

RESEARCH ARTICLE

Improving restoration success through microsite selection: an example with planting sagebrush seedlings after wildfire

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Post-fire restoration of foundation plant species, particularly non-sprouting shrubs, is critically needed in arid and semi-arid rangeland, but is hampered by low success. Expensive and labor-intensive methods, including planting seedlings, can improve restoration success. Prioritizing where these more intensive methods are applied may improve restoration efficiency. Shrubs in arid and semi-arid environments can create resource islands under their canopies that may remain after fire. Seedlings planted post-fire in former canopy and between canopies (interspace) may have different survival and growth. We compared planting Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) seedlings post-fire in former sagebrush canopy and interspace microsites at five locations. Four growing seasons after planting, seedling survival was 46 and 7% in canopy and interspace microsites, respectively. Sagebrush cover was 5.8 times greater in canopy compared to interspace microsites. Sagebrush survival and cover were likely greater because of less competition from herbaceous vegetation as well as benefiting from resource island effects in canopy microsites. Initially, post-fire abundance of exotic annual grasses was less in canopy microsites, but by the third year post-fire it was substantially greater in canopy microsites, indicating that resource availability to seedlings was greater, at least initially, in canopy microsites. These results suggest microsites with greater likelihood of success should be identified and then utilized to improve restoration success and efficiency. This is important as the need for restoration greatly exceeds resources available for restoration.

Key words: *Artemisia tridentata*, canopy, interspace, outplanting, resource island, wildfire

Implications for Practice

- Sagebrush seedlings should be planted in former sagebrush canopy rather than between canopy (interspace) microsites after wildfires to improve restoration efficiency.
- Seedlings of other woody vegetation should likely also be planted in former canopy microsites in efforts to restore the woody plant component after fire in arid and semi-arid communities.
- Microsite differences in restoration success should be used to prioritize restoration efforts, especially when using labor-intensive and expensive methods.
- Areas lacking shrubs pre-fire may be difficult to restore to shrubs post-fire because of a homogenizing of microsites (i.e. lack of former canopy microsites).

Introduction

Restoration efforts are often applied in semi-arid and arid ecosystems to reestablish native vegetation after disturbances. Historically, efforts largely focused on perennial grasses, but shrub restoration is becoming increasingly recognized as a need throughout the world (Wong et al. 2007; Medina-Roldán et al. 2012; Li et al. 2013; Linstadter & Baumann 2013). For example, shrub recovery is necessary to increase the establishment of trees

and to promote forest recovery in degraded Mediterranean environments (Torroba-Balmori et al. 2015; Alday et al. 2016) and abandoned fields (Cruz-Alonso et al. 2019). Reestablishing shrubs can be important because shrubs are often foundation species that provide important ecosystem services and functions (Prevéy et al. 2010; Fonseca et al. 2012; van Zonneveld et al. 2012). Restoration of shrubs in arid and semi-arid environments is challenging because its success is limited by water stress and invasive species (Porensky et al. 2014). Shrub establishment may also be hindered by competition from herbaceous vegetation (Allen 1988; Schuman et al. 1998; Hall et al. 1999; Rinella et al. 2015, 2016).

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In the western United States, restoration of big sagebrush (*Artemisia tridentata* Nutt.) is a conservation priority (Davies et al. 2011). Sagebrush was estimated to only occupy about 56% of its historic 500,000 km² range in the early 2000s (Knick et al. 2003; Schroeder et al. 2004) and more frequent and large wildfires in the last decade have furthered the loss of sagebrush and elevated the threat to sagebrush-obligate species (Davies et al. 2018). The widespread loss of sagebrush occupied rangelands has resulted in >350 sagebrush-associated organisms being identified as species of conservation concern (Suring et al. 2005; Wisdom et al. 2005). Sagebrush recovery is important because of its influence on surrounding plant biodiversity (Prevéy et al. 2010) and for habitat for sagebrush-associated wildlife (Crawford et al. 2004; Shipley et al. 2006).

Sagebrush restoration efforts are needed in many post-burn landscapes because natural recovery, if it occurs at all, may take over a century depending on site characteristics and post-fire weather (Ziegenhagen & Miller 2009; Nelson et al. 2014; Shineman & McIlroy 2016). Sagebrush restoration is particularly challenging in hotter and drier rangelands, exemplified by Wyoming big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young). Restoration of Wyoming big sagebrush by seeding is often unsuccessful (Lysne & Pellant 2004; Davies et al. 2013; Knutson et al. 2014), though there are exceptions when spring precipitation is above normal (Davies et al. 2018). In contrast with seeding, planting Wyoming big sagebrush seedlings has been more successful (Davies et al. 2013; McAdoo et al. 2013), although, survival of planted seedlings can be low (Davidson et al. 2019). Planting sagebrush seedlings, however, is expensive and labor-intensive (McAdoo et al. 2017). Therefore, strategically planting sagebrush seedlings in areas where the likelihood of success is greater would improve restoration efficiency.

Spatial variability in restoration responses can be used to improve restoration success by prioritizing efforts (Brudvig et al. 2017; Davies et al. 2017). Establishment of shrub seedlings differs with spatial variability across post-fire landscapes (Davies & Bates 2017; Davidson et al. 2019). Plant establishment may also vary within a plant community based on microsite differences (Rice 1993; Jurena & Archer 2003; Alday et al. 2016). Shrubs can serve as nurse plants for the establishment of other species because of their effects on microenvironments (Torroba-Balmori et al. 2015; Alday et al. 2016; Cruz-Alonso et al. 2019). Sagebrush and other woody vegetation in arid and semi-arid ecosystems can create resource islands under their canopies compared to interspaces between canopies (Doescher et al. 1984; Jackson & Caldwell 1993a, 1993b; Davies et al. 2007). Resource islands are the accumulations of soil nutrients under woody vegetation canopies (Schlesinger et al. 1996). These resource islands, primarily greater inorganic nitrogen and carbon, may remain after fire (Stubbs & Pyke 2005; Davies et al. 2009; Boyd & Davies 2012; Hoover & Germino 2012) and provide a favorable environment for plant establishment (Boyd & Davies 2010; Germino et al. 2018). Soil surface temperatures are also higher in former canopy microsites after burning, largely a result of

darker surface soils in these microsites (Davies et al. 2009; Boyd & Davies 2012). Soil resource heterogeneity caused by resource islands may influence post-fire community assembly (Davies et al. 2009).

Fire is more severe under woody vegetation canopies, leading to much greater mortality of understory vegetation in these microsites (Boyd et al. 2015). This results in less vegetation immediately post-fire in former canopy microsites than surrounding areas, and therefore seedlings may experience less competition in these microsites (Davies et al. 2009, 2017; Bates & Davies 2016). Shrubs may preferentially establish in microsites where disturbances have reduced the grass layer (Jurena & Archer 2003). Planting sagebrush seedlings in former sagebrush canopies may be more successful than planting in former interspaces because of reduced competition and greater resource availability. Bitterbrush (*Purshia tridentata* [Pursh] DC) seedlings in former western juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook) canopy locations had 10-fold greater survival compared to interspaces (Davies et al. 2017). Western junipers (10 to >15 m tall), however, are much larger than Wyoming big sagebrush (<1 m tall) and likely their former canopy locations influence resources and competition differently. Thus, it would be valuable to determine if there is spatial variability in sagebrush seedling survival between microsites post-fire.

The purpose of this study was to investigate if targeting former shrub canopy microsites for post-fire restoration efforts could improve success. The objective of this study was to evaluate the survival of planted sagebrush seedlings in former sagebrush canopy and interspace microsites after wildfire. We hypothesized that survival of planted sagebrush seedlings and sagebrush cover would be greater in the former sagebrush canopy compared to interspace microsites in a post-wildfire environment.

Methods

Study Area

Five study sites were located in the Buzzard Wildfire Complex 50–60 km southeast of Burns, OR. The Buzzard Wildfire Complex was started by multiple lightning ignitions on 14 July, 2014 and burned 160,153 ha (395,747 acres). All study sites were Wyoming big sagebrush-bunchgrass communities prior to burning. Sagebrush was removed from study sites by the wildfire as sagebrush is intolerant of burning. Common perennial bunchgrasses varied among sites and included Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), prairie Junegrass (*Koeleria macrantha* [Ledeb.] J.A. Schultes), and Sandberg bluegrass (*Poa secunda* J. Presl). Study sites were up to 16 km apart and occurred on two different land ownerships. These sites were historically and currently used as grazing lands for domestic livestock. Elevation of study sites ranged from 1,278 to 1,464 m above sea level. Slopes ranged from 4° to 13° and aspects were northwest, northeast, southeast, and southwest. Study sites were located on RO23XY212OR-Loamy

10-12 PZ (500,166 ha), R023XY216OR-Clay Pan 12-16 PZ (200,270 ha), R023XY300OR-South Slope 10-12 PZ (85,249 ha), R023XY3100OR-North Slopes 12-16 PZ (45,224 ha), and R023XY308OR-North Slope 10-12 PZ (16,529 ha) ecological sites (NRCS 2019), representing a large area of sagebrush steppe. The Natural Resource Conservation Service defines ecological sites as “as a distinctive kind of land with specific soil and physical characteristics that differ from other kinds of land in its ability to produce a distinctive kind and amount of vegetation and its ability to respond similarly to management actions and natural disturbances” (NRCS 2020). Long-term (1981–2010) average annual precipitation was 283 mm (PRISM 2019). Crop year (October–September) precipitation in 2014–2015, 2015–2016, 2016–2017, and 2017–2018 was 99, 100, 118, and 74% of the long-term average, respectively (PRISM 2019). No post-fire treatments were applied to our study sites. Cattle were excluded the first 2 years post-fire. Subsequent livestock use occurred between December and early March. This was dormant season grazing (grazing when forage is not growing) and utilization levels were <50% consumption of available forage. Dormant season grazing by livestock in this ecosystem has limited effects on native herbaceous vegetation and does not alter the competitive relationships among sagebrush and herbaceous vegetation (Davies et al. 2016). Native ungulates and other wildlife occupied the study area and were not excluded from study sites.

Experimental Design and Measurement

We used a randomized complete block design with sites being the blocking variable. Each study site ($n = 5$) was located on a different ecological site. Treatments were: former sagebrush canopy (canopy) and former between sagebrush canopies (interspace) microsites. At each site, 50 canopy and 50 interspace microsites were randomly selected. A Wyoming big sagebrush seedling was planted in each selected microsite between 23 and 26 November, 2014. Sagebrush seedlings were grown by our staff by sowing five locally (general region) collected sagebrush seeds in seedling cone containers (3.8 cm diameter \times 21 cm tall) in August 2014. Seedlings were thinned to one individual per cone container 3 weeks after emergence and were approximately 7 cm tall at the time of planting. Seedlings were grown in a grow room for the first 2 months, then they were cold, wind, and solar hardy by placing them outdoors for increasing periods of time until they were spending 10–12 hours/day outside prior to planting. Seedlings were planted by digging a hole approximately 21 cm deep \times 5 cm wide, extracting the seedling from the container, placing the seedling in the hole, and pressing soil around the roots of the seedling. Seedling locations were marked with rebar and their positions recorded with a handheld GPS unit (Trimble GeoExplorer 6000 Series GeoXT, Trimble, Inc., Sunnvale, CA, U.S.A.).

Vegetation measurements were conducted in June of 2015, 2016, 2017, and 2018. Vegetation cover and density were

Table 1. ANOVA results for fixed effects on density groups and sagebrush survival.

Variable	Effect	Degrees of Freedom	F value	p Value
Sagebrush	Microsite	1, 4	26.68	0.007
	Year	3, 24	32.72	<0.001
	Block	4, 4	4.59	0.084
	Year \times microsite	3, 24	10.13	<0.001
Sandberg bluegrass	Microsite	1, 4	11.12	0.029
	Year	3, 24	1.16	0.346
	Block	4, 4	1.91	0.274
	Year \times microsite	3, 24	0.67	0.577
Large bunchgrass	Microsite	1, 4	11.13	0.029
	Year	3, 24	1.99	0.143
	Block	4, 4	4.35	0.092
	Year \times microsite	3, 24	1.47	0.248
Perennial forb	Microsite	1, 4	1.21	0.334
	Year	3, 24	4.07	0.018
	Block	4, 4	3.77	0.113
	Year \times microsite	3, 24	0.24	0.869
Exotic annual grass	Microsite	1, 4	29.61	0.006
	Year	3, 24	21.54	<0.001
	Block	4, 4	37.22	0.002
	Year \times microsite	3, 24	3.35	0.036
Annual forb	Microsite	1, 4	3.90	0.119
	Year	3, 24	7.63	<0.001
	Block	4, 4	1.06	0.479
	Year \times microsite	3, 24	0.43	0.732
Sagebrush survival	Microsite	1, 4	26.68	0.007
	Year	3, 24	32.72	<0.001
	Block	4, 4	4.59	0.084
	Year \times microsite	3, 24	10.13	<0.001

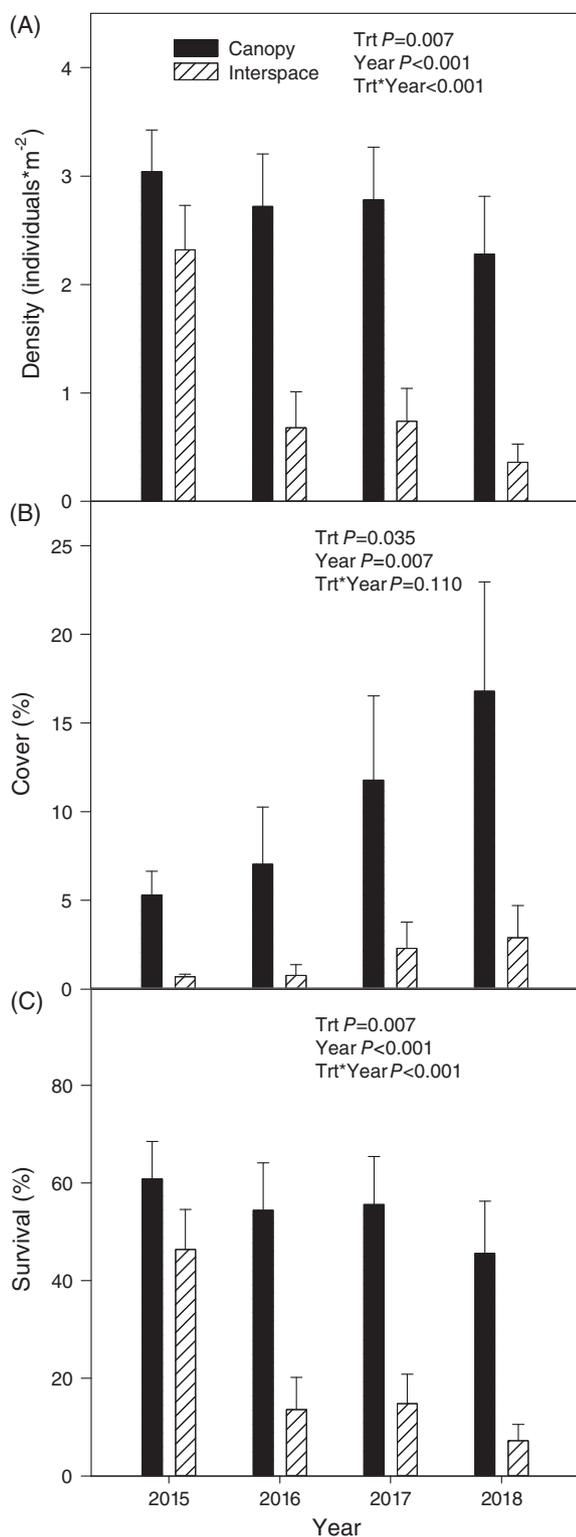


Figure 1. Sagebrush density (A), cover (B) and survival (C) (mean + SE) with planting sagebrush seedlings in former sagebrush canopy and interspace microsites after the 2014 Buzzard Wildfire Complex.

measured in fifty 40 cm × 50 cm quadrats per treatment replication. Each quadrat was centered on the location where a sagebrush seedling was planted. Vegetation cover by species was

visually estimated to the nearest 1% in the quadrats. Bare ground and litter cover were also estimated in the 40 cm × 50 cm quadrats. Density of perennial vegetation by species was measured by counting all plants rooted in the quadrats in each microsite at each site. Density of annual vegetation was counted in a 10% area of the quadrats. Sagebrush survival (%) was calculated as the ratio, in percentage, of the number of live plants at the monitoring period to the initial number of planted seedlings.

Statistical Analyses

Repeated measures analysis of variance (ANOVA) using a mixed model in SAS 9.4 (SAS Institute, Inc., Cary, NC, U.S.A.) was used to investigate microsite effects on sagebrush and vegetation characteristics. Year was the repeated variable and microsite was considered a fixed variable. Block and block by microsite interactions were treated as random variables in models. The appropriate covariance structure was selected using Akaike’s information criterion (Littell et al. 1996). For analyses, vegetation was separated into six groups: sagebrush, Sandberg bluegrass, large perennial bunchgrasses, perennial forbs, exotic annual grasses, and annual forbs. Sandberg bluegrass was separated from other bunchgrasses because it is smaller in stature, phenological development occurs earlier, and responds differently to disturbances (McLean & Tisdale 1972; Yensen et al. 1992). The exotic annual grass group consisted of cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski). Data that violated ANOVA assumptions were log-transformed prior to analyses. All data were presented in their original dimensions (i.e. non-transformed). Statistical significance was set at $p \leq 0.05$. Means were reported with standard errors (SEs). Stepwise linear regression was used to investigate the relationship between initial microsite vegetation characteristics and final sagebrush cover and density.

Results

Sagebrush density was influenced by the microsite × year interaction (Table 1, Fig. 1A; $p < 0.001$). The first year sagebrush density was 31% greater in the canopy compared to the interspace. Four years after planting, however, sagebrush density was 633% greater in canopy compared to interspace microsites, because of a substantial decline in sagebrush abundance in interspaces. Sagebrush cover differed between microsites and varied among years (Table 2, Fig. 1B; $p = 0.035$ and 0.007 , respectively). Four years after planting sagebrush cover was 5.8 times greater in canopy compared to interspace microsites. Sagebrush cover increased with time, especially in canopy microsites. Sagebrush survival, derived from density measurements, was influenced by the microsite × year interaction (Fig. 1C; $p < 0.001$). The first year sagebrush survival was slightly less in the interspace than the canopy, but in subsequent years survival was 4- to 6-fold greater in canopy compared to interspace microsites. Stepwise linear regression final model revealed that initial large perennial bunchgrass cover was the most significant variable explaining variation in final sagebrush cover and density

Table 2. ANOVA results for fixed effects on cover groups.

Variable	Effect	Degrees of Freedom	F value	p Value
Sagebrush	Microsite	1, 4	9.84	0.035
	Year	3, 24	5.19	0.007
	Block	4, 4	2.77	0.174
	Year × microsite	3, 24	2.23	0.110
Sandberg bluegrass	Microsite	1, 4	9.79	0.035
	Year	3, 24	8.63	<0.001
	Block	4, 4	1.82	0.289
	Year × microsite	3, 24	3.77	0.024
Large bunchgrass	Microsite	1, 4	17.04	0.015
	Year	3, 24	5.13	0.007
	Block	4, 4	8.96	0.028
	Year × microsite	3, 24	3.01	0.050
Perennial forb	Microsite	1, 4	0.96, 7.32	0.382
	Year	3, 24	7.32	0.001
	Block	4, 4	5.38	0.066
	Year × microsite	3, 24	0.76	0.527
Exotic annual grass	Microsite	1, 4	19.42	0.012
	Year	3, 24	33.29	<0.001
	Block	4, 4	9.54	0.025
	Year × microsite	3, 24	4.37	0.014
Annual forb	Microsite	1, 4	20.72	0.010
	Year	3, 24	5.97	0.003
	Block	4, 4	0.64	0.660
	Year × microsite	3, 24	1.97	0.145
Bare ground	Microsite	1, 4	0.69	0.453
	Year	3, 24	87.66	<0.001
	Block	4, 4	0.71	0.624
	Year × microsite	3, 24	0.92	0.444
Litter	Microsite	1, 4	0.01	0.935
	Year	3, 24	116.32	<0.001
	Block	4, 4	1.38	0.382
	Year × microsite	3, 24	0.28	0.840

(adjusted $r^2 = 0.422$ and 0.476 , $p = 0.025$ and 0.016). Sagebrush cover and density was inversely correlated to large perennial bunchgrass cover.

Sandberg bluegrass and large perennial bunchgrass densities were greater in interspace compared to canopy microsites (Fig. 2A & 2B; $p = 0.029$ and 0.029 , respectively) but did not differ among years (Table 1; $p = 0.346$ and 0.143 , respectively). On average, the abundance of Sandberg bluegrass was 2.6 times greater in interspace compared to canopy microsites. Large perennial bunchgrass density was on average 3.6 times greater in interspace compared to canopy microsites. Perennial forb density was highly variable and was not influenced by microsite nor the microsite × year interaction (data not shown; $p = 0.334$ and 0.869 , respectively). Perennial forb density varied among years ($p = 0.018$), but no clear pattern emerged. Exotic annual grass density was influenced by the microsite × year interaction (Fig. 2C; $p = 0.036$). Initially, exotic annual grass density was less in canopy compared to interspace microsites, but by the third year post-fire it was greater in canopy microsites. Annual forb density did not differ between microsites and was not influenced by the microsite × year interaction (Fig. 2D; $p = 0.119$ and 0.732 , respectively) but varied among years ($p < 0.001$).

Sandberg bluegrass cover was influenced by the microsite × year interaction (Table 2, Fig. 3A; $p = 0.024$). Sandberg bluegrass cover was greater in interspace compared to canopy microsites, but the difference decreased over time. Large perennial bunchgrass cover was influenced by the microsite × year interaction (Fig. 3B; $p = 0.050$). Large perennial bunchgrass cover was 6.6 times greater in the interspace in the first year after fire, but decreased to only 2.3 times greater by the fourth year post-fire. Perennial forb cover did not differ between microsites (data not shown; $p = 0.382$) and was not influenced by the microsite × year interaction ($p = 0.527$). Perennial forb cover varied among years ($p = 0.001$), with it generally being greatest in 2016 and lowest in 2017 and 2018. Exotic annual grass cover was influenced by the microsite × year interaction (Fig. 3C; $p = 0.014$). Exotic annual grass cover was similar between microsites the first year post-fire, but was approximately two times greater in canopy compared to interspace microsites in the second through fourth year post-fire. Annual forb cover was greater in canopy compared to interspace microsites (Fig. 3D; $p = 0.010$) and varied among years ($p = 0.003$). Bare ground and litter were not different between microsites (Fig. 3E & 3F; $p = 0.453$ and 0.935 , respectively), but varied among years ($p < 0.001$).

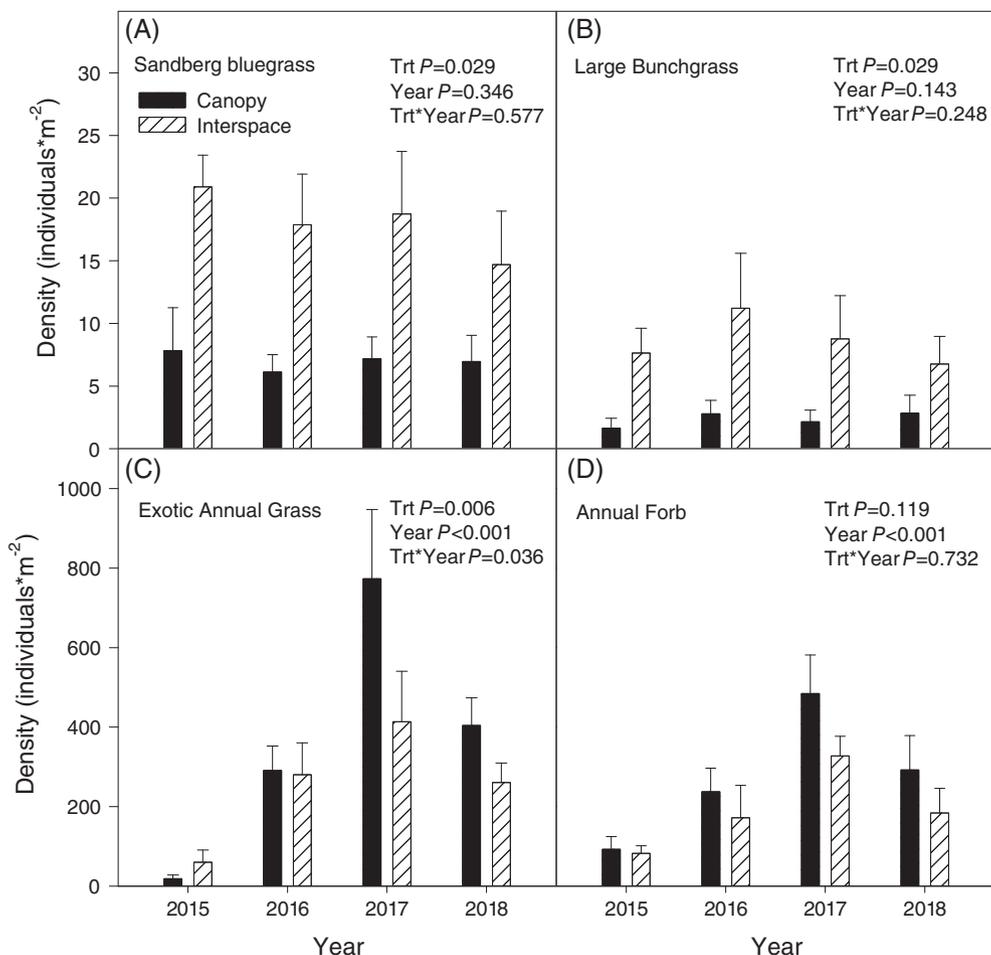


Figure 2. Density (mean + SE) of herbaceous plant groups in former sagebrush canopy and interspace microsites after the 2014 Buzzard Wildfire Complex.

Bare ground was greatest and litter cover was the least the first year post-fire.

Discussion

Selecting former shrub canopy microsites for planting seedlings can be used to improve restoration success for shrubs and likely other plant functional groups. Our results were consistent across five different ecological sites, representing almost 1 million hectares (>2 million acres). This suggests that these results likely broadly apply and would be valuable to consider in restoration of other shrub-steppe communities. Our results suggest that spatial variability needs to be identified and then utilized to increase the likelihood of restoration success. Sagebrush survival was 46% in former canopy microsites, but only 7% in interspace microsites four growing seasons after planting. Clearly, planting sagebrush seedlings in former canopy microsites is a more sensible strategy rather than planting seedlings haphazardly across a post-fire landscape. Seeded perennial grasses also had greater establishment in former sagebrush canopy microsites compared to interspace microsites post-fire (Boyd & Davies 2010). Likewise, survival of planted bitterbrush seedlings was >50% and 5% in former juniper tree canopy and interspace microsites,

respectively (Davies et al. 2017). Our study reaffirms that woody vegetation creates post-fire microsites that can be favorable to seedling establishment and survival.

Prior work has established that shrubs can act as nurse plants for other species by creating more favorable microsites under their canopies (Torroba-Balmori et al. 2015; Alday et al. 2016; Cruz-Alonso et al. 2019). Our results demonstrate that shrubs can continue to facilitate establishment and growth of plants even after they are gone. The more favorable environment for seedling establishment and growth in former canopy microsites resulted in sagebrush cover exceeding 16% on average 4 years post-fire; in contrast, interspace microsites averaged less than 3% cover. Bitterbrush growth was similarly greater in former juniper canopy than interspace microsites (Davies et al. 2017). These results suggest that recovery of shrub cover can be enhanced by planting shrub seedlings in former shrub canopy compared to interspace microsites. It is important to note that sagebrush cover was measured by centering quadrats over locations where seedlings were planted. Therefore, these cover estimates are not representative of cover at the community scale.

The greater cover and abundance of sagebrush in former canopy compared to interspace microsites were probably related to resource island effects and differences in post-fire herbaceous

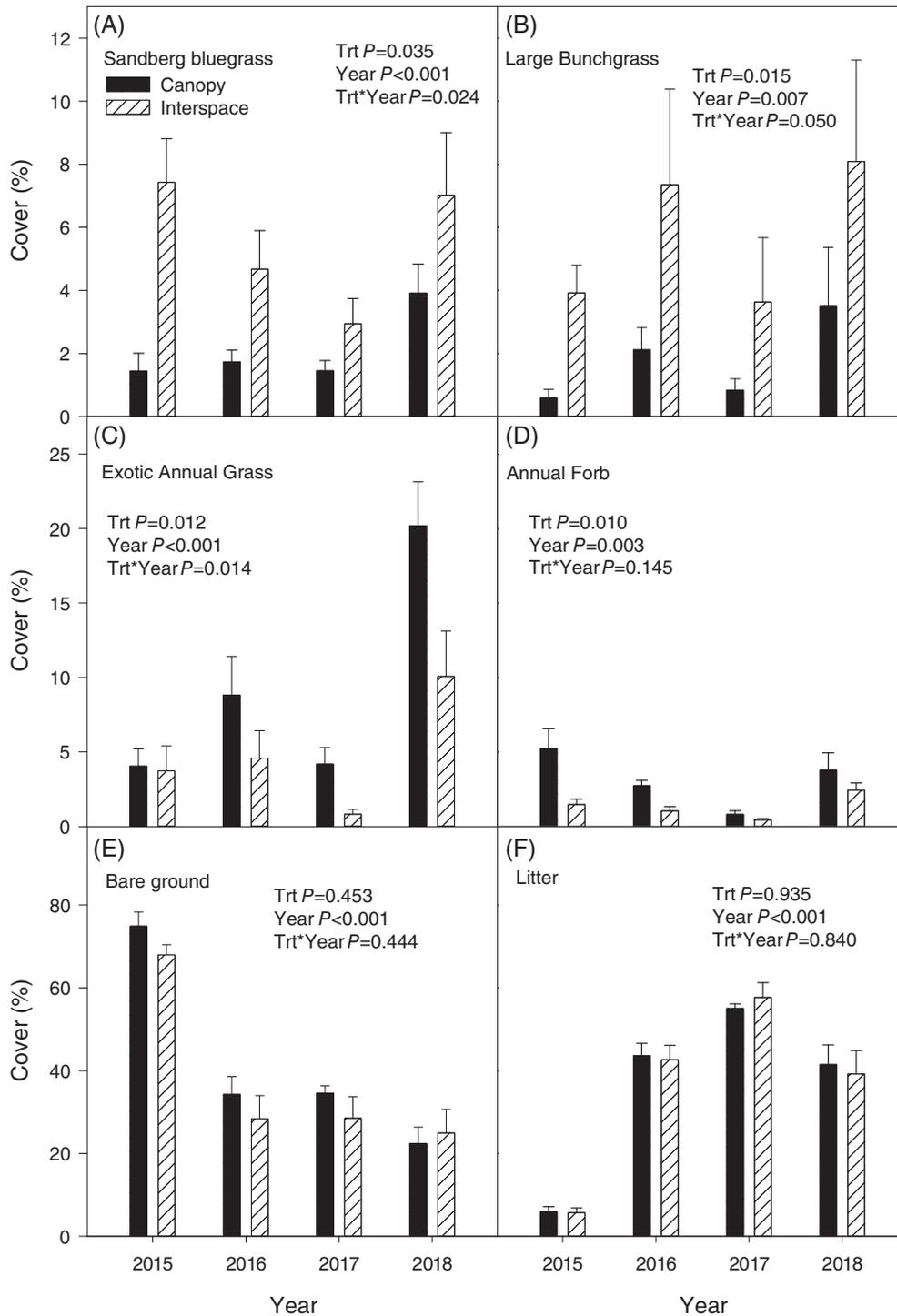


Figure 3. Cover (mean + SE) of cover groups in former sagebrush canopy and interspace microsites after the 2014 Buzzard Wildfire Complex.

vegetation. Sagebrush and other woody vegetation create resource islands under their canopies in arid and semi-arid environments (Doescher et al. 1984; Jackson & Caldwell 1993a, 1993b; Davies et al. 2007), which may remain after fire (Stubbs & Pyke 2005; Davies et al. 2009). Abundance and cover of large perennial bunchgrass and Sandberg bluegrass was less

in former canopy compared to interspace microsites. Less herbaceous vegetation in canopy microsites likely translates to reduced competition. The negative correlation between initial large perennial bunchgrass cover and final sagebrush density and cover further supports that less vegetation in the canopy microsite resulted in a favorable microsite for sagebrush

establishment and growth. Perennial bunchgrasses are highly competitive with other vegetation and dominate the understory in these ecosystems (Davies et al. 2006; James et al. 2008). Therefore, reduced vegetation in canopy microsites probably contributed to increased survival of planted sagebrush seedlings through reduced competition for limited resources. Competition from herbaceous vegetation has limited shrub establishment in other restoration attempts (Allen 1988; Schuman et al. 1998; Hall et al. 1999; Rinella et al. 2015, 2016). In particular, competition from perennial grasses is a widespread factor limiting woody vegetation establishment and growth (Midoko-Iponga et al. 2005; DeFalco et al. 2007; Rinella et al. 2015). Woody plant establishment in grasslands has been speculated to be a function of the availability of gaps with low biomass of grasses (Jurena & Archer 2003), which is supported by the results from our regression analysis. The increase in exotic annual grasses, large perennial grasses, and Sandberg bluegrass with time in former sagebrush canopy microsites further suggests that competition was limited in these microsites, at least initially post-fire. Initially, the abundance of exotic annual grass was less in canopy microsites, but by the third year of the study was substantially greater in canopy than interspace microsites, again suggesting excess resource availability post-fire.

Exotic annual grass increased substantially in both microsites after the first year post-fire. Increases in exotic annual grasses are concerning as they threaten the long-term sustainability of these communities. Exotic annual grass invasion can increase fire frequency, further promoting greater dominance by exotic annual grasses (D'Antonio & Vitousek 1992; Brooks et al. 2004). This potentially leads to an exotic annual grass–fire cycle, where frequent fire and exotic annual grass competition exclude native perennial species (D'Antonio & Vitousek 1992; Rossiter et al. 2003). This risk will need further evaluation and suggests that efforts to control exotic annuals and restore perennial herbaceous vegetation may be needed.

Sagebrush survival in the first growing season, prior to summer drought, appeared promising in both microsites. However, most mortality of planted sagebrush occurred after this sampling period, particularly in interspace microsites. This suggests that surviving the first summer drought is critically important to sagebrush establishment, as also found in other environments and for other species (Torroba-Balmori et al. 2015). Summer drought is likely a bottleneck for establishing sagebrush seedlings and, subsequently, we caution against assessing restoration success in only the first growing season. This agrees with our field experience in sagebrush communities, where sagebrush seedlings may be abundant during the late spring and early summer, but by the fall they are largely gone as they have suffered mortality during the summer drought.

Our research implies that shrublands that have lost their shrubs prior to fire may be difficult to restore. The entire area is essentially interspace because herbaceous vegetation has become more homogeneous across the community without shrubs creating distinct post-fire microsites. Restoration of shrubs is likely even more challenging if competitive exotic plants have invaded the community. Exotic annual grass-dominated areas may be exceedingly difficult to reestablish

sagebrush because of elevated competition. Planted sagebrush seedling survival (Davidson et al. 2019) and seeded sagebrush first growing season density (Germino et al. 2018) decreased with increasing exotic annual grass cover in Idaho and Oregon. Post-fire restoration of shrubs, therefore, may be critical to the ability to restore shrubs after the next fire because of the post-fire microsites they create.

Our research suggests that post-fire restoration in other shrub ecosystems may be more successful if shrubs or other priority species are planted in former canopy microsites. Shrub-induced resource islands occur around the world in arid and semi-arid ecosystems (Vetaas 1992; Jackson & Caldwell 1993a, 1993b; Schlesinger et al. 1996). Woody vegetation also burns hotter and longer than herbaceous vegetation (Gibson et al. 1990; Thaxton & Platt 2006), increasing the likelihood of fire-induced mortality of plants under and near their canopies. This could lead to microsites, similar to our current study, with reduced vegetation competition. The combination of resource islands and reduced competition likely results in a favorable microsite for establishment of shrubs and other species that are restoration priorities.

Prioritizing restoration efforts in locations with a higher probability of success will likely improve restoration efficiency. Different probabilities of restoration success can be important within landscapes at the landform or community scale (Davies & Bates 2017; Davidson et al. 2019) and, as our current study demonstrates, within communities at the microsite scale. Restoration of rangelands is challenging and results are often less than desirable (Knutson et al. 2014; Svejcar et al. 2017). Exploiting spatial variability in restoration efforts may improve restoration efficiency. Identifying favorable locations for restoration is critical, as restoration needs greatly exceed resources available for those efforts. Areas of greater resource availability and areas with less competition are likely favorable locations for restoration efforts. Identifying and utilizing these microsite differences would be particularly valuable for species that are difficult to restore, are in limited availability, or importance to the ecosystem warrant more intensive efforts.

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