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Furrows and, to a Lesser Extent, Seed Priming Improve Restoration Success in the Sagebrush Steppe☆

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ABSTRACT

Seeding of native perennial species commonly fails in the presence of invasive annual weeds. The ability of weeds to deplete soil moisture through early germination and rapid growth gives them a competitive advantage. A possible solution to help native species compete with weeds is to enhance their germination rate and growth. We primed seeds of bluebunch wheatgrass *(Pseudoroegneria spicata)* and Lewis flax *(Linum lewisii)* in a matrix of compost, clay, and biostimulants for 4–7 d. We used an extrusion technique to incorporate the seed and priming matrix into pellets for the priming duration that had the quickest germination. We evaluated primed seeds in pellets at two field sites against seeds in pellets that were not primed and seeds left untreated (control). Seed treatments were planted in shallow (1-cm) and deep (15-cm) furrows, in a complete factorial design, with the expectation that the deep furrow treatment would provide an enhanced microsite to improve plant growth. Results indicated that deep furrows were the strongest driver in enhancing seedling establishment, while priming showed a smaller contribution. In the first month after planting, a combination of priming and furrowing increased seedling emergence by 128% and 303%, for bluebunch wheatgrass and Lewis flax, respectively, compared with control seed planted in shallow furrows. The following year, primed bluebunch wheatgrass and Lewis flax seeds in deep furrows increased plant biomass by 158% and 110%, respectively, compared with control seed in shallow furrows. Overall, this study generally indicates that the rapid germination of primed seeds and the use of deep furrows may assist seedlings in establishing, which may allow them to better compete with invasive weeds.

Introduction

The degradation of ecosystems worldwide is a growing biological and economic issue (Merritt and Dixon 2011; James et al. 2013). It is estimated that globally, \$1.6 trillion yr^{-1} is spent to restore these degraded sites and that restoration costs are expected to increase (Merritt and Dixon 2011). For example, in the western United States, fires, overgrazing, drought, and other natural and anthropogenic disturbances have damaged rangelands in the sagebrush-steppe biome (Perrings and Walker 1997; James et al. 2013). These disturbances have allowed for invasive annual grass species to move into formerly native perennial grass and shrub areas (Dantonio and Vitousek 1992; Booth et al. 2003; Bradley et al. 2018). To assist in the recovery of disturbed sagebrush steppe sites that have decreased in native species abundance and diversity, land managers will commonly seek to restore these sites through direct seeding. Unfortunately, the success of these seeding efforts is highly variable due to high mortality during the early stages of plant development (Lysne and Pellant 2004; James et al. 2013; Germino et al. 2018; Shriver et al. 2018).

Seed enhancement technologies can potentially improve the likelihood of restoration success through the application of materials and treatments that enhance germination, emergence, and early seedling growth (Madsen et al. 2016). Invasive weed species capable of rapidly colonizing dryland systems could help guide the development of new seed enhancement technologies. Cheatgrass (*Bromus tectorum* L.) is a common invasive annual weed in the sagebrush-steppe biome. Its rapid seed germination is thought to give it an advantage over slower-germinating perennial species

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(Wilson et al. 1974; Roundy et al. 2007). Seed priming is commonly used on crops to accelerate and synchronize germination time (Paparella et al. 2015). Priming is done by hydrating a seed to initiate metabolic activity and progress toward germination, but the seed is dried before radicle emergence occurs (Paparella et al. 2015). Priming has the potential to improve plant establishment by providing native species with similar germination characteristics as invasive weed species, such as cheatgrass. Research has shown that priming can decrease germination time of cool-season grass species commonly seeded in the sagebrush steppe (Hardegree 1994, 1996; Hardegree and Van Vactor 2000; Hardegree et al. 2002). It is predicted that this earlier germination may give seedlings an advantage by exposing them to a longer period of available resources and protection from disease and predators (Mercer et al. 2011).

Solid-matrix priming is an approach that has been shown to increase germination timing in agriculture (Taylor et al. 1988; Pandita et al. 2010; Farooq et al. 2019) and native dryland seeds (Rogis et al. 2004; Madsen et al. 2018). Through this approach, seeds are mixed with a solid-matrix carrier that is moistened with water to achieve a desired water potential for priming. Madsen et al. (2018) demonstrated that seeds incorporated in a solid priming matrix could be extruded into pellets after priming was complete. Through this approach, the seed does not need to be extracted from the priming matrix material before planting and the priming matrix can aid in improving the microsite of the seed by increasing moisture and nutrient conditions.

In addition to promoting seed germination in optimal periods, direct seeding success rates are higher if the seed is deposited within a “safe-site,” which has increased shade (Eckert et al. 1986), higher humidity (Harper et al. 1965), elevated and prolonged moisture (Winkel and Roundy 1991), and more moderate temperatures (Winkel et al. 1991). The availability of natural safe sites is often low in degraded areas (Elmarsdottir et al. 2003). Traditional rangeland drills create safe sites for seeds, which enhances seeding success (Asher and Eckert 1973; Haferkamp et al. 1987; Ott et al. 2016). The drill creates a V-shaped furrow in which seed is deposited and lightly covered. Rangeland drill furrows are generally 3–6 cm deep, depending on the soil texture (Clary 1989). This depth provides the seed with moderate temperatures and typically higher and more consistent soil moisture for a greater period (Chambers 2000).

The objectives of this study were to 1) determine how germination timing is influenced by the priming duration within the matrix used to form extruded pellets; 2) compare seedling emergence timing and plant growth of untreated seed, pelleted seed, and primed and pelleted seed; and 3) evaluate how these different seed treatments perform within shallow and deep furrows. We hypothesized that 1) primed seeds would have faster seed germination rates, which would lead to greater seedling emergence and plant growth; 2) deep furrows would improve seedling growth and survival; and 3) the combination of primed seeds and deep furrows would be the highest-performing treatment.

Materials and Methods

A laboratory trial was initiated to determine the priming conditions that would allow for the quickest germination timing. Results from the laboratory trial were then used to treat and evaluate primed seeds in the field within deep and shallow furrows.

Laboratory trial

Laboratory research was performed at Brigham Young University on ‘Anatone’ bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve) and Lewis flax (*Linum lewisii* [Pursh]). Bluebunch wheatgrass is a palatable forage for a wide variety of wildlife and livestock and is considered a drought-tolerant species that is adapted to stabilize disturbed soils (USDA 2018). Lewis flax provides desirable forage for wildlife while also being of value for erosion control, fire suppressant in a greenstrip planting, and beautifying disturbed sites (USDA 2018).

Seeds were primed in a matrix consisting of 91 g of calcium bentonite powder (American Colloid Company, Hoffman Estates, IL), 288 g of ground compost, and 25 g of Azomite (Azomite Mineral Products, Inc., Nephi, UT) Table 1S. The mixture of the matrix material and seed was hydrated to a water potential of −1.5 MPa with a solution of 690 mL of water, 0.027 g of Captan fungicide (Southern Agricultural Insecticides, Inc., Palmetto, FL), and 0.107 g of ASET-4001 surfactant (Aquatrols Corporation of America, Paulsboro, NJ). Water potential was found by using a WP4C Dewpoint Potential Meter (METER Group, Pullman, WA) and adjusting the moisture content until the desired water potential was met. Priming was performed at 20°C in a Precision Plant Growth Chamber (Thermo Fischer Scientific, Waltham, MA) set to a 12-h light period in a 24-h cycle. Bluebunch wheatgrass and Lewis flax seeds were primed at five different daily intervals ranging from 1 to 5 and 3 to 7 d, respectively. The range of days seeds were primed was determined from preliminary trials indicating that germination occurred after 5 and 7 d for bluebunch wheatgrass and Lewis flax, respectively. After priming, seeds were sieved from the solid matrix and air-dried.

Seeds from the different priming durations and untreated control were placed separately in 9-cm diameter Petri dishes (25 seeds dish^{-1}) containing two layers of blue blotter paper moistened with water as needed throughout the study. Petri dishes were placed in the same growth chambers used for priming, which were set at 5°C, 10°C, 15°C, 20°C, and 25°C. Each temperature by species by priming time combination was replicated five times, and the replicates were arranged in blocks. Blocks were enclosed in plastic bags to prevent seeds from drying out. Germination was recorded every 1–3 d. Seeds were considered germinated once the radicle reached 2 mm in length.

Laboratory statistical analysis

From the germination data, the following indices were calculated: mean germination time (MGT), time to 50% germination (T_{50}), and final germination percentage in the program AutoGerm (Richardson et al. 2018). MGT was calculated by using the following equation:

$$\bar{t} = \frac{\sum_{i=1}^{k} n_i t_i}{\sum_{i=1}^{k} n_i}$$

where $\bar{t}$ = mean germination time, t_i = time from the start of the experiment to the i^{th} observation, n_i = number of seeds germinated in the i^{th} time, and k = last time of germination. Time to reach T_{50} was calculated as follows:

$$T = \left[\left(\frac{t_a - t_b}{n_a - n_b}\right)(N - n_b)\right] + t_b$$

where T = time (d) to subpopulation germination, t_a = incubation day when subpopulation germination was reached, t_b = incubation day before subpopulation germination was reached, n_a = number of germinated seeds on day that subpopulation germination was reached, n_b = number of germinated seeds on day before subpopulation germination was reached, and N = number of germinated seeds equal to 50% of the total population.

MGT, T_{50}, and final germination were analyzed using a standard least-squares analysis in JMP version 13 (SAS Institute Inc., Cary, NC). Temperature, species, and priming duration were considered fixed factors, and block was random in a full factorial analysis. MGT and T_{50} data underwent a log transformation to obtain a normal distribution, while final germination data did not require a transformation. For each of the indices measured at each of the five temperatures, we performed pairwise comparisons between treatments using the Tukey HSD pairwise comparison test. Differences were considered significant when $P < 0.05$. Mean values are reported with unique letters in the text and figures to denote significant differences.

Field trial

Field research was conducted at two degraded rangeland sites in Utah. The Lookout Pass site (40.139003, −112.507367) is located near the historic Pony Express Trail at 1 686 m of elevation, east of the Onaqui Mountains, approximately 8.4 km from Vernon, Utah. This site was seeded to "Hycrest" *Agropyron cristatum* (L.) Gaertn. (crested wheatgrass) in the fall of 1996, following the Aqueduct fire. Lookout Pass is a semidesert gravelly loam ecological site that receives an average of 287 mm of precipitation per year (websoilsurvey.nrcs.usda.gov). The Santaquin site (39.907287, −111.816306) is located at the southern end of Utah County at 1 562-m elevation, approximately 16 km south of Santaquin, Utah. The area is primarily dominated by bulbous bluegrass (*Poa bulbosa* L.), field bindweed (*Convolvulus arvensis* L.), jointed goatgrass (*Aegilops cylindrical* Host), and cheatgrass. The area is classified as a Mountain Gravelly Loam ecological site (https://wildlife.utah.gov/range-trend.html) that receives an average of 481 mm of precipitation per year (websoilsurvey.nrcs.usda.gov).

In preparation for seeding, both sites were sprayed in April of the previous year and 2 wk before planting, with 280 g ai ha^{-1} of glyphosate (Accord Concentrate, Dow AgroSciences, Indianapolis, IN). Plant material not killed by the herbicide was removed by hand on the day seeds were sown. Seeds were planted at Santaquin and Lookout Pass on 17 and 18 March, 2017, respectively. Both sites were fenced to keep livestock and wildlife (including rodents) out of the enclosure.

Field experimental design

The study was set up as a randomized block split-plot design with 10 blocks at each site. Furrow depth comprised the split-plot factor. The study incorporated a total of three seed treatments for bluebunch wheatgrass and Lewis flax, including primed seeds within a pellet (primed), pelleted seeds that were not primed (pelleted), and seeds where no treatment was applied (control). At both sites, the three seed treatments for each of the two species were sown in deep-wide U-shaped furrows (15 cm deep, 25 cm wide, and 1.5 m long) and shallow furrows (1 cm deep, 25 cm wide, 1.5 m long), for a total of 12 treatments. Each furrow contained ~ 125 pure live seeds. The furrows were formed by hand using a hoe. Excavated soil from the furrows was deposited along the outside edge of the furrow. Seeds were planted at the bottom of the furrows and covered with ~ 5 mm of soil.

The priming duration with the quickest germination timing from the laboratory trial was used to prime seeds for the field trial, which was 4 d and 7 d for bluebunch wheatgrass and Lewis flax, respectively. Once priming was completed, 18.7 g of Stockabsorb 660 (Evonik Stockhausen, Greensboro, NC) and 690 mL of liquid (same ingredients aforementioned) was applied to the matrix to assist flow through the 5-mm extruder. Pellets were then cut to a length of ~1.5 cm. Once pellets were formed, they were dried using a forced-air dryer at 43°C (Universal Coating Systems, Independence, OR). Pelleted seeds were created using the same methods used for the primed pellets; only the seed was not primed. For each of the pellet treatments, the number of seeds per gram of pellet material was calculated from seven replicate samples of approximately 3.15 g to estimate the weight of pellets needed to plant the targeted seeding rate.

Seed-bed soil moisture and temperature conditions were measured every hour, using TEROS 21 (MPS-6) dielectric water potential sensors (METER Group, Pullman, WA) that were randomly buried 2 cm below the surface with five replicate sensors each in deep and shallow furrows at each site. Long-term and monthly precipitation measurements during the study period were derived from models developed by PRISM's (Parameter-elevation Regressions on Independent Slopes Model) Oregon Climate Service (PRISM Climate Group 2018). Annual average precipitation and temperature were estimated from 1981 to 2010.

Seedlings were marked across the entire row every month with plastic toothpicks to track emergence and seedling survival from 20 April to 14 July and 11 April to 5 June at Lookout Pass and Santaquin, respectively. Total tillers and stems in a row were counted on 25 May during the second growing season at Lookout Pass. On 26 June, during the second growing season, the number of surviving plants was recorded and biomass was collected by clipping the entire row of established plants 2.5 cm from the soil surface. Clipped biomass was then dried in a plant drier at 60°C for 1 wk and weighed. Seedling density, tiller density, and biomass per unit area were calculated by dividing the value obtained from the seeded row by the product of the distance between the rows and the row length.

Field statistical analysis

Monthly average (±standard error) temperature and water potential values were calculated for each site. In JMP version 13 (SAS Institute Inc., Cary, NC), seedling density data were assessed using a repeated-measures mixed-model analysis. In the model, site, species, furrow depth, and treatment were considered fixed factors; the sampling period was designated as a repeated measure; and block was random. All fixed factors were included in a full factorial comparison. A log transformation was used on the data to meet the assumption of normality. All variables were included in the initial model as a full factorial; however, to simplify models, all insignificant four- and three-way interactions were removed from further models (Table 2S). We used a mixed-model analysis to analyze final plant density, tiller density, and biomass obtained from the second growing season. In the model, site, species, furrow depth, and treatment were considered fixed factors, and block was random. Mean values were separated when significant effects were found using the least square means differences Student's *t*-test. In the first year, mean estimates of plant density were analyzed separately by site and sampling period. Final plant density, tiller density, and biomass were analyzed by site. Second-year growing season metrics were not analyzed for the Santaquin site due to a grasshopper infestation removing all of the aboveground biomass. A significance level of $P < 0.1$ was used for all statistical field comparisons.

Results

Laboratory trial

In general, germination speed increased with the duration seeds were primed, and treatment response was the greatest at colder temperatures (Fig. 1). For example, at 5°C bluebunch wheatgrass primed for 5 d decreased T_{50} by 8.6 d and MGT by 9.7 d (see Fig. 1; Fig. S1, available online at …). Above 15°C, while significant differences were found, the decrease in germination timing was generally minimal. Final germination of bluebunch wheatgrass was not influenced by priming (Fig. S2, available online at …).

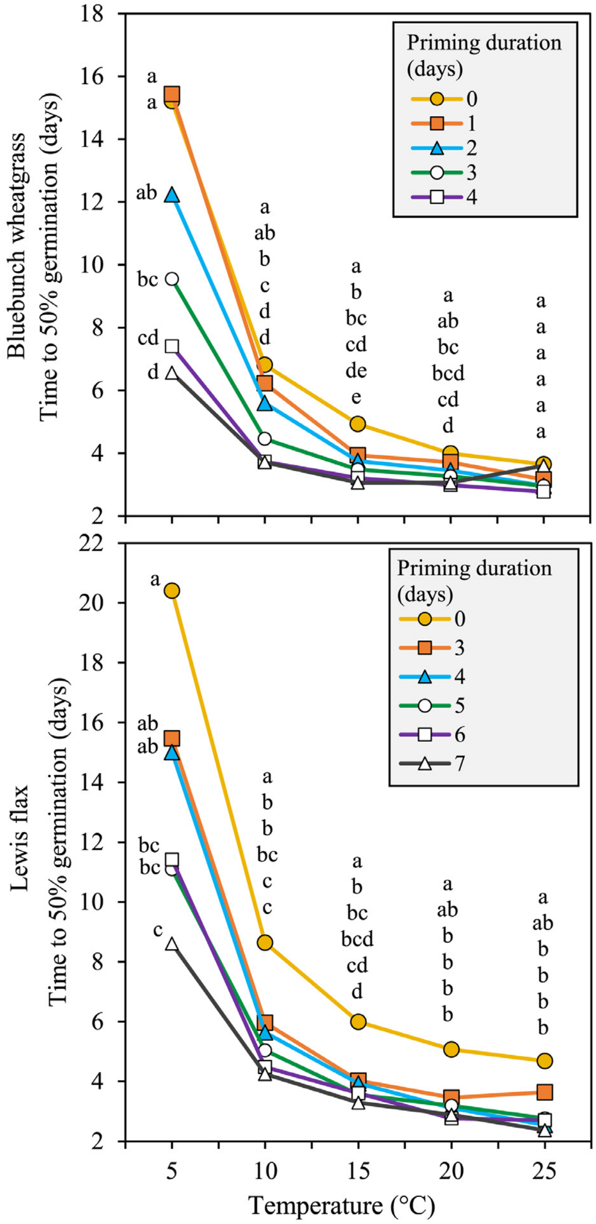

Fig. 1. Time to 50% germination of "Anatone" bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve) and Lewis flax (*Linum lewisii* [Pursh]) seed that was treated under varying priming durations and then incubated at constant temperatures ranging from 5°C to 25°C. Scale bars differ between species to emphasize differences among treatments. Unique letters denote significant differences ($P < 0.05$).

Lewis flax responded similarly to priming as bluebunch wheatgrass, with priming for 7 d exhibiting the quickest germination response. Seeds primed at 7 d showed a decrease in T_{50} at 5°C by 11.8 d (see Fig. 1) and a decrease in MGT by 10.9 d (see Fig. S1). Final germination was not influenced by priming except with a 7-d priming duration, where it decreased values by 15% at 5° C and 15°C; however, this priming treatment improved germination by 17% at 25°C (see Fig. S2).

Field trial

Annual precipitation was below the 30-yr average at Lookout Pass (286 mm) and Santaquin (470 mm). However, precipitation from January to April was above average (Fig. 2). In March 2017, when the plots were planted, there was 94% and 24% more precipitation than average at Lookout Pass and Santaquin, respectively. The annual temperature was consistent with the 30-yr average (see Fig. 2).

Daily fluctuations in soil temperature, measured in the bottom of the furrow, were typically more moderate in the deep furrows (furrow depth 15 cm below the soil surface) than in the shallow furrows (furrow depth 1 cm below the soil surface; Fig. 3). For example, in April, when most of the seedlings emerged from the soil (Fig. 4), the average daily maximum temperatures were 3.4°C and 3.5°C cooler in deep furrows, for Lookout Pass and Santaquin, respectively (see Fig. 3A). The average daily minimum temperatures were 0.8°C and 1.7°C warmer for the same field sites during this same period. These differences in temperatures within shallow and deep furrows continued to increase with time, especially during the hottest months of the year, July and August (see Fig. 3B).

Soil water potential, also measured in the bottom of the furrow, was typically higher in the deep furrows than in the shallow furrows (see Fig. 3). By April, differences between the furrow treatments became apparent (see Fig. 3A). Deep furrows maintained on average a water potential greater than −1.5 MPa through May, while shallow furrows were only above this level through March and April at Lookout Pass and Santaquin, respectively (see Fig. 3B).

The repeated measures mixed-model analysis indicated several three-way interactions (Table 2S). Two of the three-way interactions included site combined with species and month ($P < 0.01$) and species and treatment ($P = 0.04$). Another three-way interaction included species, furrow, and treatment ($P = 0.03$). Models were examined where sites and species were separated to understand these interactions better. At Lookout Pass, in the first month, primed seed of bluebunch wheatgrass and Lewis flax sowed in deep furrows improved emergence by 46% and 127%, respectively, compared with control seed sown in deep furrows (Fig. 4). The priming treatment effect was amplified when combined with deep furrows. For example, in the first month, primed seed of bluebunch wheatgrass and Lewis flax sown in deep furrows improved emergence by 128% and 303% compared with shallow furrows sown with control seed (see Fig. 4). At the end of the growing season, emergence from primed seed was similar to emergence from control seed in their respective furrow depths. However, primed and control seed of bluebunch wheatgrass in deep furrows had 113% and 105% more emergence than control seed in shallow furrows. Lewis flax demonstrated a similar response with primed and control seeds in deep furrows, increasing emergence by 184% and 112%, respectively, compared with control seeds in shallow furrows.

The following year, at Lookout Pass (433 d post planting), primed bluebunch wheatgrass and Lewis flax seed in deep furrows increased plant establishment by 64% and 100%, respectively, compared with control seed in shallow furrows (Fig. 5A). Primed bluebunch wheatgrass seed in deep furrows produced 158% more tillers, respectively, compared with control seed in shallow furrows (see Fig. 5B). Additionally, deep furrows resulted in a 195% and 124% biomass increase for primed and control bluebunch wheatgrass seed, respectively, compared with control seed in shallow furrows (see Fig. 5C). Primed and pelleted Lewis flax demonstrated a similar response by improving the number of stems by 56% and 68%, respectively, compared with control seed in shallow furrows. Also, primed and control Lewis flax seed planted in deep furrows exhibited a 110% and 100% increase in plant biomass than control seed in shallow furrows (see Fig. 5C).

Similar to treatments at Lookout pass, at Santaquin primed seed of bluebunch wheatgrass and Lewis flax in deep furrows improved emergence in the first month following seeding by 169% and 233%, respectively, compared with the control seed in shallow furrows (see Fig. 4). In May, 3 mo after planting, primed bluebunch wheatgrass seed in deep furrows had 33% higher emergence in com-

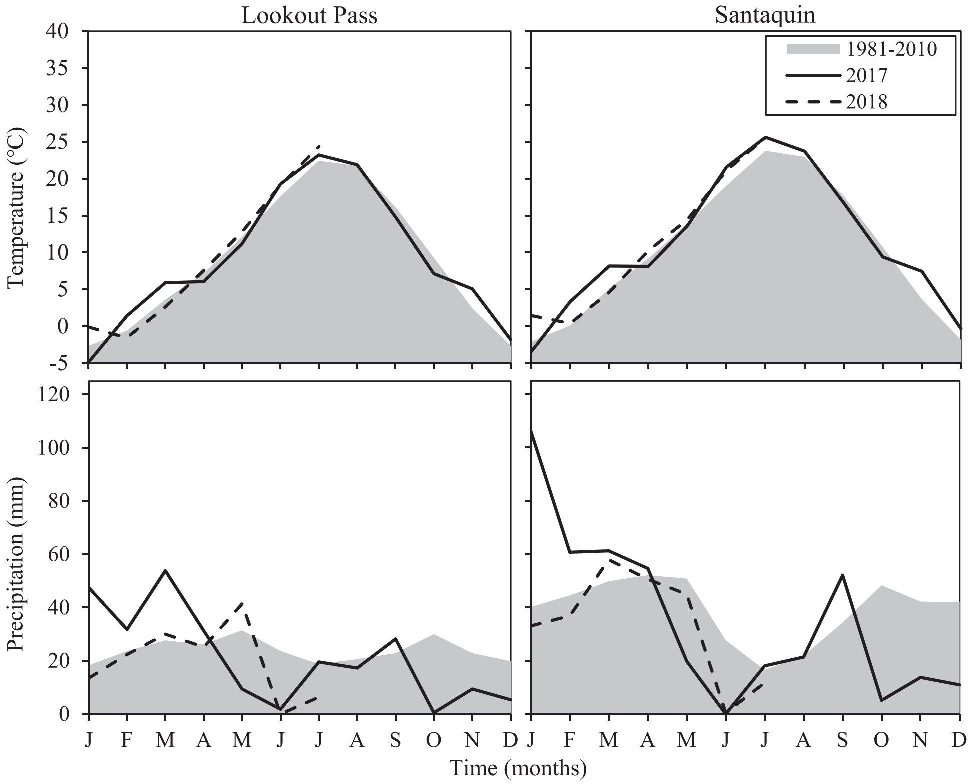

Fig. 2. A comparison of 2017–2018 monthly temperature and precipitation levels at Lookout Pass and Santaquin study sites against the 30-yr average (1981–2010).

parison with the control seed planted in shallow furrows, while primed seed of Lewis flax was similar to the control (see Fig. 4). We were not able to measure treatment responses in the second yr of the study for the Santaquin site due to a grasshopper invasion that removed all of the aboveground biomass in the study.

Discussion

Seedling survival is a major developmental bottleneck in the progression from seed to an established plant (Harper 1977; James et al. 2019). Leger et al. (2019) found that accelerated germination rates and fast-growing roots were general characteristics associated with plants that were more successful at establishing in the western United States sagebrush steppe. It is possible that priming and deep furrows may artificially provide plants with these benefits. Priming can stimulate early germination, while deep furrows offer a microsite that can substitute for fast-growing roots by giving the plant access to soil moisture reserves at deeper soil depths. Our results generally support our first hypothesis, where primed seeds would have faster seed germination rates, which in some instances lead to greater seedling emergence and plant growth. Our findings also generally support our second hypothesis that deep furrows would improve seedling emergence, growth, and plant survival. Overall, deep furrows alone appeared to have a greater effect on improving seeding success than priming. In addition, our results partially support our third hypothesis that the combination of primed seed and deep furrows would be the highest-performing treatment.

Accelerating germination and emergence through seed priming

This study demonstrated through laboratory trials and generally through field trials that primed seeds have the potential to influence rangeland restoration efforts, specifically for a spring planting (see Figs. 1 and 4). In the laboratory, priming accelerated seed germination for both species used in the trial with the greatest treatment response at a constant temperature of 5°C. Having a strong treatment response at cold temperatures is particularly advantageous as this is the soil condition most similar to when seeds would be germinating in the field, particularly in the cold desert regions of western North America. For example, James et al. (2019) estimated across 33 sites that the mean soil temperature during a 30-d period before seed germination ranged from −0.98°C to 6.8°C. Priming's ability to accelerate seed germination under cold temperatures (see Fig. 1) may be of particular value in years and sites when soil moisture and temperature are marginal or inadequate for germination (Richardson et al. 2018; Leger et al. 2019). Additionally, in regions where summer precipitation is minimal, such as our study area, early germination may improve seedling survival by allowing the plant to have an extended period of growth (Goldberg et al. 1999; Mangla et al. 2011) and possibly to produce longer roots that can assist with depleting moisture as it declines from the soil surface during the summer (Peek et al. 2005; Leger et al. 2019).

Our field research indicates that a priming treatment can result in higher seedling emergence during the initial part of the growing season, but a treatment effect was generally only significant when primed seeds were combined with a deep furrow treatment (see Fig. 4). In our study, priming exhibited its greatest treatment effect during the first 3 mo of the growing season (see Fig. 4), which may indicate, as did our laboratory trials, that priming can decrease germination time (see Fig. 1) and subsequently lead to earlier emergence. Despite improved seedling emergence, we did not see a strong treatment response from priming by the end of the growing season. During this study, rain events extending throughout the spring likely promoted untreated seeds to have similar final emergence by the end of the season as primed seeds (see Fig. 4). If this study had been sown on a year when precipitation was not

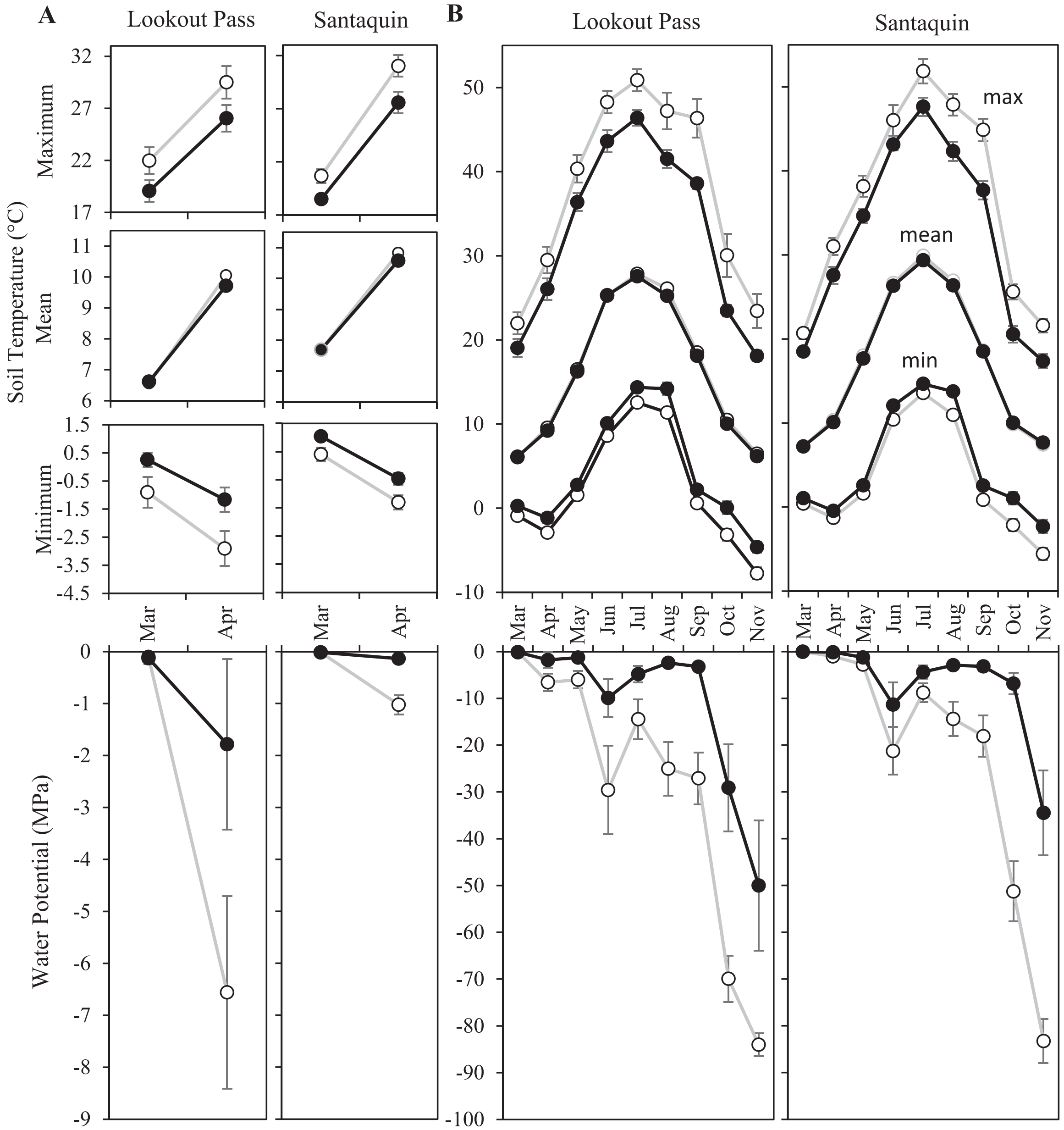

Fig. 3. Monthly average (±standard error) maximum, mean, and minimum soil temperature and mean water potential in shallow (○) and deep (●) furrows at Lookout Pass and Santaquin study sites. Shallow and deep furrows were made 1 cm and 15 cm below the soil surface, with soil excavated from the furrow placed on the outside edge of the furrow. Sensors were placed in the soil 2 cm below the bottom of the furrow. Data are shown for **A,** period when the majority of the seeds would germinate (March–April), and **B,** the entire period of the study.

as consistent during the spring, we might have seen a prolonged treatment effect from priming.

Future research should be done to evaluate primed seeds in the presence of invasive annual grasses. Vaughn and Young (2015) researched short-term priority effects between exotic annual grasses and perennial grasses. They found native perennial grasses had higher establishment when planted 2 wk earlier than exotic annual grasses. Had our study been done in the presence of invasive annual grasses, early emergence produced by primed seeds could have made the seeded species more competitive. This priming technique may also assist other native species in competing with invasive species in early demographic stages.

Primed seeds may have benefited from the pelleting material and through priming. Pelleted seed coupled with deep furrows did not demonstrate early seedling emergence, but for all other measured plant metrics (i.e., plant density, tillers/stem density, and biomass), pellets outperformed control seed in shallow furrows (see Fig. 5). It is possible that the compost, surfactant, fungicide, and Stockosorb 660 powder used in the pelleting matrix benefited plant establishment and growth. Compost may have provided nutrients and beneficial soil microbes to assist with plant establishment. Fungicides may help seeds and seedlings in their early demographic stages when they are most vulnerable to pathogen attack (Gilbert 2002). Surfactants used in seed coatings have been shown to improve seedling drought tolerance, particularly in the presence of water-repellent soils (Madsen et al. 2012; Madsen et al. 2013; Madsen et al. 2014). Additionally, Stockosorb 660 may have assisted seeds and seedlings in their ability to absorb and retain moisture, which could have diminished the effects of summer drought. The ability of these ingredients to improve conditions

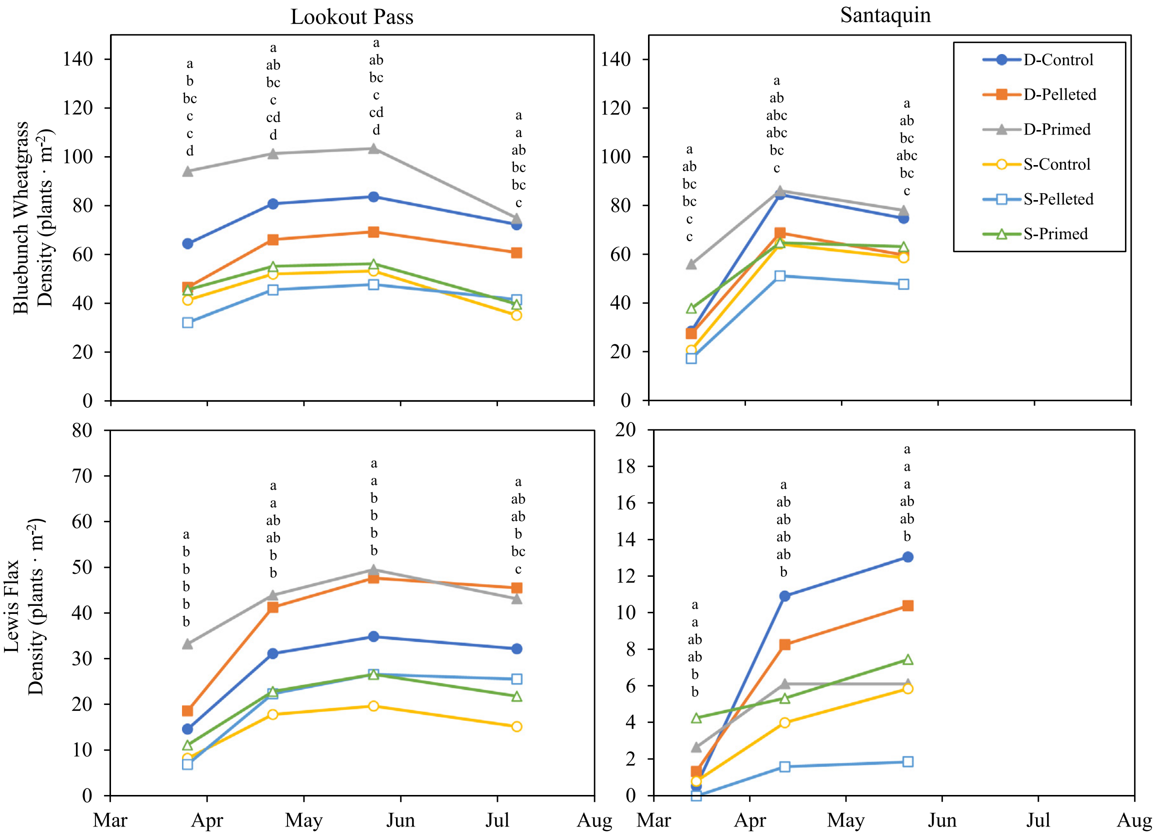

Fig. 4. Plant density of bluebunch wheatgrass and Lewis flax at Lookout Pass and Santaquin study sites. Seeds of each species were either primed, pelleted, or left untreated (control) and planted in deep (D) or shallow (S) furrows. Emergence counting stopped at the end of May at Santaquin due to a grasshopper invasion that removed all aboveground biomass. Unique letters denote significant differences ($P < 0.1$). Scale bars differ between site and species to emphasize differences among treatments.

for seedling growth and establishment may have been one of the drivers for improved plant growth in the second year.

While this study demonstrates the success of priming for spring planting, it does not indicate that priming would be successful for fall planting. For some species, seeds may naturally prime over the winter, so germination occurs rapidly in the spring. For species with relatively quicker germination times, priming may cause premature germination before or during the winter when conditions are unsuitable for plant survival (Boyd and Lemos 2013). However, for slow-germinating species, priming may provide some benefit in years with comparatively low spring precipitation by increasing the time for root development before entering a prolonged dry period (Boyd and Lemos 2015).

Improving microsite conditions by deep furrow implementation

Our results support previous research that suggests that enhancing a seed's microsite can improve plant survival and establishment (Asher and Eckert 1973; Haferkamp et al. 1987; Clary 1989; Terry et al. 2021). This study demonstrated that deep furrows could produce earlier seedling emergence (see Fig. 4) and, in most instances, higher plant densities (see Fig. 5A), tiller/stem densities (see Fig. 5B), and aboveground biomass (see Fig. 5C). Terry et al. (2021) also found that bluebunch wheatgrass had greater success when it was planted in deep furrows (that were constructed the same as in our study) in comparison with planting in shallow furrows. Our study is unique from Terry et al. (2021) in that it directly quantifies the impact furrowing had on seedbed hydrothermal properties. Improvements in plant establishment may be due, in part, to the furrow's having higher soil moisture availability and moderated soil temperatures (see Fig. 3). Increased soil moisture and moderate soil temperatures provided by the furrow would directly assist seeds in progressing toward germination (Hardegree and Van Vactor 1999; Hardegree et al. 2008), promote seedling emergence, and enhance plant growth and survival (James et al. 2019). This was especially evident at our Lookout Pass study site, where deep furrows had more than twice as many seedlings than shallow furrows (see Fig. 4). This trend persisted into the second growing season by producing two times the amount of biomass in deep furrows than shallow furrows (see Fig. 5C). Hence, the results of this study provide justification for more studies to take place to evaluate the use of deep furrows across various soil types and plant species to determine their full utility.

The results of our water potential readings should be interpreted with caution. This is due to the TEROS 21 water potential sensor's relatively large size compared with the seed. In our study, the top of the sensor was 0.5 cm below the soil surface and the bottom of the 1.5-cm thick sensor was at a 2.0 cm depth. Thus, the sensor is located within a greater depth in the soil than experienced by the seed. While the TEROS 21 sensor may not accurately measure the direct conditions within the seed zone, the results of this study are most likely correlated with the conditions experienced by the seed and demonstrate relative differences between deep and shallow furrows.

Deep furrows may be an increasingly useful tool for improving restoration efforts in the face of climate change, which is manifested by warmer ambient and soil temperatures (Karl et al. 2009; Barros et al. 2014). Specifically, soils have become dryer and hotter, resulting in less favorable conditions for plant establishment (James et al. 2019). Deep furrows are a potential solution to counteract restoration challenges that are associated with a changing

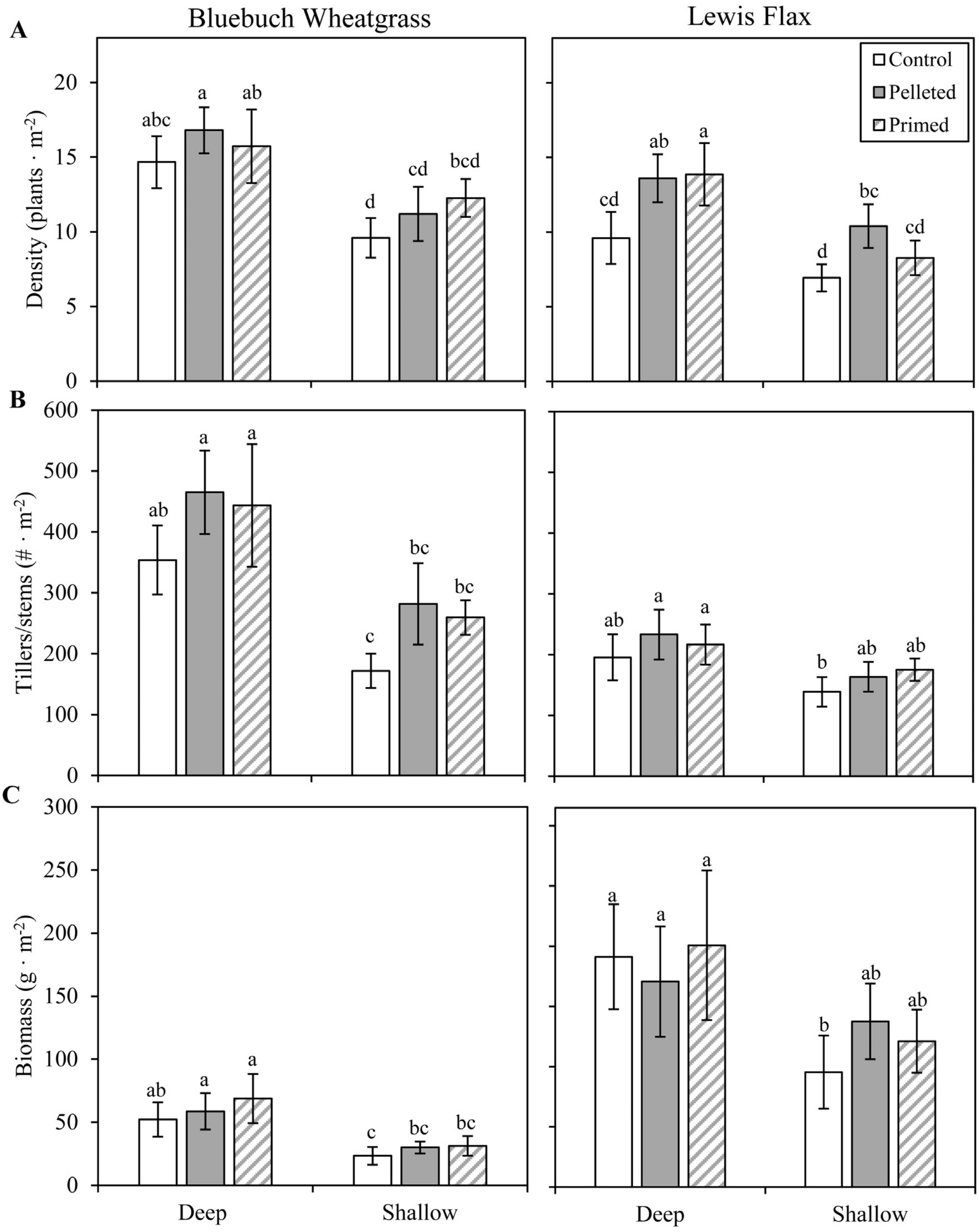

Fig. 5. A–C, Plant density, tiller/stem density, and biomass at the end of the second growing period from bluebunch wheatgrass and Lewis flax growing at the Lookout Pass study site. At planting, seed of each species was either primed, pelleted, or left untreated (control) and sown in either deep or shallow furrows. Bars reflect means with standard errors. Unique letters denote significant differences ($P < 0.1$).

climate by providing seeds with a more favorable environment for germination and plant survival.

Furrows can give an advantage to native seeded species and reduce the competitiveness of weed species (Kettler et al. 2000) by sidecasting weed seeds from the furrow and burying them at a depth that restrains their emergence (Young et al. 2014). Additionally, a rough surface, such as furrows, may trap weed seeds near the edge of a restoration site, limiting their spatial distribution and propagule pressure (Johnston 2019).

Priming and deep furrows

This study demonstrated that combining priming and deep furrows could significantly improve plant establishment. This technique provides a two-prong benefit by stimulating early germination (see Fig. 4) when adequate moisture is available and providing germinated seeds and seedlings with prolonged moisture within furrows (see Fig. 3). In most cases, seed in deep furrows had improved emergence, density, tillers/stems, and biomass compared with seed planted in shallow furrows (see Figs. 4 and 5). However, the combination of priming with deep furrows consistently outperformed untreated seed planted in shallow furrows. With an increase in plant establishment provided by priming and deep furrows, it may be possible for land managers to lower their seeding rate. In this study, it could have been advantageous to reduce the seeding rate as there appeared to be a high amount of intraspecific competition in the treatment with a combination of primed seed and deep furrows.

Management Implications

This study contributes to a growing body of knowledge that seed-enhancement technologies and improved planting techniques can advance restoration efforts (Madsen et al. 2016; Erickson et al. 2018; Hoose et al. 2019; Pedrini et al. 2020; Anderson et al. 2021; Brown et al. 2021; Terry et al. 2021). This study is unique in that it demonstrates how seed priming and deep furrow treatments can be used in combination to improve seeding success in degraded sagebrush steppe sites. Specifically, this research demonstrates two areas for improving seeding efforts: 1) seed priming accelerates germination, which in some cases improves emergence, establishment, and plant biomass; and 2) deep furrows provide longer periods of moisture and more moderate near-surface soil temperature, which directly promotes seedling emergence and plant growth. In comparing effect sizes, our data indicate that land managers could improve seeding success to a greater degree by applying deep furrows over just applying a seed priming treatment. However, we recommend using both treatments as additional gains to a restoration effort can be realized with the combination of priming and deep furrows. Future research is merited to continue evaluating priming and deep furrow planting techniques to determine if land managers should adopt these technologies.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2023.01.006.

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