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Long-term evaluation of restoring understories in Wyoming big sagebrush communities with mowing and seeding native bunchgrasses☆,☆☆

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ABSTRACT

Restoring degraded plant communities is a global challenge and a major priority for land managers and conservationists. Degraded Wyoming big sagebrush communities (*Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) have high sagebrush cover with a depleted perennial herbaceous understory. They are widespread in western North America and are a priority for restoration because they provide habitat for sagebrush-associated species and an important forage base for livestock production. Mechanically reducing sagebrush with mowing has been attempted to restore the understory in these communities but often fails because large native perennial bunchgrasses do not increase and exotic annual grasses proliferate. Seeding large native perennial bunchgrasses after mowing sagebrush may increase their density or cover and thereby limit exotic annual grasses. Native perennial bunchgrasses are slow growing; thus, long-term studies are needed to evaluate this treatment strategy. We evaluated mowing followed by drill-seeding large native perennial bunchgrasses in southeastern Oregon for 11 yr post treatment. Large bunchgrass cover and density were approximately 2 × greater with mowing followed by seeding compared with the untreated control. However, mowing, with and without seeding, increased exotic annual grasses and decreased biological soil crusts. Sagebrush cover was less in mowed treatments compared with the untreated control, but sagebrush cover increased over time. Mowing and seeding native bunchgrasses was less successful than desired, particularly since exotic annual grasses increased substantially. This treatment may be improved by reducing the disturbance associated with mowing and drill seeding, decreasing exotic annual grass competition, and increasing the establishment of native perennial bunchgrasses. The results of our study indicate that seeding native bunchgrasses into degraded Wyoming big sagebrush communities has potential as a restoration treatment but needs refinement to improve success.

Introduction

Land degradation is a widespread problem that affects nearly a quarter of the global land area, with a disproportionate greater extent in drylands (Stavi and Lal 2015). Land degradation decreases ecosystem goods and services, and plant communities may cross irreversible thresholds. Widespread degradation of native plant communities can result in declines in wildlife dependent on them, reduce biodiversity, and threaten the economic livelihoods of people who use them. This is particularly evident in rangelands, where the vast expanse of these uncultivated lands provides essential habitat for many wildlife species, a reservoir of biodiversity, and support for rural economies. Therefore, restoring degraded plant communities is a global priority and a major challenge (Suding 2011).

In western North America, degraded Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) communities are a priority for restoration. Wyoming big sagebrush communities occupy vast areas of the western United States (Miller et al. 1994; West and Young 2000), providing

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critical wildlife habitat for sagebrush-associated wildlife and an important forage base for livestock production (Connelly et al. 2000; Crawford et al. 2004; Davies et al. 2006). Historical overuse by sheep, cattle, and horses decreased native large perennial bunchgrasses (bunchgrasses excluding Sandberg bluegrass [*Poa secunda* J. Presl]) and increased sagebrush dominance in many big sagebrush communities (Davies et al. 2011a). These degraded communities were estimated to comprise 25% of the big sagebrush ecosystem approximately 2 decades ago (West 2000). Wyoming big sagebrush communities make up a disproportionate amount of the degraded sagebrush communities because they are generally less resilient than other common big sagebrush types (Miller and Eddleman 2000; Davies et al. 2011a). Because Wyoming big sagebrush communities are important to wildlife and livestock production, their restoration is paramount.

Restoring degraded Wyoming big sagebrush communities decreases their potential for transition to exotic annual grasslands. Degraded Wyoming big sagebrush communities are likely to transition to exotic annual grasslands with fire, a periodic disturbance in this ecosystem, because resilience and resistance to exotic annual grass invasion decrease when large perennial bunchgrasses decline (Chambers et al. 2007, 2014). Mature large perennial bunchgrasses are critical to limiting exotic annual grasses, in part because their resource use overlaps substantially with exotic annual grasses (Davies 2008; James et al. 2008).

Substantial invasion of Wyoming big sagebrush communities by exotic annual grasses, largely cheatgrass (*Bromus tectorum* L.), is generally irreversible. Exotic annual grass invasion is especially problematic because these species increase fine fuel continuity and fire frequency (Stewart and Hull 1949; Balch et al. 2013), which reduces native perennial vegetation, and leads to a positive feedback that favors a short exotic annual grass-fire cycle (D'Antonio and Vitousek 1992; Brooks et al. 2004). Exotic annual grasses are also highly competitive with seedlings of native vegetation and often preempt resources, resulting in the exclusion of native species (Melgoza et al. 1990; Nasri and Doescher 1995; Rafferty and Young 2002; Humphrey and Schupp 2004). To date, no large-scale cost-effective strategies exist to control exotic annual grasses across the vast areas they have invaded (Stohlgren and Schnase 2006). Therefore, it is critical to restore community resilience in depleted Wyoming big sagebrush communities before they transition to exotic annual grasslands.

Restoring the large perennial bunchgrass component in degraded Wyoming big sagebrush communities is particularly important because they dominate the understory in resilient communities (Davies et al. 2006), are the plant lifeform best able to limit exotic annual grass invasion and dominance (Chambers et al. 2007; Davies 2008; James et al. 2008), and are crucial to providing resilience to fire in this ecosystem (Chambers et al. 2014). However, restoration of the large native perennial bunchgrass component of a sagebrush-bunchgrass community is difficult. Excluding livestock to restore large perennial bunchgrasses in sagebrush communities has generally been unsuccessful, especially when sagebrush cover is high (Sneva et al. 1980; West et al. 1984; Davies et al. 2016). Competition from sagebrush is likely limiting the recovery of understory species in these degraded communities. Management may need to reduce sagebrush to promote recovery of the understory (Sneva et al. 1980; Boyd and Svejcar 2011). Reducing sagebrush as a stand-alone treatment in degraded Wyoming big sagebrush communities often does not promote the native herbaceous understory and can result in an increase in exotic annuals (Davies et al. 2012; Davies and Bates 2014; Swanson et al. 2016). The native herbaceous understory may not increase because these species may be largely lacking from degraded sagebrush communities and their seedbank may be limited (Young and Evans 1975; Chamber 2000). Therefore, in degraded Wyoming big sagebrush communities, sagebrush reduction followed by seeding may be necessary to facilitate increases in the native understory.

In Oregon, mowing to reduce sagebrush, followed by seeding native large perennial bunchgrasses in degraded Wyoming big sagebrush communities, approximately doubled the density of large bunchgrasses in a short-term study (Davies and Bates 2014). However, large bunchgrass cover was not different than the untreated control and exotic annual grasses increased substantially (Davies et al. 2014). The short-term nature of this study precluded knowing if large perennial bunchgrass cover may increase over time in this treatment and potentially reduce exotic annual grasses. Native perennial grasses in semiarid and arid ecosystems are slow growing (Holmes and Rice 1996; James et al. 2009); thus, a longer-term evaluation is needed to determine if this treatment strategy (mowing and seeding) will result in desired outcomes, especially further recruitment of large bunchgrasses and increases in their cover.

The purpose of this study was to investigate if mowing and seeding large native perennial bunchgrasses in degraded Wyoming big sagebrush communities would promote the recovery of large native bunchgrasses and limit exotic annual grasses over extended time frames (10+ yr). To accomplish this, we annually sampled experimental plots from Davies et al. (2014) for 11 yr post treatment. We hypothesized that 1) large perennial bunchgrass cover and density would be greater with mowing followed by seeding, 2) exotic annual grass cover and density would increase with mowing and seeding but decrease over time as large perennial bunchgrasses increase, and 3) exotic annual grass cover and density would be greatest in areas mowed but not seeded.

Methods

Study Area

The study was conducted in degraded Wyoming big sagebrush plant communities in southeastern Oregon 40–50 km southwest of Burns, Oregon. The overstory was primarily Wyoming big sagebrush. Bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), squirreltail (*Elymus elymoides* [Raf.] Swezey), and Sandberg bluegrass occurred at the study sites. Bluebunch wheatgrass and Thurber's needlegrass would have been dominant perennial bunchgrasses in these plant communities if they were not degraded (NRCS 2013). Study sites were on the Loamy 10-12PZ (R023XY212OR) ecological site (NRCS 2013). The exotic annual grass, cheatgrass, was common across study sites, but its cover was low (< 1%) before treatment (Davies et al. 2014). We considered the herbaceous understory as "depleted" at study sites because the density and cover of native large perennial bunchgrasses and native perennial forbs were insufficient to prevent transition to exotic annual grass community following disturbance. Foliar cover of sagebrush, Sandberg bluegrass, large perennial bunchgrass, and perennial forb averaged 14.9%, 1.7%, 1.5%, and 0.5% across study sites before treatment, respectively (Davies et al. 2014). Cover of native herbaceous perennial plant groups was lower at the study sites than in relatively intact Wyoming big sagebrush communities (Davies et al. 2006; Davies and Bates 2010). The most substantial deviation was that native large perennial bunchgrass cover was 5.9- to 6.7-fold less at the study sites than in relatively intact Wyoming big sagebrush communities (Davies et al. 2006; Davies and Bates 2010). Sagebrush cover was 20–50% greater at the study sites than the average for relatively intact Wyoming big sagebrush steppe in this region (Davies et al. 2006; Davies and Bates 2010), suggesting that sagebrush may be limiting herbaceous vegetation. Elevations at study sites were 1 263–1 350 m, and slopes were

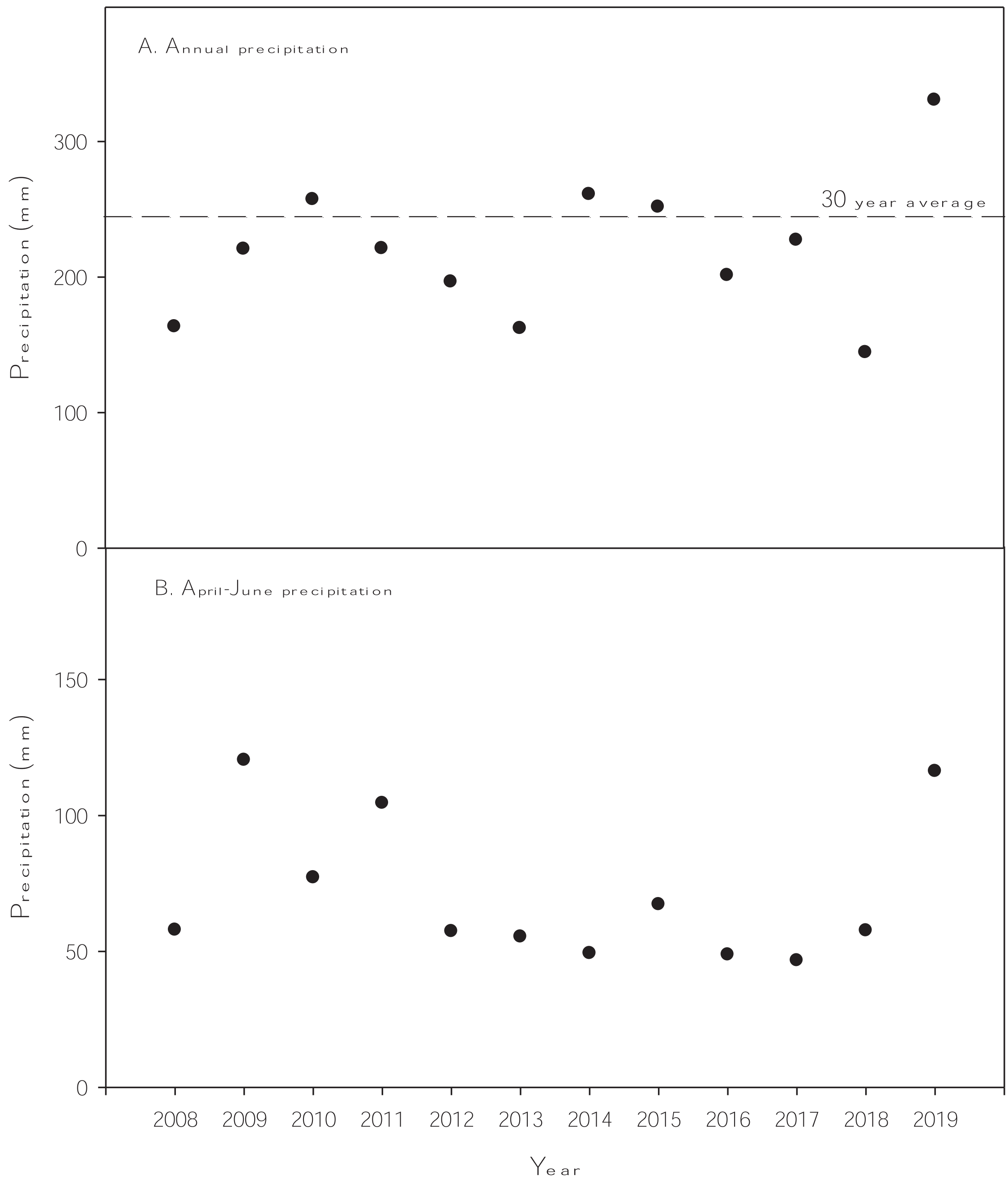

Fig. 1. Annual (**A**) and April through June (**B**) precipitation in the study area from 2008 to 2019. *Dashed line* in panel A represents the long-term (1981–2010) average annual precipitation for the study area (PRISM 2020).

flat (0–4%). Soils at study sites were loamy, well drained, and 50–100 cm deep. Soil surfaces had a physical crust with vesicular pores. Climate across the study area is characteristic of the northern Great Basin. Most precipitation occurs during the cool, wet winter and spring months, and summers are hot and dry. Long-term (1981–2010) average annual precipitation was 244 mm (PRISM 2020). Annual precipitation was variable over the duration of the study (Fig. 1). Study sites were fenced to exclude livestock from experiment plots.

Experimental Design and Measurements

A randomized complete block design with study site ($n = 5$) being the blocking variable was used in this study. Blocks varied in vegetation, soil, and elevation (Davies et al. 2014). Each block comprised three 30×50 m plots, with a 2-m buffer between plots. Treatments were 1) mowed and seeded with native perennial bunchgrasses (MOW-SEED), 2) mowed (MOW), and 3) untreated control (CONTROL). Treatments were randomly applied to one of the 30×50 m plots at each study site. Mowing was applied at a 20-cm height in September 2008 with a Schulte XH 1500 rotary cutter (Schulte Equipment Co., Englefield, Saskatchewan, Canada). After mowing, seeding was applied with a Laird Rangeland Drill (Laird Welding & Manufacturing Works, Merced, CA) in the MOW-SEED treatment. The disks on the rangeland drill were 30 cm apart, and 5-cm diameter metal pipes were dragged behind the drill to cover seeds. The seed mix was locally adapted bottlebrush squirreltail, bluebunch wheatgrass, and basin wildrye (*Leymus cinereus*

[Scribn. & Merr.] Á. Löve), with each grass species seeded at 5.6 kg·ha^{-1} pure live seed (PLS).

Vegetation, bare ground, litter, and biological soil crusts were measured each June for 11 yr post treatment (2009−2019). Four 50-m transects spaced 5 m apart were used to sample treatment plots. Herbaceous canopy cover by species was visually estimated in 40 × 50 cm quadrats located at 3-m intervals along the 50-m transects (15 quadrats per transect, 60 quadrats per plot). Bare ground, litter, and biological soil crusts cover were also measured in the 60 quadrats in each plot. Cover estimates were based on markings dividing the quadrats into 1%, 5%, 10%, 25%, and 50% segments. Density of perennial herbaceous vegetation was measured by counting by species all individuals rooted in the 40 × 50 cm quadrats. Density of annuals was measured by counting all individuals by species rooted in a 10% section delineated on the 40 × 50 cm quadrats. Shrub canopy cover by species was measured using the line intercept method on each of the 50-m transects. Shrub density by species was measured by counting all shrubs rooted in 2 × 50 m belt transects positioned over each 50-m transect.

Statistical Analyses

Repeated measures analysis of variance (ANOVA) using the mixed models procedure (Proc Mixed) in SAS version 9.4 (SAS Institute Inc., Cary, NC) was used to evaluate treatment effects. Treatment was considered a fixed variable in analyses. Year was the repeated factor and block and block-by-treatment interactions were treated as random variables in models. The appropriate covariance structure was selected for each model using the Akaike's Information Criterion (Littell et al. 1996). For analyses, herbaceous vegetation was grouped into five plant functional groups: Sandberg bluegrass, large perennial bunchgrasses, exotic annual grasses, perennial forbs, and annual forbs. Sandberg bluegrass was treated as a separate plant functional group from the other native bunchgrasses because it is smaller and develops phenologically earlier (James et al. 2008). Shrub cover and density were separated into two groups: Wyoming big sagebrush and green rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.). Data that violated assumptions of normality were log or square root transformed. Figures and text used nontransformed, original data. Treatment means were reported with standard errors (mean ± S.E.) and separated using LSDs ($P \le 0.05$). All main effects were reported, but treatment-year interactions were only reported if significant ($P \le 0.05$).

Results

Cover

Large perennial bunchgrass cover varied among treatments and years (Fig. 2A; $P = 0.006$ and < 0.001). Large perennial bunchgrass cover was greater in the MOW-SEED compared with the MOW and CONTROL treatments ($P = 0.004$ and 0.006) but did not differ between the MOW and CONTROL ($P = 0.707$). At the conclusion of the study, perennial bunchgrass cover was 1.9 × greater in the MOW-SEED treatment compared with the other treatments. Sandberg bluegrass cover was similar among treatments (data not shown; $P = 0.186$) but varied among years ($P < 0.001$). Exotic annual grass cover varied among treatments and among years (see Fig. 2B; $P = 0.020$ and < 0.001). Exotic annual grass cover was greater in the MOW-SEED and MOW treatments compared with the CONTROL ($P = 0.031$ and 0.008) but was similar between the MOW-SEED and MOW treatments ($P = 0.412$). Cover of exotic annual grasses was greater in the final 2 yr of the study in all treatments. Perennial forb cover did not vary among treatments (data not shown; $P = 0.1382$) but varied among years ($P < 0.001$), being greatest in 2011. Annual forb cover varied among treatments and years (see Fig. 2C; $P = 0.005$ and < 0.001). Annual forb cover was greater in the MOW-SEED and MOW treatments compared with the CONTROL ($P = 0.011$ and 0.002) but was similar between the MOW-SEED and MOW treatments ($P = 0.293$). Sagebrush cover was influenced by the treatment-year interaction (see Fig. 2D; $P = 0.013$). Sagebrush cover was greater in the CONTROL compared with the MOW-SEED and MOW treatments ($P < 0.001$), but the difference became smaller over time as sagebrush cover steadily increased in the MOW-SEED and MOW treatments. Green rabbitbrush cover did not vary among treatments or years (data not shown; $P = 0.329$ and 0.131). Bare ground varied among treatments and years (Fig. 3A; $P < 0.001$). Bare ground was greater in the CONTROL compared with the MOW-SEED and MOW treatments ($P < 0.001$) but was similar between the MOW-SEED and MOW treatments ($P = 0.417$). Litter was influenced by the treatment-year interaction (see Fig. 3B; $P = 0.015$). Litter was greater in the MOW-SEED and MOW treatments compared with the CONTROL ($P < 0.001$), but the magnitude of the difference decreased over time. Litter was similar between the MOW-SEED and MOW treatments ($P = 0.515$). Biological soil crust varied among treatments and years (see Fig. 3C; $P < 0.001$ and 0.009). Biological soil crust was greater in the CONTROL compared with the MOW-SEED and MOW treatments ($P < 0.001$) and greater in the MOW compared with the MOW-SEED ($P = 0.012$).

Density

Large perennial bunchgrass density varied among treatments (Fig. 4A; $P = 0.001$) but not among years ($P = 0.213$). Density of large perennial bunchgrasses was greater in the MOW-SEED treatment compared with MOW and CONTROL treatments ($P < 0.001$ and 0.001) but was similar between the MOW and CONTROL ($P = 0.621$). At the conclusion of the study, large perennial bunchgrass density was more than 2 × greater in the MOW-SEED treatment compared with the other treatments. Sandberg bluegrass density was similar among treatments (data not shown; $P = 0.539$) but varied among years ($P < 0.001$). Exotic annual grass density varied among treatments and years (see Fig. 4B; $P = 0.006$ and < 0.001). Exotic annual grass density was less in the CONTROL compared with MOW-SEED and MOW treatments ($P = 0.008$ and 0.003) but did not differ between MOW-SEED and MOW treatments ($P = 0.354$). Perennial forb density did not vary among treatments (data not shown; $P = 0.057$) but varied among years ($P < 0.001$). Annual forb density varied among treatments and years (see Fig. 4C; $P < 0.001$). Annual forb density was greater in the MOW-SEED and MOW treatment compared with the CONTROL ($P < 0.001$) and less in the MOW-SEED compared with the MOW treatment ($P = 0.026$). Sagebrush density varied among treatments (see Fig. 4D; $P < 0.001$) but did not vary among years ($P = 0.053$). Sagebrush density was greater in the CONTROL compared with the MOW-SEED and MOW treatments ($P < 0.001$) but was similar between the MOW-SEED and MOW treatments ($P = 0.144$). Green rabbitbrush density did not vary among treatments or years (data not shown; $P = 0.303$ and 0.999).

Discussion

Restoring large native bunchgrasses in degraded Wyoming big sagebrush communities will increase resilience and resistance to inevitable disturbance, improve wildlife habitat, and provide a better forage base for livestock production. Mowing followed by seeding native bunchgrasses partially achieved these objectives but also had some undesired effects. Negative effects included substantial increases in exotic annual grasses and forbs and decreases

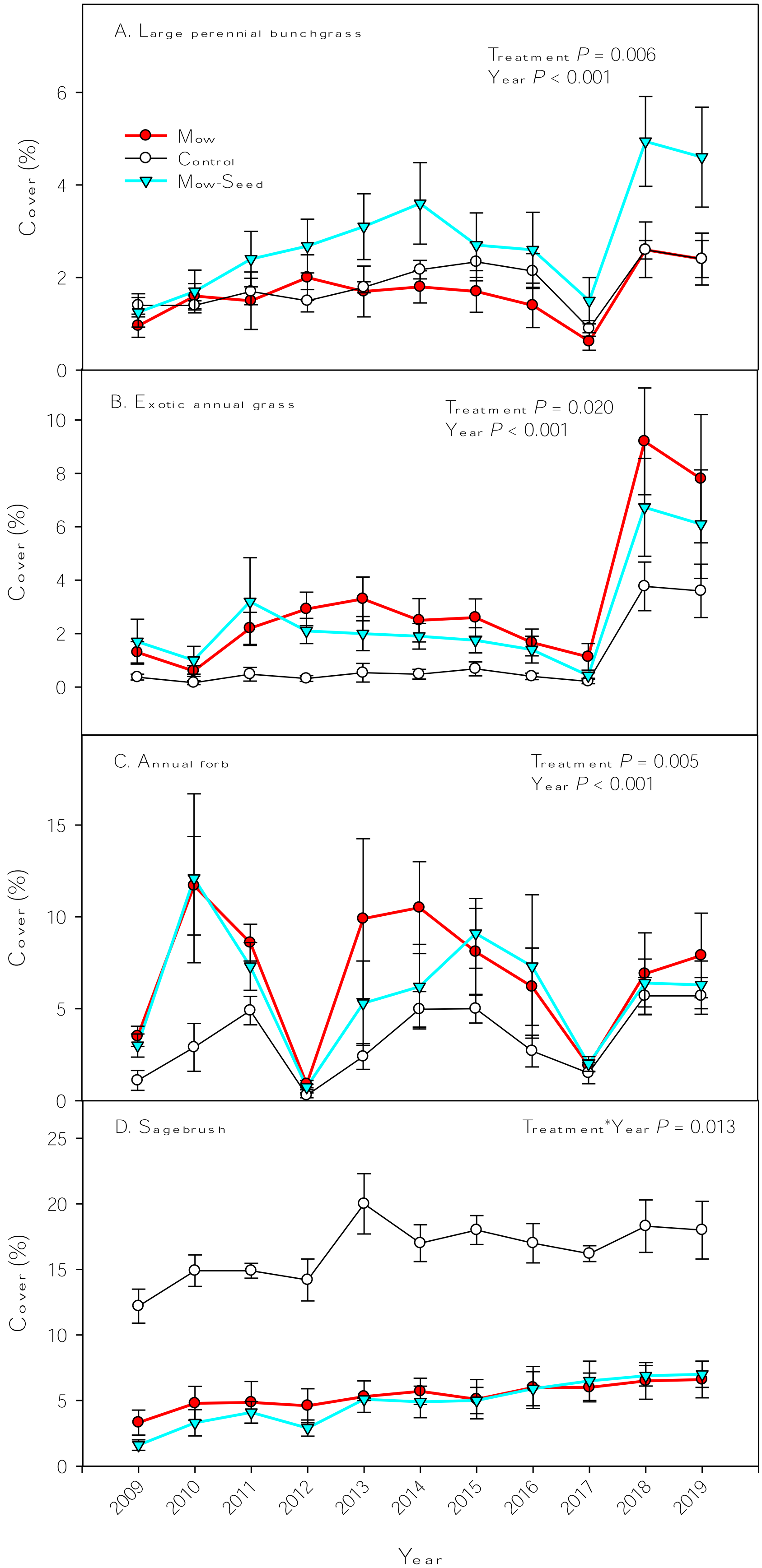

Fig. 2. Cover (mean ± standard of error) of major plant groups in the MOW, MOW-SEED, and untreated CONTROL treatments in degraded Wyoming big sagebrush communities in southeastern Oregon for 11 yr post treatment.

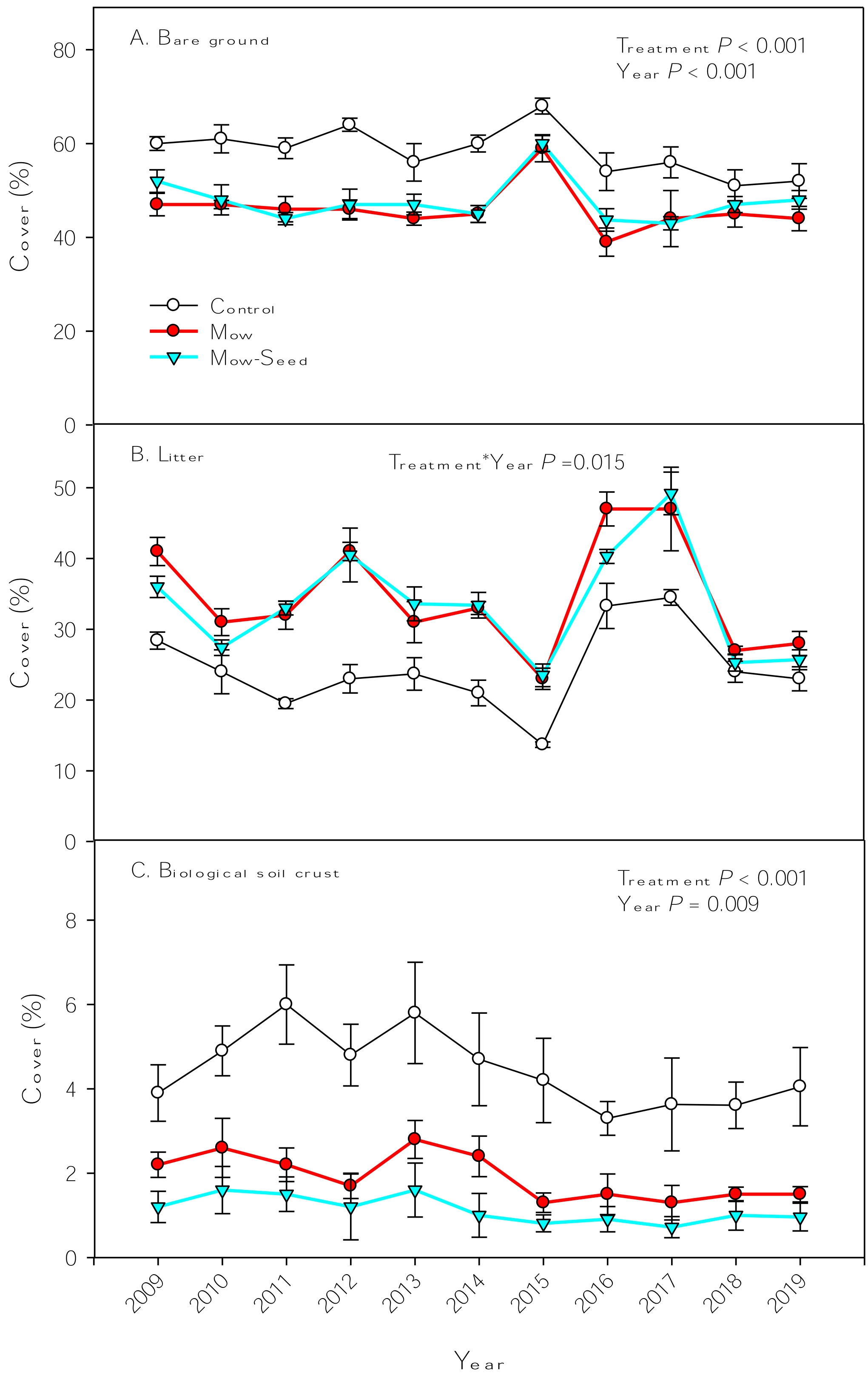

Fig. 3. Cover (mean ± standard of error) of ground cover groups in the MOW, MOW-SEED, and untreated CONTROL treatments in degraded Wyoming big sagebrush communities in southeastern Oregon for 11 yr post treatment.

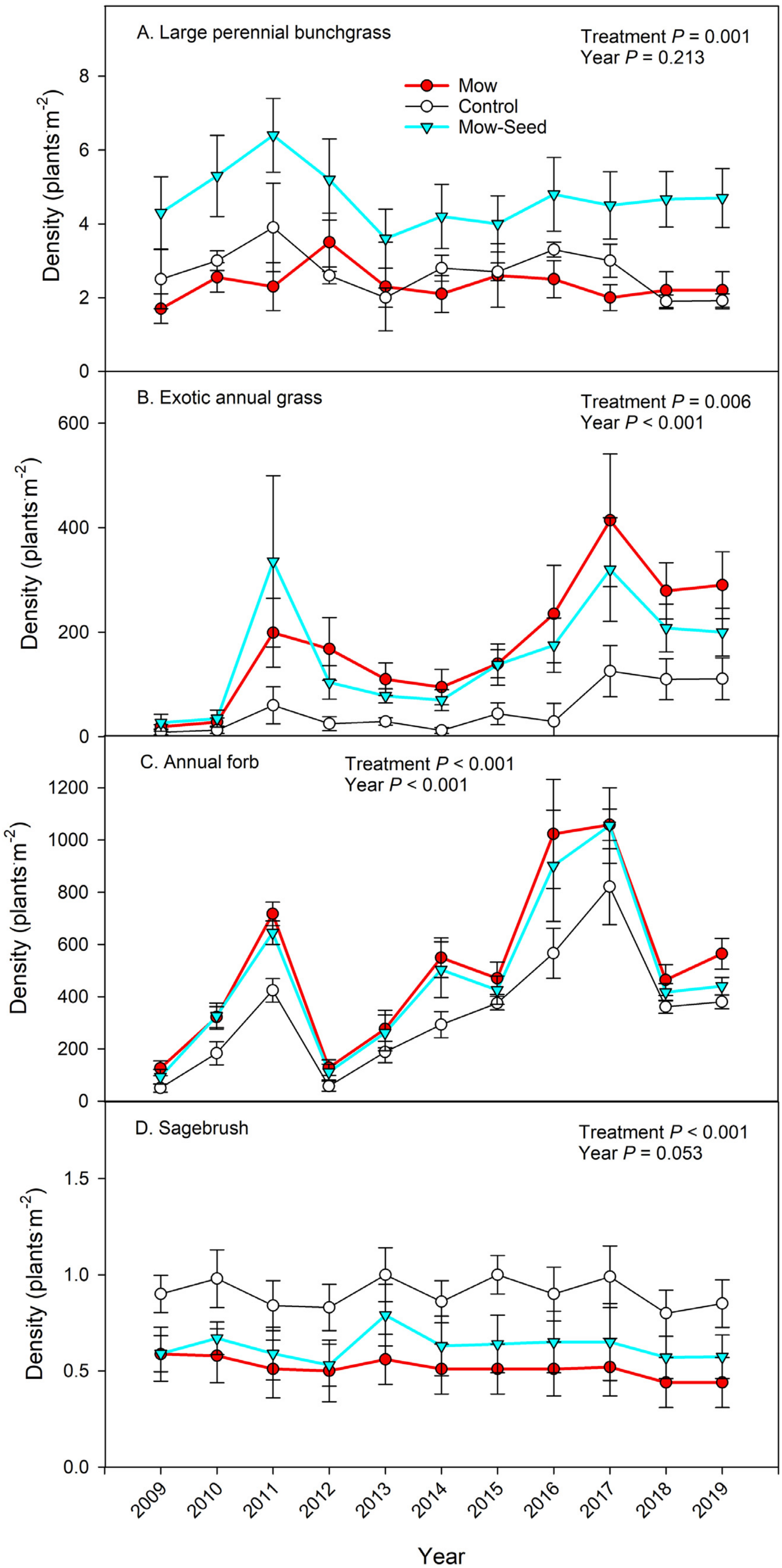

Fig. 4. Density (mean ± standard of error) of major plant groups in the MOW, MOW-SEED, and untreated CONTROL treatments in degraded Wyoming big sagebrush communities in southeastern Oregon for 11 yr post treatment.

in biological soil crusts. However, mowing and seeding approximately doubled large perennial bunchgrass cover and density. This was a substantial improvement but did not approach the levels found in intact Wyoming big sagebrush communities. Intact Wyoming big sagebrush community with the same dominant perennial bunchgrasses as our study sites in this part of Oregon average 9−13% large perennial bunchgrass cover (Davies et al. 2006; Bates and Davies 2019), but at the conclusion of our current study, large perennial bunchgrass cover was 4.6% in the MOW-SEED treatment. Density of large perennial bunchgrasses at the end of our study in the MOW-SEED treatment was approximately half of the density found in intact Wyoming big sagebrush community types in this region (Bates and Davies 2019).

Our results suggest that large native bunchgrasses were seed limited in these degraded Wyoming big sagebrush communities. Evidence for this conclusion was the lack of increase in large bunchgrass density in areas mowed but not seeded, as well as short-term (3−4 yr) studies in degraded Wyoming big sagebrush communities (Davies et al. 2012; Davies and Bates 2014). Similarly, native perennial herbaceous vegetation was seed limited in conifer-encroached mountain big sagebrush (*Artemisia tridentate* subsp. *vaseyana*) communities (Allen et al. 2008). In contrast, when seed limitation was overcome with seeding and mowing reduced sagebrush competition, the density of large perennial bunchgrasses doubled. In Utah, seeding after sagebrush reduction with two-way chain harrowing also increased perennial grasses in degraded Wyoming big sagebrush communities (Monaco et al. 2018). Clearly, in our study, to increase the density of large perennial bunchgrasses seeding these species was necessary.

Exotic annual grasses, predominantly cheatgrass, increased substantially with mowing, likely because of reduced competition and the physical disturbance of mowing. Reduction of perennial vegetation (i.e., sagebrush) may result in increased exotic annual grasses because competition from perennial vegetation for resources is critical to limiting exotic annual grasses (Chambers et al. 2007, 2014; Davies 2008; Davies and Johnson 2017). The soil disturbance associated with mowing and the decrease in sagebrush can increase soil nutrient concentrations (Davies et al. 2011b), favoring exotic annual grasses as they respond more rapidly to elevated soil resources than do native plants (Young & Allen 1997; Vasquez et al. 2008). Exotic annual grasses are generally more successful with elevated water and soil nutrient availability (Huenneke et al. 1990; Burke & Grime 1996; Davis et al. 2000). Similarly, greater soil surface litter after mowing probably favored exotic annual grasses because it improves microsite characteristics for establishment of exotic annual grasses (Evans & Young 1970, 1972; Whisenant 1990; Newingham et al. 2007). Declines in biological soil crusts may have also contributed to increases in exotic annual grasses. Exotic annual grass increases are often correlated with declines in biological soil crusts (Ponzetti et al. 2007; Dettweiler-Robison et al. 2013a). The combined effects of mowing created an environment that was likely favorable to exotic annual grasses.

The increase in exotic annual grasses likely limited further increases in large native bunchgrasses. After the initial establishment, the lack of increases in large bunchgrass abundance in the mowed and seeded treatment for over a decade is compelling evidence that their establishment was obstructed. Exotic annual grasses are highly competitive with native vegetation, especially at the seedling life stage, and may prevent their recruitment (Melgoza et al. 1990; Nasri and Doescher 1995; Clausnitzer et al. 1999; Rafferty and Young 2002). Once exotic annual grasses become abundant, control is often necessary to allow native species to increase (Marushia and Allen 2011; Nafus and Davies 2014). We may have been able to achieve further increases in native bunchgrasses if exotic annual grasses were controlled. Preemergent herbicide control of exotic annual grasses can facilitate increases in bunchgrasses (Davies and Sheley 2011). Similarly, targeted grazing can be used to decrease exotic annuals and increase perennial grasses (Schmelzer et al. 2014; Porensky et al. 2020). At present, the high density of exotic annual grasses in mowed treatments suggests that it is unlikely that the abundance of native large perennial bunchgrasses will increase without further intervention.

Sagebrush was recovering from the mowing treatment. By the end of the study, sagebrush cover had increased from 1.6% and 3.3% to 6.9% and 6.5% in the MOW-SEED and MOW treatment, respectively. Thus, the effect of mowing on sagebrush cover was transient. Other studies have also found transient effects from mechanical treatment on sagebrush cover (Watts and Wambolt 1996; Summers and Roundy 2018). The opportunity to increase native perennial bunchgrasses after mowing dense sagebrush stands may be temporally limited because competition from sagebrush likely increases over time. As big sagebrush cover increases, native perennial grasses decrease because of greater competition (McDaniel et al. 2005; Davies and Bates 2019). However, sagebrush cover at the end of our study in mowed treatments was likely not great enough to have a substantial effect on bunchgrasses. Thus, we suspect that at the conclusion of the current study, exotic annual grasses were the primary factor limiting increases in large perennial bunchgrasses.

Biological soil crusts were negatively impacted by mowing for the duration of our study. The disturbance associated with drill seeding appeared to result in further declines in cover of biological soil crusts. Other studies have found that biological soil crusts were reduced with mowing treatments (Davies et al. 2011b, 2012; Davies and Bates 2014; Condon and Gray 2020) and other soil surface disturbances (Ponzetti & McCune 2001; Ponzetti et al. 2007; Root & McCune 2012; Dettweiler-Robinson et al. 2013b). The lack of any evidence of recovery of biological soil crusts in the current study is concerning as it suggests that this may be a long-term or possibly a permanent reduction. This agrees with prior research that found biological soil crusts were generally slow to recover (Hilty et al. 2004). After mowing reduced biological soil crusts, increases in exotic annual grasses likely hindered their recovery. Increases in exotic annual grasses are one of the major factors resulting in declines in biological soil crusts (Belnap et al. 2006; Dettweiler-Robison et al. 2013a). Thus, we expect that the reductions in biological soil crusts are likely to be permanent without control of exotic annual grasses. These long-term declines in biological soils crust are of concern because they provide some ecosystem services and contribute to community stability in arid rangelands (Belnap et al. 2001; Harper & Belnap 2001; Belnap 2006). However, in the current study, biological soils crusts are quite low in communities without treatment and, thereby, likely contribute little to their resilience and resistance to exotic annual grass invasion. Thus, long-term reductions in already low biological soil crusts may be an acceptable trade-off for increases in native bunchgrasses.

Multiple barriers appear to limit restoration of degraded Wyoming big sagebrush communities. For the current study, these limitations include 1) insufficient seed of large native bunchgrasses, and likely perennial forbs, in the seed bank; 2) overabundance of sagebrush is also limiting the understory; 3) exotic annual grasses probably suppress the native understory once sagebrush is reduced; and 4) environmental variables limiting establishment of perennial vegetation. Thus, for successful restoration of degraded Wyoming big sagebrush communities, multiple barriers must be overcome. This will likely be expensive because multiple treatments often will be necessary and may need to be sequential, not simultaneous. Alternatively, improvements in initial establishment of native perennial species, before substantial increases in exotic annual grasses, could preclude the need for additional treatments. Advancements in seed delivery, timing of seed delivery, and seed enhancement technologies may meet this need in the future (Madsen et al. 2016; Copeland et al. IN PRESS). Degraded Wyoming big sagebrush communities are difficult to restore because these communities have low resistance to exotic annual grass invasion (Davies et al. 2011a; Chambers et al. 2014), and native perennial species only establish sporadically from seed and are slow growing. Thus, even when seed limitations and competition from sagebrush are mediated, restoration of the perennial herbaceous understory remains uncertain because other factors may prevent success.

Management Implications

Wyoming big sagebrush plant communities with depleted understories are a management challenge. Wildfire is inevitable in most of these degraded sagebrush communities, and without restoration of large bunchgrasses these communities are likely one fire away from transitioning to exotic annual grasslands. Restoration attempts in degraded Wyoming big sagebrush communities are generally unsuccessful and often increase exotic annual grasses. Our current effort increased large native bunchgrasses but also substantially increased exotic annual grasses. Thus, the use of this treatment to restore the understory in degraded Wyoming big sagebrush communities is inconclusive based on our mixed results. Refinement of this strategy and development of other strategies to restore degraded sagebrush communities are clearly needed. We suggest that researchers develop tools and strategies to improve the establishment of seeded species, investigate methods to seed into sagebrush communities with minimal disturbance, and evaluate integrating treatments to seed desired species and control exotic annual grasses. The results of this study question the appropriateness of applying mowing followed by seeding large native bunchgrasses to restore the understory in degraded Wyoming big sagebrush communities, as this increased exotic annual grasses, which increases the likelihood of more frequent fire (Stewart and Hull 1949; Balch et al. 2013). However, the increase in large native bunchgrasses and decrease in sagebrush cover with mowing and seeding bunchgrasses probably slightly improved the resilience of the plant community to fire. Though mowing followed by seeding achieved some desired plant community effects, these treatments should probably not be applied in degraded Wyoming big sagebrush communities without having a plan and the resources to control exotic annual grasses as needed. The partial success of mowing followed by seeding and cost of additional treatments likely necessary to improve success suggests preventing degradation of these communities and restoring these communities when they still have a greater abundance of large perennial bunchgrasses should be a management priority.

Declaration of Competing Interest

None.

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