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Restoration of Sagebrush in Crested Wheatgrass Communities: Longer-Term Evaluation in Northern Great Basin☆

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ABSTRACT

Crested wheatgrass (*Agropyron cristatum* [L] Gaertm. and *Agropyron desertorum* [Fisch.] Schult.), an introduced bunchgrass, has been seeded on millions of hectares of sagebrush steppe. It can establish near-monocultures; therefore, reestablishing native vegetation in these communities is often a restoration goal. Efforts to restore native vegetation assemblages by controlling crested wheatgrass and seeding diverse species mixes have largely failed. Restoring sagebrush, largely through planting seedlings, has shown promise in short-term studies but has not been evaluated over longer timeframes. We investigated the reestablishment of Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) in crested wheatgrass communities, where it had been broadcast seeded (seeded) or planted as seedlings (planted) across varying levels of crested wheatgrass control with a herbicide (glyphosate) for up to 9 yr post seeding/planting. Planting sagebrush seedlings in crested wheatgrass stands resulted in full recovery of sagebrush density and increasing sagebrush cover over time. Broadcast seeding failed to establish any sagebrush, except at the highest levels of crested wheatgrass control. Reducing crested wheatgrass did not influence density, cover, or size of sagebrush in the planted treatment, and therefore, crested wheatgrass control is probably unnecessary when using sagebrush seedlings. Herbaceous cover and density were generally less in the planted treatment, probably as a result of increased competition from sagebrush. This trade-off between sagebrush and herbaceous vegetation should be considered when developing plans for restoring sagebrush steppe. Our results suggest that planting sagebrush seedlings can increase the compositional and structural diversity in near-monocultures of crested wheatgrass and thereby improve habitat for sagebrush-associated wildlife. Planting native shrub seedlings may be a method to increase diversity in other monotypic stands of introduced grasses.

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Introduction

Seeding exotic forage species is a widespread vegetation manipulation that may result in near-monocultures of the seeded species. In the western United States, crested wheatgrass (*Agropyron cristatum* [L.] Gaertm. and *Agropyron desertorum* [Fisch.] Schult.) is a non-native perennial bunchgrass that is one of the most commonly seeded species in rangelands (Roger and Lorenz, 1983; Maryland et al., 1992; Henderson and Naeth, 2005). Millions of hectares of sagebrush rangeland, predominantly Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis* [Beetle & A. Young] S.L. Welsh), have been planted to crested wheatgrass, often to prevent exotic plant dominance. Crested wheatgrass was originally introduced in sagebrush rangelands to compete with the exotic forb, halogeton (*Halogeton glomeratus* [M. Bieb.] C.A. Mey), a plant toxic to sheep (Miller, 1956; Frischknecht, 1968; Young et al., 1979; Pemberton, 1986). Crested wheatgrass was also used to reclaim abandoned dry-land farms and increase forage production on overgrazed sagebrush rangelands (Morris et al., 2014). It also establishes well, decreases erosion and runoff risk, and increases livestock forage (Pellant and Lysne, 2005; Romo, 2005; Waldron et al., 2005; Hansen and Wilson, 2006). In Wyoming big sagebrush communities, crested wheatgrass is often seeded after disturbances instead of native bunchgrasses because it establishes better (Robertson et al., 1966; James et al., 2012; Davies et al., 2015), is less

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expensive, and is more available (Asay et al., 2001; Epanchin-Niell et al., 2009; Boyd and Davies, 2010, 2012). The use of crested wheatgrass has continued, especially for postfire rehabilitation (Davies et al., 2011; Knutson et al., 2014), where it can suppress exotic annual grasses (Arredondo et al., 1998; Davies et al., 2010; Davies et al. 2015), which otherwise may dominate after wildfires in drier sagebrush communities (Chambers et al., 2007).

Crested wheatgrass can alter the composition, function, and structure of plant communities, often forming near-monocultures because it is highly competitive with native vegetation (Hull and Klomp, 1967; Asay et al., 2001), outrecruits native vegetation by 10-fold (Nafus et al., 2015; Hamerlynck and Davies, 2019), dominates the seedbank, and interferes with the recruitment and growth of native vegetation (Marlette and Anderson, 1986; Henderson and Naeth, 2005; Gunnell et al., 2010). Crested wheatgrass near-monocultures are often characterized as new steady states (Hull and Klomp, 1967; Looman and Heinrichs, 1973; Marlette and Anderson, 1986), though there are exceptions (McAdoo et al., 1989; Nafus et al., 2016; Williams et al., 2017). These novel plant communities often do not provide the habitat required by sagebrush obligate wildlife (McAdoo et al., 1989). Therefore, increasing native vegetation in crested wheatgrass near-monocultures is desired to increase diversity and improve habitat for native wildlife (Vale, 1974; Reynolds and Trost, 1981; Parmenter and MacMahon, 1983; McAdoo et al., 1989).

Efforts to substantially increase native plant species in crested wheatgrass have largely failed in the sagebrush steppe as crested wheatgrass rapidly recovers from control treatments and native vegetation often fails to establish at these sites even with reduced crested wheatgrass competition because of environmental stress (e.g., Hulet et al., 2010; Fansler and Mangold, 2011; McAdoo et al., 2017). Repeated control of crested wheatgrass is likely necessary to open crested wheatgrass stands for native vegetation establishment (Morris et al., 2019) but may also facilitate invasion by exotic annual grasses and forbs (Hulet et al., 2010; McAdoo et al., 2017). Successful restoration of crested wheatgrass–dominated sagebrush rangelands to a diverse composition of native species at meaningful scales is, therefore, improbable using the current most commonly applied and economical techniques.

Instead of attempting to restore the full complement of native plant species or functional groups, it may be more opportune to focus on restoring Wyoming big sagebrush. Sagebrush has a large influence on resources in sagebrush communities because they are the overstory species and create microenvironments within the community (Davies et al., 2007a; Prevéy et al., 2010). Reestablishing sagebrush in crested wheatgrass stands may assist in mitigating the widespread loss of habitat for sage grouse and other sagebrush-associated wildlife (Knick et al., 2003; Schroeder et al., 2004; Davies et al., 2011). Reducing the monotypic characteristics of crested wheatgrass by transitioning to sagebrush-crested wheatgrass communities would increase habitat for sagebrush-associated wildlife (McAdoo et al., 1989; Kennedy et al., 2009). Successful addition of sagebrush to crested wheatgrass stands would also diversify the structure and function of these exotic grasslands. Crested wheatgrass hinders sagebrush seedling survival, but once established, sagebrush plants are likely to persist because of high niche differentiation (Gunnell et al., 2010). This suggests that, once established, sagebrush would be less likely to be displaced by crested wheatgrass than herbaceous vegetation.

Limited information exists regarding establishing sagebrush in crested wheatgrass stands. Establishing sagebrush from seed in crested wheatgrass stands has largely been unsuccessful (Hulet et al., 2010; Fansler and Mangold, 2011; Davies et al., 2013; McAdoo et al., 2017). However, at high rates of crested wheatgrass control, some sagebrush has established from broadcasted seed (Davies et al., 2013). Crested wheatgrass is highly competitive (Marlette and Anderson, 1986; Henderson and Naeth, 2005; Gunnell et al., 2010), therefore reducing crested wheatgrass is likely needed when attempting to reestablish sagebrush from seed. Greater natural recovery of sagebrush occurred in long-term grazed compared with not-grazed crested wheatgrass stands, probably because grazing reduced the competitiveness of crested wheatgrass (Nafus et al., 2016). Crested wheatgrass is most competitive with emergent sagebrush seedlings (Gunnell et al., 2010); therefore, it may be more effective to plant sagebrush seedlings to bypass the vulnerable seed to seedling stage. Furthermore, previous research suggests that sagebrush can be successfully established as planted seedlings in crested wheatgrass stands (e.g., Davies et al., 2013; McAdoo et al., 2013). However, prior work has generally been short term and thereby the longer-term effects of broadcast seeding sagebrush and planting sagebrush seedlings in crested wheatgrass stands are largely unknown.

The purpose of this study was to evaluate the longer-term effects of broadcast seeding sagebrush and planting sagebrush seedlings across varying levels of crested wheatgrass control. We accomplished this by resampling experimental plots established by Davies et al. (2013) for up to 9 yr post seeding/planting. We expected sagebrush density and cover to be greater in crested wheatgrass stands with 1) increased crested wheatgrass control and 2) planting sagebrush as seedlings compared with broadcast seeding. We also expected that herbaceous cover and density would be lower in stands where sagebrush establishment was more successful because greater sagebrush cover typically causes decreased herbaceous vegetation (Rittenhouse and Sneva, 1976; Davies and Bates, 2019).

Methods

We conducted the study on the Malheur National Wildlife Refuge (42°57′40″N, 118°49′30″W), approximately 75 km south of Burns, Oregon. The study sites were drill seeded with crested wheatgrass in 1981 after a wildfire. Before crested wheatgrass control treatments, study sites were monotypic crested wheatgrass stands with no sagebrush. On the basis of site characteristics, potential natural vegetation would have largely consisted of Wyoming big sagebrush, Thurber needlegrass (*Achnatherum therberianum* [Piper] Barkworth), bluebunch wheatgrass (*Psuedoregneria spicata* [Pursh] A. Löve), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), and Sandberg bluegrass (*Poa secunda* J. Presl). Soils at the study sites were Xeric Haplodurids and Xeric Aridurids. Elevation ranged from 1 275 to 1 300 m above sea level, and average annual precipitation ranged from 280 to 300 mm. Slopes were slight (0–5%), and aspect ranged from south to east. Crop yr precipitation (Oct. 1–Sept. 30) in the planting/seeding yr and next 2 yr after were 99% (2009), 100% (2010), and 150% (2011) of the long-term (30 yr) average at the Burns, Oregon airport weather service office. Study sites had not been grazed by livestock for > 10 yr before initiating the study and livestock were excluded during the study. Wildlife were not restricted from the study sites.

Experimental Design and Measurements

A randomized complete block design with six blocks was used to evaluate establishing sagebrush in monotypic crested wheatgrass stands. Sites were 0.5–1 km from each other and were used to account for differences in environmental characteristics (soils, slope, and aspect). Environmental characteristics were uniform within blocks. Each site consisted of eight 3 × 6 m treatment plots with 0.5-m buffers between them. Treatments were randomly assigned to 3 × 6 m plots within block. Treatments were the factorial combination of four different rates of glyphosate and two different sagebrush establishment methods. Glyphosate (Pronto Big N' Tuf) was mixed 50:50 with water and brushed on 0%, 25%, 50%, or 75% of the crested wheatgrass plants in treatment plots in late April and early June 2009. Wyoming big sagebrush was broadcast (by hand) seeded at 1 000 PLS per m^2 (seeded) or planted as seedlings (planted) at densities of one seedling per m^2 in treatment plots in September 2009. Density Wyoming big sagebrush in fully occupied communities in this region is 0.5 individuals per m^2 (Davies and Bates, 2010). Wyoming big sagebrush seedlings were grown by sowing five sagebrush seeds in seedling cone containers in a three-season greenhouse in May 2009. Cone containers were 3.8 cm diameter at the top and 21 cm tall. Seedlings were thinned to one individual per cone container 3 wk after emergence and were 10 – 15 cm tall at time of planting. Seedlings were planted by digging a hole ~21 cm deep, extracting the seedling from the container, placing the seedling in the hole, and pressing soil around the roots of the seedling.

Herbaceous vegetation foliar cover and density were measured along two, 6-m transects in each treatment plot in July of 2016, 2017, and 2018 (seventh, eighth, and ninth yr post seedling/planting). Transects were spaced 1 m from the treatment plot edge and each other. On each transect, five 0.2-m^2 quadrats were located at 1-m intervals. Herbaceous vegetation cover by species, litter, and bare ground was visually estimated in the 0.2-m^2 quadrats. Herbaceous density by species was also measured by counting all individuals rooted in the 0.2-m^2 quadrats. Sagebrush density was measured in July of 2016, 2017, and 2018 by dividing the treatment plot into thirds, each third being 1 × 6 m, and counting all sagebrush rooted inside the 1 × 6 m subplots. Sagebrush height and canopy area were determined by measuring all sagebrush plants in each treatment plot in July of 2016, 2017, and 2018. Sagebrush height was measured from the ground to the highest point of the sagebrush plant (excluding reproductive stems). Canopy area was determined by measuring the longest diameter of the sagebrush canopy and then the diameter perpendicular to the center of the first measurement. Canopy area was then calculated as elliptical area using the two measured diameters of the sagebrush canopy. Sagebrush cover was calculated by summing all the sagebrush canopy areas from the plot, dividing by the plot area, and multiplying by 100. Sagebrush canopy volume was calculated using the elliptical area and height measurement (Thorne et al., 2002).

Statistical Analyses

We used repeated measures analysis of variance (ANOVA) using the mixed models procedure (Proc Mixed) in SAS v. 9.4 (SAS Institute Inc., Cary, NC) with year as the repeated variable to determine the influence of different levels of crested wheatgrass control and establishment method (seeds or seedlings) on response variables. Fixed variables were control level, planting method, and their interactions. Site and site by treatment interactions were considered random effects. Covariance structure was determined using Akaike's Information Criterion (Littell et al., 1996). For analyses, herbaceous cover and density were separated into five groups: Sandberg bluegrass, large perennial bunchgrass (almost completely [> 99%] composed of crested wheatgrass), exotic annual grasses, perennial forbs, and annual forbs. The annual forb group largely consisted of an exotic annual, desert matwort (*Alyssum desertorum* Stapf). The perennial forb group was solely composed of native species. Sandberg bluegrass was treated as a separate group from other bunchgrasses because it matures early, is shorter in stature, and responds differently to disturbance. The exotic annual grass group was almost solely (> 99%) composed of cheatgrass (*Bromus tectorum* L.). Tukey's honestly significant difference was used for mean separations. Significance level for all tests was set at $P \leq 0.05$. Means were reported with standard errors. Interactions were only reported if significant ($P \leq 0.05$).

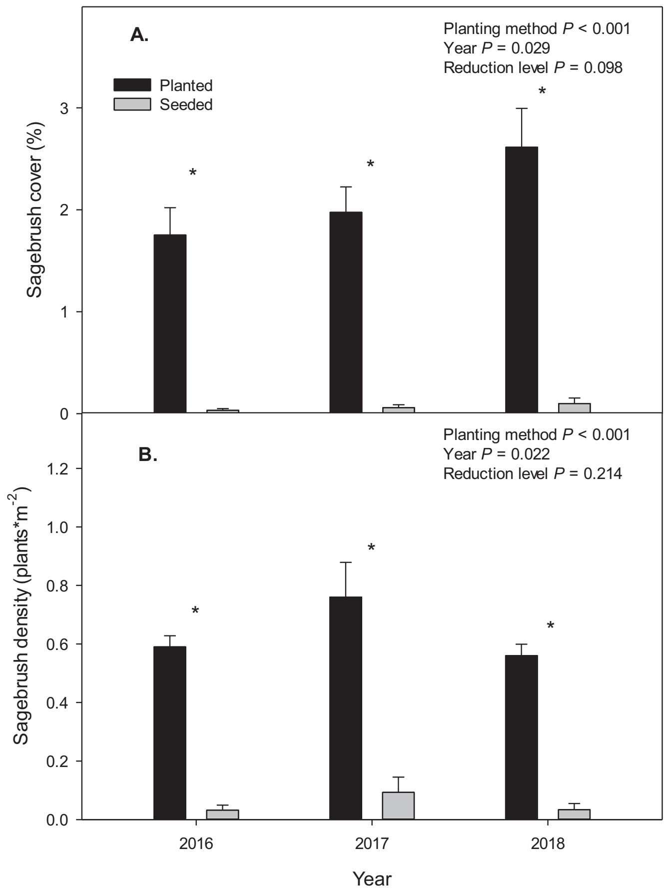

Figure 1. Sagebrush cover (**A**) and density (**B**) in the planted (planting sagebrush seedlings) and seeded (broadcast seeding sagebrush) treatments in 2016, 2017, and 2018 (seventh, eighth, and ninth yr post seedling/planting). Asterisk (*) indicates difference ($P < 0.05$) between treatments in that year.

Results

Sagebrush

Sagebrush cover varied by planting method and across years (Fig. 1A, $P < 0.001$ and $= 0.029$, respectively). Sagebrush cover was greater in the planted than seeded treatment. Sagebrush cover increased with time, particularly with planting seedlings. Level of crested wheatgrass control did not influence sagebrush cover across planting methods ($P = 0.098$). Sagebrush density varied by planting method and among years (see Fig. 1B; $P < 0.001$ and $= 0.022$, respectively), but not by reduction level ($P = 0.214$). Sagebrush density was on average 12× greater where seedlings were planted compared with seeded areas. Sagebrush canopy volume was greater in areas planted with seedlings compared with areas that were broadcast seeded (Fig. 2A; $P < 0.001$). Sagebrush canopy volume increased over time ($P = 0.002$) and was not influenced by crested wheatgrass control level ($P = 0.371$). Sagebrush height was influenced by the interaction between planting method and reduction level ($P < 0.001$) but did not vary among years ($P = 0.053$). In the broadcast seeding treatment, sagebrush height increased with greater reductions of crested wheatgrass but was generally similar among reduction levels when planting seedlings. Sagebrush height was greater in the planted compared with the seeded treatment (see Fig. 2B; $P < 0.001$).

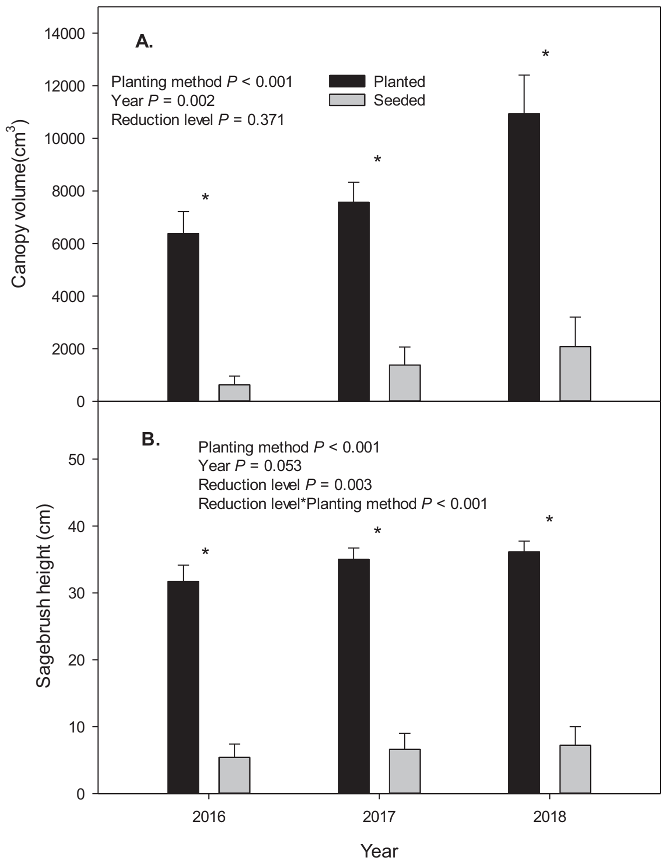

Figure 2. Sagebrush canopy volume (**A**) and height (**B**) in the planted (planting sagebrush seedlings) and seeded (broadcast seeding sagebrush) treatments in 2016, 2017, and 2018 (seventh, eighth, and ninth yr post seedling/planting). Asterisk (*) indicates difference (P < 0.05) between treatments in that year.

Understory Cover

Sandberg bluegrass cover was low and did not vary among years and reduction levels, nor between planting methods (P = 0.823, 0.257, and 0.241, respectively). Large perennial grass (primarily crested wheatgrass) and exotic annual grass cover were greater in the seeded treatment compared to the planted treatment (Fig. 3; P = 0.050 and 0.042, respectively) and varied among years (P < 0.001 and = 0.004, respectively). Perennial and annual grass cover were generally less in 2017 than 2016 and 2018. We found no evidence that perennial grass and annual grass cover differed among reduction levels 7–9 yr post treatment (P = 0.059 and 0.587, respectively). Perennial forb cover was low (Fig. 3) and was not influenced by reduction level, planting method, or year (P = 0.396, 0.320, and 0.371). Annual forb cover differed between planting method (Fig. 3; P = 0.003) and among years (P < 0.001), but not among reduction levels (P = 0.404). Annual forb cover was 1.6 × greater in the seeded compared with the planted treatment. Annual forb cover was greater in 2018 compared with 2016 and 2017. Total herbaceous vegetation cover varied among years (P < 0.001) and between planting methods (Fig. 3; P = 0.004), but not among reduction levels (P = 0.120). Total herbaceous cover was 1.2 × greater in the seeded compared with the planted treatment and less in 2017 compared with 2016 and 2018. Bare ground did not vary among reduction levels and between planting methods (P = 0.720 and 0.952, respectively) but was greater in 2017 compared with 2016 and 2018 (P < 0.001). Ground litter differed between planting methods (Fig. 3; P = 0.037) and declined over time (P < 0.001) but did not differ among reduction levels (P = 0.598). Litter was 1.1 × greater in the planted compared with the seeded treatment.

Understory Density

Sandberg bluegrass density did not differ among years and reduction levels or between planting methods (P = 0.783, 0.229, and 0.142, respectively). Perennial grass density differed among reduction levels and years (P = 0.003 and 0.003, respectively) but was similar between planting methods (Fig. 4; P = 0.363). Perennial grass density was greater in 2018 than 2016 and 2017. Perennial grass density was greater in the 0% reduction treatment (11.5 ± 0.84 plants • m^{-2}) than the 25% (8.9 ± 0.32 plants • m^{-2}) and 50% (7.7 ± 0.45 plants • m^{-2}) crested wheatgrass reduction treatments (P = 0.006 and < 0.001) but was not different than the 75% (9.9 ± 0.61 plants • m^{-2}) reduction (P = 0.080). Perennial grass density was greater in the 75% reduction compared with the 50% reduction treatment (P = 0.018) but was similar between the 25% and 50% reduction treatments (P = 0.208). Annual grass density did not vary among years or reduction levels (P = 0.556 and 0.924, respectively).

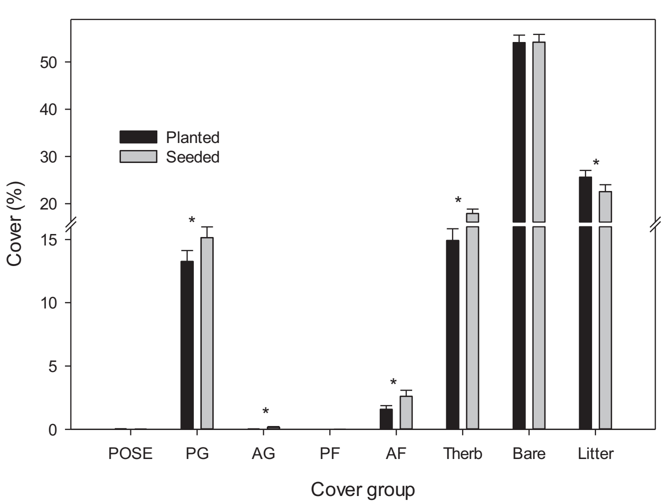

Figure 3. Cover groups cover in the planted (planting sagebrush seedlings) and seeded (broadcast seeding sagebrush) treatments summarized over the 3 sampling yr (2016, 2017, and 2018). Asterisk (*) indicates difference (P < 0.05) between treatments. POSE, Sandberg bluegrass; PG, perennial grasses excluding POSE; AG, exotic annual grasses; PF, perennial forbs; AF, annual forbs; Therb, total herbaceous vegetation; Bare, bare ground; Litter, ground litter.

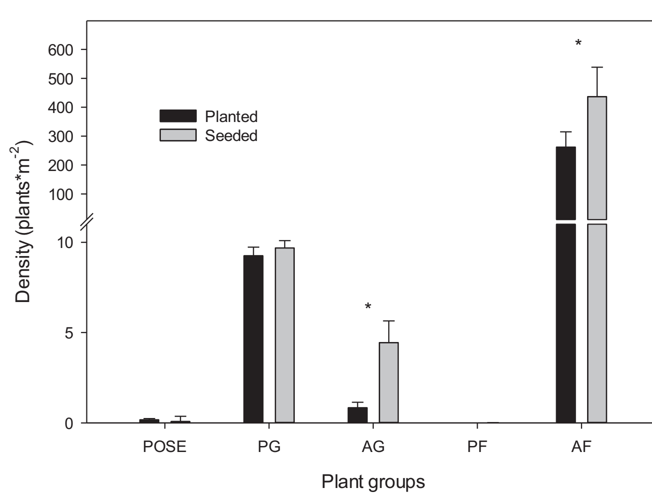

Figure 4. Density of plant groups in the planted (planting sagebrush seedlings) and seeded (broadcast seeding sagebrush) treatments summarized over the 3 sampling yr (2016, 2017, and 2018). Asterisk (*) indicates difference (P < 0.05) between treatments. POSE, Sandberg bluegrass; PG, perennial grasses excluding POSE; AG, exotic annual grasses; PF, perennial forbs; AF, annual forbs.

Annual grass density was low in both planting methods but more than five times greater in the seeded compared with the planted treatment (Fig. 4; $P = 0.002$). Perennial forbs were almost nonexistent, and their density was similar among reduction levels and years ($P = 0.396$ and 0.371, respectively). Perennial forb density was also similar between planting methods (Fig. 4; $P = 0.320$). Annual forb density varied among years and between planting method ($P = 0.020$ and 0.049, respectively) but not among reduction levels ($P = 0.651$). Annual forb density was 1.7× greater in the seeded compared with the planted treatment (Fig. 4). Annual forb density was greater in 2016 compared with 2017 and 2018.

Discussion

Planting seedlings were more effective than broadcast seeding at promoting Wyoming big sagebrush recovery in near-monocultures of crested wheatgrass. Planting seedlings was likely more effective than broadcast seeding as it bypasses the seed to seedling stage during which mortality risk is highest (Davies and Johnson, 2017). Sagebrush density was slightly less than at the end of the short-term study (Davies et al., 2013) at these sites, suggesting few plants suffered mortality over the next 4 − 7 yr. Planted Wyoming big sagebrush have persisted almost a decade and appear to have stabilized at ≈ 0.6 plants $\cdot$ m^{-2}, a level suggesting full recovery of sagebrush abundance when compared with average densities for intact Wyoming big sagebrush communities (Davies and Bates, 2010; Bates and Davies, 2019). In contrast, most areas broadcast seeded with Wyoming big sagebrush have failed to establish sagebrush plants, likely because Wyoming big sagebrush can be difficult to establish from seed (Lysne and Pellant, 2004; Brabec et al., 2015; Davies et al., 2018). Only at the highest levels of crested wheatgrass control did a few sagebrush establish from seed and survive.

Sagebrush cover has not recovered in the planted seedlings treatment, as cover remained lower than what would be expected in intact Wyoming big sagebrush communities in this region (Davies et al., 2006, 2009; Davies and Bates, 2010; Bates and Davies, 2019). Sagebrush cover, however, was increasing, suggesting that it will recover over time. Sagebrush cover in the broadcast seeding treatment was almost nonexistent. This was partly because of a much lower sagebrush abundance and also substantially smaller sagebrush plants in the broadcast seeded compared with the planted seedling treatment. Planting sagebrush seedlings probably greatly accelerated the ability of sagebrush to achieve some niche differentiation from crested wheatgrass. Crested wheatgrass greatly limits growth of sagebrush seedlings until they are large enough for niche differentiation to occur (Gunnell et al., 2010). Alternatively, the greater size of sagebrush in the planted seedlings treatment may mostly be an artifact of these plants starting out larger, as they were 10 − 15 cm tall when planted.

Early growth of sagebrush seedlings was enhanced by higher levels of crested wheatgrass control, probably due to increased resource availability (Davies et al., 2013). Competition between crested wheatgrass and sagebrush for resources may substantially affect their early growth (Cook and Lewis, 1963). These early advantages to sagebrush growth from crested wheatgrass control do not appear to persist. We found no evidence that sagebrush cover or size was influenced by the level of crested wheatgrass control when planting seedlings in this longer-term evaluation. However, in Utah, herbicide control of crested wheatgrass greatly increased the survival and growth of transplanted Wyoming big sagebrush (Newhall et al., 2011). Dissimilar to our study, Newhall et al. (2011) was attempting complete control of crested wheatgrass. Crested wheatgrass often recovers rapidly after control (McAdoo et al., 2017), likely resulting in similar crested wheatgrass competition with sagebrush within a few years post control in our study. Control of crested wheatgrass was also not necessary for survival of planted seedlings (Davies et al., 2013) and did not influence longer-term sagebrush density when planting seedlings. This, therefore, suggests that control of crested wheatgrass may not be necessary for successful establishment of planted sagebrush seedlings nor the longer-term recovery of sagebrush cover when planting seedlings, at least in average to above-average precipitation years.

Planting seedlings is expensive and time consuming (Palmerlee and Young, 2010; McAdoo et al., 2017) and, thus, only limited areas can likely be treated compared with broadcast seeding sagebrush. The success of broadcast seeding Wyoming big sagebrush is also highly variable (Lysne and Pellant, 2004; Brabec et al., 2015; Davies et al., 2018); thus, relying on it might not be the best approach. Therefore, seed enhancement technology and using a bet-hedging approach, in which more than one method and potentially multiple seeding events occur (Davies et al., 2018), need to be investigated to increase the likelihood of affordable and successful restoration of sagebrush across large landscapes. However, until such research advancements are made, when sagebrush restoration is a high priority, especially on sites where sagebrush establishment from seed is difficult (e.g., Wyoming big sagebrush communities), planting sagebrush seedling appears to have a clear advantage to broadcast seeding.

High levels of crested wheatgrass control resulted in increases in exotic annual species (cheatgrass and desert matwort) in the immediate post-treatment years at our study sites (Davies et al., 2013). Exotic annuals also posed a substantial threat after control of crested wheatgrass in Utah (Hulet et al., 2010) and Nevada (McAdoo et al., 2017). Disturbances in Wyoming big sagebrush communities often promote increases in exotic annuals (Chambers et al., 2007; Davies et al., 2009; Boyd and Svejcar, 2011). The increase in exotic annual species where crested wheatgrass was controlled did not persist in our study, probably because of the recovery of crested wheatgrass. The ability of crested wheatgrass to rapidly recover is likely one of the reasons these communities can limit exotic annuals (Davies et al., 2010; Davies et al. 2015). The rapid recovery of crested wheatgrass, however, poses a substantial challenge to restoring native species in these communities (Hulet et al., 2010; Fansler and Mangold, 2011; McAdoo et al., 2017).

Cover and density of herbaceous plant groups were generally lower in the planted seedlings compared with the broadcast seeding treatments. Increased competition from sagebrush in the planted seedlings treatment likely reduced resources available to herbaceous vegetation. Mature sagebrush competes effectively with herbaceous vegetation for limited resources in this ecosystem (Robertson, 1947; Cook and Lewis, 1963; Williams et al., 1991). Increases in sagebrush result in declines in herbaceous vegetation (Cook and Lewis, 1963; Rittenhouse and Sneva, 1976; Davies and Bates, 2019), and removal of sagebrush generally produces severalfold increases in herbaceous production (Mueggler and Blaisdell, 1958; Hedrick et al., 1966; Davies et al., 2007b). Though we didn't measure forage production response, declines in herbaceous vegetation cover are correlated to declines in herbaceous production (Davies et al., 2007b, 2012). Ground litter was greater in the planted seedlings treatment, which would seem counterintuitive since herbaceous vegetation was lower in this treatment. However, beneath sagebrush canopies, litter is generally greater than surrounding interspaces because of dropped sagebrush leaves (Davies et al., 2007a); thus, more sagebrush cover likely increased ground litter. Sagebrush recovery will also result in a trade-off with herbaceous vegetation (Davies and Bates, 2019), resulting in decreased forage production (Hull and Klomp, 1967; Rittenhouse and Sneva, 1976).

Dissimilar to most crested wheatgrass plant communities, our study sites were not grazed. Recovery of sagebrush cover observed in our study was probably conservative compared with crested wheatgrass stands grazed by cattle. Grazing would likely place crested wheatgrass, a highly palatable species, at a competitive disadvantage with sagebrush, which is generally unpalatable. Removal of photosynthetic tissue places defoliated plants at a competitive disadvantage with nondefoliated plants (Caldwell et al., 1987; Briske and Richards, 1995). For example, heavy spring grazing of native rangelands increased sagebrush by decreasing competing herbaceous vegetation (Laycock, 1967). Further suggesting that grazing may increase sagebrush recovery, grazed compared with ungrazed crested wheatgrass communities had greater abundance and cover of Wyoming big sagebrush (Nafus et al., 2016). We expect that sagebrush cover would have been even greater if cattle grazing was not excluded from our study area.

This research suggests that establishing Wyoming big sagebrush by planting seedlings may be more successful than attempting to restore the full assemblage of native herbaceous and woody species from seed in near-monocultures of crested wheatgrass. Attempts to restore diverse assemblages of native vegetation in crested wheatgrass communities have generally been unsuccessful (Hulet et al., 2010; Fansler and Mangold, 2011; McAdoo et al., 2017; Morris et al., 2019). The general lack of success with establishing native species from seed in Wyoming big sagebrush communities (Eiswerth et al., 2009; Knutson et al., 2014), rapid recovery of crested wheatgrass (Hulet et al., 2010; Fansler and Mangold, 2011), and the ability of crested wheatgrass to outrecruit native species by an order of magnitude (Nafus et al., 2015; Hamerlynck and Davies, 2019) suggests that efforts to reestablish a broad assemblage of native species in crested wheatgrass stands are likely to fail. In our study, in contrast, sagebrush plants established from planted seedlings were still persistent 9 yr after planting. Wyoming big sagebrush is also a long-lived (70+ yr) species (Perryman and Olson, 2000); thus, it is likely to continue to be a component of these communities barring a disturbance such as wildfire.

Recovery of sagebrush is also often a management goal because of the widespread decline in sagebrush. Sagebrush occupied ≈ 56% of its historic range in 2004 (Schroeder et al., 2004) and, subsequently, vast acreages of sagebrush rangelands have burned in the past decade and a half. The decline of sagebrush-occupied rangelands has been linked to the decline of sagebrush-associated wildlife (Suring et al., 2005; Aldridge et al., 2008). Sagebrush restoration is critical for the conservation of sagebrush-associated wildlife (Crawford et al., 2004; Shipley et al., 2006). Focusing on sagebrush restoration in near-monocultures of crested wheatgrass may be a strategy to help mitigate the widespread loss of sagebrush and provide habitat for species of conservation concern, including sage grouse. Sagebrush cover on areas where sagebrush seedlings were planted was lower than optimum habitat for sage grouse (Connelly et al., 2000), but was increasing over time. These areas were also providing a diversity in vegetation structure that is lacking in grasslands.

Future research should investigate if planted sagebrush plants recruit new sagebrush individuals into crested wheatgrass stands and if management can improve recruitment. Determining optimum spacing of seedlings to meet different management objectives may improve the efficiency of sagebrush restoration efforts. It would also be valuable to determine the effects of different levels and timing of grazing on sagebrush survival and growth in crested wheatgrass communities.

Management Implications

This longer-term evaluation confirmed that planting Wyoming big sagebrush seedlings was more successful at promoting sagebrush recovery in near-monocultures of crested wheatgrass than broadcast seeding sagebrush. Critically important, sagebrush persisted and increased in cover; thereby, diversifying the composition and structure of near-monocultures of crested wheatgrass. Importantly, crested wheatgrass control was not necessary when planting sagebrush seedlings as sagebrush cover, abundance, and size increased regardless of crested wheatgrass control. This would be a significant cost savings when reintroducing Wyoming big sagebrush into crested wheatgrass monocultures. In contrast, high levels of herbicide control of crested wheatgrass control were necessary to obtain minimal sagebrush establishment when broadcast seeding sagebrush. Exotic annuals initially increased with high levels of crested wheatgrass control (Davies et al., 2013); however, crested wheatgrass recovered and greatly limited them. Planting sagebrush seedlings may be a component of implementing a low-disturbance strategy to alter monotypic crested wheatgrass stands, thereby avoiding increases in exotic annual species. Planting sagebrush seedlings reduced herbaceous vegetation over time. Land managers and restoration practitioners will need to consider the trade-off between herbaceous vegetation and increasing sagebrush cover. Planting patches or strips of Wyoming big sagebrush seedlings in crested wheatgrass-dominated landscapes may be a strategy to facilitate sagebrush recovery while balancing the desire to maintaining high forage production, as well as address the cost-prohibitive nature of planting seedlings across large landscapes. In contrast to efforts that have generally failed to establish native vegetation by seeding a diverse assemblage of species in crested wheatgrass stands (e.g., Hulet et al., 2010; Fansler and Mangold, 2011; McAdoo et al., 2017; Morris et al., 2019), planting sagebrush seedlings successfully established sagebrush and is converting the introduced grassland to a shrub steppe. This increases compositional and structural diversity of monotypic crested wheatgrass stands and, thereby, may improve habitat for sagebrush-associated wildlife. Converting crested wheatgrass grassland to Wyoming big sagebrush-crested wheatgrass communities may be a method to mediate the loss of sagebrush habitat, especially in drier, lower-elevation winter habitats. In other seeded exotic grass communities, planting seedlings of native shrubs may be a strategy to diversity these communities and improve habitat for shrub-dependent wildlife.

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