall; (2) the burn treatment will tend to have positive impacts on plant growth and reproduction by increasing soil resource availability; and (3) functional group differences among seed species will likely respond differently with grasses and forbs being more responsive to the burn treatment and earlier seeding and precipitation timing than shrub species due to their less stringent germination requirements and faster growth rates.

Methods

Experimental System

This study used soil cores collected from Rush Valley in Tooele County, UT, U.S.A. (40.051°N, 112.305°W, elevation 1,650 m

above sea level [asl]) on the eastern side of the Great Basin Desert ecoregion. There was no evidence of fires and/or grazing activity in the areas where soil cores were extracted as indicated by well-developed biological soil crusts, and no evidence of non-native plant invasion. The plant community consisted of mature Wyoming big sagebrush (*Artemisia tridentata* Nutt ssp. *wyomingensis* Beetle & Young) and the perennial grass bottlebrush squirrel-tail (*Elymus elymoides* [Raf.] Swezey). Rush Valley is a mid-low elevation sagebrush steppe ecosystem with silty, mixed mesic Haplic Natragrid Taylors Flat Loam (Soil Survey Staff 2015). We transplanted the soil cores to a common garden, outdoors at the Brigham Young University Life Sciences bare field plots with no surrounding vegetation (BYU, Provo, UT, U.S.A., 40.252°N, 111.649°W, elevation 1,450 m asl), 48 km east of Rush Valley. All experimental units were subject to natural weather conditions from early September 2016 until mid-June 2017, the study duration. Provo's mean annual temperature is 12.3°C with a July mean of 24.2°C and January mean of -1.1°C and mean annual precipitation of 411 mm. The mean temperature and precipitation for the duration of the experiment (September 2016–June 2017) were 10.7°C and 389 mm (not including simulated rainfall treatment).

Experimental Design

We extracted soil in 15 cm diameter and 40 cm deep polyvinyl chloride cylinders collected from intershrub spaces outside of plant canopies (hereafter referred to as “soil cores”). We wet the soil to prevent cracking and disruption of the soil crusts. Based on visual inspection, soil crusts remained intact. We secured a wire mesh screen to the bottom of each soil core to maintain soil structure and allow root penetration during the

experiment. We transplanted and buried the soil cores in the ground at BYU to provide native soil conditions from Rush Valley and daily access for simulated rainfall applications, with the top 1 cm above ground. To deter herbivory we installed a 2-m welded-wire fence around the garden with 30 cm below ground. We watered each core to saturation to germinate any seed bank 3 weeks before beginning the experiment. Very few seedlings emerged and those that did were carefully removed. This study was a 2 × 2 full-factorial block design replicated four times with burning and seeding/precipitation timing treatments randomly positioned within each block. The study included four treatment combinations: burned–early fall seeding and precipitation; burned–mid-fall seeding and precipitation; unburned–early fall seeding and precipitation; and unburned–mid-fall seeding and precipitation (Bishop et al. 2020).

We selected plant species for the seed mix based on a Bureau of Land Management rehabilitation mix widely used in the Great Basin for postdisturbance rehabilitation projects (Bureau of Land Management Salt Lake Field Office, UT, U.S.A.). The mix contained a variety of native and non-native species belonging to different functional groups: grasses, forbs, and shrub species, with different general life history characteristics (Table 1). The Great Basin Research Center, Utah Division of Wildlife Resources (Ephraim, UT, U.S.A.) provided the seeds and the Wyoming Seed Analysis Laboratory (Powell, WY, U.S.A.) verified seed viability. We cleaned seeds from all chaff and individual hand-selected filled (thereby assumed viable) seeds for this experiment. We calculated the seeding densities of selected species used for the experiment (Table 1) based on the densities used in the rehabilitation mix scaled to the surface area of the soil core. Seeding took place after the fire treatment to simulate a typical rehabilitation scenario for this system.

Table 1. List of the species and number of seeds per core used from the rehabilitation seed mix with both scientific and common names based on the USDA PLANTS database naming convention. Functional group totals and proportions are given for the beginning and end of the study. All species were planted in each core and received a randomly selected treatment: burned–early precipitation, burned–late precipitation, unburned–early precipitation, and unburned–late precipitation.

Species Name	Native Status	Seeds Per Core	Begin Prop	End Prop
Grasses		67	0.55	0.68
Anatone bluebunch wheatgrass	<i>Pseudoroegneria spicata</i> (Pursh) Á. Löve	Native	4	
Thickspike wheatgrass	<i>Elymus lanceolatus</i> (Scribn. & J.G. Sm.) Gould	Native	4	
Snake River wheatgrass	<i>Elymus wawawaiensis</i> J. Carlson & Barkworth	Native	5	
Sandberg bluegrass	<i>Poa secunda</i> J. Presl	Native	14	
Canby bluegrass	<i>Poa canbyi</i> (Scribn.) Howell	Native	13	
Crested wheatgrass	<i>Agropyron cristatum</i> (L.) Gaertn.	Non-native	7	
Siberian wheatgrass	<i>Agropyron fragile</i> (Roth) P. Candargy	Non-native	8	
Russian wildrye	<i>Psathyrostachys (Elymus) junceus</i> (Fisch.) Nevski	Non-native	12	
Forbs		25	0.2	0.27
Lewis blueflax	<i>Linum lewisii</i> Pursh	Native	6	
Western yarrow	<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC.	Native	13	
Alfalfa	<i>Medicago sativa</i> L.	Non-native	6	
Shrubs		30	0.25	0.05
Fourwing salt bush	<i>Atriplex canescens</i> (Pursh) Nutt.	Native	10	
Antelope bitterbrush	<i>Purshia tridentata</i> (Pursh) DC.	Native	10	
Wyoming big sagebrush	<i>Artemisia tridentata</i> Nutt. ssp. <i>wyomingensis</i> Beetle & Young	Native	10	

Burn Treatment

For the burn treatment, we aimed to simulate a postfire environment commonly found in the Great Basin that has been invaded by cheatgrass (*Bromus tectorum* L.). Cheatgrass has invaded large areas of the Great Basin contributing to the spread of fire, which has increased the need for postfire restoration and/or rehabilitation (reviewed in Germino et al. 2016). We collected cheatgrass straw from Rush Valley and sterilized it in an autoclave. We placed an aluminum cylinder containing 526 g/m² of sterilized cheatgrass straw on top of eight randomly assigned cores and ignited it with a lighter to create a low-severity burn treatment. Fuel loads were similar to nearby areas in Rush Valley estimated at 462 ± 20 g of cheatgrass biomass/m² (St. Clair et al. 2016). We left the remnant ash from the fully combusted straw on top of the soil surface resulting in an estimated 9.9 g of N/m² input (St. Clair et al. 2016).

Seeding Timing and Simulated Precipitation Treatment

We conducted seeding and simulated precipitation treatments together at two different time points: (1) early fall treatment and (2) late fall treatment. We scattered seeds evenly on the soil core surfaces following the burn treatments. To increase soil contact and reduce the potential for wind loss we lightly imprinted seeds by hand. Seed mixes were added to the cores on 6 September for the early fall treatment and on 12 October for the late fall treatment. Climate projections indicate a shift toward earlier and larger fall precipitation events in the Great Basin (Gonzalez et al. 2018; IPCC 2021) thus we applied the simulated precipitation in conjunction with the seeding treatments to evaluate how coordinating planting efforts with shifted precipitation would affect restoration outcomes. All cores were subject to natural weather conditions during the entire study period regardless of which seeding treatment they received. We watered cores with 1.5 mm of water once every morning and afternoon for a total of 3 mm water per day using a flattened colander to simulate raindrops (Fig. 1). This represents an approximately 30% increase in overall fall precipitation during the 2-week watering period (Alder et al. 2013; Gonzalez et al. 2018). Anecdotally, we did not notice hydrophobicity as we imposed watering treatments. We watered the early seeded cores between 6 and 19 September 2016, and the late seeded cores between 12 and 25 October 2016, starting the same day as planting. Two natural rain events occurred during the treatment period on 14 September (10 mm) and 24–25 October (7 mm); we did not water on those days. Only one natural rain event occurred outside the simulated precipitation treatment period on 23–24 September (9 mm). The total cumulative amount of water received by soil cores was an estimated 431 mm from 6 September 2016 until plant collection in mid-June 2017 (Fig. 1).

Plant Measurements

Plant measurements included seedling emergence counts, plant density, biomass of aboveground plant tissues, and total seed production per core. We counted seedling emergence 1 month

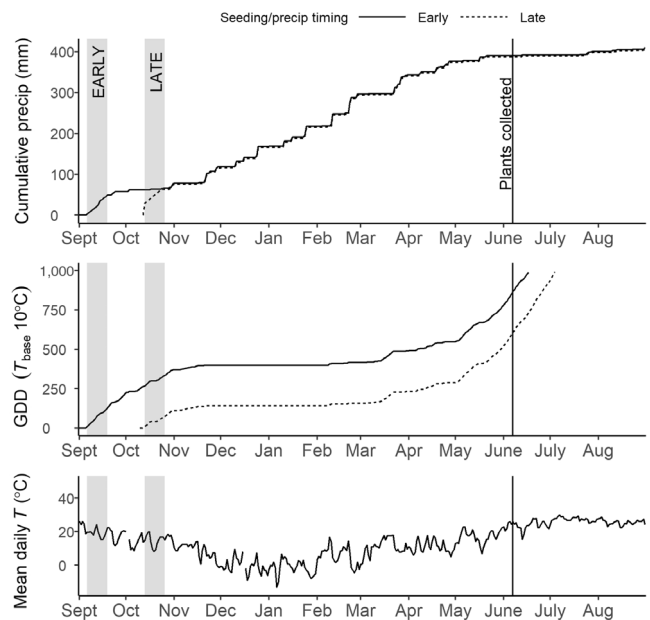


Figure 1. Timing and cumulative precipitation of the two seeding timing/precipitation treatments (top), accumulated growing degree days (GDD) with a base temperature of 10°C (middle), and daily mean temperature (°C) for the study period. The time spanning each seeding timing and simulated precipitation treatment (early and late) is denoted by the two vertical gray bars. Cumulative precipitation and GDD lines for each seeding timing/precipitation treatment (solid and dotted) are jittered to avoid overlap. The time of plant harvest is denoted by the vertical black line.

after seeding, 11–12 October for early seeded cores, and 14–15 November for late seeded cores. We counted the density of individual forb and shrub plants and each grass tiller (with and without seed) that grew by early June 2017. We destructively harvested all plants by removing all aboveground biomass and snipping at ground level. After all harvested plants were dried at room temperature and stored for 9 months, we then weighed all biomass on a mass balance. We counted filled seeds individually for all plants that produced seeds.

Statistical Analysis

We used linear mixed-effects analysis of variance to analyze treatment effects on the seedling emergence, density, biomass, and seed production of the total plant community, each functional group (grasses, forbs, and shrubs), and each identifiable species (except for grasses) using R package “nlme” (Pinheiro et al. 2022). The timing of seeding/precipitation and burn treatments were designated as fixed effects with experimental block as a random effect. To meet homogeneity of variance assumptions we used a varIdent covariance structure for the fixed effects when needed. We used zero-inflated generalized mixed-effects models for shrub species using R package “glmmTMB” (Brooks et al. 2017). We could not identify all grasses to species although some individuals were identifiable to genera such as native bluegrass (*Poa* spp.) or native wheatgrass (*Elymus* spp.); therefore, we present statistics for grasses

as a functional group. We provide mean values for identifiable *Poa* spp. and *Elymus* spp., though no analyses were conducted. We conducted all analyses in R version 3.5.2 (R Core Team) and made figures using R package “ggplot2” (Wickham 2016).

Results

Seeding and Simulated Precipitation Timing

Total plant community growth and reproduction had a strong positive response to the early fall seeding and precipitation treatment (Fig. 2). Initial seedling emergence in the early fall

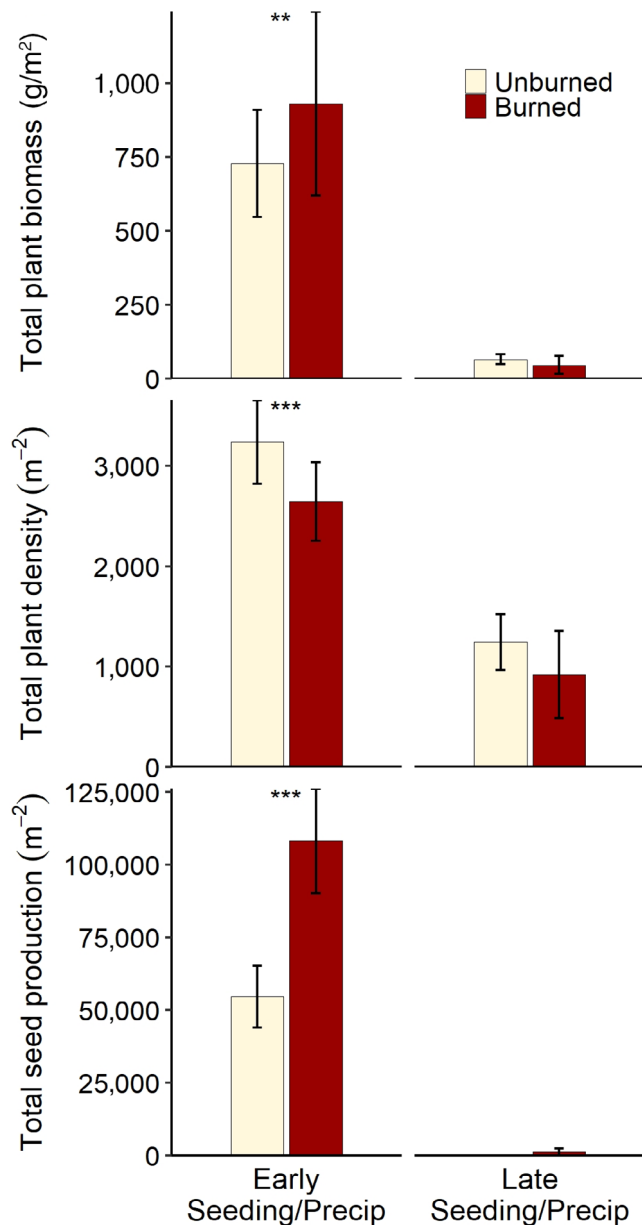


Figure 2. Growth and establishment of all plant species modified by seeding timing/precipitation and burn treatment combinations. Means ($\pm$ SE) presented. F -statistics and p -value significance are provided in Table S1.

treatment was less than half that of the late fall seeding with simulated precipitation treatment ($F = 17.5$, $p < 0.01$; Table S1; Fig. 3). However, by the end of the study, early fall treatment cores increased total plant community biomass nearly 15-fold ($F = 30.0$, $p < 0.01$), density nearly 3-fold ($F = 23.0$, $p < 0.01$), and seed production almost 140-fold ($F = 60.0$, $p < 0.01$) compared with the late fall treatment (Table S1; Fig. 2). Early fall treatment increased growth responses of nearly every plant species in the study.

Early fall seeding and simulated precipitation decreased initial forb seedling emergence over 2-fold ($F = 15.4$, $p < 0.01$) compared to the late fall treatment (Table S2; Fig. 3). Early fall treatment increased forb biomass nearly 17-fold ($F = 16.0$, $p < 0.01$), and density 2-fold ($F = 10.9$, $p < 0.01$) compared to late fall treatment cores by the end of the study (Table S2; Fig. 4). Even though harvesting occurred during an average fruiting window for these forb species, there was no forb seed production in late fall treatment cores, whereas average seed production was $22,827 \pm 1,226$ seeds/m² in early fall treatment cores at the time of harvest ($F = 4.1$, $p = 0.03$; Table S2; Fig. 4). All species of forbs increased in density, biomass, and seed production in response to early fall seeding and precipitation treatment compared with late fall treatment (Table S2; Fig. 4).

Early fall seeding and simulated precipitation treatment initially decreased the number of grass seedlings that emerged almost 2-fold ($F = 32.3$, $p < 0.01$) in late fall treatment cores (Table S3; Fig. 3). However, the early fall treatment significantly increased grass density 4-fold ($F = 13.0$, $p < 0.01$), biomass 7-fold ($F = 5.4$, $p = 0.03$), and seed production near 100-fold ($F = 22.0$, $p < 0.01$) compared to the late fall treatments (Table S3; Fig. 4) by the end of the study. Native bluegrass responded positively to early fall treatments where average biomass ($F = 18.7$, $p < 0.01$), density ($F = 7.7$, $p = 0.01$), and seed production ($F = 19.0$, $p < 0.01$) increased 6.5-, 17-, 32-, and 97-fold compared to late fall treatment cores (Table S3).

Early fall seeding and simulated precipitation treatment decreased the shrub seedling emergence 2-fold ($F = 5.4$, $p = 0.02$; Fig. 3) but increased shrub biomass 3-fold ($F = 3.2$, $p = 0.07$; Table S4; Fig. 4). However, each shrub species had differing responses to seed timing and simulated precipitation treatments (Table S4). Early seeding with simulated precipitation increased Wyoming big sagebrush average biomass 3-fold ($F = 3.4$, $p = 0.04$) and density 2.6-fold ($F = 6.5$, $p = 0.02$) (Table S4). In contrast, seed timing and simulated precipitation did not affect bitterbrush biomass ($F = 0.9$, $p = 0.4$) or density ($F = 0.1$, $p = 0.55$; Table S4).

Burned Seedbed Effects

Burned seedbeds did not significantly affect the biomass, density, or total seed production of the total plant community by the end of the study ($F = 2.0$, 1.7, and 1.3 respectively, $p > 0.1$; Table S1; Fig. 2) but decreased the mean emergence of seedlings 1 month postsowing ($F = 17.5$, $p < 0.01$; Table S1; Fig. 3). There was also a significant interaction between burn treatment and seeding/precipitation timing that

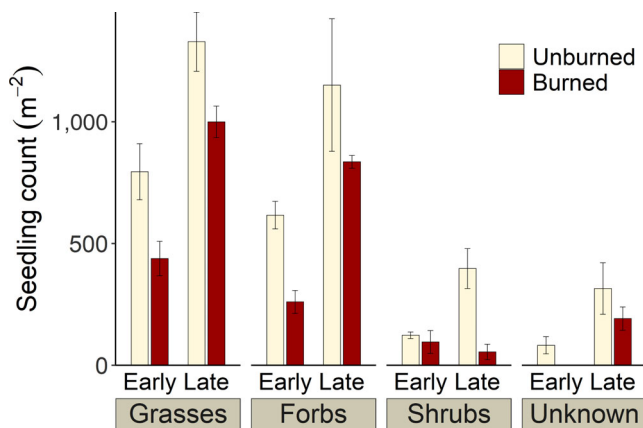


Figure 3. Seedling emergence counts of functional plant groups modified by seeding timing/precipitation and burn treatment combinations. Seedlings were counted 1 month postsowing and initiation of seeding timing/precipitation treatment. Means ($\pm$ SE) presented. F -statistics and p -value significance are provided in Table S1.

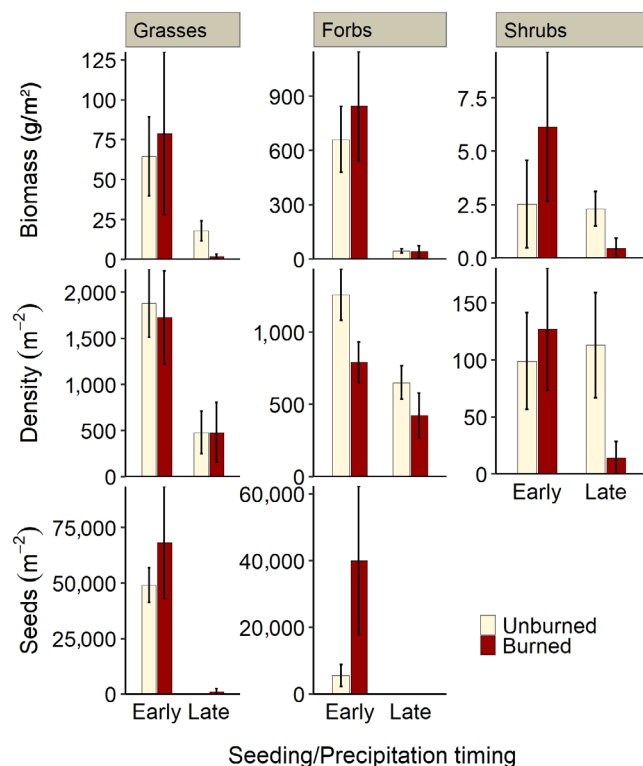


Figure 4. Growth, establishment, and seed production of functional plant groups modified by seeding timing/precipitation and burn treatment combinations. Means ($\pm$ SE) presented. F -statistics and p -value significance are provided in forbs—Table S2; grass—Table S3; and shrubs—Table S4).

led to a 2-fold increase in total seed production in burned–early seeding/precipitation cores compared to the other treatments ($F = 6.0$, $p = 0.03$; Table S1; Fig. 2).

Burn effects were highly variable depending on species, particularly among forbs. Burned seedbeds decreased forb seedling

emergence 1.6-fold ($F = 5.6$, $p = 0.02$; Table S2; Fig. 3), and total forb density 1.6-fold ($F = 5.5$, $p = 0.02$; Table S2; Fig. 4) compared with unburned cores. The burned seedbed environment had no significant effect on overall forb seed production ($F = 2.4$, $p = 0.14$; Table S2; Fig. 4) or forb biomass ($F = 0.3$, $p = 0.5$; Table S2; Fig. 4). Lewis blue flax and alfalfa density decreased in burned seedbeds. The biomass and seed production of western yarrow responded positively to burned seedbeds ($p < 0.05$; Table S2). Western yarrow biomass increased over 33-fold in response to the burn treatment ($F = 9.3$, $p = 0.01$; Table S2). Western yarrow seed production was highest in burned–early seeded/precipitation cores (6-fold greater) compared to unburned–early seeded/precipitation cores as indicated by the significant burn $\times$ seed timing/precipitation interaction (Table S2). No other significant treatment interactions were present for forb species (Table S2).

Grasses had minimal response to the burned seedbed treatment. The number of emerged grass seedlings was 1.5-fold fewer in burned seedbeds compared to unburned seedbeds ($F = 12.6$, $p < 0.01$; Table S3; Fig. 3). There was no significant response of biomass, density, or seed production among grass species to the burn treatment (all $p > 0.1$; Table S3; Fig. 4).

The burn treatment decreased the emergence of shrub seedlings 5-fold ($F = 13.6$, $p < 0.01$) compared to unburned cores (Table S4; Fig. 3). Shrub biomass and final density had no significant response to the burn treatment ($F = 0.1$, $p > 0.1$ and $F = 0.8$, $p > 0.1$, respectively; Table S4; Fig. 4). Also, no shrub species produced seed under any treatment during the experiment, as expected. Burned seedbeds decreased antelope bitterbrush density (6-fold) ($F = 4.0$, $p = 0.04$; Table S4) and biomass ($F = 2.1$, $p = 0.08$; Table S4). Burned seedbeds did not significantly affect Wyoming big sagebrush density ($F = 0.6$, $p > 0.1$; Table S4) but slightly increased biomass ($F = 1.9$, $p = 0.08$; Table S4). Four-wing saltbush failed to emerge in the soil cores (Table S4). Shrub biomass was greatest in burned–early seeded/precipitation cores, relative to the other three treatment conditions resulting in significant burn $\times$ seed timing/precipitation interactions ($F = 3.8$, $p = 0.06$; Table S4; Fig. 4). No other interactions between burned seedbed and seeding timing/precipitation treatments were statistically significant for shrub species.

Discussion

Our results underscore the importance of testing plant species responses to modifications in seeding timing in the context of future climate scenarios. Related to our first hypothesis, we found evidence that differences in the timing of fall seeding during periods of increased soil moisture strongly alter plant emergence, growth, and reproduction. From a management perspective, this could mean shifting priorities for seeding timing based on weather forecasting to identify windows of resource opportunity. We did not find support for our second hypothesis that the altered seedbed environment related to the burn treatment would have a widespread positive effect on plant growth. While our burned seedbed treatment did affect emergence for some species, effects tended to be muted or negative

and did not appear to be as dramatic as the impacts of more severe fires created by perennial woody vegetation (Booth et al. 2003; Germino et al. 2018; Bishop et al. 2020). There was mixed support for our third hypothesis, where the effects of seeding/precipitation timing and burning differed among species and functional groups.

Effects of Seed/Precipitation Timing on Emergence, Growth, and Seed Production

Precipitation and temperature patterns strongly influence seed germination timing (Kildisheva et al. 2019) and soil nutrient availability. Earlier seeding accompanied by precipitation increased growth responses of the plant communities in our study, likely because of readily available soil moisture during a period of warmer temperatures in the early fall that promotes earlier germination (Kildisheva et al. 2019). Longer periods of wet soil during the warmer temperatures of early fall can also increase nitrogen fixation in biological soil crusts increasing soil N availability (Belnap & Lange 2003; Pregitzer & King 2005). Increased soil N promotes plant growth and enhances seedling hardiness to frost events later in the fall period (Belnap 2002; Pregitzer & King 2005; Schlaepfer et al. 2014). Though we saw fewer emerging seedlings in the early seeding treatment (1 month postsowing), the increased robustness, possibly due to the aforementioned mechanisms, may have decreased winter seedling mortality. Also, with the extended growing period, more seedlings could have emerged after the 1-month mark in the earlier seeding treatment.

Growth rate and phenological traits can create variable germination and emergence timing that can affect competitive ability (Uselman et al. 2015; discussed in Buisson et al. 2017). Our results are supported by a growing body of evidence suggesting that the timing of seeding can be a factor in determining seedling establishment success (e.g. James et al. 2011, 2012; Richardson et al. 2018; Bennett et al. 2019). The growing season is changing for much of the Great Basin ecoregion (Tang et al. 2015) and changes in precipitation timing can affect sagebrush systems (Bates et al. 2006; Prev  y et al. 2010), with important implications for restoration practices. This is a relevant management consideration particularly as soil resource availability, which impacts plant establishment, is shifting with climate change (Jansson & Hofmockel 2020).

Effects of Burned Seedbeds on the Plant Community

We had expected burned seedbeds to provide a more hospitable microsite environment for seed germination and emergence (Allen et al. 2011; Bowman et al. 2011; Bishop et al. 2020) across all plant functional groups and species. However, forbs were the most responsive to the burned seedbed treatments. Alfalfa and Lewis blue flax responded similarly to Davies et al. (2014) where these species failed to establish in postfire environments. However, western yarrow established well in postfire environments as found in Sheley and Bates (2008). In burned landscapes in the western United States, species such as western yarrow and bottlebrush squirrel-tail grass (*Elymus*

spp.) are facultative early seral species and can increase the likelihood of native shrub species' eventual return by competing with invasive plants (Nelle et al. 2000; Booth et al. 2003). Based on our results, western yarrow and bottlebrush squirrel-tail grass may be key target species for rehabilitation of postfire landscapes where a fire is less severe. Fires are commonly associated with nutrient pulses and biological soil crust damage (Allen et al. 2011; Sankey et al. 2012) which may have also contributed to positive responses to the burned seedbeds by these early seral species (Deines et al. 2007; Boyd & Obradovich 2014; Ferrenberg et al. 2017; Germino et al. 2018; Bishop et al. 2020). This underscores the need for using a priority effects framework in management practices such as species selection and landscape treatments.

Restoration for Future Climates

Similar opportunities to match seeding timing with changing climate conditions are likely to exist in other arid ecosystems where changing landscape conditions, such as plant invasions and novel fire regimes, driven by changing climate, increasingly constrain the establishment of desirable species (i.e. Gelviz-Gelvez et al. 2015). For example, in the Mojave Desert, Custer et al. (2022) showed that intraspecific variation in growth response of two dominant perennial shrubs was largely determined by precipitation regimes and local adaptation. As shifts in precipitation timing can benefit earlier seeded native, non-native preferred, and non-native weedy species alike (Prev  y & Seastedt 2015; Horn et al. 2017; Pilliod et al. 2017; Bishop 2019; Bishop et al. 2020), competition for soil resources can become a bottleneck for native plant community success (Booth et al. 2003; Ulrich & Perkins 2014). We found earlier seeding with accompanying shifts in simulated precipitation may have led to more density-dependent competition resulting in fewer but larger individuals for some of the seeded species. Increased growth and reproductive response of native forbs and grass species in response to earlier seeding may be beneficial when attempting to preempt space and resources in invaded ecosystems (Werner et al. 2016; Young et al. 2017). More generally across ecosystems, new studies and reviews show that restoration outcomes in future climate scenarios and shifting disturbance and management regimes are poorly understood (Sch  dler et al. 2019; Lemmer et al. 2021). Therefore, as management efforts adapt to changing landscape conditions (i.e. fire regime changes) (Epanchin-Niell et al. 2009; Cochrane & Bowman 2021), those efforts should also take into consideration shifting precipitation patterns (Tietjen & Jeltsch 2007; Ram  n Vallejo et al. 2012; Korell et al. 2020).

Characterizing seed mix performance in response to changing climate conditions is critical to successful restoration and rehabilitation projects (Wilsey 2021). As our study shows, changing climate may influence vegetation responses, which highlights the imperative need for further studies that examine projected changes in precipitation and changing fire regimes across ecosystems (Johnson et al. 2015; Wilsey 2021). Longer field experiments are needed to extend these initial results (e.g. Ott et al. 2019) for restoration and rehabilitation species, though

the responses in our study have been documented for invasive *Bromus* species (Horn et al. 2015; Bishop et al. 2020). Seed germination and seedling emergence modeling efforts (Bradford 2002 and others) have increased the capacity to support integration of future climate scenarios with the timing of seeding events. It is important to note, however, that in some ecoregions with high interannual variability in precipitation, coupled with warming temperature (Hardegree et al. 2020) these practices should be approached with caution and field-tested to validate modeling efforts. Nevertheless, the increased availability of seed enhancement technology (e.g. priming, coatings;) could work synergistically with modified seeding times (Pedrini et al. 2020). Increased availability of user-friendly and flexible weather forecasting (USGCRP 2017, 2018) and visualization tools (i.e. Southwest FireCLIME n.d.; Alder et al. 2013), and increased network collaboration (i.e. RestoreNET) could help land managers make rapid decisions on when to seed a specific region.

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LITERATURE CITED

- Aanderud ZT, Bahr J, Robinson DM, Belnap J, Campbell TP, Gill RA, McMillian B, St. Clair SB (2019) The burning of biocrusts facilitates the emergence of a bare soil community of poorly-connected chemoheterotrophic bacteria with depressed ecosystem services. *Frontiers in Ecology and Evolution* 7:467. <https://doi.org/10.3389/fevo.2019.00467>
- Abatzoglou JT, Kolden CA (2011) Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. *Rangeland Ecology & Management* 64:471–478. <https://doi.org/10.2111/REM-D-09-00151.1>
- Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences* 113:11770–11775. <https://doi.org/10.1073/pnas.1607171113>
- Abella SR, Engel EC (2013) Influences of wildfires on organic carbon, total nitrogen, and other properties of desert soils. *Soil Science Society of America Journal* 77:1806–1817. <https://doi.org/10.2136/sssaj2012.0293>
- Alder J, Hostetler S, Williams D (2013) An interactive web application for visualizing climate data. *Eos, Transactions American Geophysical Union* 94:197–198. <https://doi.org/10.1002/2013EO220001>
- Allen EB, Steers RJ, Dickens SJ (2011) Impacts of fire and invasive species on desert soil ecology. *Rangeland Ecology & Management* 64:450–462. <https://doi.org/10.2111/REM-D-09-00159.1>
- Bates JD, Svejcar T, Miller RF, Angell RA (2006) The effects of precipitation timing on sagebrush steppe vegetation. *Journal of Arid Environments* 64:670–697. <https://doi.org/10.1016/j.jaridenv.2005.06.026>
- Belnap J (2002) Nitrogen fixation in biological soil crusts from southeast Utah, U.S.A. *Biology and Fertility of Soils* 35:128–135. <https://doi.org/10.1007/s00374-002-0452-x>
- Belnap J, Eldridge D (2001) Disturbance and recovery of biological soil crusts. Pages 363–383. In: Belnap J, Lange OL (eds) *Biological soil crusts: structure, function, and management*. Vol 150. Springer Berlin Heidelberg, Berlin, Heidelberg, Germany. https://doi.org/10.1007/978-3-642-56475-8_27
- Belnap J, Lange OL (eds) (2003) *Biological soil crusts: structure, function, and management*. Springer Berlin Heidelberg, Berlin, Heidelberg, Germany. <https://doi.org/10.1007/978-3-642-56475-8>
- Bennett J, Smart A, Perkins L (2019) Using phenological niche separation to improve management in a Northern Glaciated Plains grassland. *Restoration Ecology* 27:745–749. <https://doi.org/10.1111/rec.12932>
- Bishop TBB (2019) Of fire, mammals, and rain: mechanisms of plant invasions. Theses and dissertations. Brigham Young University
- Bishop TBB, Nusink BC, Lee Molinari R, Taylor JB, St. Clair SB (2020) Earlier fall precipitation and low severity fire impacts on cheatgrass and sagebrush establishment. *Ecosphere* 11:e03019. <https://doi.org/10.1002/ecs2.3019>
- Blank RR, Morgan T (2012) Suppression of *Bromus tectorum* L. by established perennial grasses: potential mechanisms—part one. *Applied and Environmental Soil Science* 2012:1–9. <https://doi.org/10.1155/2012/632172>
- Bonner FT, Karrfalt RP (eds) (2008) *The woody plant seed Manual*. Agriculture Handbook No. 727. U.S. Department of Agriculture, Forest Service, Washington, DC, 1223 Page
- Booth MS, Caldwell MM, Stark JM (2003) Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* 91:36–48. <https://doi.org/10.1046/j.1365-2745.2003.00739.x>
- Bowman DMJS, Balch J, Artaxo P, Bond WJ, Cochrane MA, D'Antonio CM, et al. (2011) The human dimension of fire regimes on Earth: the human dimension of fire regimes on Earth. *Journal of Biogeography* 38:2223–2236. <https://doi.org/10.1111/j.1365-2699.2011.02595.x>
- Boyd CS, James JJ (2013) Variation in timing of planting influences bluebunch wheatgrass demography in an arid system. *Rangeland Ecology & Management* 66:117–126. <https://doi.org/10.2111/REM-D-11-00217.1>
- Boyd CS, Lemos JA (2015) Evaluating winter/spring seeding of a native perennial bunchgrass in the sagebrush steppe. *Rangeland Ecology & Management* 68:494–500. <https://doi.org/10.1016/j.rama.2015.07.009>
- Boyd CS, Obradovich M (2014) Is pile seeding Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*) an effective alternative to broadcast seeding? *Rangeland Ecology & Management* 67:292–297. <https://doi.org/10.2111/REM-D-13-00107.1>
- Bradford KJ (2002) Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Science* 50:248–260. [https://doi.org/10.1614/0043-1745\(2002\)050\[0248:AOHTTQ\]2.0.CO;2](https://doi.org/10.1614/0043-1745(2002)050[0248:AOHTTQ]2.0.CO;2)
- Bradley BA, Curtis CA, Fusco EJ, Abatzoglou JT, Balch JK, Dadashi S, Tuanmu M-N (2018) Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. *Biological Invasions* 20:1493–1506. <https://doi.org/10.1007/s10530-017-1641-8>
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9:378–400. <https://doi.org/10.32614/RJ-2017-066>
- Buisson E, Alvarado ST, Le Stradic S, Morello LPC (2017) Plant phenological research enhances ecological restoration. *Restoration Ecology* 25:164–171. <https://doi.org/10.1111/rec.12471>
- Butterfield BJ, Copeland SM, Munson SM, Roybal CM, Wood TE (2017) Prestoration: using species in restoration that will persist now and into the future: pre-storing for climate change. *Restoration Ecology* 25:S155–S163. <https://doi.org/10.1111/rec.12381>
- Caldwell M (1985) Cold desert. Pages 198–212. In: *Physiological ecology of North American plant communities*. Springer, Dordrecht, The Netherlands. https://doi.org/10.1007/978-94-009-4830-3_9

- Chambers JC, Pellant M (2008) Climate change impacts on northwestern and intermountain United States rangelands. *Rangelands* 30:29–33. [https://doi.org/10.2111/1551-501X\(2008\)30\[29:CCIONA\]2.0.CO;2](https://doi.org/10.2111/1551-501X(2008)30[29:CCIONA]2.0.CO;2)
- Chambers JC, Wisdom MJ (2009) Priority research and management issues for the imperiled Great Basin of the western United States. *Restoration Ecology* 17:707–714. <https://doi.org/10.1111/j.1526-100X.2009.00588.x>
- Cochrane MA, Bowman DMJS (2021) Manage fire regimes, not fires. *Nature Geoscience* 14:455–457. <https://doi.org/10.1038/s41561-021-00791-4>
- Condon L, Weisberg PJ, Chambers JC (2011) Abiotic and biotic influences on *Bromus tectorum* invasion and *Artemisia tridentata* recovery after fire. *International Journal of Wildland Fire* 20:597. <https://doi.org/10.1071/WF09082>
- Custer NA, Schwinning S, DeFalco LA, Esque TC (2022) Local climate adaptations in two ubiquitous Mojave Desert shrub species, *Ambrosia dumosa* and *Larrea tridentata*. *Journal of Ecology* 110:1072–1089. <https://doi.org/10.1111/1365-2745.13747>
- Davies KW, Bates JD, Madsen MD, Nafus AM (2014) Restoration of mountain big sagebrush steppe following prescribed burning to control western juniper. *Environmental Management* 53:1015–1022. <https://doi.org/10.1007/s00267-014-0255-5>
- Deines L, Rosentreter R, Eldridge DJ, Serpe MD (2007) Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. *Plant and Soil* 295:23–35. <https://doi.org/10.1007/s11104-007-9256-y>
- Easterling DR, Arnold JR, Knutson T, Kunkel KE, LeGrande AN, Leung LR, Vose RS, Waliser DE, Wehner MF (2017) Precipitation change in the United States. Pages 207–230. In: Wuebbles DJ, Fahey DW, Hibbard KA, Dokken DJ, Stewart BC, Maycock TK (eds) *Climate science special report: fourth national climate assessment. Vol I.* U.S. Global Change Research Program, Washington, DC, USA. <https://doi.org/10.7930/J0H993CC>
- Epanchin-Niell R, Englin J, Nalle D (2009) Investing in rangeland restoration in the Arid West, U.S.A.: countering the effects of an invasive weed on the long-term fire cycle. *Journal of Environmental Management* 91:370–379. <https://doi.org/10.1016/j.jenvman.2009.09.004>
- Esque TC, Kaye JP, Eckert SE, DeFalco LA, Tracy CR (2010) Short-term soil inorganic N pulse after experimental fire alters invasive and native annual plant production in a Mojave Desert shrubland. *Oecologia* 164:253–263. <https://doi.org/10.1007/s00442-010-1617-1>
- Ferrenberg S, Tucker CL, Reed SC (2017) Biological soil crusts: diminutive communities of potential global importance. *Frontiers in Ecology and the Environment* 15:160–167. <https://doi.org/10.1002/fee.1469>
- Frischie SL, Rowe HI (2012) Replicating life cycle of early-maturing species in the timing of restoration seeding improves establishment and community diversity. *Restoration Ecology* 20:188–193. <https://doi.org/10.1111/j.1526-100X.2010.00770.x>
- Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079–1081. <https://doi.org/10.1038/nature05719>
- Fusco EJ, Finn JT, Balch JK, Nagy RC, Bradley BA (2019) Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proceedings of the National Academy of Sciences* 116:23594–23599. <https://doi.org/10.1073/pnas.1908253116>
- Gelviz-Gelvez SM, Pavón NP, Illoldi-Rangel P, Ballesteros-Barrera C (2015) Ecological niche modeling under climate change to select shrubs for ecological restoration in Central Mexico. *Ecological Engineering* 74:302–309. <https://doi.org/10.1016/j.ecoleng.2014.09.082>
- Germino MJ, Chambers JC, Brown CS (eds) (2016) *Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications.* Springer International Publishing, Cham, Switzerland. <https://doi.org/10.1007/978-3-319-24930-8>
- Germino MJ, Barnard DM, Davidson BE, Arkle RS, Pilliod DS, Fisk MR, Applestein C (2018) Thresholds and hotspots for shrub restoration following a heterogeneous megafire. *Landscape Ecology* 33:1177–1194. <https://doi.org/10.1007/s10980-018-0662-8>
- Gill RA, O'Connor RC, Rhodes A, Bishop TBB, Laughlin DC, St. Clair SB (2018) Niche opportunities for invasive annual plants in dryland ecosystems are controlled by disturbance, trophic interactions, and rainfall. *Oecologia* 187:755–765. <https://doi.org/10.1007/s00442-018-4137-z>
- Gillies RR, Wang SY, Booth MR (2012) Observational and synoptic analyses of the winter precipitation regime change over Utah. *Journal of Climate* 25:4679–4698. <https://doi.org/10.1175/JCLI-D-11-00084.1>
- Gonzalez P, Garfin GM, Breshears DD, Brooks KM, Brown HE, Elias EH, et al. (2018) Southwest. Pages 1101–1184. In: Reidmiller DR, Avery CW, Easterling DR, Kunkel KE, Lewis KLM, Maycock TK, Stewart BC (eds) *Impacts, risks, and adaptation in the United States: fourth national climate assessment. Vol II.* U.S. Global Change Research Program, Washington, DC, USA. <https://doi.org/10.7930/NCA4.2018.CH25>
- Hardegree SP, Moffet CA, Walters CT, Sheley RL, Flerchinger GN (2017) Hydrothermal germination models: improving experimental efficiency by limiting data collection to the relevant hydrothermal range. *Crop Science* 57:2753–2760. <https://doi.org/10.2135/cropsci2017.02.0133>
- Hardegree SP, Roundy BA, Walters CT, Reeves PA, Richards CM, Moffet CA, Sheley RL, Flerchinger GN (2018) Hydrothermal germination models: assessment of the wet-thermal approximation of potential field response. *Crop Science* 58:2042–2049. <https://doi.org/10.2135/cropsci2017.11.0666>
- Hardegree SP, Sheley RL, James JJ, Reeves PA, Richards CM, Walters CT, Boyd CS, Moffet CA, Flerchinger GN (2020) Germination syndromes and their relevance to rangeland seeding strategies in the intermountain western United States. *Rangeland Ecology & Management* 73:334–341. <https://doi.org/10.1016/j.rama.2019.11.004>
- Harris JA, Hobbs RJ, Higgs E, Aronson J (2006) Ecological restoration and global climate change. *Restoration Ecology* 14:170–176. <https://doi.org/10.1111/j.1526-100X.2006.00136.x>
- Harvey AJ, Simanonok SC, Rew LJ, Prather TS, Mangold JM (2020) Effect of *Pseudoroegneria spicata* (bluebunch wheatgrass) seeding date on establishment and resistance to invasion by *Bromus tectorum* (cheatgrass). *Ecological Restoration* 38:145–152. <https://doi.org/10.3368/er.38.3.145>
- Havrilla CA, Munson SM, McCormick ML, Laushman KM, Balazs KR, Butterfield BJ (2020) RestoreNet: an emerging restoration network reveals controls on seeding success across dryland ecosystems. *Journal of Applied Ecology* 57:2191–2202. <https://doi.org/10.1111/1365-2664.13715>
- Horn KJ, Nettles R, St. Clair SB (2015) Germination response to temperature and moisture to predict distributions of the invasive grass red brome and wild-fire. *Biological Invasions* 17:1849–1857. <https://doi.org/10.1007/s10530-015-0841-3>
- Horn KJ, Bishop TBB, St. Clair SB (2017) Precipitation timing and soil heterogeneity regulate the growth and seed production of the invasive grass red brome. *Biological Invasions* 19:1339–1350. <https://doi.org/10.1007/s10530-016-1348-2>
- Huxman TE, Snyder KA, Tissue D, Leffler AJ, Ogle K, Pockman WT, Sandquist DR, Potts DL, Schwinning S (2004) Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141:254–268. <https://doi.org/10.1007/s00442-004-1682-4>
- IPCC (2021) *Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on Climate Change.* In: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI, Huang M, Leitzell K, Lonnoy E, Matthews JBR, Maycock TK, Waterfield T, Yelekçi O, Yu R, Zhou B (eds) Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, In press. <https://doi.org/10.1017/9781009157896>
- James JJ, Svejcar TJ, Rinella MJ (2011) Demographic processes limiting seedling recruitment in arid grassland restoration: seedling recruitment and aridland restoration. *Journal of Applied Ecology* 48:961–969. <https://doi.org/10.1111/j.1365-2664.2011.02009.x>
- James JJ, Rinella MJ, Svejcar T (2012) Grass seedling demography and sagebrush steppe restoration. *Rangeland Ecology & Management* 65:409–417. <https://doi.org/10.2111/REM-D-11-00138.1>

- Jansson JK, Hofmockel KS (2020) Soil microbiomes and climate change. *Nature Reviews Microbiology* 18:35–46. <https://doi.org/10.1038/s41579-019-0265-7>
- Johnson LC, Olsen JT, Tetreault H, DeLaCruz A, Bryant J, Morgan TJ, Knapp M, Bello NM, Baer SG, Maricle BR (2015) Intraspecific variation of a dominant grass and local adaptation in reciprocal garden communities along a US Great Plains' precipitation gradient: implications for grassland restoration with climate change. *Evolutionary Applications* 8:705–723. <https://doi.org/10.1111/eva.12281>
- Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications* 6:7537. <https://doi.org/10.1038/ncomms8537>
- Kildisheva OA, Erickson TE, Madsen MD, Dixon KW, Merritt DJ (2019) Seed germination and dormancy traits of forbs and shrubs important for restoration of North American dryland ecosystems. *Plant Biology* 21:458–469. <https://doi.org/10.1111/plb.12892>
- Kitchen SG (1994) Perennial forb life-history strategies on semiarid rangelands: implications for revegetation. Pages 342–346. In: Monsen SB, Kitchen SG (compilers) *Proceedings: ecology and management of annual rangelands*. Gen. Tech. Rep. INT-313. US Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah
- Korell L, Auge H, Chase JM, Harpole S, Knight TM (2020) We need more realistic climate change experiments for understanding ecosystems of the future. *Global Change Biology* 26:325–327. <https://doi.org/10.1111/gcb.14797>
- Leger EA, Baughman OW (2015) What seeds to plant in the Great Basin? Comparing traits prioritized in native plant cultivars and releases with those that promote survival in the field. *Natural Areas Journal* 35:54–68. <https://doi.org/10.3375/043.035.0108>
- Lemmer J, Andrzejak M, Compagnoni A, Knight TM, Korell L (2021) Climate change and grassland management interactively influence the population dynamics of *Bromus erectus* (Poaceae). *Basic and Applied Ecology* 56: 226–238. <https://doi.org/10.1016/j.baaec.2021.06.012>
- Matzek V, Gornish ES, Hulvey KB (2017) Emerging approaches to successful ecological restoration: five imperatives to guide innovation: five imperatives for innovative approaches. *Restoration Ecology* 25:S110–S113. <https://doi.org/10.1111/rec.12630>
- McGill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21:178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Neary DG, Klopatek CC, DeBano LF, Ffolliott PF (1999) Fire effects on below-ground sustainability: a review and synthesis. *Forest Ecology and Management* 122:51–71. [https://doi.org/10.1016/S0378-1127\(99\)00032-8](https://doi.org/10.1016/S0378-1127(99)00032-8)
- Nelle PJ, Reese KP, Connelly JW (2000) Long-term effects of fire on sage grouse habitat. *Journal of Range Management* 53:586. <https://doi.org/10.2307/4003151>
- Ott JE, Kilkenny FF, Summers DD, Thompson TW (2019) Long-term vegetation recovery and invasive annual suppression in native and introduced postfire seeding treatments. *Rangeland Ecology & Management* 72:640–653. <https://doi.org/10.1016/j.rama.2019.02.001>
- Pedriani S, Balestrazzi A, Madsen MD, Bhalsing K, Hardegree SP, Dixon KW, Kildisheva OA (2020) Seed enhancement: getting seeds restoration-ready. *Restoration Ecology* 28:S266–S275. <https://doi.org/10.1111/rec.13184>
- Pilliod DS, Welty JL, Arkle RS (2017) Refining the cheatgrass–fire cycle in the Great Basin: precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7:8126–8151. <https://doi.org/10.1002/ece3.3414>
- Pinheiro J, Bates D, R Core Team (2022) nlme: linear and nonlinear mixed effects models. R package version 3.1-158. <https://CRAN.R-project.org/package=nlme>
- Pregitzer KS, King JS (2005) Effects of soil temperature on nutrient uptake. Pages 277–310. In: BassiriRad H (ed) *Nutrient acquisition by plants: an ecological perspective*. Ecological Studies Springer, Berlin, Heidelberg, Germany. https://doi.org/10.1007/3-540-27675-0_10
- Prevéy JS, Seastedt TR (2015) Effects of precipitation change and neighboring plants on population dynamics of *Bromus tectorum*. *Oecologia* 179: 765–775. <https://doi.org/10.1007/s00442-015-3398-z>
- Prevéy JS, Germino MJ, Huntly NJ, Inouye RS (2010) Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. *Plant Ecology* 207:39–51. <https://doi.org/10.1007/s11258-009-9652-x>
- Ramón Vallejo V, Smanis A, Chirino E, Fuentes D, Valdecantos A, Vilagrosa A (2012) Perspectives in dryland restoration: approaches for climate change adaptation. *New Forests* 43:561–579. <https://doi.org/10.1007/s11056-012-9325-9>
- Rau BM, Blank RR, Chambers JC, Johnson DW (2007) Prescribed fire in a Great Basin sagebrush ecosystem: dynamics of soil extractable nitrogen and phosphorus. *Journal of Arid Environments* 71:362–375. <https://doi.org/10.1016/j.jaridenv.2007.05.006>
- Richardson WC, Whitaker DR, Sant KP, Barney NS, Call RS, Roundy BA, Aanderud ZT, Madsen MD (2018) Use of auto-germ to model germination timing in the sagebrush-steppe. *Ecology and Evolution* 8:11533–11542. <https://doi.org/10.1002/ece3.4591>
- Sankey JB, Germino MJ, Sankey TT, Hoover AN (2012) Fire effects on the spatial patterning of soil properties in sagebrush steppe, U.S.A.: a meta-analysis. *International Journal of Wildland Fire* 21:545. <https://doi.org/10.1071/WF11092>
- Schädler M, Buscot F, Klotz S, Reitz T, Durka W, Bumberger J, et al. (2019) Investigating the consequences of climate change under different land-use regimes: a novel experimental infrastructure. *Ecosphere* 10:e02635. <https://doi.org/10.1002/ecs2.2635>
- Schlaepfer DR, Lauenroth WK, Bradford JB (2014) Natural regeneration processes in big sagebrush (*Artemisia tridentata*). *Rangeland Ecology & Management* 67:344–357. <https://doi.org/10.2111/REM-D-13-00079.1>
- Sheley RL, Bates JD (2008) Restoring western juniper- (*Juniperus occidentalis*) infested rangeland after prescribed fire. *Weed Science* 56:469–476. <https://doi.org/10.1614/WS-07-131.1>
- Shriver RK, Andrews CM, Arkle RS, Barnard DM, Duniway MC, Germino MJ, Pilliod DS, Pyke DA, Welty JL, Bradford JB (2019) Transient population dynamics impede restoration and may promote ecosystem transformation after disturbance. *Ecology Letters* 22:1357–1366. <https://doi.org/10.1111/ele.13291>
- Smith SD, Monson RK, Anderson JE (1997) Case study: *Artemisia tridentata*. Pages 75–93. In: *Physiological ecology of North American desert plants*. Springer-Verlag, Berlin, Heidelberg, Germany, New York
- Snyder KA, Evers L, Chambers JC, Dunham J, Bradford JB, Loik ME (2019) Effects of changing climate on the hydrological cycle in cold desert ecosystems of the Great Basin and Columbia Plateau. *Rangeland Ecology & Management* 72:1–12. <https://doi.org/10.1016/j.rama.2018.07.007>
- Soil Survey Staff (2015) Natural resources conservation service, United States Department of Agriculture. Web Soil Survey. <http://websoilsurvey.sc.egov.usda.gov/> (accessed Sep 2015)
- Southwest FireCLIME (n.d.) Vulnerability assessment. <https://swfireclime.org/vulnerability-assessment/>
- St. Clair SB, Bishop TBB (2019) Loss of biotic resistance and high propagule pressure promote invasive grass-fire cycles. *Journal of Ecology* 107: 1995–2005. <https://doi.org/10.1111/1365-2745.13156>
- St. Clair SB, O'Connor R, Gill R, McMillan B (2016) Biotic resistance and disturbance: rodent consumers regulate post-fire plant invasions and increase plant community diversity. *Ecology* 97:1700–1711. <https://doi.org/10.1002/ecs.1391>
- Tang G, Arnone JA III, Verburg PSJ, Jasoni RL, Sun L (2015) Trends and climatic sensitivities of vegetation phenology in semiarid and arid ecosystems in the US Great Basin during 1982–2011. *Biogeosciences* 12:6985–6997. <https://doi.org/10.5194/bg-12-6985-2015>
- Tietjen B, Jeltsch F (2007) Semi-arid grazing systems and climate change: a survey of present modelling potential and future needs: grazing systems and climate change. *Journal of Applied Ecology* 44:425–434. <https://doi.org/10.1111/j.1365-2664.2007.01280.x>
- Turner MG (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849. <https://doi.org/10.1890/10-0097.1>
- Ulrich E, Perkins L (2014) *Bromus inermis* and *Elymus canadensis* but not *Poa pratensis* demonstrate strong competitive effects and all benefit from

- priority. *Plant Ecology* 215:1269–1275. <https://doi.org/10.1007/s11258-014-0385-0>
- Uselman SM, Snyder KA, Leger EA, Duke SE (2015) Emergence and early survival of early versus late seral species in Great Basin restoration in two different soil types. *Applied Vegetation Science* 18:624–636. <https://doi.org/10.1111/avsc.12175>
- USGCRP (2017) Climate science special report: fourth national climate assessment. In: Wuebbles DJ, Fahey DW, Hibbard KA, Dokken DJ, Stewart BC, Maycock TK (eds) Vol I. U.S. Global Change Research Program, Washington, DC, USA, 470 Page. <https://doi.org/10.7930/J0J964J6>
- USGCRP (2018) Impacts, risks, and adaptation in the United States: fourth national climate assessment. In: Reidmiller DR, Avery CW, Easterling DR, Kunkel KE, Lewis KLM, Maycock TK, Stewart BC (eds) Vol II. U.S. Global Change Research Program, Washington, DC, USA, 1515 Page. <https://doi.org/10.7930/NCA4.2018>
- Werner CM, Vaughn KJ, Stuble KL, Wolf K, Young TP (2016) Persistent asymmetrical priority effects in a California grassland restoration experiment. *Ecological Applications* 26:1624–1632. <https://doi.org/10.1890/15-1918.1>
- Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York. <https://ggplot2.tidyverse.org>
- Wilsey B (2021) Restoration in the face of changing climate: importance of persistence, priority effects, and species diversity. *Restoration Ecology* 29: e13132. <https://doi.org/10.1111/rec.13132>
- Xue T, Tang G, Sun L, Wu Y, Liu Y, Dou Y (2017) Long-term trends in precipitation and precipitation extremes and underlying mechanisms in the US Great Basin during 1951–2013. *Journal of Geophysical Research: Atmospheres* 122:6152–6169. <https://doi.org/10.1002/2017JD026682>
- Young TP, Stuble KL, Balachowski JA, Werner CM (2017) Using priority effects to manipulate competitive relationships in restoration. *Restoration Ecology* 25:S114–S123. <https://doi.org/10.1111/rec.12384>

Supporting Information

The following information may be found in the online version of this article:

Table S1. Statistical results of total plant growth linear mixed-effects models.

Table S2. Statistical results of forb plant growth linear mixed-effects models.

Table S3. Statistical results of plant growth linear mixed-effects models.

Table S4. Statistical results of shrub plant growth linear mixed-effects models.

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