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Original Research

Comparison of Postfire Seeding Practices for Wyoming Big Sagebrush[☆]

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ABSTRACT

Wildfires in the Great Basin have resulted in widespread loss of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young), an ecologically important shrub that has proven difficult to establish from seed. We sought to identify optimal seeding practices for Wyoming big sagebrush in the context of postfire seeding operations involving rangeland drills. In an experiment replicated at three burned sites in the northern Great Basin, we compared Wyoming big sagebrush establishment across treatments differing by seed delivery technique, timing, and rate of seed application. A seed mix containing bunchgrasses was drill-seeded in alternate rows using one of two drill-types (conventional or minimum-till), and a mix containing sagebrush was either delivered by drill to the soil surface in remaining rows or broadcast by hand (simulating aerial seeding) following drilling in fall or winter. Drill-delivery of sagebrush seed was accompanied by drag chains (conventional drill) or imprinter wheels (minimum-till drill) to improve seed-soil contact and was carried out at multiple seeding rates (ca. 50, 250, and 500 pure live seed m^{-2}). During 2 yr following seeding, sagebrush establishment was lower at two sites (yr 1: ≤ 1.2 plants m^{-2}; yr 2: ≤ 0.8 plants m^{-2}) compared with a third site (yr 1: ≤ 4.1 plants m^{-2}; yr 2: ≤ 2.0 plants m^{-2}) where treatment differences were more pronounced and significant. Wherever density differed between treatments, it was consistently higher in certain treatment levels (minimum-till > conventional drill, drill-delivery > broadcast-delivery, fall broadcast > winter broadcast, and higher rates > lower rates). Densities declined between years at two sites, but we did not find evidence that declines were due to density-dependent mortality. Results indicate that seeding success can likely be enhanced by using a minimum-till imprinter seeding method and using seeding rates higher than typical postfire seeding recommendations for Wyoming big sagebrush.

Introduction

Land management agencies of the United States have developed programs for actively seeding degraded areas on public lands, including areas affected by wildfire and invasive weeds (DOI and USDA, 2006; DOI, 2015). As the focus of seeding has increasingly shifted toward restoration of native plant communities, the importance of delivering “the right seed in the right place at the right time” has become a central concern (PCA, 2015). Many native species require special attention to ensure that seed quantity, placement, and timing of seeding are optimized to promote germination and establishment (Monsen and Stevens, 2004). These considerations are especially crucial in arid or semiarid environments where restoration efforts have historically had limited success (Allen, 1995; Whisenant, 1995; James et al., 2013).

Seeding is commonly carried out following wildfire in degraded sagebrush communities of the Great Basin where lack of postfire perennial recruitment could otherwise lead to dominance by cheatgrass (*Bromus tectorum* L.) or other exotic annuals (Epanchin-Niell et al., 2009; Pyke et al., 2013; Knutson et al., 2014). Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) is a priority restoration plant because of its importance to biodiversity, ecosystem functioning, and wildlife habitat (Lambert, 2005b; Welch, 2005; Prater et al., 2006; Prevey et al., 2010; Beck et al., 2012). Concerns over population declines of greater sage-grouse *(Centrocercus urophasianus)*, a sagebrush-obligate species, have contributed to interest in restoring Wyoming big sagebrush habitats affected by wildfire (Arkle et al., 2014; Pyke et al., 2015).

Postfire recovery of Wyoming big sagebrush can be slow due to its inability to resprout, short-lived seed banks, and dependence on seed dispersal from unburned areas (Lesica et al., 2007; Schlaepfer et al., 2014; Shinneman and McIlroy, 2016). Efforts to hasten Wyoming big sagebrush recovery through postfire seeding have been undertaken

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for many years but have often failed to achieve desired results (Lysne, 2005; Knutson et al., 2014). Transplanting is an alternative to direct seeding (Dettweiler-Robinson et al., 2013; McAdoo et al., 2013; Palma and Laurance, 2015) but presents logistical challenges for treating large areas affected by wildfire.

The poor success of Wyoming big sagebrush seedings can be attributed in part to the general difficulty of plant establishment in areas with low moisture availability and exotic annual grass competition (Boyd and Obradovich, 2014; Knutson et al., 2014; Brabec et al., 2015), as well as the possibility that seed used in past seedings was not well-adapted to local conditions (Brabec et al., 2015, 2017; Richardson et al., 2015). Poor establishment of seeded Wyoming big sagebrush could also be a consequence of suboptimal seeding practices, including improper timing of seeding, insufficient seeding rates, unsuitable seedbeds, or failure to place seeds in appropriate microsites (Monsen and Stevens, 2004). A variety of different options are currently available for seeding Wyoming big sagebrush in postfire settings, but not all options have been widely applied or rigorously tested (Boltz, 1994; McArthur and Stevens, 2004; Lambert, 2005b; Lysne, 2005; Shaw et al., 2005; Welch, 2005; Meyer and Warren, 2016).

Postfire seeding commonly involves the use of rangeland drills to sow grass-dominated seed mixes during the fall season (Monsen and Stevens, 2004; Knutson et al., 2014). Drill-seeding works well for relatively large seeds that can tolerate burial at 0.6 cm or more (Stevens and Monsen, 2004), and seeding carried out in the fall allows overwintering seeds to break dormancy, if needed, and emerge as soon as conditions become favorable in spring (Monsen and Stevens, 2004; Hardegree et al., 2013). However, standard drill-seeding techniques are not ideal for sagebrush species whose small seeds (technically achenes, < 3.0 mg seed^{-1}; Richardson et al., 2015) may require light for germination (Meyer et al., 1990) and whose seedlings may fail to emerge when seeds are buried deeper than 0.3 − 0.5 cm (Jacobson and Welch, 1987; McArthur and Stevens, 2004). Furthermore, minimal seed dormancy in Wyoming big sagebrush (Meyer and Monsen, 1992) means that fall-planted seeds might germinate precociously and risk frost-induced mortality during winter (Sakai and Larcher, 1987; Boyd and Lemos, 2013).

For situations where both large-seeded species (e.g., perennial grasses) and small-seeded species (e.g., sagebrush) are desired components of postfire seed mixes, separate seeding operations for each seed size have been recommended (Stevens and Monsen, 2004; Shaw et al., 2005). One option is to drill the larger seeds followed by aerial broadcasting of smaller seeds (Stevens and Monsen, 2004). This approach has the disadvantages of added cost for separate drilling and broadcasting procedures and presents the possibility that broadcast seeds will land in suboptimal microsites, including drill furrows where they might become buried, or on surfaces between furrows where they might have insufficient soil contact. Another option is to plant both large and small seeds using modified rangeland drills capable of placing different seed mixes in separate rows (Stevens and Monsen, 2004; Shaw et al., 2005; Truax Co., Inc, 2016). Drill disks can be removed or raised above ground level on rows designated for small seeds, which ensures that small seeds are kept away from drill furrows and spatially segregated from potentially more competitive large-seeded species. The addition of chains or imprinter wheels on rows with small seeds may further enhance their establishment by improving seed-soil contact (Shaw et al., 2005; Ott et al., 2016; Truax Co., Inc., 2016).

The question of how much sagebrush seed to use for postfire seedings requires careful consideration. Seeding rates[1] for Wyoming big sagebrush in the range of ca. 50 − 265 pure live seed (PLS) m^{-2} have been recommended by several authors (Plummer et al., 1968; McArthur and Stevens, 2004; Lambert, 2005a; Meyer, 2008; Jacobs et al., 2011; Meyer and Warren, 2016), but few studies have experimentally tested multiple rates or examined rates above this recommended range. Boltz (1994) reported instances of higher sagebrush densities at ca. 620 PLS m^{-2} compared with ca. 200 PLS m^{-2} in postfire seeding trials, and mine reclamation studies have demonstrated that sagebrush density can increase in response to increased seeding rates up to ca. 1400 PLS m^{-2} (Booth et al., 1999; Williams et al., 2002; Hild et al., 2006). These findings suggest that sagebrush establishment in postfire seedings might be enhanced by using seeding rates higher than typical recommendations. However, the benefits of higher seeding rates should be weighed against not only increased monetary costs but also possible diminishing returns due to density-dependent mortality at higher seedling densities (Harper, 1977; Burton et al., 2006). Some studies suggest that competition within dense stands of sagebrush seedlings may have a negative effect on survivorship (Owens and Norton, 1989; Boyd and Obradovich, 2014).

Continuing research on postfire seeding of Wyoming big sagebrush is warranted given current uncertainty over best seeding practices and the possibility that underutilized options might prove advantageous for future seeding efforts. We report results from an operational-scale experiment comparing the efficacy of practices for seeding Wyoming big sagebrush following fire in the northern Great Basin. This paper expands on previous work covering responses of Wyoming big sagebrush and other species to drill-seeding using different drill types (Ott et al., 2016); we present results of additional treatments including simulated aerial broadcast seeding in fall and winter and multiple seeding rates. Ott et al. (2016) found that Wyoming big sagebrush establishment was higher when seed was delivered through a minimum-till drill as opposed to a conventional drill, but they did not examine seeding rate effects nor compare drill-delivery with broadcasting. We hypothesized that seed delivery using either drill type would be more effective than broadcasting due to better seed placement and seed-soil contact. We also hypothesized that winter broadcasting would lead to higher establishment than fall broadcasting due to reduced incidence of frost damage associated with earlier germination. We expected that seedling densities would be higher at higher seeding rates, although mortality due to seedling competition might also be higher. We also anticipated that seeding success might vary among three contrasting sites included in our study.

Methods

Study Area

Three Wyoming big sagebrush sites in the northern Great Basin were selected following summer wildfires in 2007, 2008, and 2010 (Table 1). Each site was occupied by mature sagebrush before burning but burned with sufficient intensity to kill existing shrubs. The fire at Mountain Home likely burned with lower intensity than fires at the other sites, as evidenced by higher residual litter and rapid postfire

Table 1
Attributes of postfire seeding study sites in the northern Great Basin.[1]

	Mountain Home	Scooby	Saylor Creek
Location	42°58'42"N, 115°37'57"W	41°51"16"N, 113°2'46"W	42°39'43"N, 115°28'18"W
County, state	Elmore, ID	Box Elder, UT	Elmore, ID
Wildfire date	6 July 2007	22 September 2008	29 June 2010
Fall seeding date	29-30 October 2007	18-19 November 2008	27-28 October 2010
Winter seeding date	18 January 2008	29 January 2009	15 February 2011

[1] See Ott et al. (2016) for an expanded version of this table with ecological site and soils information.

[1] Seeding rates originally given on a per-weight basis are standardized here using the conversion factor 2.14 million seeds/lb. for Wyoming big sagebrush (Meyer, 2008).

establishment of cheatgrass (Ott et al., 2016). The Mountain Home and Saylor Creek sites are located on similar silty/loamy soils, ca. 40 km apart on the Snake River Plain in southwestern Idaho but differ in elevation (911 m at Mountain Home, 1204 m at Saylor Creek) and proximity to irrigated agricultural fields (< 1 km at Mountain Home, > 18 km at Saylor Creek). The Scooby site is located on loamy/sandy soils at ca. 1450 m in the Wildcat Hills north of the Great Salt Lake in northern Utah.

Weather data for the postfire study period at each site (Wang et al., 2012; CFCG, 2014) indicate that Scooby was generally colder and had more precipitation as snow than the other sites (Fig. S1). Above-average precipitation (> 80 mm) fell at Scooby during the first postfire summer and at Saylor Creek during the first winter and spring, whereas precipitation at Mountain Home was below average (< 50 mm) during each season from the first fall through the second winter (see Fig. S1). Further details about site characteristics, including postfire density and cover of dominant species, are described in Ott et al. (2016).

Experimental Treatments

Fall seeding treatments were applied in October — November of the wildfire years (Table 1) using the same equipment at each site. The experimental design was a randomized complete block with treatments assigned to rectangular, 30 m × 70 m plots within each of five blocks per site. Plots were separated by 3.05-m wide buffer strips seeded with bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve) and Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth). Drilling treatments were carried out with drill rows aligned parallel to the long axis of each plot. Blocks were fenced to exclude livestock during the course of the experiment.

Drill-seeding was done with a P & F Services "Kemmerer" rangeland drill and a Truax Co., Inc. "Roughrider" minimum-till drill (hereafter "conventional drill" and "minimum-till drill," respectively). Rice hulls were added to the seed mixes to facilitate drill calibration and seed flow from the drills (St. John et al., 2005). Both drills had 10 seed drops spaced 30.5 cm apart and were configured to place two different seed mixes in alternate rows. One mix contained relatively large seeds that were placed in drill furrows, while the other mix contained smaller seeds (including Wyoming big sagebrush) that were dispensed onto the soil surface between furrows (Table 2). We used the term "drill-delivery" when referring to this technique for dispensing small seeds, emphasizing the use of a drill apparatus but the lack of drill furrows.[2] On small-seed rows of the minimum-till drill, disks were removed and replaced with patterned imprinter wheels that pressed seeds into the soil. The conventional drill's disks could not be removed but were raised to prevent furrowing on small-seed rows, and seed tubes on these rows were pulled from the disk assembly and replaced with aluminum pipes to channel seeds closer to the soil surface. The conventional drill did not have imprinter wheels but utilized drag chains to improve seed-soil contact. These drill configurations were duplicated in all seeding treatments, as well as nonseeded controls where drilling was carried out with empty seed boxes using both drill types.

Seed mixes and seeding rates were adjusted for each site on the basis of site characteristics and seed availability (see Table 2). We sought the most local seed available from commercial vendors. Different source populations of Wyoming big sagebrush were seeded at Mountain Home (Lincoln/Blaine/Jerome Co, ID, 1230 m), Scooby (Sanpete Co, UT, 1460 m), and Saylor Creek (Power Co, ID, 1390 m). At each site, we applied three sagebrush seeding rates designated 1X (50-52 PLS m^{-2}), 5X (234-262 PLS m^{-2}), and 10X (495-525 PLS m^{-2}) (see Table 2). The 1X and 5X rates correspond approximately to the lower and higher ends, respectively, of standard recommended rates for Wyoming big sagebrush in postfire seedings, while the 10X rate is approximately twice the higher end of standard recommendations. Seeding rates of other seed-mix species were kept constant in all treatments; mixes thus differed only by sagebrush seeding rate (see Table 2).

Table 2
Postfire seed mixes and seeding rates at study sites in the northern Great Basin.

	Pure live seed m^{-2}		
	Mountain Home	Scooby	Saylor Creek
Broadcast mix			
Artemisia tridentata spp. *wyomingensis* (Wyoming big sagebrush)			
1X[1]	52	52	50
5X	262	234	250
10X	525	495	500
Ericameria nauseosa (Rubber rabbitbrush)	86	86	85
Poa secunda (Sandberg bluegrass, Mt. Home Germplasm)	91	91	100
Achillea millefolium (Western yarrow, Eagle Germplasm)	–	100	100
Penstemon deustus (Scabland penstemon)	76	–	–
Penstemon cyaneus (Blue penstemon)	–	76	–
Penstemon speciosus (Royal penstemon)	–	–	15
Drill mix			
Pseudoroegneria spicata (Bluebunch wheatgrass, Anatone Germplasm)	67	67	60
Elymus elymoides (Squirreltail, Toe Jam Creek & Emigrant Germplasm)	47	47	35
Achnatherum hymenoides ('Rimrock' Indian ricegrass)	51	51	50
Achnatherum thuberianum (Thurber's needlegrass)	–	–	30
Hesperostipa comata (Needle-and-thread)	–	–	20
Sphaeralcea munroana (Munro's globemallow)	93	93	40
Eriogonum umbellatum (Sulphur-flower buckwheat)	8	11	–
Astragalus filipes (Basalt milkvetch)	–	–	14

[1] Seeding rates differed for Wyoming big sagebrush but not other species.

Broadcast treatments were designed to simulate broadcasting from an aircraft over drilled surfaces in fall and winter. These treatments were identical to the 5X drill-delivery treatments with respect to seed mix composition, seeding rates (see Table 2) and seeding of the large-seed mix in alternate rows; but they differed in that the small-seed mix was broadcast by hand instead of delivered through the drills. Workers scattered 5X quantities of seed evenly across broadcast plots rather than in rows. The fall broadcast treatment was applied immediately following drilling in October — November, while the winter broadcast treatment was delayed until January — February (see Table 1). At all but one site (Saylor Creek), snow cover was present at the time of winter broadcasting.

Data Collection and Analysis

Density data for sagebrush and other seeded species were collected from experimental plots during May — June of the first 2 yr following seeding. Density was estimated by counting plants in 20 quadrats per plot (four quadrats on each of five transects) following protocols modified from Herrick et al. (2005) and Wirth and Pyke (2007). Transects were aligned parallel to the short axis of each plot, perpendicular to drill rows and separated by 10-m intervals. Along each transect, the first quadrat was placed at a randomly selected distance between 0 and 99 cm and subsequent quadrats were placed at 6-m intervals. Where necessary, quadrats were manually shifted to ensure that each quadrat contained exactly two drill furrows and two small-seed rows. Quadrats were 1 m × 0.5 m with the long side oriented parallel to the transect axis, except at Saylor Creek, where 1 m × 1 m transects were used during the first year. Data were collected from the same transects both years, but quadrat placements were rerandomized the second year. Density values were standardized to account for different quadrat sizes and summed across quadrats within plots before analysis.

We used a generalized linear mixed modeling approach (GLIMMIX procedure in SAS 9.3; SAS Institute, Inc., 2011) to infer effects of seeding

[2] The term "drill-broadcast" as used by Ott et al. (2016) is equivalent to "drill-delivery" of the small seed mix onto the soil surface.

technique, timing, seeding rate and drill-type on sagebrush density during the 2-yr study period at each site. Treatments were grouped into two sets that were analyzed separately for each site (Table 3). The first set contained all 5X treatments, allowing comparison of different drill types (conventional vs. minimum-till), seed-delivery techniques (drill vs. broadcast), and timing of broadcast seeding (fall vs. winter) at a constant (5X) seeding rate (see Table 3). The second set contained multiple seeding rates (1X, 5X, 10X) for drill-delivery treatments applied in the fall using both drill-types (see Table 3). Drilled/nonseeded treatments were included as controls in both sets of analyses (see Table 3). Drill type, delivery/timing treatment (or seeding rate) and year, plus interactions of these variables, were treated as fixed effects with block as a random effect in statistical models. We applied a $\log(x+1)$ transformation to sagebrush density values to improve data properties for modeling using a Gaussian reference distribution. Tukey's HSD was used for mean comparisons of fixed effects at $\alpha = 0.05$, after removing nonsignificant interaction terms from our models. Results were graphed using the R package "ggplot2" (Wickham, 2009; R Core Team, 2012).

We also examined whether year-to-year changes in density were proportionally different among seeding rates and drill types using a binomial counts modeling approach in GLMMIX (SAS Institute, Inc., 2011). Our response variable was second-year density as a proportion of the total density for both years. As in other analyses described earlier, we modeled each site separately, with drill type and seeding rate (1X, 5X, and 10X) as fixed effects and block as a random effect.

Results

Seeding Technique and Timing

When comparing treatments differing by seed delivery technique and timing, we found significant treatment effects on sagebrush density at all sites, although the pattern and magnitude of effects differed among sites, years, and drill types (see Fig. 1, Table S1). The delivery/timing × drill-type interaction was significant only at Saylor Creek (see Table S1), where drill-delivery with the minimum-till drill (equipped with imprinter wheels) resulted in higher sagebrush density than either drill-delivery with the conventional drill (equipped with drag chains) or broadcasting in the fall following minimum-till drilling (Fig. 1C). Other seeding treatment combinations at Saylor Creek (fall broadcast following conventional drilling and winter broadcast following either type of drilling) had low sagebrush densities that were not significantly different from the nonseeded control treatments (see Fig. 1C). Densities in winter broadcast treatments at Mountain Home and Scooby likewise did not differ from nonseeded controls (see Fig. 1A−B). Fall broadcast and drill-delivery treatments at Mountain Home and Scooby had higher densities than controls during at least 1 of 2 yr, but the magnitude of these treatment differences was generally lower than at Saylor Creek (see Fig. 1). Between yr 1 and 2, sagebrush density either decreased or remained stable within treatments at Saylor Creek and Mountain Home but increased slightly at Scooby (see Fig. 1).

Seeding Rate

Higher seeding rates generally resulted in higher sagebrush densities, although density differences between adjacent rate increments were not always significant (Fig. 2). Densities at the 1X rate were not significantly greater than nonseeded controls at any site with either drill type (see Fig. 2). The 5X rate had higher densities than 1X at Mountain Home and Saylor Creek but not Scooby for both drill types (see Fig. 2). The 10X rate had higher densities than 5X at Scooby (both drill types) and at Saylor Creek when seeded with the minimum-till drill (see Fig. 2).

Drill type effects and/or drill type × seeding rate interactions were significant at all sites when modeling sagebrush density (Table S2), and wherever densities differed between drill types at a given rate, the minimum-till drill always had higher density (see Fig. 2). Sagebrush density appeared to be highest at Saylor Creek, especially in the minimum-till 10X treatment, where densities reached 4.1 plants m^{-2} in yr 1 and 2.0 plants m^{-2} in yr 2 (see Fig. 2). By comparison, yr 2 densities in the minimum-till 10X treatment were 0.8 plants m^{-2} at Scooby and 0.3 plants m^{-2} at Mountain Home (see Fig. 2). Density decreased between years at Mountain Home and Saylor Creek (see Fig. 2).

Binomial count models showed that the proportion of yr 2 density counts relative to total (yr 1 + yr 2) density counts did not differ significantly between drill-type and seeding rate treatments at Saylor Creek (Table S3), suggesting that observed density decreases from the first to second year were proportionally equivalent among treatments. We were unable to obtain results from this modeling approach for Mountain Home and Scooby because models did not converge, likely due to high numbers of zeros in datasets for these sites.

Discussion

The rationale for seeding Wyoming big sagebrush following wildfire is to accelerate recovery, which would otherwise depend on depleted residual seed banks and seed dispersal from unburned stands (Lesica et al., 2007; Schlaepfer et al., 2014; Shinneman and McIlroy, 2016). Consistent with the expected pattern, Wyoming big sagebrush recruitment during the first 2 postfire yr at our study sites was negligible in the absence of active seeding but was higher in at least some seeding treatments. We found that drill-delivery was a more effective technique than fall broadcast seeding (on recently drilled surfaces), but only at Saylor Creek, the site where overall seedling densities were highest and conditions presumably most favorable for establishment. Likewise, the greater effectiveness of drill-delivery with the minimum-till drill compared with the conventional drill (see also Ott et al., 2016) was

Table 3
Experimental treatments included in analyses of sagebrush establishment following fire and seeding at study sites in the northern Great Basin. The six treatments shown were duplicated using two contrasting drill types (conventional and minimum-till) and were replicated in five blocks at each site (each block containing one plot of each treatment/drill-type combination). Analyses compare different seed delivery techniques/timings at a uniform (5X) seeding rate (Set 1; see Fig. 1) or different seeding rates with a uniform (drill) delivery technique (Set 2; see Fig. 2).

Treatment name	Seeded	Seed delivery[1]	Seeding timing[2]	Seeding rate[3]	Analysis Set 1	Analysis Set 2
Drilled/nonseeded (Control)	No	—	—	—	No seed	No seed
Drill-delivery (1X)	Yes	Drill	Fall	1X	—	1X
Drill-delivery (5X)	Yes	Drill	Fall	5X	Drill	5X
Drill-delivery (10X)	Yes	Drill	Fall	10X	—	10X
Fall broadcast	Yes	Broadcast	Fall	5X	Fall broadcast	—
Winter broadcast	Yes	Broadcast	Winter	5X	Winter broadcast	—

[1] Seed delivery techniques for Wyoming big sagebrush/small-seed mix: drill indicates seed dispensed from a drill onto soil surface; broadcast, seed scattered by hand following drill-seeding of large-seed mix.
[2] Seeding timing for Wyoming big sagebrush/small-seed mix; see Table 1.
[3] Seeding rates for Wyoming big sagebrush; see Table 2.

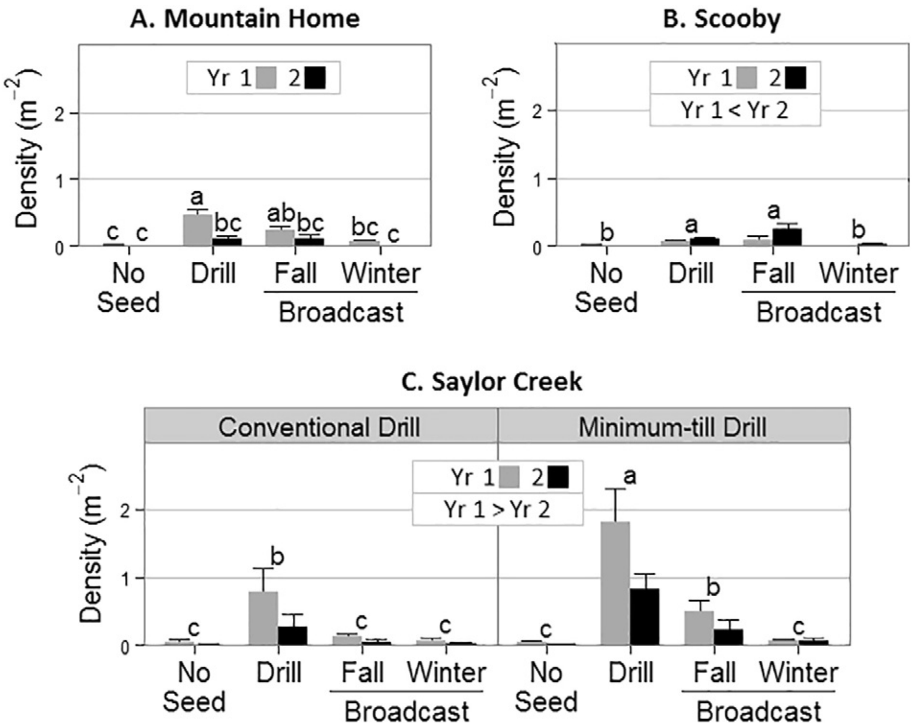

Figure 1. Wyoming big sagebrush density during 2 postfire yr at three sites in the northern Great Basin (A, Mountain Home; B, Scooby; C, Saylor Creek), showing effects of treatments differing by seed delivery technique (drill and broadcast) and timing of broadcast seed delivery (fall and winter) (see Table 3). Two different drill-types (conventional and minimum-till) were used in each case with either empty seed boxes (control treatment, "no seed"), large and small seeds in separate boxes (drill treatment), or large seeds drilled from boxes followed by broadcasting small seeds (fall and winter broadcast treatments). Wyoming big sagebrush was included in the small-seed mix at ca. 250 PLS m^{-2} (see Tables 2-3). Bars are means, and error bars are standard errors. Within sites, means with the same letter are not significantly different ($P < 0.05$). Drill types are not displayed for Mountain Home and Scooby because the effect of drill type was not significant. Significant year effects are shown for Scooby and Saylor Creek, whereas separate letters for each year at Mountain Home indicate a significant treatment × year interaction (see also Table S1).

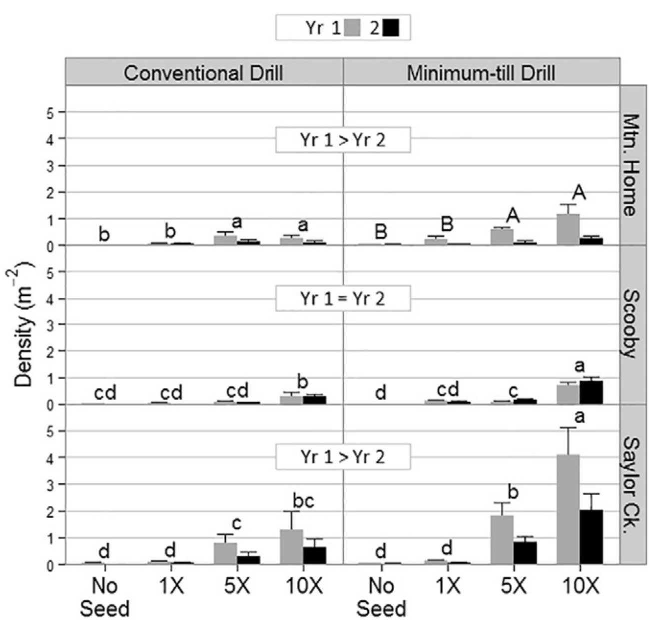

Figure 2. Wyoming big sagebrush density during 2 postfire yr at three sites in the northern Great Basin (Mountain Home [Mtn. Home], Scooby, and Saylor Creek [Saylor Ck.]), showing effects of seed delivery using different drill types (conventional and minimum-till) at different seeding rates (No Seed = 0 PLS m^{-2}, 1X = ca. 50 PLS m^{-2}, 5X = ca. 250 PLS m^{-2}, 10X = ca. 500 PLS m^{-2}) (see Table 3). Bars are means, and error bars are standard errors. Within sites (horizontal panels), means with the same case letter are not significantly different ($P < 0.05$). Different case letters for Mountain Home indicate a significant effect of drill type (minimum-till > conventional) but a nonsignificant drill type × year interaction, unlike Scooby and Saylor Creek, where this interaction was significant. Seeding rate × year interactions were nonsignificant, but year effects were significant at Mountain Home and Saylor Creek (see also Table S2).

most apparent under more favorable conditions (Saylor Creek) and/or at higher seeding rates. These results highlight the interacting effects of seeding technique, seeding rate, and site conditions for determining seeding effectiveness. Studies involving other species have also demonstrated that limiting conditions at the time of seeding (e.g., Young et al., 1994; Caldwell et al., 2009; Bernstein et al., 2014) or inadequate seeding rates (e.g., Frances et al., 2010; Hulvey and Aigner, 2014) can mask the effects of otherwise suitable seeding techniques.

Higher sagebrush establishment in drill-delivery than broadcast treatments at Saylor Creek was likely due to enhanced seed placement. Many of the evenly scattered seeds of the broadcast treatment could have landed in drill furrows, where they would be susceptible to excessive burial and competition with seeded grasses if they germinated. Sagebrush seeds delivered through the drill, in contrast, were concentrated in strips between drill furrows and were also likely better integrated into the soil through the action of imprinters or drag chains. Of the two drill types tested, the minimum-till drill with imprinters resulted in higher sagebrush establishment than the conventional drill with drag chains, not only in drill-delivery treatments (as noted previously by Ott et al., 2016) but also in the fall broadcast treatment. In the latter case, the effect of drill type on sagebrush establishment must have been indirect (e.g., due to differences in soil surface characteristics created by each drill). The minimum-till drill appears to have provided a better surface for broadcast seeds than the conventional drill, perhaps because narrower furrows of the minimum-till drill led to fewer seeds encountering furrow-related problems.

Poor sagebrush establishment in the winter broadcast treatment contradicted our hypothesis that delayed seeding would reduce the risk of frost-induced mortality on germinating seedlings. Frost sensitivity of Wyoming big sagebrush in the germination/emergence stage is poorly understood (Schlaepfer et al., 2014), although adverse effects of low temperatures have been documented at later stages (Loik and Redar, 2003; Brabec et al., 2017). We hypothesized that newly germinated Wyoming big sagebrush would exhibit frost sensitivities similar to those documented for perennial bunchgrasses of sagebrush habitats (Boyd and James, 2013; Boyd and Lemos, 2013, 2015). However, our results suggest that any deleterious effects of increased frost exposure in fall-seeded plants were overshadowed by advantages of earlier seeding; for example, early-germinating plants that survive the winter would have an advantage arising from greater growth before periods of dessication stress in spring or summer (Boyd and Lemos, 2015). An alternative possibility is that seedbed conditions were better in the fall, providing more safe sites for broadcast seeds. Because natural dispersal of Wyoming big sagebrush seeds tends to occur in the fall (Schlaepfer et al., 2014), seeds might be better adapted for integration into the soil before the onset of winter conditions.

Although Klott and Ketchum (1991) found that broadcasting onto snow was an effective strategy for seeding mountain big sagebrush (*A. tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle), we found that snow cover at Mountain Home and Scooby made little difference compared with Saylor Creek, where snow was lacking at the time of winter broadcasting. Different results might be expected at mountain big sagebrush sites, where winter snows are deeper and more lasting than the Wyoming big sagebrush sites we studied.

The pattern of increasing density with increasing seeding rate that we observed is consistent with results of other studies examining sagebrush seeding rates (Boltz, 1994; Booth et al., 1999; Williams et al., 2002; Hild et al., 2006). We found that Wyoming big sagebrush establishment in drill-delivery treatments was statistically indistinguishable from background recruitment when seeded near the lower end of standard recommended seeding rates (1X: ca. 50 PLS m^{-2}), whereas notably higher establishment could be achieved using seeding rates near the upper end (5X: ca. 250 PLS m^{-2}), and especially at even higher rates approximately double typical recommendations for postfire seedings (10X: ca. 500 PLS m^{-2}). Although the percentage of seeds reaching the seedling stage was < 1% in all cases, seedling establishment was nevertheless high enough in some cases to consider the treatments successful. If we define "success" as attainment of target densities comparable with mature Wyoming big sagebrush stands (i.e., mean densities ≥ 0.5 plants m^{-2}; Davies and Bates, 2010), we would conclude that there were three instances of successful 10X treatments (minimum-till and conventional drill at Saylor Creek, minimum-till drill at Scooby) and one instance of a successful 5X treatment (minimum-till at Saylor Creek) at the time of second-year data collection (see Fig. 2). Given the possibility of continuing seedling mortality with little new recruitment in subsequent years (Schuman and Belden, 2002; Hild et al., 2006), target densities at the 2-yr mark might need to be set even higher if they are expected to translate to mature stand densities within a single generation. In practice, however, lower target densities (on the order of 0.1 plants m^{-2}) are often considered sufficient for Wyoming big sagebrush during the early years following postfire seeding (Anne Halford, pers. comm.), under the assumption that gradual infilling of low-density stands will occur once seeded plants mature and produce seeds (McArthur and Stevens, 2004). Seed production could potentially begin 2 − 3 yr after seedling establishment under optimal circumstances (Schlaepfer et al., 2014). At a target mean density of 0.1 plants m^{-2}, most of the 10X and 5X treatments would be considered successful in yr 2 at all three sites. The 1X treatments, on the other hand, would likely be considered unsuccessful under any evaluation scheme because establishment was marginal relative to the alternative of not seeding.

We hypothesized that competition among establishing sagebrush seedlings might be more intense at higher seeding rates, leading to density-dependent mortality, but did not find evidence in support of this hypothesis. Although density decreased between years at Mountain Home and Saylor Creek, the decrease appeared to be (at least at Saylor Creek where binomial counts modeling was successful) directly proportional to total density independent of the magnitude of the total. In other words, the net loss of sagebrush observed from yr 1 to 2 at Saylor Creek was not proportionally higher in treatments with higher sagebrush establishment, as might be expected if density-dependent competitive effects were the cause of mortality. In contrast to our results, Owens and Norton (1989) found evidence of density-dependent mortality among seedlings of basin big sagebrush (*A. tridentata* Nutt. ssp. *tridentata*) during periods of water stress, especially among seedlings with an available area < 300 mm^2. The sagebrush seedlings at our study sites were likely much more widely spaced that those observed by Owens and Norton (1989), even when taking into account seedling concentration in rows, and we suspect that our seedlings had not reached a critical density at which seedling competition might cause mortality.

Because the closest neighbors to sagebrush seedlings would in most cases have been members of other species, interspecific competition was probably more intense than intraspecific competition at our study sites. Negative effects of neighboring herbaceous species on sagebrush seedling growth and survival have been documented (Schuman et al., 1998; DiCristina and Germino, 2006; Brabec et al., 2015), although positive effects are also possible (Schuman and Belden, 2002). As we have noted, competition between sagebrush seedlings and species of the large-seed mix was likely reduced in treatments where they were segregated into different rows, but the sagebrush in these treatments would have still be exposed to competition from other species of the small-seed mix (see Table 2), as well as nonseeded species such as cheatgrass. Sagebrush seedlings might have been better shielded from competition had sagebrush been seeded in rows of its own, but only if the net effect of the other small-seed mix species was actually negative rather than positive or neutral, which we were not able to determine from our study. Our experiment was not designed to test the effects of different combinations and seeding rates of species seeded alongside Wyoming big sagebrush, but such experiments would offer further insights into optimal seeding practices.

Sagebrush density at Scooby remained stable or even increased between years in some treatments (see Figs. 1-2). These density increases might reflect establishment that occurred during the summer following first-year data collection but could also have arisen from seeds that carried over into the cool season of the second year. Despite a general pattern of nondormancy for Wyoming big sagebrush seeds (Meyer and Monsen, 1992), establishment has been reported from seeds that apparently did not germinate until 1 − 3 yr following seeding (Schuman et al., 1998; Hild et al., 2006). Such cases of seed carry-over might involve seeds that become dormant upon burial followed by release of dormancy upon relocation to the surface (Wijayratne and Pyke, 2012). Although seed carryover has the potential to lengthen the window of Wyoming big sagebrush establishment following postfire seeding, chances of successful establishment during the second year and beyond may be diminished in areas where exotic annual populations undergo a postfire rebound (Shinneman and McIlroy, 2016).

As discussed by Ott et al. (2016), different postfire conditions at our three study sites likely contributed to different levels of seeded plant establishment and mortality. High first-year establishment of Wyoming big sagebrush at Saylor Creek relative to lower establishment at Mountain Home and Scooby appears to be related to precipitation differences, especially precipitation during the first winter and spring, which was approximately two to three times higher at Saylor Creek than the other sites (see Fig. S1). Winter/spring precipitation is important for Wyoming big sagebrush because most seed germination and seedling emergence occurs during this period (Schlaepfer et al., 2014; Shinneman and McIlroy, 2016). Summer is typically a period of mortality for young sagebrush seedlings (Owens and Norton, 1989; Williams et al., 2002; Boyd and Obradovich, 2014; Schlaepfer et al., 2014), but favorable summer conditions (e.g., high precipitation/low temperatures) may enhance seedling survival and even allow new seedling recruitment (Schuman et al., 1998). Second-year declines of Wyoming big sagebrush at Saylor Creek and Mountain Home likely reflect mortality during summers when precipitation was below average (< 30 mm), in contrast to Scooby where summer precipitation approached 100 mm (see Fig. S1). Competition from cheatgrass and other exotic annuals could have also contributed to second-year seedling mortality at Mountain Home and Saylor Creek, but this competition effect was probably weaker at Scooby, where exotic annual cover remained relatively low during the timeframe of our study (Ott et al., 2016). Other relevant factors that might have affected sagebrush mortality include low winter temperatures (Loik and Redar, 2003; Brabec et al., 2017), jackrabbit herbivory (McAdoo et al., 2013), and the degree to which seeded sagebrush plant materials were locally adapted (Brabec et al., 2015; Richardson et al., 2015).

Implications

Keeping in mind that our study sites represent only a portion of the range of Wyoming big sagebrush, and that significant treatment differences were observed primarily at only one of the sites, we assert that our study provides useful information for postfire sagebrush seeding efforts. Our results do not contradict previous appraisals of the difficulty of establishing Wyoming big sagebrush due to limiting weather conditions but do suggest that the chances of successful establishment can be increased by following certain practices. Where possible, seed delivery using a drill, especially with a minimum-till drill/imprinter combination, would be preferable to aerial broadcasting. Drill-delivery appears to favor sagebrush establishment by optimizing both lateral and vertical seed placement. If aerial broadcasting is deemed the best option, it should be done in the fall soon after drilling operations rather than during the winter.

Furthermore, drill-delivery of Wyoming big sagebrush seed is likely to be most successful when applying seeding rates higher than typical previous recommendations. Our results call into question the common practice of using conservative seeding rates for sagebrush on postfire seedings, which may have contributed to the limited success of past seeding attempts. Conservative seeding rates can be defended with the argument that natural spread from low-density stands may be sufficient for long-term recovery (Stevenson et al., 1995; McArthur and Stevens, 2004), but managers hoping for more rapid postfire recovery may wish to consider using higher rates, as have been used in mine reclamation settings with a clear-cut need for bond release within a designated time period (Williams et al., 2002). Our results suggest that these practices should enhance sagebrush establishment over the short term (1 − 2 years), which in turn should improve the odds of maintaining sagebrush over the longer term, although further research is needed to verify long-term effects of these practices on development and persistence of sagebrush stands.

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