

RESEARCH ARTICLE

Postwildfire seeding to restore native vegetation and limit exotic annuals: an evaluation in juniper-dominated sagebrush steppe

Kirk W. Davies^{1,2} , Jon D. Bates¹, Chad S. Boyd¹

Reestablishment of perennial vegetation is often needed after wildfires to limit exotic species and restore ecosystem services. However, there is a growing body of evidence that questions if seeding after wildfires increases perennial vegetation and reduces exotic plants. The concern that seeding may not meet restoration goals is even more prevalent when native perennial vegetation is seeded after fire. We evaluated vegetation cover and density responses to broadcast seeding native perennial grasses and mountain big sagebrush (*Artemisia tridentata* Nutt. spp. *vaseyana* [Rydb.] Beetle) after wildfires in the western United States in six juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook)-dominated mountain big sagebrush communities for 3 years postfire. Seeding native perennial species compared to not seeding increased perennial grass and sagebrush cover and density. Perennial grass cover was 4.3 times greater in seeded compared to nonseeded areas. Sagebrush cover averaged 24 and less than 0.1% in seeded and nonseeded areas at the conclusion of the study, respectively. Seeding perennial species reduced exotic annual grass and annual forb cover and density. Exotic annual grass cover was 8.6 times greater in nonseeded compared to seeded areas 3 years postfire. Exotic annual grass cover increased over time in nonseeded areas but decreased in seeded areas by the third-year postfire. Seeded areas were perennial-dominated and nonseeded areas were annual-dominated at the end of the study. Establishing perennial vegetation may be critical after wildfires in juniper-dominated sagebrush steppe to prevent the development of annual-dominated communities. Postwildfire seeding increased perennial vegetation and reduced exotic plants and justifies its use.

Key words: annual grasses, broadcast, cheatgrass, seeding, shrubs, western juniper

Implications for Practice

- Postfire seeding can increase native vegetation and limit exotic plants.
- After wildfire in juniper-dominated sagebrush steppe, perennial vegetation should be seeded to restore ecosystem services and limit exotic annual grasses.
- Broadcast seeding native perennial grasses and sagebrush is a viable restoration method after fire in juniper-dominated sagebrush communities.
- Research is needed to increase restoration efficiency by determining optimal broadcast seeding rates and seeding mixtures.
- Preventing conifer-dominance of sagebrush communities should be a management priority to limit the need for postfire restoration.

Introduction

Postfire restoration of native vegetation is often needed in imperiled ecosystems. Restoring native vegetation is critical because some native fauna require specific habitat components that only native vegetation can provide. As areas burned annually increase in some regions (Krawchuk et al. 2009; Adams 2013), restoration of native vegetation will only become a more pressing issue.

This need will likely increase in many areas because larger and more frequent and severe wildfires are expected with climate change and increasing CO₂ levels (Fried et al. 2004; Fulé 2008; Yue et al. 2013).

Seeding after wildfires is a commonly used management tool applied with the goal of increasing vegetation cover and reducing the abundance of exotic species (Robichaud et al. 2000; Beyer 2004). Seeding vegetation after fire is assumed to increase seeded species that will utilize resources that would otherwise be available to exotic species. However, seeding after fire has generally not achieved the goal of increasing native vegetation cover and reducing exotic species (Peppin et al. 2010; Stella et al. 2010). Furthermore, seeding native species after wildfires has been limited and there is little published information on the effectiveness of postfire seeding of native species (Beschta et al. 2004). One notable exception is Thompson et al. (2006)

Author contributions: all authors conceived and designed the study; KWD carried out the experiment, analyzed the data, and wrote the manuscript; all authors edited the manuscript.

¹USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center, 67826-A Hwy 205, Burns, OR 97720, U.S.A.

²Address correspondence to K. W. Davies, email kirk.davies@ars.usda.gov

Published 2018. This article is a U.S. Government work and is in the public domain in the USA.
doi: 10.1111/rec.12848

who reported seeding native and non-native species in sagebrush (*Artemisia L.*) steppe communities in Utah, United States, increased perennial vegetation and limited exotic plants.

The sagebrush steppe is an ecosystem that is imperiled from multiple threats (Knick et al. 2003; Davies et al. 2011) and, consequently, multiple sagebrush-associated species are of conservation concern (Crawford et al. 2004; Suring et al. 2005; Shipley et al. 2006). The sagebrush steppe developed with infrequent fire (Wright & Bailey 1982; Mensing et al. 2006); however, exotic annual grasses have altered its recovery after fire (Davies et al. 2009). Periodic fire is necessary for limiting conifer encroachment in higher elevation sagebrush communities (Miller & Tausch 2001; Miller et al. 2005). However, once a conifer woodland has developed, the potential for a more severe fire is elevated because of increased fuel loads (Tausch 1999; Miller et al. 2008; Stebleton & Bunting 2009). Higher severity fire in fully developed woodlands increases the probability of a substantial exotic annual grass invasion (Bates et al. 2014). Limiting exotic annual grasses is important because they compete with native vegetation (Melgoza et al. 1990; Humphrey & Schupp 2004) and promote frequent wildfires that are detrimental to native species (D'Antonio & Vitousek 1992). Increases in exotic annual grass abundance are also correlated with exponential declines in native plant species and biodiversity (Davies 2011).

Reestablishing native perennial-dominated plant communities after wildfire in western juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook)-encroached mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) is important because postfire exotic plant invasion can be substantial in some locations (e.g. Bates et al. 2014; Davies & Bates 2017). Furthermore, restoring native vegetation in mountain big sagebrush communities is important because these are some of the most productive sagebrush communities (Hironaka et al. 1983; Davies & Bates 2010a, 2010b). This is an issue on millions of hectares of mountain big sagebrush that have been or are at risk of juniper encroachment in the northern Great Basin and Columbia Plateau (Miller et al. 2000; Miller et al. 2005).

Information on postwildfire seeding of native vegetation in juniper-dominated sagebrush communities is lacking. What information is available focuses on seeding after prescribed fire (Sheley & Bates 2008; Davies et al. 2014, 2017; Davies & Bates 2017). These studies were also limited as they only seeded sagebrush (Davies et al. 2017; Davies & Bates 2017), included non-native species (Davies et al. 2014), or used small plot design (2 × 2 m) that did not include sagebrush (Sheley & Bates 2008). Seeding mountain big sagebrush is often successful (Davies et al. 2014, 2018; Davies & Bates 2017). Herbaceous vegetation, particularly non-native species, may limit shrub establishment (Rinella et al. 2015, 2016; Davies et al. 2017). The effects, however, of seeding sagebrush in combination with native herbaceous vegetation are unknown. Exotic annual species can be limited when native perennial species become established in high numbers in Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) communities (Davies & Johnson 2017), but this has not been tested in mountain big sagebrush communities. Evaluating the

ability of seeded native species to establish after wildfire in juniper-dominated mountain big sagebrush is critically needed to assist land managers developing postfire restoration plans, especially in plant communities at risk of exotic annual grass invasion after wildfire.

There is a prevailing assumption that mountain big sagebrush communities recover after fire without the need for active restoration efforts (e.g. seeding). This view likely developed because mountain big sagebrush plant communities are considered more resilient to wildfire and resistant to exotic annual grass invasion than lower elevation sagebrush communities (Davies et al. 2011; Chambers et al. 2014). Mountain big sagebrush also historically burned more frequently than less productive sagebrush communities (Miller et al. 2005) and intact (i.e. nonconifer encroached) mountain big sagebrush communities often recover after fire without seeding (Lesica et al. 2007; Nelson et al. 2014). Another common assumption is that if burned mountain big sagebrush communities need seeding, introduced species should be used to rapidly occupy the site and prevent exotic plant invasion. This likely evolved from experiences in hotter, drier Wyoming big sagebrush communities where seeding introduced species is much more successful at increasing perennial vegetation and limiting exotic annual species than seeding native species (Eiswerth et al. 2009; Boyd & Davies 2010; Davies et al. 2015). Therefore, it is important to determine if seeding is needed and if seeding native vegetation can increase perennial vegetation and limit exotic annual species after wildfire in juniper-dominated mountain big sagebrush communities.

The purpose of this study was to evaluate the effects of seeding native perennial vegetation after wildfire in western juniper-dominated mountain big sagebrush communities that may be at risk of postfire exotic annual grass invasion and dominance. We hypothesized that seeding native perennial grasses and sagebrush after wildfire in juniper-dominated mountain big sagebrush communities would increase sagebrush and perennial grass cover and density and limit exotic annual grass and annual forb cover and density compared to unseeded areas.

Methods

Study Area

The study was conducted in southeastern Oregon in areas burned in the Buzzard wildfire complex and the Glass Butte wildfire in 2014. Study sites were located between 52 km west and 90 km southeast of Burns, Oregon. At the time of the wildfires, study sites were fully developed western juniper woodlands (i.e. dominated by juniper) established on mountain big sagebrush-bunchgrass plant communities. Juniper cover ranged from 23 to 42% across the sites prior to burning. Sagebrush was largely displaced from the communities by juniper encroachment prior to the wildfires. Wildfires killed 100% of the junipers at the study sites. Historical fire return intervals for these communities would have been less than 50 years and may have been as common as every decade (Miller et al. 2005). Common perennial grasses postfire included bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), Thurber's

needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), Idaho fescue (*Festuca idahoensis* Elmer), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), and Sandberg bluegrass (*Poa secunda* J. Presl). Study sites ranged in elevation from 1,499 to 1,683 m above sea level. Slopes ranged from 0 to 45° with aspects facing north, south, east, and west. Soils ranged from silty clay to loamy among study sites. Regional climate consists of cool, wet winters and hot, dry summers. Long-term annual precipitation (1981–2010) ranged from 300 to 426 mm among the study sites (PRISM 2018). Crop year (1 October–30 September) precipitation averaged 91, 87, and 101% of the long-term average in 2014–2015, 2015–2016, and 2016–2017, respectively. Livestock were excluded for the duration of study. Wildlife was not excluded but we saw little evidence of wildlife use.

Experimental Design and Measurements

We used a randomized complete block design with six blocks (sites) to evaluate the effects of seeding native perennial vegetation after wildfire in juniper-dominated mountain big sagebrush communities. Blocks were separated by up to 133 km. Treatments were: (1) broadcast seeded with sagebrush and native perennial grasses (seeded), and (2) not seeded (control). Treatments were randomly assigned to one of two 10 × 30 m plots at each block. Seeding treatments were applied on 18 and 19 November of 2014. The native seed mix contained mountain brome (*Bromus marginatus* Nees ex Steud.), thickspike wheatgrass (*Elymus lanceolatus* [Scribn. & J.G. Sm.] Gould), Sherman big bluegrass (*Poa secunda* J. Presl), prairie Junegrass (*Koeleria macrantha* [Ledeb.] Schult.), Idaho fescue, Snake River wheatgrass (*Elymus wawawaiensis* J. Carlson & Barkworth), bottlebrush squirreltail, bluebunch wheatgrass, Sandberg bluegrass, and mountain big sagebrush. We originally intended to seed each species at 1.45 kg/ha but a technical error in the application resulted in each species being seeded at 5.8 kg/ha.

Vegetation measurements were conducted in early July of 2015, 2016, and 2017 using four, parallel 30-m transects spaced 2 m apart in each treatment plot in each block. Herbaceous foliar cover by species was estimated in 0.2 m⁻² quadrats located every 3 m along each 30-m transect (starting at 3 m and ending at 27 m). Bare ground, litter, biological soil crust, and rock cover were also estimated in the 0.2 m⁻² quadrats. Herbaceous density by species was measured by counting all plants rooted in the 0.2 m⁻² quadrats. Rhizomatous species density was estimated by dividing quadrats into quarters and counting quarters that contained the species. Shrub cover by species was measured using the line-intercept method along each 30-m transect. Shrub density by species was measured by counting shrubs rooted inside a 2 × 30-m belt transect placed over each 30-m transect. Sagebrush density was also recorded as juvenile or mature. Sagebrush was considered mature if it had reproductive stems.

Statistical Analyses

Repeated measures analysis of variance (ANOVA) using the mixed models procedure (Proc Mixed) in SAS v. 9.4 (SAS

Institute Inc., Cary, NC, U.S.A.) was used to compare between treatments and years. Block and block by treatment interactions were considered random effects and year of sampling was the repeated variable. Covariance structure was determined using Akaike's information criterion (Littell et al. 1996). Data that violated ANOVA assumptions were square root transformed prior to analyses to better meet the assumptions of ANOVAs. All data presented are in their original dimensions (i.e. nontransformed). For analyses, herbaceous cover and density were separated into five groups: Sandberg bluegrass, perennial grasses, exotic annual grasses, perennial forbs, and annual forbs. Sandberg bluegrass was treated as its own plant group because it is smaller in stature, develops phenologically earlier, and responds differently to disturbances than other perennial grasses of the sagebrush steppe. Sherman big bluegrass, though currently classified as a variety of Sandberg bluegrass, was grouped with the other perennial grasses in the analyses because it is larger and matures later than the more common Sandberg bluegrass in this ecosystem. The exotic annual grass group was predominately comprised of cheatgrass (*Bromus tectorum* L.) with some medusahead (*Taeniatherum caput-medusae* [L.] Nevski). Shrubs were separated into sagebrush and other shrubs for analyses. Significance level for all tests was set at $p \leq 0.05$ and response variable means were reported with standard errors.

Results

Perennial grass cover differed between treatments and among years ($p = 0.026$ and 0.012 , respectively; Fig. 1A). Perennial grass cover was 4.3 times greater in the seeded treatment compared to the controls 3 years postfire. Sandberg bluegrass cover did not differ between treatments ($p = 0.069$; Fig. 1B) but varied by year ($p < 0.001$) and generally declined over time. Perennial forb cover did not vary between treatments ($p = 0.848$) or among years ($p = 0.815$) and averaged $1.3 \pm 0.5\%$ and $1.5 \pm 0.5\%$ in the seeded treatment and controls at the end of the study, respectively. Exotic annual grass cover varied by the interaction between treatment and year ($p = 0.001$; Fig. 1C). In the controls, exotic annual grass cover increased over time but in the seeded treatment, annual grass cover peaked the second postfire year and then declined the third-year postfire. Nonseeded controls had 8.6 times greater exotic annual grass cover compared to the seeded treatment at the end of the study. Annual forb cover varied between treatments and among years ($p = 0.003$ and < 0.001 , respectively; Fig. 1D). Annual forb cover was 2.4 times greater in the controls compared to the seeded treatment 3 years postfire. Bare ground and rock cover did not differ between treatments ($p = 0.642$ and 0.274 , respectively) but both varied among years ($p < 0.001$; Fig. 2A & 2B). Bare ground and rock generally declined over time in both treatments. Litter was similar between treatments ($p = 0.141$) but varied among years ($p < 0.001$; Fig. 2C). Litter increased over time in both treatments. Biological soil crust cover was similar between treatments and among years ($p = 0.810$ and 0.086 , respectively). At the end of the study, biological soil crust cover was 0.005 ± 0.005 and $0.006 \pm 0.004\%$ in the seeded treatment and controls, respectively. Sagebrush cover varied by the

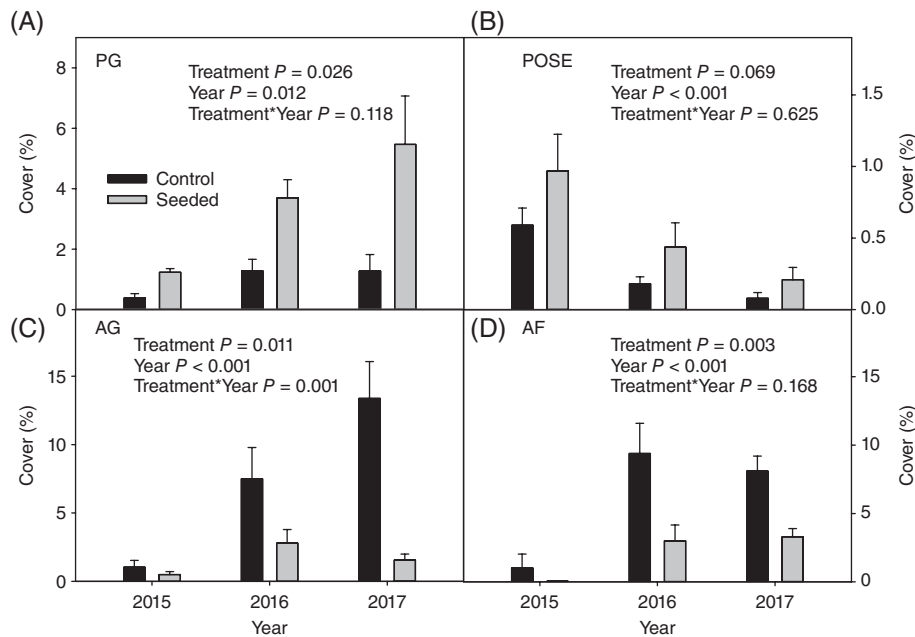


Figure 1. Herbaceous functional group cover (mean + SE) in the seeded and control treatments in 2015, 2016, and 2017. PG, perennial grass (A), POSE, Sandberg bluegrass (B), AG, exotic annual grass (C), and AF, annual forb (D).

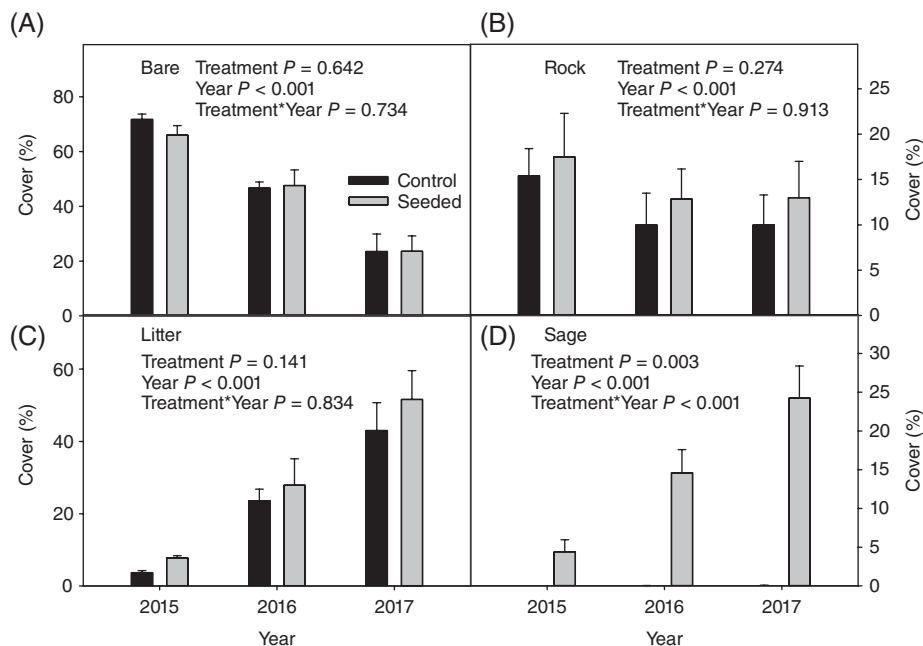


Figure 2. Cover groups cover (mean + SE) in the seeded and control treatments in 2015, 2016, and 2017. Bare, bare ground (A); rock, rock (B); litter, ground litter (C); and sage, sagebrush (D).

interaction between treatment and year ($p < 0.001$; Fig. 2D). Sagebrush cover increased over time in the seeded treatment but remained low and constant in the control treatment. By the end of the study, sagebrush cover average $24 \pm 4\%$ and $0.06 \pm 0.06\%$ in the seeded treatment and controls, respectively. Other shrub cover was similar between treatments and among years ($p = 0.206$ and 0.101 , respectively). Other shrub cover was

$1.7 \pm 1.6\%$ and $1.7 \pm 1.2\%$ in the seeded treatment and controls at the conclusion of the study, respectively.

Perennial grass density was greater in the seeded treatment compared to the controls ($p = 0.007$, respectively; Fig. 3A) and varied among years ($p < 0.001$). In the final sampling year, perennial grass density was 3.3 times greater in the seeded treatment compared to the controls. Perennial grass density

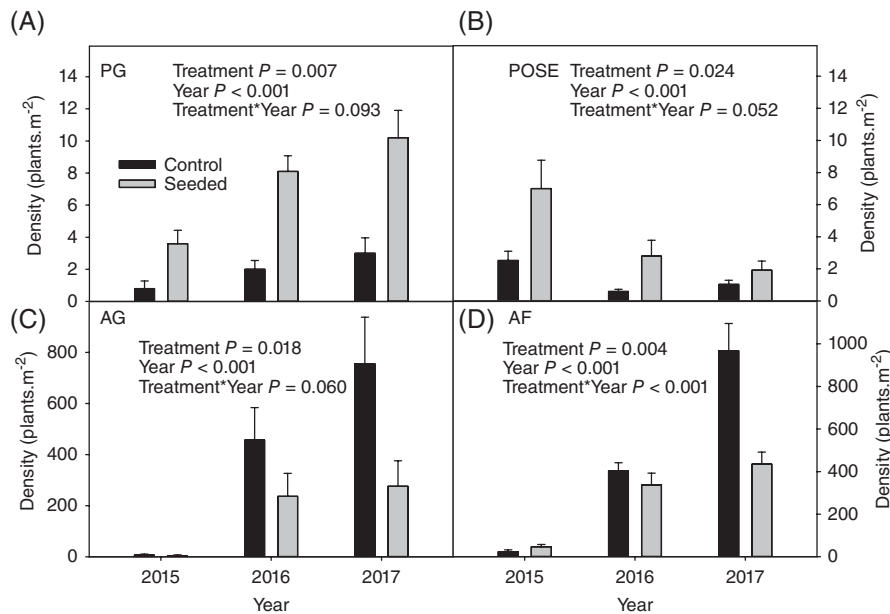


Figure 3. Herbaceous functional group density (mean + SE) in the seeded and control treatments in 2015, 2016, and 2017. PG, perennial grass (A); POSE, Sandberg bluegrass (B); AG, exotic annual grass (C); and AF, annual forb (D).

increased with time since seeding. Sandberg bluegrass density was greater in the seeded treatment compared to the controls and varied among years ($p = 0.024$ and < 0.001 , respectively; Fig. 3B). Sandberg bluegrass density generally decreased over time. Perennial forb density was similar between treatments and among years ($p = 0.948$ and 0.610 , respectively). In the final sampling year, perennial forb density was 3.6 ± 1.8 and 4.2 ± 1.2 plants/m² in the seeded treatment and controls, respectively. Exotic annual grass density was greater in the controls compared to the seeded treatment ($p = 0.018$; Fig. 3C) and varied among years ($p < 0.001$). The controls had 270% greater exotic annual grass abundance than the seeded treatment 3 years after seeding. Exotic annual grass density increased with time in both treatments. Annual forb density was influenced by the interaction between treatment and year ($p < 0.001$; Fig. 3D). Annual forb density was more similar between the controls than the seeded treatment in the first year, slightly greater in the controls than the seeded treatment in the second year, and more than two times greater in the controls compared to the seeded treatment in the third year. In the third sampling year, annual forb density was 532 plants/m² greater in controls compared to the seeded treatment. Juvenile sagebrush density was greater in the seeded treatment compared to the controls ($p < 0.001$; Fig. 4A) but did not vary among years ($p = 0.075$). Mature sagebrush density varied by the interaction between treatment and year ($p = 0.004$; Fig. 4B). In the first year, neither treatment contained any mature sagebrush. However, in the second and third postfire year, mature sagebrush density was over 200 times greater in the seeded treatment compared to the controls (Fig. 4B). Sagebrush was only detected at two of the six unseeded controls. Density of other shrubs did not differ between treatments or among years ($p = 0.460$ and 0.082 , respectively). In the final sampling year, other shrub density was

0.49 ± 0.43 and 0.38 ± 0.32 plants/m² in the controls and seeded treatment, respectively.

Discussion

Our results support the rationale for seeding after wildfires to increase perennial vegetation and limit exotic plants. The results of our study specifically support our hypotheses that seeding native perennial vegetation can increase perennial grass and sagebrush cover and density and reduce exotic annual grass and annual forb response after wildfire in western juniper-dominated sagebrush steppe in the western United States. These results suggest that seeding native perennial vegetation after wildfires may be needed to promote recovery and prevent exotic annual grass dominance in juniper-encroached sagebrush steppe. Importantly, our results suggest that seeding native vegetation after wildfire in juniper-encroached sagebrush communities is a viable restoration strategy. With the increase in area burned in wildfires in many regions (Krawchuk et al. 2009; Adams 2013), establishing that seeding native perennial species can increase perennial vegetation and limit exotic plants after wildfires provides critically needed guidance for postfire restoration. This is particularly important as other research (e.g. Stella et al. 2010) has suggested that postwildfire seeding is ineffective at reducing exotic plants.

Prior research demonstrated that exotic annual grasses could increase after prescribed fire in some juniper-encroached mountain big sagebrush communities with risk of annual grass dominance increasing with greater woodland development and with decreasing site resistance and resilience (Bates et al. 2014; Roundy et al. 2014; Davies & Bates 2017). The results from our unseeded plots further indicate that exotic annual grass invasion and dominance after fire in juniper-dominated mountain

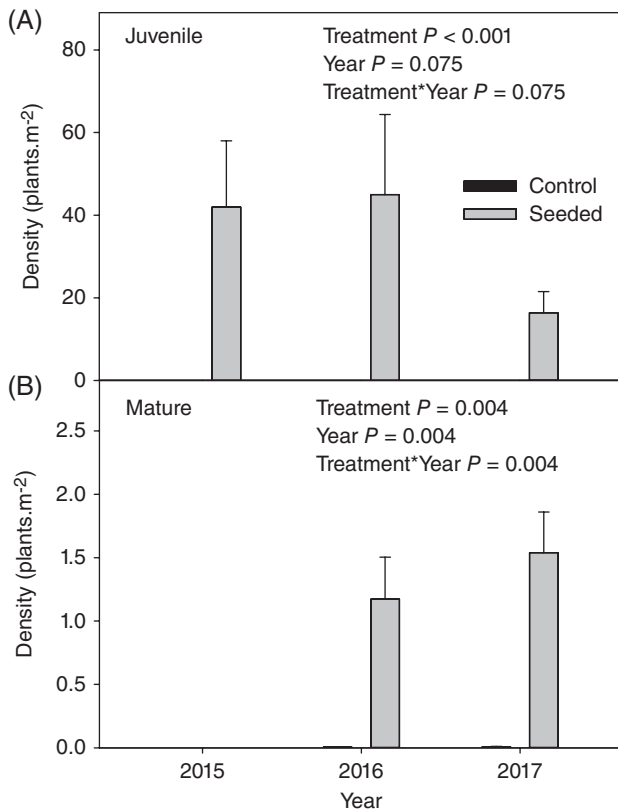


Figure 4. Sagebrush density (mean + SE) in the seeded and control treatments in 2015, 2016, and 2017. Juvenile, juvenile sagebrush (A) and mature, mature sagebrush (B).

big sagebrush steppe is of concern. This likely occurs because junipers decrease herbaceous vegetation as they dominate a site (Miller et al. 2000; Bates et al. 2005) and after fires the former juniper canopy locations are often devoid of vegetation and have high soil resource availability (Bates & Davies 2017; Davies et al. 2017). The abundance of soil resources and reduction in herbaceous vegetation, in particular perennial grasses, creates a perfect scenario for exotic annual grass invasion and dominance (Chambers et al. 2007).

Our results agree with prior research that establishing perennial vegetation is critical to limiting exotic annual species (Davies et al. 2015; Davies & Johnson 2017). This is particularly important after wildfires in areas susceptible to exotic annual grass invasion and dominance. Although exotic annual grass cover increased each year in areas not seeded, in areas seeded with native perennial vegetation, exotic annual grass cover peaked in the second-year postfire and declined almost 50% by the third-year postfire. This indicates that seeded vegetation may limited resources available to exotic annual grasses. Furthermore, this also suggests that the trajectory for the seeded areas is continued perennial vegetation dominance. At the end of the study, the areas not seeded were dominated by annual species (exotic annual grasses and annual forbs). The future trajectory of these communities is unknown but there is a high probability of continued exotic annual species dominance given

the low abundance of perennial grasses in these areas. Exotic annual grass dominance increases the risk of an annual grass-fire cycle developing because annual grasses dry out earlier and increase fine fuel loads and continuity compared to native vegetation (D'Antonio & Vitousek 1992). Increased fire frequency is especially detrimental to native vegetation that evolved with less frequent fire (D'Antonio & Vitousek 1992).

Sagebrush recovered rapidly after seeding with cover averaging 24% by the third-year postfire. However, sagebrush was largely absent from areas not seeded with sagebrush cover averaging less than 0.1% at the end of the study. Seeding sagebrush after juniper control with fire has generally accelerated the recovery of sagebrush cover and density (Davies et al. 2014; Davies & Bates 2017), except when herbaceous vegetation was allowed to recover prior to seeding sagebrush (Davies et al. 2017). These findings and the current study suggest the loss of sagebrush with juniper encroachment followed by fire that imposes strong juniper mortality results in a scenario of slow sagebrush recovery. This is counter to the assumption that sagebrush will often naturally recover rapidly after conifer control (Barney & Frischknecht 1974; Tausch & Tueller 1977; Skousen et al. 1989; Miller et al. 2005). Rapid recovery of sagebrush is needed because sagebrush is a crucial habitat component for sagebrush-associated wildlife species that are of conservation concern (Crawford et al. 2004; Shipley et al. 2006; Aldridge et al. 2008).

One caveat of our study was the high seeding rate, which was three or more times the rate often applied by land management agencies, especially for sagebrush. This may be one of the reasons that our results differ from other studies suggesting that postwildfire seeding is not effective (Peppin et al. 2010; Stella et al. 2010). Broadcast seeding after wildfires in juniper-dominated sagebrush communities as well as many other communities has not been empirically tested to establish optimal seeding rates. The high establishment of sagebrush and subsequent high cover of sagebrush probably limited perennial grass cover. As sagebrush cover increases, perennial grass production decreases (Cook & Lewis 1963; Rittenhouse & Sneva 1976). Our results, however, suggest that sagebrush and native perennial grasses can be seeded together. Additional research evaluating different seeding rates and ratios of different plant groups and species in seed mixtures would be valuable in establishing optimal seeding rates and mixtures. This is important because habitat requirements for sagebrush-associated wildlife often require a mixture of sagebrush and herbaceous species (e.g. Crawford et al. 2004).

Though our seeding rate was high, our study demonstrated that seeding native perennial vegetation after wildfire can promote recovery of perennial grasses and sagebrush and limit exotic annual grasses. Importantly, this suggests that seeding introduced species is not necessary to achieve management objectives after fire in mountain big sagebrush communities. This is a stark contrast to Wyoming big sagebrush communities, where seeded native vegetation often fails to establish (Eiswerth et al. 2009; Boyd & Davies 2010; Davies et al. 2015); however, there are exceptions (see Davies et al. 2018). Mountain big sagebrush communities are cooler and wetter than Wyoming

big sagebrush communities (West et al. 1978; Winward 1980; Hironaka et al. 1983) and this likely explains why seeded native vegetation often successfully establishes in these communities.

The high abundance and cover of exotic annual grasses in nonseeded areas at the end of the study suggests that seeding perennial vegetation is needed after wildfires in juniper-dominated sagebrush steppe to prevent exotic annual grass dominance and restore ecosystem services. This can be achieved by broadcast seeding native perennial grasses and sagebrush. Refinement of seeding mixtures and rates would be beneficial to improve restoration success and efficiency. We suggest that restoration practitioners consider seeding perennial vegetation after fires in juniper-dominated sagebrush communities, especially those at risk of exotic plant invasion.

Tree encroached-shrublands in Australia (Rundel et al. 2014), Africa (Holmes & Cowling 1997; Rundel et al. 2014), and South America (Sarasola et al. 2006; Langdon et al. 2010) may, similar to our current study, be at risk of postfire exotic plant invasion. Tree mortality from fire reduces competition and opens the plant community to exotic plant invasion. This may be even more problematic if tree encroachment or the fire that controls the trees reduces understory species that are keys for resistance to exotic plant invasion. Our results demonstrate that seeding native perennial vegetation after wildfire is a method that can counter this threat.

Acknowledgments

We thank W. Strachan and numerous student technicians for assisting with data collection and entry. We are also grateful for thoughtful reviews of earlier versions of this manuscript by D. Johnson and E. Hamerlynck. Constructive reviews by the associate editor and anonymous reviewers were also greatly appreciated. Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA or the authors and does not imply its approval to the exclusion of other products. USDA is an equal opportunity provider and employer.

LITERATURE CITED

- Adams MA (2013) Mega-fires, tipping points and ecosystem services: managing forests and woodlands in an uncertain future. *Forest Ecology and Management* 294:250–261
- Aldridge CL, Nielsen SE, Beyer HL, Boyce MS, Connelly JW, Knick ST, Schroeder MA (2008) Range-wide patterns of greater sage-grouse persistence. *Diversity and Distributions* 14:983–994
- Barney M, Frischknecht N (1974) Vegetation changes following fire in the pinyon-juniper type of west-Central Utah. *Journal of Range Management* 27:91–96
- Bates JD, Davies KW (2017) Effects of conifer treatments on soil nutrient availability and plant composition in sagebrush steppe. *Forest Ecology & Management* 400:631–644
- Bates JD, Miller RF, Svejcar TJ (2005) Long-term successional trends following western juniper cutting. *Rangeland Ecology & Management* 58:533–541
- Bates JD, Sharp RN, Davies KW (2014) Sagebrush steppe recovery after fire varies by development phase of *Juniperus occidentalis* woodland. *International Journal of Wildland Fire* 23:117–130
- Beschta RL, Rhodes JJ, Kauffman JB, Gresswell RE, Minshall GW, Karr JR, Perry DA, Hauer FR, Frissell CA (2004) Post-fire management of forested public lands of the western United States. *Conservation Biology* 18:957–967
- Beyer JL (2004) Post-fire seeding for erosion control: effectiveness and impacts on native plant communities. *Conservation Biology* 18:947–956
- Boyd CS, Davies KW (2010) Shrub microsite influences post-fire perennial grass establishment. *Rangeland Ecology & Management* 63:248–252
- Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs* 77:117–145
- Chambers JC, Bradley BA, Brown CS, D'Antonio C, Germino MJ, Grace JB, Hardegree SP, Miller RF, Pyke DA (2014) Resilience to stress and disturbance and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. *Ecosystems* 17:360–375
- Cook CW, Lewis CE (1963) Competition between big sagebrush and seeded grasses on foothill ranges in Utah. *Journal of Range Management* 16:245–250
- Crawford JA, Olson RA, West NE, Mosley JC, Schroeder MA, Whitson TD, Miller RF, Gregg MA, Boyd CS (2004) Ecology and management of sage-grouse and sage-grouse habitat. *Journal of Range Management* 57:2–19
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87
- Davies KW (2011) Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. *Oecologia* 167:481–491
- Davies KW, Bates JD (2010a) Native perennial forb variation between mountain big sagebrush and Wyoming big sagebrush plant communities. *Environmental Management* 46:452–458
- Davies KW, Bates JD (2010b) Vegetation characteristics of mountain and Wyoming big sagebrush plant communities in the northern Great Basin. *Rangeland Ecology & Management* 63:461–466
- Davies KW, Bates JD (2017) Restoring big sagebrush after controlling encroaching western juniper with fire: aspect and subspecies effects. *Restoration Ecology* 25:33–41
- Davies KW, Johnson DD (2017) Established perennial vegetation provides high resistance to reinvasion by exotic annual grasses. *Rangeland Ecology & Management* 70:748–754
- Davies KW, Svejcar TJ, Bates JD (2009) Interaction of historical and nonhistorical disturbances maintains native plant communities. *Ecological Applications* 19:1536–1545
- Davies KW, Boyd CS, Beck JL, Bates JD, Svejcar TJ, Gregg MA (2011) Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144:2573–2584
- Davies KW, Bates JD, Madsen MD, Nafus AM (2014) Restoration of mountain big sagebrush steppe following prescribed burning to control western juniper. *Environmental Management* 53:1015–1022
- Davies KW, Boyd CS, Johnson DD, Nafus AM, Madsen MD (2015) Success of seeding native compared to introduced perennial vegetation for revegetating medusahead-invaded sagebrush rangeland. *Rangeland Ecology & Management* 68:224–230
- Davies KW, Bates JD, Hulet A (2017) Attempting to restoring mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) four years after fire. *Restoration Ecology* 25:717–722
- Davies KW, Boyd CS, Madsen MD, Kerby J, Hulet A (2018) Evaluating a seed technology for sagebrush restoration efforts across an elevation gradient: support for bet hedging. *Rangeland Ecology & Management* 71:19–24
- Eiswerth ME, Krauter K, Swanson SR, Zielinski M (2009) Post-fire seeding on Wyoming big sagebrush ecological sites: regression analyses of seeded nonnative and native species densities. *Journal of Environmental Management* 90:1320–1325
- Fried JS, Torn MS, Mills E (2004) The impact of climate change on wild-fire severity: a regional forecast for northern California. *Climate Change* 64:169–191
- Fulé PZ (2008) Does it make sense to restore wildland fire in changing climate? *Restoration Ecology* 16:526–531

- Hironaka MM, Fosberg M, Winward AH (1983) Sagebrush-grass habitat types of southern Idaho. University of Idaho, Moscow. Bulletin 35
- Holmes PM, Cowling RM (1997) Diversity, composition, and guild structure relationships between soil stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. *Plant Ecology* 133:107–122
- Humphrey LD, Schupp EW (2004) Competition as a barrier to establishment of a native perennial grass (*Elmus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405–422
- Knick ST, Dobkin DS, Rotenberry JT, Schroeder MA, Vander Haegen WM, Riper CV (2003) Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611–634
- Krawchuk MA, Moritz MA, Parisien MA, Van Dorn J, Hayhoe K (2009) Global pyrogeography: the current and future distribution of wildfire. *PLoS One* 4:1–12
- Langdon B, Pauchard A, Aguayo M (2010) *Pinus contorta* invasion in Chilean Patagonia: local patterns in a global context. *Biological Invasions* 12:3961–3971
- Lesica P, Cooper SV, Kunray G (2007) Recovery of big sagebrush following fire in Southwest Montana. *Rangeland Ecology & Management* 60:261–269
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) SAS system for mixed models. SAS Institute Inc., Cary, North Carolina
- Melgoza G, Nowak RS, Tausch RJ (1990) Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7–13
- Mensing S, Livingston S, Barker P (2006) Long-term fire history in Great Basin sagebrush reconstructed from macroscopic charcoal in spring sediments, Newark Valley, Nevada. *Western North American Naturalist* 66:64–77
- Miller RF, Tausch RJ (2001) The role of fire in pinyon and juniper woodlands: a descriptive analysis. Tall Timbers Research Station Miscellaneous Publication 11:15–30
- Miller RF, Svejcar TJ, Rose JR (2000) Impacts of western juniper on plant community composition and structure. *Journal of Range Management* 53:574–585
- Miller RF, Bates JD, Svejcar TJ, Pierson FB, Eddleman LE (2005) Biology, ecology, and management of western juniper. Oregon State University Agricultural Experiment Station Technical Bulletin No. 152, Corvallis, OR
- Miller RF, Tausch RJ, McArthur ED, Johnson DD, Sanderson SC (2008) Age structure and expansion of piñon–juniper woodlands: a regional perspective in the Intermountain West. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado. Research Paper RMRS-RP-69
- Nelson ZJ, Weisberg PJ, Kitchen SG (2014) Influence of climate and environment on post-fire recovery of mountain big sagebrush. *International Journal of Wildland Fire* 23:131–142
- Peppin D, Fulé PZ, Sieg CH, Beyers JL, Hunter ME (2010) Post-wildfire seeding in forests of the western United States: an evidence-based review. *Forest Ecology & Management* 260:573–586
- PRISM (2018). PRISM climate group database. <http://prism.nacse.org/explorer/> (accessed 28 Mar 2018)
- Rinella MJ, Hammond DH, Bryant AM, Kozar BJ (2015) High precipitation and seeded species competition reduce seeded shrub establishment during dryland restoration. *Ecological Applications* 25:1044–1053
- Rinella MJ, Espeland EK, Moffat BJ (2016) Studying long-term, large-scale grassland restoration outcome to improving seeding methods and reveal knowledge gaps. *Journal of Applied Ecology* 53:1565–1574
- Rittenhouse LR, Sneva FA (1976) Expressing the competitive relationship between Wyoming big sagebrush and crested wheatgrass. *Journal of Range Management* 29:326–327
- Robichaud PR, Beyers JL, Neary DG (2000) Evaluating the effectiveness of post-fire rehabilitation treatments. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado General Technical Report RMRS-GTR63
- Roundy BA, Miller RF, Tausch RJ, Young K, Hulet A, Rau B, Jessop B, Chambers JC, Eggett D (2014) Understory cover responses to piñon–juniper treatments across tree dominance gradients in the Great Basin. *Rangeland Ecology & Management* 67:482–494
- Rundel RW, Dickie IA, Richardson DM (2014) Tree invasions into treeless areas: mechanisms and ecosystem process. *Biological Invasions* 16:663–675
- Sarasola M, Rusch V, Schlichter T, Ghersa C (2006) Invasión de coníferas forestales en áreas de estepa y bosques de ciprés de la cordillera en la región Andino Patagónica. *Ecología Austral* 16:143–156
- Sheley RL, Bates JD (2008) Restoring western juniper (*Juniperus occidentalis*) infested rangeland after prescribed fire. *Weed Science* 56:469–476
- Shipley LA, Davila TB, Thines NJ, Elias BA (2006) Nutritional requirements and diet choices of the pygmy rabbit (*Bachylagus idahoensis*): a sagebrush specialist. *Journal of Chemical Ecology* 32:2455–2474
- Skousen JG, Davis JN, Brotherson JD (1989) Pinyon–juniper chaining and seeding for big game in Central Utah. *Journal of Range Management* 42:98–104
- Stebleton A, Bunting S (2009) Guide for quantifying fuels in sagebrush steppe and juniper woodlands of the Great Basin. Bureau of Land Management, Denver, Colorado. Technical Note 430
- Stella KA, Sieg CH, Fulé PZ (2010) Minimal effectiveness of native and non-native seeding following three high-severity wildfires. *International Journal of Wildland Fire* 19:746–758
- Suring LH, Rowland MM, Wisdom MJ (2005) Identifying species of conservation concern. Pages 150–162. In: Wisdom MJ, Rowland MM, Suring LH (eds) Habitat threats in the sagebrush ecosystem – methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, Kansas
- Tausch RJ (1999) Transitions and thresholds: influences and implications for management in pinyon and Utah juniper woodlands. Pages 61–65. In: Monsen SB, Stevens R, Tausch RJ, Miller R, Goodrich S (eds) Proceedings of the ecology and management of pinyon–juniper communities within the interior west, 15–18 September 1999, Provo, UT. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah. Proceedings RMRS-P-9
- Tausch RJ, Tueller PT (1977) Plant succession following chaining of pinyon–juniper woodlands in eastern Nevada. *Journal of Range Management* 30:44–49
- Thompson TW, Roundy BA, McArthur ED, Jessop BD, Waldron B, Davis JN (2006) Fire rehabilitation using native and introduced species: a landscape trial. *Rangeland Ecology & Management* 59:237–248
- West NE, Tausch RJ, Rea KH, Tueller PT (1978) Taxonomic determination, distribution, and ecological indicator values of sagebrush within the pinyon–juniper woodlands of the Great Basin. *Journal of Range Management* 31:87–92
- Winward AH (1980) Taxonomy and ecology of sagebrush in Oregon. Oregon State University, Corvallis, Oregon. Oregon Agricultural Experiment Station Bulletin 642
- Wright HA, Bailey AW (1982) Fire ecology: United States and southern Canada. John Wiley & Sons, Inc, New York
- Yue X, Micklely LJ, Logan JA, Kaplan JO (2013) Ensemble projections of wildfire activity and carbonaceous aerosol concentrations over the western United States in the mid-21st century. *Atmospheric Environment* 77:767–780

Coordinating Editor: Lora Perkins

Received: 11 May, 2018; First decision: 5 June, 2018; Revised: 12 June, 2018; Accepted: 13 June, 2018; First published online: 12 July, 2018