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# Using Postfire Spatial Variability to Improve Restoration Success with Seeded Bitterbrush☆

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ABSTRACT

Seed-based restoration of wildlife-important shrubs following wildfire is a management priority in many ecosystems. However, postfire restoration success is spatiotemporally variable and establishment from seed frequently fails in arid and semiarid rangelands. There may be opportunities to improve restoration success by taking advantage of small-scale spatial variability in environmental characteristics. Woody plants create distinct postfire microsites, which may influence establishment and growth of seeded species, under their canopies (canopies) compared with between their canopies (interspaces). Immediately after fire, former canopies generally have less vegetation and greater soil nutrient concentrations compared with interspaces. Thus, former canopy compared with interspace microsites may be more favorable for establishment and growth of seeded species, but rapid exotic plant invasion of former canopy microsites may hinder success. We evaluated seeding bitterbrush (*Purshia tridentata* Pursh DC) after wildfire in former western juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook) canopy compared with interspace microsites at six locations for 3 yr post seeding. Bitterbrush abundance was 3.6-fold greater in former canopy compared with interspace microsites after 3 yr. Bitterbrush height was 1.5 to 2.5-fold greater in former canopy compared with interspace microsites. The first year after fire, exotic annual grass cover was 15.6-fold greater in interspace compared with canopy microsites. Abundance and cover of other herbaceous vegetation were generally also greater in the interspace. Exotic annual grass and native bunchgrass abundance increased substantially over time in former canopy microsites, suggesting abundant resource availability. Less herbaceous competition and presumably greater resource availability in former canopies probably resulted in greater success of seeded bitterbrush. These results suggest that capitalizing on spatial variability in environments can be used to increase restoration efficiency. After fire in western juniper–encroached rangelands, former juniper canopy microsites are a favorable environment for establishment and growth of seeded bitterbrush and could be targeted for restoration efforts to improve efficiency.



## Introduction

Postfire restoration of fire-sensitive plant species can be critical for native wildlife and to return ecosystem function. Restoration of native species is expensive, and success is widely variable through time and space, especially in arid and semiarid rangelands (Svejcar et al. 2017; Shackelford et al. 2021). Spatial variability of restoration outcomes is evident across landscapes (Boyd and Davies 2010; Davies and Bates 2017; Davidson et al. 2019) and within plant communities (Rice 1993; Jurena and Archer 2003; Davies et al. 2020). Strategically applying restoration efforts in areas with a higher probability of success could increase efficiency and effectiveness of restoration investments (Germino et al. 2018; Davies et al. 2020). This could also create islands of fire-sensitive species that could serve as refugia for wildlife and as a seed source for the recovery of these plants across the landscape

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(Hulvey et al. 2017). Identifying areas where the probability of success is highest at both large and small scales is critical to strategic application of restoration efforts.

Antelope bitterbrush (*Purshia tridentata* DC) is a native shrub in North America that has decreased in many areas because of tree encroachment, wildfires, heavy defoliation by wildlife and livestock, and limited recruitment (Billings 1952; Tueller and Tower 1979; Miller et al. 2000). The decline of bitterbrush is of concern because many animal species use it. Bitterbrush provides critical fall and winter browse for wild ungulates (Kufeld et al. 1973; Vavra and Sneva 1978; Shaw and Monsen 1986). Livestock also use bitterbrush in the late summer, fall, and winter when herbaceous vegetation is low in digestible protein (Ganskopp et al. 1999; Clements and Young 2002). Bitterbrush enhances the late-season diets of ungulates because its crude protein remains above 8% year-round (Hickman 1975; Kituku et al. 1992). Bitterbrush seeds are also an important food source for some rodents (Everett et al 1978; Vander Wall 1994). For these reasons, bitterbrush is often a restoration priority after wildfire in rangelands.

Bitterbrush restoration success is highly variable with many unsuccessful attempts (Hubbard 1964; Clemens and Young 2000; Davies et al. 2017). Restoration failures of bitterbrush are often caused by inadequate growth between emergence and seasonal summer drought (Davies et al. 2017). Insufficient growth makes seedlings more vulnerable to heat and drought stress, which likely drives high mortality of seedlings in the first year (Davies et al. 2017). Limited seedling growth is likely the result of low resource availability, primarily moisture, the product of the environment and competition. Clements and Young (2002) speculated that competition for moisture was the most limiting barrier to bitterbrush establishment in many postfire rangelands. Bitterbrush and other shrub establishment can be hindered by competition from herbaceous vegetation (Porensky et al. 2014; Rinella et al. 2015; Davies et al. 2017). Therefore, bitterbrush restoration efforts may be more successful in areas with elevated resources and lower competition from other vegetation.

In semiarid and arid rangelands, woody vegetation can create distinct microsites under their canopies (canopy) and between canopies (interspace), resulting in resource islands (increased soil nutrient concentrations) in canopy compared with interspace microsites (Jackson and Caldwell 1993; Herman et al. 1995). These microsite differences contribute to heterogeneity in herbaceous vegetation in shrublands (Doescher et al. 1984; Burke et al. 1987; Wight et al. 1992; Davies et al. 2007). Though fire alters microsites, differences in abiotic and biotic characteristics between canopy and interspace microsites remain (Davies et al. 2009; Bates and Davies 2016), offering two distinct restoration environments. Consequently, success of seeded bitterbrush likely differs between these microsites.

When wildfire occurs in western juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook)−encroached shrub steppe, there may be an opportunity to improve bitterbrush restoration by seeding into former juniper canopy compared with interspace microsites. Former juniper canopies compared with interspace microsites have less vegetation immediately after fire, likely in part from fire-induced mortality, and greater soil nutrient availability (Rau et al. 2007, 2008; Bates and Davies 2016; Davies et al. 2017). Establishment of other seeded vegetation after fire has been greater in former shrub canopy compared with interspace microsites (Boyd and Davies 2010; Germino et al. 2018). Survival of planted bitterbrush and sagebrush seedlings was greater in former juniper and sagebrush canopy microsites, respectively, further suggesting that former canopy microsites may be a favorable environment for establishment of seeded bitterbrush (Davies et al. 2017; Davies et al. 2020). Rapid postfire invasion of former canopy microsites by exotic annual grasses (Bates and Davies 2016; Davies et al. 2017), however, could hinder survival and growth of seeded bitterbrush. Seeded seedlings may be especially vulnerable to competition relative to planted seedlings because seeded bitterbrush does not bypass the smallest size classes that are most likely to suffer mortality (Shriver et al. 2019). Therefore, determining whether seeded bitterbrush recruitment and growth differ between microsites is necessary to guide restoration efforts.

The purpose of this study was to investigate seeded bitterbrush establishment and growth in former juniper canopy and interspace microsites after a wildfire in western juniper−encroached shrub steppe. We also compared vegetation and ground cover characteristics between microsites to assist in explaining seeded bitterbrush response. We expected that bitterbrush density and growth would be greater in former canopy compared with interspace microsites and that initial herbaceous cover and density would be lower in former canopy compared with interspace microsites.

## Methods

### *Study area*

Six study sites were located in the 21 231-ha Cinder Butte Wildfire 25−35 km west and southwest of Riley, Oregon. The human-caused Cinder Butte Wildfire occurred in early August of 2017. Before burning, vegetation at the study sites was western juniper−encroached shrub steppe. The shrub component was dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) with bitterbrush intermixed. The understory was dominated by native perennial bunchgrasses. Common perennial bunchgrasses included Idaho fescue (*Festuca idahoensis* Elmer), bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), prairie Junegrass (*Koeleria macrantha* [Ledeb.] Schult.), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), and Sandberg bluegrass (*Poa secunda* J. Presl). The exotic annual grass, cheatgrass (*Bromus tectorum* L.), was present in low abundance across the study area before the wildfire. Climate across the study area is typical of the Intermountain West with hot, dry summers and cool, wet winters. Long-term average precipitation (1981−2010) ranged from 261 to 331 mm among study sites (PRISM 2021). Precipitation at study sites was 90−93%, 59−65%, 113−130%, and 69−72% of the long-term average in 2017 (year of the fire), 2018 (first year post seeding), 2019, and 2020, respectively (PRISM 2021). Aspects ranged from southeast, east, and northeast, and slopes ranged from 4º to 13º among study sites. Elevation ranged from 1 453 to 1 679 m above sea level. Soil surfaces were gravelly fine sandy loam, gravelly silt loam, and very stony clay loam (NRCS 2021). Livestock were excluded for the duration of the study from the study sites, but wildlife had unrestricted access to the study sites.

### *Experimental design and measurements*

We used a complete block design with six sites (blocks) to investigate seeding bitterbrush into former western juniper canopy and interspace microsites after wildfire. Blocks were separated by up to 19 km. Each block consisted of two treatments: 1) former juniper canopy (canopy) and 2) interspace (interspace) microsites. Each block consisted of five $6 \times 6$ m canopy and interspace microsites at each site. Microsites had to be greater than $6 \times 6$ m to be included in the study. Canopy microsites were identified by the tree skeleton and darker soil created by the combustion of the tree. Former canopy microsites were centered on the trunk of the dead juniper tree, and interspace microsites were placed in the center of the area between canopies. Each microsite location was marked with rebar and a metal tag and recorded with a Global Positioning System unit (Trimble GeoExplorer 6000 Series GeoXT, Trimble Inc., Sunnvale, California). Five bitterbrush seeds were planted in a group in a 2-cm deep hole in each square meter of each treatment replicate in November of 2017. Bitterbrush seeds were harvested from native stands < 100 km south of the study sites.

Vegetation characteristics were measured in late June of 2018, 2019, and 2020. Bitterbrush density was determined by counting every bitterbrush in each microsite in each block. Height, longest canopy diameter, and canopy diameter perpendicular to the longest diameter were measured on every bitterbrush plant. Herbaceous vegetation cover and density were measured in four, 0.2-$m^2$ frames randomly located in every microsite in each treatment replicate (20 per treatment in each block). Bare ground, rock, and litter cover were also estimated using the 0.2-$m^2$ frames.

### *Statistical analyses*

We used repeated measures analysis of variance (ANOVA) using the mixed-model procedure (Proc Mixed) in SAS v. 9.4 (SAS Institute Inc., Cary, North Carolina) to investigate bitterbrush establishment and growth in former canopy and interspace microsites. Year was the repeated variable, block and block • treatment interactions were treated as random effects in analyses. Covariance structure was selected using Akaike's Information Criterion (Littell et al. 1996). Data that violated ANOVA assumptions were log or square root transformed before analysis. Data in the text and figures are presented in their original, nontransformed dimensions. Herbaceous vegetation was separated into five groups for analyses: Sandberg bluegrass, perennial bunchgrasses, exotic annual grasses, perennial forbs, and annual forbs. Sandberg bluegrass was analyzed independently from the other bunchgrasses because it develops phenologically earlier, is smaller in stature, and responds differently to management and disturbances (McLean and Tisdale 1972; Davies et al. 2021). The exotic annual grass group was composed solely of cheatgrass. The perennial forb group was entirely composed of native species. The annual forb group was dominated by exotic species. Significance level for all tests was set at $P \leq 0.05$, and response variable means are reported with standard errors.

## Results

Bitterbrush density was influenced by the microsite • year interaction (Fig. 1A; $P = 0.038$). Bitterbrush density was greater in the canopy in all years but decreased between the first and second sampling period while the density in the interspace remained similar among years. At the end of the study, bitterbrush density was 3.6-fold greater in former canopy compared with interspace microsites. Bitterbrush height was 1.5- to 2.5-fold greater in the canopy compared with the interspace (see Fig. 1B; $P = 0.050$) and generally increased with time ($P < 0.001$). Bitterbrush longest and perpendicular canopy diameters did not differ between microsites (see Fig. 1C and 1D; $P = 0.257$ and 0.053, respectively) but varied among years ($P < 0.001$ and $P = 0.006$, respectively). Bitterbrush canopy diameters were generally greatest in the second year in the former canopy and the third year in the interspace.

Sandberg bluegrass density was greater in the interspace than the canopy (Fig. 2A; $P = 0.049$) but did not differ among years ($P = 0.592$). Perennial bunchgrass density was influenced by the microsite • year interaction (see Fig. 2B; $P = 0.033$). Perennial bunchgrass density increased with time in the canopy but remained similar across years in the interspace. Exotic annual grass

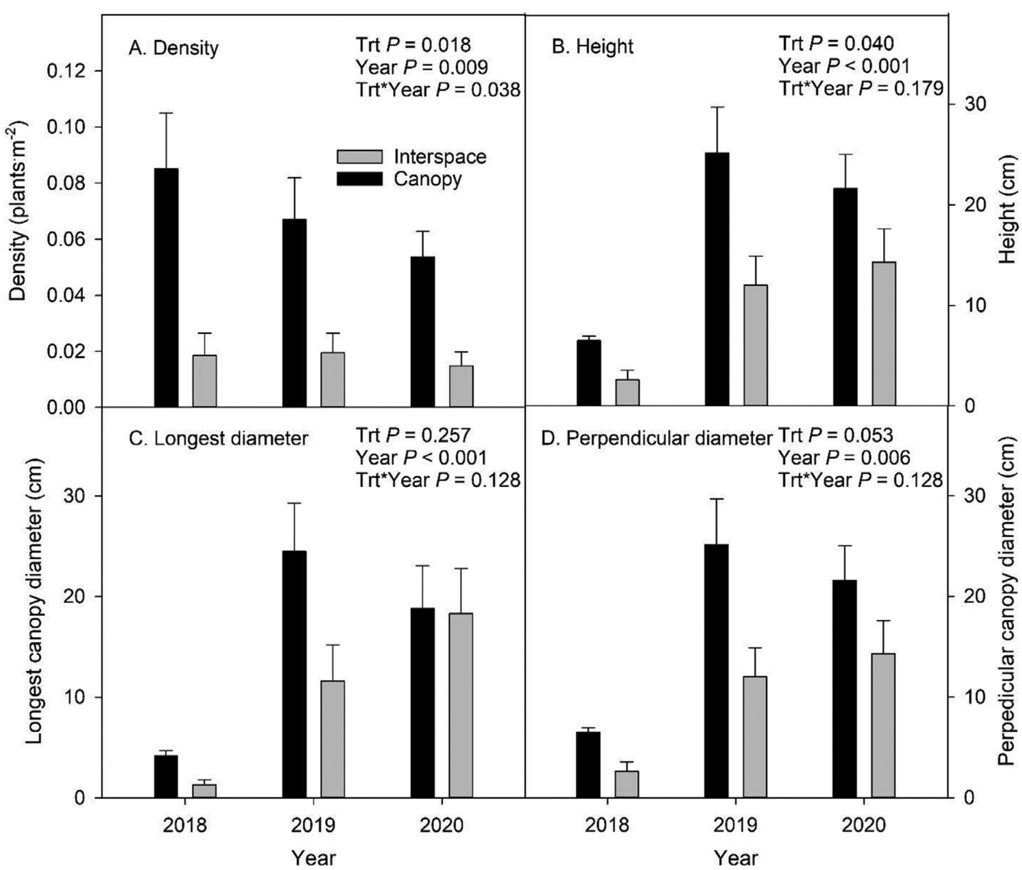


**Figure 1. A–D,** Bitterbrush density, height, longest canopy diameter, and canopy diameter perpendicular to the longest diameter (mean + standard of error) in former juniper canopy and interspace microsites where bitterbrush was seeded after a 2017 wildfire in the first through third year post seeding (2018–2020).

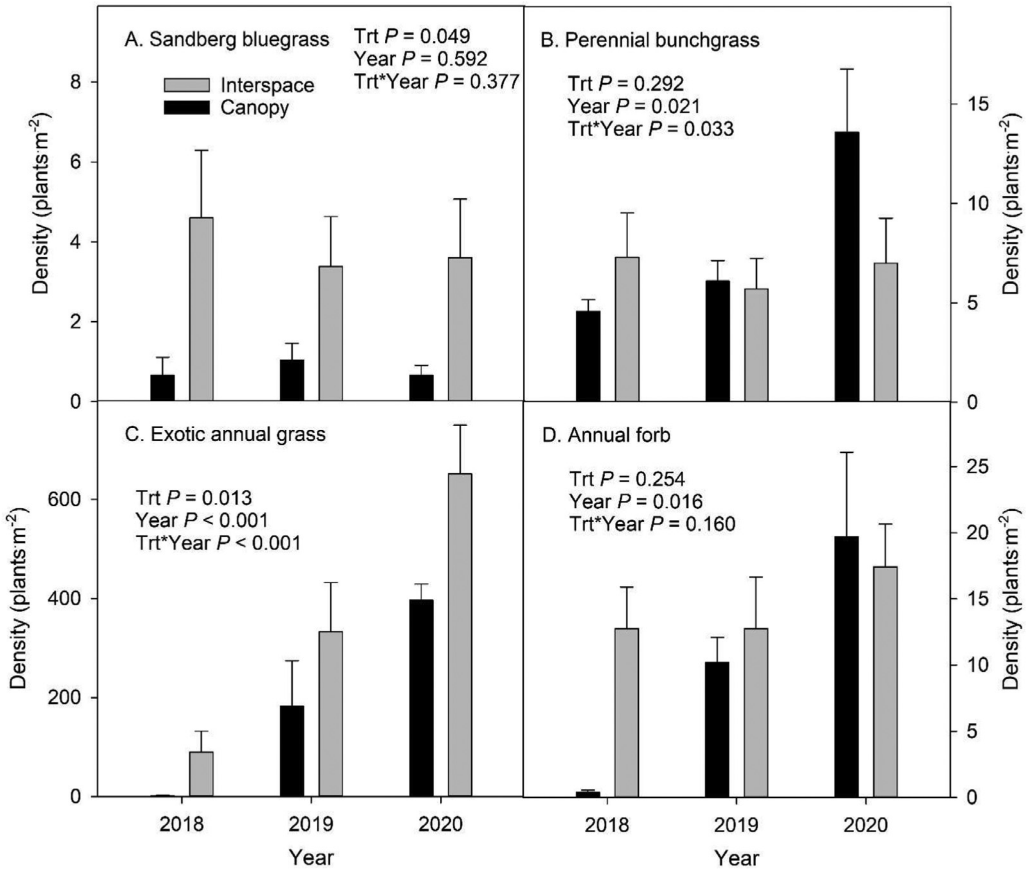


**Figure 2.** Plant group densities (mean + standard of error) in former juniper canopy and interspace microsites where bitterbrush was seeded after a 2017 wildfire in the first through third year post seeding (2018–2020).

density was influenced by the microsite∗year interaction (see Fig. 2C; $P < 0.001$). The interspace had greater exotic annual grass abundance than the canopy, but the magnitude of the difference decreased with time. Perennial forb density did not differ between microsites or vary among years (data not shown; $P = 0.355$ and 0.936, respectively). Annual forb density did not differ between microsites (see Fig. 2D; $P = 0.254$) but varied among years ($P = 0.016$). Annual forb density was greatest in the final year of the study.

Sandberg bluegrass cover was greater in the interspace compared with the canopy (Fig. 3A; $P = 0.037$) but did not vary among years ($P = 0.663$). Perennial bunchgrass cover did not differ between microsites (see Fig. 3B; $P = 0.328$) but increased over time ($P = 0.001$). Exotic annual grass cover differed between microsites and varied among years (see Fig. 3C; $P = 0.024$ and $< 0.001$, respectively). The first year after fire, exotic annual grass cover was 15.6-fold greater in the interspace compared with the canopy. At the end of the study, exotic annual grass cover was 1.6-fold greater in the interspace compared with the canopy. Perennial forb cover did not differ between microsites or vary among years (data not shown; $P = 0.577$ and 0.055, respectively). Annual forb cover was influenced by the microsite∗year interaction (see Fig. 3D; $P = 0.005$). Annual forb cover was greater in the interspace the first year after fire, but in all subsequent years it was greater in the canopy. Total herbaceous cover was influenced by the microsite∗year interaction (see Fig. 3E; $P = 0.011$). Total herbaceous cover was less in the canopy compared with the interspace in the first year, but after that it was similar between microsites. Bare ground did not differ between microsites (see Fig. 3F; $P = 0.244$) but decreased with time ($P < 0.001$). Rock and litter cover also did not differ between microsites (data not shown; $P = 0.612$ and 0.221, respectively) but varied among years ($P < 0.001$). Rock cover followed a similar trend as bare ground, and litter cover was the inverse of bare ground across time.

## Discussion

Our results supported our hypothesis that bitterbrush density and growth would be greater in former juniper canopy compared with interspace microsites. This suggests that using spatial variability to strategically apply restoration efforts within plant communities can improve efficiency. This requires determining where restoration success is more probable. Our research adds to the growing body of literature that suggests that former shrub or tree canopy compared with interspace microsites in postfire rangelands are more favorable for establishment of species targeted for restoration (e.g., Boyd and Davies 2010; Davies et al. 2017; Germino et al. 2018; Davies et al. 2020). At the conclusion of our study, bitterbrush density was 3.6× greater in former canopy compared with interspace microsites, strongly suggesting that bitterbrush seeding efforts should focus on former canopy microsites. Similar to our current work, planted bitterbrush seedling survival was > 50% after 3 yr in former juniper canopy compared with only 5% in interspace microsites (Davies et al. 2017). Greater growth of bitterbrush, indicated by height in our current study, also suggests that former canopy microsites are a favorable environment for shrub growth. The greater survival of bitterbrush seedlings (Davies et al. 2017) and greater density and growth of seeded bitterbrush in former canopies in our current study provide robust evidence that bitterbrush restoration success can be improved by focusing efforts on these microsites.

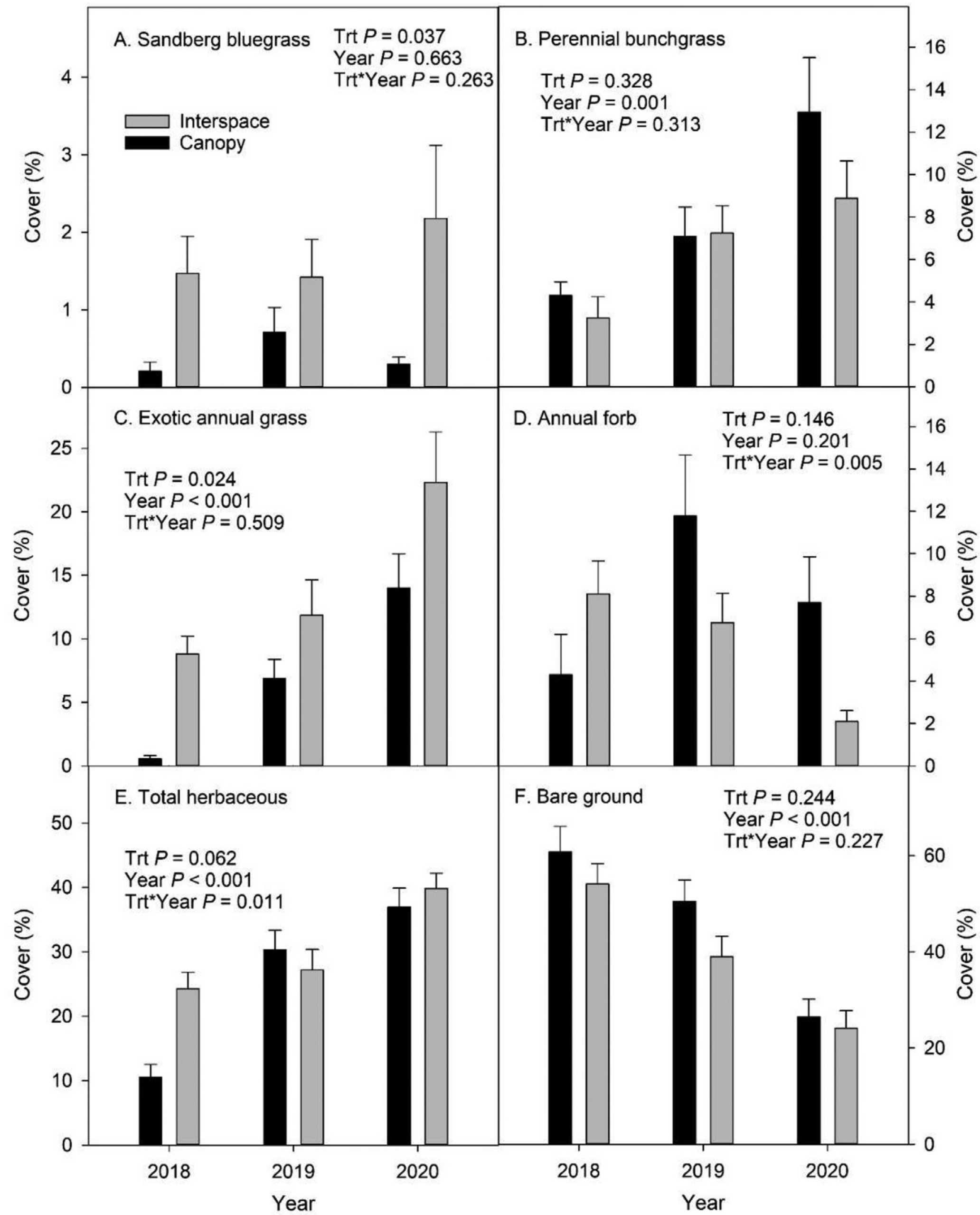


**Figure 3.** Plant group cover and bare ground (mean + standard of error) in former juniper canopy and interspace microsites where bitterbrush was seeded after a 2017 wildfire in the first through third year post seeding (2018–2020).

Bitterbrush canopy diameters were expected to differ between microsites. However, they did not meet our significance level to be considered different. Unexpectedly, in former canopy microsites, bitterbrush canopy diameters and height generally declined from the second to third year after seeding (see Fig. 1B-D). In contrast, bitterbrush height and canopy diameters generally increased with time in the interspace. In the third year, we observed substantial browsing of bitterbrush plants in former canopy microsites and expect this caused the reduction in bitterbrush height and canopy diameters. Bitterbrush did not appear to be as heavily browsed in interspace microsites, possibly because they were smaller in stature and thus their canopies were more obstructed visually and physically by herbaceous vegetation.

The greater density and growth of seeded bitterbrush in former canopies was probably, at least partially, a result of less competition from herbaceous vegetation. Exotic annual grass abundance and cover were greater in interspace compared with former canopy microsites. The greater abundance of exotic annual grasses in the interspace, especially in the first year post seeding, likely reduced the establishment of bitterbrush. Competition from exotic annual grasses is often the greatest limiting factor to bitterbrush establishment in postfire rangelands (Clements and Young 2002). Greater Sandberg bluegrass cover and density and total herbaceous cover (at least in the first year) in the interspace compared with the former canopy further suggests that competition was greater in the interspace, likely hindering bitterbrush establishment and growth. In support of our assumption that competition was limiting bitterbrush in the interspace, herbaceous competition has been repeatedly found to impede bitterbrush and other shrub establishment (Porensky et al. 2014; Rinella et al. 2015; Davies et al. 2017). Therefore, less herbaceous competition likely contributed to the greater success of seeded bitterbrush in former canopies compared with interspace microsites.

The resource island effect of former juniper canopies probably also contributed to greater bitterbrush abundance and growth in former canopies compared with interspace microsites. Woody vegetation in rangelands can increase undercanopy soil nutrient concentrations, resulting in resource islands (Doescher et al. 1984; Burke et al. 1987; Jackson and Caldwell 1993; Herman et al. 1995; Davies et al. 2007). Postfire former canopy microsites often have greater soil nutrient concentrations than interspace microsites, providing evidence that the resource island effect remains after fire removes the woody vegetation (Stubbs and Pyke 2005; Rau et al. 2007; Davies et al. 2009; Bates and Davies 2016). Greater soil nutrient concentrations in former canopy locations likely favor bitterbrush growth and survival (Davies et al. 2017). Thus, the resource island effect and reduced competition likely makes former canopy microsites a favorable environment for seeded bitterbrush establishment and growth. The growth conditions of postfire canopy microsites would likely be beneficial for other species as well.

Further suggesting former canopy microsites were a favorable environment for plant establishment, perennial bunchgrass and exotic annual grass density increased substantially in former canopy microsites over time. In contrast in the interspace, perennial bunchgrass density did not change and the magnitude of increase in exotic annual grass density was much less over time. Similarly, seeded bunchgrass establishment was substantially greater in former sagebrush canopy compared with interspaced microsites (Boyd and Davies 2010). In general, former canopy microsites are likely a favorable environment for vegetation establishment, particularly in postfire restoration efforts.

The first year establishment of bitterbrush in this study occurred in a drought year, 59−65% of long-term average precipitation occurred across study sites. Dissimilar to the establishment in the canopy microsite in our study, most reports of seeding success in rangelands occur in years when annual precipitation was average or above average (Hardegree et al. 2011). Many rangeland restoration efforts are unsuccessful because seeded vegetation fails to establish as a result of inadequate postseeding precipitation (Svejcar et al. 2017). The benefit of being seeded in a former juniper canopy microsite after wildfire, likely because of greater soil moisture, may have offset some of the negative effects of drought on seedlings. Inadequate soil moisture is often the most limiting barrier to bitterbrush postfire establishment (Clements and Young 2002). For example, in a bitterbrush restoration study, drought likely resulted in mortality of almost all planted seedlings (Davies et al. 2022). Less herbaceous vegetation in former canopy microsites, especially immediately after fire, suggests that soil moisture was probably more available to seeded vegetation. Considering that drought is a frequent barrier to establishment of seeded species in many rangelands, seeding in former canopy microsites may be an effective strategy for overcoming this impediment to restoration success.

## Management Implications

Restoration efficiency can be improved by focusing efforts in areas where success is more likely. This requires identifying locations that are favorable for restoration based on their abiotic and biotic characteristics. In postfire juniper-encroached shrub steppe, former juniper canopy microsites are a favorable environment for seeded bitterbrush establishment and growth compared with interspaces. Former tree and shrub canopy microsites have also been favorable for planted shrub seedling survival (Davies et al. 2017; Davies et al. 2020) and seeded grass establishment (Boyd and Davies 2010). Combined with the current study, these results suggest that former canopy microsites in shrub steppe communities can be targeted for restoration efforts to increase the probability of success. This is particularly important when using expensive and labor-intensive restoration actions or when desired plant material is limited. Restoration can be improved by identifying spatial heterogeneity in abiotic and biotic characteristics within and across plant communities and then capitalizing on locations with greater probability of success. Therefore, more research is warranted to determine spatial variability in abiotic and biotic characteristics and their effects on restoration outcomes. Future research also needs to identify when "favorable" abiotic and biotic characteristics can be broadly applied to restoration efforts and when they are specific to individual species or plant functional groups. In western juniper−encroached shrub steppe, former juniper canopy microsites are a favorable environment after fire for seeded bitterbrush establishment and, subsequently, can be targeted to improve bitterbrush restoration efficiency.

## Declaration of Competing Interest

We do not have any conflict of interest to declare.

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