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A Fine-Scale Understanding of Sagebrush Islands to Improve Restoration Outcomes in the Intermountain West

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A FINE-SCALE UNDERSTANDING OF SAGEBRUSH ISLANDS TO IMPROVE RESTORATION OUTCOMES IN THE INTERMOUNTAIN WEST

by

Sofia Koutzoukis

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

In

Ecology

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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

A fine-scale understanding of sagebrush islands to improve restoration outcomes in the Intermountain West

by

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Utah State University, 2023

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Department: Wildland Resources

In the Intermountain West, USA expansion of non-native grasses, primarily cheatgrass, has altered fire regimes by promoting a positive feedback loop between fire and further invasion, creating stands of sagebrush that lack perennial understory cover and are neither resistant to cheatgrass invasion nor resilient after a disturbance. Traditional methods to break the cheatgrass-fire cycle are generally insufficient to reliably reduce cheatgrass cover and promote native establishment.

Utilizing nurse shrub effects of sagebrush canopies is a novel, under-utilized method to potentially increase perennial cover in depauperate stands, but this approach requires an understanding of the tradeoffs between benefits and drawbacks of canopies. In drylands, shrub canopies are often considered “good” microsites for establishing understory vegetation and interspaces, between canopies, are considered “bad,” but this dichotomy may overly simplistic. Rather, nurse shrub effects may extend from the canopy into the interspace, making interspaces more favorable than expected, while competition with established vegetation under the canopy may make the canopy less favorable. This dissertation centers around the role of intact sagebrush canopies in influencing establishment of understory grasses and forbs at multiple sites across the Intermountain West.

I found that the establishment of two transplanted native forb species, Munro's globemallow and common yarrow, was highest at intermediate distances between the sagebrush canopy dripline and the position as far as possible from that sagebrush and its nearest shrub neighbor, while native bunchgrass survival (squirreltail and bluebunch wheatgrass) was not affected by proximity to the sagebrush canopy. However, when established from seed, the same grass species sometimes exhibited higher emergence close to the canopy, but fungicides- an emerging strategy for improving emergence rates of seeded individuals- did not affect emergence likely due to low precipitation during the study period. Third, I found that most attributes of the favorable shrub canopy were maintained well into the interspace. Finally, I found that bluebunch wheatgrass and Munro's globemallow were shade tolerant and did not decrease allocation to roots at the expense of shoots when subjected to low light levels, suggesting a mechanism for field observations of drought and shade tolerance of these species under the canopy.

(197 pages)

PUBLIC ABSTRACT

A fine-scale understanding of sagebrush resource islands to improve restoration outcomes in the Intermountain West

Sofia Koutzoukis

In the Intermountain West, rapid expansion of non-native grasses, primarily cheatgrass, has created a repeating cycle where cheatgrass easily ignites and after a fire, more cheatgrass establishes in the burned area, leading to more fire, and more cheatgrass. The primary method to prevent further fires is to plant grass and shrub seeds after a fire because they can deter cheatgrass from establishing and reduce the chance of fire. However, this approach does not always work. There is a need and interest in alternative ways to establish native grasses and forbs.

Sagebrush, the dominant shrub of lower-elevation regions of the Intermountain West, may act as a nurse plant: a plant that alters the environment around itself in a way that is beneficial to other plants. Capitalizing on the attributes that make sagebrush nurse plants, like shade and higher soil moisture, may help the establishment of grasses and forbs before a fire occurs, increasing the likelihood that cheatgrass will not dominate that system. While the area around nurse plants generally is thought of as a favorable place for grasses and forbs to grow, that may not always be the case. There may be minimal differences in the microenvironment between the canopy and interspace and there can be competition under the canopy between newly established plants and other vegetation that is already present.

I found that the sagebrush canopy influenced the survival of two native wildflower species, Munro’s globemallow and common yarrow, when they were transplanted as seedlings, but survival of two native transplanted grass species, bluebunch wheatgrass and squirreltail, was unaffected by the sagebrush canopy. However, when those same grasses were planted as seeds, if the seeds emerged, their emergence was highest near the canopy. Some of the attributes that make the canopy a “good” place for grasses and wildflowers to grow extend into the interspace, making the interspace potentially similarly “good.” I found that bluebunch wheatgrass and globemallow were shade tolerant and grew in ways that may allow them to be competitive under the canopy and persist in the interspaces, outside of what is generally considered a “good” nurse shrub microenvironment.

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My father, a keen naturalist and observer of the natural world, once drove twelve hours to help me pull transect tapes in middle-of-nowhere Nevada, and my mother always picked up the phone when I missed the bus and encouraged me to stay well rounded. My brother, an artist, introduced me to the concept of restoration ecology at a young age and helped keep my optimism alive. I want to express my bottomless gratitude and love to my husband, Scott Zimmer, who will remain, unilaterally, the best part of graduate school and the greatest achievement of my life.

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PREFACE

Because this dissertation has been prepared in journal format, there is some redundancy between chapters. Chapters 2 and 3 have been submitted to peer-reviewed journals and are in review. Chapters 4 and 5 will be submitted for peer-reviewed publication in the near future. Each chapter has been or will be published with coauthors; as such, the pronoun “we” is used throughout the thesis.

CHAPTER 1

INTRODUCTION

Sagebrush ecosystems in the Western United States are threatened by changing fire regimes, catalyzed by cheatgrass (*Bromus tectorum*), an invasive annual grass (D'Antonio & Vitousek 1992; Balch et al. 2013). Cheatgrass is the greatest threat to ecosystem functioning and services in low-elevation sites with little understory perennial cover (Chambers et al. 2014). A positive feedback loop occurs between cheatgrass invasion and fire, where cheatgrass greatly increases the likelihood of fire, which further promotes cheatgrass invasion (D'Antonio & Vitousek 1992). Vegetation composition is simplified through each successive fire and disturbance, from complex stands with woody canopies of multiple ages and understory perennial herbaceous cover, to intact stands of sagebrush canopies with depauperate understories, to eventual cheatgrass monocultures (Davies et al. 2012) that provide few ecosystem services (Weltz et al. 2014).

Low-elevation sagebrush stands generally do not passively recover after disturbances and require intervention to establish desirable vegetation (i.e. sagebrush and bunchgrasses) and reduce cheatgrass cover (Chambers et al. 2014). Most interventions, namely aerial and drill seeding, take place after a fire, once sagebrush is top killed and cover is removed (Pilliod et al. 2017).Those revegetation projects are largely unsuccessful, often with higher invasive annual grass cover after the revegetation project than before (Knutson et al. 2014; Shackelford et al. 2021; but see Simler-Williamson & Germino 2022). There is a growing interest in and need for novel restoration techniques and strategies to increase the success rate of restoration in the Intermountain West (Copeland et al. 2021).

Sagebrush can facilitate understory vegetation establishment and growth. Generally, soil moisture, nitrogen availability, potassium, phosphorus, and soil organic matter are higher under sagebrush canopies than in surrounding interspaces (Jackson & Caldwell 1993), and vegetation is more abundant under canopies than in surrounding interspaces (Holthuijzen & Veblen 2015). In post-fire settings in the Intermountain West (i.e., after sagebrush canopies have been killed by fire), both seeded and transplanted understory plants exhibit higher establishment rates in the remnant, burned canopy microsites (Boyd & Davies 2010, 2012; Davies et al. 2017, 2020). In these settings, sagebrush's aboveground facilitative effects, primarily shading are not at play, but because aboveground microclimate amelioration is more influential on seedling survival than belowground resource availability in some semi-arid systems (Gómez-Aparicio et al. 2005), not capitalizing on pre-fire nurse shrub effects may be a missed opportunity to increase establishment rates. I investigated nurse shrub effects in the absence of fire, a scenario in which living shrub canopies have the potential to influence understory establishment both above- and belowground.

However, there are several reasons that growing under sagebrush may not always be beneficial for understory plants, four of which I address in this dissertation. First, competition with existing understory vegetation can dampen facilitative effects (Pescador et al. 2014) and those facilitative effects can shift with interannual changes in precipitation, or other sources of "stress," to competitive effects (Cruz-Alonso et al. 2020; Swanson et al. 2021). Secondly, the abiotic attributes that make the shrub canopy a favorable microenvironment for establishment, like increased soil moisture (Davies et al. 2007), may also make seeds planted in the canopy more susceptible to fungal pathogens during winter stratification (Gornish et al. 2015; Mackin et al. 2021), but fungicide-coated seeds may escape the limitation to emergence posed by soil fungal pathogens (Hoose et al. 2022).Thirdly, the high resource abundance that leads to generalization of nurse plant canopies being considered “good” microsites and interspaces “bad” is likely oversimplistic and site-specific. Because roots can extend from the canopy into interspaces (Ryel et al. 1996; Rau et al. 2009), and root function is associated with organic inputs and soil moisture (Caldwell & Richards 1989; Kononova 2013), it is likely that the attributes that make canopies a beneficial planting microsite extend into the interspace. Fourthly, while the shade from the sagebrush canopy is associated with a beneficial microclimate, namely lower evapotranspiration (Prater & DeLucia 2006) and increased soil moisture (Davies et al. 2007), shade may also negatively influence seedling biomass allocation patterns in a way that reduces competitive fitness. In response to fluctuating resource availability in a given environment, plants can plasticly increase aboveground biomass when light is limiting or increase belowground when other resources, like nitrogen or soil moisture, are limiting (Hodge 2004). Plants are most competitive for limited soil resources with high root biomass relative to shoot biomass (Rowe & Leger 2011), but shade can cause plants to increase shoot biomass at the expense of root biomass, decreasing their competitive fitness (Poorter et al. 2012).

There is tension between facilitation from canopy effects and competition from existing vegetation (Pescador et al. 2014), and the net-effect of competition and facilitation may push the microsites that best support high survival outside of the canopy into the interspace. A more nuanced paradigm that investigates the possibility that establishment can be high outside of the canopy requires an investigation into the fine-scale distribution of the above- and below-ground attributes that make up the favorable microenvironment around sagebrush, whether those attributes are highly clustered at the canopy versus more diffuse, and how conserved those patterns are across landscapes. For example, soil resource availability can remain elevated from the canopy to interspace (Mudrak et al. 2014; De Boever et al. 2015), but the relationship between soil resources and proximity to the canopy are highly site-specific (Doescher et al. 1984).

Research summary

Focusing on intermediate states of degradation, where bunchgrass communities have been removed but sagebrush canopies remain intact, represents an underexploited restoration strategy but requires an understanding of the spatial distribution of the favorable microenvironments under or around sagebrush plants and the mechanistic role that microenvironment plays in seedling growth. My dissertation focuses on two central themes around sagebrush canopies: (1) how to utilize sagebrush canopies to improve understory establishment in depauperate stands and (2) describing canopy-interspace dynamics of abiotic attributes and their effects on seedling growth.

Study sites and species

Field experiments (Chapters 2-4) occurred at all or a subset of seven 1-acre plots that I established in 2018 and 2019 across the Intermountain West. The study sites were in five Major Land Resource Areas in five states: Columbia Basin, Washington (Saddle Mountain), Great Salt Lake Area, Utah (Onaqui), Snake River Plain (Birds of Prey, Roberts), Malheur High Plateau (Rock Creek/Grey Butte), and the Owyhee High Plateau (Wilson; Figure 1.1). Saddle Mountain, Rock Creek, Grey Butte, and Onaqui were located within control plots of a long-term vegetation manipulation study (McIver et al. 2010). All study sites' soils were loamy aridisols (Soil Survey Staff USDA-NRCS 2020) and dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* [Beetle & Young] S.L. Welsh). Sites spanned a range of elevation (260-1650 m) and 30-year normal (1991-2020) temperature (6-11°C), and precipitation (204-297 mm; PRISM Climate Group 2014). All sites were dominated by mature sagebrush canopies with variable native perennial grass and non-native annual cheatgrass cover (mean ± 1SD: 14 ± 9% perennial grass; 8 ± 11% cheatgrass). Our focal species were two grasses, bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey ssp. *elymoides*; hereafter squirreltail), bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), and two forbs, Munro's globemallow (*Sphaeralcea munroana* [Douglas] Spach: hereafter globemallow), and common yarrow (*Achillea millefolium* L.: hereafter yarrow). All the focal species are common native perennial plants in the Intermountain West and commonly used in restoration or are in development for broadscale post-fire restoration in this region.

Summary: Sagebrush influence on transplanted seedling survival

The first data chapter of my dissertation (Chapter 2) examines how microsites within stands of sagebrush influence the survival of transplanted globemallow, yarrow, squirreltail, and bluebunch wheatgrass seedlings in two different years. I planted each species at all seven study sites in 2018 and 2019, which received above-normal and below-normal precipitation during the growing season, respectively, and I followed survival for four years after planting. I predicted that the highest survival would be closer to the sagebrush canopy in drier years, indicative of net facilitation and farther in wetter years. I hypothesized that survival for all planted species would be higher farther from the canopy in the second year compared to the first year post-planting due to increased competitive effects on the more mature planted seedlings from sagebrush and other understory plants. I also hypothesized that soil surface cover characteristics (measured as percent cover of biological soil crust, moss, physical crust, and rock) and existing plant community (measured as cheatgrass, Sandberg bluegrass [*Poa secunda*], and all perennial native grass cover) would influence survival.

I found that, for seedlings planted in the wetter year, survival of globemallow and yarrow was highest in the interspace region between the sagebrush canopy edge and the maximum distance between sagebrush canopies, but only for the first year post-planting. Contrary to my expectations, globemallow and yarrow survival were not affected by proximity to the sagebrush canopy when planted in the drier year, likely due to either a breakdown of facilitation at extreme stress, or a byproduct of low sample sizes and survival. Both first- and second-year survival of the grass species, squirreltail and bluebunch wheatgrass, were unaffected by proximity to the sagebrush canopy either year they were planted. Globemallow survival was associated with high biological soil crust and rock cover and low litter cover.

Summary: Sagebrush canopy effects on emergence of fungicide-coated seeds

The second data chapter of my dissertation investigated the possibility of planting fungicide-coated seeds in intact Wyoming big sagebrush stands and whether there was an interaction between fungicide coating and proximity to nurse shrub canopies. I planted uncoated and fungicide-coated bluebunch wheatgrass and squirreltail seeds in small furrows extending from the sagebrush canopy dripline into the interspace at four sites (Grey Butte, Roberts, Onaqui, Saddle Mountain) across the Intermountain West in two years (2020 and 2021). I hypothesized that under high precipitation scenarios, fungicide coatings would improve emergence rates but emergence would be low close to the sagebrush canopy, and the opposite would hold true under low precipitation scenarios.

In both years, 2020-2021 and 2021-2022, precipitation was below-normal at most sites, with sites receiving between 53-73% of normal precipitation during the 2020 growing season and 62-98% of normal precipitation during the 2021 growing season. Overall rates of emergence were extremely low in both years, and I observed complete seeding failure across treatments, at three out of the four sites in both years. At the lowest elevation site in the drier year, all seed coating treatments exhibited the highest emergence at the canopy dripline. Fungicide had no effect on emergence likely because precipitation was below-normal throughout the study period. This work highlights the site- and climate-specificity of the success of seed coating amendments and the need for restoration solutions that are successful in the driest years and sites.

Summary: Spatial clustering of above- and belowground nurse shrub effects around sagebrush canopies

The third data chapter of my dissertation focuses on the extent of sagebrush canopies' influence on resource island effects. At four sites (Rock Creek, Roberts, Onaqui, Saddle Mountain), I examined how the fine-scale distribution of aboveground (radiation, vapor pressure deficit) and belowground (soil organic matter, soil moisture, phosphorus, potassium, nitrate, ammonium) attributes of sagebrush canopy effects changed from the canopy to the interspace at four sites across the Intermountain West. I hypothesized that attributes of shrub islands associated with shrub canopies (e.g., shade and vapor pressure deficit) would immediately change from the canopy edge into the interspace whereas belowground attributes of shrub islands (e.g. organic matter, soil moisture, potassium) would remain elevated between the canopy edge and interspace microsites.

My hypothesis was partially supported. Rather than simple partitioning of patterns by above- versus belowground, attributes strongly associated with and derived from the canopy changed abruptly at the canopy edge, whereas attributes less associated with the canopy were more diffuse. Of all attributes analyzed, radiation and potassium were highly clustered at the canopy edge. Radiation is directly influenced by shading from the canopy whereas potassium is leached from sagebrush litter, most of which falls directly under the canopy. Belowground variables (organic matter, soil moisture, ammonium, nitrate, potassium) coincided with established patterns of root biomass in Wyoming big sagebrush stands, where root biomass can be equally high from directly next to a perennial plant into the interspace. Like previously observed patterns in root biomass, I found that belowground variables showed either no change or minimal changes between the canopy and maximum interspace microsites suggesting that interspaces can potentially support survival.

Summary: Role of shade, organic matter, and watering frequency on seedling growth and biomass allocation

My fourth data chapter was a growth chamber study, isolating how two attributes of nurse-shrub microenvironment, shade and water holding capacity, affected growth patterns (relative growth rate, root and shoot biomass, root:shoot ratio) of two species (globemallow and bluebunch wheatgrass). I investigated how growth patterns were influenced by water holding capacity (high and low), and shade (shaded and unshaded) and watering (high watering, low watering). In response to varying resource availability (light and soil moisture in this study), plants allocate a finite amount of resources to maximize their fitness- to roots when soil resources are limiting and to aboveground structures when light is limiting. Reductions to belowground biomass at the expense of aboveground biomass can reduce an individual's ability to compete for soil resources. I predicted that shade would decrease biomass allocation to roots in response to increased shoot biomass allocation to maintain maximum photosynthetic capacity and that both shade and organic matter would buffer seedlings against negative effects of infrequent and lower volume watering events.

Both species were shade tolerant, with no differences in overall root and shoot dry weight or root:shoot dry mass ratio (R:S) or root mass fraction by shade treatment. Bluebunch wheatgrass growth (leaf length, number of leaves, number of tillers, leaf area) was faster under shade during the first four weeks of the experiment, and globemallow growth was then faster under shade during the last two weeks. Bluebunch wheatgrass exhibited the highest root:shoot ratio in the treatment that received the most water, whereas globemallow's highest root:shoot ratio was in the treatment receiving the least amount of water. Root allocation (root dry biomass, R:S, root mass fraction) was unaffected by the shade treatment for both species in both soil and watering regimes. These results suggest that there is no negative effect of growing in the canopy for these two species: canopy seedlings have the same root:shoot ratio as seedlings not growing in shade, indicating no reduction in their ability to compete for soil resources. At the same time, can still capitalize on higher soil moisture found under the canopy. The infrequent/low water treatment only negatively affected seedling growth (biomass, R:S) in the soil with the lowest water holding capacity.

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Figures

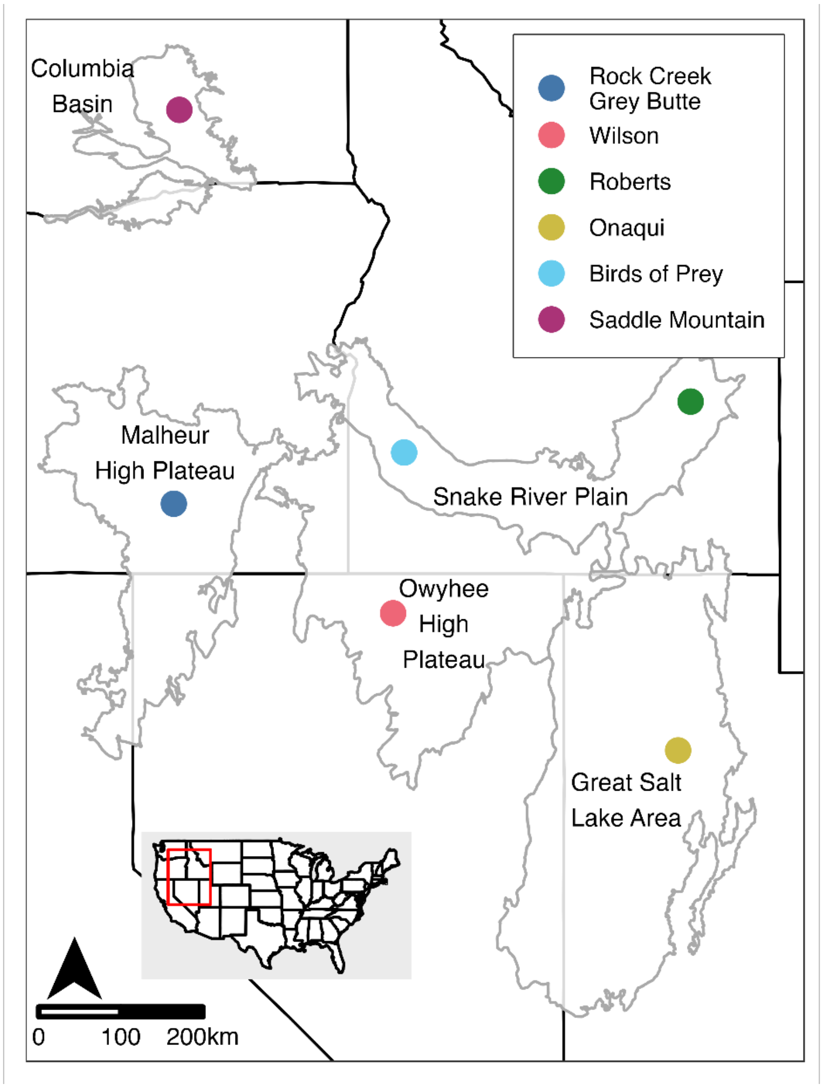

Figure 1.1: Map of site locations of all field sites. Sites are listed according to descending annual temperature and ascending annual precipitation. Rock Creek burned in fall of 2019 and a new site was established 6 km away at Grey Butte. Shading and labels indicate Natural Resources Conservation Service (NRCS) Major Land Resource Areas (MLRA).

CHAPTER 2

GOLDILOCKS FORBS: SURVIVAL IS HIGHEST OUTSIDE – BUT NOT TOO FAR OUTSIDE – OF WYOMING BIG SAGEBRUSH CANOPIES

Abstract

In arid and semiarid systems, positive effects of nurse shrubs generally occur immediately underneath and around shrub canopies, creating microsites that can be targeted to promote plant establishment in restoration settings. Alternatively, the best microsites may occur in the interspace zone immediately surrounding nurse shrubs if positive abiotic effects extend beyond nurse shrub canopy boundaries and if competition with nurse shrubs is reduced in that zone. In the Intermountain West, USA, we investigated survival of transplanted herbaceous seedlings at different distances from Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) canopies. We planted two native perennial forb species, Munro's globemallow (*Sphaeralcea munroana*) and common yarrow (*Achillea millefolium*), and two native perennial grass species, bluebunch wheatgrass (*Pseudoroegneria spicata*) and bottlebrush squirreltail (*Elymus elymoides*), at four distances from sagebrush canopies at six sites across the Intermountain West, repeated across two years. Under above-normal precipitation, proximity to sagebrush influenced first-year survival of the forb, but not grass, species. Globemallow and yarrow survival were highest mid-way between the canopy dripline and maximum interspace distance between neighboring sagebrush plants. Ground cover characteristics and globemallow survival covaried with respect to distance from shrub, suggesting ground cover characteristics as indicators of suitable planting microsites.

Under drier conditions, survival of all species was low and unaffected by distance from canopies. Our results demonstrate the value of fine-tuning the canopy-interspace paradigm to more carefully consider how plant performance may differ across zones within the interspace region between plants, especially when the goal is to maximize plant establishment in non-drought years.

Introduction

In arid and semiarid systems, nurse shrubs can be critical for the establishment and persistence of understory plant species, and are increasingly viewed as important tools for revegetation and restoration in those systems (Padilla & Pugnaire 2006; Pyke et al. 2020). Nurse shrubs can be used to promote colonization of understory seedlings both passively through natural recolonization (e.g., Liu et al. 2011) and actively, through selectively planting seedlings into remnant shrub canopies to increase survival (e.g., Boyd & Davies 2012). However, nurse shrubs also can compete with understory plants, and interspecific relationships are not static in time or space. Rather, the strength and effect of interactions can change from positive to negative with changes in resource availability (Holland & DeAngelis 2009), stress-gradients (Maestre et al. 2009; Callaway & Walker 1997), and plant traits (Graff & Aguiar 2017). For example, nurse shrubs can facilitate emergence and persistence of understory seedlings by providing a favorable abiotic environment under drought conditions but may not do so under “normal” conditions when net competitive effects from the nurse shrub and other understory plants prevail (Swanson et al. 2021; Verwijmeren et al. 2013; Maestre et al. 2009).

Positive effects of nurse shrubs are generally thought to coincide with the area under or near the shrub itself, but could extend farther into the interspace between shrub canopies, depending on the broader environmental context. Existing vegetation diversity and abundance can change continuously, for example gradually attenuating from the shrub canopy into the interspace (Schafer et al. 2012; Segoli et al. 2012). Simultaneously, abiotic drivers of nurse shrub effects, like soil moisture and micronutrient availability, in some cases, show corresponding gradual patterns of attenuation from the canopy into the interspace (Mudrak et al. 2014; Ryel et al. 1996).

Given the increasing unpredictability of growing season precipitation in arid and semi-arid systems (Hardegree et al. 2018), focusing planting efforts in interspaces near nurse plant canopies, but avoiding microsites that occur at the maximum interspace distances between the nurse plant and its neighbors (i.e., the most “interior” interspace locations), could act as a spatial and temporal bet-hedging strategy. Spatially, this approach would allow seedlings to partially avoid competition with the nurse plant and other understory plants, while still capitalizing on at least some benefits of nurse plants (e.g., abiotic resources) that extend beyond the edge of the canopy. The strength of these patterns could also change temporally. For example, at a given position outside but near the shrub canopy, consumer-resource theory (Holland & DeAngelis 2009) would predict that plants could reap the benefits of facilitation that extend beyond the shrub canopy in a more “stressful” year (e.g. drier), whereas, in that same position during a less “stressful” year (e.g. wetter) when competition is expected to be stronger, they could at least partially avoid strong competition associated with growing directly beneath the canopy. Tradeoffs between competition and facilitation may further vary temporally across different plant life stages, where seedlings are associated with nurse plants, but adults are not (Callaway & Walker 1997). Thus, the optimal microsites to escape competition while still receiving abiotic benefits of nurse shrubs may fall at intermediate distances between the nurse plant canopy and the microsite that occurs at the maximum distance between a nurse plant and its neighbor. Optimal distances also could vary with different species (e.g., deep versus shallow rooted) and physical environments (e.g., warm dry versus cool wet; Callaway & Walker 1997).

The Intermountain West of the United States is characterized by vast expanses of big sagebrush (*Artemisia tridentata*) with understories often dominated by fire-prone invasive species due to changing fire regimes (Davies et al. 2012) and land use history (Filazzola et al. 2020). Previous research has found that, in post-fire restoration settings commonly encountered in this region, remnant, dead sagebrush canopy microsites can greatly increase survival of both transplanted woody and seeded herbaceous species (Boyd & Davies 2010; Davies et al. 2020, 2017). However, in intact, unburned semi-arid systems, aboveground canopy ameliorations are considered more influential than belowground resource availability on seedling survival (Gómez-Aparicio et al. 2005; Liu et al. 2021). In the Intermountain West, intact systems are also more likely to be characterized by intact biological soil crust communities which can increase (or decrease) establishment and by lower invasive annual grass cover which can improve plant establishment (Condon & Gray 2020; Havrilla et al. 2019; Bradley et al. 2018). Living sagebrush may further improve establishment of restoration species via abiotic microclimate ameliorations, like increased soil moisture from hydraulic redistribution, regulated soil temperature, and reduced evapotranspiration (Caldwell & Richards 1989; Davies et al. 2007), as well as via biotic protection from large ungulate grazing and small mammal herbivory (Jaksic & Fuentes 1980; Allington & Valone 2014). Therefore, exploring the effects of living sagebrush canopies on plant establishment may reveal an unexploited opportunity to improve outcomes in pre-fire restoration settings. Conversely, positive abiotic effects of nurse shrubs in these contexts may be offset by negative, competitive effects from the nurse shrub itself, other established native vegetation, or exotic annual grasses that are more abundant in sagebrush understories (Griffith 2010; Holthuijzen & Veblen 2015).

To examine the canopy-interspace dynamics of understory plant establishment patterns, we investigated the effects of distance from sagebrush canopy on survival of four understory herbaceous perennial species across different climate regimes in the Intermountain West in both above- and below-normal precipitation years. Initiating this experiment in two successive years allowed us to infer precipitation effects between years, which is rarely done in ecological experiments (Werner et al. 2020). We focused on transplanted understory seedlings because traditional methods of revegetation, namely direct seeding, have been met with variable success (Knutson et al. 2014) and there is growing interest in transplanting seedlings of focal species to increase establishment rates (Pyke et al. 2020; Davies et al. 2020). We predicted that survival would be highest in the interspace zone between the sagebrush canopy dripline and the maximum (i.e., most interior) interspace distance between nurse plants. But we also predicted that, within that interspace zone, survival would be higher closer to the sagebrush canopy in drier years, indicative of net facilitation, and farther from the canopy in wetter years, characteristic of net competition. We hypothesized that, for all planted species, survival would be maximized closer to the canopy for seedlings in their first than second year of growth due to reduced potential for competition (via niche differentiation) between younger plantings and mature sagebrush and other canopy-associated plants. We also hypothesized that biological soil crust would be associated with higher survival of plantings.

Methods

We tested how distance to focal sagebrush plants influenced ground cover characteristics (e.g., biological soil crust cover) and survival of two native grass and two native forb seedlings that were planted in each of two years, monitoring each cohort's survival for three years after planting.

Study sites and seedling stock

We established six study sites during the 2018 primary growing season for herbaceous species (May-June) on public land managed by the Bureau of Land Management or U.S. Fish and Wildlife Service across the Intermountain West, USA (Figure 2.1, Table 2.1). The Rock Creek site burned in a wildfire in September 2019 (Poker Fire, 9500 ha) post-planting, so we established a new site for our second planting year at Grey Butte, six kilometers away with similar soils and climate (Table A1). The study sites are in five Major Land Resource Areas (USDA-NRCS 2021) in five states: Columbia Basin, Washington (Saddle Mountain), Great Salt Lake Area, Utah (Onaqui), Snake River Plain, Idaho (Birds of Prey, Roberts), Malheur High Plateau, Oregon (Rock Creek/Grey Butte), and the Owyhee High Plateau, Nevada (Wilson).

All study sites were dominated by mature Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* [Beetle & Young] S.L. Welsh) with variable native perennial grass and non-native annual cheatgrass (*Bromus tectorum* L.) cover (mean ±

1SD: 25 ± 17% perennial grass; 16 ± 26% cheatgrass; Table A1). Average basal gap size between perennial vegetation ranged from 1.36 m to 5.22 m (Table A1). All soils were loamy aridisols (Soil Survey Staff USDA-NRCS 2020). Sites spanned a range of elevation (260-1650 m), 30-year normal (1991-2020) temperature (6-11°C), and precipitation (204-297 mm; PRISM Climate Group 2014; Table A1). Precipitation for the first planting cohort's first growing season (October 2018-June 2019) was consistently above 30-year climate normals (133-156% normal precipitation; Table 2.1). The second planting cohort's first growing season, (October 2019-June 2020) was more varied but overall drier, from 74% to 122% of normal precipitation (Table 2.1).

All study sites were historically grazed by domestic livestock, but have been excluded at three sites for at least 15 years (Roberts, fenced in 2006; Saddle Mountain, 2007; Rock Creek/Grey Butte, 1999). Wilson and Onaqui are unfenced and have evidence of cattle presence (fresh dung, hoof prints, direct observation; Table A1), but most use at Wilson occurs along "trails" parallel to the road outside the plot. Onaqui has wild horse presence, and horse grazing can be high, but varies in intensity (J. Bullock, BLM, personal communication). Birds of Prey is also unfenced in an allotment that is actively grazed but does not have evidence of recent cattle presence in our study plots (A. Welke, BLM, personal communication).

Our focal species were two grasses, bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey ssp. *elymoides*; hereafter "squirreltail") and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), and two forbs, Munro's globemallow (*Sphaeralcea munroana* [Douglas] Spach: hereafter "globemallow") and common yarrow (*Achillea millefolium* L.: hereafter "yarrow"). All species are common native perennial plants in the Intermountain West, commonly used in restoration and/or in development for broadscale post-fire restoration in this region, and relatively shade tolerant (Hamerlynck & Ziegenhagen 2020; Bourdôt et al. 1984). Squirreltail is a medium-rooted bunchgrass while bluebunch wheatgrass is a deep-rooted bunchgrass. Yarrow has a shallow, fibrous, rhizomatous root system and globemallow has a deep taproot. Both grasses and yarrow are fire resistant (Hogenbirk & Sarrazin-Delay 1995; Monsen et al. 2004) and while globemallow is top-killed by fire, it can resprout from its caudex (Wasser & Shoemaker 1982). The grasses are palatable forage species for domestic and wild ungulates as well as smaller mammals, especially in the spring (Hutchings 1953; Monsen et al. 2004). The forbs are spring and summer food sources for the greater sage grouse (*Centrocercus urophasianus*; Braun et al. 1977), an endemic wildlife species of concern in the region (Dudley et al. 2021).

We grew seedlings from seeds that originated as close as possible to their respective planting sites out of available varieties, cultivars, and sources at BLM seed warehouses in 2017 (ranging from the same county to 1000 km away; Table A2).

Seedlings were grown at the Utah State University Research Greenhouses (Logan, UT, USA) in PVC SC-10 cone-tainers (Stuewe & Sons, Inc., Corvallis, OR, USA; 20 cm deep 4 cm diameter) starting the February before planting, except yarrow which was started in May since it germinated and grew faster than the other species. The soil medium was a 4:2:1 ratio of sphagnum moss, sand, and perlite. Seedlings were fertilized with a low nutrient fertilizer (10-9-5 NPK with micronutrients) every two weeks and watered twice per week in the winter and spring and up to five times per week in the summer. Greenhouse temperatures were 20-23°C in the winter, 15-25°C in the spring and summer, and 10-15°C in the fall before planting. We hardened off seedlings by gradually reducing watering to once per week and moving them outside for two weeks before planting where they regularly experienced sub-freezing nighttime temperatures.

Field sampling and planting

Prior to planting, we characterized the study sites by monitoring along four 37.5 m-long transects extending from the center to the four corners of a 100 m by 50 m plot at each of the six original sites during the 2018 growing season (May-June). The seventh site, Grey Butte, was monitored in June 2020 after being established in October 2019. We measured plant cover by line point intercept dropping a pin every 50 cm and measured gap sizes between bases of all perennial plants along transects. As an index of animal use at our sites, we counted dung piles identified to species/functional group in 2-4 m wide belt transects along each transect (Herrick et al. 2017).

We planted from October 23 to November 29 2018, and from October 23 to December 6, 2019. We started at the cooler, higher elevation sites (Rock Creek/Grey Butte and Wilson) and ended at the warmest and lowest elevation site (Saddle Mountain) in both years (Table 2.1). We planted approximately 100 seedlings of each species at each site, depending on seedling losses in the greenhouse and during transport to the sites (Table 2.1). To ensure seedlings were planted at multiple distances from the canopy of the focal nurse shrub into the interspace, seedlings were divided approximately equally among four microsites: 1) canopy dripline, 2) maximum interspace distance (i.e., equidistant) between canopy dripline of the focal shrub and the canopy of the nearest neighboring sagebrush greater than 40 cm canopy diameter, 3) 25% of the distance from canopy dripline to the maximum interspace distance, and 4) 50% of the distance from canopy dripline to the maximum interspace distance (Figure 2.2). We did not include a fifth microsite type directly under sagebrush canopies because plants growing directly under sagebrush canopies would likely be exposed to fatal headloads and die during future fires (Hulet et al. 2015). For each planting, we measured the exact distance (in centimeters) and size of the focal sagebrush (widest diameter, perpendicular diameter in centimeters). We used these measurements to create a "scaled shrub distance" metric for analysis (Figure 2.2), similar to that used by Caldwell et al. (2008).

Microsite locations were randomly chosen, and seedlings (~100 per species per site) were then randomly assigned to each microsite. To guide planting and randomization of microsite locations, at each site we established 18-21 parallel 50 m planting transects 5 m apart. Along each transect, we randomly assigned one of the four microsite types to each of 15-30 sagebrush plants per transect. Microsites were placed in a direction from a sagebrush plant that maximized distance to perennial grasses and also avoided areas of high annual grass or forb cover, slick spots (anomalously silty and clayey soil with high exchangeable sodium), and animal disturbances like burrows or ant mounds. Seedlings were planted along the same transects in 2018 and 2019. Some 2019 plantings shared an interspace with 2018 plantings but were associated with different focal shrubs and were at least 50 cm away from other plantings to minimize competition (Reisner 2010). To plant seedlings, we used dibble sticks (Saddle Mountain, Roberts) and augers with 4-inch diameter bits at rockier and clayier sites (Birds of Prey, Wilson, Rock Creek, Grey Butte, Onaqui).

We monitored survival in May to June for three years following planting for the 2019 cohort and four years for the 2018 cohort (approximately 6, 19, 30, 40 months post-planting). We recorded whether seedlings were alive or dead and any qualitative evidence of major disturbance like frost heaving, herbivory, trampling by cattle, or disturbance by animal burrows. At all planting microsites, in the first May-June following planting, we made visual estimates of ground cover (lichen, moss, physical crust, litter, rock) and grass cover (cheatgrass, Sandberg bluegrass [*Poa secunda* J. Presl], all perennial grasses including Sandberg bluegrass) in two 100 cm^2 square quadrats placed adjacent to, but outside of the soil that was disturbed by planting each seedling; cover classes were 0%, 1-5%, 6-25%, 26-50%, 50-75%, 76-95%, 96-100%.

Analysis

We performed four separate analyses to infer relationships among survival and environmental drivers: 1) survival by distance from sagebrush canopy for each planted species, 2) ground cover characteristics by distance from sagebrush canopy, 3) survival by ground cover characteristics for each species, and 4) disturbance by distance from the sagebrush canopy. We could not use more complex models because we had low statistical power due to generally low survival rates (Table 2.1). For models that included distance from sagebrush canopy, we calculated “scaled shrub distance” (Figure 2.2), a unitless metric that considers relationships between nurse shrub size and the areal extent of shrub island effects (e.g., Varela et al. 2017; Caldwell et al. 2008). Scaled shrub distance is the average radius of the focal sagebrush canopy (cm; calculated from the widest canopy diameter and perpendicular diameter) divided by the distance between the planting microsite and the sagebrush base (cm). For example, a seedling planted 50 cm from the base of a sagebrush with a radius of 50 cm would have a scaled shrub distance of one, whereas a seedling planted 100 cm from the same sagebrush would have a scaled shrub distance of two (Figure 2.2). Additionally, in any analysis that included survival as a dependent variable, we excluded seedlings that had qualitative evidence of disturbance, including frost heaving, herbivory, trampling, and animal burrows (Tables 2.1, S3). Although we report descriptive statistics for all sites (Table 2.2), we also excluded the Birds of Prey site from statistical analyses due to high rates of disturbance (94% of seedlings 7 months post-planting; Tables 1, S3), as well as Rock Creek due to low survival (1-6% survival across species in the first year). For all models, we used the R package, *DHARMa* (Hartig 2020), to check for zero-inflation and model assumptions (constant variance, over/under dispersion, outliers, normality).

For our first set of analyses, we tested how seedling survival varied with scaled distance from sagebrush canopy. We separately analyzed each combination of cohort (2018, 2019), year ("Year 1", "Year 2", which were, respectively approximately 6 and 18 months post-planting), and species (globemallow, yarrow, bluebunch wheatgrass, squirreltail) using binomial linear models with logit links similar to the form of a continuation ratio, where a given year's survival is relative to the previous year's survival. For models that included Year 1 survival, the seedlings that died before Year 1 were coded as "0", and seedlings that survived to Year 1 or Year 2 were coded as "1". For models that included Year 2 survival, the seedlings that had not survived to Year 1 were dropped, seedlings that survived to Year 1 but not Year 2 were coded as "0", and seedlings that survived to Year 2 were coded as "1". In all models, we only included sites where at least 5 seedlings of a given species survived (Table A3). We limited predictors (all fixed effects) to site, scaled shrub distance, and orthogonal 2nd order scaled shrub distance due to the limited sample size of live seedlings. The quadratic term allowed for non-linear relationships between distance and survival. Orthogonal polynomials reduce collinearity between linear and quadratic covariates. We only report descriptive statistics for 3- and 4-year survival (approximately 30, 40 months post-planting) of each cohort due to low survival and weak spatial patterns in 2-year survival (Table 2.2).

In a second set of analyses, to understand how microsite ground cover characteristics varied by site and proximity to sagebrush, we used separate models for each ground cover characteristic (% cover of biological soil crust, physical crust, moss, rock, litter, all perennial grass, Sandberg bluegrass, and cheatgrass), with scaled shrub distance, orthogonal 2nd order polynomial scaled shrub distance, and site as fixed effects. Because there was evidence of zero-inflation for these variables in our original analysis that used a Poisson linear regression with a log link, we ultimately used a zero-inflated Poisson generalized linear model with a log link using the R package glmmTMB (Brooks et al 2017). We used the median of each cover class in analysis (0, 2, 16, 38, 63, 85, 98%). We excluded Saddle Mountain from the rock model due to no rock cover and Wilson from the physical crust model because we sampled on a rainy day when physical crust could not be assessed.

For the third set of analyses, we used logistic regressions to understand how Year 1 survival of each species in the 2018 cohort related to microsite ground cover characteristics. For each species, we used separate generalized linear regression models with logit links to regress survival of 2018 seedlings in Year 1, excluding all plantings with signs of disturbance (see below), against each ground cover characteristic. We applied a Bonferroni correction for multiple comparisons ($\alpha = 0.006$). All sites were included in each model, except Saddle Mountain and Wilson were excluded from the rock and physical crust models. We did not repeat this analysis for the other three cohort-year combinations due to low survival in Year 2 (Table 2.2).

We performed a fourth set of analyses to test whether there was a relationship between disturbance and distance from sagebrush canopy. For each cohort-year combination, we used a generalized linear regression model with logit link where presence/absence of disturbance (which had been recorded for each seedling each spring) was predicted by linear and second order polynomial scaled shrub distance and site. To maintain statistical power, we pooled all species together and only included sites that had been retained in two or more survival by distance models.

Results

Survival, distance from the canopy, and ground cover characteristics

For both 2018 and 2019 cohorts, globemallow generally exhibited the highest mean (± 1SD) first-year survival relative to other species, although there was wide variation among sites (29.2 ± 26.5% and 23.4 ± 36.0% for cohorts 2018 and 2019, respectively; Table 2.2). The other three species exhibited similarly moderate average survival in the 2018 cohort (11.2-13.5% across species; Table 2.2), and more variable survival in the 2019 cohort (4.3-16.0% across species; Table 2.2). For the 2018 cohort, by the end of the third-year post-planting (June 2021), globemallow still exhibited the highest survival (14.13 ± 17.3%), followed by bluebunch wheatgrass (9.8 ± 19.7%), squirreltail (7.9 ± 10.7%), and yarrow (1.6 ± 1.6%). The 2019 cohort, on the other hand, showed consistently low survival in the third-year post-planting (April 2022) across all species (1.2 ± 2.2%; Table 2.2).

For seedlings in the 2018 cohort, globemallow and yarrow, experienced the highest survival outside of the sagebrush canopy, but maximum survival occurred at different distances for the two forb species (Figure 2.3, Table A4). First-year survival of the 2018 cohort of globemallow was highest near the sagebrush canopy dripline at 1.8 scaled distance units from the sagebrush stem, whereas survival of yarrow was highest at 2.9 scaled distance units (where 1 scaled distance unit indicates the canopy edge; Figure 2.2, Table A5). Neither forb species' survival in this cohort responded significantly to distance from sagebrush in their second year of growth (Table A4).

All ground cover characteristics varied significantly with distance from the sagebrush stem (distance effect $p < 0.001$, Table A6), with maximum biological soil crust and rock cover and minimum litter cover at intermediate distances from the shrub canopy (2.8, 3.3, 3.1 scaled distance units, respectively, Figure 2.4). For the 2018 cohort, Year 1 globemallow survival showed trends of positive association with higher biological soil crust and rock cover, but negative association with litter cover ($X^2 = 4.99$ $df = 1$ $p = 0.025$, $X^2 = 6.04$ $df = 1$ $p = 0.014$, $X^2 = 4.78$ $df = 1$ $p = 0.029$, respectively, though in all cases, relationships are no longer significant when the conservative Bonferroni correction [$\alpha = 0.006$] for multiple comparisons is applied; Figure S1,Table A7).

For the 2018 cohort, neither bluebunch wheatgrass nor squirreltail survival was significantly affected by distance from a sagebrush canopy in either year post-planting ($p > 0.05$; Figure 3 2., Table A4). However, for the 2018 cohort, bluebunch wheatgrass survival showed a trend of negative association with physical crust cover (LR $X^2 = 4.81$ $df = 1$ $p = 0.028$; Figure S1, Table A7), which itself varied significantly with distance from the sagebrush stem (LR $X^2 = 1270.55$ $df = 1$ $p < 0.001$; Figure 2.4, Table A6). Squirreltail survival was not significantly associated with ground cover (Table A7).

Seedlings in the 2019 cohort, which generally experienced a much drier first-year (Table 2.1), did not respond significantly to distance from sagebrush canopy for any species 1- or 2-years post-planting (Figure 2.3, Table A4). Although probability of disturbance varied across sites, there was no relationship between disturbance and distance from sagebrush stem for any cohort-year combination (Table A8).

Precipitation and disturbance

Although we could not explicitly test how precipitation interacted with disturbance to influence survival, we found that the sites planted last (Saddle Mountain, Birds of Prey, and Onaqui) received the highest precipitation in the 21 days following planting (Table 2.1) but had varied disturbance rates. In 2018, for sites with qualitative signs of disturbance, herbivory accounted for 34% of disturbed seedlings at Wilson, 69% at Rock Creek, 78% at Birds of Prey, 85% at Onaqui, and 99% at Roberts. In both 2018 and 2019 planting years, of the three high precipitation sites, Saddle Mountain had moderate precipitation in the 21 days immediately after planting coupled with low disturbance (17, 23 mm precipitation, and 0, 3% of seedlings disturbed for 2018, 2019 cohorts, respectively; Table 2.1), and 1-year seedling survival was high (45, 69% for 2018, 2019 cohorts; Table 2.1). Conversely, Birds of Prey had higher precipitation than Saddle Mountain (Table 2.1), but disturbance was extremely high (94 ,100% for 2018, 2019 cohorts; Table 2.1) and 1-year survival was very low (1, 0.3% for 2018, 2019 cohorts; Table 2.1). The 2019 Onaqui cohort exhibited a similar pattern: high precipitation (37 mm), but high disturbance (48%) and low survival (5%; Table 2.1). This contrasted with the 2018 Onaqui cohort which experienced lower precipitation for 21 days post-planting (10 mm), but low herbivory (5%) and moderate 1-year survival (23%; Table 2.1).

Discussion

Nurse shrubs improve seedling survival across multiple semiarid systems (Poulos et al. 2014; Macek et al. 2018), yet most studies focus on spatial binaries associated with nurse shrubs: canopy versus interspace microsites. This paradigm often implicitly assumes that canopies are generally “good” microsites and interspaces are “bad” for establishment and survival of some species. We present evidence that, for two forb species native to sagebrush communities in the western U.S. and commonly used in restoration, survival is optimized in the zone between the shrub canopy dripline and the “interspace maximum” which we define as the microsite equidistant between the focal nurse shrub and its neighbor shrub. Understanding survival in this “intermediate zone” requires more nuance than the simple canopy-interspace paradigm allows. Had we used the binary categories of canopy-interspace, we would have found higher survival of the forbs at the canopy dripline than in the interspace maximum, but we would have missed the even higher species-specific peaks of survival in the intermediate zone between the extremes. Within our study ecosystem, our finding that nurse shrub effects of live sagebrush extend beyond the canopy dripline fills a knowledge gap left open by previous studies that have focused primarily on post-fire landscapes with dead sagebrush. More generally, our results enhance our understanding of how nurse shrub effects might more effectively be applied in restoration contexts.

Distance effects on survival

We hypothesized that the net effects of competition and facilitation would lead to the highest survival of transplants just outside the sagebrush canopy where seedlings could partially avoid competition with established vegetation while still benefiting from nurse shrub effects. Yarrow and globemallow are competitively suppressed by bunchgrasses (Parkinson 2008; Kildisheva & Davis 2012), which are more abundant under the canopy (Holthuijzen & Veblen 2015). Thus, that their peak survival was highest in the intermediate zone between canopy and interspace maximum, is consistent with the idea that they survived best when they could grow as close to the canopy as possible without being suppressed by established vegetation under the canopy. Although the negative effects of competition from established grasses under the canopy likely vary with planting type (e.g., seeds versus seedlings) and planting-year weather, our data nonetheless suggest no disadvantage in the first or second year of survival to planting grasses near nurse plant canopies.

We found that the location within the intermediate zone at which highest survival occurred varied across species. For the 2018 cohort, first-year survival of globemallow was highest outside but near the sagebrush canopy dripline, while survival of the other forb species, yarrow, peaked farther from the sagebrush, mid-way between the canopy and interspace maximum. Globemallow may have benefited from growing closer to the sagebrush canopy because its deeper roots (Pendery & Rumbaugh 1993) allowed it to access the higher soil moisture typically associated with sagebrush canopies due to hydraulic redistribution (Caldwell & Richards 1989). Growing close to sagebrush canopies may have been less advantageous for yarrow, however, with its shallow, fibrous, and lateral roots (Warwick & Black 1982) because hydraulic redistribution only increases soil moisture deeper than 10 cm (Cardon et al. 2013). Peak survival of yarrow that occurred farther into the interspace may instead have been at a distance that was characterized by other abiotic ameliorations (e.g., elevated nutrients) that extend beyond sagebrush canopies, as well as by reduced competition from sagebrush and other understory plants.

In contrast to the two forbs species, we found that neither grass species responded to proximity to sagebrush. Grass survival was likely consistent across different distances from sagebrush because it was minimally affected by competition. Bluebunch wheatgrass is shade tolerant and is not out-competed for root space by established sagebrush (Huber-Sannwald & Pyke 2005). Squirreltail is also a competitive species as evidenced by its ability to establish from seed in invasive grass-dominated stands (Hironaka & Sindelar 1973) and compete against forb species (Parkinson 2008). Root systems of both grasses, which are fibrous and relatively deep (Reynolds & Fraley 1989; Cline et al. 1977) may have helped them survive in the interspace better than the forbs, which are fibrous (yarrow) or deep-rooted (globemallow), but not both. Previous studies show that squirreltail and bluebunch wheatgrass exhibit higher establishment in and around the sagebrush canopy, but those studies focus on mature plants that have experienced barriers at multiple life stages (Holthuijzen & Veblen 2015) or occur in post-fire settings where the barriers to establishment differ to those in our intact system (Boyd & Davies 2012).

Our findings may also be applicable outside of both the Intermountain West and semi-arid rangelands. For instance, the tension between benefits versus drawbacks of canopy microsites has been shown to drive establishment in the intermediate zone between canopy and interspace maximum in an alpine Mediterranean system, where clumps of perennial grasses act as nurse plants for other grasses and forbs (Pescador et al. 2014). Because the strength of nurse shrub effects on the abiotic microenvironment is generally weaker where abiotic stress is lower (e.g., more mesic, north-facing, higher elevation; Davies et al. 2007) increased seedling establishment may occur farther from the canopy (e.g., at maximum interspace distances) in more mesic systems. Additionally, our results suggest species- and functional group-level responses could potentially correspond with traits such as root morphology (e.g., taproot vs. fibrous roots).

Temporal dynamics

We had hypothesized that peak survival relative to the canopy would change between growth-years because, theoretically, the favorable microenvironment for survival and growth can change across different plant life stages (Schupp 2007). We found that distance from the canopy acted as a first-year bottleneck: once forb seedlings established in the intermediate zone in the first year, they were not further affected by proximity to sagebrush canopy in the second year. Facilitation and mutualism can shift to competition with increases in plant size, density, and age (Nakazawa 2020), likely minimizing nurse shrub effects as plants increase in size or density. Our observed initial nurse-shrub effect that dampens over time has been observed in other semiarid systems but not explicitly linked to distance from the nurse shrub (Nuñez et al. 2009).

We also found that our results appear to contrast with Swanson et al. (2021), the only study we found that experimentally tested facilitative effects of sagebrush canopies under different precipitation conditions. These authors found that the benefits of sagebrush canopy effects were stronger under drought than ambient conditions, consistent with spatial patterns of mature plants across precipitation gradients in this system (Holthuijzen & Veblen 2015). We, however, found that first-year survival of the 2019 cohort, following a drier than normal growing season, was not affected by proximity to sagebrush. Given the very low first-year survival of transplanted seedlings at most sites that year, presumably due to dry conditions, our sample size may have been too small to detect significant patterns of survival.

Ground cover characteristics

We found that ground cover characteristics and seedling survival covaried with respect to distance from shrubs, in patterns that would have remained unexplained by canopy-interspace models that ignore the potential for variability throughout the interspace. Like first year survival of the 2018 globemallow cohort, cover of biological soil crust (BSC) and rock cover were highest in the "intermediate zone" between sagebrush canopy and interspace maximum. It may be that globemallow and BSC simply share microsite requirements. It is also possible that seedling survival responded positively to BSC and rock because both have been found to increase the growth of non-nitrogen fixing forbs and cool-season grasses (Nobel et al. 1992; Havrilla et al. 2019) by increasing soil moisture (Chamizo et al. 2016; Nobel et al. 1992) and soil fertility (Ferrenberg et al. 2018).

Regardless of the mechanisms driving covariation between groundcover characteristics and seedling survival, our results suggest that when these patterns exist, they could be used as indicators or guides for identifying ideal planting microsites. In our study system, we note tradeoffs to using BSC cover as a guide because disruption to BSC during planting could increase cover of exotic annual grasses (Havrilla & Barger 2018).

We did, however, observe partial recovery of biocrusts two to three years post-planting (S. Koutzoukis, pers. obs.), a process that could potentially be hastened by inoculating planting microsites with BSC (Velasco Ayuso et al. 2017).

Precipitation and disturbance

Because post-planting precipitation strongly influences seedling survival (O'Connor et al. 2020) we expected sites that experienced the highest precipitation in the three weeks immediately post-planting to result in the greatest survival. But herbivory can be as or more influential on establishment than abiotic conditions (Cuevas et al. 2013). As such, one of the highest precipitation sites (Birds of Prey) experienced the lowest survival, likely due to high rates of disturbance, which was comprised primarily of herbivory (78% of disturbed seedlings showed signs of herbivory). Meanwhile, the site with the highest survival (Saddle Mountain) experienced both high precipitation and low herbivory. Although herbivory can reinforce clustering of vegetation around shrubs (Adler et al. 2001; Verwijmeren et al. 2013), we found that there was no relationship between disturbance and distance from sagebrush stem within sites.

Targeting the intermediate zone

Our results indicate that targeting transplanting to the intermediate zone would be particularly advantageous when practitioners are already targeting non-drought periods or otherwise trying to maximize post-planting precipitation, as is becoming increasingly imperative in drylands (see Table A4; Hardegree et al. 2018). Additionally, planting greenhouse-grown seedlings helps bypass seed-to-seedling barriers to establishment (see James et al. 2011) when used in place of traditional drill or broadcast-seeding approaches that have met limited success (Knutson et al. 2014). There are two other potential long-term benefits to increasing establishment in the intermediate zone in these fire-prone landscapes: 1) plants growing outside the canopy are less likely to be exposed to fatal head-loads and more likely to survive future fires (Hulet et al. 2015) and 2) plantings in the intermediate zone could be used to close large gaps between perennial plants in intact sagebrush stands at risk for invasion (Chambers et al. 2014). Reisner et al. (2013) suggests that, in this system, sites with larger gaps between perennial vegetation are more susceptible to cheatgrass invasion and associated fire risk, and increased perennial plant cover is associated with both pre-fire resistance to invasive annual grass establishment post-fire resilience (Chambers et al. 2014). Testing whether plant establishment can be increased by targeting restoration plantings in favorable intermediate zones between nurse shrub canopies and interspace maximums also has potential utility in other semi-arid systems where resistance and resilience can be improved by increasing plant densities.

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Tables

Table 2.1: Site descriptions and seedling cohort information for two planting cohorts (2018 and 2019). The Rock Creek site was planted in 2018, but later burned and was replaced by a nearby site, Grey Butte, for the 2019 cohort. In fall of each year, seedlings were planted at six sites, with order in the table indicating planting order (Rock Creek/Grey Butte first, Saddle Mountain last). Normal precipitation is 30-year climate normal. Study period precipitation is total precipitation from October of planting year to the following June, while % is the percent of normal precipitation for that period, and the value in parenthesis is precipitation (mm) in the 21 days after planting (PRISM Climate Group 2004). For each cohort (2018/2019), Year 1 survival is percent of seedlings alive in May/June following (fall) planting, and Year 1 disturbance is the percent of seedlings that showed qualitative signs of disturbance in the May/June following planting relative to the total number of seedlings originally planted.

Site	Elevation (m)	30 Year Normal Precipitation (mm)	2018 Cohort				2019 Cohort			
			Study Period Precipitation	Sedlings Planted	Year 1 survival (%)	Year 1 disturbance (%)	Study Period Precipitation	Sedlings Planted	Year 1 survival (%)	Year 1 disturbance (%)
Rock Creek	1489	267	291 mm, 133% (1 mm)	356	3	64	—	—	—	—
Grey Butte	1510	265	—	—	—	—	171 mm, 79% (0 mm)	413	6	44
Wilson	1646	297	387 mm, 160% (1 mm)	402	7	23	287 mm, 118% (0 mm)	380	3	62
Roberts	1477	259	240 mm, 156% (3 mm)	384	16	57	145 mm, 94% (3 mm)	415	8	14
Onaqui	1670	297	325 mm, 154% (10 mm)	399	23	5	157 mm, 74% (35 mm)	391	5	48
Birds of Prey	972	274	344 134% (34 mm)	362	1	97	313 mm, 122% (24 mm)	340	0	100
Saddle Mountain	257	213	218 mm, 150% (23 mm)	406	45	0	128 mm, 88% (17 mm)	354	69	3

Table 2.2: Percent survival across all planting sites for herbaceous seedlings planted in Oct-Dec of 2018 (2018 Cohort) and 2019 (2019 Cohort). Species include globemallow (*S. munroana*), yarrow (*A. millefolium*), bluebunch wheatgrass (*P. spicata*), and squirreltail (*E. elymoides*). Table values (mean ± 1SD) are percent survival relative to number of seedlings originally planted. Values in parentheses (mean ± 1SD) are relative to number of seedlings that had survived to the previous year and only include sites (n) where there were living seedlings for that species the previous year. Seedlings were monitored for survival post-planting at 6-7 months (Year 1), 18-19 months (Year 2), 30-31 months (Year 3), and 40-41 months (Year 4). One site, Rock Creek, burned after Year 1 and is not included in calculations for the 2018 Cohort Year 2, 3 or 4 and was replaced by a nearby site, Grey Butte, for the 2019 cohort.

	Year 1	Year 2	Year 3	Year 4
		2018 cohort		
Globemallow	29.15 ± 26.46	23.35 ± 20.68	14.13 ± 17.3	6.16 ± 7.58
	—	(68.2 ± 24.38, n=4)	(53.83 ± 38.16, n=4)	(50.2 ± 35.26, n=4)
Yarrow	11.25 ± 18.04	7.6 ± 12.98	1.29 ± 1.62	0.66 ± 0.93
	—	(56.03 ± 35.26, n=4)	(24.06 ± 22.08, n=4)	(50 ± 50, n=3)
Bluebunch Wheatgrass	13.53 ± 21.7	10.22 ± 20.68	7.87 ± 17.59	6.18 ± 12.35
	—	(41.86 ± 31.51, n=5)	(20.83 ± 41.67, n=4)	(62.86, n=1)
Squirreltail	12.42 ± 12.18	6.71 ± 10.9	4.75 ± 9.64	3.68 ± 8.24
	—	(40.75 ± 32.35, n=4)	(37.3 ± 42.35, n=3)	(46 ± 65.05, n=2)
Total	**16.53 ± 16.17**	**11.85 ± 13.63**	**6.66 ± 9.00**	**4.29 ± 5.75**
	—	**(52.1 ± 28.6, n=5)**	**(37.17 ± 35.28, n=5)**	**(52.5 ± 30.42, n=4)**
		2019 cohort		
Globemallow	23.36 ± 36.01	10.55 ± 20.73	2.25 ± 4.48	—
	—	(26.93 ± 20.7, n=5)	(34.56 ± 35.32, n=4)	—
Yarrow	4.3 ± 4.28	0.87 ± 0.76	1.03 ± 1.68	—
	—	(23.48 ± 19.76, n=5)	(50 ± 57.74, n=4)	—
Bluebunch Wheatgrass	12.49 ± 27.56	3.67 ± 8.13	1.31 ± 2.44	—
	—	(26.62 ± 25.16, n=3)	(15.79 ± 22.33, n=2)	—
Squirreltail	15.98 ± 29.62	2.06 ± 2.72	1.78 ± 2.74	—
	—	(36.25 ± 39.35, n=3)	(52.78 ± 24.06, n=3)	—
Total	**15.21 ± 26.58**	**4.59 ± 8.21**	**1.24 ± 2.21**	—
	—	**(24.07 ± 18.33, n=6)**	**(31.41 ± 29.95, n=5)**	—

Figures

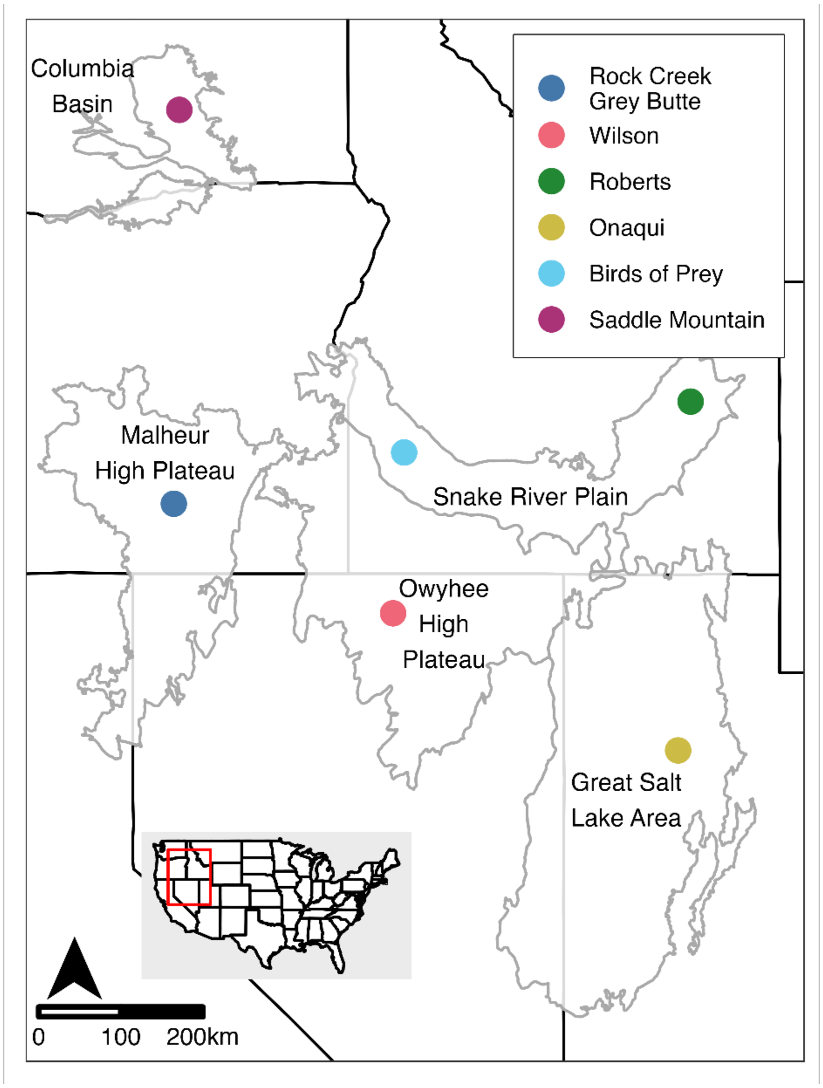

Figure 2.1: Map of site locations. Sites are listed according to descending annual temperature and ascending annual precipitation. Rock Creek burned in fall of 2019 and a new site was established 6 km away at Grey Butte. Shading and labels indicate Natural Resources Conservation Service (NRCS) Major Land Resource Areas (MLRA).

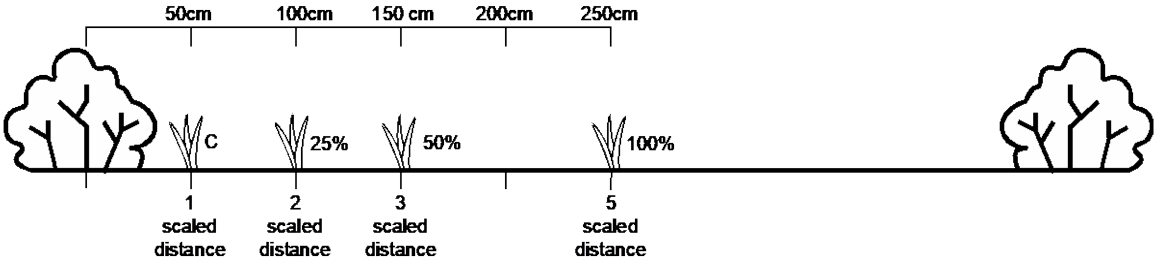

Figure 2.2: Schematic describing the planting design and analytical units. Planting microsites were chosen at random to be one of four possible locations: the canopy dripline (C), the farthest distance between neighboring sagebrush (100%, the "maximum interspace distance") and 25% and 50% of the distance from the canopy to the maximum interspace distance. When planting, only one microsite type was assigned per focal sagebrush. In analyses, distances were converted to "scaled shrub distance", a unitless metric that accounts for the relationship between the areal extent of nurse shrub effects and the size of the nurse shrub. Scaled shrub distance is the sagebrush radius divided by distance of the seedling from the sagebrush base. In this example, the radius of the sagebrush is 50 cm, and the canopy microsite is at 50 cm from the sagebrush base resulting in a value of "1" scaled distance. The 25%, 50%, and 100% microsites are, respectively at 100, 150 and 250 cm from the base, corresponding to 2, 3 and 5 scaled distances.

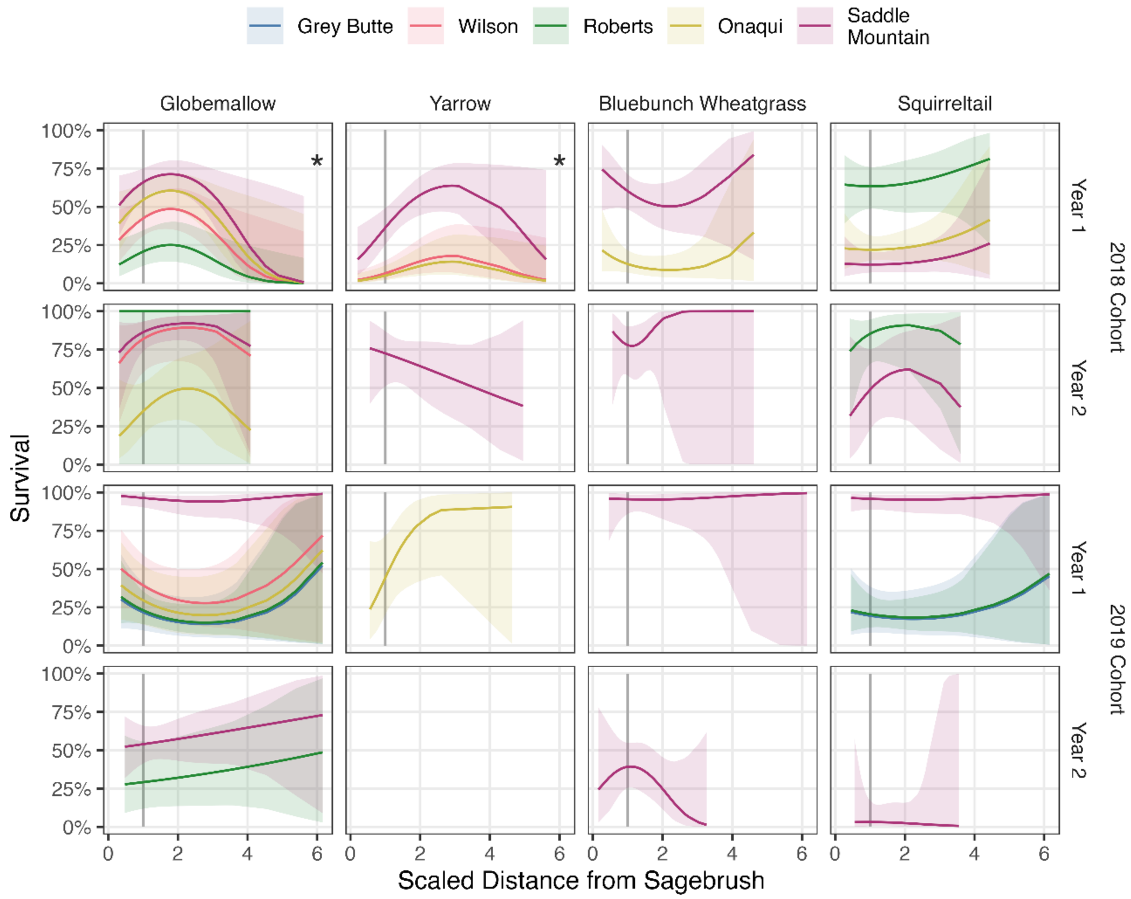

Figure 2.3: Modeled estimated marginal mean survival for each of four herbaceous plant species planted across 5 sites in the Intermountain West, USA. Rows represent different combinations of cohort (2018, 2019) and post-planting period (Year 1 and Year 2). Scaled distance from sagebrush (x axis) is sagebrush radius divided by distance of seedling from sagebrush base (where the grey vertical line at 1 indicates the canopy edge). Error ribbons indicate 95% confidence interval. For each cohort, Year 2 survival only includes, and is relative to the number of, seedlings that survived to Year 1. Sites were only included in each cohort-planting period model if at least 5 individuals survived. Asterisks indicate a significant relationship between survival and distance from the sagebrush ($p < 0.05$).

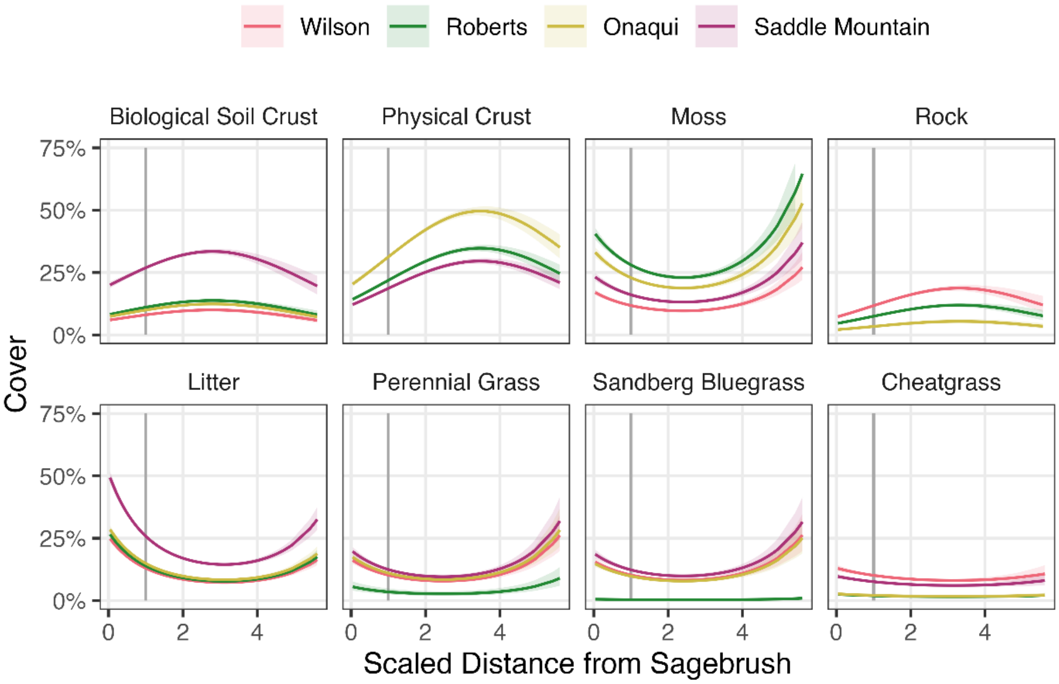

Figure 2.4: Estimated marginal mean cover for eight ground cover types measured at different distances from sagebrush canopies across five sites in the Intermountain West, USA. Scaled distance from sagebrush (x axis) is sagebrush radius divided by the distance between the sagebrush base and the microsite where the ground cover variable was measured (where the grey vertical line at 1 indicates the canopy edge). Error ribbons indicate 95% confidence intervals. All variables significantly differed by site and scaled distance from the sagebrush.

CHAPTER 3

UNDER DROUGHT CONDITIONS, FUNGICIDE COATING DOES NOT INCREASE EMERGENCE OF TWO NATIVE GRAS SPECIES IN SAGEBRUSH STANDS OF THE INTERMOUNTAIN WEST

Abstract

Coating seeds with amendments to increase germination, emergence, and establishment is a promising avenue of research in dryland restoration. Fungicide treatments represent a potential seed coating ingredient for use in Western US rangelands, where fungal pathogens can cause seed mortality during winter stratification between late fall seeding and spring germination. In this system the effectiveness of the fungicide treatment can be dictated by climate and the microenvironment within a site. We tested how fungicide coating influenced seedling emergence of native grasses within sagebrush stands by planting fungicide-coated, uncoated, and blank-coated (i.e., coated but without an active fungicide ingredient) seeds in furrows that extended from the canopy dripline of sagebrush plants (*Artemisia tridentata* ssp. *wyomingensis*) into the interspace at four sites across the Intermountain West two successive years. We planted two native grasses, bluebunch wheatgrass (*Pseudoroegneria spicata*) and bottlebrush squirreltail (*Elymus elymoides*). Emergence was extremely low in both years. We observed complete seeding failure where zero seedlings emerged, across treatments, at two sites in the first year and at three sites in the second year. At the site where enough plants emerged to statistically analyze data, fungicide had no effect on emergence. In the drier year at this site, which was the lowest in elevation, the highest emergence was at the canopy dripline. We

conclude that under anomalously dry and nearly normal precipitation conditions, fungicide does not, but proximity to sagebrush canopy might, increase emergence. This work highlights the site- and weather-specificity of the success of seed coating amendments.

Introduction

Over 50% of global drylands are considered degraded and require intervention to restore ecosystem function and services (Volis 2019; Mahata & Sharma 2021). Seeding is the most common method to revegetate degraded sites because it can be implemented at broad scales, which is often required of these restoration projects (Kildisheva et al. 2016). Still, the success of revegetation by seeding is subject to several limitations, both biotic and edaphic (James et al. 2011). Coating seeds with amendments to help them overcome biotic and edaphic barriers to germination and emergence is an approach borrowed from commercial agriculture and horticulture (reviewed in Jamieson 2008), but more recently being tested in wildland restoration settings (Madsen et al. 2016; Brown et al. 2021; Svejcar et al. 2022). Some seed amendments commonly tested in restoration settings include surfactants, pelletized seeds, and herbicide protectants (Madsen et al. 2016). However, the ecological conditions associated with wildland restoration settings are highly variable across space and time. Using seed-coating amendments in these settings requires a thorough understanding of the ecological contexts in which they are most or least effective at improving plant establishment, across years, sites, and at a microsite-level within a site.

Fungal pathogens are widespread and thought to be a common cause of the loss of seed viability in drylands (Gornish et al. 2015), suggesting that anti-fungal seed amendments may be a promising approach to improve plant establishment in restoration settings. In temperate zones, seed-based revegetation projects often are conducted in fall to delay germination and emergence until spring when soil moisture is highest (Monsen et al. 2004). But, seeds are vulnerable to soil fungal pathogens during the two- to three-month stratification period between sowing and germination (Gornish et al. 2015). Seeds coated with fungicide can increase establishment by as much as 59% by defending seeds against soil fungal pathogens (Hoose et al. 2022), but fungicide coatings do not always affect emergence (Gornish et al. 2015; Hoose et al. 2022).

At a given site, inter-annual variation in weather appears to influence the effectiveness of fungicide coatings, improving establishment rates when precipitation is above-normal, but not affecting emergence when precipitation is at or below normal (Hoose et al. 2022). Additionally, the competitive fitness of pathogens can be reduced or enhanced by soil moisture and temperature (Mackin et al. 2021), factors that can vary at a microsite scale. In drylands, areas under or near shrubs can often provide microclimates typically advantageous to seedlings because they are characterized by increased soil moisture and decreased temperature compared to surrounding interspaces (Davies et al. 2007). However, shrub canopies are also associated with increased microbial activity (Cardon et al. 2013), including increased fungal abundance (Ochoa-Hueso et al. 2018), which may include pathogens that target seeds during the period preceding germination and emergence.

Wildfires and legacies of improper grazing have left western US drylands in various stages of degradation (Davies et al. 2012), requiring active restoration to establish desired native species and break the positive feedback loop between fire and exotic annual grass invasion (D'Antonio & Vitousek 1992; Chambers et al. 2014). However, efforts to establish desirable native species by seeding frequently fail (Knutson et al. 2014). Adoption of precision strategies that target biotic and abiotic limitations to plant establishment is critical to improving restoration outcomes (Copeland et al. 2021). We investigated spatial patterns in fungicide-coated seed emergence associated with microsites that span the distance between canopy dripline and the maximum interspace distance between sagebrush shrubs for two grass species, bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve) and bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), native to sagebrush rangelands of the western U.S. We predicted that fungicide-coated seeds would have higher establishment closer to the canopy than would uncoated seeds because coated seeds would be more resistant to fungal pathogens that may be higher closer the canopy. We predicted that, if precipitation was at or below-normal, fungicide would have no effect on emergence, regardless of microsite, but if precipitation was above-normal, fungicide-coated seeds would exhibit higher emergence than uncoated seeds.

Methods

Site selection and focal species

We selected four sites across the Intermountain West representative of the elevation and climate ranges of Wyoming big sagebrush (*Artemisia tridentata* Nutt. var. *wyomingensis* (Beetle & Young) S.L. Welsh; see Innes 2019; Table 3.1). The sites were in four Major Land Use Resource Areas in four states: Columbia Basin, WA (Saddle Mountain), Great Salt Lake Area, UT (Onaqui), Snake River Plain, ID (Roberts), and Malheur High Plateau, OR (Grey Butte; USDA NRCS 2021). All sites were aridisols

(Soil Survey Staff 2020) but varied in texture (Table 3.1). Sites ranged in elevation from 257m to 1670m, with mean annual temperature of 6-11°C and mean annual precipitation of 213-296 mm (PRISM Climate Group 2014; Table 3.1). All sites were located on public lands managed by the Bureau of Land Management (Roberts, Onaqui) or Fish and Wildlife Service (Saddle Mountain, Grey Butte).

Squirreltail (*Elymus elymoides*) and bluebunch wheatgrass (*Pseudoroegneria spicata*) are medium and deep rooted, respectively, perennial bunchgrasses common to the Intermountain West (Reynolds & Fraley 1989; Canadell et al. 1996). Squirreltail is currently found at all four sites and their surrounding areas. Bluebunch wheatgrass is currently found at all sites except Roberts, although it is included in the site's reference conditions (NRCS 2020).

Seed source and preparation

We used commercially released varieties of squirreltail and bluebunch wheatgrass seeds sourced from L&H Seeds (Connell, WA, USA). We purchased new lots of seeds for each year of the experiment but used the same varieties. We planted Anatone bluebunch wheatgrass (Monsen et al. 2003) and Toe Jam squirreltail (Jones et al. 2004) at the more mesic, cooler sites (Roberts, Grey Butte; Table 3.1) and Columbia bluebunch wheatgrass (Jones & Mott 2016) and Turkey Lake squirreltail (Jones 2016) at the more xeric, warmer sites (Saddle Mountain, Onaqui; Table 3.1). We tested three treatments: seeds left untreated (uncoated), seeds treated with a coating containing fungicides (coated-fungicide), and seeds coated with no active ingredient (coated-blank). The fungicide coating contained four fungicides that address the pathogens that Gornish et al. (2015) identified as common fungal pathogens affecting bluebunch wheatgrass seeds over winter (Table B1). The fungicides (mefenoxam, fludioxonil, azoxystrobin, difenoconazole) inhibit cellular respiration, interfere with DNA, RNA, and cell wall synthesis, and interrupt signal transduction with half-lives that range from 9 to 220 days (Table B1). The fungicides were bound to the seeds using Agrimer SCP II polymer binder (Ashland Inc., Covington, KY, USA) and calcium carbonate powder (Clayton Calcium; Parma, ID, USA). The coated-blank seeds were prepared with the same materials and methods as the coated-fungicide seeds, except fungicides were not added to the seeds. This treatment was added as a control to observe the effects of the coating alone without the influence of the fungicides. Both coating types were applied in a rotary drum seed coater (Universal Coating Systems, Independence, OR, USA) in our lab at Brigham Young University (Provo, UT, USA). See Hoose et al. (2022) for application rates and more detailed methods.

Planting

We planted along 1m long furrows that extended from the dripline (i.e., outside edge) of a sagebrush canopy towards the interspace between that focal sagebrush and its nearest sagebrush neighbor. To guide selection of focal sagebrush plants, at each site we established a 0.15 ha plot within which we located 7-12 transects, 5 m apart, that were either 25 m or 50 m long. The number of transects and their lengths varied across sites to allow us to avoid patches of dense cheatgrass cover, animal trails, fences, and roads. Along each transect we selected approximately 20–40 focal sagebrush, depending on transect length. At each focal sagebrush we established a 1 m furrow, in a random azimuth, that began at the canopy dripline and extended into the interspace. Half of the transects were planted in each year (2020 or 2021).

At each of the four study sites, in each year, we planted 120 furrows, which were divided equally (i.e., 20 furrows each) and randomly among our six treatment-species combinations (coated-fungicide, coated-blank, and uncoated treatments, each applied to both squirreltail and bluebunch wheatgrass). We planted following methods and training by the authors of Hoose et al. (2022), using the same people in both years of our study. Furrows were approximately 15 cm wide, 2-4 cm deep, with a smaller 1 cm wide, 1cm deep furrow centered in the middle of the larger furrow. The deeper furrows increase soil moisture and can greatly increase emergence, and the smaller furrow keeps the seeds in place (Anderson et al. 2023). We planted 75 seeds evenly throughout the length of the smaller furrow and covered them with a few millimeters of soil (November 4-11, 2020; November 11-December 5, 2021). We assessed emergence in the spring following planting (June 04-18, 2021; April 30-June 05, 2022) by recording the exact distance (cm) of each emerged seedling from the sagebrush canopy edge. We also measured the height and crown diameter of the focal sagebrush plants.

Analysis

Due to low emergence rates (Table B2), we were only able to analyze data from one site (Saddle Mountain) planted in 2020. We used a Poisson linear mixed effect model with a log link to model emergence. The response variable, number of emerged seedlings, was binned according to distance from canopy dripline; we used the exact distances measured in the field to tally the number of emerged seedlings in each of 11 bins (0-10 cm, 11-20 cm, etc. to 101-111 cm as the final bin). The fixed effects were the distance bin, coating treatment, species, and the interaction of distance bin and coating treatment, and the random effect was the focal sagebrush associated with the planting transect, using

R package *glmmTMB* (Brooks et al. 2017). The model was checked for zero inflation and model assumptions (normality, dispersion, heteroskedasticity) using the R package *DHARMa* (Hartig 2021). Analyses were conducted in R version 4.4.1 (R Core Team 2021).

Results

All sites in the 2020 cohort experienced an anomalously dry period from the June before planting to the time of monitoring (Figure 3.1a, Table 3.1). The 2021 cohort experienced high precipitation for five months before planting, but during the period from planting to monitoring, precipitation was at-normal at Saddle Mountain and below-normal precipitation at the other three sites (Figure 3.1a; Table 3.1). For the 2020 cohort, December - January was anomalously warm at Saddle Mountain and normal at all other sites, while the 2021 cohort saw anomalously cold December - January temperatures at all sites except Grey Butte where temperatures were above-normal (Figure 3.1b, Table 3.1).

For the 2020 cohort, we observed emergence at only two of four sites; at Saddle Mountain, 318 seedlings emerged at 77 furrows across all species and treatments, and 5 seedlings emerged at 4 furrows at Roberts. For the 2021 cohort, Onaqui was the only site with emergence, with 19 seedlings emerging across 16 furrows (Table B2).

At Saddle Mountain (2020 cohort), emergence was highest at the canopy and declined to nearly zero by the end of the 1-meter planting furrow (distance bin effect: $X^2=58.4$, $df=1$, $p<0.001$; Figure 3.2, Table B3). Emergence did not differ by species ($X^2=0.45$, $df=1$, $p=0.5$), by coating ($X^2=1.16$, $df=2$, $p=0.56$), or the interaction between distance from the canopy and coating ($X^2=3.61$, $df=2$, $p=0.16$; Figure 3.2, Table B3).

Discussion

Seed coating is an exciting approach to overcome barriers to establishment in failure-prone systems because often it does increase emergence and establishment (Madsen et al. 2016; Berto et al. 2021; Dadzie et al. 2022) while potentially being scalable for large revegetation projects. Specifically, fungicides have improved establishment rates in the Intermountain West (Fund et al. 2019; Hoose et al. 2022) where fungal pathogen pressure during winter stratification is a bottleneck to establishment (Gornish et al. 2015). However, the exact context in which restoration, especially via novel techniques, is "successful" is subject to limitations associated with favorable climatic conditions (Hardegree et al. 2018).

We asked whether fungicide-coated seeds improve emergence and if there are species-specific patterns in emergence. We found low overall emergence regardless of treatment, where only 0.48 % of all seeds planted emerged, which we attribute to low precipitation during our study period. Even at the one site where we observed enough emergence to statistically analyze data, fungicide did not increase establishment for either species. Our findings support Hoose et al. (2022), who, with identical fungicide formulations as our study, found that fungicide does not improve emergence rates when precipitation is anomalously low or nearly normal for bluebunch wheatgrass (*Pseudoroegneria spicata*). Our results indicate this to also be the case for the previously untested species, squirreltail (*Elymus elymoides*). Under dry soil conditions, overall fungal abundance (Talley et al. 2002) and their pathogenic effects on seed survival (Mordecai 2012) are less pronounced. Given that our results and those of Hoose et al. (2022) indicate that fungicide coatings do not work when precipitation is at or below-normal, and Svejcar et al. (2017) found that precipitation is below-normal about 50% of the time in the Intermountain West, it follows that fungicide coatings might only increase emergence about 50% of the time. Additionally, we seeded in areas with existing perennial vegetation, a factor that may have limited soil moisture availability; while sagebrush increase under-shrub soil moisture via shading (Liu et al. 2021) and hydraulic lift (Prieto et al. 2011), existing perennial and annual grasses may decrease soil moisture throughout the growing season (Booth et al. 2003).

Bottlenecks between seed and established plant have been widely documented in dryland seeding projects (James et al. 2011), and each year, we observed complete seeding failure (zero emergence) in at least 50% of our sites. Potential causes of seeding failure are broad. Overall precipitation and its timing strongly controls seedling emergence (Pyle et al. 2021). Freezing between germination and emergence also is a common cause of losses of seed viability for fall-sown seeds (Boyd & Lemos 2015; Copeland et al. 2022), and seed coating amendments that delay germination have been shown to increase emergence (Madsen et al. 2016; Fund et al. 2019). The seeds in our study would have been subject to this freezing during winter months. One possible exception was Saddle Mountain in the 2020 cohort which experienced warmer-than-average winter temperatures and, accordingly, also experienced the highest seedling emergence. However, another site, Grey Butte, also saw an anomalously warm winter in the 2021 cohort but experienced total seeding failure, making it difficult to attribute emergence patterns to temperature without direct testing.

In addition to weather and its timing, choice of seed sources and growth traits can influence establishment rates. For both species, we observed almost no emergence of the variety more adapted to (and planted in) cooler, mesic conditions (Monsen et al. 2003; Jones et al. 2004). We did, however, observe some emergence of the varieties of both species more adapted to (and planted in) warmer, more xeric conditions (Jones 2016; Jones & Mott 2016). Additionally, seedlings collected from locally adapted populations can exhibit higher emergence rates (Baughman et al. 2019) with more vigorous growth patterns (e.g., higher root:shoot ratio) than commercially grown varieties (Leger et al. 2021).

Despite low overall emergence, we were able to detect statistically significant patterns with respect to microsites for both species at one site (Saddle Mountain in 2020). The favorable microenvironment provided by the sagebrush canopy, namely higher soil moisture in the early growing season, is more pronounced at sites characterized by higher stress (i.e., south-facing, lower elevation, more xeric; Davies et al. 2007). This may explain why we observed higher emergence near the canopy at Saddle Mountain which was the lowest elevation site (1220m lower than the next highest site). However, this canopy effect did not reliably increase emergence at Saddle Mountain where no emergence was observed in the second year.

Novel restoration methods are most needed in sites with low resistance and resilience (Chambers et al. 2014), particularly during dry years. Seed coating may prove to be the solution to some revegetation failures, but we found that neither the effects of fungicide coating, nor the positive microenvironment provided by sagebrush canopies were strong enough to reliably overcome establishment bottlenecks that appeared to be driven by dry conditions. Given the high likelihood of below-normal precipitation in Wyoming big sagebrush rangelands (Svejcar et al. 2017), further investigation into factors such as seed source and herbivory (Pearson et al. 2019), is needed to fine-tune precision restoration strategies (Copeland et al. 2021) and overcome site-specific barriers to plant establishment. Restoration practitioners should consider strategies that allow for bet-hedging (e.g. Davies et al. 2018) and multiple outcomes in the face of unpredictable weather and its role in influencing revegetation success (e.g. Hardegree et al. 2018).

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Tables

Table 3.1: Site characteristics at four sagebrush-dominated study sites in the Intermountain West. Temperature and precipitation data are from PRISM at 4 km resolution (PRISM Climate Group 2014). Annual Temperature and Mean Annual Precipitation are 30-year normal averages (1991-2020). Study Period Precipitation is observed precipitation (in mm) from the month of planting (November/December) to the month of monitoring (April/June), with values in parentheses indicating percent of observed precipitation compared to 30-year normal precipitation for the same time period. Soil texture was collected from ten 2.5cm diameter 10cm deep soil cores at each site where half of the samples were taken at the canopy and the other half at the corresponding interspace, textured via hydrometer and averaged across the 10 samples after finding no differences between canopy and interspace microsite samples. Texture class reflects USDA classification (Soil Science Division Staff 2017).

Site	Elevation (m)	Latitude	Longitude	Mean Monthly Temperature (°C)			Mean Annual Precipitation (mm)	Study Period Precipitation (mm)		Soil Texture		
				Min	Mean	Max		2021 Cohort	2022 Cohort	Texture Class	Sand (%)	Silt (%)
Saddle Mountain	257	46.75	-119.36	4.5	11.0	17.5	265	91 (54%)	131 (98%)	Sandy Loam	68	6
Onaqui	1670	40.2	-112.46	1.1	9.2	17.3	297	113 (53%)	84 (62%)	Loam	45	14
Roberts	1477	43.76	-112.29	-1.7	5.9	13.6	259	112 (73%)	67 (90%)	Sandy Loam	54	17
Grey Butte	1510	42.72	-119.44	-0.4	8.0	16.4	213	146 (67%)	114 (96%)	Sandy Loam	56	20

Figures

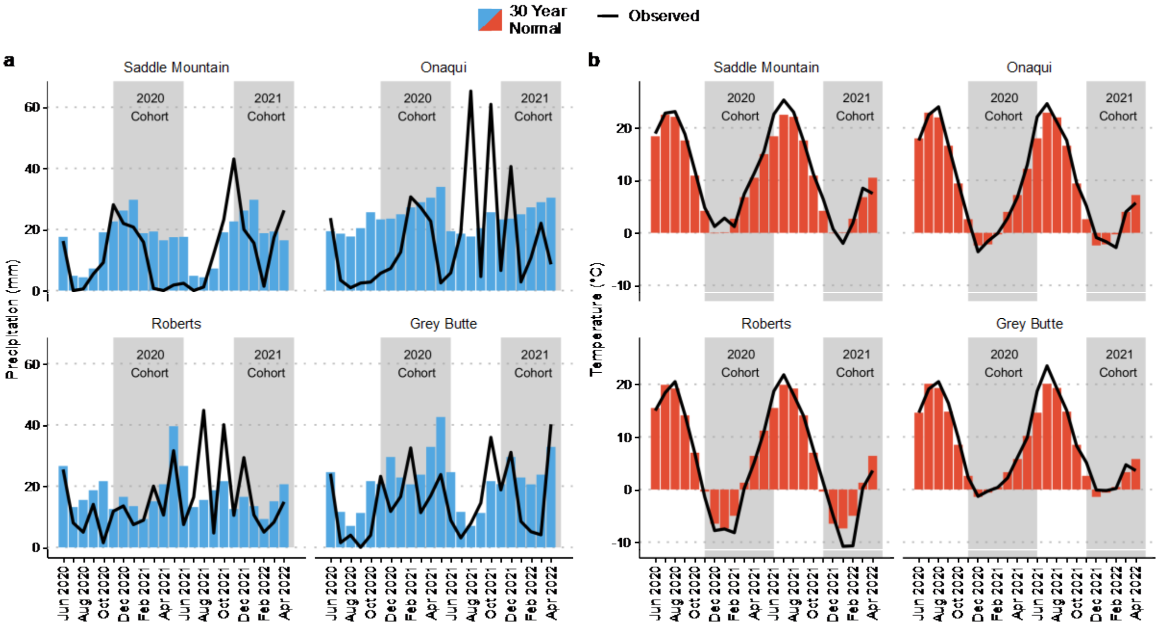

Figure 3.1: Monthly 30-year normal (1991-2020) and observed precipitation (a) and mean temperature (b) at four Wyoming big sagebrush dominated sites in the Intermountain West from June 2020 to April 2022. Line indicates monthly precipitation (a) and temperature (b) and boxes indicate 30-year normal climate. Precipitation and temperature data are at 4 km resolution (PRISM Climate Group 2014). Grey boxes indicate the study period (planting to monitoring) for each cohort, 2020 and 2021.

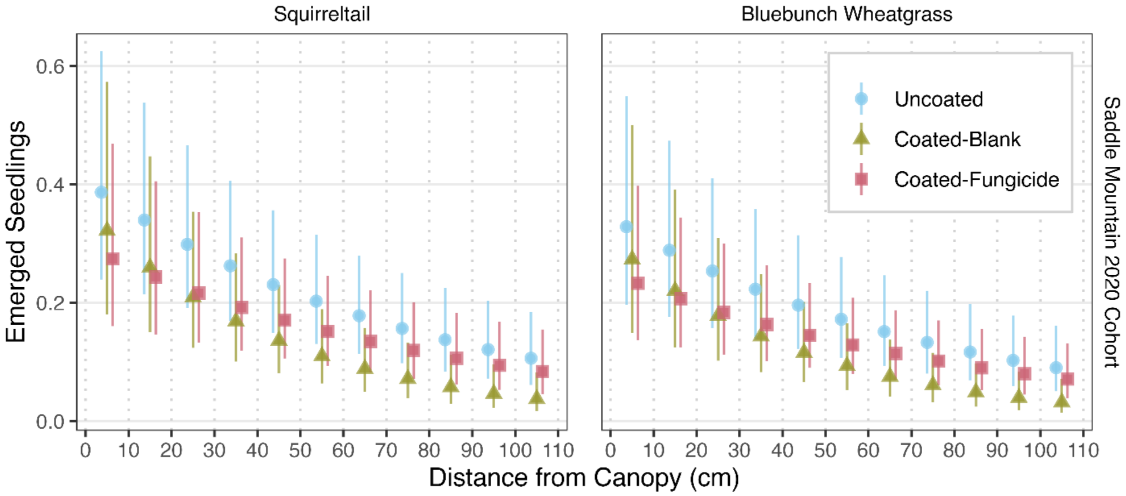

Figure 3.2: Estimated mean emergence of uncoated, coated-blank, and coated-fungicide squirreltail and bluebunch wheatgrass seeds at one site (Saddle Mountain) in the Intermountain West planted November 2020 and monitored in June 2021. Coated-fungicide seeds were coated with a polymer, limestone binder and fungicides, whereas coated-blank were coated with the polymer and limestone binder, but no fungicide. Error bars indicate 95% confidence intervals.

CHAPTER 4

CLUSTERING OF ABOVE- AND BELOWGROUND NURSE SHRUB EFFECTS IN WYOMING BIG SAGEBRUSH ISLANDS IN THE INTERMOUNTAIN WEST

Abstract

The microenvironments surrounding existing canopy vegetation in patchily vegetated systems are often seen as critical microsites for understory establishment in semi-arid systems. In sagebrush stands of the Intermountain West, these “shrub islands” are associated with sagebrush canopies, with microenvironments typically considered to be favorable near the canopy and unfavorable in the interspace, as far as possible from all sagebrush canopies. The degree to which the favorable microenvironment is clustered around the canopy and whether some attributes of shrub islands drastically change or remain elevated at intermediate distances between the canopy microsites and maximum interspace microsites is understudied. If attributes of shrub islands are not strongly clustered around canopies, the interspace region between canopy dripline and the maximum interspace distance sagebrush canopies may be advantageous for growth or establishment of some understory plants. We hypothesized that attributes of shrub islands associated with shrub canopies (e.g., shade and vapor pressure deficit) would immediately change from the canopy edge into the interspace whereas belowground attributes of shrub islands (e.g., organic matter, soil moisture, potassium, would remain elevated between the canopy edge and interspace microsites. At four sites across the Intermountain West, we sampled aboveground variables (radiation, and vapor pressure deficit) and belowground variables (organic matter, soil moisture, potassium, phosphorus) at the canopy dripline microsite, the interspace microsite (maximum distance away from neighboring sagebrush canopies), and two microsites between the canopy and interspace microsites. I found two attributes of the shrub island microenvironment had a strong association with the canopy (radiation and potassium) while other attributes (organic matter, soil moisture, and phosphorus) stayed at levels as high as the canopy in the interspace. Aside from the strong clustering of radiation and potassium, most variables showed only weak associations with the canopy, suggesting that levels of those variables are compatible with plant growth in the interspaces.

Introduction

Vegetation in arid and semiarid systems is spatially heterogeneous where, often, resource-rich "shrub islands" are interspersed within a matrix comprised of microenvironments less suitable for plant establishment (Pugnaire et al. 1996; Sala & Aguiar 1996; Schlesinger et al. 1996; Ochoa-Hueso et al. 2018).These shrub islands often serve as "islands of fertility" that shape plant community composition (Pescador et al. 2014) by providing microenvironments that promote understory plant establishment (Davies et al. 2007). The abiotic conditions associated with the areas beneath shrub canopies promote spatial clustering of new plant establishment with existing vegetation. These shrub island effects are generally thought to coincide with the area directly beneath shrubs. However, there is also evidence that some abiotic variables can remain elevated beyond shrub driplines, well into the interspace zone between plants (Segoli et al. 2012; Cuevas et al. 2013; Mudrak et al. 2014) and that the degree to which abiotic conditions change relative to distance from canopy is site-specific (Doescher et al. 1984).

Shrub islands are the product of a positive feedback between biotic and abiotic processes that occur above- and belowground, reinforcing more favorable microenvironmental conditions in or near islands than in the surrounding interspaces. In shrublands, aboveground processes that drive formation of shrub islands are largely associated with shrub canopies. Established vegetation shades the soil underneath the shrub, keeping temperatures cooler (Maestre et al. 2001; Davies et al. 2007) and reducing evapotranspiration (Prater & DeLucia 2006; Kidron 2009), and litter falls beneath the shrub, sometimes acting as both a favorable substrate for germination (Jia et al. 2018) and a source of organic matter (Burke 1989; Kononova 2013). At the same time, belowground drivers, associated with root turnover and function (e.g., organic matter, ammonium, nitrate), extend beyond the canopy dripline (Jackson & Caldwell 1993a; Ryel et al. 1996; Rau et al. 2009), obscuring distinctions between canopy and interspace. Most attributes of shrub microenvironments do not act solely above- or belowground, and the magnitude of change between the canopy and interspaces likely derives from the relative influence of above- versus belowground processes. For instance, soil organic matter is driven not only aboveground by litterfall, but also belowground, where root biomass remains high from the canopy dripline into interspaces (Ryel et al. 1996; Rau et al. 2009), by fine root turnover (Hooker et al. 2008). Thus, soil organic matter may remain elevated from the canopy into the interspace whereas an attribute such as shade would be highly clustered around the canopy, immediately changing between the canopy edge and interspace.

In many shrublands, biological soil crusts are critical to ecosystem function (Belnap 2003) and may both respond to and reinforce abiotic conditions associated with shrub islands (Eldridge et al. 2020). Biological soil crusts fix nitrogen at high rates of and prevent nutrient leaching compared to bare soil (Belnap 2003). Therefore, plants growing in biological soil crust often exhibit greater above- and belowground biomass (Pendleton et al. 2003), thereby also increasing organic inputs (soil organic matter) to the soil, which are then mineralized back into available forms of nitrogen (ammonium, nitrate) by biological soil crust (Zhang et al. 2016) and free-living microbes (Van Der Heijden et al. 2008). Soil surface characteristics, including relative cover of biological soil crusts, vary at the microsite (canopy vs. interspace) level within sites, but also vary at broader across-site scales (Holthuijzen & Veblen 2015).

In the semi-arid big sagebrush (*Artemisia tridentata*) rangelands of the Intermountain West, USA, vegetation is generally clustered around sagebrush canopies (Holthuijzen & Veblen 2015). Like in other semi-arid systems, empirical studies of shrub islands in sagebrush rangelands usually follow the paradigm of focusing on relative abundance or availability in resources or attributes in shrub canopies versus the interspaces between shrubs. Canopy versus interspace dynamics have been well studied in the Intermountain West, where the canopy microsite is at or under the canopy edge and the interspace microsite is often the farthest microsite from all neighboring sagebrush. But these studies have left the region between canopy microsites and interspace microsites, which we describe in this study as “the intermediate zone”, underexplored or underexploited.

To describe fine-scale spatial patterns associated with shrub island microenvironments, we evaluated attributes of shrub islands at multiple distances from Wyoming sagebrush canopies at four sites across the Intermountain West. We investigated how levels of two aboveground attributes, vapor pressure deficit and radiation, and six belowground attributes – soil organic matter, soil moisture, ammonium, nitrate, phosphorus, and potassium – differed between canopy and interspace microsites. We asked 1) whether spatial patterns of these abiotic attributes of shrub islands are consistent with a more nuanced view of the binary canopy-interspace paradigm such that some attributes maintain canopy values into the surrounding interspace, 2) whether the patterns of change between the canopy and interspace are similar across attribute type (e.g., aboveground versus belowground), and 3) whether spatial patterns of abiotic attributes correlated with ground cover characteristics.

Methods

Study sites

We established four study sites in the summer of 2018. They are distributed across the Intermountain West, USA (Figure 4.1) on public land managed by the Bureau of Land Management (BLM) or Fish and Wildlife Service (FWS) (Figure 4.1, Table 4.1). The Poker Jim Ridge Fire (9600 hectares) burned one of the sites (Rock Creek) in September 2019. All study sites are loamy Aridisols (USDA-NRCS WSS 2020) and dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp.*wyomingensis* (Beetle & Young) S.L. Welsh). The sites span a range of mean annual temperature (6-11°C) and precipitation (203-294 mm) (PRISM Climate Group 2014), and elevations range from 260 m to 1670 m (Table 4.1). Sites were dominated by sagebrush canopies with 4-58% native perennial grass cover and 1-20% cheatgrass cover.

Two sites, Roberts and Saddle Mountain, were fenced with 3-strand 1-meter-high barbed wire fencing in 2006 and 2007, respectively, to prevent cattle, but not wildlife, from entering the study area as part of a different study (McIver et al. 2010). Rock Creek is located in a National Wildlife Refuge that has excluded cattle since 1999. The fourth site, Onaqui, is not fenced and is in a BLM allotment that is grazed by cattle from November to June and is within a BLM Horse Management Area with significant wild horse presence (J. Bullock, BLM, personal communication).

Sample collection and processing

At each site we established 18-21 parallel 50 m transects 5 meters apart, along which we randomly selected ~5 focal sagebrush islands per transect to sample. At these sagebrush islands, we collected soil cores for lab analysis and made field measurements along short transects extending from each sagebrush canopy to a corresponding interspace, with the transect oriented randomly but to avoid large perennial grasses, rocks, or atypical soil, like slick spots or game trails. We sampled at four distances along each transect (Figure 4.2), at the canopy dripline (C, or "canopy"), in the interspace at the farthest point from any neighboring shrubs larger than 40 cm diameter (I, or "interspace"), and two intermediate distances between the canopy and interspace: 25% of the distance between the canopy and interspace ("25%"), and 50% of the distance between the canopy and interspace ("50%").

For each sampling of the four microsite types (C, 25%, 50%, I), we measured its azimuth from the focal sagebrush base and the size of the nearest sagebrush (widest diameter, perpendicular diameter, height). We also recorded ground cover (biological soil crust, moss, physical crust, litter, rock, cheatgrass, perennial grasses) in two 10 cm^2 quadrats placed adjacent to and on either side of where soil cores had been collected. Ground cover variables were assigned to cover classes (0%, 1-5%, 6-25%, 26-50%, 50-

75%, 76-95%, 96-100%).

We sampled in three successive summers, sampling a different randomly selected set of sagebrush islands each summer. During the first summer (09 May to 24 June 2019), we collected soil cores to analyze for soil organic matter (SOM), soil moisture (SM), nitrate (NO_3^-), and ammonium (NH_4^+) at 100 focal shrubs per site, at four sites (400 shrubs total). During the second summer (12 May-24 June 2020) we measured air temperature and relative humidity at 25 focal shrubs at three sites (75 total shrubs). During the third summer, we collected soil cores to analyze Olsen P and K and measured radiation at the same sites but different shrubs as the previous summer (03-18 June 2021; 25 shrub islands at 3 sites, 75 total). We sampled only three of four sites in the second and third summers (2020 and 2021) because one site, Rock Creek, had burned after our first sampling (2019). For all soil sampling, we collected four 2.5 cm diameter, 0-10 cm deep cores, placed as close to each other as possible, at each microsite.

For the soil organic matter (SOM) and gravimetric soil moisture (SM) sampling, we collected soil cores at each of four microsites (C, 25%, 50%, I) for a total of 1600 samples (4 microsites * 100 sagebrush islands * 4 sites). We sieved soil samples to 2.5 mm to remove large organic matter and gravels and measured gravimetric soil moisture of the samples immediately upon return from the field by first weight 10g of soil, then drying it in a 70°C oven for 48 hours and then calculating the difference in weight before and after drying. The time between sampling and precipitation, and the amount of that precipitation varied by site: Saddle Mountain received 6 mm of precipitation ten days before sampling with no precipitation seven days prior. There was precipitation in the seven days before sampling at all other sites: 6 mm at Onaqui, 11 mm at Roberts, 13.3

mm at Grey Butte (PRISM Climate Group 2014). We analyzed organic matter via loss-on-ignition, where dry soil samples were placed in crucibles and burned in a muffle furnace at 550°C for 5 hours. Organic matter was then calculated as the difference in dry sample weight before and after burning.

For ammonium (NH_4^+) and nitrate (NO_3^-), we only analyzed soil collected at C and I microsites (2 microsites, 100 sagebrush, 4 sites for 800 samples). Samples for ammonium and nitrate were prepared in the field by transferring approximately 5 g of unsieved soil into 2M KCl and brought back to the lab and analyzed via flow injection method (Lachat Instruments, Loveland, CO USA).

For potassium (Olsen K) and phosphorus (Olsen P), we collected soil cores at each of four microsites (4 microsites * 25 sagebrush islands * 3 sites = 300 samples). We air-dried and sieved soil samples to 2.5 mm to remove large organic matter and gravels and sent those to the Utah State University Analytical Laboratory (Logan, UT, USA) to be analyzed with the Olsen methodology (Olsen & Sommers 1983) because all soils are alkaline (Soil Survey Staff USDA-NRCS 2020)).

We measured air temperature, relative humidity, and radiation at each of four microsites (4 microsites * 25 sagebrush islands * 3 sites = 300 samples) between 11 am and 1 pm at 10cm above the soil surface to more closely capture the microenvironment experienced by a seedling. We used a single thermistor (Vaisala HMP60; Vaisala, Helsinki, Finland) to instantaneously read air temperature and relative humidity. We used a LI-COR 140 datalogger (LI-COR Biosciences, Lincoln, NE, USA). We calculated vapor pressure deficit (VPD) from the thermistor readings with the following formula (Allen et al. 2005) where T_a is air temperature (°C) and RH is relative humidity:

$$VPD = \left(0.618e^{\frac{(17.27 \times T_a}{(T_a + 273.3)}}\right) - \left(\frac{RH}{100} * 0.618\, e^{\frac{(17.27 \times T_a)}{(T_a + 273.3)}}\right)$$

To measure radiation, we used two pyranometers (LI-200; LI-COR Biosciences, Lincoln, NE, USA) at the canopy and 25% microsite simultaneously, and then the 50% and interspace microsites simultaneously.

Data analysis

We fit separate models for each shrub island variable: soil organic matter, gravimetric soil moisture, ammonium, nitrate, phosphorus (Olsen P), potassium (Olsen K), vapor pressure deficit, and solar radiation. All belowground variables except ammonium and nitrate (i.e., organic matter, soil moisture, phosphorus, potassium) were modeled with microsite (C, 25, 50, I), site (Saddle Mountain, Onaqui, Roberts, and Rock Creek), the interaction of microsite and site, cardinal direction (N, S, E, W), surface litter (%), and shrub volume (cm^3), as fixed effects and the shrub as the random effect. Although azimuths of microsites relative to focal shrubs were chosen at random, for analysis, the azimuths were binned into cardinal directions as factors (N: 337.6-37.5°, E: 37.6-157.5°, S: 157.6-247.5°, W: 247.6-337.5°). Shrub volume (V) was calculated according to the ellipsoid formula (Thorne et al. 2002):

$$V = \left(\frac{2}{3}\right)\pi H\left(\frac{A}{2}\right)\left(\frac{B}{2}\right)$$

where H is shrub height, A is diameter of the longest canopy axis, and B is the canopy axis perpendicular to A. Shrub volume and surface litter were centered by the site mean. Covariates were chosen based on mechanistic associations found in literature (litter: Burke 1989; cardinal direction: Mudrak et al. 2014; shrub volume: Liu et al. 2020).Ammonium and nitrate were analyzed with the same models, except there were only two levels of microsite (C, I).

The models for aboveground variables (radiation and VPD) took a similar form to the belowground variables. Radiation was modeled by microsite, site, and the interaction of microsite and site as fixed effects and the shrub as the random effect. Cardinal direction was not included because radiation was measured in transects parallel to the shadows cast by the shrub canopy. Vapor pressure deficit was modeled separately for each site because variances were very different across sites; VPD was modeled with microsite, shrub volume, and cardinal direction as fixed effects and shrub as the random effect.

Predictor variables were log-transformed (organic matter, potassium, phosphorus, ammonium, nitrate) or square root transformed (soil moisture) to meet the assumption of constant variance. We used AICc (appropriate for small sample sizes) to compare five random effect covariance structures (no covariance structure, heterogeneous unstructured, heterogeneous Toeplitz, heterogeneous compound symmetry, heterogeneous diagonal). Most models were best fit without covariance structures, except organic matter (heterogeneous compound symmetry), and radiation (heterogeneous diagonal covariance structure). We tested pairwise differences among microsites (C, 25%, 50%, I) within each site using Tukey-adjusted p-values. If a variable was log or square root transformed, all statistical tests were conducted on the transformed predictors, but data and results are presented on the original scale.

We also modeled microsite differences among soil surface cover variables using linear mixed effect models. We used the soil surface data associated with the organic matter/soil moisture soil samples (400 microsites across 100 focal sagebrush at Saddle

Mountain, Onaqui, Roberts, and Rock Creek each). In the field we collected soil surface characteristics in cover classes (0%, 1-5%, 6-25%, 26-50%, 50-75%, 76-95%, 96-100%) but analyzed the midpoints of each cover class, rounded to integers for use in the Poisson model. Each soil surface characteristic (biological soil crust, moss, physical crust, litter, rock, cheatgrass, perennial grass) was modeled by site, microsite, and the interaction between site and microsite as fixed effects and the shrub associated with each measurement as the random effect using a zero-inflated Poisson model. Saddle Mountain was excluded from the rock model due to the complete absence of rock. We tested pairwise differences among microsites within each site using Tukey-adjusted p-values.

We correlated each belowground attribute (soil moisture, ammonium, nitrate, potassium, phosphorus, organic matter) with each soil surface characteristic (biological soil crust, cheatgrass, litter, moss, physical crust, rock, cheatgrass, perennial grass) using a Kendall rank correlation coefficient because soil surface characteristics were collected in cover classes, then converted to percent cover. For each correlation, data for all microsite types were pooled into a single analysis. Due to the strong site effects in the analyses of shrub island attributes and soil surface responses to microsites, we correlated each soil surface characteristic by belowground attribute separately at each site. We evaluated significance with a Bonferroni correction for multiple comparisons because each belowground attribute was correlated with eight soil surface characteristic, where $\alpha = 0.00625$. At Saddle Mountain, all correlations with rock were excluded due to complete absence of rock, and we did not test correlations with phosphorus and potassium at Rock Creek because we sampled those attributes after the site had burned.

We used *tidyverse* (Wickham et al. 2019), *misty* (Yanagida 2021), and *naniar*

(Tierney et al. 2021) to prepare data, MuMIn (Bartoń 2020) to compare covariance structures*,* *DHARMa* (Hartig 2020) to evaluate model fit, and *glmmTMB* (Brooks et al. 2017) to fit the models, and *car* (Fox & Weisberg 2019), *emmeans* (Lenth 2020), *ggeffects* (Lüdecke 2018), and *multcomp* (Hothorn et al. 2008) to model the data and present results.

Results

Shrub island attributes relative to distance from the canopy

For most attributes of shrub islands analyzed, there were significant differences between canopy (C) and interspace (I) microsites (Figure 4.3, Table 4.2), but the magnitudes of those differences were less than 10% of canopy values for all characteristics except radiation, potassium, and nitrate (Figure 4.3). Across all sites, radiation was significantly lower in the canopy than interspace, while potassium and nitrate were higher in the canopy than interspace. Organic matter also was higher in the canopy than interspace across all sites, but the interspace values were only 10% lower than canopy organic matter. For at least two out of the three or four sites measured, there were significant differences, though small in magnitude, between the canopy and interspace for ammonium (C>I), soil moisture (C>I), and vapor pressure deficit (C<I) (Figure 4.3, Table 4.3).

The two canopy-associated attributes that showed the strongest and most consistent cross-site patterns, radiation and potassium, showed the most extreme values directly under sagebrush canopy driplines (i.e., C microsites) at two of three sites (Figures 4.3). Radiation increased abruptly between the C and 25% microsites where radiation at the 25% microsite was 225% and 140% of canopy radiation at Roberts and

Onaqui, respectively ($p < 0.001$, Table 4.2), but radiation remained similar between the 25% microsite, 50% and I microsites. Potassium decreased abruptly outside the canopy where values at the 25% microsites were only 24% and 22% of the canopy values, respectively, at Onaqui and Saddle Mountain ($p < 0.001$; Figures 4.3 and 4.4, Table 4.2), and remained low farther into the interspace (i.e., at 50% and I microsites; Figure 4.3, Table 4.3).

For the remaining shrub island attributes, differences between C and I microsites were small in magnitude, and values changed more gradually with increasing distance from canopy (i.e., from C to 25% to 50% to I). For one canopy-associated variable, VPD, and two belowground variables, organic matter and soil moisture, 25% and 50% microsite values consistently were intermediate in magnitude between C and I microsite values (Figure 4.3, Table 4.3). Phosphorus, a belowground variable, showed no significant pairwise differences among microsites (Figure 4.3). Nitrogen and ammonium, which were only measured at the canopy (C) and interspace (I) microsites exhibited opposite patterns, with nitrate increasing between the canopy and interspace at two out of three sites and ammonium decreasing between the canopy and interspace at three out of four sites (Figure 4.3, Table 4.3)

Organic matter, soil moisture, and nitrate values across microsites increased with shrub volume ($p = 0.023$, 0.018, 0.027 for organic matter, soil moisture, and nitrate, respectively; Table 4.2).

Soil surface patterns and correlations

Litter, cheatgrass, perennial grass, and moss cover were higher in canopy (C) than interspace (I) microsites (Figure 4.4). Of these, litter showed the strongest and most consistent response where, across sites, 25% microsite values were 42 to 53% of canopy values and interspace values were 67 to 87% of canopy values (Figure 4.5). Litter also was a significant predictor of organic matter (*p* = 0.022; Table 4.2) and significantly positively correlated with organic matter at three out of four sites (Table 4.4). Litter was significantly and positively associated with higher soil moisture, ammonium, and potassium at the microsite scale for at least two sites (of three or four, depending on the variable) (Table 4.4). Biological soil crust, physical crust, and rock cover were lower in canopy (C) than interspace (I) microsites although patterns varied across sites (Figure 4.5).

Discussion

Studies of shrub islands frequently employ a simple paradigm: what is happening under the canopy of a woody plant versus the interspace between plants? (e.g. Davies et al. 2007, Carrera and Bertiller 2013, Tucker and Reed 2016, Varela et al. 2017, Ochoa-Hueso et al. 2018, Liu et al. 2020). We found that levels of several attributes indeed differed between the canopy and maximum interspace distance between plants, but by sampling intermediate distances additionally revealed different degrees of clustering of those attributes around the canopy. Some aboveground attributes clustered around the canopy while belowground attributes were more diffuse. Understanding the degree to which above- and belowground shrub island effects cluster around shrub islands reveals the spatial extent of abiotic conditions that may facilitate establishment and persistence near canopies, may represent microsites that can be abiotically favorable for emergence, establishment, or persistence outside of canopies.

Clustering of some, but not all aboveground attributes

Because it is so strongly modulated by shading from the canopy, we were not surprised to find evidence that radiation, an aboveground attibute, was clustered around the canopy. Shrub canopies modulate radiation by intercepting incoming radiation, with more radiation intercepted when canopies are denser or larger (Tracol et al. 2011; Liu et al. 2020) and little to no interception in shrub-free interspaces. This pattern would change throughout the day and year, as shadows extend from the canopy, and by orientation, with more radiation on the south-side of a sagebrush in the summer (June-August). Shade, regardless of time of day, reduces water demand by reducing radiation (Lambers & Oliveira 2019), but this is especially pronounced at mid-day when radiation is highest and evaporative demand peaks (Begg et al. 1964).

Despite also influencing the aboveground microclimate and being similarly modulated by the canopy, vapor pressure deficit (VPD), a key factor controlling evaporative demand (Penman & Keen 1948), did not follow our expectations. Woody canopies in other systems are characterized by higher relative humidity from insulating air and lower temperature from shading (Tracol et al. 2011), conditions that lower VPD. Yet despite these theoretical associations between canopy cover and VPD, we found VPD remained elevated into the interspaces. Our results may be an artifact of having sampled in hot, dry conditions, in which VPD was low at all microsites. The canopy architecture of sagebrush may have been too sparse to sufficiently insulate the air inside the canopy from mixing with air outside the canopy (see Tracol et al. 2011). Additionally, our sampling design, at a single point in time, may have overemphasized daily variation in weather (wind, clouds, temperature), Additionally, because we sampled each site at a single point in time small, daily effects of weather (wind, clouds, temperature, air pressure) strongly influenced our results and limits our scope of inference.

We also found that potassium frequently clustered around the canopy. Although it is measured belowground, potassium is strongly associated with leaching from (aboveground) leaf litter (Duchesne et al. 2001; Sardans & Peñuelas 2015), which we found to be highest in canopy microsites consistently across all study sites. Sagebrush leaf litter has the highest potassium content of common litter inputs in sagebrush systems (Blank et al. 1994) and in previous studies, has been shown to be highly clustered around perennial vegetation through the growing season (Ryel et al. 1996).

Phosphorus is similarly measured belowground and associated with litterfall, so we expected phosphorus to be high in the canopy, similar to potassium and to patterns of phosphorus elsewhere in the Intermountain West (Jackson & Caldwell 1993a; Cross & Schlesinger 2001). But phosphorus did not show evidence of clustering. This may be because phosphorus enters a system through both litterfall (Etherington 1975) and soil weathering (Smeck 1973). Soil weathering is generally uniform across landscapes at the scale of our study sites and therefore less likely to contribute to phosphorus differences at the scale of microsites within a site. Another reason we did not find discernible spatial patterning of phosphorus may be that by the time we sampled in mid-summer, all available phosphorus had been assimilated by perennial vegetation during the growing season (Caldwell et al. 1987; Matzner & Richards 1996).

Diffuse belowground attributes

Despite being higher in the canopy than interspace as expected, organic matter did not show evidence of clustering; rather, we found relatively high organic matter not only in the canopy, but in the intermediate zone between the canopy and interspace. Unlike attributes we consider to be strongly canopy-associated (radiation and potassium), organic matter is also derived from and strongly influenced by root systems, entering the soil not only through litter inputs, but via fine root turnover (Hooker et al. 2008). Our results suggest a greater relative contribution of organic matter from roots which are similarly abundant in interspaces as under perennial vegetation (Jackson & Caldwell 1993a; Mitra et al. 2014). Our results agree with other studies in the Intermountain West that found higher organic matter under canopies (Bates et al. 2007), but we reveal that organic matter levels can extend farther into the interspace.

Soil moisture, which is measured belowground but influenced by both above- and belowground processes, showed weak or no patterns of clustering. Aboveground, we would have expected the strong association of shade (i.e., lower radiation) with sagebrush canopies to increase soil moisture (Liu et al. 2020), but similar to VPD, soil moisture was not strongly associated with canopy microsites. While we observed lower radiation under the canopy, this pattern was not mirrored by lower VPD under the canopy. We further would have expected any canopy-interspace differences to be reinforced belowground where roots redistribute soil moisture from deeper to shallower layers (Richards & Caldwell 1987). However, in sagebrush systems, roots, responsible for hydraulic redistribution, can be equally dense under the canopy as they are in the interspaces (Jackson & Caldwell 1993a; Mitra et al. 2014), potentially reducing any differences between canopy and interspace. Moreover, any small differences may have been difficult to detect because hydraulic lift does not affect soil moisture in the upper 10 cm of the soil

(Cardon et al. 2013) where we sampled. Additionally, if we had sampled earlier in the growing season when overall soil moisture is highest and differences between canopy and interspace microsites are greatest (Davies et al. 2007; Wu et al. 2016) we may have seen a greater influence of the canopy on soil moisture, and VPD.

Although we did not sample intermediate distances, we found ammonium was higher in the canopy than the maximum interspace ("I"), as expected. This pattern was consistent with more general patterns of small differences in organic matter between canopy and interspace microsites. Nitrogen mineralization is controlled by substrate (organic matter) and moisture availability, both of which are generally higher in the canopy than in the interspace (Burke 1989). Nitrate showed opposite patterns from ammonium, being higher in the interspace than canopy. The direction and magnitude of canopy-interspace differences of nitrate are variable throughout the growing season (Stubbs & Pyke 2005; Norton et al. 2008), suggesting ephemerality. The pattern of low nitrate abundance in the canopy and high abundance in the interspace may be influenced by two simultaneous processes. In this study system, annual grasses are more common under the shrub canopy and preferentially uptake nitrate over ammonium (Monaco et al. 2003), decreasing nitrate in the canopy. At the same time, the nitrate pool in the interspace increases over the hot, dry summer, when we sampled, while uptake rates are low (Booth et al. 2003a; Booth et al. 2003b).

Drivers of shrub islands

Microsite-level patterns associated with shrub islands in the Intermountain West are often site-specific and what drives these differences in unclear (Doescher et al. 1984). Although in many cases is often because studies occur at a single site (Jackson &

Caldwell 1993a, 1993b), we too found high site-specificity when we examined four sites across a range of elevations, climate, grazing, and soil age. In many ways this is not surprising because shrub island formation is known to be caused many interacting processes such as shrub size (Varela et al. 2017; Liu et al. 2020), grazing (Allington & Valone 2014), litterfall (Burke et al. 1989), soil development (Noumi et al. 2016), and hydraulic lift (Cardon et al. 2013).

Some of the canopy-interspace differences that we observed appear to be partially driven by litter, a pattern which has been observed in semiarid systems outside of the Intermountain West (Carrera & Bertiller 2013). The magnitude of difference between the canopy and interspace for litter was greater than for the soil attributes that we found to be correlated with litter cover (organic matter, ammonium, potassium). Litter is the substrate that, in concert with soil moisture and microbes, is decomposed and mineralized into organic matter and available forms of nitrogen (Bates et al. 2007). The lack of microsite differences in soil moisture may have dampened microsite differences in litter-derived soil attributes. Differences between canopy and interspace microsites also may have been driven by shrub size. Larger shrubs influence the surrounding islands more than smaller shrubs (Varela et al. 2017; Liu et al. 2020) and we found that organic matter, soil moisture, and nitrate availability increased with shrub size, perhaps because large shrubs simply produce and accumulate more litter over time.

Some hypothesize that resource-rich shrub islands are a byproduct of grazing (Allington & Valone 2014), where livestock both compact soils and preferentially graze easily accessible vegetation in interspaces (van de Koppel et al. 2002), leading to resource-poor interspaces and resource-rich refugia under the canopy (Lin et al. 2010).

Our only site that was in a BLM allotment and actively grazed, Onaqui, saw the strongest canopy-interspace differences for ammonium, nitrate, and potassium compared to all other sites, lending support to the grazing-byproduct hypothesis. Additional sampling in nearby long term vegetation monitoring studies where livestock grazing has been excluded since 2006 (described in McIver et al. 2010), may elucidate the grazing-byproduct hypothesis at Onaqui.

Both short- and long-term processes influence shrub island development (Noumi et al. 2016) and we provide evidence that short term processes, like litter accumulation, were correlated with some shrub island metrics, like organic matter. Although we did not have replication at the site-level, we also qualitatively found evidence that cross-site patterns were consistent with the influence of long-term processes. For example, our Onaqui site has parent material of lacustrine sediment from Pleistocene-era Lake Bonneville and as a result, its soils have high clay content. Clay content is positively correlated with organic matter (Schimel et al. 1994) and both clay and organic matter can increase soil moisture (Hudson 1994). Accordingly, we found high organic matter content and soil moisture across all microsites at Onaqui. This is contrasted with soils at Saddle Mountain, which were not present during the Pleistocene due to periodic cataclysmic mega flooding to bedrock (Baker 2009). Correspondingly, clay content, organic matter, and soil moisture were lower.

Conclusions

Our findings, that some attributes of shrub microenvironments do not immediately change between the canopy edge and interspace, are seemingly at odds with the patchiness and heterogeneity of vegetation in Wyoming sagebrush systems. In intact sagebrush stands, understory vegetation is clustered around the sagebrush canopy (Holthuijzen & Veblen 2015), yet we found that most attributes were diffuse. Despite levels of attributes like soil organic matter, nitrate, and phosphorus being similar between the canopy and interspace, the amelioration of water-stress associated with clustering of radiation and potassium may be the overarching factor influencing the hospitability of the microenvironment associated with Wyoming big sagebrush canopies in the Intermountain West. In other systems, shading by the canopy is more influential to seedling establishment than belowground attribute availability (Liu et al. 2021), and this may be the case in Wyoming big sagebrush stands of the Intermountain West. The two attributes clustered around the canopy, radiation and potassium, can influence the ability of vegetation to establish and persist in the understory by alleviating water demands and increasing water use efficiency. Shading alters leaf energy balance and decreases evapotranspiration (Lambers & Oliveira 2019) and simultaneously under the canopy, higher levels of potassium may allow plants to maintain high carbon assimilation levels under low light conditions (sensu Wang et al. 2020). Additionally, the higher levels of potassium increase root osmotic potential (Bradbury & Malcolm 1977) and stomata modulation (Cochrane & Cochrane 2009), allowing plants to regulate transpiration and thus water stress more efficiently. Our results, that canopy-derived attributes are generally clustered around the canopy while belowground attributes are diffuse can guide species-specific restoration. For example, it may be that planting of species with low water use efficiency or that are highly sensitive to leaf energy balance could be targeted to the canopy while stress-tolerant species could be planted throughout the interspace, from the canopy dripline to the interspace microsite as far as possible from neighboring sagebrush canopies, where most belowground resource availability is equally high (see Pyke & Archer 1991). Shrub island dynamics have direct implications for land management in the Intermountain West, a region subject to extensive restoration efforts (Svejcar et al. 2017) as shrub islands have been used as focal planting areas to increase understory (Boyd & Davies 2010, 2012). If interspace areas outside of shrub islands themselves are equally suitable for transplanting seedlings as canopies, land managers may be underexploiting restoration opportunities by only targeting canopies, rather than also including the zone encompassing intermediate distances between canopy and interspace. Likewise, because the patterns of shrub islands are not conserved across sites, planting into intermediate distances may be less suitable at some sites than others. For example, (Davies et al. 2007) found differences in soil moisture, pH, total carbon, total nitrogen, air temperature between canopy and interspace microsites at a low elevation site but no differences at a higher elevation site, while Doescher et al. (1984) found no consistent patterns across multiple sites. Planting into interspaces where perennial vegetation is sparse can greatly increase resistance and resilience of sagebrush systems (Reisner et al. 2013).

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Tables

Table 4.1: Site locations, 30 year normal (1991-2020) monthly average temperature ranges and yearly precipitation and texture in the top 10cm of soil. Soil texture was analyzed via hydrometer and averaged over 10 soil samples at each site. We used paired t-tests to compare canopy and interspace texture and found no significant differences in texture between canopy and interspace samples, so table textural values reflect averages across site.

Site	Elevation (m)	Latitude	Longitude	Mean Monthly Temperature (°C)			Annual Precipitation (mm)	Soil Texture		
				Min.	Mean	Max.		% Sand	% Clay	% Silt
Saddle Mountain	257	46.75	-119.36	4.5	11	17.5	203.68		Sandy Loam	
								68	6	26
Roberts	1482	43.77	-112.29	-1.7	5.9	13.6	222.61		Sandy Loam	
								54	17	29
Rock Creek	1520	42.72	-119.44	1.0	8.3	15.7	272.14		Sandy Loam	
								56	20	24
Onaqui	1677	40.20	-112.46	1.1	9.2	17.3	294.13		Loam	
								45	14	41

Table 4.2: Analysis of Variance Table) results for generalized linear mixed effect regression models with soil organic matter, gravimetric soil moisture, phosphorus, potassium, ammonium, nitrate, vapor pressure deficit, and radiation as response variables. Some response variables are log-transformed or square-root transformed. For all variables except radiation and vapor pressure deficit (VPD), the fixed effects were site, microsite, shrub volume, cardinal direction, soil surface litter cover, and the interaction between site and microsite, evaluated using Type III ANOVA. For radiation, the fixed effects were site, microsite, and the interaction between site and microsite, evaluated using Type III ANOVA. VPD models were analyzed separately by site to meet model assumptions, with microsite and shrub volume as fixed effects, evaluated using Type II ANOVA. The random effect in every model was the shrub that the microsite samples are associated with. Covariance structures varied by model. Results significant at alpha of 0.05 in bold.

	Organic Matter			**Soil Moisture**			**Phosphorus**		
	Chi Sq	**Df**	**Pr(>Chi Sq)**	**Chi Sq**	**Df**	**Pr(>Chi Sq)**	**Chi Sq**	**Df**	**Pr(>Chi Sq)**
Intercept	1207.266	1	**< 0.001**	1424.896	1	**< 0.001**	**Chi Sq**	**Df**	**Pr(>Chi Sq)**
Site	1227.18	3	**< 0.001**	2573.983	3	**< 0.001**	111.257	2	**< 0.001**
Microsite	10.098	3	**0.0178**	3.297	3	0.348	27.346	3	**< 0.001**
Shrub Volume	4.849	1	**0.0277**	5.577	1	**0.0182**	6.701	1	**0.00963**
Litter	5.913	1	**0.015**	0.682	1	0.409	0.164	1	0.686
Cardinal Direction	7.786	3	0.0506	15.881	3	**0.0012**	0.922	3	0.82
Site:Microsite	14.776	9	0.0973	46.89	9	**< 0.001**	29.754	6	**< 0.001**

	Potassium			**Ammonium**			**Nitrate**		
	Chi Sq	**Df**	**Pr(>Chi Sq)**	**Chi Sq**	**Df**	**Pr(>Chi Sq)**	**Chi Sq**	**Df**	**Pr(>Chi Sq)**
Intercept	2456.284	1	**< 0.001**	61.842	1	**< 0.001**	632.013	1	**< 0.001**
Site	183.955	2	**< 0.001**	303.487	3	**< 0.001**	377.192	3	**< 0.001**
Microsite	20.663	3	**< 0.001**	14.216	1	**< 0.001**	0.516	1	0.473
Shrub Volume	0.42	1	0.517	0.455	1	0.5	4.465	1	**0.0346**
Litter	4.972	1	**0.0258**	3.242	1	0.0718	1.168	1	0.28
Cardinal Direction	5.472	3	0.14	0.109	3	0.991	8.123	3	**0.0435**
Site:Microsite	13.466	6	**0.0362**	8.949	3	**0.03**	4.224	3	0.238

	Radiation					**Vapor Presure Deficit**		
	Chi Sq	**Df**	**Pr(>Chi Sq)**			**Chi Sq**	**Df**	**Pr(>Chi Sq)**
Intercept	41.45	1	**< 0.001**	**Saddle Mtn**	**Microsite**	18.725	3	**< 0.001**
Site	19.742	2	**< 0.001**		**Shrub Volume**	0.023	1	0.878
Microsite	94.547	3	**< 0.001**		**Cardinal Dir.**	1.316	3	0.725
Shrub Volume	0.16	1	0.689	**Onaqui**	**Microsite**	74.012	3	**< 0.001**
Site:Microsite	20.629	6	**0.00214**		**Shrub Volume**	0.191	1	0.662
					Cardinal Dir.	6.616	3	0.0852
				Roberts	**Microsite**	107.965	3	**< 0.001**
					Shrub Volume	0.853	1	0.356
					Cardinal Dir.	1.001	3	0.801

Table 4.3: Pairwise contrast estimates among microsites in sagebrush stands at Saddle Mountain, Onaqui, Roberts, and Rock Creek study sites in the Intermountain West, USA. Values are contrast on the response scale ± 1 standard error. Nitrate and ammonium were measured at canopy and maximum interspace distance between sagebrush plants (I) microsites, and all other variables were measured in C and I microsites as well as microsites at 25% of the distance from C to I (25) and 50% of the distance from C to I (50). Rock Creek burned before we sampled radiation, vapor pressure deficit, potassium, and phosphorus. Asterisks indicate Tukey-adjusted significance (* < 0.05, ** < 0.01, *** < 0.001).

	Contrast	Saddle Mountain	Roberts	Rock Creek	Onaqui
Organic Matter	C - 25	0.06 ± 0.04	0.12 ± 0.06	0.38 ± 0.08 ***	0.24 ± 0.08 *
	C - 50	0.05 ± 0.04	0.09 ± 0.06	0.42 ± 0.08 ***	0.26 ± 0.08 **
	C - I	0.12 ± 0.04 **	0.23 ± 0.06 **	0.61 ± 0.08 ***	0.45 ± 0.08 ***
	25 - 50	-0.01 ± 0.04	-0.03 ± 0.06	0.04 ± 0.08	0.02 ± 0.07
	25 - I	0.06 ± 0.04	0.11 ± 0.06	0.23 ± 0.08 *	0.21 ± 0.07 *
	50 - I	0.07 ± 0.04	0.14 ± 0.06	0.2 ± 0.08 *	0.19 ± 0.07 *
Soil Moisture	C - 25	-0.09 ± 0.07	0.11 ± 0.12	0.51 ± 0.14 **	-0.03 ± 0.17
	C - 50	-0.11 ± 0.07	0.06 ± 0.12	0.72 ± 0.15 ***	0.24 ± 0.18
	C - I	-0.1 ± 0.07	0.12 ± 0.12	0.87 ± 0.14 ***	0.65 ± 0.18 **
	25 - 50	-0.03 ± 0.07	-0.05 ± 0.12	0.21 ± 0.14	0.27 ± 0.17
	25 - I	-0.02 ± 0.07	0.02 ± 0.12	0.36 ± 0.14 *	0.68 ± 0.17 ***
	50 - I	0.01 ± 0.07	0.07 ± 0.12	0.15 ± 0.13	0.41 ± 0.17
Potassium	C - 25	31.43 ± 9.37 **	12.01 ± 35.35	–	120.44 ± 37.21 **
	C - 50	39.43 ± 9.59 ***	40.21 ± 35.25	–	115.83 ± 39.87 *
	C - I	30.97 ± 10.09 *	5.61 ± 36.44	–	136.64 ± 38.87 **
	25 - 50	7.99 ± 6.6	28.2 ± 32.7	–	-4.62 ± 28.67
	25 - I	-0.47 ± 7.28	-6.4 ± 33.91	–	16.19 ± 27.5
	50 - I	-8.46 ± 6.86	-34.6 ± 32.66	–	20.81 ± 27.21
Phosphorus	C - 25	0.35 ± 0.31	-0.98 ± 1.15	–	0.84 ± 0.88
	C - 50	-1.17 ± 0.39 *	0.84 ± 1.04	–	1.24 ± 0.93
	C - I	0.3 ± 0.34	-0.89 ± 1.13	–	0.43 ± 0.95
	25 - 50	-1.52 ± 0.35 ***	1.82 ± 1.12	–	0.41 ± 0.81
	25 - I	-0.04 ± 0.29	0.09 ± 1.2	–	-0.4 ± 0.85
	50 - I	1.48 ± 0.35 ***	-1.73 ± 1.06	–	-0.81 ± 0.82
Nitrate	C - I	-0.01 ± 0.01	-0.07 ± 0.02 **	-0.03 ± 0.02	-0.29 ± 0.09 **
Ammonium	C - I	0.33 ± 0.09 ***	0.17 ± 0.05 **	0.02 ± 0.04	0.29 ± 0.07 ***
Radiation	C - 25	-183.5 ± 77.07	-445.33 ± 88.99 ***	–	-256.07 ± 89.15 *
	C - 50	-405 ± 70.88 ***	-587.89 ± 81.85 ***	–	-314.03 ± 82.19 ***
	C - I	-568.58 ± 63.3 ***	-653.22 ± 73.09 ***	–	-329.19 ± 75.45 ***
	25 - 50	-221.5 ± 72.07 *	-142.56 ± 83.22	–	-57.96 ± 73.97
	25 - I	-385.08 ± 64.63 ***	-207.89 ± 74.63 *	–	-73.12 ± 66.4
	50 - I	-163.58 ± 57.11 *	-65.33 ± 65.95	–	-15.16 ± 56.72
Vapor Pressure Deficit	C - 25	-0.05 ± 0.02	-0.04 ± 0.01 *	–	-0.04 ± 0.02 *
	C - 50	-0.06 ± 0.02	-0.09 ± 0.01 ***	–	-0.08 ± 0.02 ***
	C - I	-0.1 ± 0.02 ***	-0.12 ± 0.01 ***	–	-0.13 ± 0.02 ***
	25 - 50	-0.01 ± 0.02	-0.05 ± 0.01 ***	–	-0.04 ± 0.02
	25 - I	-0.06 ± 0.02	-0.09 ± 0.01 ***	–	-0.09 ± 0.02 ***
	50 - I	-0.04 ± 0.02	-0.04 ± 0.01 *	–	-0.05 ± 0.02 *

Table 4.4: Kendall's tau correlation coefficient for correlations between each soil surface characteristic (biological soil crust, moss, physical crust, litter, rock, cheatgrass, perennial grass) and each belowground attribute (organic matter, soil moisture), ammonium, nitrate, potassium (Olsen K), phosphorus (Olsen P), modeled separately by site (Saddle Mountain (SM), Onaqui, Roberts, Rock Creek (RC)). For each correlation, data for all microsite types were pooled into a single analysis. Potassium and phosphorus were not sampled at Rock Creek due to wildfire in September 2019, and rock cover was zero at all microsites at Saddle Mountain, those variables were not analyzed. Bold Kendall's tau coefficients indicate significance with Bonferroni correction (p=0.00625).

	Saddle Mtn	Onaqui	Roberts	Rock Creek
	Soil Organic Matter			
Cheatgrass	0.026	0.031	-0.0087	0.11
Biological Soil Crust	-0.017	0.0098	-0.064	**0.35**
Litter	**0.11**	**0.15**	0.099	**0.14**
Moss	0.052	0.052	**0.11**	0.096
Physical Crust	-0.03	-0.1	0.033	**-0.22**
Perennial Grass	0.099	**0.18**	0.11	-0.097
Rock	–	-0.025	**-0.11**	**-0.35**
	Soil Moisture			
Cheatgrass	-0.07	-0.024	0.038	**0.14**
Biological Soil Crust	0.075	-0.043	**-0.12**	**0.16**
Litter	-0.037	0.083	-0.045	**0.16**
Moss	-0.0092	0.1	0.047	0.079
Physical Crust	-0.017	**-0.13**	-0.1	**-0.19**
Perennial Grass	-0.017	0.054	0.035	-0.09
Rock	–	-0.01	**0.19**	**-0.25**
	Ammonium			
Cheatgrass	0.13	-0.019	0.076	0.091
Biological Soil Crust	**-0.16**	-0.12	-0.073	0.022
Litter	**0.24**	**0.28**	**0.22**	0.091
Moss	0.017	**0.2**	0.12	0.016
Physical Crust	-0.076	**-0.23**	-0.047	-0.081
Perennial Grass	0.079	**0.23**	0.042	0.07
Rock	–	-0.12	**-0.16**	-0.027
	Nitrate			
Cheatgrass	-0.058	0.0017	-0.17	0.087
Biological Soil Crust	-0.013	-0.049	0.13	0.15
Litter	-0.13	0.051	**-0.22**	-0.046
Moss	-0.081	0.043	**-0.21**	**-0.19**
Physical Crust	**0.19**	-0.045	0.11	0.12
Perennial Grass	-0.078	0.058	0.0081	**-0.19**
Rock	–	-0.00088	**0.3**	-0.033
	Potassium			
Cheatgrass	0.13	0.12	0.12	–
Biological Soil Crust	-0.073	**-0.24**	0.0058	–
Litter	**0.25**	**0.27**	0.19	–
Moss	0.22	0.078	0.043	–
Physical Crust	-0.2	-0.12	-0.13	–
Perennial Grass	0.059	0.091	0.054	–
Rock	–	-0.19	**-0.22**	–
	Phosphorus			
Cheatgrass	-0.03	0.089	0.029	–
Biological Soil Crust	-0.12	0.00079	-0.19	–
Litter	0.14	**0.28**	0.069	–
Moss	-0.022	-0.052	0.21	–
Physical Crust	0.048	-0.12	-0.075	–
Perennial Grass	**-0.23**	0.13	0.072	–
Rock	–	0.0031	**-0.13**	–

Figures

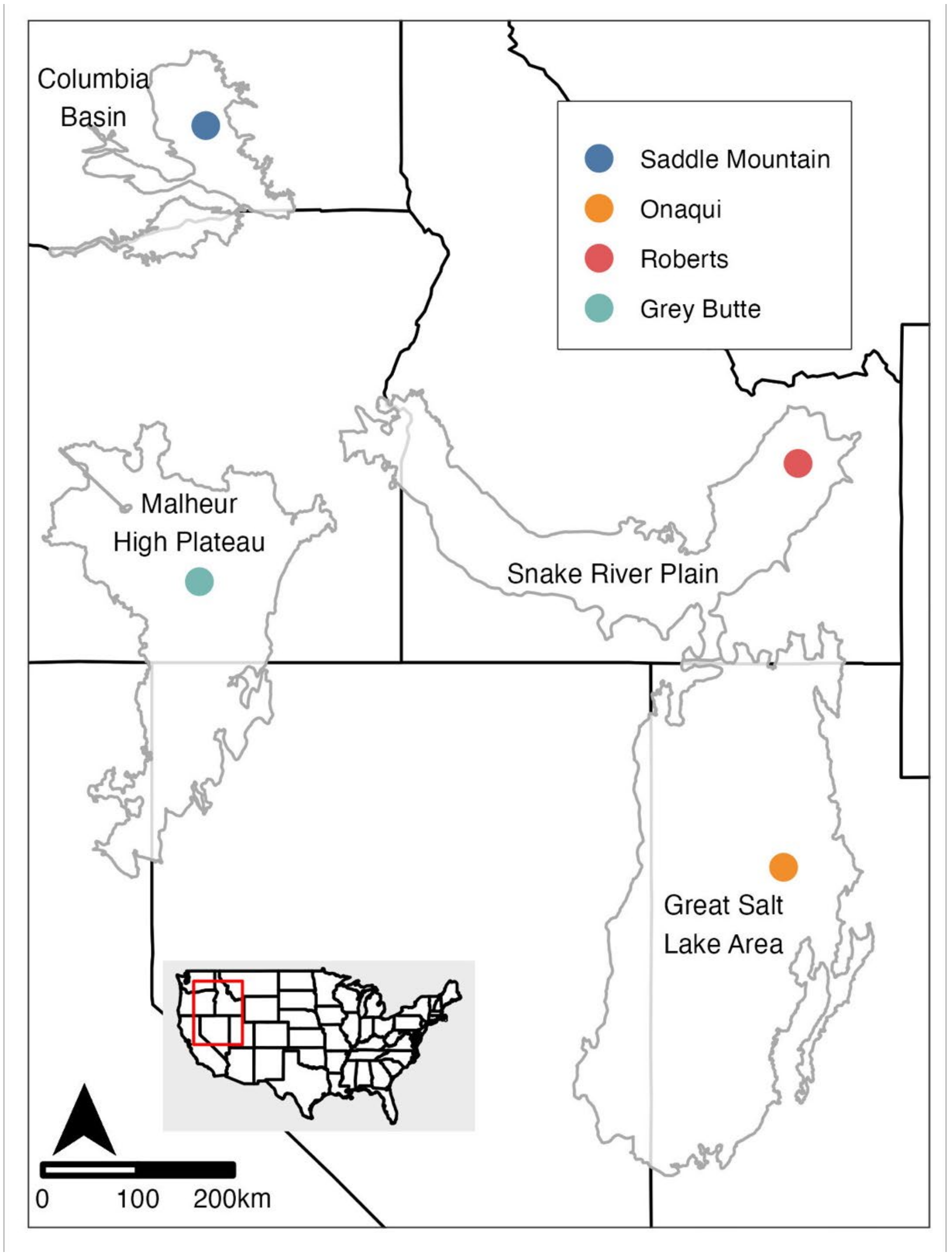

Figure 4.1: Map of site locations. Sites are listed in descending order of annual temperature and ascending annual precipitation. Rock Creek burned in September 2019. Shading and labels indicate Natural Resources Conservation Service (NRCS) Major Land Resource Areas.

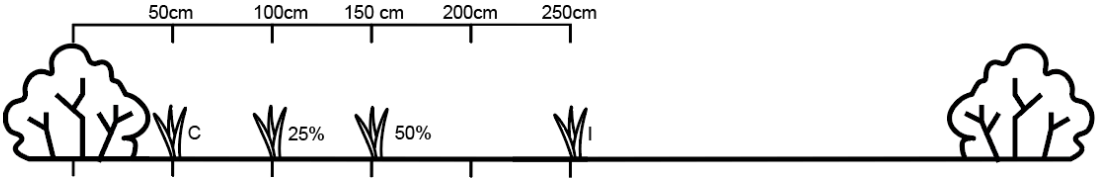

Figure 4.2: Schematic describing sampling design. Soil cores and relative humidity, air temperature, and radiation measurements were taken at four microsites at each focal sagebrush: The canopy edge (C), the farthest interspace distance from all neighboring sagebrush (I) and two locations between the two extremes, 25% and 50% of the distance from the C to I. In this example, the canopy sample was taken at 50cm from the sagebrush base, the interspace samples were taken at 250cm from the sagebrush base, the 25% microsite is at 100 cm from the base and the 50% microsite is at 150 cm.

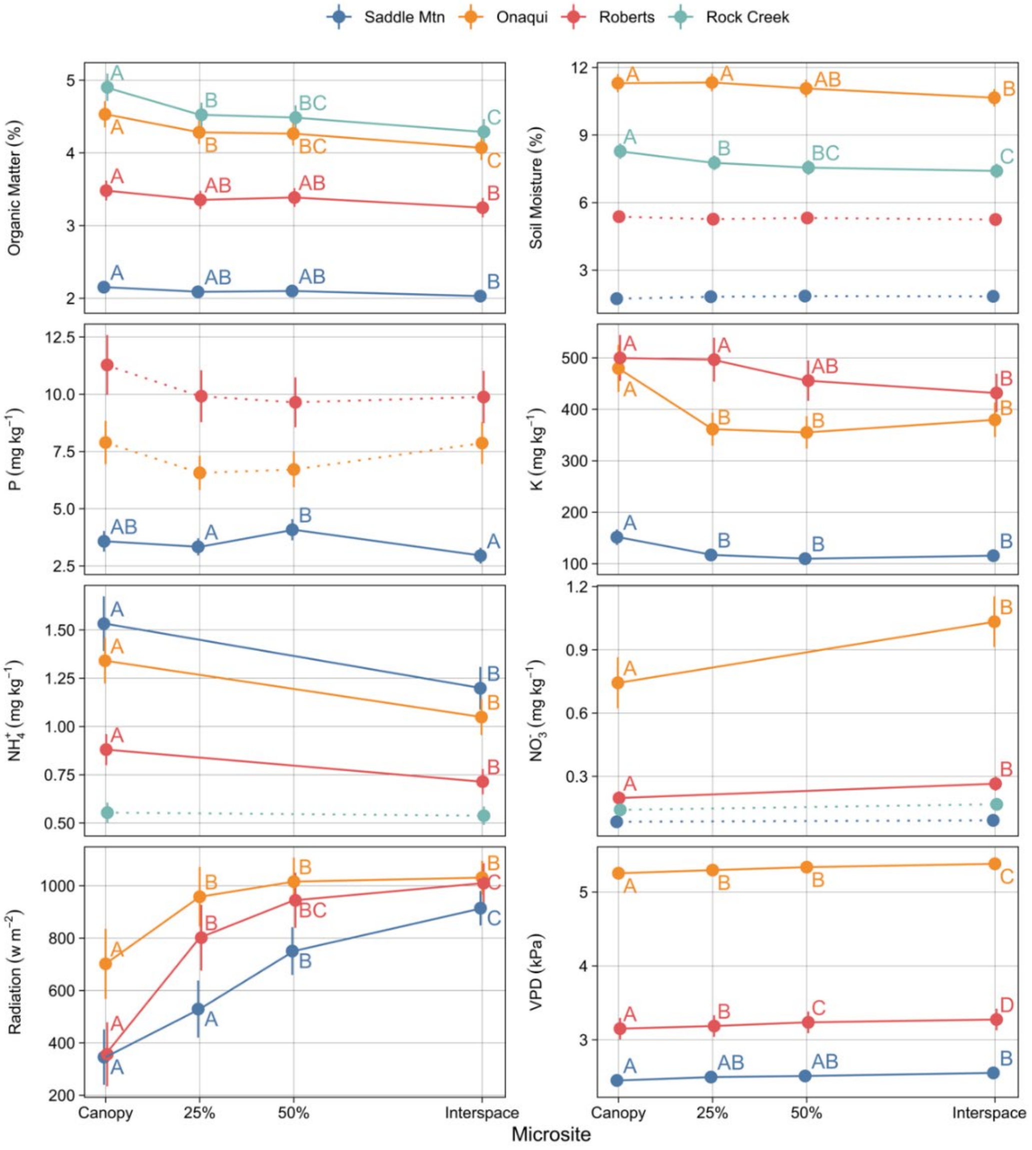

Figure 4.3: Modeled estimated marginal mean value for each of eight variables associated with shrub islands in sagebrush stands at sites across the Intermountain West, USA. Resources were measured at four microsites: canopy edge (C), the farthest interspace distance from all neighboring sagebrush (I) and two locations between the two extremes, 25% and 50% of the distance from the C to I, except for ammonium and nitrate which were only measured at the canopy and interspace. Potassium, phosphorus, radiation, and VPD (vapor pressure deficit) were not measured at Rock Creek before the site burned in September 2019. Error bars indicate 95% confidence intervals. Shared letters indicate no significant pairwise differences (Tukey-adjusted) between microsites within a given site, and dotted lines indicate no significant pairwise differences among any microsites at a given site. Significance was determined at 0.05.

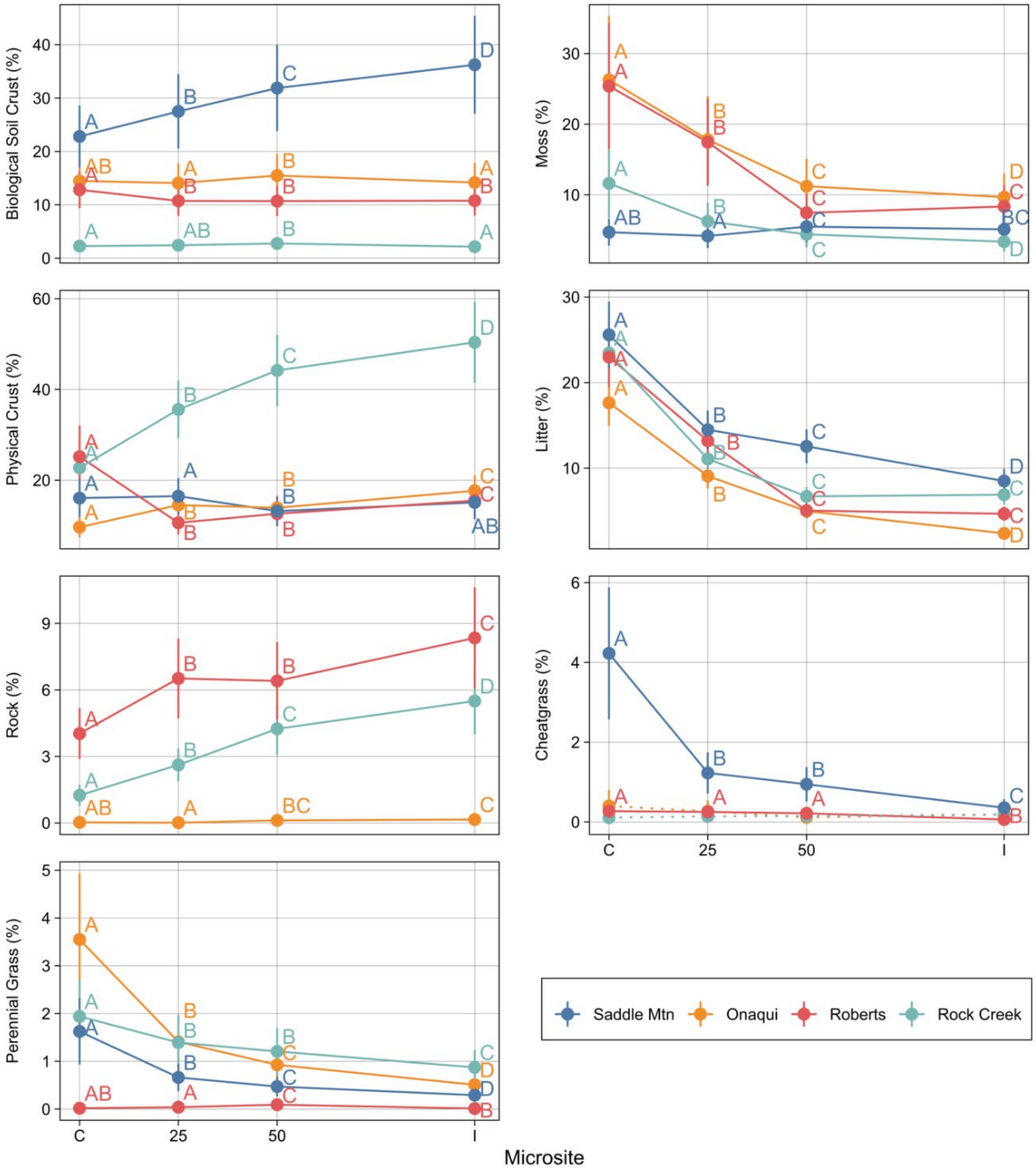

Figure 4.4: Modeled estimated marginal mean percent cover for each of seven soil surface characteristics at four sites in the Intermountain West, USA. Soil surface characteristics were measured at four microsites: canopy edge (C), the farthest interspace distance from all neighboring sagebrush (I) and two locations between the two extremes, 25% and 50% of the distance from the C to I. Error bars indicate 95% confidence intervals. Shared letters indicate no significant pairwise differences (Tukey-adjusted) between microsites within a given site, and dotted lines indicate no significant pairwise differences among any microsites at a given site. Significance was determined at 0.05. Rock Cover was 0% at Saddle Mountain and not included.

CHAPTER 5

SHADE TOLERANCE AND ROOT ALLOCATION PATTERNS OF TWO NATIVE GREAT BASIN HERBACEOUS SPECIES

Abstract

In sagebrush rangelands of the Intermountain West, like in other semiarid systems, canopies of the dominant shrub (sagebrush, *Artemisia tridentata*) modify their surrounding microenvironment in ways that can facilitate understory establishment and act as nurse shrubs to seedlings. High organic matter found under the canopy, by increasing water holding capacity, can act as a buffer during periods of drought. At the same time under the canopy, shade may negatively influence seedling growth by decreasing root allocation, thereby decreasing their competitive ability. We asked how one aboveground nurse shrub microclimate effect, shade (0%, 50% shade), and two belowground effects, soil organic matter (high, low) and watering level (high, low), each affected patterns of root:shoot dry mass allocation for one native perennial bunchgrass (*Pseudoroegneria spicata*) and one native perennial forb (*Sphaeralcea munroana*) to understand possible mechanisms of establishment under the sagebrush canopy. We found that shade increased specific leaf area of both species, which appeared to allow plants to maximize photosynthetic capacity without decreasing allocation to root dry mass, as evidenced by root:shoot dry mass ratio and root mass fraction being similar between shade treatments. Globemallow increased root allocation with decreasing water availability as expected, but bluebunch wheatgrass maintained high root:shoot ratio even at low water availability. While most plants under low light conditions allocate more

growth to aboveground structures at the expense of root growth, the lack of a shade response to root allocation for both species suggested a pathway to persistence under the canopy: seedlings can access higher soil resource availability under the canopy without lowering their competitive fitness by reducing their root:shoot ratio. . Artificial shade structures may be a promising restoration technique for these species, potentially increasing seedling establishment without being subject to tradeoffs to belowground biomass allocation.

Introduction

Semiarid and arid systems are often characterized by patchy vegetation and shrub distribution, where understory vegetation establishes at higher rates under and around existing vegetation canopies, compared to the surrounding interspaces (Pugnaire et al. 1996; Sala & Aguiar 1996; Schlesinger et al. 1996; Ochoa-Hueso et al. 2018). Shrub canopies can act as nurse shrubs, ameliorating harsh aboveground microclimates and increasing resource availability belowground (Gómez-Aparicio et al. 2005).

Microclimatic conditions under shrub canopies are not unilaterally beneficial to seedlings. The benefits of higher soil moisture, reduced air temperature, and increased relative humidity under canopies (Tracol et al. 2011) can be mitigated by resource consumption by other understory vegetation and the nurse plant itself (Pescador et al. 2014; Cruz-Alonso et al. 2020) . Additionally, while shading can enhance seedling survival under canopies by enhancing soil moisture in the upper soil layers (Liu et al. 2021), it may also have some drawbacks for seedling growth. Plants allocate growth where resources are limiting: to shoots when light is limiting and roots when moisture or other soil resources are limiting (Shipley & Meziane 2002). Under shade, most plants will increase their shoot allocation at the expense of root allocation if light is limiting to photosynthesis (Poorter et al. 2012) in part by increasing leaf area and specific leaf area (SLA; see Liu et al. 2016), thereby decreasing their ability to compete with other plants also growing under shade for scarce soil resources (Wang et al. 2010). Growing under the canopy requires coexistence with other plants also growing under the canopy (Pescador et al. 2014), where root allocation and competitive ability are critical to access limited resources.

The effects of shade and soil resource availability under the canopy may interact to produce plastic responses in root and shoot allocation that alter herbaceous competitive ability for relatively scarce soil moisture. Belowground, soil organic matter is among the primary soil attributes that the nurse shrub influences through root turnover and litterfall (Kononova 2013). In the short term, organic matter increases water holding capacity (WHC) by acting as a sponge, retaining water (Hudson 1994), acting as a buffer during periods of low precipitation or drought. Aboveground, the canopy modulates shade which in part, increases soil moisture (Liu et al. 2021). The combination of low light and high soil resources may influence seedlings under the canopy to have high shoot biomass to compete for low light at the expense of root biomass, decreasing a seedling's ability to compete for soil resources when those resources become scarce (Cahill 1999) or understory plant density increases (Kiær et al. 2013).

Rangelands of the Intermountain West are characterized by a dominant woody shrub species, sagebrush (*Artemisia tridentata*), which influences community composition and structure. However, more than a million acres of sagebrush habitat are lost annually from invasive annual grass expansion and subsequent wildfires (D'Antonio

& Vitousek 1992; Balch et al. 2013) with negative consequences for obligate species like the greater sage grouse (*Centrocercus urophasianus*; Doherty et al. 2022) and for ecosystem services (Davies et al. 2011) Understanding the role of sagebrush in shaping community composition and recruitment dynamics of native plants is important to best protect and restore degraded sagebrush systems (Maestas et al. 2022). At a landscape scale, understory vegetation is clustered under sagebrush canopies (Holthuijzen & Veblen 2015), especially at low-elevation sites, but the spatial extent of soil resources and their overall availability under and around sagebrush canopies varies both across a landscape and at the microsite level (Doescher et al. 1984), and understanding abiotic drivers of resource islands on seedling growth and allocation patterns may be predictive of how understory plant distributions respond to resource islands.

There are strong barriers to seedling establishment in Wyoming big sagebrush systems (James et al. 2011), and seedlings are highly sensitive to water deficits (O’Connor et al. 2020). In sagebrush systems, soil moisture is higher under the canopy during the early growing season (Davies et al. 2007), and this could be a driver of higher herbaceous plant establishment under the canopy. Increased soil moisture could be due to higher organic matter (which increases WHC; Hudson 1994), reduced soil-water evaporation due to shading (Gómez-Aparicio et al. 2005; Liu et al. 2021), or both. In both the Intermountain West and other semi-arid systems, there is growing interest in small mitigations that can be applied to revegetation projects to increase establishment rates (Havrilla et al. 2020). For example, shade-providing dead shrubs increase sagebrush seedling establishment in the Intermountain West (McAdoo & Davies 2018) in Hawaiian dry forests shade structures increased both soil moisture and herbaceous establishment

(Thaxton et al. 2012) and in mesic Hawaiian forests, shade structures allowed native shade tolerant species to outcompete shade intolerant exotic species (Funk & McDaniel 2010) .

Here we used a controlled growth chamber setting to isolate the effects of soil WHC, shade, and their interactions as drivers of understory plant establishment. Target species were two native perennial species commonly used in restoration projects in sagebrush rangelands of the Intermountain West, a forb, Munro's globemallow (*Sphaeralcea munroana* (Douglas) Spach), and a grass, bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve). Our research aims are centered around the principle that shade beneficially increases soil moisture but often at the expense of how much of a plant's biomass is allocated to root (versus shoot) material, and we tested how the effect of shade on plant growth patterns may shift with changes in soil water content. We grew seedlings in two different soils varying in water holding capacity (WHC, the ability of a given soil texture to hold water), two levels of light (high and shade), and two watering levels to serve as a surrogate for interspecific water competition. We evaluated three predictions: 1) Both species would have lower root allocation (R:S, RMF) under shade, compared to individuals of the same soil and watering treatments; 2) Higher shoot allocation under shade would initially increase seedling growth (leaf area, leaf length) compared to unshaded seedlings, but the difference in growth rates between shaded and unshaded seedlings would decrease as specific leaf area increases; 3) root biomass will increase with decreasing soil water content.

Methods

Our experimental design followed a 2x2x2 split block design in which we fully crossed soil type (high WHC, low WHC), water availability (high, low), and species (globemallow and bluebunch wheatgrass) within blocks that were split into shaded vs. unshaded. There were 6 blocks, and each block had two subsamples of each WHC, water availability, species, shade combination.

To create high and low soil water holding capacities (WHC), we used a field-collected clay loam from the AP horizon of a previously cultivated field near Millville, Utah with 3.5% soil organic matter (23.7% sand, 29.8% clay, 46.5% silt). Soil was unaltered for the high WHC treatment. We diluted the high WHC soil with field-collected fine sand from Preston, Idaho in a 3:2 ratio of clay loam to sand to create a low WHC soil with 2.1% organic matter (50.3% sand, 18.9% clay, 30.8% silt). Both soils were sent to Brigham Young University Environmental Analytical Lab (Provo, UT) for texture analysis by the hydrometer method, total soil organic matter by loss on ignition. Soils were also analyzed for soil water content (SWC%) at two soil matric water potentials: -0.03 MPa, ~field capacity and -1.5 MPa, ~permanent wilting point. Because we did not sterilize the soil, some seeds from the soil seed bank germinated throughout the experiment but were removed immediately (mostly *Salsola tragus*).

We germinated bluebunch wheatgrass (Anatone Selected Class Germplasm, Asotin Co., WA) and Munro's globemallow seeds (scarified for 10 minutes in 12M sulfuric acid; Fulbright & Flenniken 1987) in germination boxes filled with approximately 5 mm of fine sandy soil. We then covered them with germination paper to keep seeds moist and kept boxes at 4°C in the dark until radicals and coleoptiles had emerged. Then, we filled 192 (n = 96 for each species) 470 ml plastic cups (60mm bottom diameter, 90mm opening diameter, 120 mm tall) filled with 500 g of dry soil and transplanted the germinated seedlings into these cups. We transplanted four globemallow seedlings and two bluebunch wheatgrass seedlings per cup because we found that globemallow were more likely to die during this initial growth stage during previous trials. The cups were kept moist for 10 days at 25°C before being thinned to one seedling (the only remaining living seedling or the largest seedling) and placed in a growth chamber (model PGW40, Conviron, Winnipeg, Canada). During the initial ten days before placing plants in the growth chamber, nine globemallow plants died and did not have a replacement, so 184 seedlings were placed in the growth chamber.

In the growth chamber, photosynthetically active radiation (PAR; 400-700 nm) was set to 1000 μmol m^{-2} s^{-1} with a combination of incandescent and LED bulbs on a 14/10-hour day/night diurnal schedule where daytime settings were 23°C and 40% relative humidity (RH) and the nighttime settings were 12°C and 80% RH. The seedlings in the unshaded treatment were grown under ambient light (~1000 μmol m^{-2} s^{-1}) while the seedlings that were assigned to the shade treatment were placed under a neutral density shade structure that reduced photosynthetically active radiation (PAR; 400-700 nm) by 50% (see Monaco & Briske 2000).For the first week of the experiment, we imposed watering treatments based on SWC values associated with lab-determined field capacity and permanent wilting points of our soils. In the high WHC soils, the lab-determined SWC at field capacity was 23.0% and the lab-determined permanent wilting point was 13.8%. In the low WHC soils, the lab determined permanent wilting point and field capacity SWCs were 5.4 and 14 %, respectively. We watered all cups of a given WHC-watering treatment combination when one cup dropped below the permanent wilting point to either field capacity (high water) or the midway point between field capacity and permanent wilting point (low water). In the high water treatment, we watered to field capacity, and in the low water treatment, we watered to midway between permanent wilting point and field capacity. After using lab-determined field capacity and permanent wilting point for the first week of the experiment, we observed high mortality in the low watering treatment (10 seedlings, 5% of individuals). In response to the high mortality, we increased the permanent wilting point by 30%: from 13.8 to 17.8% in high WHC; and 5.4 to 7% in low WHC). Because thehe difference in soil water content at permanent wilting point and field capacity is the soil water available to a plant, the available water content, we then adjusted field capacity to reflect the same available water content as with lab-determined values (23 to 27% in high WHC; 14 to 16.2% in low WHC). Throughout the 44 days in the growth chamber, we weighed the cups and recorded those weights every one to two days to track both evaporation and maintain the watering regimes.

When cups were first brought into the growth chamber, and every 2 weeks thereafter for their 44 days in the growth chamber, we measured plant size. We recorded the length of the longest leaf, numbers of tillers, and numbers of leaves for bluebunch wheatgrass. For globemallow, we took an overhead photograph of the cup and included a 2.5mm diameter red circle in the frame to calibrate the size of the image using Photoshop (see Xiao et al. 2005; Adobe Systems, San Jose, CA). We then used Canopeo, an automatic color threshold image analysis tool mobile phone application (Patrignani & Ochsner 2015) to calculate the percentage of the photo that was green. We multiplied the photo area by the percent green to determine the area (cm^2) of the photo that was green.

After 44 days, we harvested seedlings and separated shoots from roots. First, we obtained digital images of stems and leaves together and analyzed images to determine leaf area (WinRHIZO Pro 2020, Regent Instruments, Québec, Canada). Then, we washed roots twice using sieves with 850 µm openings. The stems/leaves and roots were left to dry for 48 hours under lights (stems/leaves) or in a 25°C greenhouse (roots) and then weighed for shoot dry mass and root dry mass respectively.

We used the scanned leaf area and final shoot dry mass to calculate the specific leaf area:

$$SLA = \frac{leaf\ area\ (cm^2)}{shoot\ dry\ mass\ (g)}$$

and we used the final root and shoot dry masses to calculate the root-to-shoot ratio (R:S):

$$R{:}S = \frac{root\ dry\ mass\ (g)}{shoot\ dry\ mass\ (g)}$$

and root mass fraction (RMF).

$$RMF = \frac{root\ dry\ mass\ (g)}{shoot\ dry\ mass\ (g) + root\ dry\ mass\ (g)}$$

To validate the aboveground leaf area measurements from Canopeo, we used Pearson product-moment correlation of the leaf area from Canopeo vs. WinRhizo (Figure C1) collected on the same day (day 44).

Analysis

Each block had two subsamples of each treatment combination (soil WHC, watering treatment, shade, species), so we averaged measurements across subsamples within a block for each species. Due to the relatively low sample size (6 blocks), we modeled each species separately and combined WHC and watering treatments into a single 4-level factor we call “moisture regime” (high WHC high water, high WHC low water, low WHC high water, low WHC low water) that follow a gradient of soil moisture. All models took the same form: mixed effect linear model with the response variable modeled by the interaction of moisture regime and shade as fixed effects and block as the random effect. Two individuals, including one globemallow and one bluebunch wheatgrass, survived but did not grow over the course of the experiment (whereas other replicates of the same treatment did grow). We removed them from the data set before averaging because we believe the root tips were damaged during transplanting, which occurred after the root radical had emerged.

We analyzed specific leaf area (SLA), root dry mass, shoot dry mass, and root to shoot dry mass ratio, and leaf area fraction for both species at the end of the 44 day experiment. In addition, we calculated relative growth rates for plant height, tiller number, and the leaf number for bluebunch wheatgrass and leaf area for globemallow using the equation:

$$RGR = \frac{ln(S2) - ln(S1)}{T2 - T1}$$

Where T1 is the day of the experiment of the first measurement, S1, and T2 is the time of the final harvest (44 days) measurement, S2.

Models were broken up into 4 groups of response variables: (1) the relative growth rate of leaves, height, tillers, and leaf area between the start of the experiment and final harvest (44 days), (2) specific leaf area (3) root dry mass, shoot dry mass, root:shoot dry mass ratio, and root mass fraction, and (4) water loss per day to evapotranspiration. We used pairwise contrasts to look at soil moisture regime-soil combinations for each model with Tukey-adjusted p values. All analyses were conducted in R version 4.2.1 (R

Core Team 2021) with the packages *tidyverse* (Wickham et al. 2019), *plyr* (Wickham 2011), *zoo* (Zeileis & Grothendieck 2005), and *lubridate* (Grolemund & Wickham 2011) to aggregate and tidy the data, *car* (Fox & Weisberg 2018), *emmeans* (Lenth 2020), *multcomp* (Hothorn et al. 2008*)*, and *glmmTMB* (Brooks et al. 2017)to model and visualize the results.

Results

Influence of shade

Shade affected the relative growth rates of bluebunch wheatgrass and globemallow. For bluebunch wheatgrass, shade increased the relative growth rate of leaf length and decreased the number of tillers and leaves (Figure 5.1, Table 5.1). For globemallow, we found that shade had no effect on leaf area over the length of the experiment (Figure 5.1, Table 5.1).

The specific leaf area (SLA) of globemallow was similar between shaded and unshaded treatment for all moisture regimes except for in the low WHC high watering treatment (Figure 5.2, Table 5.2). The SLA for bluebunch wheatgrass was higher under shade in the regime with the lowest available soil water content, low WHC low water (Figure 5.2, Table 5.2). Despite its effects on SLA, shade, for the most part, did not affect biomass allocations. For both species, root dry mass, root:shoot dry mass ratio, and root mass fraction (RMF) were similar between shaded and unshaded treatments (Figure 5.3, Table 5.3). Bluebunch wheatgrass shoot biomass was marginally significantly higher ($p = 0.049$; Table 5.3) under shade compared to ambient light.

Of the 7 globemallow individuals that died in the first week of the experiment 71% were unshaded (n=5) and 29% were shaded (n = 2). However, shade did not reduce the amount of water lost to evapotranspiration at any point in the study (Table C1).

Influence of moisture regimes

Moisture regime effects on relative growth rates and final root/shoot metrics (shoot dry biomass, root dry biomass, R:S, RMF) were similar between the two species. Generally, the high WHC treatment exhibited higher RGRs than the low WHC treatment (Figure 5.1, Table 5.1). The only exception to the high WHC versus low WHC differences were in unshaded globemallow leaf area RGR, where there were no pairwise differences between high and low WHC RGRs in the unshaded treatment. When there were pairwise differences within moisture regimes, the differences were never between the two highest soil moisture treatments (high WHC high watering and high WHC low watering) and more often were between the two lowest soil moisture regimes (low WHC low watering, low WHC low watering; Figure 5.1). The few instances that water regimes were not similar within a soil type (e.g., high WHC high water versus high WHC low water), the differences among low WHC high water and low WHC low water. The effects of high versus low watering in the low WHC soils were observed for final bluebunch wheatgrass shoot dry biomass (Figure 5.3), unshaded RGR number of leaves (Figure 5.2), and unshaded RGR number of tillers (Figure 5.2).

Bluebunch wheatgrass root:shoot ratio and RMF indicated that the highest root allocation occurred in the two moisture regimes with the highest soil moisture (high WHC high water, high WHC low water). Globemallow showed opposite patterns to bluebunch wheatgrass in root allocation, where the lowest moisture regime (low WHC, low watering) had significantly higher root:shoot ratios than the other regimes (Figure 5.3, Table 5.3).

Discussion

Our results illustrate that both light and soil moisture influence seedling growth (dry mass, plasticity in allocation to roots vs shoots, relative growth rates) for both globemallow and bluebunch wheatgrass. The general shade tolerance of both species, as evidenced by similar root allocation patterns between shaded and unshaded treatments, may facilitate both persistence and competitive ability under the canopy.

Role of shade

Bluebunch wheatgrass exhibited high RGRs in leaf length under shade. This faster RGR in leaf length likely compensated for the slower growth rate in number of leaves and tillers because, at the end of the experiment, there were no differences in aboveground dry mass between shaded and unshaded seedlings. Globemallow leaf area growth rate, on the other hand, did not differ by shade treatments, also yielding similar aboveground dry mass at the end of the experiment.

Specific leaf area (SLA) increases under low light conditions (Shipley & Almeida-Cortez 2003) and can offset low relative growth rates aboveground dry biomass under shade to yield plants of equal size (measured as leaf density) to ambient treatments (Shipley 2000). Accordingly, both bluebunch wheatgrass and globemallow had increased SLA in response to shade at the end of the experiment. Under the shade treatment, leaves became thinner over the course of the experiment (as opposed to increasing their dry mass) to maximize photosynthetic capacity, but they did so without decreasing allocation to root dry mass. That is, we found no decreases in root allocation (R:S, RMF) in response to shade, corroborating the shade tolerance of bluebunch wheatgrass (Nowak & Caldwell 1986; Huber-Sannwald & Pyke 2005). Notably, Munro's globemallow did not respond to 50% reductions in PAR, providing new information about the shade tolerance of this species as well.

One alternative explanation for the lack of shade effects on dry mass allocation is that our shade treatment may have been inadequate. We achieved a 50% reduction of PAR under the shade treatment, from approximately 1000 μmol m^{-2} s^{-1} to approximately 500 μmol m^{-2} s^{-1}. This is similar to the PAR under sagebrush canopies under field settings and representative of field settings and the conditions faced by seedlings in under-canopy microsites (Huber-Sannwald & Pyke 2005; Liu et al. 2020). However, our shade treatment may have nonetheless been insufficient to stimulate stronger changes in dry mass allocations in the first 6 weeks of seedling growth. Additionally, while the shade treatment decreased PAR as intended, we also had expected evapotranspiration to be lower under shade, either as a byproduct of decreased radiation (Lambers & Oliveira 2019) or due to the insulating effects of the shade structure. Instead, we found similar evaporation rates between the shaded and unshaded treatment, likely a byproduct of the lower infrared radiation compared to field settings and constant air circulation in the growth chamber that reduced the leaf boundary layer, the thin layer of air adjacent to the leaf surface that provides resistance to transpiration by reducing heat transfer between the leaf and its surroundings – thinner boundary layers are associated with higher transpiration rates than thicker boundary layers (Grace & Wilson 1976; Boulard et al. 2004).

Watering regimes and soil types

Growth is commonly allocated to plant structures to compensate for the most limiting resource: shoots when light is limiting and roots when water and nutrients are limiting (Shipley & Meziane 2002). We did not observe a root allocation response to shade, but we did observe responses to decreasing soil water content in our watering regimes. We expected root biomass allocation (R:S, RMF) to increase drought stress for both species, which we observed for globemallow with increasing R:S and RMF with decreasing soil water content. But we found that for bluebunch wheatgrass, R:S and RMF decreased with decreasing soil water content. Root mass fraction (RMF; root dry mass divided by total dry mass) typically increases in response to drought treatments at the expense of aboveground dry mass when plants are subject to severe drought (Poorter et al. 2012).

Species-specific responses

Coexisting species can display different responses in aboveground traits to the same stressors (Sultan et al. 1998; Hill et al. 2006; Grassein et al. 2010), even more so when the species are more unrelated (Albert et al. 2010; Lü et al. 2012), like bluebunch wheatgrass (a monocot) versus globemallow (a dicot). Bluebunch wheatgrass and globemallow showed opposite dry mass allocation patterns (R:S and RMF) in response to soil and watering regimes. Most species increase R:S and RMF with decreasing water availability to improve access to soil moisture (Poorter & Nagel 2000). Globemallow followed this pattern, increasing RMF with decreasing soil moisture. Bluebunch wheatgrass, on the other hand, showed increasing R:S with higher available water. This is contradictory to our expectation but similar to other studies that found bluebunch wheatgrass maintained high RMF and R:S across a soil moisture gradient (Blicker et al. 2003; Zheng et al. 2019). Unsurprisingly, we found that both globemallow and bluebunch wheatgrass exhibited the greatest dry mass when soil moisture was highest, but interestingly, this pattern was not altered by light levels. Our results suggest that bluebunch wheatgrass and globemallow could capitalize on high soil moisture by increasing both above and belowground biomass regardless of microsites (under shrub canopies versus outside shrub canopies). This increase in root dry mass allows for them to be competitors for soil resources when resources are abundant, but then tolerate drought when resources are less abundant (Zheng et al. 2019), regardless of whether they are growing in microsites under vs. outside of the canopy. This growth pattern is additionally beneficial because water use efficiency of bluebunch wheatgrass is highest when soil moisture is high, further capitalizing on beneficial soil moisture (Blicker et al. 2003). Importantly, we show that shade does not affect that growth pattern that allows for high growth rates when soil moisture is high.

Implications

The shade tolerance of both bluebunch wheatgrass and globemallow suggests a strong advantage for these species of growing under the sagebrush canopy. First, seeds growing under the shade of the canopy have similar root allocation patterns to seedlings growing under ambient light, like conditions found in interspaces. Shaded seedlings therefore presumably have a similar (higher) ability to access soil moisture as do unshaded seedlings. Root traits are linked to higher resource acquisition (Wang et al. 2010; Leger & Goergen 2017) and specifically, increased R:S is associated with competitive tolerance to cheatgrass (*Bromus tectorum*), an introduced grass ubiquitous in the Intermountain West (Rowe & Leger 2011). Secondly, soil moisture can be higher under sagebrush canopies in the early growing season (Caldwell & Richards 1989; Davies et al. 2007; Cardon et al. 2013).

Because shade did not affect the opportunistic growth patterns of bluebunch wheatgrass or the high R:S of globemallow, artificial shade structures that decrease radiation and evapotranspiration should be considered in restoration settings. Structures that mimic nurse shrub effects of sagebrush canopies, like artificial structures that trap loess and seeds (Fick et al. 2016) or dead sagebrush that provide shade to understory seedlings (Poulos et al. 2014), have been shown to increase seedling cover and density. Artificial shade structures could similarly be used to improve establishment rates. In the Intermountain West, large gaps between perennial vegetation, like between sagebrush individuals, make sagebrush stands more susceptible to cheatgrass invasion (Reisner et al. 2013). Artificial shade structures placed in large gaps and seeded with bluebunch wheatgrass and globemallow may improve traditionally low establishment outcomes. However, the facilitative effects of living sagebrush canopies extend to invasive annual grasses (Lucero et al. 2021) and it is possible that annual grasses would also be higher under an artificial shade structure. This association may not doom the efficacy of artificial shade structures as a restoration technique because other perennial grasses with similar R:S patterns as bluebunch wheatgrass (see Zheng et al. 2019)are able to establish from seed in invasive-dominant stands (Hironaka & Sindelar 1973), or herbicides could be applied to reduce invasive annual grass cover. More simply, seeding in canopies may also yield high establishment rates (Young & Evans 1975) and we illustrate that globemallow and especially bluebunch wheatgrass, may remain competitive for soil resources against established perennial and exotic annual vegetation.

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Tables

Table 5.1: Analysis of Variance table (type III test) results for generalized mixed effect regression models of relative growth rate (RGR) for bluebunch wheatgrass leaf length, number of leaves, and number of tillers, and Munro's globemallow leaf area between the start and end of the experiment (44 days). RGR was calculated as the difference between the natural log of each response variable between the day that the seedlings were placed in the growth chamber (day 1) and the end of the experiment (day 44). The fixed effects are moisture regime (high water holding capacity [WHC] high water, high WHC low water, low WHC high water, low WHC low water) and light (shaded, unshaded), and the random effect is the experimental block. Results in bold are significant at alpha of 0.05.

			Chi Sq	df	Pr (> Chi Sq)
Bluebunch Wheatgrass	RGR Leaf Length	Intercept	206.855	1	**<0.001**
		Regime	88.778	3	**<0.001**
		Shade	38.395	1	**<0.001**
		Regime : Shade	1.241	3	0.743
	RGR # of Leaves	Intercept	2869.055	1	**<0.001**
		Regime	127.305	3	**<0.001**
		Shade	10.203	1	**0.001**
		Regime : Shade	2.861	3	0.414
	RGR # of Tillers	Intercept	2687.047	1	**<0.001**
		Regime	230.448	3	**<0.001**
		Shade	16.207	1	**<0.001**
		Regime : Shade	3.519	3	0.318
Globemallow	RGR Leaf Area	Intercept	442.617	1	**<0.001**
		Regime	31.638	3	**<0.001**
		Shade	0.074	1	0.786
		Regime : Shade	1.606	3	0.658

Table 5.2: Analysis of Variance table (type III test) results for generalized mixed effect regression models of specific leaf area for bluebunch wheatgrass and Munro's globemallow. The fixed effects are moisture regime (high water holding capacity [WHC] high watering, high WHC low watering, low WHC high watering, low WHC low watering) and light (shaded, unshaded), and the random effect is the experimental block. Results significant in bold at alpha of 0.05.

		Chi Sq	Df	Pr(>Chi Sq)
Bluebunch Wheatgrass	Intercept	1407.46	1	< **0.001**
	Regime	8.18	3	**0.043**
	Shade	21.3	1	< **0.001**
	Regime:Shade	2.36	3	0.501
Globemallow	Intercept	580.12	1	< **0.001**
	Regime	2.16	3	0.54
	Shade	24.8	1	< **0.001**
	Regime:Shade	11.02	3	**0.012**

Table 5.3: Analysis of Variance table (type III) results for generalized mixed effect regression models of shoot and root biomass, root:shoot ratio, and leaf mass fraction for bluebunch wheatgrass and Munro's globemallow. The fixed effects are moisture regime (high water holding capacity [WHC] high water, high WHC low water, low WHC high watering, low WHC low water) and light (shaded, unshaded), and the random effect is the experimental block. Results significant in bold at alpha of 0.05.

		Blubunch Wheatgrass			Globemallow		
		Chi Sq	Df	Pr(>Chi Sq)	Chi Sq	Df	Pr(>Chi Sq)
Root Biomass	Intercept	665.443	1	**< 0.001**	167.676	1	**< 0.001**
	Regime	261.341	3	**< 0.001**	32.148	3	**< 0.001**
	Shade	0.816	1	0.366	0.839	1	0.36
	Regime : Shade	1.98	3	0.577	3.072	3	0.381
Shoot Biomass	Intercept	1035.743	1	**< 0.001**	281.624	1	**< 0.001**
	Regime	317.54	3	**< 0.001**	98.614	3	**< 0.001**
	Shade	3.885	1	**0.049**	0.189	1	0.664
	Regime : Shade	1.248	3	0.741	2.621	3	0.454
Root:Shoot	Intercept	690.661	1	**< 0.001**	511.96	1	**< 0.001**
	Regime	38.475	3	**< 0.001**	17.533	3	**< 0.001**
	Shade	1.345	1	0.246	0.19	1	0.663
	Regime : Shade	2.269	3	0.518	2.406	3	0.492
Root Mass Fraction	Intercept	2391.341	1	**< 0.001**	2036.944	1	**< 0.001**
	Regime	30.59	3	**< 0.001**	22.148	3	**< 0.001**
	Shade	3.417	1	0.065	0.117	1	0.732
	Regime : Shade	2.66	3	0.447	0.891	3	0.828

Figures

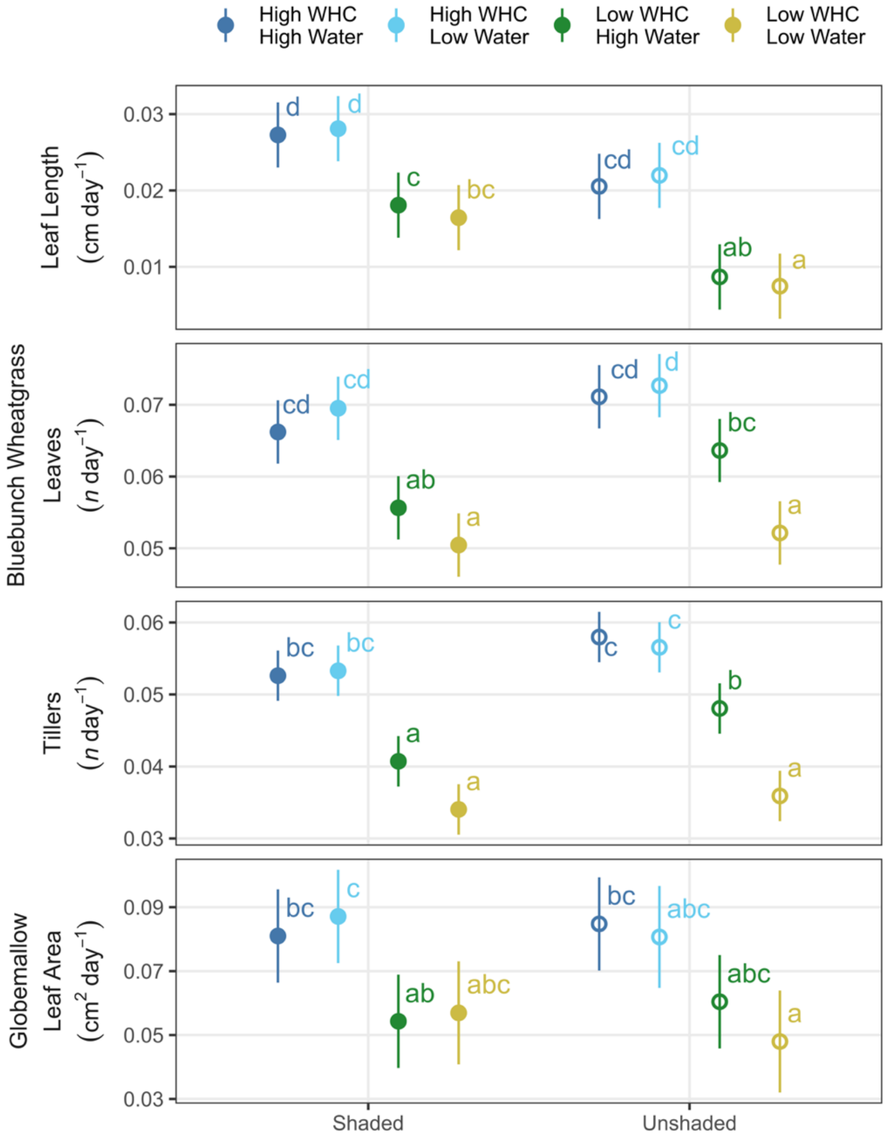

Figure 5.1: Modeled mean relative growth (RGR), calculated as the difference between the natural log of each response variable (bluebunch wheatgrass leaf length, number of leaves, and number of tillers, and Munro’s globemallow leaf area) between the start (day 1) and end of the experiment (day 44) Colors indicate soil moisture regimes: high water holding capacity [WHC] high water, high WHC low water, low WHC high water, low WHC low water and filled points indicate light treatments (shaded, unshaded). Shared letters indicate no Tukey-adjusted pairwise differences among treatment levels (all 8 moisture regime- shade combinations).. Error bars indicate 95% confidence intervals.

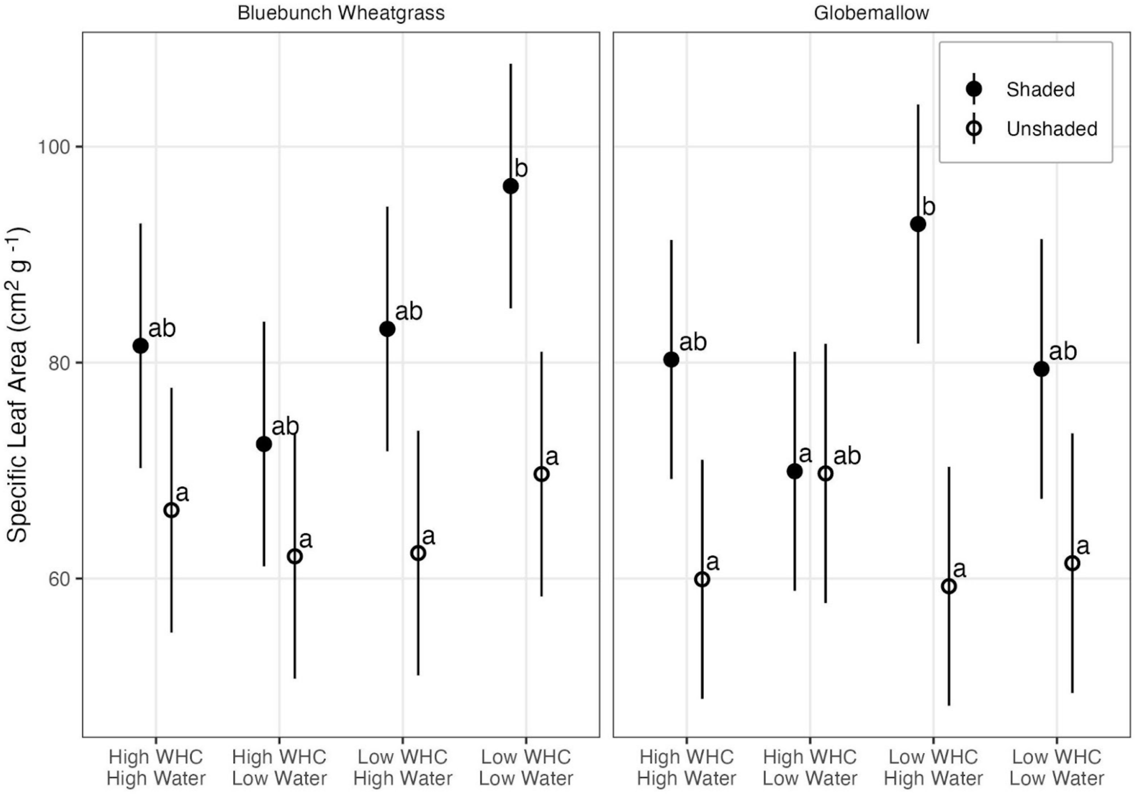

Figure 5.2: Modeled mean specific leaf area for bluebunch wheatgrass and Munro’s globemallow specific leaf area after 44 days in the growth chamber under two levels of light (shaded, unshaded) and four moisture regimes (high water holding capacity [WHC] high water, high WHC low water, low WHC high water, low WHC low water). Shared letters indicate no Tukey-adjusted pairwise differences among treatment levels (all 8 moisture regime- shade combinations). Error bars indicate 95% confidence intervals.

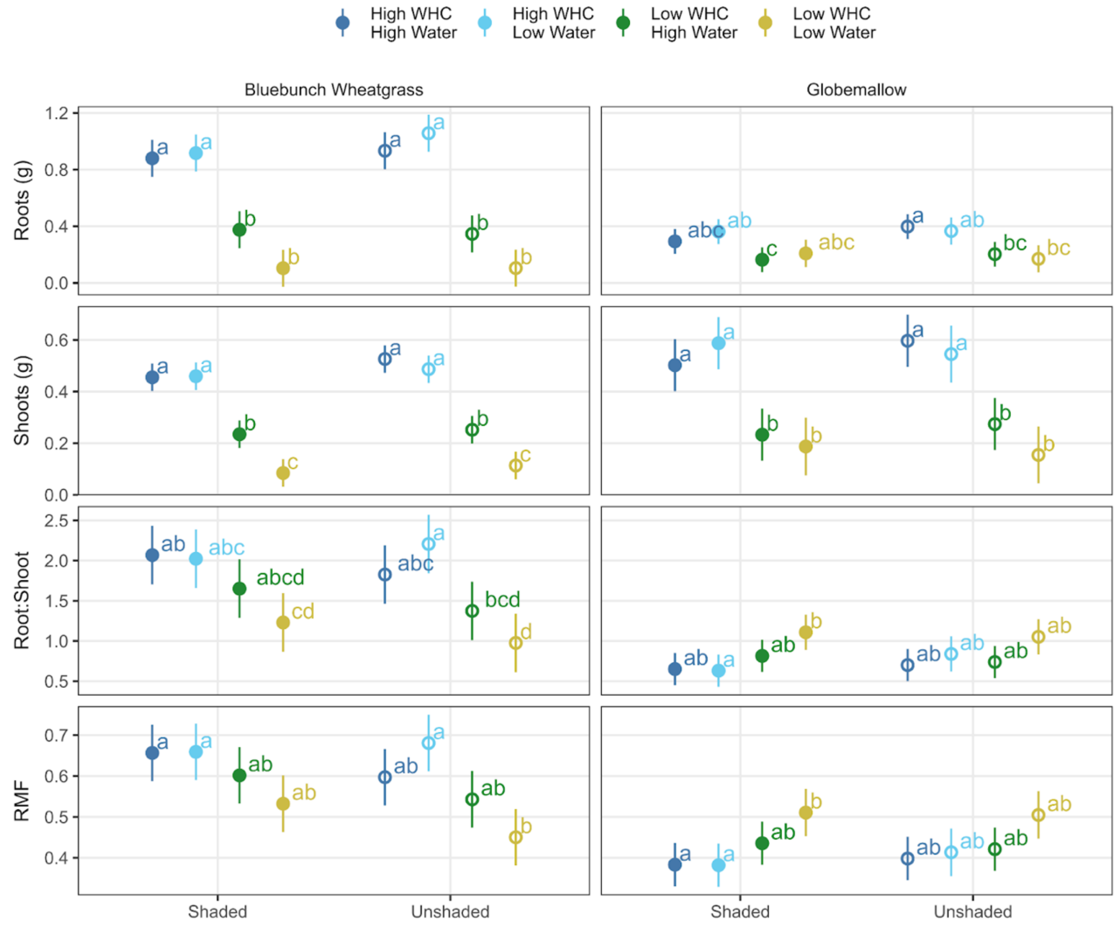

Figure 5.3: Modeled mean specific leaf area for bluebunch wheatgrass and Munro's globemallow root biomass (Roots), shoot biomass (Shoots), root:shoot ratio (Root:Shoot), and root mass fraction (RMF) after 44 days in the growth chamber at two light levels (shaded, unshaded) and four moisture regimes: high water holding capacity [WHC] high water, high WHC low water, low WHC high water, low WHC low water. Shared letters indicate no Tukey-adjusted pairwise differences among treatment levels (all 8 moisture regime- shade combinations). Error bars indicate 95% confidence intervals.

CONCLUSION

Traditional methods of restoration in Wyoming big sagebrush systems of the Intermountain West have been largely insufficient to successfully break the fire-cheatgrass cycle (Pyke et al. 2013; Knutson et al. 2014; Shackelford et al. 2021). There are increasing calls for alternative methods and restoration paradigms that protect stands of sagebrush steppe where sagebrush remains, rather than attempting to restore these systems from seed (Smith et al. 2022; Maestas et al. 2022; Johnson et al. 2022). Increasing resistance to further cheatgrass invasion and increasing a community's resilience to future fires can be achieved by increasing understory perennial grass and forb cover (Chambers et al. 2014). This dissertation focused on understanding how sagebrush's nurse shrub effects and resource island formation can best be capitalized to increase perennial grass and forb establishment in depauperate sagebrush stands of the Intermountain West. I used experimental manipulations in both the field and a controlled growth chamber environment to test the tradeoffs between the positive nurse shrub effects of sagebrush on understory vegetation and negative effects from the established vegetation, pathogens, and the canopy itself. My results show that while canopies do increase survival of some transplanted species and do not negatively affect growth patterns of some understory plants, most belowground resources that are thought of as driving nurse shrub effects are not exclusively found around the canopy, but instead remain high from the canopy into the interspace.

In the first data chapter, I studied how the survival of transplanted seedlings is affected by the net effects of a favorable canopy microenvironment versus competition with established vegetation. I found that for the first cohort, when precipitation was above-normal, forb seedlings (*Sphaeralcea munroana* and *Achillea millefolium*) planted midway between the canopy and maximum interspace distance between sagebrush plants exhibited the highest survival, associated with increased biological soil crust cover, while grass (*Elymus elymoides* and *Pseudoroegneria spicata*) survival was similar at all distances between the canopy and interspace. For the second cohort, when precipitation was at- or below-normal, both grasses and forbs had similar probabilities of survival at all distances from the canopy. I suggest that the peak-survival of *S. munroana* and *A. millefolium* in the area outside and immediately surrounding the canopy is the net effect of interspecific competition pushing survival away from the canopy and nurse shrub facilitation pulling survival towards the canopy, a phenomenon Pescador et al. (2014) calls "facilitation in the halo."

In the second data chapter, I studied the how fungicide and nurse shrub effects can be utilized to improve emergence rates of seeded native grasses. Seed-coating is a promising avenue of restoration that allows planted seeds to overcome biotic and edaphic barriers to seedling establishment (Madsen et al. 2016) while remaining scalable for large-scale restoration projects, but the efficacy of different seed coatings is subject to weather and climate (Davies et al. 2018; Hoose et al. 2022).Fungicide-coated seeds can greatly improve emergence rates when precipitation is high (Hoose et al. 2022) but have no effect on emergence when precipitation is low. Capitalizing on favorable nurse shrub microenvironments may also improve emergence rates but is similarly subject to interannual variation in weather. Nurse shrub effects can increase understory cover when precipitation is anomalously dry (Swanson et al. 2021), we did observe higher emergence under the canopy at the one site where seedlings did emerge, but proximity to the shrub canopy did not reliably increase emergence. I found that when precipitation is at- or below-normal, fungicide has no effect on seedling emergence, supporting previous findings by Hoose et al. (2022). Hoose et al. (2022) only tested fungicide coatings on bluebunch wheatgrass and we found that bluebunch wheatgrass and another native perennial bunchgrass, squirreltail, respond similarly to fungicide in low precipitation years. My results highlight the need to repeat ecological field experiments in multiple years (Vaughn & Young 2010; Werner et al. 2020).

In the third data chapter, I investigated how the favorable microenvironment characteristics around shrub islands (organic matter, soil moisture, available nitrogen, phosphorus, potassium, radiation, vapor pressure deficit) change between the canopy and interspace. Building on the first data chapter results that showed some species established best outside of sagebrush canopies, I was interested if resource-rich shrub island microenvironments extend into the interspace. While this type of study where various attributes of shrub microenvironments are analyzed at multiple distances from the canopy to interspace has occurred in the Intermountain West previously (Jackson & Caldwell 1993b, 1993a; Ryel et al. 1996) results have been site-specific (Doescher et al. 1984). In this chapter I showed that litter may be a mechanistic driver of resource availability under and around sagebrush canopies. I found that only radiation and potassium were clustered around the canopy while the remaining attributes of shrub islands (organic matter, soil moisture, available nitrogen, phosphorus, vapor pressure deficit) remained equally or near equally high across microsites that ranged from the canopy to interspace.

The fourth data chapter was motivated by my finding in the third data chapter that radiation was far lower at the canopy edge compared to interspace microsites and that modulation of light from the sagebrush canopy has the possibility of increasing seedling establishment by decreasing evapotranspiration (Lambers & Oliveira 2019). I therefore investigated the potentially negative influence of shade and its interaction with water availability on seedling growth. Plants with high root allocation are more competitive for soil resources and are more drought tolerant than plants with low root allocation (Rowe & Leger 2011; Zheng et al. 2019). Shade can negatively impact seedling growth and competitive ability by diverting growth from roots to shoots. We corroborated a previous study that found that bluebunch wheatgrass is shade tolerant (Huber-Sannwald & Pyke 2005) and newly revealed that Munro's globemallow is also shade tolerant. The lack of a shade response to root allocation for both species suggests that canopy microsites can be highly advantageous because seedlings growing under shaded conditions can access the resource-rich microenvironment generally found under canopies without decreasing their root:shoot ratio in response to low light. Artificial shade structures may be a promising restoration technique, potentially increasing establishment without tradeoffs to belowground biomass allocation.

My dissertation research highlights that the binary distinction of canopies as "good" and interspaces as "bad" microenvironments for seedling establishment is insufficient to describe the spatial and temporal variation in resource-rich islands and nurse shrub effects. Rangelands are characterized by high spatial and temporal variation (Reeves et al. 2021), coupled with mosaics of management and land use histories (Knapp 1996; Sayre 2005). The interspecific relationships that drive community assembly and restoration outcomes (Werner et al. 2020) are not static but change with resource availability (Holland & DeAngelis 2009), stress-gradients (Callaway & Walker 1997;

Maestre et al. 2009), and plant traits (Graff & Aguiar 2017). While simplified paradigms can be beneficial to understand some processes, in Western rangelands, the drivers of dynamism are numerous and widespread, and given the cost and scope of restoration activities occurring the region, those drivers must be considered.

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APPENDICES

Appendix A – Supplementary Information for Chapter 2

Table A1: Supplementary site information for seven study sites in the Intermountain West, USA. Six sites were established May-June 2018 and a seventh (Grey Butte) was established October 2019 to replace Rock Creek after it burned. Precipitation data is total precipitation for 21 days after each cohort was planted, and temperature is the 30 year normal (1990-2020) minimum, mean, and maximum for each site (4 km resolution; PRISM Climate Group 2014). Soil taxonomy and soil series are from Web Soil Series (Soil Survey Staff 2020). Line point-intercept, basal gap between perennial plants (avg. per. gap), sagebrush density (collected in belt transects), and dung counts were collected May-June 2018, except Grey Butte, which was monitored June 2019. Line point-intercept reflects absolute, not relative cover.

Site	Lat., Lon.	Temp (Min Mean Max °C)	Soil Taxonomy	Avg. Per. Gap (m)	Line Point Intercept (%)							Sagebrush Sizes by Height (count/cm2)				Animals (dung count/ha)					
					Bare Ground	Litter	Intro. Forb	Cheatgrass	Native PG	Native Forb	Native Shrub	Seedling	< 15cm	< 50cm	>100 cm	Cow	Lagomorph	Coyote	Pronghorn	Elk/ Deer	Squirrel
Rock Creek	42.73 -119.49	1.0 8.3 15.7	Loamy-skeletal, mixed, active, mesic Xeric Haplocalcids	3.3	26	37	0	9	31	9	21	0	0.087	0.79	0.37	0	22800	100	0	0	0
Grey Butte	-119.44 42.72	0.3 8.2 16.0	Fine-loamy, mixed, superactive, frigid Xeric Argidurids	1.4	43	48	0	4	16	5	18	0	0.007	0.31	0.33	0	16900	0	300	0	0
Wilson	41.60 -116.40	-0.4 8.0 16.4	Fine, smectitic, mesic Xeric Argidurids	5.2	6	91	10	72	10	3	40	0	0.007	0.36	1.03	800	5700	0	0	0	500
Roberts	43.76 -112.29	-1.7 5.9 13.6	Fine-loamy, mixed, calcareous, frigid Xeric Torriorthents	5.3	29	65	21	4	3	2	25	0.47	0.76	1.76	0.84	0	28000	0	0	0	0
Onaqui	40.20 112.46	1.1 9.2 17.3	Loamy-skeletal, mixed, active, mesic Xeric Haplocalcids	1.4	18	77	3	1	45	1	25	0	0.013	0.81	1.01	1600	1900	0	100	100	0
Birds of Prey	43.25 -116.25	3.5 10.6 17.6	Fine-loamy, mixed, mesic Xerollic Calciorthids	1.4	26	68	20	0	26	0	26	0.16	0.21	1.25	0.66	1100	800	0	0	0	0
Saddle Mtn	46.75 -119.36	4.5 11.0 17.5	Coarse-silty, mixed, superactive, mesic Xeric Haplocambids	2.1	14	75	0	19	48	1	32	0	0.007	0.027	0.74	0	8000	0	0	0	0

Table A2: Seed provenance, provided by BLM seed warehouses, for each species and variety planted at six sites across the Intermountain West in both years the experiment was initiated.

Site	Yarrow		Globemallow		Squirreltail		Bluebunch Wheatgrass	
	Variety	Source County & Elevation (m)	Variety	Source County & Elevation (m)	Variety	Source County & Elevation (m)	Variety	Source County & Elevation (m)
Rock Creek/ Grey Butte	Eagle	Ada, ID 850m	Munro's	Uintah, UT 1550m	Emigrant	Harney, OR 1450-1554m	Anatone	Latah, ID 1005m
Wilson	Eagle	Ada, ID 850m	Munro's	Uintah, UT 1550m	Toe Jam	Elko, NV 1830m	Sheeps Head	Malheur, OR 1415-1485m
Roberts	Eagle	Ada, ID 850m	Munro's	Uintah, UT 1550m	Fish Creek	Blaine, ID 1445m	Anatone	Latah, ID 1005m
Onaqui	Eagle	Ada, ID 850m	Munro's	Uintah, UT 1550m	Site ID	Duchesne, UT 1740m	Sheeps Head	Malheur, OR 1415-1485m
Birds of Prey	Eagle	Ada, ID 850m	Munro's	Uintah, UT 1550m	Turkey Lake	Franklin, WA 305m	Sheeps Head	Malheur, OR 1415-1485m
Saddle Mtn	Yakima	Franklin, WA 175m	Munro's	Uintah, UT 1550m	Turkey Lake	Franklin, WA 305m	Horse Heaven	Benson, WA 255m

Table A3: Summary of descriptive survival and disturbance for four species of herbaceous seedlings planted in Oct-Dec of 2018 (2018 Cohort) and 2019 (2019 Cohort) at seven sites in the Intermountain West. Species are referred to by their 4-letter USDA Plant code (globemallow SPMU; yarrow ACMI; bluebunch wheatgrass PSSP; squirreltail ELEL). Seedlings were monitored for survival and qualitative signs of disturbance (frost heaving, herbivory, trampling, animal burrows) at 7-8 months (Year 1), 19-20 months (Year 2), 31-32 months (Year 3), and 40 months (Year 4) post-planting. "n" refers to total number planted for each species-cohort combination. % dist is percent of seedlings with signs of disturbance. % survival is percent of seedlings that survived relative to the initial number planted.

site	species	n	Year 1		Year 2		Year 3		Year 4	
			% dist.	% survival	% dist.	% survival	% dist.	% survival	% dist.	% survival
2018 Cohort										
Saddle Mtn	SPMU	97	0	65.1	0	56.6	1.7	42.5	2.22	9.4
	ACMI	51	0	47.5	0	30.7	0	4	0	2
	PSSP	99	0	57.3	0	47.2	0	39.3	0	24.7
	ELEL	107	0	13.6	0	7.3	0	1.8	0	0
Birds of Prey	SPMU	88	89.7	0	—	—	—	—	—	—
	ACMI	65	95.5	0	—	—	—	—	—	—
	PSSP	93	94.6	4.3	100	1.08	100	0	—	—
	ELEL	94	95.3	0	—	—	—	—	—	—
Onaqui	SPMU	93	10.6	51.1	4.17	17.0	0	2.1	0	1.1
	ACMI	92	3.5	7	0	1.2	0	0	—	—
	PSSP	107	4.1	11.2	0	0	—	—		—
	ELEL	99	2.5	22.3	0	0	—	—	—	—
Roberts	SPMU	100	50	22.0	50	19	0	18	0	18
	ACMI	77	57.1	2.6	0	2.6	0	1.3	0	1.3
	PSSP	93	61.3	2.2	50	1.1	0	0	—	—
	ELEL	114	58.8	30.7	17.14	25.4	0	21.9	0	18.4
Rock Creek	SPMU	90	74.4	1.1	—	—	—	—	—	—
	ACMI	94	72.3	2.1	—	—	—	—	—	—
	PSSP	74	56.8	2.7	—	—	—	—	—	—
	ELEL	98	51	6.2	—	—	—	—	—	—
Wilson	SPMU	87	17.2	35.6	3.23	24.1	28.6	8.1	14.3	2.3
	ACMI	85	20	8.2	0	3.5	0	1.2	0	0
	PSSP	114	27.2	3.5	0	1.8	0	0	—	—
	ELEL	116	24.1	1.7	50	0.9	100	0	—	—
2019 Cohort										
Saddle Mtn	SPMU	97	4.1	95.9	1.1	52.6	2	11.3		
	ACMI	51	2	5.9	0	2	0	3.9		
	PSSP	99	3	68.7	2.9	20.2	0	6.1		
	ELEL	107	2.8	75.7	0	2.8	0	1.9		
Birds of Prey	SPMU	88	100	0	—	—	—	—		
	ACMI	65	100	1.5	100	0	—	—		
	PSSP	93	100	0	—	—	—	—		
	ELEL	94	100	0	—	—	—	—		
Onaqui	SPMU	93	77.4	7.5	0	—	—	—		
	ACMI	92	79.4	12	0	1.1	0	0		
	PSSP	107	19.6	0	—	—	—	—		
	ELEL	99	21.2	0	—	—	—	—		
Roberts	SPMU	97	12.4	17.5	5.9	6.2	0	1		
	ACMI	88	5.7	2.3	0	1.1	0	2.3		
	PSSP	117	6.8	1.7	0	—	—	—		
	ELEL	113	30.1	10.6	8.3	2.7	0	7.1		
Grey Butte	SPMU	89	64	6.7	16.7	1.1	0	—		
	ACMI	96	67.7	4.2	25	1	0	—		
	PSSP	112	11.6	3.6	50	1.8	0	1.8		
	ELEL	116	38.8	8.6	0	6.9	0	1.7		
Wilson	SPMU	88	68.2	12.5	27.3	3.4	0	1.1		
	ACMI	85	76.5	0	—	—	—	—		
	PSSP	102	45.1	1	0	0	—	—		
	ELEL	105	61	1	0	0	—	—		

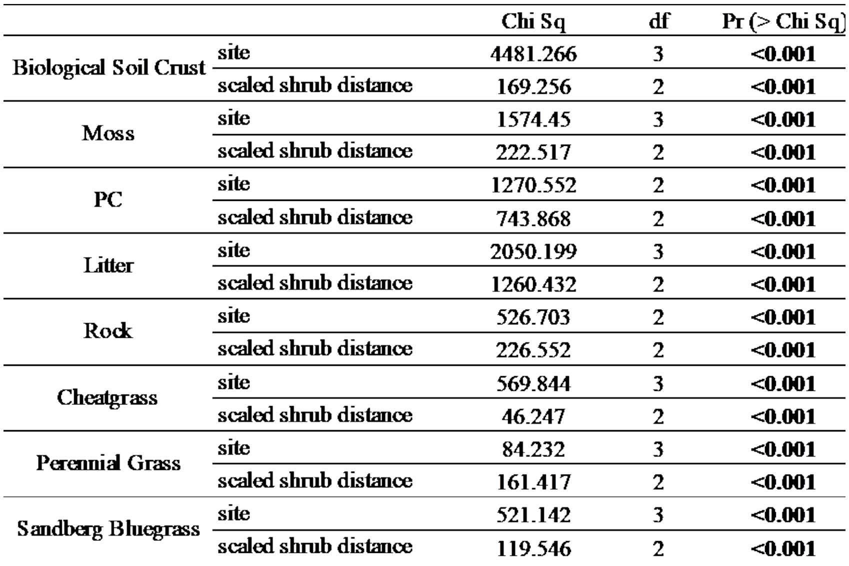
Table A4: Analysis of Variance Table (type II test) results of logistic regression models for each of four herbaceous species (globemallow [*S. munroana*], yarrow [*A. millefolium*], bluebunch wheatgrass [*P. spicata*], and squirreltail [*E. elymoides*]) planted at multiple distances from sagebrush canopies in each of two cohorts (2018, 2019) across 5 sites in the Intermountain West, USA and monitored in two post-planting periods (Year 1, Year 2). Separate models were run for each species-cohort-year combination. Year 1 assessed survival 7-8 months post-planting and Year 2 assessed survival of those same individuals 15-18 months post-planting. For each analysis only sites with > 5 living seedlings were included, so number of sites included within species-cohort-year combinations range from 1 (i.e., no test of site) to five. Fixed effects are site and orthogonal 2nd order scaled shrub distance (distance from sagebrush stem divided by shrub diameter). Results significant at α < 0.05. All seedlings with evidence of disturbance between planting and monitoring were removed from all analyses.

		LR Chisq	Df	Pr(>Chisq)	LR Chisq	Df	Pr(>Chisq)
		2018 Cohort					
		Year 1			Year 2		
Globemallow	scaled shrub distance	7.740	2	**0.021**	1.954	2	0.376
	site	30.883	3	**< 0.001**	33.661	3	**< 0.001**
Yarrow	scaled shrub distance	8.585	2	**0.014**	1.303	2	0.521
	site	43.379	2	**< 0.001**	—	—	—
Bluebunch Wheatgrass	scaled shrub distance	1.988	2	0.37	2.610	2	0.271
	site	45.071	1	**< 0.001**	—	—	—
Squirreltail	scaled shrub distance	0.582	2	0.747	0.673	2	0.714
	site	40.869	2	**< 0.001**	5.524	1	**0.019**
		2019 Cohort					
		Year 1			Year 2		
Globemallow	scaled shrub distance	2.082	2	0.353	0.542	2	0.763
	site	146.977	4	**< 0.001**	3.466	1	0.063
Yarrow	scaled shrub distance	4.044	2	0.132	—	—	—
	site	—	—	—	—	—	—
Bluebunch Wheatgrass	scaled shrub distance	0.147	2	0.929	4.330	2	0.115
	site	—	—	—	—	—	—
Squirreltail	scaled shrub distance	0.303	2	0.86	0.121	2	0.942
	site	139.123	2	**< 0.001**	—	—	—

Table A5: Distance of peak survival for globemallow and yarrow seedlings planted at variable distances from the canopy edge of a focal sagebrush "nurse plant" in 2018 and 2019 at seven study sites. Table displays the average radius of small, medium and large focal sagebrush plants at each site and the corresponding distance from the canopy edge where survival of globemallow and yarrow was highest (Fig. 2). Radius of small, medium, and large sagebrush categories reflect the radius of a focal sagebrush plant in the 25th, 50th, and 75th percentile of individuals, respectively, at each site. A unitless metric called scaled distance (average sagebrush canopy radius divided by distance from the sagebrush base) was used to model survival probabilities relative to the sagebrush canopy, where 1 indicates the canopy edge. Globemallow and yarrow survival were highest at 1.8 and 2.9 scaled distance units, respectively. Here, scaled distance was used to derive the peak survival distance (cm) values displayed in the table by multiplying the scaled distance unit with peak survival by the average sagebrush radius for each site.

	Small Sagebrush			Medium Sagebrush			Large Sagebrush		
	Sagebrush Radius (cm)	Peak Survival Distance From Canopy Edge (cm)		Sagebrush Radius (cm)	Peak Survival Distance From Canopy Edge (cm)		Sagebrush Radius (cm)	Peak Survival Distance From Canopy Edge (cm)	
		Globemallow	Yarrow		Globemallow	Yarrow		Globemallow	Yarrow
Rock Creek	29	23	55	38	31	73	52	41	98
Grey Butte	35	28	66	46	37	88	63	51	120
Wilson	40	32	76	50	40	95	60	48	114
Roberts	26	21	50	32	26	61	40	32	75
Onaqui	31	25	59	38	31	73	47	38	89
Birds of Prey	29	23	55	36	29	68	47	37	88
Saddle Mtn	48	38	90	61	49	116	78	62	147

Table A6: Analysis of Variance Table (type II test) results for zero-inflated Poisson regression models with soil surface characteristics (biological soil crust, moss, physical crust [PC], litter and rock) and plant cover (cheatgrass [*Bromus tectorum*]), perennial grasses, and Sandberg's bluegrass [*Poa secunda*]) as the response variable for all seedlings planted Oct-Dec 2018 and monitored 7-8 months post-planting (May-June 2019). Fixed effects are site and 2^{nd} order polynomial scaled shrub distance (distance from sagebrush stem divided by shrub radius). Results significant at $\alpha < 0.05$ in bold.



		Chi Sq	df	Pr (> Chi Sq)
Biological Soil Crust	site	4481.266	3	**<0.001**
	scaled shrub distance	169.256	2	**<0.001**
Moss	site	1574.45	3	**<0.001**
	scaled shrub distance	222.517	2	**<0.001**
PC	site	1270.552	2	**<0.001**
	scaled shrub distance	743.868	2	**<0.001**
Litter	site	2050.199	3	**<0.001**
	scaled shrub distance	1260.432	2	**<0.001**
Rock	site	526.703	2	**<0.001**
	scaled shrub distance	226.552	2	**<0.001**
Cheatgrass	site	569.844	3	**<0.001**
	scaled shrub distance	46.247	2	**<0.001**
Perennial Grass	site	84.232	3	**<0.001**
	scaled shrub distance	161.417	2	**<0.001**
Sandberg Bluegrass	site	521.142	3	**<0.001**
	scaled shrub distance	119.546	2	**<0.001**

Table A7: Analysis of Variance Table (type II test) results of logistic regression models of seedling survival for each of four herbaceous species (globemallow [*S. munroana*], yarrow [*A. millefolium*], bluebunch wheatgrass [*P. spicata*], and squirreltail [*E. elymoides*]) by soil surface characteristics (biological soil crust, moss, physical crust, litter and rock) and plant cover (cheatgrass [*B.* tectorum], all perennial grass, Sandberg bluegrass only [*P. secunda*]). Seedlings were planted Oct-Dec 2018 and monitored 7-8 months post-planting (May-June 2019). Fixed effects are site, 2nd order polynomial scaled shrub distance (distance from sagebrush stem divided by shrub radius). For each analysis only sites with > 5 living seedlings were included, so number of sites included within species-cohort-year combinations range from 1 (i.e., no test of site) to five. Results significant at α = 0.006 with a Bonferroni correction in bold.

		LR Chi Sq	df	p value		LR Chi Sq	df	p value		LR Chi Sq	df	p value		LR Chi Sq	df	p value
Globemallow	**Biological Soil Crust**	4.99	1	0.025	**Moss**	2.874	1	0.09	**Cheatgrass**	0.649	1	0.421	**Physical Crust**	0.02	1	0.887
	Site	22.892	3	**<0.001**	**Site**	29.079	3	**<0.001**	**Site**	29.446	3	**<0.001**	**Site**	26.696	2	**<0.001**
	Litter	4.78	1	0.029	**Rock**	6.04	1	0.014	**Perennial Grass**	2.107	1	0.147	**Sandberg Bluegrass**	0.351	1	0.553
	Site	32.906	3	**<0.001**	**Site**	18.339	2	**<0.001**	**Site**	30.867	3	**<0.001**	**Site**	29.432	3	**<0.001**
Yarrow	**Biological Soil Crust**	2.719	1	0.099	**Moss**	0.128	1	0.72	**Cheatgrass**	0.684	1	0.408	**Physical Crust**	0.779	1	0.377
	Site	28.913	2	**<0.001**	**Site**	41.992	2	**<0.001**	**Site**	46.513	2	**<0.001**	**Site**	28.72	1	**<0.001**
	Litter	0.144	1	0.705	**Rock**	1.179	1	0.278	**Perennial Grass**	0.044	1	0.834	**Sandberg Bluegrass**	0.099	1	0.753
	Site	45.589	2	**<0.001**	**Site**	0.036	1	0.849	**Site**	46.594	2	**<0.001**	**Site**	46.953	2	**<0.001**
Bluebunch Wheatgrass	**Biological Soil Crust**	0.02	1	0.888	**Moss**	1.178	1	0.278	**Cheatgrass**	1.017	1	0.313	**Physical Crust**	4.809	1	0.028
	Site	41.248	1	**<0.001**	**Site**	46.276	1	**<0.001**	**Site**	42.431	1	**<0.001**	**Site**	35.769	1	**<0.001**
	Litter	0.55	1	0.458	**Rock**	0.14	1	0.708	**Perennial Grass**	0.473	1	0.492	**Sandberg Bluegrass**	0.416	1	0.519
	Site	40.391	1	**<0.001**	—	—	—	—	**Site**	46.336	1	**<0.001**	**Site**	46.292	1	**<0.001**
Squirreltail	**Biological Soil Crust**	0.1	1	0.752	**Moss**	0.406	1	0.524	**Cheatgrass**	0.022	1	0.882	**Physical Crust**	0.122	1	0.727
	Site	35.542	2	**<0.001**	**Site**	39.764	2	**<0.001**	**Site**	38.875	2	**<0.001**	**Site**	40.943	2	**<0.001**
	Litter	0.234	1	0.629	**Rock**	0.404	1	0.525	**Perennial Grass**	0.005	1	0.944	**Sandberg Bluegrass**	0.006	1	0.936
	Site	40.183	2	**<0.001**	**Site**	23.978	1	**<0.001**	**Site**	38.944	2	**<0.001**	**Site**	38.999	2	**<0.001**

Table A8: Analysis of Variance Table (type II test) results for logistic regression of disturbance to seedlings, planted in two cohorts (2018, 2019) and monitored 7-8 and 14-15 months post-planting (Year 1, Year 2) for qualitative signs of disturbance (frost heaving, trampling, herbivory, animal burrows). Response variable is whether a seedling exhibited signs of disturbance and fixed effects are site, 2^{nd} order polynomial scaled shrub distance (distance from sagebrush stem divided by shrub diameter). Results significant at $\alpha < 0.05$ in bold. In some cohort-year combinations, there were zero living seedlings and were not included in survival models, so in this analysis, we only included sites that were in two or more survival models (Figure 2.2). For example, the 2019 Cohort Year 2 model does not include site because Saddle Mountain was the only site where 2 or more species has more than 5 living seedlings, the criterion for being included in a survival model.

		LR Chi Sq	Df	Pr(>Chi Sq)
2018 Cohort Year 1	scaled shrub distance	3.281	2	0.194
	site	509.374	3	**<0.001**
2018 Cohort Year 2	scaled shrub distance	0.884	2	0.643
	site	57.677	2	**<0.001**
2019 Cohort Year 1	scaled shrub distance	5.29	2	0.071
	site	214.036	2	**<0.001**
2019 Cohort Year 2	scaled shrub distance	1.529	2	0.466

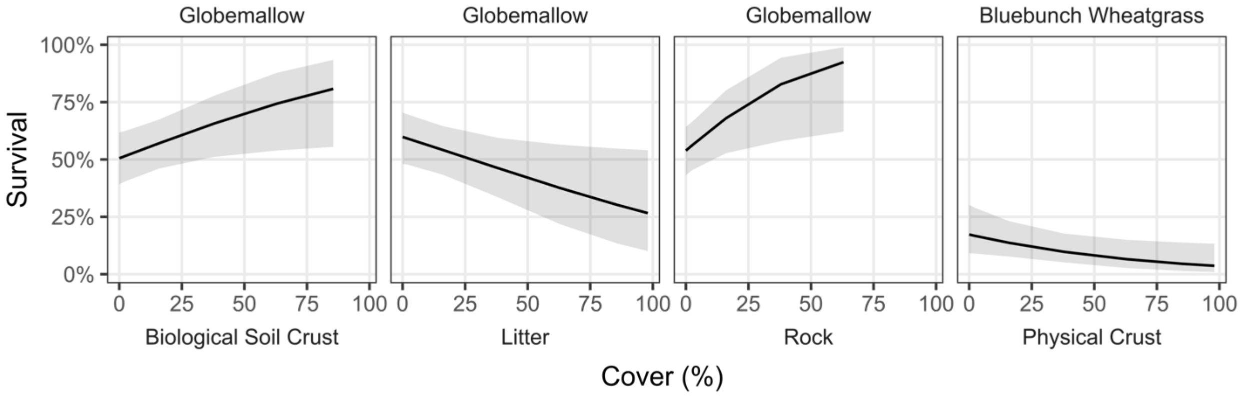


Figure A1: Estimated marginal mean Year 1 survival of plant species (globemallow [*S. munroana*] and bluebunch wheatgrass [*P. spicata*]) relative to ground cover characteristics (biological soil crust, moss, physical crust [PC], litter and rock) and plant cover (cheatgrass [*Bromus tectorum*]), perennial grasses, and Sandberg's bluegrass [*Poa secunda*]) across four sites in the Intermountain West, USA. Only graphs for species-ground cover combinations where the relationship between seedling survival and ground cover variable was significant ($\alpha = 0.05$) for the 2018 cohort are presented. None were significant with a Bonferroni correction ($\alpha = 0.006$).

Appendix B – Supplementary Information for Chapter 3

Table B1: Fungicides applied to bluebunch wheatgrass and squirreltail seeds, the corresponding active ingredients, target pathogens, and half-lives.

Active Ingredient	Fungicide Trade Name	Examples of Target Pathogens	Half-life (days)
Mefenoxam	Apron XL	Pythium, Phytophthora	35
Difenoconazole	Dividend	Verticillium, Septoria	9
Azoxytrobin	Dynasty	Rhizoctonia, Broad Spectrum	14
Fludioxonil	Maxim 4Fs	Fusarium, Rhizoctonia	142-220

Table B2: Emergence by site, species (squirreltail *Elymus elymoides*, bluebunch wheatgrass *Pseudoroegneria spicata*), treatment (coated-fungicide, coated-blank, uncoated), and cohort (2020, 2021). Transects with emergence refers to number of transects where at least one seedling emerged, with percent of transects with emergence in parenthesis. Emerged seedlings refers to total number of emerged seedlings across transects for a given site-species-coating-cohort combination, with percent seeds that emerged in parenthesis. Seventy five seeds were planted in each transect.

			2020 Cohort			2021 Cohort		
Site	Species	Coating	# Transects	Transects with Emergence	Emerged Seedlings	# Transects	Transects with Emergence	Emerged Seedlings
Saddle Mountain	Squirreltail	coated-blank	16	14 (87.5%)	46 (0.04%)	21	0	0
		coated-fungicide	20	11 (55%)	49 (0.03%)	20	0	0
		uncoated	23	18 (78.26%)	83 (0.05%)	19	0	0
	Bluebunch Wheatgrass	coated-blank	15	6 (40%)	24 (0.02%)	19	0	0
		coated-fungicide	20	14 (70%)	55 (0.04%)	20	0	0
		uncoated	18	14 (77.78%)	61 (0.05%)	21	0	0
Onaqui	Squirreltail	coated-blank	20	0	0	20	3 (15%)	5
		coated-fungicide	20	0	0	20	2 (10%)	2
		uncoated	19	0	0	20	4 (20%)	5
	Bluebunch Wheatgrass	coated-blank	18	0	0	20	0	0
		coated-fungicide	19	0	0	20	4 (20%)	4
		uncoated	21	0	0	20	3 (15%)	3
Grey Butte	Squirreltail	coated-blank	20	0	0	19	0	0
		coated-fungicide	19	0	0	20	0	0
		uncoated	20	0	0	20	0	0
	Bluebunch Wheatgrass	coated-blank	21	0	0	20	0	0
		coated-fungicide	20	0	0	20	0	0
		uncoated	20	0	0	21	0	0
Roberts	Squirreltail	coated-blank	20	1 (5%)	1	20	0	0
		coated-fungicide	20	1 (5%)	2	20	0	0
		uncoated	20	0	0	19	0	0
	Bluebunch Wheatgrass	coated-blank	20	1 (5%)	1	20	0	0
		coated-fungicide	20	1 (5%)	1	20	0	0
		uncoated	20	0	0	21	0	0

Table B3: Analysis of Variance Table (type III test) results for generalized Poisson mixed effect regression models with number of emerged seedlings as the dependent variable. Species (bluebunch wheatgrass vs. squirreltail), distance from the canopy edge (10 cm bins in furrows extending from the edge of a sagebrush canopy into the interspace: 0-10cm, 11-20cm, 21-30cm, etc.), coating treatment (uncoated, coated-blank, coated-fungicide), and the interaction between the distance from the canopy and coating treatment were treated as fixed effects, and the random effect was the sagebrush shrub that the planting furrow was associated with. Results in bold significant at alpha = 0.05.

	Saddle Mountain 2020 Cohort		
	Chi Sq	**Df**	**Pr > (Chi Sq)**
Intercept	61.94	1	**< 0.001**
Species	0.47	1	0.49
Distance Bin	58.42	1	**< 0.001**
Coating	1.16	2	0.56
Distance:Coating	3.61	2	0.16

Appendix C – Supplementary Information for Chapter 5

Table C1: Analysis of Variance (type III) of mixed effect linear model of water loss per cup per day (evapotranspiration, which ranged from 13 g/day [low WHC low water] to 30 g/day [high WHC high water]) over the study period modeled by fixed effects of soil/watering regime (high water holding capacity (WHC) high water, high WHC low water, low WHC high water, low WHC low water) and light (shaded, unshaded) and the random effect is the experimental block. Results are significant in bold at alpha of 0.05.

	Bluebunch Wheatgrass			Globemallow		
	Chi Sq	**Df**	**Pr(>Chi Sq)**	**Chi Sq**	**Df**	**Pr(>Chi Sq)**
Intercept	4258.33	1	**< 0.001**	3162.97	1	**< 0.001**
Regime	407.63	3	**< 0.001**	301.83	3	**< 0.001**
Shade	0.62	1	0.430	0.06	1	0.802
Regime : Shade	4.04	3	0.257	5.05	3	0.168

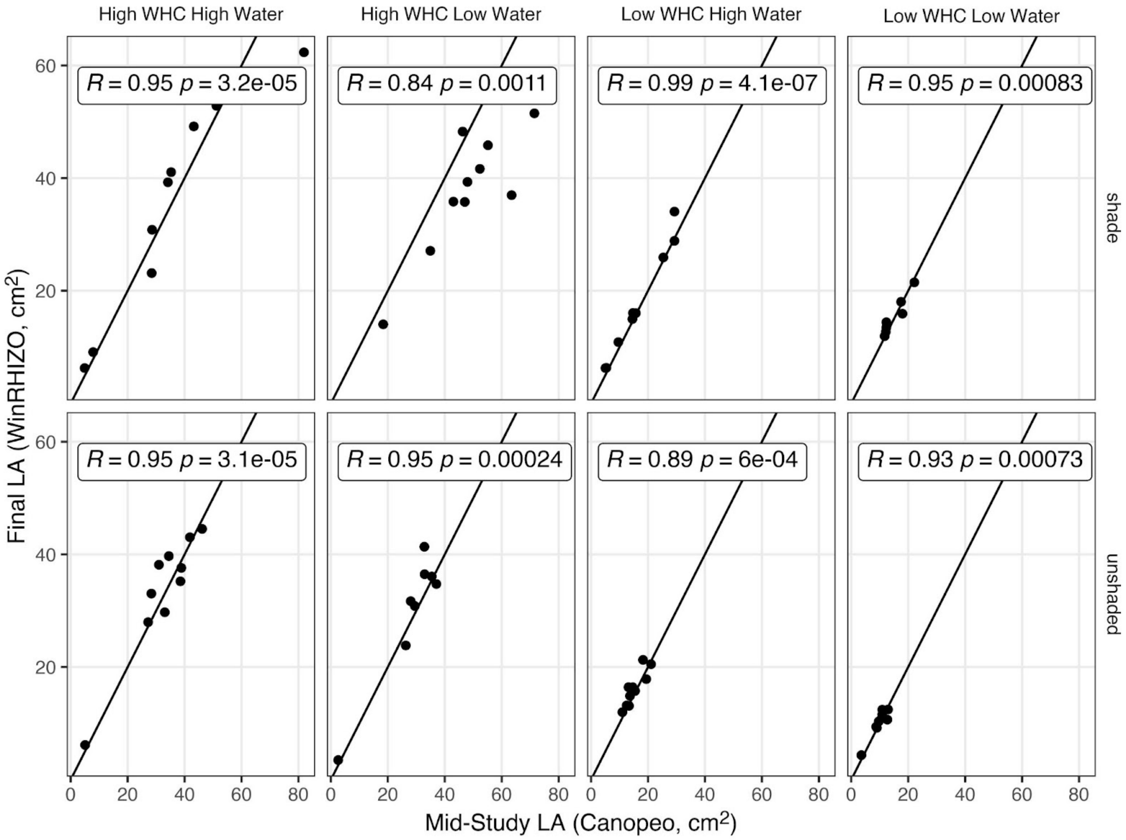


Figure C1: Pearson product-moment correlation coefficient (R) and significance of relationship (p value) between leaf area derived from Canopeo and leaf area (LA) derived from WinRHIZO at the end of the experiment (44 days) to evaluate the accuracy of Canopeo to measure leaf area. We correlated the two measures of leaf area for each level of soil/watering regime (high water **holding** capacity (WHC) high water, high WHC low water, low WHC high water, low WHC low water) and light (shaded, unshaded).

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EDUCATION

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PROFESSIONAL EXPERIENCE

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Two-year fellowship focused on developing and executing interdisciplinary research that supports climate adaptation and mitigation
Studio Project: *Collaborative Knowledge Braiding for Climate-Adapted Restoration: Informing the Desired Future Condition of the Shoshone's Boa Ogoi Site* (Advised by Dr. Sarah Klain)
Internship: *Connecting remotely sensed vegetation indexes with field observations and water balance modeling to understand vegetation sensitivities on the Colorado Plateau.*
Hosted by National Park Service (Advised by Dr. David Thoma and Dana Witwicki)
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Research Topics: Urban and arid systems, urban tree physiology, soil biogeochemistry
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PUBLICATIONS

Wang J, Castro-Garcia L, Jenerette GD, Chandler M, Ge C, Kucera D, Koutzoukis S, Zeng J (2022) Resolving and Predicting Neighborhood Vulnerability to Urban Heat and Air Pollution: Insights From a Pilot Project of Community Science. GeoHealth 6:e2021GH000575

Calzado Martinez C, MW Brunson, *S Koutzoukis*, JA Baggio, KE Veblen (2023) Addressing barriers to proactive restoration for at-risk sagebrush communities: A causal layered analysis. Restoration Ecology 10.1111/rec.13897

Koutzoukis S, DA Pyke, MW Brunson, JA Baggio, KE Veblen. Goldilocks forbs: survival is highest outside – but not too far outside – of Wyoming big sagebrush canopies. *In review.* Restoration Ecology

Koutzoukis S, MD Madsen, KE Veblen. Under drought conditions, fungicide coating does not increase emergence of two native grass species in sagebrush stands of the Intermountain West. *In review*. Restoration Ecology

Owen M, KE Veblen, J Boettinger, *S Koutzoukis*, T Monaco. Native Seedling Establishment in Biocrust-Areas of a Salt Desert Shrubland Varies by Species and Season of Planting. *In revision.* Ecology & Evolution

PRESENTATIONS *OP=oral presentation* *PP=poster presentation*

Koutzoukis S, DA Pyke, J Baggio, MW Brunson, KE Veblen. 2021. Above and belowground resource patterns associated with sagebrush islands of fertility in the Intermountain West. 106h ESA Annual Meeting, Virtual (OP)

Calzado C, MW Brunson, *S Koutzoukis*, KE Veblen, J Baggio. 2021. Addressing barriers to proactive restoration for at-risk sagebrush communities: A Causal Layered Analysis. International Association for Society and Natural Resources, Virtual (OP)

Huntly N, B Schumacher, *S Koutzoukis*, W Munger, L Capito, K Todecheene, D Parry, B Parry, S Klain, MW Brunson, T Nicholls. 2021. Community Engaged Science: How the Climate Adaptation Science Program & Its Trainees Engage Beyond the Academy for Persisting Change. Utah State University Community Engagement Center Community Engagement Session (PP)

Riley E, KE Veblen, *S Koutzoukis*, J Burton. 2021. Phenology and climate change in the TW Daniel Experimental Forest meadow. Utah State University Student Research Symposium (PP)

Parry D, S Klain, W Munger, C Stocker, L Capito, *S Koutzoukis*, N Huntly, T Nicholls, P Kelly, K Todecheene. 2021. Supporting Reverence, Regeneration, and Resilience: Weaving Knowledge for Tribal Stewardship of the Boa Ogoi Massacre Site. Utah State University Department of Environment and Society Seminar (OP)

Koutzoukis S, D Thoma, D Witwicki, S Munson. 2021. Connecting water balance, field cover, and NDVI to understand landscape-scale vegetation responses to drought on the

Colorado Plateau. National Park Service Northern Colorado Plateau Network Annual Meeting (OP)

Koutzoukis S, KE Veblen. 2020. Distance from sagebrush canopy influences seedling survival in the Intermountain West. Utah State University Wildland Resources Department Symposium (OP).

Koutzoukis S, DA Pyke, C Calzado, MW Brunson, KE Veblen. 2020. Distance from sagebrush canopy influences seedling survival in the Intermountain West. 105th ESA Annual Meeting, Virtual (PP)

Brunson MW, N Huntly, S Bogen, L Capito, M Christman, *S Koutzoukis,* B Morgan, W Munger, KA Spangler. 2020. Integrating ecological and social systems models and data: An application of the 4DEE approach for graduate education. 105th ESA Annual Meeting, Virtual (Invited OP)

Pinto D, C Morrisett, *S Koutzoukis*, M Christman. 2020. Graduate researchers collaborating on interdisciplinary climate adaptation science. 105th ESA Annual Meeting, Virtual (PP)

Klain S, W Munger, *S Koutzoukis*, L Capito, C Stocker. 2020. Reconciling indigenous ecological restoration goals with a changing climate: Co-production of a land stewardship plan at Boa Ogoi Cultural and Interpretive Center. 105th ESA Annual Meeting, Virtual (OP)

Koutzoukis S, DA Pyke, C Calzado, MW Brunson, J Baggio, KE Veblen. 2020. Microenvironment and distance from sagebrush canopy influence seedling survival along a landscape gradient in the Intermountain West. Great Basin Society for Ecological Restoration Annual Meeting. Boise, Idaho (canceled due to COVID-19)

C Calzado, MW Brunson, *S Koutzoukis*, KE Veblen, J Baggio, DA Pyke. 2020. Addressing barriers to proactive restoration for at-risk sagebrush communities: A Causal Layered Analysis. Society for Range Management Annual Meeting. Denver, Colorado (PP)

Koutzoukis S, KE Veblen. 2018. Preemptive restoration and the role of microenvironment in
restoring the Intermountain West. Utah State University Wildland Resources Department Symposium (OP).

Koutzoukis S, GD Jenerette, M Chandler, J Wang, L Castro, C Ge, J Ripplinger. 2017. Regional and local meteorology influences high-resolution tropospheric ozone concentration in the Los Angeles Basin. American Geophysical Union Fall Meeting. New Orleans, Louisiana (PP)

Ripplinger J, GD Jenerette, Wang J, Chandler M, Ge C, *S Koutzoukis*. 2017. Understanding climate variability of urban ecosystems through the lens of citizen science. American Geophysical Union Fall Meeting. New Orleans, Louisiana (PP)

Jenerette GD, J Wang, M Chandler, J Ripplinger, *S Koutzoukis*, C Ge, L Castro, D Kucera, X Liu. 2017. Resolving uncertainties in the urban air quality, climate, and vegetation nexus through citizen science, satellite imagery, and atmospheric modeling. American Geophysical Union Fall Meeting. New Orleans, Louisiana (OP)

Koutzoukis S, S Crum, H Andrews, GD Jenerette. 2017. Dynamic microclimate effects of vegetation throughout a 1600 m elevation transect in Southern California, USA. 102nd ESA Annual Meeting. Portland, Oregon (OP)

Teller N, *S Koutzoukis*, GD Jenerette, T Bean. 2017. Phenocam monitoring for management of *Salsola tragus* (Russian thistle). California-Invasive Plant Council Symposium. Palm Springs, California (PP)

Koutzoukis S, A Simler, M Metz. 2016. Post-disturbance resprouting is more advantageous than seeding in redwood-tanoak forests of Big Sur, CA. 101st ESA Annual Meeting. Ft. Lauderdale, Florida (PP)

GRANTS, FELLOWSHIPS & SCHOLARSHIPS

2022 Utah State University Ecology Center Student Research Grant ($2,800)
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2018-2020 Climate Adaptation Science Fellowship, NSF-NRT ($34,000, graduate tuition and fees)
2015 Rogers Science Research Internship, Lewis & Clark College ($5,350)
2012-2016 Trustee Endowment Scholarship, Lewis & Clark College ($48,000)

TEACHING & MENTORING

Fall 2021-Teaching Assistant (USU WILD 4750 - Monitoring and Assessment in Natural Resource and Environmental Management)
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SERVICE

USU Wildland Resources Dept. Faculty Search Committee Graduate Student Representative: Fall 2021
USU Student Research Symposium Evaluator: Fall 2020
USU SJ Quinney College of Natural Resources Graduate Student Council: Social Coordinator 2019-2020
USU Ecology Center Seminar Series Committee 2019-2020
USU SJ Quinney College of Natural Resources Graduate Student Council: Medical Liaison 2018-2019

PROFESSIONAL MEMBERSHIPS

Ecological Society of America
American Geophysical Union

PRESS and OUTREACH

Do Science that Matters: Climate Adaptation Science at Utah State's Ecology Center

Boa Ogoi (NSF - CAS Project):

- USU Team Working With Shoshone Nation To Restore Bear River Massacre Site | UPR Utah Public Radio
- Boa Ogoi: Restoring Sacred Land 150 years after the Bear River Massacre
- USU assisting the Northwest Band of Shoshone to prepare memorial at Massacre Site, Cache Valley Today
- A Healing Ground - Utah State Magazine

USDA-AFRI (Dissertation project):

- Invasive species affect everyone
- Fact sheet: "Preemptive restoration of sagebrush stands in the Great Basin" (in prep)