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Legacy microsite effect on the survival of bitterbrush outplantings after prescribed fire: capitalizing on spatial variability to improve restoration

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Restoration of shrubs in arid and semi-arid rangelands is hampered by low success rates. Planting shrub seedlings is a method used to improve success in these rangelands; however, it is expensive and labor intensive. The efficiency of shrub restoration could be improved by identifying microsites where shrub survival is greater. Bitterbrush (*Purshia tridentata* Pursh DC) is an important shrub to wildlife that has declined because of conifer encroachment, excessive defoliation, wildfires, and low recruitment. We investigated planting bitterbrush seedlings in western juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook) encroached shrublands after prescribed fire was used to control trees. Bitterbrush seedlings were planted in under (canopy) and between (interspace) former juniper canopies at five blocks and evaluated for three growing seasons. Bitterbrush survival was greater than 50% in the former canopy, but only 5% in the interspace microsite by the third growing season. Growth of bitterbrush was also greater in the former canopy compared with the interspace, potentially due to markedly less perennial vegetation in this microsite. Exotic annual grasses and annual forbs became prevalent in the former canopy in the second and third growing season, suggesting that soil resource availability was greater in this microsite. These results suggest that restoration success will vary by specific locations within a burned landscape and that this variability can be used to improve restoration efficiency. In this situation, bitterbrush restoration can be improved by planting seedlings in former canopy compared with interspace microsites.

Key words: burning, canopy, cheatgrass, interspace, juniper, *Purshia tridentata*, seedling

Implications for Practice

- In postfire landscapes, bitterbrush seedlings should be planted in former juniper canopies compared with interspace microsites because survival was 10 times greater.
- Efforts should focus on identifying microsites where abiotic and biotic conditions increase the likelihood of successful restoration.
- Restoration efforts should capitalize on spatial variability in postburn environments to improve efficiency.
- We recommend other shrub seedlings also be planted in former canopy microsites in postfire landscapes to restore shrublands.

Introduction

The need for shrub restoration is becoming increasingly recognized in Europe (Medina-Roldán et al. 2012), Africa (Linstadter & Baumann 2013), Australia (Wong et al. 2007), North America (Davies et al. 2011), and Asia (Li et al. 2013), because many shrubs are keystone species that provide critical ecosystem services (Prevéy et al. 2010; Fonseca et al. 2012; van Zonneveld et al. 2012). Shrub restoration in arid and semi-arid rangelands is hindered by water stress, invasive species, and erosion (Porensky et al. 2014). In North America, antelope bitterbrush (*Purshia tridentata* Pursh DC) is often a priority for restoration because it serves as a keystone species that is important to wildlife. Bitterbrush is critical fall and winter browse for some wild ungulates and is also used by livestock (Kufeld et al. 1973; Vavra & Sneva 1978; Shaw & Monsen 1986), and its seeds are an important food source for rodents (Everett et al. 1978; Vander Wall 1994). Bitterbrush restoration is needed because this species has decreased due to conifer encroachment, wildfires, excessive defoliation, and limited recruitment (Billings 1952; Tueller & Tower 1979; Winward & Alderfer-Findley 1983; Miller et al. 2000). Restoration of bitterbrush, similar to other shrubs in arid and semi-arid environments, has often been unsuccessful (Hubbard 1964; Kituku et al. 1995), but exceptions exist (e.g. see Clements & Young 2002).

Critical to improving restoration efficiency is identifying and focusing efforts in areas where success is more likely. Heterogeneous postfire environments can have vastly different

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probabilities of restoration success even over relatively small spatial scales (Boyd & Davies 2012; Davies & Bates 2017). Thus, the first step is to identify locations that vary in abiotic and biotic characteristics and then evaluate restoration success between these locations. In a postfire environment, abiotic and biotic characteristics can vary between former woody plant canopy (under canopy from the trunk to the drip line) and interspace (between woody plant canopies) microsites (Davies et al. 2009; Bates & Davies 2016).

Conifers encroaching into shrublands are often controlled with fire because it is one of the most effective treatments across extensive landscapes (Miller et al. 2005; Bates et al. 2011; Davies et al. 2014). Conifer encroachment in the western United States has occurred since European settlement decreased fire frequency (Miller & Wigand 1994; Miller & Rose 1995; Gruell 1999; Weisberg et al. 2007). In the Intermountain West, western juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook) has increased from 0.3 million ha to 3.5 million ha since the mid-1800s as junipers have expanded and in-filled from historic fire-safe areas (Miller & Rose 1995; Miller et al. 2000). Western juniper encroachment is concerning because as tree cover increases keystone shrubs important to wildlife such as sagebrush (*Artemisia* L.) and bitterbrush decrease, herbaceous production and diversity can decline, and erosion and runoff potential increase (Miller et al. 2000; Bates et al. 2005; Pierson et al. 2007). Thus, there is a critical need to restore shrubs after juniper control with fire. Bitterbrush postfire restoration success, however, may differ between former juniper canopy and interspace microsites.

These two postfire microsites may have dissimilar restoration success because of abiotic and biotic differences. Former canopy microsites generally have less perennial vegetation immediately after fire than interspace microsites, in part from fire-induced mortality (Bates unpublished data; Bates & Davies 2016). This could enhance bitterbrush establishment because of reduced competition and greater resource availability. Establishment of other species has been found to be greater in former canopy microsites. For example, in burned sagebrush communities, seeded perennial grass establishment was six times greater in former sagebrush canopy compared with interspace microsites (Boyd & Davies 2010). However, exotic annual grass invasion can also be greater in former canopy than interspace microsites postfire in juniper woodlands (Bates & Davies 2016), which could negatively impact bitterbrush survival and growth. Postfire former juniper canopy microsites can also have greater nutrient availability compared with interspace microsites (Bates unpublished data; Rau et al. 2007, 2008). Similar postfire resource islands have been found in former sagebrush canopy microsites (Stubbs & Pyke 2005; Davies et al. 2009). Determining if there is spatial variability in bitterbrush survival and growth between former juniper canopy and interspace microsites would be valuable information for increasing the efficiency of restoring bitterbrush.

The purpose of this study was to evaluate survival and growth of transplanted bitterbrush seedlings in former western juniper canopy and interspace microsites after prescribed fire controlled juniper. Planting seedlings was selected because, similar to establishing other shrubs (Davies et al. 2013; McAdoo et al. 2013), it is one of the more successful methods for restoring bitterbrush (Kituku et al. 1995). Vegetation characteristics were also compared between microsites to help explain bitterbrush response. We hypothesized that in burned juniper-encroached rangeland, bitterbrush seedlings planted in former juniper canopy would have greater survival and growth compared with interspace microsites and that herbaceous vegetation cover and density would be less in former canopy compared with interspace microsites.

Methods

Study Area

Five study sites (blocks) were located on Steens Mountain approximately 80–90 km southeast of Burns, Oregon, U.S.A. All study sites were mountain shrublands encroached by western juniper prior to prescribed burning. Prior to burning, the plant communities were codominated by western juniper and shrubs, with mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) as the dominant shrub, with an understory of native perennial grasses and forbs. Idaho fescue (*Festuca idahoensis* Elmer) was the dominant perennial grass. No bitterbrush was found on the study sites, but bitterbrush was scattered across the greater study area. Bitterbrush abundance may have been low in this area from historically high, spring through fall use by sheep in the early 1900s. Heavy defoliation of bitterbrush by sheep can be detrimental to its growth and survival (Mueggler 1950; Jensen et al. 1972). Elevation of study sites was approximately 1,750 m above sea level and slopes ranged from 35 to 50%. Aspects of study sites were northeast, north, and northwest. Maximum distance between study sites was 10 km. All study sites were R023XY310OR North Slope 12–16 PZ Ecological Sites (NRCS 2016). Annual precipitation was 61, 83, and 85% of the 30-year long-term average (1981–2010) in 2013, 2014, and 2015 (PRISM 2016). Cattle were excluded the first 2 years after burning. Feral horses, native ungulates, and other wildlife occupied the study area and were not excluded from study sites.

Experimental Design and Measurements

The effect of microsite on planted bitterbrush seedlings after prescribed fire in juniper-encroached rangeland was evaluated using five 100 × 100 m blocks. In the fall of 2011, one-third of the mature juniper trees in each block were felled with chainsaws to increase surface fuels to carry a prescribed fire across experimental blocks. Blocks were burned individually in late September 2012 to control remaining western juniper. Prescribed burns were applied as head fires and mortality of western juniper and nonsprouting shrubs was 100% in each block. In each block, 12 bitterbrush seedlings (six per microsite) were planted in early March 2013 in former juniper canopy and interspace microsites. Former juniper canopy and interspace microsites were randomly selected for planting in each block. Former juniper canopy microsites were the area under the prefire drip line of the juniper tree, and interspaces were the location between former juniper canopies. Remains of juniper trees were upright for the duration of study in former juniper canopy microsites. Felled junipers, either under the former canopy or the felled tree, were not used to represent either microsite. Rebar with a metal tag was used to mark each canopy and interspace where bitterbrush was planted to aid in relocation of seedlings. Bitterbrush seedlings were 1-year-old bare root seedlings grown by Lucky Peak Nursery, Boise, Idaho, U.S.A., grown from seed collected in southwestern Idaho. Prior to planting seedlings roots were soaked for 8 hours in a solution containing soil collected from beneath bitterbrush plants to inoculate seedlings with nitrogen-fixing bacteria (*Frankia*). The solution was 480 cm^3 soil from under the bitterbrush canopy drip line from 0 to 15 cm depth mixed with 8 L of water. Seedling height averaged 20 cm at planting. Vexar mesh tubes (10 cm diameter × 41 cm height) were placed over seedlings and secured in place with a bamboo stake to discourage browsing. However, most tubes were removed, likely by feral horses, from the plants before the first sampling in July 2013 (in total four and five tubes remained in the canopy and interspace microsites, respectively). Tubes were not replaced.

Vegetation measurements were conducted in July of 2013, 2014, and 2015. Bitterbrush survival was determined by the presence of live photosynthetic tissue (leaves). Bitterbrush height, longest canopy diameter, and canopy diameter perpendicular to the longest diameter were measured on each surviving bitterbrush seedling. Vegetation characteristics were measured with 10 randomly located 0.2 m^2 quadrats in each microsite where a bitterbrush was planted in each block (10 quadrats × 6 bitterbrush seedlings × 2 microsites = 120 quadrats per block). Herbaceous cover was estimated by species to the nearest 1%. Bare ground and litter cover were also visually estimated in the 0.2 m^2 quadrats. Herbaceous density by species was measured by counting all plants rooted in the 0.2 m^2 quadrats. Shrubs, with the exception of planted bitterbrush, were not present after fire in treatment blocks.

Statistical Analyses

Repeated measures of analysis of variances (ANOVAs) using a mixed model in SAS 9.2 (SAS Institute, Inc., Cary, North Carolina, U.S.A.) was used to determine microsite effects on bitterbrush survival and plant community 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 the models. The appropriate covariance structure was selected using Akaike's Information Criterion (Littell et al. 1996). Using this criterion, compound symmetry covariance structure was selected for most models, except autoregressive covariance structure was selected for models for exotic annual grass cover, annual forb density, and total herbaceous density. Herbaceous vegetation was partitioned into five functional groups for analyses: Sandberg bluegrass (*Poa secunda* J. Presl), large perennial grasses, perennial forbs, exotic annual grasses, and annual forbs. The exotic annual grass functional group was largely comprised of cheatgrass (*Bromus tectorum* L.). The large perennial grass group was predominately Idaho fescue with some bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), squirreltail (*Elymus elymoides* [Raf.] Swezey), and prairie Junegrass (*Koeleria macrantha* [Ledeb.] Schult). The perennial and annual forb groups were solely and largely comprised of natives, respectively. Total herbaceous vegetation was determined by summing the five functional groups. Bitterbrush size was compared between the treatments in 2013 with an ANOVA using a mixed model in SAS 9.2 (PROC MIXED, SAS Institute, Inc.). Bitterbrush size was not compared between treatments in subsequent years because mortality was so high in interspaces that most were devoid of bitterbrush. Treatment means were considered different at $\alpha = 0.05$ and reported with standard errors (SE).

Results

Bitterbrush survival was greater in the former canopy than the interspace microsite (Fig. 1; $F_{[1,4]} = 29.16$, $p = 0.006$). By the third growing season after planting, bitterbrush survival was 10-fold greater in the canopy compared with the interspace. The percent of bitterbrush seedlings surviving decreased over time ($F_{[2,16]} = 16.32$, $p = 0.001$); however, the decrease between the second and third growing season was only 2% of the total planted seedlings. Bitterbrush seedlings were larger in the former canopy than interspace microsites (Fig. 2). Seedlings were 1.3-fold taller in the former canopy compared with the interspace ($F_{[1,4]} = 8.62$, $p = 0.043$). The longest bitterbrush canopy diameter and the diameter perpendicular to the longest diameter were 2-fold greater in the canopy compared with the interspace ($F_{[1,4]} = 52.63$ and 40.77, $p = 0.002$ and 0.003, respectively). By the third growing season after planting, some seedlings in the canopy microsite were up to 50 cm tall and had canopy diameters exceeding 45 cm.

Sandberg bluegrass cover was greater in the interspace compared with the former canopy microsite (Fig. 3A; $F_{1,4} = 47.97$, $p = 0.002$). Large perennial grass cover varied by the interaction between treatment (microsite) and year (Fig. 3B; $F_{[2,16]} = 5.40$, $p = 0.016$). In the first two growing seasons perennial grass cover was 7-fold greater in the interspace compared with the former canopy, but by the third growing season, cover values had started to converge. Perennial forb cover was greater in the interspace than the former canopy (Fig. 3C; $F_{[1,4]} = 61.77$, $p = 0.001$) and varied by year ($F_{[2,16]} = 17.85$, $p < 0.001$). There was a significant treatment-by-year interaction effect for annual forb cover (Fig. 3D; $F_{[2,16]} = 9.13$, $p = 0.002$). Annual forb cover was greater in the former canopy than interspace, but the magnitude of difference was much greater in second growing season than either the first or third growing season. Exotic annual grass cover was greater in the former canopy compared with the interspace microsite (Fig. 3E; $F_{[1,5.19]} = 6.60$, $p = 0.048$). By the third growing season, exotic annual grass cover was more than 3-fold greater in the former canopy compared with the interspace. Exotic annual grass cover generally increased over time ($F_{[2,14.1]} = 9.08$ $p = 0.003$). Total herbaceous cover varied by the interaction between treatment and year (Fig. 3F; $F_{[2,16]} = 3.76$, $p = 0.046$). Total herbaceous cover was greater in the interspace

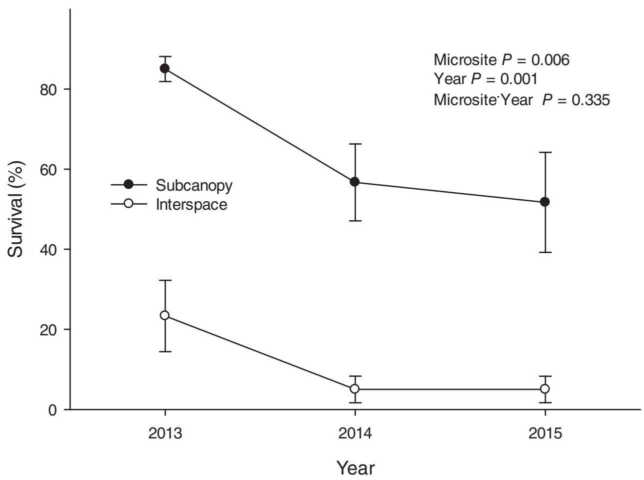

Figure 1. Survival of planted bitterbrush seedlings (mean ± SE) in former juniper canopy and interspace microsite locations.

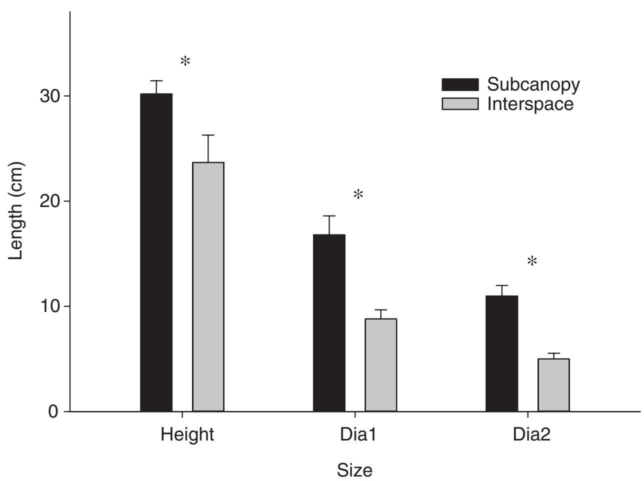

Figure 2. Height, longest diameter (Dia1), and diameter perpendicular to longest diameter (Dia2) of bitterbrush seedlings (mean + SE) planted in former juniper scanopy and interspace microsite locations in the first growing season (2013). Asterisks (*) indicates significant difference ($p < 0.05$) between microsites.

than former canopy in the first growing season, but in the second and third growing seasons, it was greater in the former canopy. Subsequently, bare ground was inverse to this pattern (Fig. 3G; $F_{[2,16]} = 31.26$, $p < 0.001$) with it being greater in the former canopy in the first growing season and then greater in the interspace in the second and third growing seasons. Litter also varied by the interaction between treatment and year (Fig. 3H; $F_{[2,16]} = 9.62$, $p = 0.002$). Litter was greater in the interspace microsite the first year, but by the third year, it was greater in the former canopy microsite.

Densities of Sandberg bluegrass and large perennial grasses were greater in the interspace than the former canopy (Fig. 4A & 4B; $F_{[1,4]} = 33.60$ and 32.85, $p = 0.004$ and 0.005, respectively), and they increased over time ($F_{[2,16]} = 4.41$ and 3.69, $p = 0.030$ and 0.048, respectively). Sandberg bluegrass density was ≥ 18-fold greater in the interspace compared with the former canopy in every growing season. Large perennial grass density was initially 5- to 8-fold greater in the interspace compared with the former canopy, but by the third growing season, perennial grass density in the interspace was only 2-fold greater than the former canopy. Perennial forb density was 2.6- to 3.7-fold greater in the interspace compared with the former canopy (Fig. 4C; $F_{[1,4]} = 26.70$, $p = 0.007$) and increased over time ($F_{[2,16]} = 4.55$, $p = 0.027$). Annual forb density varied by the interaction between treatment and year (Fig. 4D; $F_{[2,9.86]} = 12.04$, $p = 0.002$). In the first growing season, annual forb density was greater in the interspace, but in the second and third growing seasons, it was greater in the former canopy. Exotic annual grass density was greater in the former canopy than the interspace (Fig. 4E; $F_{[1,4]} = 7.97$, $p = 0.048$) and increased with time ($F_{[2,16]} = 12.12$, $p < 0.001$). Exotic annual grass density was initially low (less than 6 individuals/m^2) in both locations, but by the third growing season, density was >800 individuals/m^2 in the former canopy and >200 individuals/m^2 in the interspace. Total herbaceous density varied by the interaction between treatment and year (Fig. 4F; $F_{[2,14.8]} = 4.73$, $p = 0.026$). In the first growing season, total herbaceous density was greater in the interspace; however, because of increasing annuals, it was greater in the former canopy the second and third growing seasons.

Discussion

Our results suggest that capitalizing on spatial variability in restoration success could be used to improve restoration efficiency. In postfire environments, shrub restoration in former woody vegetation canopy microsites compared with interspace microsites may be more likely to be successful. In our current study, bitterbrush seedlings planted in former canopy microsites had greater than 50% survival after three growing seasons; in contrast, survival in interspace microsites was only 5%. Similarly, seeded perennial grasses had greater survival in former sagebrush canopy compared with interspace microsites after fire (Boyd & Davies 2010). Our results confirm that postfire microsites created by woody vegetation can be a favorable environment for seedling survival. The high survival of bitterbrush in the former canopy occurred despite a drought (61% of long-term average) in the first year and below average precipitation the next 2 years.

Survival of bitterbrush seedlings was probably related to differences in vegetation in former canopy and interspace microsites after fire. Abundance of Sandberg bluegrass, large perennial grasses, and perennial forbs were less in former canopy compared with interspace microsites. In agreement with our results, fall burned former juniper canopy microsites had less perennial vegetation than interspace microsites on similar sites in Oregon (Bates & Davies 2016). The greater vegetation in the interspace likely contributed to increased mortality of planted bitterbrush seedlings through competition for limiting soil resources; most likely water since a drought occurred in the planting year and was followed by two below-average

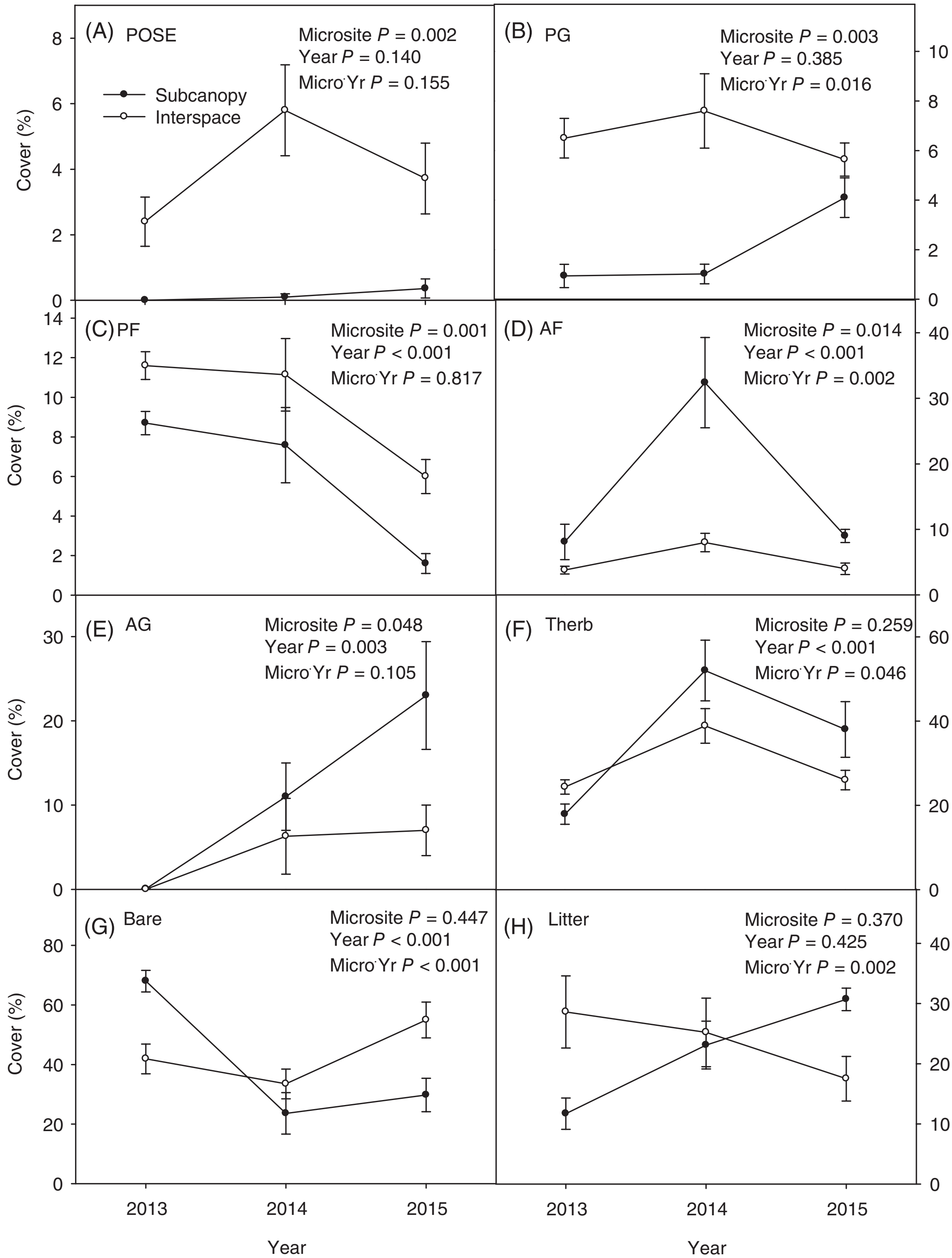

Figure 3. Herbaceous functional and cover group cover (mean ± SE) of former juniper canopy and interspace microsite locations. Micro·Yr = interaction between microsite and year. (A) POSE = Sandberg bluegrass, (B) PG = large perennial grasses, (C) PF = perennial forbs, (D) AG = annual grasses, (E) AF = annual forbs, (F) Therb = total herbaceous, (G) Bare = bare ground, and (H) Litter = ground litter. Note scales are different between left and right panels.

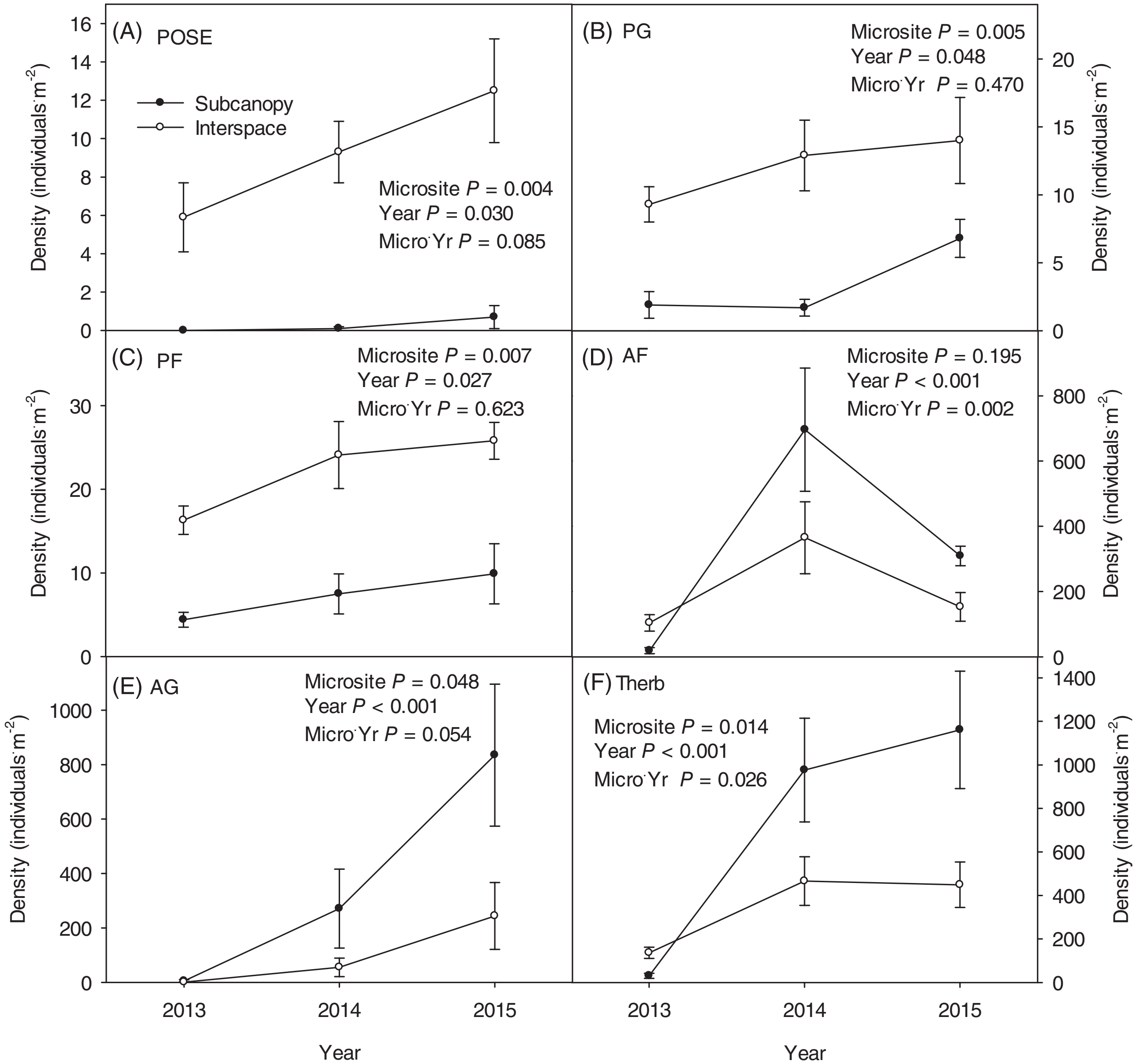

Figure 4. Herbaceous functional group density (mean ± SE) of former juniper canopy and interspace microsite locations. Micro·Yr = interaction between microsite and year. (A) POSE = Sandberg bluegrass, (B) PG = large perennial grasses, (C) PF = perennial forbs, (D) AG = annual grasses, (E) AF = annual forbs, and (F) Therb = total herbaceous. Note scales are different between left and right panels.

precipitation years. In support of this postulation, mortality of bitterbrush seedlings increased with greater competition from herbaceous vegetation (Hubbard 1957). Competition from herbaceous species has also limited other shrub species recovery (Porensky et al. 2014; Rinella et al. 2015).

Most of the mortality of planted bitterbrush occurred prior to sampling in the second growing season, suggesting that bitterbrush that survived the first year were likely to persist. Survival in the former juniper canopy microsite remained high even with increases in herbaceous vegetation. Most critical was that large increases in exotic annual grasses and annual forbs after the first year did not cause substantial mortality. This is important because small bitterbrush seedlings can be sensitive to competition from weeds and grasses (Shaw & Monsen 1986). Similar to our results, a study in south-central Oregon found survival of planted bitterbrush seedlings at the end of the first growing season was a good indicator of subsequent survival (Johnson & Okula 2006). Other shrub species have also been reported to have high mortality in the first year. For example, mortality of planted sagebrush seedlings was also greatest in the first year after planting (Davies et al. 2013). Herbaceous vegetation and small shrub seedlings overlap in resource niche occupation; however, established shrubs and competitive herbaceous vegetation can coexist because of high niche differentiation (Gunnell et al. 2010). Bitterbrush can also, over time, develop nitrogen-fixing nodules (Dalton & Zobel 1977), likely further niche differentiating from herbaceous vegetation. Our results suggest the effect of competition from herbaceous vegetation on bitterbrush survival may decrease as bitterbrush becomes more established.

Similar to survival, bitterbrush growth was greater in the former canopy compared with the interspace in the first growing season. Greater growth in the former canopy the first growing season after fire was likely a result of less competition and elevated soil nutrient concentrations. In our study, perennial herbaceous vegetation and total herbaceous cover was less in the former canopy compared with the interspace microsite the first growing season after fire. The burned canopy microsites also are likely to have greater soil nutrient concentrations because of resource islands created under juniper canopies. Juniper and other woody vegetation are well known to create resource islands under their canopies in arid and semi-arid rangelands (Doescher et al. 1987; Jackson & Caldwell 1993; Schlesinger et al. 1996; Davies et al. 2007). These resource islands persist after woody vegetation is removed by fire (Bates unpublished data; Stubbs & Pyke 2005; Rau et al. 2007, 2008; Davies et al. 2009) and likely favor bitterbrush growth in the first growing season. In our study, growth in subsequent growing seasons could not be compared between microsites because of the near complete mortality of bitterbrush in the interspaces. The increase in annuals and subsequently total herbaceous vegetation in the second and third year in the former canopy may have also mediated any microsite effect on bitterbrush growth.

The need to restore shrubs to conserve wildlife habitat and provide ecosystem services is critically needed in many ecosystems globally (Wong et al. 2007; Davies et al. 2011; Medina-Roldán et al. 2012; Li et al. 2013; Linstadter & Baumann 2013). However, shrub restoration in arid and semi-arid environments can be challenging with high rates of failure (Lysne & Pellant 2004; Knutson et al. 2014; Porensky et al. 2014). We suggest that spatial variability in abiotic and biotic characteristics can be exploited to improve restoration success; in the current study, planting bitterbrush seedlings in former juniper canopy microsites greatly improved the establishment of bitterbrush. Determining favorable microsites for other high priority species may similarly improve restoration success and decrease the cost per successfully established plant.

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