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RESEARCH ARTICLE

Restoring big sagebrush after controlling encroaching western juniper with fire: aspect and subspecies effects

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The need for restoration of shrubs is increasingly recognized around the world. In the western United States, restoration of mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) after controlling encroaching conifers is a priority to improve sagebrush-associated wildlife habitat. Conifers can be cost effectively removed with prescribed burning when sagebrush is codominant; however, burning removes sagebrush and natural recovery may be slow. We evaluated seeding mountain and Wyoming big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) on north and south aspects after western juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook) control with prescribed burning. We included seeding Wyoming big sagebrush, a more drought tolerant subspecies of big sagebrush, because it might grow better than mountain big sagebrush on hot, dry south slopes, during drought, or after juniper encroachment. Seeding mountain big sagebrush increased sagebrush cover and density compared to unseeded controls. In mountain big sagebrush-seeded plots, sagebrush cover was 19 times greater on north compared to south aspects in the fourth year after seeding. At this time, sagebrush cover was also greater on mountain compared to Wyoming big sagebrush-seeded plots. Natural recovery (i.e. unseeded) of sagebrush was occurring on north aspects with sagebrush cover averaging 3% 4 years after fire. Sagebrush was not detected on unseeded south aspects at the end of the study. These results suggest that postfire sagebrush recovery, with and without seeding, will be variable across the landscape based on topography. This study suggests seeding sagebrush after controlling junipers with burning may accelerate sagebrush recovery.

Key words: ***Artemisia tridentata*, burning, conifer control, *Juniperus*, recovery, seeding**

Implications for Practice

- Seeding mountain big sagebrush after juniper control with burning accelerated the recovery of sagebrush. Success was, however, vastly less on south aspects compared to north aspects.
- North aspects, but not south aspects, showed evidence of natural recovery of sagebrush cover and density.
- These results suggest that recovery of sagebrush after fire in juniper-encroached sagebrush communities will be heterogeneous across the landscape based on topographical features with and without seeding.
- Seeding Wyoming big sagebrush after western juniper control on sites that were formerly mountain big sagebrush communities (i.e. assisted migration) does not appear to be a viable method for restoring south slopes.
- We recommend that managers consider seeding mountain big sagebrush after fire in juniper-encroached mountain big sagebrush communities.

Introduction

Artemisia ecosystems around the world are a conservation concern because of threats from desertification, invasive plants, overharvesting of shrubs for fuels, altered fire regimes, and improper grazing (Han et al. 2008; Sasaki et al. 2008; Bedunah et al. 2010; Louhaichi & Tastad 2010; Davies et al. 2011). In the western United States, the big sagebrush (*Artemisia tridentata* Nutt.) ecosystem is a high priority for conservation, but faces many threats (Davies et al. 2011). This ecosystem serves as an important forage base for western livestock producers and provides critical habitat for sagebrush-associated wildlife species. The continued and widespread loss of the sagebrush ecosystem has resulted in more than 350 sagebrush-associated plants and animals being identified as species of conservation concern (Suring et al. 2005; Wisdom et al. 2005). Currently, sagebrush only occupies about 56% of its historic range and these plant communities are highly fragmented (Knick et al. 2003; Schroeder et al. 2004). Sagebrush plant communities are being converted to conifer (e.g. pinyon [*Pinus monophylla* Torr. and Frem.] and juniper [*Juniperus occidentalis* Hook., *J. osteosperma* [Torr.] Little]) woodlands, exotic annual grasslands, introduced perennial grasslands, and croplands as well as being degraded and fragmented by anthropogenic development (Davies et al. 2011).

Author contributions: KWD, JDB conceived and designed the study and carried out the experiments; KWD analyzed the data and wrote the manuscript; KWD, JDB edited the manuscript.

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Conifer encroachment is one of the most prevalent issues in mountain big sagebrush (*A. tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) plant communities. Conifer woodlands have expanded from historically fire-safe sites into more productive sagebrush communities with decreases in fire frequency following European settlement (Miller & Wigand 1994; Gruell 1999; Miller & Rose 1999; Weisberg et al. 2007). In the northern Great Basin and Columbia Plateau, western juniper (*J. occidentalis* ssp. *occidentalis* Hook) has increased from 0.3 to 3.5 million hectare since 1870 (Miller et al. 2000). Expansion of western juniper has primarily been in mountain big sagebrush and other productive plant communities in the northern Great Basin (Burkhardt & Tisdale 1969; Miller & Rose 1995; Miller et al. 2005). Western juniper encroachment is concerning because as tree cover increases, sagebrush is lost, forage production and diversity decrease, and runoff and erosion potential increase (Miller et al. 2000; Bates et al. 2005; Pierson et al. 2007). The decline in sagebrush with western juniper encroachment is detrimental to sagebrush-associated wildlife, especially sagebrush-obligate wildlife species (Connelly et al. 2000; Miller et al. 2005; Baruch-Mordo et al. 2013).

Restoration of sagebrush communities encroached by western juniper is a priority to conserve sagebrush habitat for wildlife (Baruch-Mordo et al. 2013) and ecosystem services (Miller et al. 2005; Pierson et al. 2007; Bates et al. 2011). One of the most cost-effective methods to control large acreages of western juniper is prescribed burning or partial cutting (cutting ¼ to ½ of mature trees to increase surface fuels) followed by prescribed burning (Bates et al. 2011; Davies et al. 2014). Burning generally results in more complete control of western juniper than mechanical treatments, because mechanical treatments often fail to control juniper seedlings and small juveniles or reduce the seed bank (Miller et al. 2005). Burning, however, also removes fire-intolerant sagebrush from these plant communities, which can be undesirable because sagebrush is a critical habitat component for sagebrush-associated wildlife (Crawford et al. 2004; Shipley et al. 2006; Aldridge et al. 2008) and sagebrush-obligates, such as sage grouse, will not occupy large burns until sagebrush recovers (Connelly et al. 2000).

Mountain big sagebrush may recover after fire; however, recovery time after fire is quite variable with estimates ranging from 15 to 100 years (Baker 2006; Ziegenhagen & Miller 2009; Nelson et al. 2014). Post-fire recovery of sagebrush may be even slower after western juniper encroachment because sagebrush density, and presumably the sagebrush seed bank, has been greatly reduced. Bates et al. (2005) reported that sagebrush recovery can be slow after cutting western juniper if sagebrush densities were low prior to treatment. Waiting several decades to a century for sagebrush recovery may not be acceptable given the current need for habitat for sagebrush-associated wildlife. Climate the first few years after fire can also significantly influence recovery of mountain big sagebrush (Ziegenhagen & Miller 2009; Nelson et al. 2014) because most sagebrush seed remain viable for only a year or two (Young & Evans 1989; Wijayratne & Pyke 2012). Wildfires and prescribed fires generally occur before big sagebrush has set seed; subsequently, recruitment must occur from seed that is already at least 1 year old. Therefore, it may be valuable to seed mountain big sagebrush after controlling western juniper with prescribed burning.

Information on the effects of seeding mountain big sagebrush after prescribed burning western juniper-encroached sagebrush communities is limited. The only literature we are aware of evaluating seeding mountain big sagebrush after prescribed burning encroaching western juniper was Davies et al. (2014). In this study, crop year (Oct.–Sept.) precipitation was between 100 and 150% of the long-term average the first 2 years after seeding, thus their results may not be applicable in drier years. Several dry years after fire may greatly lengthen the time required for recovery of mountain big sagebrush (Ziegenhagen & Miller 2009; Nelson et al. 2014). Davies et al. (2014) also only evaluated seeding on sites dominated by western juniper with little to no sagebrush remaining (late phase II and phase III woodlands; Miller et al. 2005) and therefore may not be applicable to phase II woodlands that are codominated by sagebrush and juniper. Site characteristics likely also greatly influence sagebrush recovery postfire (Davies et al. 2011; Nelson et al. 2014). For example, cooler, wetter north aspects compared to hotter, drier south aspects are probably a much more favorable environment for sagebrush seedling establishment and growth. Thus, it would also be valuable to compare the effects of seeding mountain big sagebrush after western juniper control on different aspects.

Pinyon and juniper encroachment can cause soil erosion changing the site from mountain big sagebrush community to a Wyoming big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) community (Pyke 2011). Mountain big sagebrush-dominated plant communities may also become more suited for Wyoming big sagebrush as conditions become warmer and drier with climate change (Schlaepfer et al. 2015). Furthermore, south aspects, generally drier and warmer than north slopes, may generally be less favorable to establishment of mountain big sagebrush and thus, Wyoming big sagebrush, a more drought tolerant subspecies, may establish and grow better in these environments. Wyoming big sagebrush occupies hotter and drier sites than mountain big sagebrush (Winward & Tisdale 1977; West et al. 1978; Winward 1980; Blaisdell et al. 1982; Hironaka et al. 1983) because it is better adapted to tolerate these conditions as they grow slower (McArthur and Welch 1982; Messina et al. 2002), have greater xylem cavitation resistance, and lower xylem pressure causing loss of leaf turgor (i.e. better drought adaptations) (Kolb & Sperry 1999). Wyoming big sagebrush may also establish more successfully than mountain big sagebrush at some more cool and moist locations, especially if these locations experience a postseeding drought. Furthermore, with the potential for assisted migration as a management response to climate change (McLachlan et al. 2007), it would be valuable to evaluate the effects of seeding Wyoming big sagebrush on sites formerly occupied by mountain big sagebrush.

The purpose of this research project was to investigate the effects of seeding mountain and Wyoming big sagebrush after controlling western juniper encroaching into mountain big sagebrush communities with prescribed burning on south and north aspects. We expected that natural recovery of sagebrush would occur more rapidly on north than south aspects. We also expected that seeding mountain big sagebrush would expedite sagebrush recovery on north aspects more than natural recovery (unseeded) or seeding Wyoming big sagebrush, but on south aspects that seeding Wyoming big sagebrush would result in the greatest cover and density of sagebrush.

Methods

Study Area

Study sites were located in the northern Great Basin approximately 80 km southeast of Burns, OR, between Princeton, Folly Farm, Mann Lake, and Diamond, OR, U.S.A. All study sites were mountain big sagebrush dominated plant communities prior to encroachment by western juniper. Prior to burning, the plant communities were codominated by western juniper and mountain big sagebrush with an understory of native perennial bunchgrasses and forbs. Dominant large perennial bunchgrasses were *Festuca idahoensis* Elmer and *Pseudoroegneria spicata* (Pursh) A. Löve on south aspects and *F. idahoensis* on north aspects. Juniper woodland development prior to treatment was classified as phase II (Miller et al. 2005). Elevation at study sites was 1650–1775 m above sea level. Aspects of study sites were north and south. Slopes ranged between 30 and 35%. South and north aspects were South Slopes 12-16 PZ (R023XY302OR) and North Slopes 12-16 PZ (R023XY31OR) Ecological Sites, respectively (NRCS 2016). Both aspects were frigid temperature regime and xeric moisture regime (NRCS 2016). Long-term average annual precipitation (1981–2010) was 405 mm with the majority occurring during the cool season (PRISM 2015). Annual precipitation was 89, 87, 63, and 87% of the long-term average in 2011, 2012, 2013, and 2014 (PRISM 2015). Livestock were excluded for 1 year prior and 1 year after burning on all study sites. Livestock grazing management objective for the study area was 40% utilization and applied in July through September; however, little evidence of cattle use was detected at the study sites. Wild ungulates and other wildlife were not restricted from the study sites and limited evidence of wildlife use was detected throughout the duration of the study.

Experimental Design and Measurements

The effects of seeding different subspecies of big sagebrush on north and south aspects that had been prescribed burned to remove encroaching juniper were evaluated using a split-plot design with four complete replicates of all treatment on each aspect. A north and south aspect in close proximity to each other (i.e. on the same ridge at the same elevation) were considered a block. Blocks were selected to be representative of north and south slopes. Each block consisted of three 10 × 40 m plots with a 2-m buffer between plots. Blocks were spread across an 8 km^2 area. Treatments included an unseeded control, seeding with mountain big sagebrush, and seeding with Wyoming big sagebrush, and were randomly assigned to the three plots in each block on each aspect. Total number of treatment plots was 24 (4 blocks × 2 aspects × 3 treatments). All treatment plots were prescribed burned in late September of 2011 using head-fires ignited with drip torches. All fires were complete burns resulting in 100% mortality of juniper and sagebrush plants. Relative humidity ranged from 22 to 30%, air temperature was between 24 and 32°C, and wind speed fluctuated from 10 to 24 km/hour during prescribed burns. Sagebrush seed was broadcast seeded with a handheld seeder at 500 PLS/m^2 in November of 2011. Seeded sagebrush seed was collected locally (within 75 km of study sites) and percent live seed was determined using petri dish germination method (Meyer & Monsen 1991).

Plant community characteristics were measured in July of 2013, 2014, and 2015 along two parallel 40-m transects spaced 3 m apart in each plot. Herbaceous vegetation cover was measured by species in 0.2 m^2 quadrats placed at 3-m intervals along each 40-m transect (resulting in 13 quadrats per transect and 26 quadrats per plot). Herbaceous cover was visually estimated based on markings that divided 0.2 m^2 quadrats into 1, 5, 10, 25, and 50% segments. Litter cover (plant material on soil surface and unattached to roots) and bare ground were also visually estimated in 0.2 m^2 quadrats using the segment markings. Herbaceous density was measured by counting all plants rooted in 0.2 m^2 quadrats. Shrub cover was measured by species using the line-intercept method (Canfield 1941) along each of the 40-m transects. Shrub canopy gaps less than 15 cm were included in cover estimates. Shrub density was measured by species by positioning a 2 × 40-m belt transect over each 40-m transect. Shrubs were counted if they were rooted in the 2 × 40-m belt transect.

Statistical Analyses

Repeated measures analyses of variance (ANOVAs) using the PROC MIXED procedure in SAS 9.2 (PROC MIXED SAS Institute, Inc., Cary, NC, U.S.A.) was used to determine treatment effects on plant community characteristics. Year was used as the repeated variable and treatment and aspect were considered fixed variables. Treatment, year, aspect, block, treatment*year, treatment*aspect, and treatment*aspect*year were used as explanatory variables in the models. When there was a significant treatment*aspect interaction, data were also analyzed individually by aspect using repeated measures ANOVAs. Compound symmetry covariance structure was selected using Akaike's Information Criterion (Littell et al. 1996). Data that violated assumptions of ANOVAs were log transformed to better meet assumptions. Nontransformed data (i.e. original data) were presented in the text and figures. Herbaceous vegetation was grouped into four functional groups for analyses: perennial grasses, perennial forbs, exotic annual grasses, and annual forbs. The exotic annual grass functional group was largely comprised of cheatgrass (*Bromus tectorum* L.). Treatment means were separated using Fisher's Protected least significant difference (LSD) method. Treatment means were considered different at $\alpha = 0.05$ and reported with standard errors (SE).

Results

Density

Density of perennial grasses and perennial forbs did not differ among treatments ($F_{[2,6]} = 0.12$ and 0.30, $p = 0.891$ and

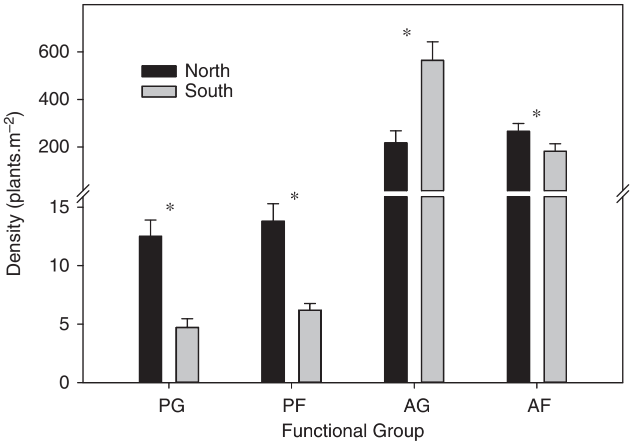

Figure 1. Herbaceous functional group density (mean + SE) by aspect summarized across treatments and years (2013–2015). PG, perennial grasses; PF, perennial forbs; AG, annual grasses, and AF, annual forbs. Asterisks (*) indicates significant difference ($p \leq 0.05$) between aspects for that functional group.

0.754, respectively). Perennial grass and perennial forb densities were 2.7- and 2.2-fold greater on north aspects compared to south aspects (Fig. 1; $F_{[1,45]} = 65.90$ and 76.47, $p < 0.001$) and both generally increased over time ($F_{[2,45]} = 52.86$ and 69.64, $p < 0.001$). Exotic annual grass density was similar among treatments ($F_{[2,6]} = 0.16$, $p = 0.858$), but was more than two times greater on south compared to north aspects (Fig. 1; $F_{[1,45]} = 43.57$, $p < 0.001$). Exotic annual grass density varied by year ($F_{[2,45]} = 47.60$, $p < 0.001$) but no clear pattern emerged. Annual forb density did not differ among treatments ($F_{[2,6]} = 1.18$, $p = 0.369$). North aspects compared to south aspects had 1.5-fold greater annual forb cover (Fig. 1; $F_{[1,45]} = 12.86$, $p = 0.001$). Annual forb density varied among years ($F_{[2,45]} = 69.70$, $p < 0.001$), but there was not a consistent trend. Treatment*year and aspect*treatment interactions did not affect the density of any herbaceous functional group ($p > 0.05$).

Sagebrush and total shrub density varied by the treatment*aspect interaction (Fig. 2; $F_{[2,45]} = 9.95$ and 15.53, $p < 0.001$). Sagebrush density was on average more than 40 times greater on the north compared to south aspect. Sagebrush density was greater in all years on both aspects on mountain big sagebrush-seeded plots compared to unseeded control plots (Fig. 2A & 2C). Sagebrush density on Wyoming big sagebrush-seeded plots generally did not differ from unseeded control plots in most years, except it was greater than the controls on the north aspect in 2015 (Fig. 2). Sagebrush density was similar in mountain and Wyoming big sagebrush-seeded plots in most years on both aspects, except for on the north aspect in 2015 when sagebrush density was greater in mountain big sagebrush-seeded plots compared to Wyoming big sagebrush-seeded plots (Fig. 2). Natural recovery of sagebrush density was not occurring on south aspects (Fig. 2C), while some sagebrush was detected on north aspects in unseeded controls (Fig. 2A). Total shrub density was greater in mountain big sagebrush-seeded plots compared to control plots on north aspects in all years (Fig. 2B). Total shrub density did not vary between Wyoming big sagebrush-seeded plots and control plots on north aspects (Fig. 2B). Total shrub density did not differ between Wyoming and mountain big sagebrush-seeded plots on north aspects in 2013 and 2014; however, in 2015 it was greater in mountain big sagebrush-seeded plots (Fig. 2B). Total shrub density on south slopes did not differ among treatments in any year (Fig. 2D). The treatment*year interaction was not significant for any measured shrub density variable ($p > 0.05$).

Cover

Perennial grass cover did not differ among treatments or between aspects ($F_{[2,6]} = 2.04$ and $F_{[1,45]} = 0.46$, $p = 0.211$ and 0.500, respectively). Perennial grass cover generally increased with time since burning ($F_{[2,45]} = 5.16$, $p = 0.010$). Perennial forb cover was similar between treatments ($F_{[2,6]} = 1.24$, $p = 0.354$). Perennial forb cover was on average 2.1 times greater on north compared to south aspects (Fig. 3; $F_{[1,45]} = 67.05$, $p < 0.001$). Perennial forb cover varied by year ($F_{[2,45]} = 8.19$, $p = 0.001$), but no trend was apparent. Cover of exotic annual grasses did not differ among treatments ($F_{[2,6]} = 1.73$, $p = 0.255$). Exotic annual grass cover was more than 2-fold greater on south than north aspects (Fig. 3; $F_{[1,45]} = 106.40$, $p < 0.001$) and generally increased with time since fire ($F_{[2,45]} = 60.07$, $p < 0.001$). Annual forb cover did not differ among treatments or years ($F_{[2,6]} = 2.45$ and $F_{[2,45]} = 0.84$ $p = 0.167$ and 0.439, respectively). Annual forb cover was 2.4-fold greater on north compared to south aspects (Fig. 3; $F_{[1,45]} = 110.36$, $p < 0.001$). Total herbaceous cover did not differ among treatments ($F_{[2,6]} = 2.01$, $p = 0.215$) or between aspects (Fig. 3; $F_{[1,45]} = 0.28$, $p = 0.600$). Total herbaceous cover increased with time since fire ($F_{[2,45]} = 45.43$, $p < 0.001$). Bare ground did not differ among treatments or years ($F_{[2,6]} = 2.20$ and $F_{[2,45]} = 3.14$, $p = 0.192$ and 0.053, respectively). Bare ground was 4.5 times greater on north aspects compared to south aspects (Fig. 3; $F_{[1,45]} = 262.07$, $p < 0.001$). Ground litter did not vary among treatments ($F_{[2,6]} = 0.57$, $p = 0.593$). South aspects on average had 2.3-fold greater ground cover by litter, largely comprised of prior years' exotic annual grass growth, than north aspects (Fig. 3; $F_{[1,45]} = 170.89$, $p < 0.001$). Litter also differed among years ($F_{[2,45]} = 12.39$, $p < 0.001$), but no trend was evident. Treatment*year and aspect*treatment interactions were not significant for any herbaceous functional group, total herbaceous, bare ground, or litter cover ($p > 0.05$).

Sagebrush and total shrub cover varied by the treatment*aspect interaction (Fig. 4; $F_{[2,45]} = 8.75$ and 8.20, $p < 0.001$ and $= 0.001$, respectively). On north aspects, sagebrush and total shrub cover did not differ between control and mountain big sagebrush-seeded plots in 2013 and 2014, but by 2015 sagebrush and total shrub cover were greater in mountain big sagebrush-seeded plots (Fig. 4A and 4B). Sagebrush and total shrub cover on north aspects in Wyoming big sagebrush-seeded plots did not differ from controls in any year and mountain big sagebrush-seeded plots in 2013 and 2014 (Fig. 4A and 4B). In 2015, sagebrush and total shrub cover on north aspects were greater in mountain big sagebrush compared

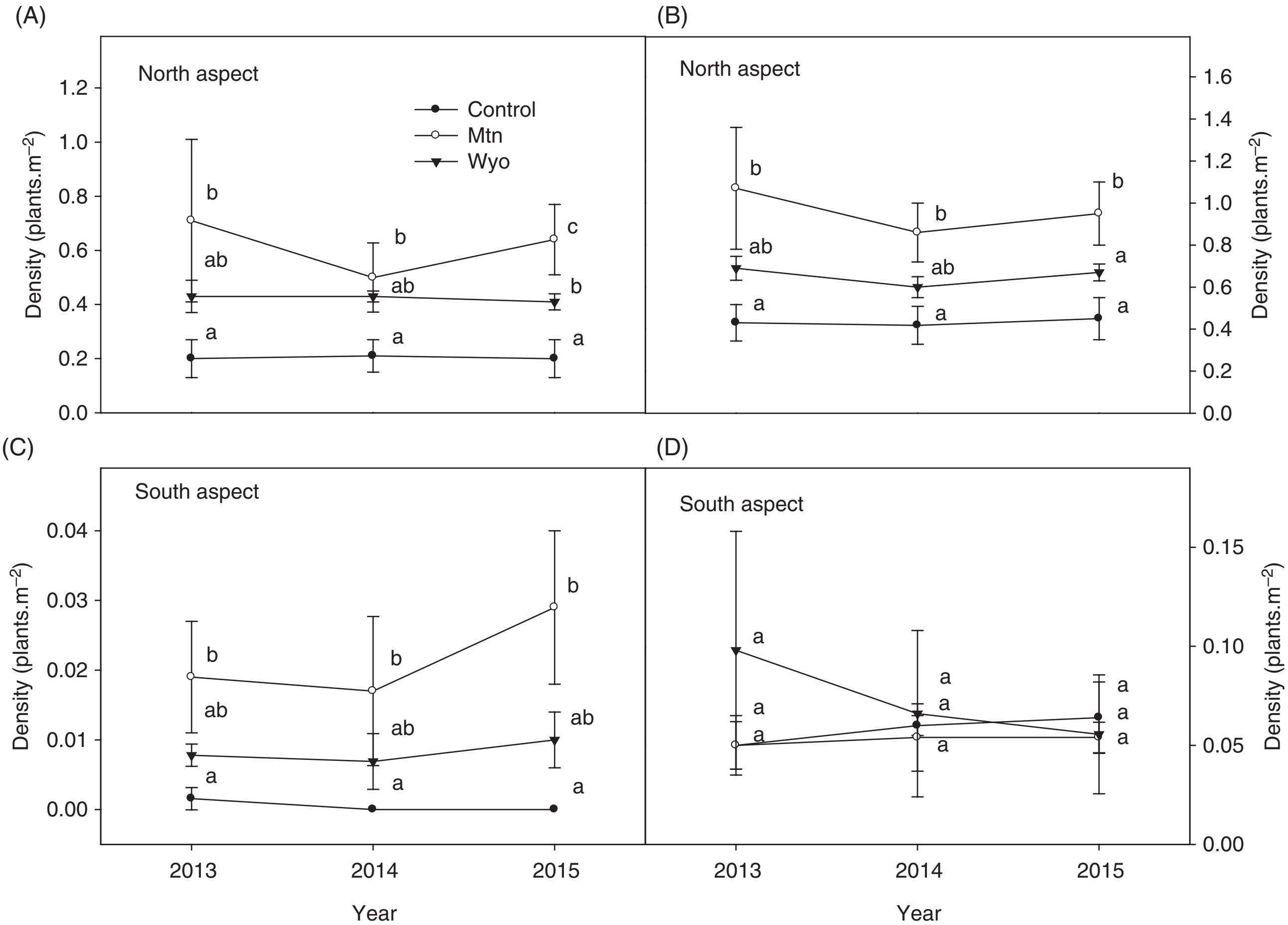

Figure 2. Sagebrush (A and C) and total shrub (B and D) density (mean ± SE) in treatments on north aspects and south aspects in 2013, 2014, and 2015. Control, unseeded control; Mtn, mountain big sagebrush seeded, and Wyo, Wyoming big sagebrush seeded. Different lower case letters signify differences ($p \leq 0.05$) between treatments in that year. Scale varies by figure panel.

to Wyoming big sagebrush-seeded plots (Fig. 4A and 4B). Sagebrush cover increased with time on north aspects (Fig. 4A; $F_{[2,18]} = 24.97$, $p < 0.001$), but did not vary with time on south aspects (Fig. 4C; $F_{[2,18]} = 3.29$, $p = 0.060$). Sagebrush cover was similar among treatments in all years on south slopes, except it was greater in mountain big sagebrush-seeded plots compared to control plots by 2015 (Fig. 4C). Total shrub cover on south aspects was not significantly different among treatments in any year (Fig. 4D). The treatment*year interaction was not significant for any measured shrub cover variable ($p > 0.05$).

Discussion

Seeding mountain big sagebrush after controlling western juniper with prescribed fire accelerated the recovery of sagebrush cover and density. Similar results were reported by Davies et al. (2014) when they seeded mountain big sagebrush in combination with perennial grasses and forbs after juniper control with partial cutting followed by prescribed burning. Davies et al. (2014) also reported wide-ranging levels of success with sagebrush cover varying from 1 to 12% among seeded sites by

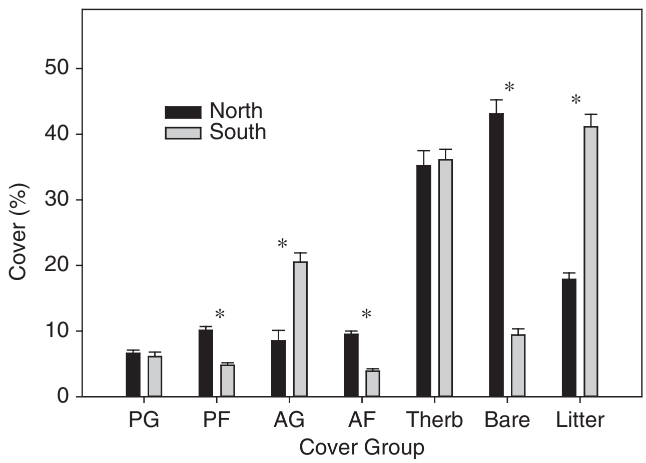

Figure 3. Herbaceous functional and cover group cover (mean + SE) by aspect summarized across treatments and years (2013–2015). PG, perennial grasses; PF, perennial forbs; AG, annual grasses; AF, annual forbs; Therb, total herbaceous; Bare, bare ground; and litter, ground litter. Asterisks (*) indicates significant difference ($p \leq 0.05$) between aspects for that cover group.

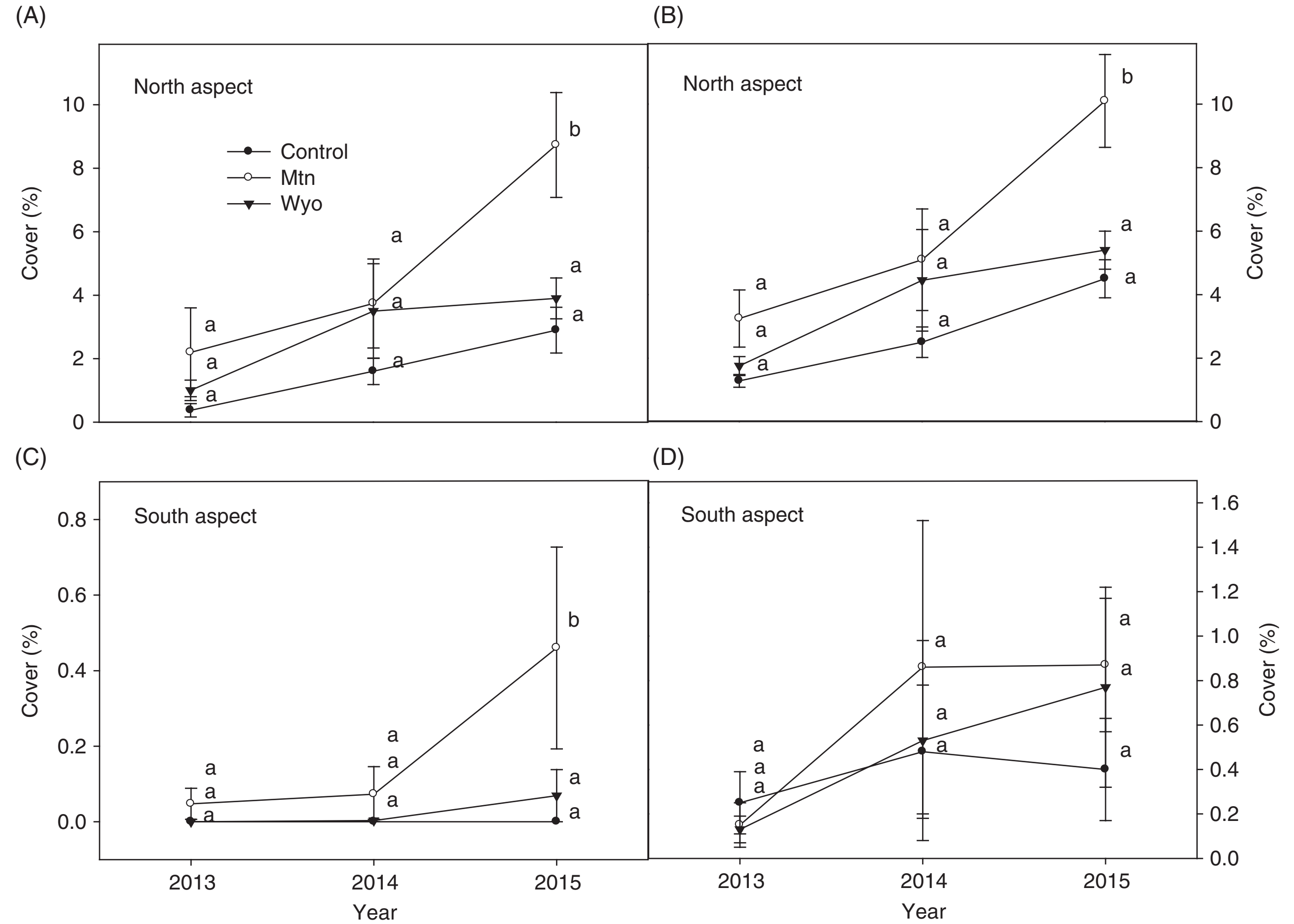

Figure 4. Sagebrush (A and C) and total shrub (B and D) cover (mean ± SE) in treatments on north aspects and south aspects in 2013, 2014, and 2015. Control, unseeded control; Mtn, mountain big sagebrush seeded; and Wyo, Wyoming big sagebrush seeded. Different lower case letters signify differences ($p \leq 0.05$) between treatments in that year. Scale varies by figure panel.

the third year postseeding. In agreement, we found recovery of sagebrush cover and density varied considerably among sites seeded with mountain big sagebrush. The majority of the variability in sagebrush cover and density in our study was related to aspect. For example, sagebrush cover in mountain big sagebrush-seeded plots was 19 times greater on north compared to south aspects in the final year of study. Though sagebrush cover and density on south aspects seeded with mountain big sagebrush were low, both were greater than the unseeded control at the end of the study. This suggests that rapid recovery of sagebrush after fire on these juniper-encroached south aspects, even with seeding, may be improbable, but seeding mountain big sagebrush does hasten sagebrush recovery.

The limited success with seeding mountain big sagebrush on south aspects was probably caused by unfavorable environmental characteristics and competition with annual grasses. Though both aspects had a frigid temperature regime and a xeric moisture regime, south aspects have lower resilience to disturbance and resistance to exotic annual grasses than north aspects with the same temperature and moisture regimes (Miller et al. 2014, 2015). South aspects are hotter and drier than north aspects often leading to water stress for plants (Van de Water et al. 2002), and are a more favorable environment for exotic annual grass invasion in the Great Basin (Leffler et al. 2013). The south aspects were heavily invaded by cheatgrass and other exotic annual grasses which may have further depleted available moisture to sagebrush seedlings. Cheatgrass depletes soil moisture earlier than native vegetation and suppresses the growth of native species (Melgoza et al. 1990). The exotic annual grass invasion also threatens to develop an annual grass-fire cycle that would likely burn too frequently for the persistence of sagebrush (D'Antonio & Vitousek 1992; Davies & Svejcar 2008; Davies & Nafus 2013). Therefore, on southerly exposed sites, natural recovery of sagebrush may be unlikely if significant annual grass invasion persists. This suggests that portioning the landscape into topographic settings for guiding restoration is imperative (Hessburg et al. 2015). In this situation, different responses between aspects suggest that practitioners should either not burn south aspects or may need to apply additional treatments to manage exotic annual grasses. Exotic annual grasses, however, often initially increase after western juniper control, but rapidly decrease with perennial grass recovery (Bates et al. 2005).

These conditions on south slopes, however, did not favor Wyoming big sagebrush establishment and growth compared to mountain big sagebrush. Counter to our assumption that sagebrush cover and density would be greater with seeding Wyoming compared to mountain big sagebrush on south aspects, sagebrush cover was less on Wyoming big sagebrush-seeded plots by the end of the study. Also contrary to our expectations, sagebrush density on south aspects was numerically less in Wyoming compared to mountain big sagebrush-seeded plots, but statistically did not differ between subspecies. Sagebrush cover and density on Wyoming big sagebrush-seeded plots on south aspects did not differ from unseeded control plots, further suggesting that seeding Wyoming big sagebrush on south slopes formerly occupied by mountain big sagebrush (i.e. assisted migration), at least those similar to our study sites, is not likely a viable sagebrush restoration strategy at this time. Mountain big sagebrush is apparently still better adapted to these sites or more competitive with existing vegetation than Wyoming big sagebrush even with climate change and invasion of exotic annual grasses, though this may not remain true with continued climate change. Mountain big sagebrush's ability to grow faster than Wyoming big sagebrush (McArthur & Welch 1982; Messina et al. 2002) may be one of the mechanisms by which mountain big sagebrush was able to achieve greater cover values than Wyoming big sagebrush on both south and north aspects.

Natural recovery of sagebrush was occurring on north slopes with approximately 3% sagebrush cover by the conclusion of the study. This level of recovery is much greater than the less than 1% sagebrush cover Davies et al. (2014) reported for natural recovery three years postburning. However, Davies et al. (2014) evaluated late phase II and phase III juniper woodlands, which likely had limited viable sagebrush seed in the seed bank as sagebrush was largely excluded from plant communities prior to juniper control and most sagebrush seed remains viable for only a few years (Young & Evans 1989; Wijayratne & Pyke 2012). In contrast, this study was evaluating sagebrush recovery after prescribed burning of phase II juniper woodlands, where sagebrush was still codominant prior to juniper control and therefore likely had a greater sagebrush seed bank. Dissimilar to north aspects, there was no evidence of natural recovery of big sagebrush on south aspects. At the end of the study, sagebrush was not detected in unseeded plots on south aspects, suggesting that natural sagebrush recovery on south slopes will be slow.

Prior researchers (Ziegenhagen & Miller 2009; Nelson et al. 2014) have reported two different recovery trajectories for mountain big sagebrush after fire: a fast track where the first couple of years postfire weather is favorable for establishment of sagebrush, and a slow track where sagebrush fails to establish in the first couple of years postfire because of unfavorable conditions. In the fast track, sagebrush likely recruits from the seed bank and is, therefore, relatively uniformly present across the postfire landscape. In contrast, the slow track may require sagebrush to be dispersed from outside the burn (due to the limited viability of sagebrush seed beyond 1–2 years), which may result in sagebrush recruitment patterns being dependent on proximity to seed sources. Our research suggests that these two vastly different recovery trajectories may occur in the same burned landscape based on the influence of landscape characteristics on the seedling establishment environment. In our study, north and south aspects appear to be following the fast and slow sagebrush recovery tracks, respectively. This is likely because topography provides a persistent physical template that dictates vegetation patterns and suggests that landscapes should be divided into topographic settings for restoration (Hessburg et al. 2015). South compared to north aspects with the same temperature and moisture regimes are less resilient to disturbance (Miller et al. 2014, 2015). The results of our study may be relevant to shrub restoration in other parts of the world as the need for shrub restoration is becoming increasingly recognized in Africa (Linstadter & Baumann 2013), Europe (Medina-Roldán et al. 2012), Australia (Wong et al. 2007), and Asia (Li et al. 2013).

We did not detect any effects of seeding sagebrush on other vegetation characteristics. Vegetation differences were largely related to aspect and time since burning. Sagebrush, however, was a small component of the total cover at the conclusion of the study and thus not detecting an effect on other vegetation was not surprising. As seeded sagebrush plants grow larger and new individuals are recruited from established plants, sagebrush will probably influence other vegetation (Davies et al. 2014). Sagebrush competes with herbaceous vegetation in this ecosystem (Robertson 1947; Cook & Lewis 1963; Williams et al. 1991) and reductions in sagebrush in fully occupied communities often result in 2- to 3-fold increases in herbaceous vegetation (Mueggler & Blaisdell 1958; Hedrick et al. 1966; McDaniel et al. 1991; Davies et al. 2007). Though seeding sagebrush will probably ultimately influence other vegetation, sagebrush's accelerated recovery would likely benefit sagebrush-associated wildlife.

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