RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Influence of shrub-induced microhabitats and biocrusts on native bunchgrass seedling establishment and growth

Kirk W. Davies[1,2], Jon D. Bates[1], Lauren N. Svejcar[1]

Abstract

Introduction: Establishment of native vegetation from seed is important to the persistence and restoration of many native plant communities. Seedling establishment and growth likely vary within a plant community and may be influenced by microhabitats and biological soil crusts (biocrusts).

Objectives: Understanding the effects of biocrusts and microhabitats on seedling establishment and growth is critical for prioritizing restoration as well as guiding management and restoration efforts.

Methods: We investigated the effects of biocrusts and microhabitats created by sagebrush in sagebrush-bunchgrass plant communities on seedling establishment and growth of two native bunchgrasses, bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) and bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey).

Results: Biocrusts limited the establishment of native bunchgrasses from seed, but did not appear to restrict the growth of established plants. This suggests that biocrusts are likely a physical barrier to establishment from seed. Under sagebrush canopies increased native bunchgrass establishment 400 to 900% compared to microhabitats between sagebrush canopies (interspaces). Seedling heights were generally greater under sagebrush canopies compared to interspaces. The north side of under sagebrush canopies favored the establishment and growth of bottlebrush squirreltail compared to south sides, but bluebunch wheatgrass appeared not to be influenced by directional side.

Conclusions: Biocrusts and microhabitats created by sagebrush substantially influence the establishment of native bunchgrass from seed and likely the spatial arrangement of vegetation in these communities. Species-specific response to directional side under sagebrush canopies suggests sagebrush promotes diversity.

Implications for Practice: Sagebrush is clearly important in these communities as it promotes diversity and creates favorable microhabitats for seedling establishment and growth. These benefits also highlight the importance of maintaining and restoring sagebrush in these communities. Though biocrusts provide important ecosystem services, biocrusts may inhibit native bunchgrass establishment, suggesting broadcast-seeding efforts should prioritize areas with low biocrust cover. Sagebrush-induced microhabitats and biocrusts have ramifications for the persistence and restoration of bunchgrasses and likely other herbaceous vegetation in sagebrush plant communities. Land management and restoration planning and prioritization likely should consider the effects of biocrusts and sagebrush microhabitats on bunchgrass seedling establishment and growth.

Key words: biological soil crusts, bluebunch wheatgrass, bottlebrush squirreltail, restoration, sagebrush

Introduction

Establishment of native perennial vegetation from seed is essential to the persistence and restoration of many native plant communities and the goods and services they provide society. With widespread degradation of drylands, the need for seed-based restoration is increasing around the globe (Abhilash 2021). In drylands, establishment of native perennial species from seed is rarely successful (Shackelford et al. 2021; Svejcar et al. 2023a). Establishment from seed varies across landscapes, but also likely varies within an individual plant community (Boyd & Davies 2012a, 2012b; Davies et al. 2022a). Determining where perennial vegetation is more likely to establish from seed and understanding how different factors influence establishment and growth within a plant community would be valuable for promoting the persistence and potentially improving the restoration of native plant communities.

Native sagebrush (*Artemisia* L.)-bunchgrass plant communities are a conservation and management priority in the western United States (Davies et al. 2011). Sagebrush plant communities are being lost at a rate of more than half a million hectares (1.3 million acres) annually (Doherty et al. 2022). The majority

Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA or the authors and does not imply its approval to the exclusion of other products.

Author contributions: KWD, JDB, LNS designed and executed the study; KWD analyzed the data and wrote and edited the manuscript; JDB, LNS edited the manuscript.

[1]US Department of Agriculture - Agricultural Research Service, 67826-A Highway 205, Burns 97720, OR, U.S.A.
[2]Address correspondence to K. W. Davies, email kirk.davies@usda.gov

Published 2025. This article is a U.S. Government work and is in the public domain in the USA. Restoration Ecology published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
doi: 10.1111/rec.70222

of the loss of sagebrush communities is attributed to invasive annual grasses (Davies et al. 2021; Doherty et al. 2022). Restoring perennial vegetation, especially bunchgrasses, can substantially limit invasive annual grasses (Davies & Johnson 2017; Davies et al. 2019). Perennial bunchgrasses are the most important plant functional group for providing resilience to disturbances in these communities and resistance to annual grass invasion because they are the most abundant herbaceous plant group and their resource acquisition patterns overlap greatly with annual grasses (Chambers et al. 2007; James et al. 2008; Davies et al. 2021). Hence, it is important to understand the influence of different factors on bunchgrass establishment and growth from seed within a plant community.

Within a sagebrush plant community, sagebrush createsunique microhabitats under sagebrush canopies compared to between sagebrush canopies (interspaces). Under sagebrush canopies are expected to be more conducive to plant growth because of moderated temperature extremes and greater soil nutrient concentrations, soil organic matter, and water availability (Doescher et al. 1984; Chambers 2001; Davies et al. 2007). This suggests that under sagebrush canopies may provide ideal microhabitats for bunchgrass seedling establishment and growth. However, competition may limit seedling establishment and growth in canopy microhabitats as herbaceous vegetation cover and density are greater in these microhabitats compared to interspaces (Davies et al. 2007, 2022b, 2023). Directional side (i.e., north vs. south) of sagebrush canopies also results in different microhabitat characteristics that shape vegetation community characteristics (Davies et al. 2023) and likely could affect establishment and growth of seedlings. Though sagebrush-induced microhabitats could influence seedling establishment and growth, the effect likely varies by precipitation and site characteristics such as soil (Swanson et al. 2021).

Prior research on the effects of sagebrush-induced microhabitats on seedlings was inconclusive. Interspace locations midway between the sagebrush dripline and the maximum distance between sagebrush canopies were more favorable for the survival of transplanted forbs than under canopies (Koutzoukis et al. 2023). In contrast, the survival of transplanted perennial bunchgrasses appeared not to be influenced by microhabitats (Koutzoukis et al. 2023). Establishment from seed is very different from transplants as using transplants bypasses the most limiting growth stages to survival (James et al. 2011; Davies et al. 2020), thus investigations with seeding are warranted. After fire has removed sagebrush, the former under canopy locations were ideal for establishment and growth of perennial vegetation from seed (Boyd & Davies 2010, 2012a, 2012b). Microhabitat characteristics, including competition, however, were altered with the removal of sagebrush with fire (Davies et al. 2009). Hence, investigations of the effects of undisturbed (i.e., not burned) microhabitats created by sagebrush on native bunchgrass seedling establishment and growth are needed.

Biological soil crusts (biocrusts) comprised of cyanobacteria, lichens, fungi, and mosses convey many benefits in arid and semi-arid ecosystems. Biocrusts can facilitate or inhibit plant species performance depending on ecological setting, biocrust composition, and plant species (Condon & Pyke 2018; Havrilla et al. 2019). Biocrusts are known to limit invasive annual grasses in the western United States (Deines et al. 2007; Hernandez & Sandquist 2011); however, this indicates that they could also impede the establishment of native bunchgrasses. In support of this, biocrusts inhibited perennial species in a study in Germany (Langhans et al. 2009), China (Song et al. 2017), and Argentina (Funk et al. 2014). Soil amended with biological soil crust materials, in contrast, increased native bunchgrass biomass in a study in the western United States (Pendleton et al. 2003). Many of these prior studies were conducted in the laboratory; thus, their findings also need to be evaluated in the field. Understanding the effects of biocrusts on native bunchgrass seedling establishment and growth in the field is needed to allow land managers and restoration practitioners to make informed management decisions and prioritize areas for restoration.

The objective of this study was to investigate the effects of microhabitats and biocrusts on the establishment and growth of native bunchgrasses from seed. We initiated the first step in determining the effects of microhabitats and biocrusts on bunchgrass seedlings with this study conducted in one area of the heterogeneous sagebrush ecosystem. We hypothesized that: (1) biocrusts limit the establishment and growth of seeded bunchgrasses because biocrusts have limited other perennials (Langhans et al. 2009; Funk et al. 2014; Song et al. 2017), (2) that under sagebrush canopies compared to interspaces between canopies would be more conducive to bunchgrass seedling establishment and growth because canopy microsites are often favorable environments for plant growth (Doescher et al. 1984; Chambers 2001; Davies et al. 2007), and (3) that bunchgrass seedling establishment and growth would be greater under the north compared to the south side of the sagebrush canopy because the north side microhabitat is likely more favorable for perennial vegetation (Davies et al. 2023).

Methods

Study Area

The study was conducted in four Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh)—bunchgrass steppe sites in southeastern Oregon south of Riley, OR (43°32′29″N, 119°30′17″W) and southwest of Burns, OR (43°34′50″N 119°03′42″W). The vegetation overstory was dominated by Wyoming big sagebrush. Common perennial bunchgrasses included bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), and Sandberg bluegrass (*Poa secunda* J. Presl). The non-native annual grass, cheatgrass (*Bromus tectorum* L.), was present in low abundance across the study sites. Common perennial forbs included *Phlox longifolia* Nutt., *Erigeron* L. spp., *Eriogonum* Michx. spp., and *Lomatium* Raf. spp. Biocrusts were largely comprised of mosses and lichens. Biocrust cover in the interspaces between sagebrush canopies was low, patchy, and contained very little moss. In contrast, biocrust cover under sagebrush canopies

was generally >20% and contained high amounts of moss. Climate is characteristic of the northern Great Basin with hot, dry summers and cool, wet winters. Long-term (30 years) average annual precipitation ranged from 235 to 237 mm (PRISM 2025). Annual precipitation ranged from 282 to 286 mm and 326 to 343 mm in 2023 and 2024, respectively (PRISM 2025). Elevation at the study sites ranged from 1,291 to 1,362 m. All the study sites were relatively flat (<2% slope). Soils were well-drained, very cobbly loams and clay loams, and were moderately deep with soil depth to bedrock between 60 and 110 cm. Livestock grazing was excluded from the study sites since 2009 using barbwire fencing. Prior to livestock exclusion in 2009, the area was moderately grazed by cattle (40–50% utilization) with a rest-deferred rotation for more than half a century. Between the late 1800s and early 1900s, the area was likely heavily grazed (>60% utilization) by sheep, horses, and cattle (Copeland et al. 2021).

Experimental Design and Measurements

We used a block design with four blocks (sites) to investigate the influence of microhabitats and biocrusts on seedling establishment and growth from seeds. Blocks were separated by up to 12 km. In each block, we applied each treatment 20 times and half were seeded with squirreltail and the other half were seeded with bluebunch wheatgrass. Treatments were: no biocrust removal in the interspace between sagebrush canopies, no removal of biocrusts under the north side of the sagebrush canopy, biocrusts removed north side under canopy, and biocrusts removed south side under canopy. A complete factorial design could not be used because the study would have been too large to keep within a site with similar characteristics, and the cover of biocrust in the interspaces was quite patchy, which would have made it difficult to find representative and repeatable locations for biocrust treatments. Under canopy locations were located 10–20 cm from the stem of the sagebrush and fully under the sagebrush canopy. Interspace locations were ≥50 cm from the nearest sagebrush canopy. Biocrusts were removed by gently scraping them off the soil surface with a soil knife. A minimal amount of soil (<1 cm) was removed with biocrust removal. Treatments were applied to a 10 × 20 cm area and then seeded with 20 seeds in late-September 2023. Seeds were locally collected from within 20 km of the study sites. While removing biocrusts confounds the effects of the disturbance with the effects of biocrusts, other options to eliminate the influence of biocrust, such as trampling (Hernandez & Sandquist 2011), have similar issues or are unlikely to be relevant to restoration scenarios, such as biocrust sterilized or fumigation. Seeds were gently pushed into the surface material (either soil or biocrust) to prevent movement after seeding. Landscaping nails and GPS coordinates were used to mark treatment plots.

In late June of 2024, seedling density, height, and number of leaves per seedling were measured in all treatment plots. Seedling density was determined by counting all seedlings rooted in each 10 × 20 cm treatment plot. Seedlings were considered established if they survived until late June. Height and number of leaves per seedling were measured on all seedlings in each treatment plot.

Statistical Analyses

We analyzed seedling density, seedling height, and number of leaves per seedling data using mixed model ANOVAs (SAS version 9.4). We analyzed the response of squirreltail and bluebunch wheatgrass individually because bunchgrass species can respond differently to microhabitats (Davies et al. 2007). Data from the ten 10 × 20 cm plots for each treatment for each bunchgrass species in a block were summed together and considered one replication (i.e., one treatment replication per species per block). For hypothesis 1, biocrust effects on seedlings were investigated by comparing no removal of biocrusts and biocrusts removed on the north side under sagebrush canopy microhabitat. Treatment was no removal or biocrusts removed. For hypothesis 2, the effects on seedlings of being under the sagebrush canopy (north side) were compared to being in the interspace between canopies in microhabitats without biocrust removal. Microhabitat was considered the treatment in these analyses. For hypothesis 3, the effect of the directional side of sagebrush canopy was investigated by comparing biocrusts removed on the north and south sides under canopy treatments. The directional side of the sagebrush canopy was considered the treatment in these analyses. The explanatory variables in the mixed models were treatment, block, and block by treatment interaction. Treatment was considered a fixed variable in all analyses. Separate models were run for each hypothesis. Block and block by treatment interaction were treated as random variables in the models. When assumptions of ANOVAs were violated, data were either log or square-root transformed to better meet assumptions. When comparing areas with and without biocrust removal, bottlebrush squirreltail and bluebunch wheatgrass heights did not meet assumptions of normality; therefore, squirreltail height was log transformed and bluebunch wheatgrass was square-root transformed prior to analyses. When comparing the directional side of sagebrush effects, both perennial bunchgrasses' seedling densities did not meet assumptions of normality; thus, they were log transformed. Non-transformed (original) data are presented in figures and text. Treatment means were considered different at $p < 0.05$ and likely different at $p < 0.10$ and reported with standard errors.

Results

Biocrusts impeded the establishment of bottlebrush squirreltail ($F_{[1,3]} = 12.78$, $p = 0.037$) and likely impeded the establishment of bluebunch wheatgrass seedlings ($F_{[1,3]} = 5.70$, $p = 0.097$) from seed (Fig. 1). Density of squirreltail and bluebunch wheatgrass seedlings was 2.0- and 1.6-fold greater in areas where biocrusts had been removed, respectively. We did not find evidence that biocrusts influenced the growth of seedlings as the height of squirreltail and bluebunch wheatgrass seedlings did not differ between no biocrust removal areas and areas with biocrusts removed (Fig. 1; $F_{[1,3]} = 2.65$, $p = 0.202$ and $F_{[1,3]} = 0.37$, $p = 0.584$, respectively). The number of

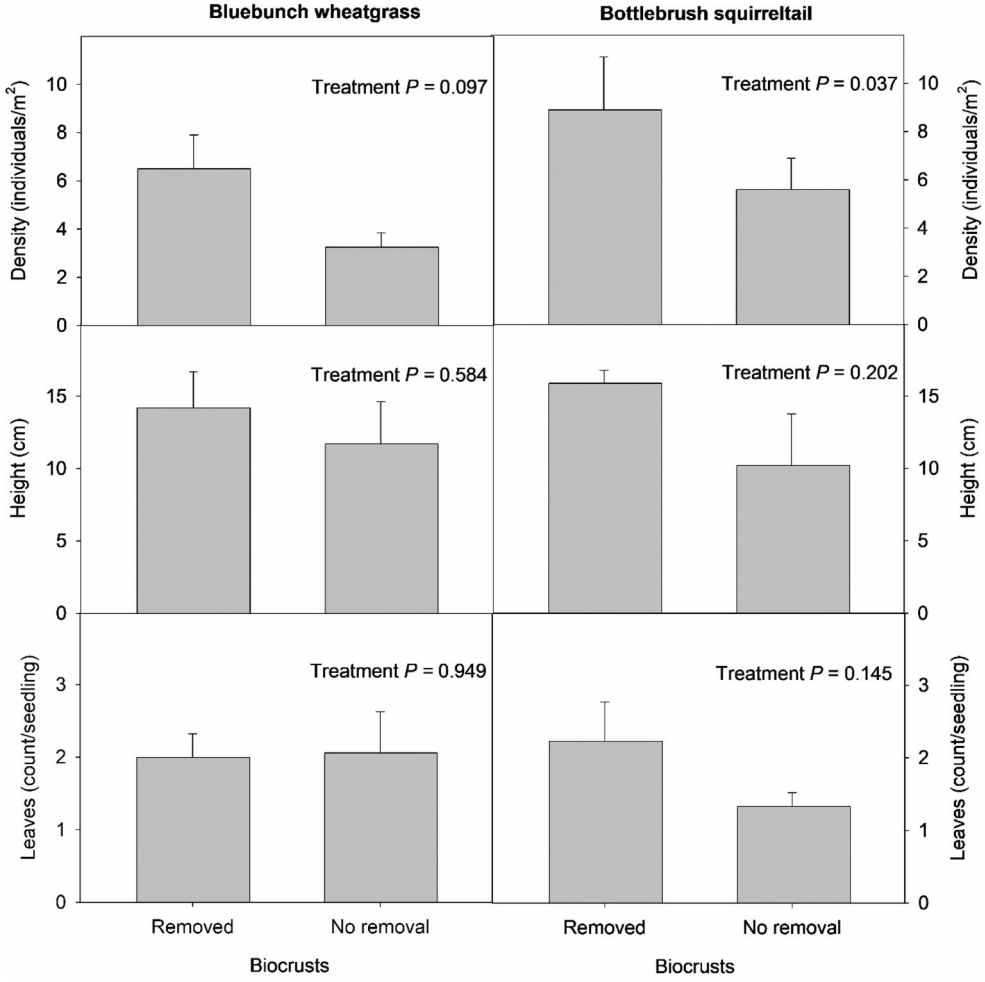


Figure 1. Seedling density, seedling height, and number of leaves per seedling (mean + SE) of bluebunch wheatgrass and bottlebrush squirreltail seeded in areas with no biological soil crusts (biocrusts) removal and biocrusts removed under the north side of sagebrush canopies.

leaves per seedling of squirreltail and bluebunch wheatgrass was also similar between biocrusts removed and no biocrust removed areas (Fig. 1; $F_{[1,3]} = 3.83$, $p = 0.145$ and $F_{[1,3]} = 0.00$, $p = 0.949$, respectively).

Microhabitat (canopy and interspace) influenced bluebunch wheatgrass and squirreltail seedling establishment (Fig. 2; $F_{[1,3]} = 22.42$, $p = 0.018$ and $F_{[1,3]} = 16.22$, $p = 0.028$, respectively). Squirreltail and bluebunch wheatgrass seedling establishment were 9.0- and 4.0-fold greater under sagebrush canopies than in interspaces, respectively. Squirreltail seeding height was 2.8-fold greater in canopy compared to interspace microsites (Fig. 2; $F_{[1,3]} = 27.52$, $p = 0.014$). Though the average height of bluebunch wheatgrass seedlings was 1.9-fold greater in canopy compared to interspace microsites, we did not find evidence that seedling height differed between microhabitats (Fig. 2; $F_{[1,3]} = 3.37$, $p = 0.164$). Leaves per squirreltail seedling were 2.3-fold greater in interspace compared to canopy microsites (Fig. 2; $F_{[1,3]} = 22.98$, $p = 0.018$). We did not find evidence that the number of leaves per bluebunch wheatgrass seedling differed between microsites (Fig. 2; $F_{[1,3]} = 3.67$, $p = 0.151$).

Directional side of the sagebrush canopy did not influence bluebunch wheatgrass seedling densities (Fig. 3; $F_{[1,3]} = 0.00$, $p = 0.974$). In contrast, the density of squirreltail seedlings was 3.1-fold greater under the north side compared to the south side of the canopy (Fig. 3; $F_{[1,3]} = 10.36$, $p = 0.049$). Seedling height of bluebunch wheatgrass did not differ between the north and south sides (Fig. 3; $F_{[1,3]} = 0.08$, $p = 0.797$). Similar to seedling density, squirreltail seedling height was 2.7-fold greater under the north side compared to the south side of the canopy (Fig. 3; $F_{1,3} = 23.97$, $p = 0.016$). The number of leaves on bluebunch wheatgrass and squirreltail seedlings did not differ between the north and south sides of the canopy (Fig. 3; $F_{[1,3]} = 0.53$, $p = 0.518$ and $F_{[1,3]} = 0.01$, $p = 0.913$, respectively).

Discussion

The response to microhabitats varied by bunchgrass species, suggesting that microhabitats likely contribute to plant community diversity and the development of heterogeneous patterns of vegetation cover and density, which has been measured within

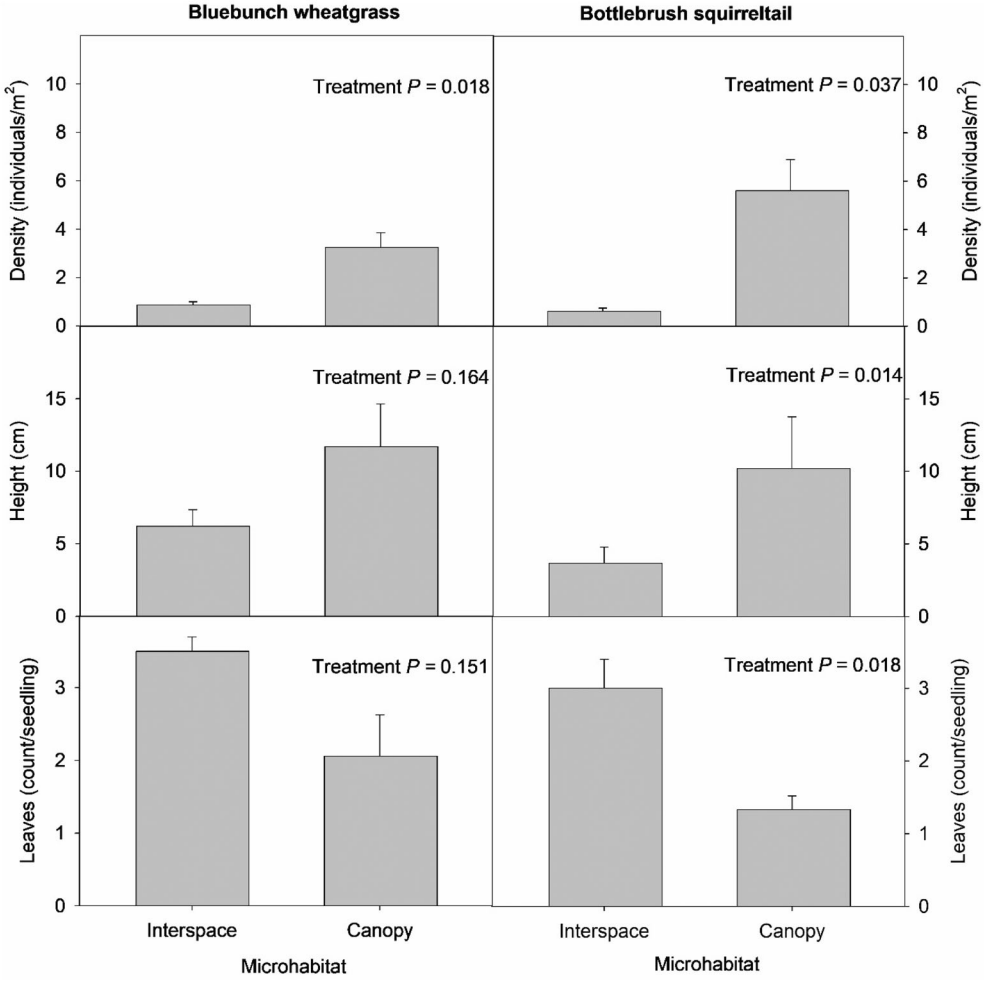


Figure 2. Seedling density, seedling height, and number of leaves per seedling (mean + SE) of bluebunch wheatgrass and bottlebrush squirreltail seeded in under sagebrush canopies (canopy) and between sagebrush canopies (interspace) microhabitats with no biocrusts removal.

sagebrush-bunchgrass plant communities (e.g., Charley & West 1977; Davies et al. 2007, 2023). Biocrusts also influenced bunchgrass establishment from seed, which probably also affected the spatial patterns of vegetation in sagebrush communities. Our study was limited because it was only conducted in one year and one area of the sagebrush ecosystem; thus, effects may vary with different years and site characteristics. Understanding the effects of microhabitats and biocrusts on herbaceous vegetation is needed for effective land management and restoration.

Biocrusts appear to be a barrier to the establishment of native bunchgrasses in Wyoming big sagebrush plant communities. However, our study is limited to one area and a single year and thus, biocrusts may influence bunchgrasses differently in other years or sites. Biocrust effects on plants vary by biocrust composition, ecological context, and plant traits (Condon & Pyke 2018; Havrilla et al. 2019). In our study, bottlebrush squirreltail and bluebunch wheatgrass seedling establishment was greater when biocrusts were removed. Biocrusts likely impede establishment because they act as a physical barrier to seedling root penetration into the soil. In a common garden study, seedlings often appeared in cracks in biocrusts, which would allow seedlings to bypass the physical barrier imposed by biocrusts (Langhans et al. 2009). Once seedling roots penetrated through the biocrusts, there appeared to not be any negative effects as seedlings were of similar size with and without biocrust removal. The lack of an effect of biocrusts on seedling growth further supports that the negative effects of biocrusts on seedling establishment were likely the result of them acting as a physical barrier.

Biocrusts likely influence natural recruitment as well as recruitment from broadcast seeding efforts. Biocrusts may limit recruitment from seed rain since they act as a barrier between the seed and soil, thus expectations of natural recovery of bunchgrasses should be tempered in areas with high biocrust cover. In areas with high biocrust cover, there is likely a tradeoff with perennial herbaceous vegetation. This is probably similar to the negative relationship between invasive annual grasses and biocrusts (Deines et al. 2007; Hernandez & Sandquist 2011; Peterson 2013). Our conclusion that biocrusts may limit

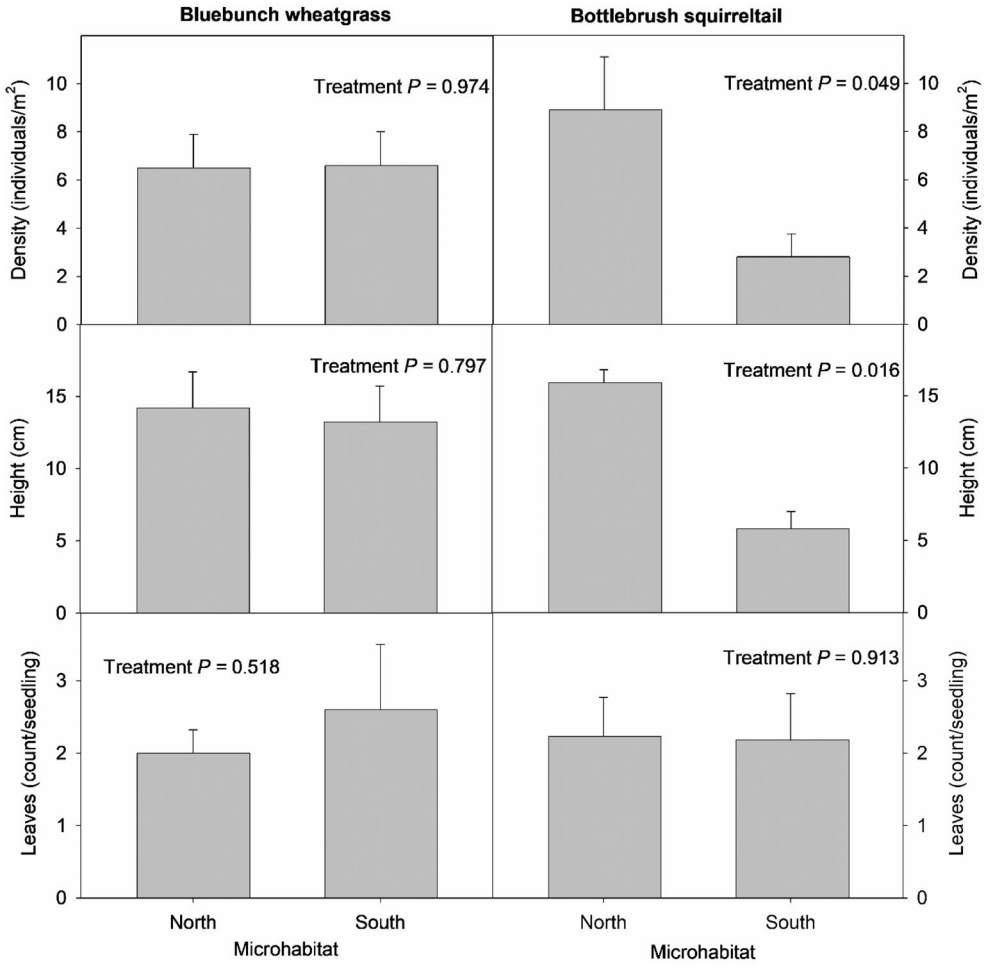


Figure 3. Seedling density, seedling height, and number of leaves per seedling (mean + SE) of bluebunch wheatgrass and bottlebrush squirreltail seeded under the north side and south side of sagebrush canopies with biocrusts removed.

bunchgrass recruitment would seem to be contradicting findings from an observational study from the Great Basin where there was a correlation between greater biocrust cover, especially moss cover, and greater native bunchgrass cover (Condon & Pyke 2018). Differences between our study and Condon and Pyke (2018) may have been from our experimental study being limited to a few sites in the northern Great Basin and examining two bunchgrass species, while Condon and Pyke (2018) observational study was across the Great Basin and examined perennial grasses as a single group. Clearly, relationships between perennial grasses and biocrusts are more complicated than just the direct effects of biocrusts on recruitment from seed. Restoration success using broadcast seeding may also be limited in areas with high biocrust cover because seeds would likely be distributed on top of biocrusts. The benefit of having high biocrust cover to limit invasive annual grasses (Deines et al. 2007; Hernandez & Sandquist 2011; Peterson 2013) probably offsets the need for immediate restoration. Already low success with broadcast seeding in Wyoming big sagebrush communities (Svejcar et al. 2023b) further suggests broadcast seeding may not be an effective restoration strategy in areas with high biocrust cover. Therefore, it may be advantageous to prioritize restoration of areas with low biocrust cover when using broadcast seeding.

Establishment and growth of bunchgrass seedlings from seed were generally influenced by microhabitat (canopy vs. interspace). The canopy microhabitat was more favorable for the establishment of bluebunch wheatgrass and bottlebrush squirreltail than the interspace microhabitat. Partially in agreement with our results, squirreltail, but not bluebunch wheatgrass, abundance was greater in the canopy compared to the interspace in intact Wyoming big sagebrush communities (Davies et al. 2007). Competition, particularly with other grasses, in the canopy microhabitat may be the reason why, even though bluebunch wheatgrass had high establishment from seed in our study, Davies et al. (2007) did not find bluebunch wheatgrass to be more abundant in canopy microhabitats. The influence of the canopy microhabitat on seedling growth was less clear. Squirreltail seedlings were taller but had fewer leaves per seedling in the canopy compared to the interspace microhabitat. This pattern was similar for bluebunch wheatgrass seedling

height and leaves per seedling. Though the effects of canopy compared to interspace were inverse for height and leaves, we still consider growth greater in the canopy locations because of the substantial seedling height differences. However, plants growing in shade are often taller, possibly because they are light limited (Allard et al. 1991; Krieger et al. 2022). Under sagebrush canopies are probably a more favorable environment for seedling establishment and growth than interspaces because of mediated temperature extremes (Davies et al. 2007; Chambers 2001), reduced solar incident radiation (Moro et al. 1997), greater soil water availability (Davies et al. 2007), reduced evapotranspiration, and greater soil nutrient concentrations (Charley & West 1977; Doescher et al. 1984).

Directional side of canopy microhabitats likely influences the establishment and growth of some herbaceous species. Density of bottlebrush squirreltail seedlings was 300% greater under the north compared to the south side canopy microhabitat. Similarly, squirreltail seedlings were 270% taller under the north compared to the south side. In contrast, bluebunch wheatgrass seedling establishment and growth were similar between canopy directional sides. Hence, north compared to south side microhabitats may be favorable for certain herbaceous species or functional groups, but not for others. Further supporting that the directional side of sagebrush canopies influences the establishment and growth of herbaceous vegetation, annual forb and annual grass abundance differed between north and south side canopy microhabitats in sagebrush plant communities near our current study area (Davies et al. 2023). The species-specific response to the directional side of the canopy suggests that sagebrush is likely critical to promoting plant community diversity. By modifying microhabitats, sagebrush creates unique niches in a plant community, which in turn favors different species and functional groups leading to more diverse plant communities.

Clearly, sagebrush plants create important microhabitats that generally favor the establishment and growth of perennial bunchgrasses from seed, as seen in our current study, as well as potentially limit large herbivore defoliation (France et al. 2008). This is similar to other research that has suggested that under sagebrush canopies promote the establishment and growth of other plant species (Pierson & Wight 1991; Callaway et al. 1996; Davies et al. 2022b). Favoring the establishment and growth of bunchgrasses is important because bunchgrasses are critical to promoting resistance to annual grass invasion (Chambers et al. 2007; Davies 2008; Davies & Johnson 2017) and preventing the development of an annual grass-fire cycle that is detrimental to native plants (D'Antonio & Vitousek 1992; Crist et al. 2023). The directional side of a sagebrush canopy can also influence the establishment and growth of some bunchgrass species from seed and is likely vital to their persistence in some sagebrush communities. The effects of sagebrush on seedling establishment and growth likely vary across the sagebrush ecosystem and among years because the strength of the effects of sagebrush on under-canopy vegetation varies with precipitation and soil characteristics (Swanson et al. 2021). Sagebrush appears to be important to the long-term persistence and restoration of diverse herbaceous understory plant communities. This suggests maintaining a sagebrush overstory in sagebrush-bunchgrass communities is crucial, as well as restoring sagebrush after it has been lost in disturbances such as wildfires.

Native perennial bunchgrass establishment and growth from seed within sagebrush communities were influenced by biocrusts and microhabitats created by sagebrush plants. This has important ramifications for the persistence and restoration of the herbaceous understory in sagebrush and other shrubland communities. Though biocrusts are important for limiting invasive annual grasses (Deines et al. 2007; Hernandez & Sandquist 2011; Peterson 2013), they also limited native perennial bunchgrass establishment from seed in our current study. Therefore, restoration practices (e.g., drill seeding) that disturb biocrusts to improve seed-soil contact will likely need to be weighed against the risk of promoting invasive annual grasses. Though we did not observe any increases in annual grasses with disturbing biocrusts in our study, we expect that if the disturbance was at a large scale and with additional time following disturbance, annual grasses would have likely increased in abundance. Areas with high biocrust cover may also be a lower priority for restoration of perennial herbaceous vegetation than areas where biocrust cover is unlikely to substantially limit establishment from seed. Perennial bunchgrass establishment and growth from seed is substantially greater under sagebrush canopies, suggesting the importance of maintaining intact communities and restoring sagebrush in burned areas. Sagebrush is probably particularly important for the persistence and restoration of perennial herbaceous species that may not be as competitive as other species when exposed to hotter and drier microhabitats. Though more research is needed, our results suggest that areas with sagebrush still occupying the community and areas where sagebrush has been recently lost (Boyd & Davies 2010, 2012a) may be more likely to be successfully restored with seed-based restoration efforts than areas where sagebrush has been absent for extended time periods. Our results provide evidence that shrubs and biocrusts likely have substantial influence on herbaceous vegetation establishment from seed and spatial vegetation patterns in drylands, though additional studies are warranted because of the broad range of ecological conditions across the sagebrush ecosystem and varying biocrust composition could influence responses. Regardless, the potential effects of shrubs and biocrusts on seedling establishment and growth should be considered in management and restoration plans.

Acknowledgments

We are grateful to C. Guetling for plot setup, fence maintenance, and data management. We also appreciate numerous summer technicians for assisting with data collection and entry. We appreciate R. O'Connor and other reviewers for thoughtful reviews of earlier versions of this manuscript. We also thank L. Condon, the Coordinating Editor, for helping to improve our manuscript.

LITERATURE CITED

Abhilash PC (2021) Restoring the unrestored: strategies for restoring global land during the UN Decade on Ecosystem Restoration (UN-DER). Land 10:201. https://doi.org/10.3390/land10020201

Allard G, Nelson CJ, Pallardy SG (1991) Shade effects on growth of tall fescue: I. Leaf anatomy and dry matter partitioning. Crop Science 31:163–167. https://doi.org/10.2135/cropsci1991.0011183X003100010037x

Boyd CS, Davies KW (2010) Shrub microsite influences post-fire perennial grass establishment. Rangeland Ecology & Management 63:248–252. https://doi.org/10.2111/REM-D-09-00025.1

Boyd CS, Davies KW (2012a) Spatial variability in cost and success of revegetation in a Wyoming big sagebrush community. Environmental Management 50:441–450. https://doi.org/10.1007/s00267-012-9894-6

Boyd CS, Davies KW (2012b) Differential seedling performance and environmental correlates in shrub vs. interspace microenvironments. Journal of Arid Environments 87:50–57. https://doi.org/10.1016/j.jaridenv.2012.06.010

Callaway RM, DeLucia EH, Moore D, Nowak R, Schlesinger WH (1996) Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. Ecology 77:2130–2141. https://doi.org/10.2307/2265707

Chambers JC (2001) *Pinus monophylla* establishment in an expanding *Pinus-Juniperus* woodland: environmental conditions, facilitation, and interacting factors. Journal of Vegetation Science 12:27–40. https://doi.org/10.2307/3236671

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77:117–145. https://doi.org/10.1890/05-1991

Charley JL, West NE (1977) Micro-patterns of nitrogen mineralization activity in soils of some shrub dominated semi-desert ecosystems of Utah. Soil Biology and Biochemistry 9:357–365. https://doi.org/10.1016/0038-0717(77)90010-4

Condon LA, Pyke DA (2018) Fire and grazing influence site resistance to *Bromus tectorum* through their effects on shrubs, bunchgrass and biocrust communities in the Great Basin (U.S.A.). Ecosystems 21:1416–1431. https://doi.org/10.1007/s10021-018-0230-8

Copeland SM, Davies KW, Boyd CS, Bates JD (2021) Recovery of the herbaceous component of degraded sagebrush steppe is unimpeded by 75 years of moderate cattle grazing. Ecosphere 12:e03445. https://doi.org/10.1002/ecs2.3445

Crist MR, Belger R, Davies KW, Davis DM, Meldrum JR, Shinneman DJ, Remington TE, Welty J, Mayer KE (2023) Trends, impacts, and cost of catastrophic and frequent wildfires in the sagebrush biome. Rangeland Ecology & Management 89:3–19. https://doi.org/10.1016/j.rama.2023.03.003

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Davies KW (2008) Medusahead dispersal and establishment in sagebrush steppe plant communities. Rangeland Ecology & Management 61:110–115. https://doi.org/10.2111/07-041R2.1

Davies KW, Bates JD, Boyd CS (2019) Post-wildfire seeding to restore native vegetation and limit exotic annuals: an evaluation in juniper-dominated sagebrush steppe. Restoration Ecology 27:120–127. https://doi.org/10.1111/rec.12848

Davies KW, Bates JD, Boyd CS, Svejcar L (2022a) Utilizing post-fire spatial variability to improve restoration success with seeded bitterbrush. Rangeland Ecology & Management 83:117–123. https://doi.org/10.1016/j.rama.2022.04.002

Davies KW, Bates JD, James JJ (2009) Microsite and herbaceous vegetation heterogeneity after burning *Artemisia tridentata* steppe. Oecologia 159:597–606. https://doi.org/10.1007/s00442-008-1231-7

Davies KW, Bates JD, Miller RF (2007) The influence of Artemisia tridentata spp. wyomingensis on microsite and herbaceous vegetation heterogeneity. Journal of Arid Environments 69:441–457.

Davies KW, Boyd CS, Bates JD, Hamerlynck EP, Copeland SM (2020) Restoration of sagebrush in crested wheatgrass communities: longer-term evaluation in northern Great Basin. Rangeland Ecology & Management 73:1–8. https://doi.org/10.1016/j.rama.2019.07.005

Davies KW, Boyd CS, Beck JL, Bates JD, Svejcar TJ, Gregg MA (2011) Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144:2573–2584. https://doi.org/10.1016/j.biocon.2011.07.016

Davies KW, Copeland SM, Bates JD (2022b) Grazing effects on shrub-induced resource islands and herbaceous vegetation heterogeneity in sagebrush-steppe communities. Global Ecology and Conservation 35:e02106. https://doi.org/10.1016/j.gecco.2022.e02106

Davies KW, Copeland SM, Clenet DR, Svejcar LN, Bates JD (2023) Influence of directional side of sagebrush canopies and interspaces on microhabitats. Basic and Applied Ecology 72:16–21. https://doi.org/10.1016/j.baae.2023.06.004

Davies KW, Johnson DD (2017) Established perennial vegetation provides high resistance to reinvasion by exotic annual grasses. Rangeland Ecology & Management 70:748–754. https://doi.org/10.1016/j.rama.2017.06.001

Davies KW, Leger EA, Boyd CS, Hallett LM (2021) Living with exotic annual grasses in the sagebrush ecosystem. Journal of Environmental Management 288:112417. https://doi.org/10.1016/j.jenvman.2021.112417

Deines L, Rosentreter R, Eldridge DJ, Serpe MD (2007) Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. Plant and Soil 295:23–35. https://doi.org/10.1007/s11104-007-9256-y

Doescher PS, Miller RF, Winward AH (1984) Soil chemical patterns under eastern Oregon plant communities dominated by big sagebrush. Soil Science Society of America Journal 48:659–663. https://doi.org/10.2136/sssaj1984.03615995004800030038x

Doherty K, Theobald DM, Bradford JB, Wiechman LA, Bedrosian G, Boyd CS, et al. (2022) A sagebrush conservation design to proactively restore America's sagebrush biome (No. 2022–1,081). US Geological Survey, Reston, VA. https://doi.org/10.3133/ofr20221081

France KA, Ganskopp DC, Boyd CS (2008) Interspace/undercanopy foraging patterns of beef cattle in sagebrush habitats. Rangeland Ecology & Management 61:389–393. https://doi.org/10.2111/06-072.1

Funk FA, Loydi A, Peter G (2014) Effects of biological soil crusts and drought on emergence and survival of a Patagonian perennial grass in Monte of Argentina. Journal of Arid Land 6:735–741. https://doi.org/10.1007/s40333-014-0022-8

Havrilla CA, Chaudhary VB, Ferrenberg S, Antoninka AJ, Belnap J, Bowker MA, et al. (2019) Towards a predictive framework for biocrust mediation of plant performance: a meta-analysis. Journal of Ecology 107:2789–2807. https://doi.org/10.1111/1365-2745.13269

Hernandez RR, Sandquist DR (2011) Disturbance of biological soil crust increases emergence of exotic vascular plants in California sage scrub. Plant Ecology 212:1709–1721. https://doi.org/10.1007/s11258-011-9943-x

James JJ, Davies KW, Sheley RL, Aanderud ZT (2008) Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. Oecologia 156:637–648. https://doi.org/10.1007/s00442-008-1015-0

James JJ, Svejcar TS, Rinella MJ (2011) Demographic processes limiting seedling recruitment in arid grassland restoration. Journal of Applied Ecology 48:961–969. https://doi.org/10.1111/j.1365-2664.2011.02009.x

Koutzoukis S, Pyke DA, Brunson MW, Baggio J, Calzado-Martinez C, Velben KE (2023) Goldilocks forbs: survival is highest outside-but not too far outside-of Wyoming big sagebrush canopies. Restoration Ecology 31:e13919. https://doi.org/10.1111/rec.13919

Krieger MT, Ditton J, Albrecht H, Linderl L, Kollmann J, Teixeira LH (2022) Effects of shading and site conditions on vegetative and generative growth of a native grassland invader. Ecological Engineering 178:106592. https://doi.org/10.1016/j.ecoleng.2022.106592

Langhans TM, Storm C, Schwabe A (2009) Biological soil crusts and their microenvironment: impact on emergence, survival and establishment of seedlings. Flora 204:157–168. https://doi.org/10.1016/j.flora.2008.01.001

Moro MJ, Pugnaire FI, Haase P, Puifdefábregas J (1997) Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semiarid environment.

Functional Ecology 11:425–431. https://doi.org/10.1046/j.1365-2435.1997.00106.x

Pendleton RL, Pendleton BK, Howard GL, Warren SD (2003) Growth and nutrient content of herbaceous seedlings associated with biological soil crusts. Arid Land Research and Management 17:271–281. https://doi.org/10.1080/15324980301598

Peterson EB (2013) Regional-scale relationship among biological soil crust, invasive annual grasses, and disturbance. Ecological Processes 2:2. https://doi.org/10.1186/2192-1709-2-2

Pierson FB, Wight JR (1991) Variability of near-surface soil temperature on sagebrush rangeland. Journal of Range Management 44:491–497. https://doi.org/10.2307/4002751

PRISM (2025) PRISM climatic group database. http://prism.nacse.org/explorer/ (accessed 8 Feb 2025)

Shackelford N, Paterno G, Winkler D, Erickson T, Leger E, Svejcar L, et al. (2021) Drivers of seedling establishment success in dryland restoration efforts. Nature Ecology & Evolution 5:1283–1290. https://doi.org/10.1038/s41559-021-01510-3

Song G, Li X, Hui R (2017) Effect of biological soil crusts on seed germination and growth of an exotic and two native species in an arid ecosystem. PLoS One 12:e0185839. https://doi.org/10.1371/journal.pone.0185839

Svejcar LN, Davies KW, Ritchie A (2023a) Ecological restoration in the age of apocalypse. Global Change Biology 29:4706–4710. https://doi.org/10.1111/gcb.16809

Svejcar LN, Kerby JD, Mackey B, Boyd CS, Svejcar TJ, Baughman OW, Madsen MD, Davies KW (2023b) Plant recruitment in drylands varies by site, year and seeding technique. Restoration Ecology 31:e13750. https://doi.org/10.1111/rec.13750

Swanson EK, Sheley RL, James JJ (2021) Shrubs facilitate perennial bunchgrass recruitment in drylands under experimental precipitation change. Journal of Arid Environments 187:104432. https://doi.org/10.1016/j.jaridenv.2020.104432

Coordinating Editor: Lea Condon

Received: 9 April, 2025; First decision: 21 April, 2025; Revised: 23 September, 2025; Accepted: 23 September, 2025