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RESEARCH ARTICLE

Plant recruitment in drylands varies by site, year, and seeding technique

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Restoration in dryland ecosystems is hindered by low establishment of seeded species. As such, evaluations of current seeding methods are critical to understanding limitations and barriers to seeding success. Drill seeding is perceived as an optimal seeding strategy in many dryland ecosystems, but broadcast seeding is more commonly used as a seeding method due to physical and logistical constraints. For example, broadcast seeding may be conducted by aerial drops where other methods are limited by topography or obstructive features in the landscape. Few studies have quantified the differences between drill and broadcast seeding through space and time. We compare 2-year recruitment of emergent *Pseudoroegneria spicata* (bluebunch wheatgrass) seedlings in the sagebrush steppe biome for drill versus broadcast seeding methods across three seeding years, three landscape aspects and two soil types using a 95% confidence interval approach to avoid the penalty of multiplicity. We found drill seeding had 2.7 times greater recruitment of seedlings after 2 years compared with broadcast seeding. However, differences were highly subject to seeding year, aspect and soil type, likely because of soil moisture and temperature variations. Drill seeding had an advantage on clay soils with flat and north aspects (10.1 and 4.6 times greater for drill than broadcast seeding, respectively). In most conditions, drill seeding had greater recruitment than broadcast seeding, though in 2014 on south aspects broadcast seeding had 2.7 times greater recruitment than drill seeding. The results of this study demonstrate a need for restoration plans that account for spatiotemporal variation in seeding success.

Key words: bluebunch wheatgrass, bunchgrass, Great Basin, rangeland restoration, sagebrush steppe biome, seeding

Implications for Practice

- Drill seeding of a key bunchgrass species, where logistically possible, is advantageous over broadcast seeding for seed delivery in restoration efforts in the northern Great Basin.
- Broadcast seeding, though not as effective as drill seeding, is an important restoration tool that can successfully establish seeded vegetation.
- Variable recruitment among seeding years and sites indicates a need for bet-hedging strategies (e.g. multiple-year seeding with novel seed treatments).

Introduction

Degradation of ecosystems is of global concern and recognized by the United Nations as one of the top ecological problems of the century (United Nations General Assembly 2019). Restoring plant communities within degraded ecosystems is a global priority but is often difficult (Suding 2011). Dryland ecosystems are particularly susceptible to degradation and are difficult to restore because of their harsh environmental conditions, specifically extreme temperature fluctuations, limited and sporadic precipitation, and high interannual variation (Reynolds et al. 2007; Bainbridge 2012). Once degraded, these systems are often incapable of autogenic recovery (Suding et al. 2004), and require active restoration to return desirable ecosystem structure and function.

In the western United States, hundreds of thousands of square kilometers of the sagebrush steppe are degraded and in need of restoration (D'Antonio & Vitousek 1992; Davies et al. 2011; Bradley et al. 2018). One cause of sagebrush steppe degradation is the alteration in fire extent and frequency (Davies et al. 2011). Following fire, lands are highly susceptible to invasion by exotic annual grasses if active restoration is not successfully conducted (Davies et al. 2021). Establishment of native bunchgrass species is not only important to maintain biodiversity and ecosystem function, but also for reducing the risk of exotic annual grass invasion and proliferation (Davies et al. 2021). Restoration

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efforts in this region are predominantly seed-based because of the logistical constraints of restoring large-scale degraded areas with nursery-grown seedlings (Pilliod et al. 2017). Millions of dollars are spent annually on seed for sagebrush steppe restoration (Pilliod et al. 2017). The desire to use native species in restoration is increasing, but establishment of native seedlings in this region is frequently low (James et al. 2011). As such, evaluations of current seeding strategies for native plants are needed.

Seed-based restoration techniques, such as drill and broadcast seeding, are common within many ecosystems globally (Merritt & Dixon 2011; Knutson et al. 2014; Broadhurst et al. 2015). Drill seeding creates linear furrows where seeds are placed into a safe site, a microsite that allows for higher chances of germination and establishment (Fowler 1988). With broadcast seeding by comparison, seed is dropped aerially and may or may not land in a safe site. Broadcast seeding can be highly successful when conducted with techniques such as rolling or raking to ensure seed penetrates into the soil (Shaw et al. 2020) as evidenced by prairie research in the Great Plains (Bakker et al. 2003; Applestein et al. 2018). Similarly, smaller seeded sagebrush steppe species may be successfully restored using broadcast seeding without pre- or post-seeding soil preparation (e.g. Davies et al. 2014, 2019). In the Great Basin of the western United States, restoration scientists and land managers suggest greater establishment is achieved with drill seeding compared with non-soil prepared broadcast seeding of bunchgrass species because of increased seed-to-soil contact (Hull & Holmgren 1964) and generally higher soil moisture content (Hull 1970). Research in prairie systems suggests a similar benefit of drill seeding compared with non-soil prepared broadcast seeding for grass species in particular (Yurkonis et al. 2010*a*, 2010*b*). However, for some regions getting equipment to a restoration site for soil preparation or post-broadcast seeding treatments may be logistically impossible (Svejcar et al. 2017).

Comparisons between drill and broadcast seeding methods are needed. But only one previous study compared drill versus broadcast seeding methods on bunchgrasses in the sagebrush steppe (Nelson et al. 1970). Nelson et al. (1970) tested seven native bunchgrass species in drill versus broadcast seeding treatments at different seeding times, fall versus spring, in tandem with controls on seed depredation, invasive species control, and seed bed preparation. Drill relative to broadcast seeding had greater recruitment of all species under all conditions, which was attributed to both reduced seed depredation and reduced fluctuations in soil water content near the seed (Nelson et al. 1970). However, the seeding was only conducted in a single year and at one site.

Variations in spatiotemporal conditions at both macro (km) and micro (cm) scales can have a major impact on seed germination and seedling recruitment (Hull 1970). The sagebrush steppe biome has high climatic (temporal) and edaphic (spatial) variability because of the geographic context of the region (Hardegree et al. 2011; Svejcar et al. 2017). Field studies testing seedling recruitment across climoedaphic gradients in the sagebrush steppe biome are not common, especially when comparing drill versus broadcast seeding. Ott et al. (2016) tested diverse seed mixes containing both perennial grasses and forbs across three different sites all with loam soils. The experiment was planted in different years following fire, but divided species by seed size such that large seeded species were drill seeded and small seeded species were broadcast seeded, and were then compared with nonseeded controls. Large differences were found within both drill and broadcast seeding treatments between the different sites (Ott et al. 2016). However, to our knowledge, within species comparisons of drill versus broadcast seeding methods across spatiotemporal gradients have not been conducted.

Understanding the spatiotemporal variability in successful establishment of broadcast seeded species is also crucial because many areas cannot be drill seeded due to logistical constraints and physical barriers. Therefore, a better understanding of the likelihood of success with broadcast seeding is invaluable for weighing whether or not to broadcast seed, for planning additional treatments and re-seeding, and for allocating limited restoration resources. The purpose of this study was to evaluate drill and broadcast seeding methods for differences in plant recruitment at the 2-year plant growth stage. We tested these seeding techniques across a spatiotemporal gradient for one of the most commonly seeded native cool-season perennial bunchgrass species in the sagebrush steppe biome, *Pseudoroegneria spicata* [Pursh] A. Löve (bluebunch wheatgrass) (Knutson et al. 2014). We hypothesized drill seeding would consistently result in greater emergence and recruitment of seedlings, but that the difference would vary temporally and spatially. Specifically, we hypothesized that recruitment would be greater on northern compared with southern and flat aspects and in wetter compared to drier years.

Methods

Study Area and Species

The experiment was conducted at the Northern Great Basin Experimental Range (NGBER), which is approximately 50 km west of Burns, OR, U.S.A. The area is semiarid with an average 286 mm precipitation per year; though this varies strongly in space and time (Svejcar et al. 2017). Precipitation mainly occurs during the cool season (October–May). The NGBER falls within the High Lava Plains physiographic province (Lentz & Simonson 1986). Soils in the area are highly heterogeneous (Svejcar et al. 2017) but are generally dominated by a well-drained, loam structure (Lentz & Simonson 1986).

The region is part of the Great Basin floristic province (Pellant et al. 2004). All study plots were co-dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and A. Young) and bluebunch wheatgrass. Sandberg's bluegrass (*Poa secunda* J. Presl), bottlebrush squirrel tail (*Elymus elymoides* [Raf.] Swezey), hawksbeard (*Crepis* L. spp.), biscuitroot (*Lomatium* Raf. spp.), milkvetch (*Astragalus* L. spp.), and tailcup lupine (*Lupinus caudatus* Kellogg) occurred on all sites. Idaho fescue (*Festuca idahoensis* Elmer) occurred only on northern aspect sites and Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth) occurred only on southern aspect sites. The exotic annual cheatgrass (*Bromus tectorum* L.) was present at all sites.

Our study used *Pseudoroegneria spicata* cv. Anatone obtained from the Utah Division of Wildlife Resources Great Basin Research Center (Ephraim, UT, U.S.A.), as the seeded species. *Pseudoroegneria spicata* is a drought-tolerant, native

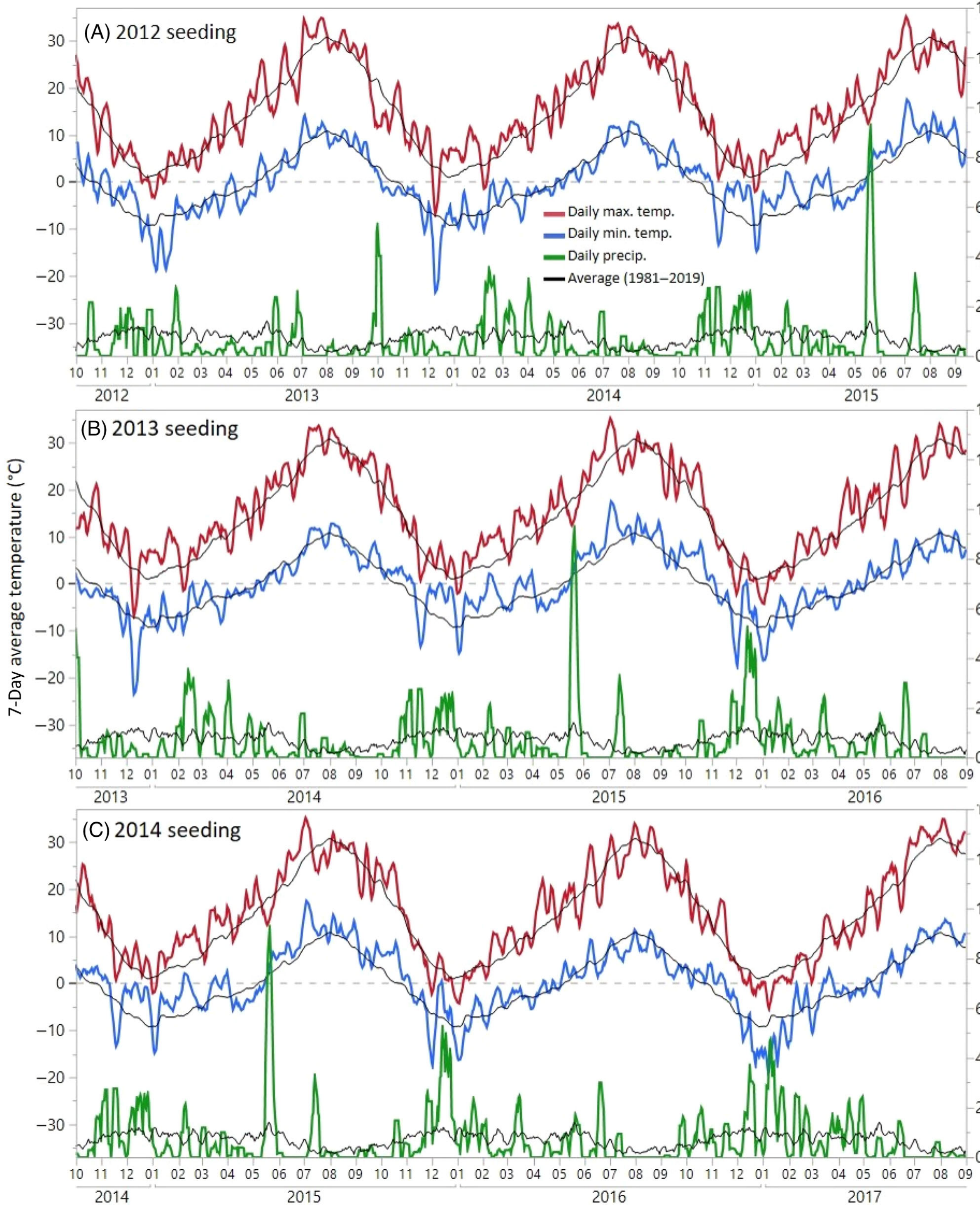

Figure 1. Maximum and minimum ambient temperature (°C) and 7-day average precipitation (mm) for the experimental area over the period from seeding (November) to final recruitment stage measurements (July) for the (A) 2012 seeding (November 2012–July 2015), (B) 2013 seeding (November 2013–July 2016), and (C) 2014 seeding (November 2014–July 2017).

cool-season perennial bunchgrass that is widespread throughout the sagebrush steppe (Plants Database USDA; https://plants.usda.gov/core/profile?symbol=pssp6 [accessed 2021]; Knutson et al. 2014) and is one of the most commonly seeded species and accessions in restoration efforts throughout the sagebrush steppe biome (Jones 2019). While many restoration efforts by land management groups entail seeding multiple species, *P. spicata* is one of the most commonly used species in the northern Great Basin due to its dominance in the landscape, wide adaptability, and commercial availability (Burns and Vale Bureau of Land Management District Offices, personal communication). Bunchgrasses are known to compete with exotic annual grasses once established (Davies 2008) and as such is a key functional group to restore to degraded sage steppe ecosystems. *Pseudoroegneria spicata* is used in this study as a model species for bunchgrasses and provides a starting point for further studies. *Pseudoroegneria spicata* plants are considered established as adults after approximately 2 years (Ogle et al. 2010).

Experimental Design and Measurements

Sites were installed on three aspects and within two ecological sites (3 aspects × 2 ecological sites = 6 total sites). The three landscape aspects were flat, south, and north facing slopes with elevations ranging from 1,383 to 1,501 m. The two ecological sites, hereafter referred to as soils, for each aspect that varied in subsurface soil horizons (NRCS 2012) included a Loamy 10–12, Carryback gravelly loam soils hereafter referred to as "Loam," and a Clayey 10–12, Actem cobbly loam soils hereafter referred to as "Clay." Surface soil samples were collected for all sites and surface soil texture, sampled to a 1.5 cm depth, was assessed for each site using the fractionation method (Bowman & Hutka 2002). While subsurface soil horizons varied, surface soil texture did not vary significantly between sites. Mean percent (± SE) of sand, silt, and clay for surface soils (0–2 cm) of the sites was 49% (± 1%), 38% (± 2%), and 13% (± 1%), respectively.

Prior to seeding each year, a previously undisturbed area at each site was prepared in a manner that simulated post-wildfire conditions with high mortality of existing native vegetation. This included a spring application of 11.7 oz/acre (0.14 L/ha) with 480 g/L of active ingredient of glyphosate followed by a prescribed fire in the fall. No soil treatments were conducted. Seedings were conducted in autumn (November) of 3 years, 2012, 2013, and 2014 (3 years × 3 aspects × 2 soils × 2 seeding treatments × 5 replications per site = 180 total plots). The seeding rate for all plots was 500 pure live seed/m^2 (3.4 kg pure live seed/ha). Plots were either drill seeded, where a small drill seeder (Push Planter Product, Kincaid Equipment Manufacturing, Haven, KS, U.S.A.) was pushed across plots, or broadcast seeded where seed was tossed by hand evenly across plots. The drill seeder created furrows and deposited seeds

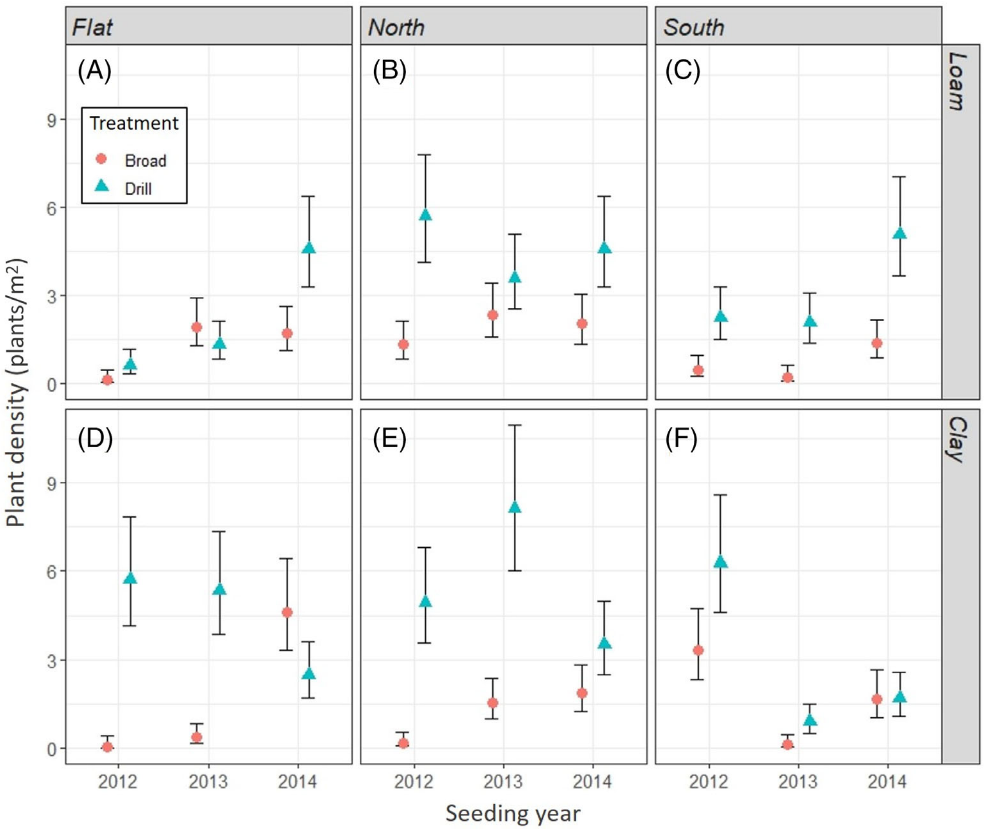

Figure 2. Treatment comparison for density of seedlings surviving 2 years after seeding. Least square means of counts were divided by monitored area (4 m^2) to obtain seedling density of both broadcast (Broad) and drill (Drill) seeding treatments. Columns are aspects and rows are soils classification. Bars represent 95% CI. Letters indicate aspect by ecological site combinations.

at a depth of approximately 2 cm, and then loosely covered seed with soil as it passed over. Plots for each treatment were 2.5×3.5 m (8.75 m^2) to account for the spacing on the drill seeder used and were arranged in a randomized complete block design.

Emergence was monitored in late spring following all seeding years, but was highly variable temporally for the broadcast seeding treatment. We may not have captured maximum emergence for that treatment so emergence was not analyzed for any treatment. Plants were then counted in mid-summer (July) 2 years following emergence for a measure of density at the recruitment stage, 2015, 2016, and 2017. The 2-year time frame is important as it is approximately when *P. spicata* plants would transition to an adult stage and have reproductive capacity (James et al. 2011). Counts of plants were conducted in a 4-m^2 area in the plot interior for plant density. One plot was compromised in 2013 (soil = Loam, aspect = South) and one in 2014 (soil = Clay, aspect = South) where $N = 29$ for each year for the broadcast seeding treatment.

Precipitation was below average in every year of the study (PRISM 2020). Cumulative annual precipitation was 178 mm for the November 2012–2013 and 2013–2014 periods and 254 mm in the 2014–2015 period. In particular, precipitation in the spring following the November 2012 seeding was low (Fig. 1A). Most years in the study followed the typical weather cycle of the area where precipitation falls as snow in winter (Svejcar et al. 2017), but in 2014 (following the November 2013 seeding) precipitation events were frequent from February to May (Fig. 1B). Two large rain events occurred in early (May 2015) and mid-summer (July 2015) for the first year following the 2014 seeding (Fig. 1C). This resulted in total summer precipitation (May–August) for 2015 reaching 97 mm, compared with 50 mm for 2013 and 40 mm for 2014.

Statistical Analysis

Drill and broadcast seeding treatments were compared after 2 years (recruitment stage) using a generalized linear mixed model approach (GLIMMIX, SAS version 9.4, SAS Institute, Cary, NC, U.S.A.). Plant densities (counts) at the recruitment stage were response variables with 0.1 added to all counts to avoid estimating problems because of counts of zero. Aspect, soil, seeding year, and seeding treatment were fixed effects. We initially tested a Poisson error distribution to account for the dependent variable being count data (Zuur et al. 2007) but we did not obtain a model fit. Thus, we assumed a negative binomial error distribution, which had a good model fit, and used a transformation through the log link function. Log-scale least squares means and 95% confidence intervals were back transformed to the original count scale (du Prel et al. 2009), and then were divided by 4 m^2 to obtain surviving seedling density for graphing purposes. Type III tests of fixed effects were used to determine significant interactions. Confidence intervals were used to determine differences instead of significance testing due to the large number of comparisons and the large penalty for multiplicity (Dushoff et al. 2019). However, model output results are available in Table S1. Analyses are reported at a 0.95 confidence level. Data figures were created in ggplot2 (Wickham 2009).

Results

Between Seeding Treatments

Data are presented to allow comparisons of treatments, seeding year, aspect, and soils against the other variables (Table S1; Figs. 2–5). Drill-seeding had greater plant densities across all combinations of sites and years after 2 years than broadcast-seeding (3.8 and 1.4 average plants/m^2, respectively; 2.7 times greater). However, differences in plant density varied by seeding year, aspect, and soil type. Differences in average plant densities between drill and broadcast seeding treatments were greatest for the 2012 seedings where drill seeding had plant densities 4.7 times greater than broadcast seeding, followed by the 2013 seedings (3.3 times greater) and lowest for the 2014 seedings (1.7 times greater). On average, north aspects had a greater difference between drill and broadcast seeding treatment plant densities than either flat or south aspects (drill seeding had 3.4, 2.2, and 2.5 times greater plant densities than broadcast seeding, respectively). The average difference in plant densities between treatments for the two soil types was similar; drill seeding had 3.3 times greater plant densities than broadcast seeding on Clay sites and 2.5 times greater plant densities on Loam sites.

The large overall difference in plant densities for drill versus broadcast seeding treatments for the 2012 seedings was driven

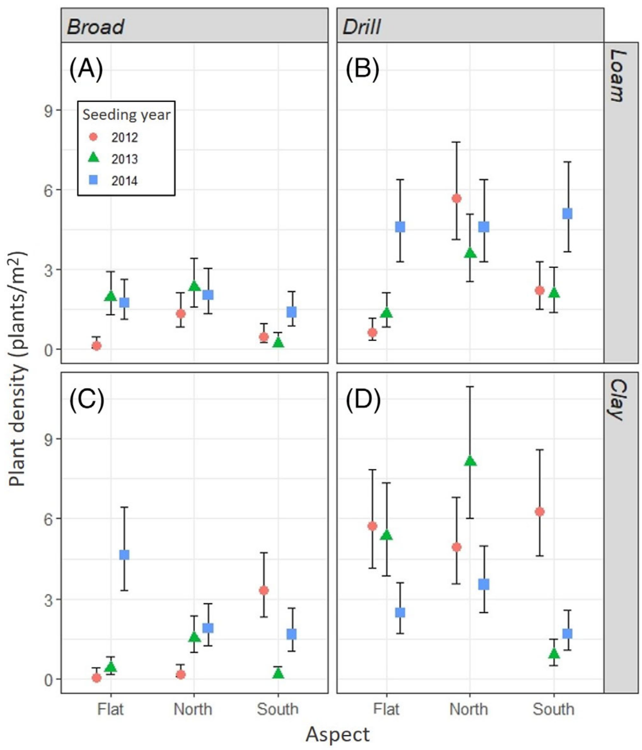

Figure 3. Year comparison for density of seedlings surviving 2 years after seeding. Least square means of counts were divided by monitored area (4 m^2) to obtain seedling density of both broadcast (Broad) and drill (Drill) seeding treatments. Columns are seeding treatments and rows are soils classification. Bars represent 95% CI. Letters indicate individual treatment by soils combinations.

by the north Loam, flat Clay and north Clay sites, which had very low densities for broadcast seedings with many plots having zero plants (drill seeding relative to broadcast seeding = 4.4, 190, and 24.5 times greater, respectively; Fig. 2B, 2D, & 2E). Similarly in the 2013 seedings, the flat Clay and north Clay sites had the greatest differences in plant densities between drill and broadcast seeding treatments (13.3 times greater plant densities for drill seeding, 5.4 times greater plant densities for drill seeding; Fig. 2D & 2E, respectively). However, in the 2014 seedings the south Loam site had the greatest difference between seeding treatments (3.6 times greater for drill seeding; Fig. 2C).

Differences within seeding methods were also found. The highest recruitment of seedlings for drill seeding treatments was in the 2013 seedings at the north Clay site (8.1 seedlings/m^2) while the lowest was in the 2012 seedings at the flat Loam site (0.6 seedlings/m^2). For broadcast seeding treatments, the flat Clay site in the 2014 seedings had the highest recruitment (4.6 seedlings/m^2) and the flat Clay site in the 2012 seedings had the lowest (0.03 seedlings/m^2).

Seeding Year: Within Seeding Treatment Effects

When averaged across sites, seedling recruitment was similar across years for both drill (2012: 4.2 seedlings/m^2; 2013: 3.6 seedlings/m^2; and 2014: 3.7 seedlings/m^2) and broadcast (2012: 0.9 seedlings/m^2; 2013: 1.1 seedlings/m^2; and 2014: 2.2 seedlings/m^2) seeding treatments. However, individual treatments had a site by year interaction (Table S1; Fig. 3). In the broadcast seedings, the flat Clay site had the greatest difference between years (2012: 0.03 seedlings/m^2; 2013: 0.4 seedlings/m^2; and 2014: 4.6 seedlings/m^2). Broadcast seeding for 2012 was equivalent to or lower than either 2013 or 2014 in every site except the south Clay site (Fig. 3C), though confidence intervals between 2012 and 2014 at this site overlapped. Seedling recruitment varied substantially between sites and years for the drill seedings. In all of the Clay sites for drill seeding, 2014 seedings were lower than or within the same confidence intervals as the 2012 and 2013 seedings (Fig. 3D), but in the Loam sites the inverse was true with 2014 seedings being greater than or within the same confidence intervals as the 2012 and 2013 seedings (Fig. 3D). Similar to broadcast seeding, the only site where 2012 drill seeding treatments were greater than 2013 or 2014 were in the south Clay site (Fig. 3D).

Aspect: Within Seeding Treatment Effects

Averaged across aspect, broadcast seeding had similar average recruitment levels among the three aspects and across years and soils (flat = 1.5 seedlings/m^2, north = 1.5 seedlings/m^2, and south = 1.2 seedlings/m^2). Seedling densities for broadcast seedings on south aspects were generally lower than or within

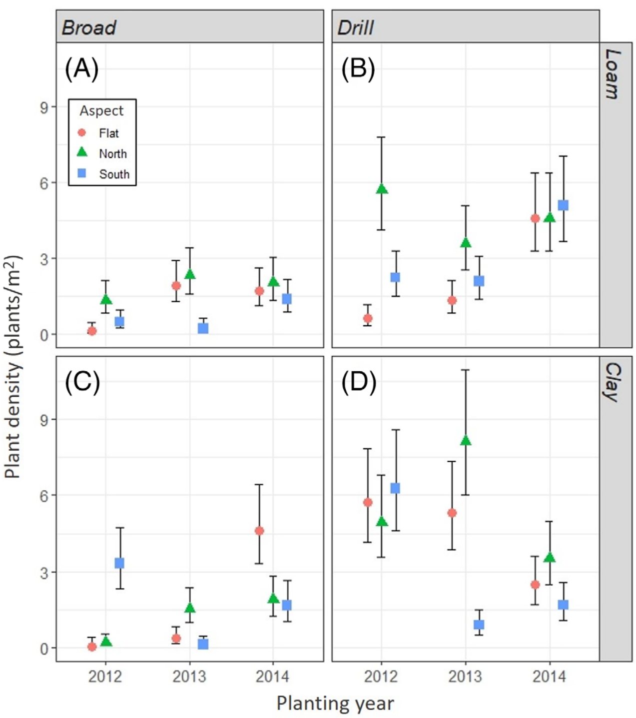

Figure 4. Aspect comparison for density of seedlings surviving 2 years after seeding. Least square means of counts were divided by monitored area (4 m^2) to obtain seedling density of both broadcast (Broad) and drill (Drill) seeding treatments. Columns are seeding treatments and rows are soils classification. Bars represent 95% CI. Letters indicate individual treatment by soils combinations.

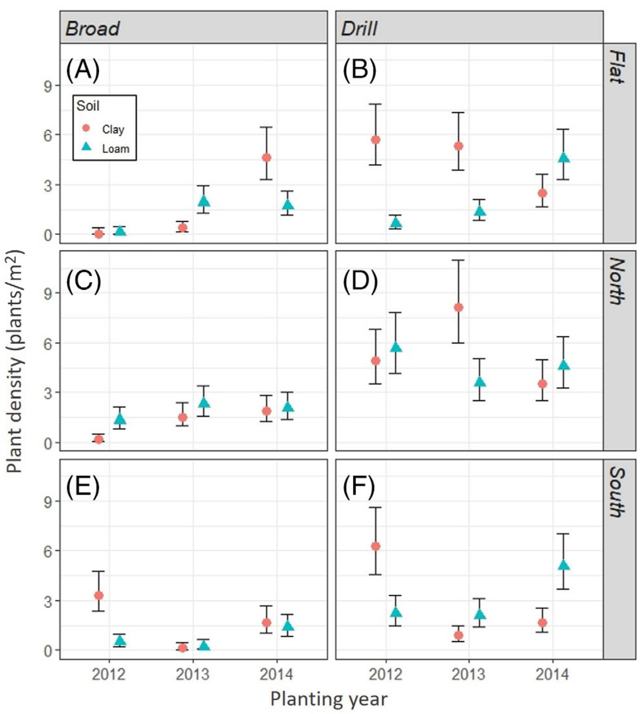

Figure 5. Soils comparison for density of seedlings surviving 2 years after seeding. Least square means of counts were divided by monitored area (4 m^2) to obtain seedling density of both broadcast (Broad) and drill (Drill) seeding treatments. Columns are seeding treatments and rows are aspect. Bars represent 95% CI. Letters indicate individual treatment by aspect combinations.

the confidence intervals of north and flat aspects (Fig. 4A & 4C), except on Clay soils in 2012 (Fig. 4C). The flat aspect was greater than south and north aspects in the Clay sites in 2014 (2.7 and 2.4 times greater, respectively; Fig. 4C). Drill seeding was overall greatest for the north aspect (1.5 times greater than flat sites and 1.7 times greater than south sites), though the only instance where the north aspect was greater than flat and south sites without confidence intervals overlapping was in 2012 at the Loam site (Fig. 4B).

Soil: Within Seeding Treatment Effects

Averages between Clay and Loam sites for broadcast seeding treatments were similar (Clay was 1.2 times greater than Loam), while drill seeding treatments were slightly greater for Clay sites than Loam sites (Clay was 1.3 times greater than Loam). Clay sites generally had higher seedling recruitment than Loam sites for both broadcast (Fig. 5A & 5E) and drill (Fig. 5B, 5D, & 5F) seeding treatments where confidence intervals did not overlap. There were only two instances of Loam sites having higher seedling recruitment than Clay sites (Fig. 5A & 5F) where confidence intervals did not overlap.

Discussion

Even with high spatiotemporal variability, our study provides strong empirical evidence for an overall benefit of drill seeding over broadcast seeding in restoration of *P. spicata* in the northern Great Basin. In 10 of the 18 site-by-year combinations we tested, seedling recruitment was greater with drill versus broadcast seeding. These results are in line with previous research that found overall higher recruitment of species in drill versus broadcast seeding treatments (Nelson et al. 1970; Ott et al. 2016). Higher recruitment of seedlings in drill seeded treatments is likely driven by drilled seeds being placed directly in a safe site, while broadcast seeds need to find a safe site (Leck et al. 2008). Sub-surface soil conditions and furrows have conditions that are more consistently optimal for seed germination and seedling emergence of seeded species than the soil surface (Hull 1970; Nelson et al. 1970). Similarly, burial of seeds may provide protection from granivore predation (Hulme 1998). Our study evaluated seeding treatments at the plot level for multiple site conditions. However, the level of benefit for drill over broadcast seeding in our study was highly dependent on spatiotemporal context. Part of the variation seen between sites, specifically for broadcast seeding, could be dependent on microsite conditions that were not captured at our plot level sampling. For example, postfire sagebrush canopies, where sagebrush had completely combusted, demonstrated lower seedling densities than interspaces for broadcast seed (Boyd & Davies 2012). Microsite variation among sites was not captured in our study and may have driven differences in broadcast seeding responses, but more research on microsite effects on broadcast seeding treatments among and between sites is needed.

Drill seeding may be advantageous because of moderation of extreme seedling microenvironments. The year with the lowest average precipitation, specifically in the spring following seeding, occurred after the 2012 fall seeding, and this seeding year had the greatest between treatment differences in seedling recruitment (drill versus broadcast). This may indicate that stressful low precipitation periods exhibit a greater benefit for drill seeding because subsurface soil conditions provide more consistent soil moisture than surface conditions (Nelson et al. 1970). However, the north aspect sites, which are known to have more consistent soil moisture than either south or flat aspects (Davies & Bates 2017), also had greater differences between treatments with drill seeding having higher seedling recruitment than broadcast seeding treatments. The difference in drill versus broadcast seeding in north aspect sites may be attributed to temperature where subsurface conditions in the cooler northern aspects may protect germinated seed from cold stress and freeze mortality (Boyd & Lemos 2013). Our results suggest that drill seeding improves the micro-environment for seedlings and this benefit is more apparent when seedling microenvironments are more stressful.

Though drill seeding was generally more successful than broadcast seeding, broadcast seeding may still be a useful treatment. Our study demonstrated one instance of broadcast seeding having potentially greater seedling recruitment than drill seeding, the flat Clay site in 2014, but confidence intervals overlapped, and in general, recruitment for all treatments was low (below the target 5 plants/m^2 target of land management agencies in this region). In contrast, Nelson et al. (1970) did not find any evidence for increased success with broadcast versus drill seeding. From a management perspective, broadcast seeding is often more logistically feasible than drill seeding because drill seeders cannot be pulled across steep, rocky terrain or used when soils are wet as the equipment can get stuck. As such, our results suggest there are spatiotemporal contexts where broadcast seeding is a useful and valid treatment. For example, on our south Clay site differences between drill and broadcast seeding were not statistically detectable for any of the seeding years so the more logistically feasible restoration method, broadcast seeding, may be selected.

Year of seeding in our study affected seedling recruitment in both drill and broadcast seeding treatments. In the Great Basin, spring (March–June) is a critical period for seedling recruitment (Boyd & James 2013). March to June of 2013, the spring period following the 2012 fall seeding, was the lowest initial spring precipitation of the three seeding years and overall seedling recruitment was lowest in this year. However, differences in seedling recruitment between years were more pronounced for drill seeding than broadcast seeding. A common target that land managers aim for with restoration is an establishment rate of 5 plants/m^2. Broadcast seeding did not reach this level in any year, whereas drill seeding achieved 5 plants/m^2 or greater in all years (three sites in 2012, two sites in 2013, and one site in 2014). This indicates that in almost all efforts for broadcast seeding, and some instances for drill seeding, multiple years of seeding for a single site may be needed.

Aspect can be an important factor determining seeding success. However, in general, broadcast seeding did not have substantial variation in seedling recruitment among aspects, possibly because of overall low recruitment. Large variation among aspects for drill seeding treatments were found with north aspect sites having 1.5–1.7 times greater overall recruitment than flat and south sites, respectively. South aspects in the sagebrush steppe biome are known to have hot, dry conditions and limited establishment of sagebrush steppe species (Davies & Bates 2017). As such, we expected greater recruitment of seedlings on north aspects. While north aspects generally had greater seedling recruitment than south aspects in the drill seed treatment, the results varied across time and soils. Clearly, aspect is important, but its influence is dependent upon the seeding treatment.

Similar to aspect, a large difference was found between Clay and Loam soils for seedling recruitment in drill seeding treatments, especially on north and flat aspects. Differences found between soils for drill seeding treatments could be due to the higher soil moisture holding capacity of clay soils. However, seedling recruitment in broadcast seeding treatments did not differ substantially between Clay and Loam soils, which could be due to similarities in surface soil conditions as well as overall low recruitment. Surface soil samples from each site demonstrated similar percentages of sand, silt, and clay, and the potential for soil physical crusting was thus similar among sites. When seed is broadcast onto the soil surface, soil physical crusting inhibits emergent seedling roots from penetrating to deeper soil horizons leading to seedling desiccation (Madsen et al. 2012). However, studies quantifying the impacts of varying surface soil conditions on seed germination and seedling establishment are needed.

The sagebrush steppe biome is known for high heterogeneity in climoedaphic conditions (Pierson & Wight 1991; Svejcar et al. 2017) and interannual climatic variability (Rajagopalan & Lall 1998; Boyd & James 2013; Svejcar et al. 2017; Davies et al. 2018). Highly variable environments, such as in the sagebrush steppe biome, often necessitate organisms to develop bet hedging strategies to improve net fitness over a range of environmental conditions (Cohen 1966). In seed-based ecological restoration, the concept of bet hedging is proposed as a means of maximizing plant recruitment under highly variable environmental conditions. This strategy may be accomplished by implementing different seeding techniques and treatments through space and time and imposing variability in seed germination, seedling emergence, and seedling tolerance through methods such as seed enhancement technologies (Davies et al. 2018). For example, time delay seed coatings may minimize mortality of fall seeded species that could germinate prior to deep winter freezes if a wet, mild autumn occurs (Madsen et al. 2016). Our results demonstrate that spatiotemporal context is critically important to seedling recruitment in post-disturbance restoration conditions. As such, there is a need to develop restoration plans that account for this variability, which includes trying to overcome factors limiting recruitment as well as recognizing that multiple seeding attempts may be necessary on some sites (Knutson et al. 2014; Davies et al. 2018; Copeland et al. 2021). Repeated seeding efforts may be especially important when broadcast seeding since it has overall lower success than drill seeding. Though drill seeding is advantageous compared to broadcast seeding, broadcast seeding will likely be an important seed delivery method across vast rangelands. In particular, drill seeding can be a challenge for land managers due to rough terrain and remoteness of sites that require restoration (Nelson et al. 1970). As such, broadcast seeding may be the only feasible option for some restoration plans (Hull & Holmgren 1964). However, in the sagebrush steppe biome, if seed resources are scarce and variable or managers have limited funding for restoration efforts, then a prioritization for areas that can be drill seeded may be beneficial and provide a greater return on investment compared to broadcast seeding. Similarly, the lack of success using broadcast seeding under certain conditions and the logistical limitations of drill seeding may justify the need and cost of novel seed enhancement technologies for development of bet hedging strategies (Davies et al. 2018).

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Supporting Information

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

Table S1. GLIMMIX model output.

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