Investigating the Effects of Mycorrhizal Inoculation on Native-Invasive Plant Interactions Post-Fire

by

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THESIS ABSTRACT

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Title: Investigating the Effects of Mycorrhizal Inoculation on Native-Invasive Plant Interactions Post-Fire

Understanding the factors that facilitate or inhibit invasive plant species establishment is a primary goal of restoration ecology, particularly in post-fire forest systems. Increasing attention is being given to arbuscular mycorrhizal fungi (AMF) as a restoration tool for the dynamic role AMF play in plant community structure where both native and invasive species are present. Acting as both mutualists and parasites depending on environmental context, native AMF may support native communities by conferring competitive advantages to native species while antagonizing invasive species. AMF communities are significantly altered by wildfire, however, and the effects of restorative AMF inoculation on native & invasive species in post-fire systems is not well understood. Here, I conduct a mechanistic greenhouse experiment and an applied field test of how AMF inoculation in a post-fire landscape influences the performance and competitive ability of three native plants (2 grasses, 1 forb) against an invasive grass, Brachypodium sylvaticum (False Brome). My results offer mixed support for my hypothesis, demonstrating high context dependency of plant responses to post-fire AMF inoculation. I found mechanistic support that inoculation with native AMF can selectively increase native species competitive ability while conferring no advantage to invasive False Brome in a controlled greenhouse setting using burned soils. However, in an applied field setting, I found that first-year survival of the three native plants decreased as a result of AMF inoculation, while other non-seeded native species (mostly forbs) were unaffected by inoculation. While my hypothesis was not supported in the field, the contexts in which AMF were mutualistic or antagonistic met expectations set forth in other studies- making repeat surveys of the field essential to definitively understand longer-term effects of AMF inoculation. However, first-year results indicate AMF inoculation is beneficial in invasion prone high-burn severity areas where restoring native forb species is a priority.

ACKNOWLEDGEMENTS

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I also am extending a special thank you to my family and friends that have unconditionally supported and loved me throughout my master's work and beyond, whether we lived close or far. Despite most of the time being far apart, you all have been close to me best we

could; and the difference that made in getting to this point in my life and career could never be overstated. To my family: Dad, Mom, Giselle, Esteban; and my closest friends ecology has brought me to: Maddie Sutton, Alaina Makowski, Matt Reala; There is no world where I am able to do all these things I love without you. Thank you!

The other acknowledgement and thanks I wish to give here is dedicated to the H.J. Andrews Forest itself. It has been an immense privilege to be able to work in, study, and call the Andrews home during parts of my master's, and most of my post-undergrad life. For a site so integral to the history of western ecological understanding of forests (particularly for long-term research and old-growth), the generosity in which the forest lends its obscure ecologies, grandiose and most shy inhabitants, and comfort to many a researcher and visitor beyond myself is humbling. Through serene afternoons with warm gentle breezes passing through open understories between 300ft giants and cold mountain creeks, and through uncertain nights watching and running from wildfires crawling across its ridges, it is a home away from home that has been central to my growth not only as a researcher, but as a person as well. The ability to learn and grow so much from the Andrews is the privilege of a lifetime, and one I wish many others after me are able to partake in as well. In so, I will carry with me the generosity, community, intensity, timelessness, and ephemerality it has shown me always.

TABLE OF CONTENTS

I. LIST OF FIGURES

II. LIST OF TABLES

Table Page

III. INTRODUCTION

Over the course of the past several decades climate change and histories of fire-suppression have combined to generate larger and more severe wildfires, particularly in the western United States (Mueller et al. 2015, Halofsky et al. 2020). Increasingly severe fires in particular pose a threat to endangered old-growth forests throughout the Pacific Northwest (Spies et al. 2018); Severe and frequent fires have the potential to disrupt the succession of old-growth forests by eliminating not only the seedbank and existing floral communities, but also essential plant-soil feedbacks largely driven by mutualists such as mycorrhizal fungi (Perry et al. 2011, Dove & Hart 2017). As fire burns through a landscape, the diversity and abundance of mycorrhizal fungi significantly decreases, leaving post-fire plant communities without their fungal mutualists and susceptible to invasion for years afterwards (van der Putten et al. 2013, Xiang et al. 2015). The restoration of native plant-fungal interactions post-fire may then be an integral tool to mitigate the spread of invasive species, as they are key for advancing native plant succession, and may inhibit invasive species success as well (Bever et al. 2023, Koziol et al. 2023). However, few studies have examined how mycorrhizal restoration influences native and invasive plant interactions, with even fewer doing so in a post-fire landscape (Hoeksema et al. 2010, Bunn et al. 2015, Fahey & Flory 2022).

Plant community structure is significantly impacted by the influence plants have on the soil around them. This feedback occurs by plants altering soil properties that in turn affect plant performance (Bever et al. 1997). These interactions, known as plant-soil feedbacks, can enact positive or negative effects on plants; negative feedbacks may entail increased selection against seedlings due to accrued pathogens, while positive feedbacks may occur through soil modifications that limit competitors or facilitate mutualisms (van der Putten et al. 2013). Positive plant-soil feedbacks are of additional interest as the faciliatory effects feedbacks enact have been shown to strengthen in abiotically stressful environments (e.g. post-fire landscapes).

Positive plant-soil feedbacks also encompass the effects of mutualisms such as mycorrhizal fungi (van der Putten et al. 2013, Beals et al. 2020). Mycorrhizal fungi (also known as mycorrhizae) are fungi that form a symbiotic association with the roots of almost all plant families, often exchanging soil nutrients (namely Phosphorus and Nitrogen) and water in exchange for photosynthates from plants (Pringle et al. 2009). The highly-conserved nature of this symbiosis has led to it being a key factor in the structure of many plant communities (Smith and Read 2008). Mycorrhizae play a significant role in advancing successional patterns of disturbed landscapes (Janos 1980). For earlier seral communities threatened by invasive species, mycorrhizae can serve as a biotic filter to slow the establishment of invasive species via direct and/or indirect means (Bunn et al. 2015, Koziol & Bever 2017).

Mycorrhizal fungi directly inhibit invasive species by parasitizing the plant it forms a symbiosis with. While mycorrhizae are commonly thought of as mutualists with their host plants, mycorrhizal fungi exist on a continuum ranging from mutualistic to parasitic (Johnson et al. 1997). Whether a symbiosis with mycorrhizae becomes beneficial or antagonistic for a plant depends on several factors- namely host identity, nutrient and light availability, and development stage of the symbiosis. For example, when nutrients like nitrogen and phosphorus are readily available for plants, there is little benefit to forming mycorrhizal partnerships; however, if the symbiosis still forms, the plant is then shuttling sugars and carbon to the fungus with little in return (Smith and Read 2008).

Mycorrhizae may indirectly inhibit invasive species establishment by forming preferential mutualisms with native species, making native species better competitors

(Klironomos 2003). Preferential mutualisms often manifest as increases in plant growth that are greater than those experienced by invasive species when partnering with the same mycorrhizal fungi; this in turn offers increased competitive ability against invasive species (Bunn et al. 2015, Shen et al. 2024). It is also important to note that in certain contexts, invasive species may also benefit from mutualistic behaviors of native mycorrhizae, facilitating further invasion (Reinhart and Calloway 2006, Workman and Cruzan 2016).

When a disturbance such as fire alters a landscape, the diversity and abundance of arbuscular mycorrhizal fungi, which are the most common type of mycorrhizal fungi, significantly decreases, leaving post-fire plant communities without their succession-driving fungal mutualists, which in turn makes plant communities particularly susceptible to invasion for years following a disturbance (Bever et al. 2001, Pringle et al 2009, Alba et al. 2015, Xiang et al. 2015, Dove & Hart 2017, Brambila et al. 2023). Invasive plant species, if established before native communities, can then begin to cultivate a novel soil mycorrhizal community via their own plant-soil feedbacks that benefit the invasive species and inhibits the reestablishment of native arbuscular mycorrhizal communities; this positive feedback of invasive mycorrhizal communities thus slows, if not halts, the succession of native plant communities (Reinhart & Callaway 2006, Pringle 2009, van der Putten et al. 2013, Grove et al. 2017).

At particular risk of invasion and mycorrhizal community shifts are pacific northwestern forests experiencing fire for the first time in several decades (Reilly et al. 2022). As fire works its way back on the landscape of the pacific northwest, several invasive species pose severe threats to forests left vulnerable after fire. Therefore, it is critical to gain an understanding of how immediate post-fire restoration of mycorrhizal fungi may alter how native and invasive species interact.

In this thesis I investigate how arbuscular mycorrhizal inoculation in a post-fire landscape influences the performance and competitive ability of native plants against an invasive species, *Brachypodium sylvaticum* (False Brome). I hypothesize that inoculating plant communities with native mycorrhizae will increase the performance and competitive ability of native plants post-fire. Alternatively, should *Brachypodium sylvaticum* benefit from partnering with native mycorrhizal fungi, inoculation of post fire communities may enhance invasive species performance and facilitate invasion. I test these hypotheses both mechanistically in a greenhouse competition experiment, isolating the effects of mycorrhizal inoculation on native plants grown alone and in competition with *B. sylvaticum;* as well as in an applied post-fire restoration field setting, where I experimentally apply mycorrhizal inoculum to compliment roadside seedings across a burn severity gradient. Addressing this question not only advances ecological understanding of the role mycorrhizae play in plant communities and competitive interactions, but also generates significant restoration and management recommendations. This is especially important for landscapes like the Pacific Northwest, whose old-growth forests are facing increasingly dynamic fire regimes (Spies et al. 2018, Reilly et al. 2022).

IV. METHODS

Site and Focal Species Selection

Here I conduct two experiments to mechanistically and observationally assess how mycorrhizal inoculation of post-fire plant communities influences native and invasive species interactions. To assess the effects of mycorrhizal inoculation in a post-fire landscape, both of my experiments surround the 2023 Lookout Fire. In August 2023, a lightning strike initiated the Lookout Fire in Oregon's western Cascades mountain range. In total, the Lookout Fire burned approximately 25,751 acres of mostly old-growth forest in a mix of low-severity (72%), moderate (13%), and high-severity (2%) soil burn patches (Willamette National Forest 2023). The Lookout Fire encompassed a significant portion of the H.J. Andrews Experimental Forest (HJA), a long-term ecological research site established in 1948 near Blue River, OR that has collected demographic data on old-growth forest since the 1970's. Approximately 70% of the HJA burned to differing severities, creating a burn severity mosaic (Willamette National Forest 2023). Additionally, the HJA faces invasion threats from *Brachypodium sylvaticum* (Kim 2015). Together, these factors made the HJA an ideal study system to study how mycorrhizal fungi affect invasion dynamics post-fire.

In response to the 2023 Lookout Fire, the U.S. Forest Service created a Burn Area Emergency Response (BAER) Team to assess post-fire threats to life, property, and critical resources, as well as recommend management strategies to mitigate immediate risks such as the spread of invasive species, particularly *Brachypodium sylvaticum*. *B. sylvaticum* is a bunchgrass native to Eurasia and Northern Africa that occurs across elevations and gradients of light availability in both its native range and invasive range in Oregon (Roy et al. 2011). False brome's ability to thrive in partial shade environments has allowed it to successfully spread throughout the understory of Douglas-fir dominated canopies characteristic of western Oregon (Roy et al. 2011). Once established, false brome, like other invasive species, may begin to alter soil microbial communities as well as form thick thatch after each growing season (Reinhart & Callaway 2006). The accumulation of false brome thatch in the understory generates a significant amount of fuel for fire, increasing fire frequency which in turn promotes further false brome proliferation (Workman & Cruzan 2016). Additionally, like other invasive species, false brome performs best in disturbed soils without native mycorrhizae or competitors (Workman & Cruzan 2016).

To prevent establishment of *B. sylvaticum*, the team implementing BAER recommendations seeded several native grass and forb species along roadsides in the burn footprint of the Lookout Fire that are most vulnerable to further false brome encroachment. In collaboration with the Forest Service and HJA, we selected three native plants to seed in the HJA: *Elymus glaucus* (Blue Wild Rye), *Bromus carinatus* (California Brome), and *Achillea millefolium* (Western Yarrow). Each of these selected species already occur within the boundaries of the HJA and have demonstrated establishment success in roadside seedings after invasive species removal treatments and after prior fires in the Willamette National Forest (Willamette National Forest. *Personal Communication*. Jan. 16, 2024).

Inoculum Preparation

For both experiments I cultured a mycorrhizal inoculum that is specific to western Oregon forests and mutualistic with my native focal species. Commercial mycorrhizal inoculum was not used to avoid introducing non-native fungal species to the HJA and surrounding old-growth forests. Instead, my experiments used a crude root inoculum of arbuscular mycorrhizal fungi species local to the HJA. Crude root inoculum consists of an applicable media of host plant roots colonized by the desired mycorrhizal fungi. While Pacific Northwest old-growth forests are generally ectomycorrhizal (EMF) dominated, local arbuscular mycorrhizal fungi (AMF) inoculant was used. My focal species are AMF associated, and several native tree and forb species found here are AMF associated as well (namely *Acer* and *Taxus* species). Crude root inoculum for my experiments was grown on *Zea mays* (corn), as corn readily forms partnerships with many species of AMF, and corn roots bore little possibility of propagating or passing diseases specific to seeded or other native plant species (Habte & Osario 2001, Hoeksema et al. 2010). My inoculum is sourced from rhizosphere soil surrounding AMF associated species found in the HJA (*Taxus brevifolia, Acer sp.*). Using the wet-sieving technique described in Boyno et al. 2023, mycorrhizal spores from rhizosphere soil samples were isolated and then evenly applied to *Zea mays* seedlings growing in doubly autoclaved soil (99 minutes at 123°C, Lane Forestry Products “Super Natural Potting Mix”). Seedlings then grew in a greenhouse for approximately 3 months prior to the start of each experiment, receiving 16-hour light/days and watering every other day. After 3 months, roots from *Z. mays* were then harvested and cut into small pieces to be used as inoculum. This method of developing crude root inoculum ensures that what is applied to experimental plots in the field is exclusively native mycorrhizal fungi, and any foreign pathogens/other microbes are not transported to the HJA.

Greenhouse Experiment

To assess how mycorrhizal inoculation mechanistically influences native-invasive plant interactions, I conducted a greenhouse competition experiment to assess how experimental inoculation with HJA sourced AMF inoculum influences competitive interactions between native species and false brome. Individuals of each of our three native focal species and invasive false brome were grown alone or in competition (native vs. invasive), with and without mycorrhizal inoculum, to assess how inoculation influences competitive ability (measured by plant heights and biomasses). This experimental assessment of plant biomass responses to inoculation resulted in four block groups: growing alone with inoculation, alone without inoculation, in competition with inoculation, and in competition without inoculation (Figure 1b).

Seeds of either *E. glaucus*, *B. carinatus*, or *A. millefolium* were planted in 4”x4”x12” seedling pots with seeds of *B. sylvaticum* to create one-on-one pairwise competition pots; all four species in the experiment were also seeded alone in equal dimension pots for alone treatments (Figure 1a). Native seeds were provided by the Forest Service, and seeds of false brome were collected from sites around Eugene, OR in November 2023 and tested for viability. Each of the three native species growing alone and in competition with invasive false brome received 2 different inoculation treatments: inoculated and non-inoculated. Ten replicates of each competition combination (*E. glaucus* x *B. sylvaticum*; *B. carinatus* x *B. sylvaticum; A. millefolium* x *B. sylvaticum; E. glaucus alone; B. carinatus alone; A. millefolium alone, B. sylvaticum alone*) for both mycorrhizal treatments (inoculated and non-inoculated) were created-totaling to 140 pots (Figure 1a). In total the greenhouse experiment featured 200 total plants. All pots in the greenhouse experiment use soil collected from a high severity burn area in the footprint of the Lookout Fire to simulate degraded mycorrhizal communities encountered in the field (Collected Soil Coordinates: 44.190667, -122.192167). Plants in the greenhouse were grown for 60 days. After the 60-day growth period, plants were harvested and weighed to collect root, shoot, and total biomasses. After weighing roots, samples of the roots from half of the replicates were collected and stored in 50% ethanol solution for later staining and quantification of mycorrhizal colonization analysis. Shoots were then dried for one month at 60°C and weighed again to obtain dry shoot biomass.

To determine significance between treatments, each of the four species in the experiment (3 native and 1 invasive) had separate ANOVAs analyzing dry shoot biomass as a response of treatment (inoculated vs. non-inoculated) and competition group (alone vs. in competition). Since the three native species only had one competitor (*B. sylvaticum*), there were only two levels of competition group for those models. Since false brome experienced competition against all three native species, the false brome model has four levels, one for alone and three others for each of the native species it competed against. A Games-Howell post-hoc test was then run on ANOVA results to adjust for multiple comparisons.

I used R to clean and manage all data, generate results figures, and calculate statistics (R version 4.2.3). Since samples of plant roots were collected upon harvest, the biomasses of roots were modified; subsequently no roots were dried for collecting dry root biomasses later on. I report out dried shoot (aboveground) biomass here, which is a standard indicator of plant competitive ability (Freckleton & Watkinson 2000).

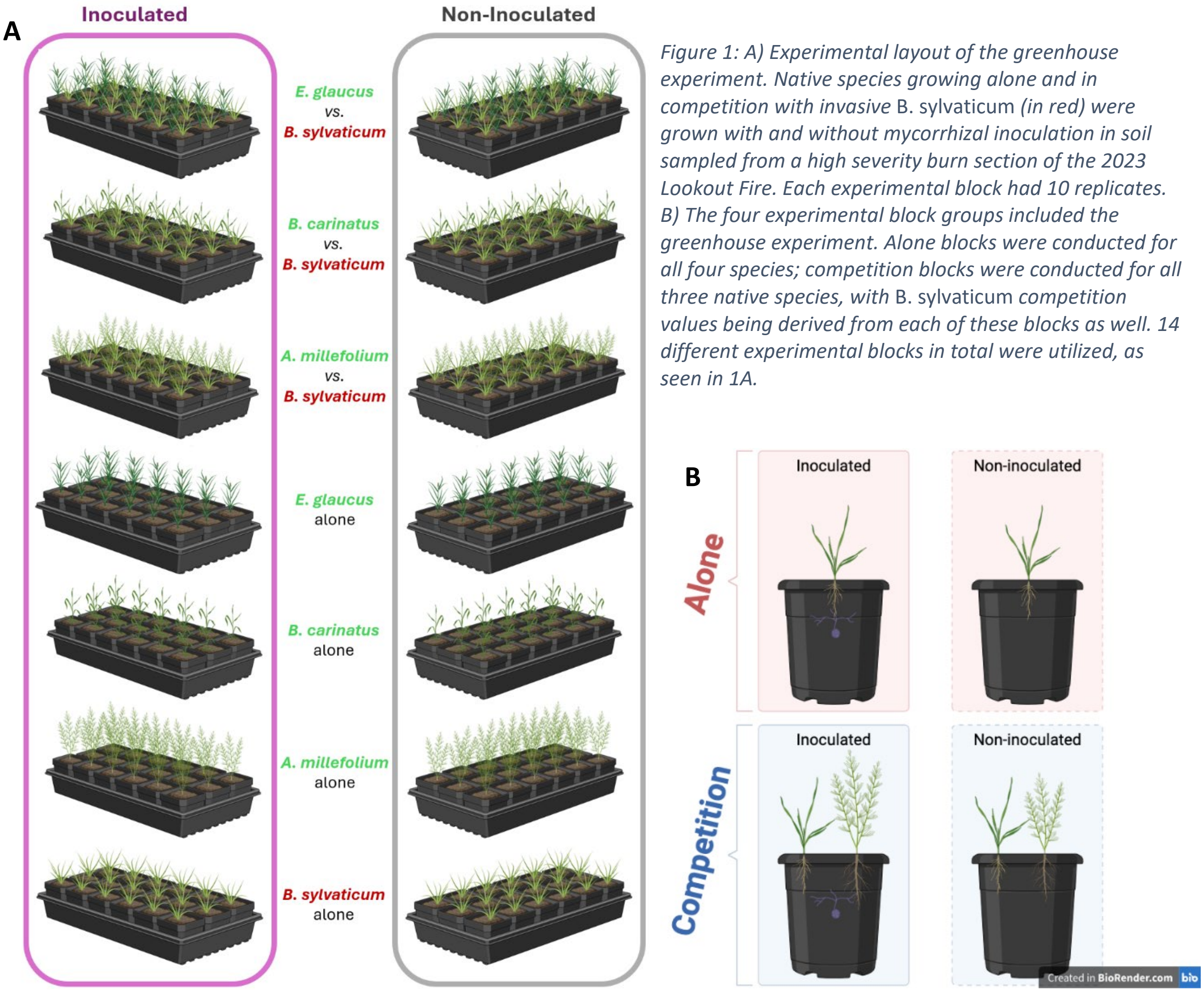


Figure 1: A) Experimental layout of the greenhouse experiment. Native species growing alone and in competition with invasive B. sylvaticum *(in red) were grown with and without mycorrhizal inoculation in soil sampled from a high severity burn section of the 2023 Lookout Fire. Each experimental block had 10 replicates. B) The four experimental block groups included the greenhouse experiment. Alone blocks were conducted for all four species; competition blocks were conducted for all three native species, with* B. sylvaticum *competition values being derived from each of these blocks as well. 14 different experimental blocks in total were utilized, as seen in 1A.*

Root Staining and Mycorrhizal Colonization Quantification

To verify the efficacy of mycorrhizal treatments, roots from the greenhouse experiment underwent a staining procedure to be able to identify mycorrhizal structures under a microscope. Stained roots can also be utilized to quantify percentages of roots colonized by mycorrhizal fungi, providing a metric by which we can measure how strong mycorrhizal partnerships are between species.

Staining protocols were adapted from Vierheilig et al. 1998. Samples of roots of individual plants from five replicates of all four treatments were collected upon harvest and stored in 50% ethanol solution until ready to stain. Samples were then placed into cassettes, brought to a boil in 5% potassium hydroxide (KOH) solution and left to rest for an hour. Once tannins and other compounds that would otherwise obstruct viewing of mycorrhizal structures were leached from the roots, the root cassettes were rinsed in tap water before being placed into a 5% ink-vinegar solution (Schaeffer's black fountain pen ink) and briefly brought to a boil. The root cassettes were once again rinsed with tap water and then left in a diluted vinegar solution to de-stain or about 20 minutes. Once de-stained, the roots from each sample were then prepared onto microscopy slides- plating 10-12 root fragments greater than 1cm in length vertically per slide. Slide covers were fixed to the slide using PVLG. Slides from inoculated and non-inoculated samples were then viewed under a microscope at 40x magnification to confirm the presence of mycorrhizal structures in the inoculated samples (Fig. 16), and absence thereof in the non-inoculated samples.

Field Experiment

To assess how mycorrhizal inoculation influences native plant performance in an applied post-fire restoration setting, I conducted a field experiment to assess how mycorrhizal inoculation influenced native plant performance (measured as first-year germinate survival) in the first year following fire. In collaboration with the U.S. Forest Service and local Walama Restoration Project, Walama Restoration Project seeded our three selected native focal species throughout the HJA along burned roadsides where threats of false brome spread were thought to be the strongest. I then established 1m^2 vegetation monitoring plots in rows perpendicular to seeded roadsides in the HJA where false brome was known to be present prior to the Lookout Fire. The 1m^2 vegetation plots occur across 5 sites of varying burn severity within the footprint of the Lookout Fire, with 8 plots being established at each site, except one site with 10 plots (42 total plots across 5 sites). At each site, half of the plots were inoculated with ~1 pound of crude root inoculum, while the other plots were left untreated (21 inoculated, 21 non-inoculated plots in total). Plots were inoculated by using a core aerator (Corona 40.0-Inches Composite Core aerator) to create space in the soil to plug with crude root inoculum- taking care not to damage any plants already established in the plot. This was also repeated in the non-inoculated plots to replicate the effect of soil disturbance in the inoculated plots. Additional metadata collected at each plot include coordinates, elevation, distance to road, canopy cover, slope, and aspect. Canopy Cover was measured using a spherical densiometer at the plot scale. After establishment, and every 2 weeks until the end of summer 2024, stem counts and percent cover of every species were recorded for each plot to determine how mycorrhizal inoculation affected the performance of native species in the first year after seeding. No surveys were conducted between 07/17/24 and 08/22/24 due to the nearby 2024 Ore Fire prompting the U.S. Forest Service to close the HJA.

Data from the field experiment consisted of raw counts and percent cover of all plants within the survey plots. Due to the difficulty of identifying seeded grass species immediately after germination, consistent measurements of their species-specific abundances could not be collected. However, while seeded species could not be differentiated from one another, they were distinguishable from other non-seeded, naturally regenerating species. From this I was able to accurately measure abundances for all seeded species over time. Since plots were established after germination occurred to ensure inoculation treatments were applied to viable sites, raw abundances are not reported as results due to variable starting abundances of seeded species. To account for variable initial abundances, proportional changes of seeded species from peak abundance were reported instead (calculated as final abundance ÷ peak abundance) and interpreted as first-year germinate stem survival.

To assess the significance of mycorrhizal inoculation on first-year survival of seeded and non-seeded species abundances, I fit my data to a linear mixed effects regression model. Since the distribution of proportional stem abundance changes was non-normal, it was log transformed for the model. The log of proportional stem abundance change was examined in response to parameters of inoculation status, canopy cover, distance to road, and site (burn severity) as a random effect. Site was included as a random effect to avoid pseudoreplication in assessing burn severity affects. Models with and without site as a random effect were compared using ANOVA analysis to assess for the significance of a site effect.

Shannon's diversity was calculated using the vegan package in R with survey data from the final survey conducted (Aug. 23, 2024) (Oksanen et al. 2022). Abundances of all native species, seeded and non-seeded, were included in the diversity analysis.

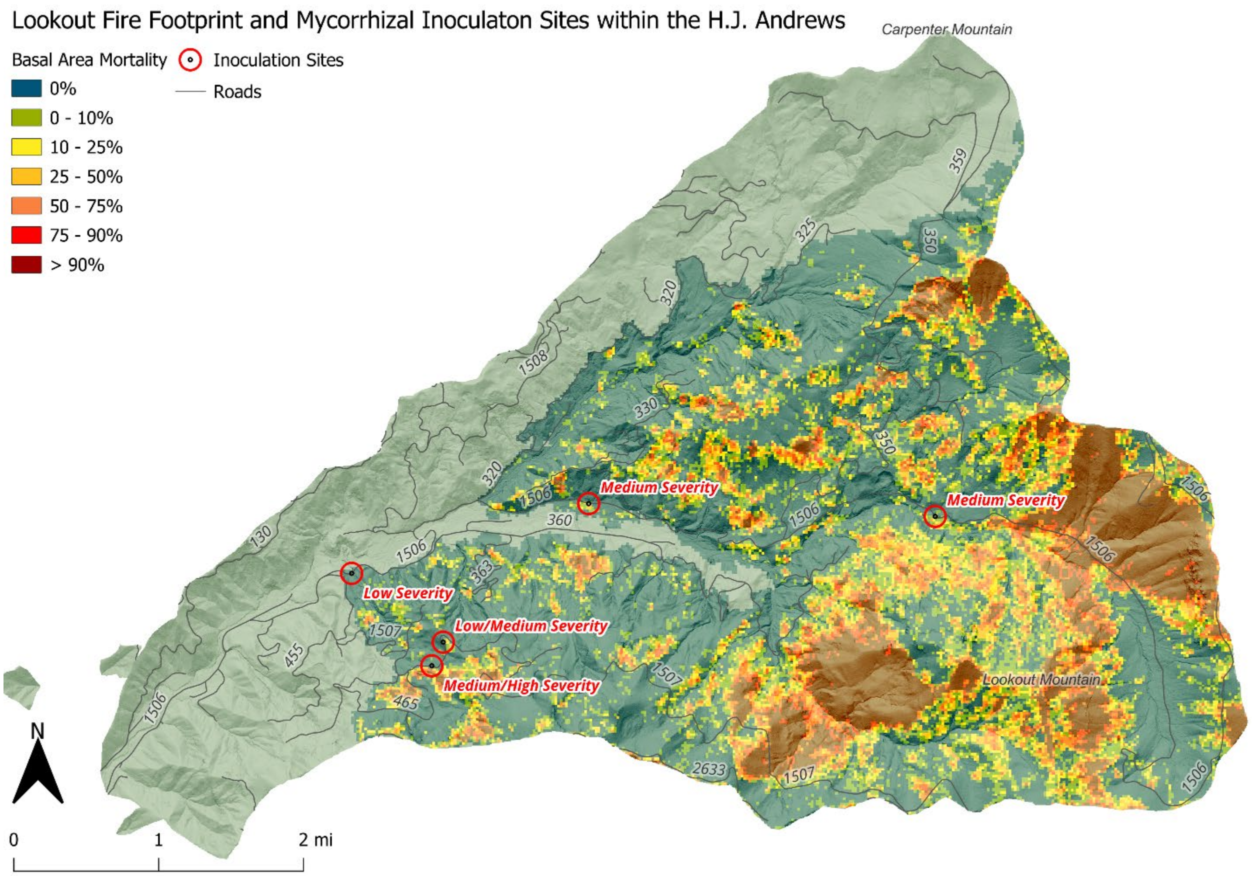


Figure 2: Portions of the H.J. Andrews Experimental Forest that were burned in the 2023 Lookout Fire. Inoculation and survey plot sites were established mostly along the 1506 and 1507 roads. Data for the burn severity and hillshade layers comes from the U.S. Forest Service and H.J. Andrews. This map was created using QGIS.

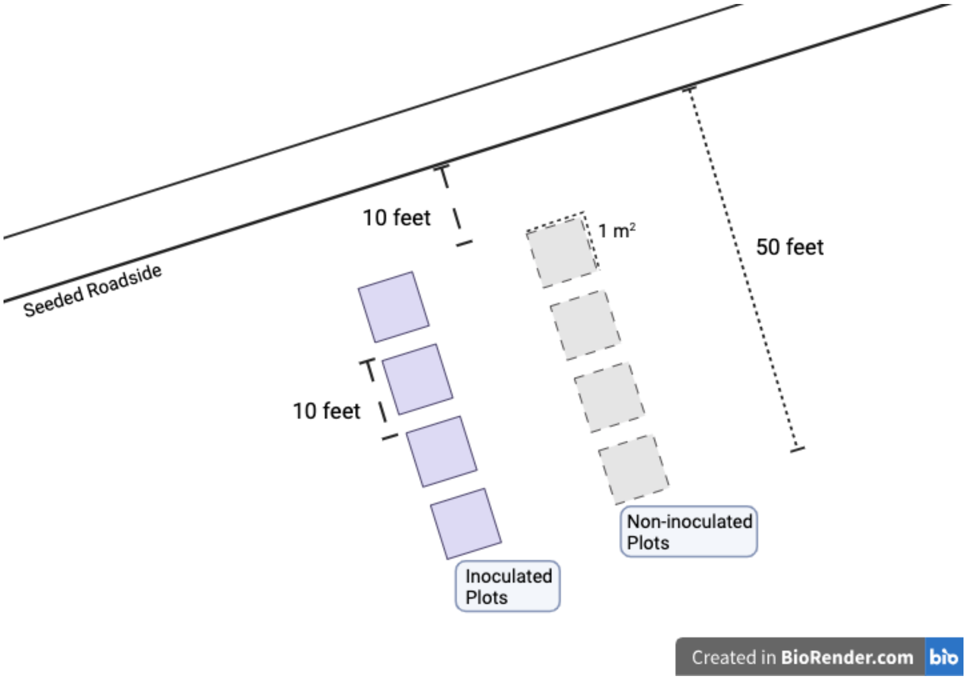


Figure 3: Site design of the field experiment. 8 1m2 plots were established at each site from 10ft to the road every 10 feet up to 50ft from the roadside, with the exception of the low burn severity site containing 10 plots total. Half of the plots at each site received mycorrhizal inoculum.

V. RESULTS

Greenhouse Experiment

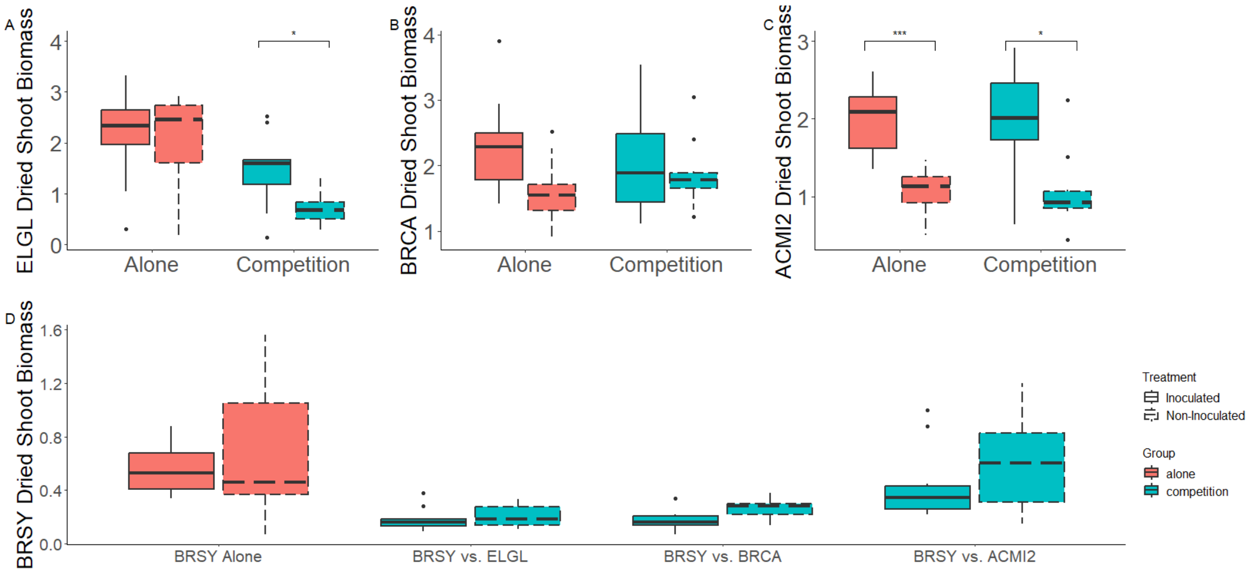
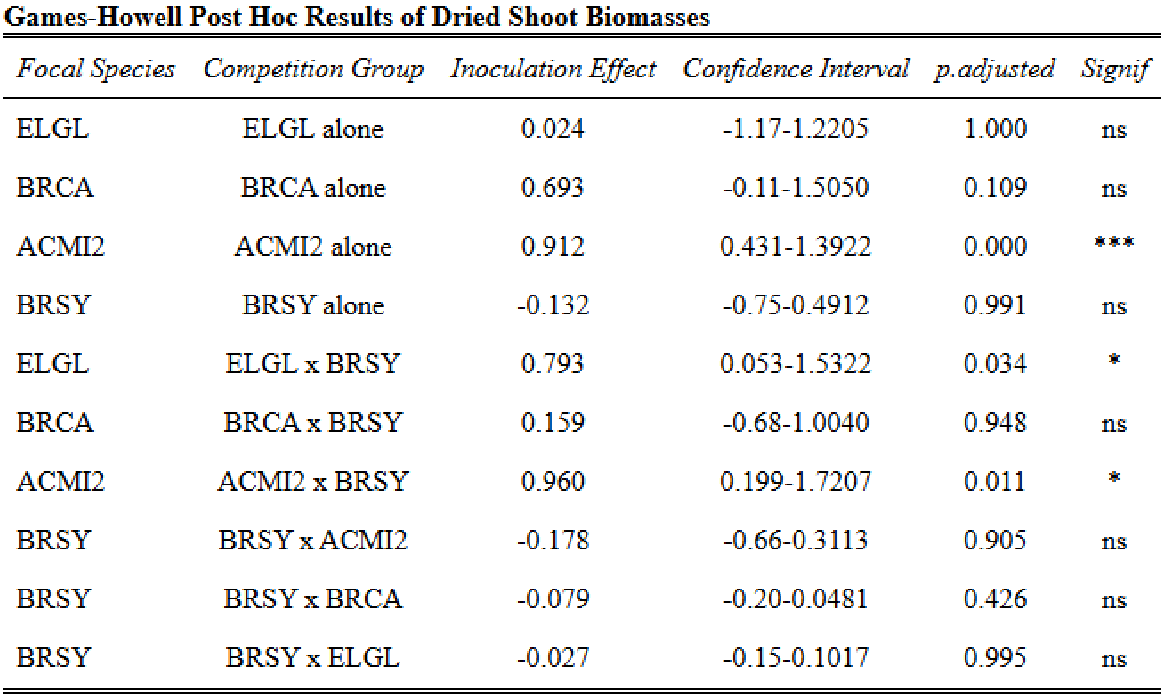


Figure 4: Dried shoot biomass of all four species inoculated (solid) and non-inoculated (dashed) in the greenhouse experiment when growing alone (red) and in one-on-one competition (blue). Panel D shows the dried shoot biomasses of false brome (BRSY) under different treatments and competition groupings. Panel A, B, and C show the dried shoot biomass responses of native species Elymus glaucus *(ELGL),* Bromus carinatus *(BRCA), and* Achillea millefolium *(ACMI2), respectively. Significant differences are denoted by stars.*

Inoculation resulted in increased dried shoot biomass in both alone and competition settings, however this varied by species. Inoculation boosted the biomass of *Elymus glaucus* when growing in competition against false brome (p.adj = 0.034), but not when growing alone (p.adj = 1). *E. glaucus* was also negatively influenced by competition (p.adj < 0.006), however this effect was negated by the aforementioned biomass boost provided by inoculation (p.adj = 0.364). *Bromus carinatus* received no significant boost in biomass from inoculation when competing against false brome (p.adj = 0.948), but had a near significant increase in biomass from inoculation when growing alone (p.adj = 0.109). *B. carinatus* was not negatively impacted by competition whether inoculated or not (p.adj > 0.474). *Achillea millefolium* received significant increases in biomass from inoculation when in competition against false brome (p.adj = 0.011), as well as when grown alone (p.adj = 3.23×10^{-4}). *A. millefolium* was not negatively impacted by competition whether inoculated or not (p.adj > 0.999).

Notably, inoculation offered no competitive boosts to *Brachypodium sylvaticum* in any competition grouping, nor when growing alone (all p.adj > 0.426). Instead, while not significant, inoculation often resulted in lower biomasses for *B. sylvaticum* (Table 1). These results offer mechanistic support for my hypothesis, demonstrating inoculation with native AMF preferentially increases competitive ability of native species, while conferring no advantage to invasive *B. sylvaticum*.



Games-Howell Post Hoc Results of Dried Shoot Biomasses

Focal Species	*Competition Group*	*Inoculation Effect*	*Confidence Interval*	*p.adjusted*	*Signif*
ELGL	ELGL alone	0.024	-1.17-1.2205	1.000	ns
BRCA	BRCA alone	0.693	-0.11-1.5050	0.109	ns
ACMI2	ACMI2 alone	0.912	0.431-1.3922	0.000	***
BRSY	BRSY alone	-0.132	-0.75-0.4912	0.991	ns
ELGL	ELGL x BRSY	0.793	0.053-1.5322	0.034	*
BRCA	BRCA x BRSY	0.159	-0.68-1.0040	0.948	ns
ACMI2	ACMI2 x BRSY	0.960	0.199-1.7207	0.011	*
BRSY	BRSY x ACMI2	-0.178	-0.66-0.3113	0.905	ns
BRSY	BRSY x BRCA	-0.079	-0.20-0.0481	0.426	ns
BRSY	BRSY x ELGL	-0.027	-0.15-0.1017	0.995	ns

Table 1: Results of games howell post-hoc tests of ANOVA's analyzing the effects of inoculation between competition and alone groups.

Field Experiment

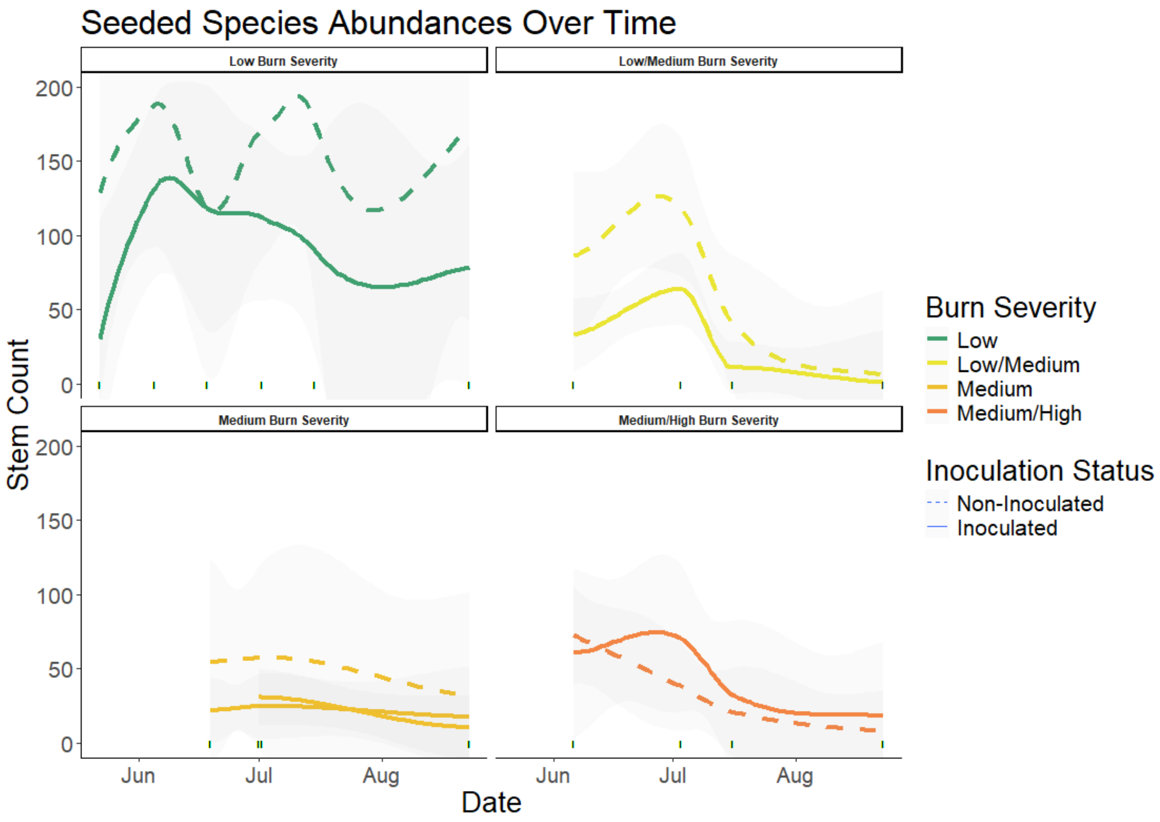


Figure 5: Timeseries of mean seeded species abundances (stem counts) at each site. Solid lines represent inoculated plots' means, whereas dashed lines represent those that did not receive mycorrhizal inoculum. Dashes along the x-axis denote dates at which surveys were conducted.

As a result of plots needing to be established after germination occurred, plots at all sites contain initial stem abundances of seeded species at establishment. At all sites, seeded species stem abundances did not significantly vary with inoculation status. The low severity sites are established earlier than the others on account of their germination occurring earlier in the summer due to their lower elevation compared to other sites. The Low severity site occurs at 1833ft; the Low/Medium severity site occurs at 2873ft; Medium severity sites occur at 1940ft and 2689ft, and the Medium/High severity site occurs at 2761ft. Stem abundances generally peaked around early July, before declining to their lowest levels by the end of August. Low severity sites did not follow this trend, and instead continually fluctuated in abundance throughout the summer. Sites categorized with higher burn severities generally had lower abundances of seeded species compared to lower burn severity sites (Fig. 5).

Non-seeded plant communities varied from seeded species and were largely dominated by *Chamaenerion angustifolium* (fireweed)*, Lysimachia latifolia* (starflower), and *Berberis nervosa* (dwarf Oregon grape) (Fig. 14). Somewhat unexpectedly, no individuals of *Brachypodium sylvaticum* had confirmed observations in any of the plots. Non-seeded native species' stem abundances also did not respond to receiving crude root inoculum. However, abundances of non-seeded species were more similar across burn severities, with medium/high burn severity plots generally having higher average stems compared to low burn severity plots.

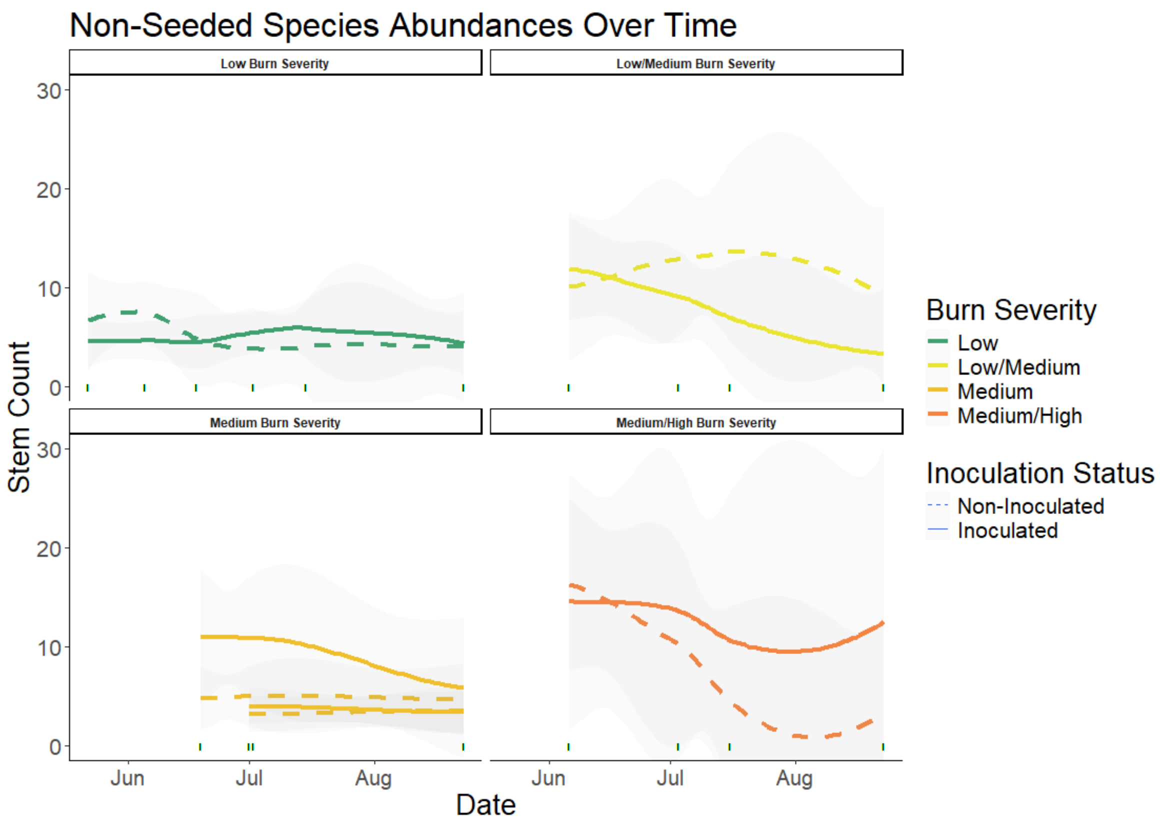


Figure 6: Timeseries of mean non-seeded species abundances (stem counts) at each site. Solid lines represent inoculated plots' means, whereas dashed lines represent those that did not receive mycorrhizal inoculum. Dashes along the x-axis denote dates at which surveys were conducted.

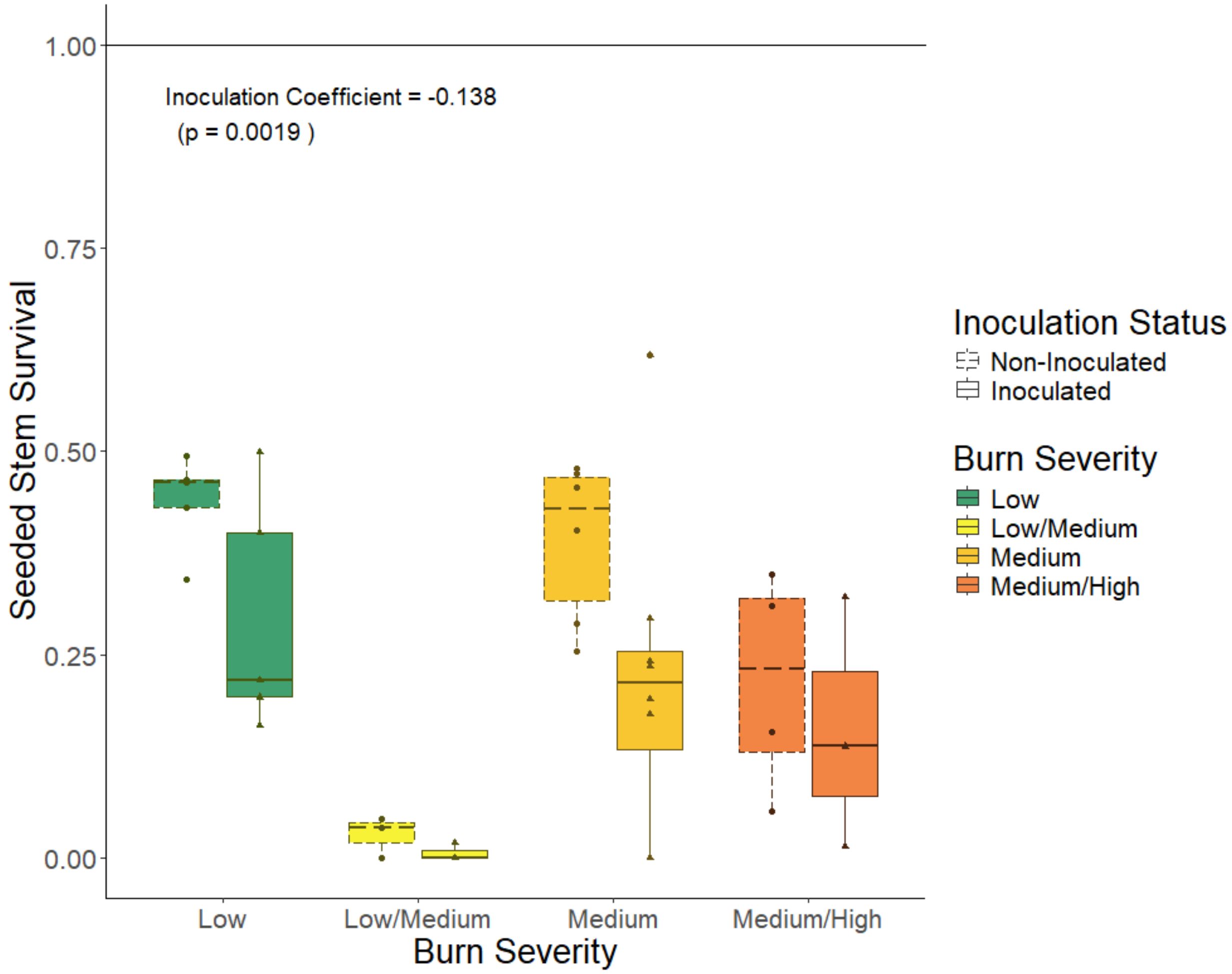


Figure 7: Effect of mycorrhizal inoculation on first-year germinate seeded species survival (calculated as stems remaining at final survey since peak abundance) at each site. Inoculated plots for each burn severity are denoted by solid lines, and non-inoculated plots are denoted with dashed lines. Model estimates of inoculation effects are listed in the upper left corner.

Inoculation had a significant negative effect on first year germinate survival, contradicting my hypothesis (p = 0.002). Canopy Cover had a near significant positive effect on first year stem retention, with plots with higher canopy cover experiencing greater germinate survival (p = 0.056). Distance to road had a minor, but non-significant, negative effect on log first year stem retention as well (p = 0.117). This effect appeared to flip between low and medium/high burn severity sites, however including an interaction in the model did not yield any significant results

(Fig. 9). Comparison of models with and without site as a random effect using an ANOVA uncovered a significant site effect on first-year germinate survival (p = 0.0012).

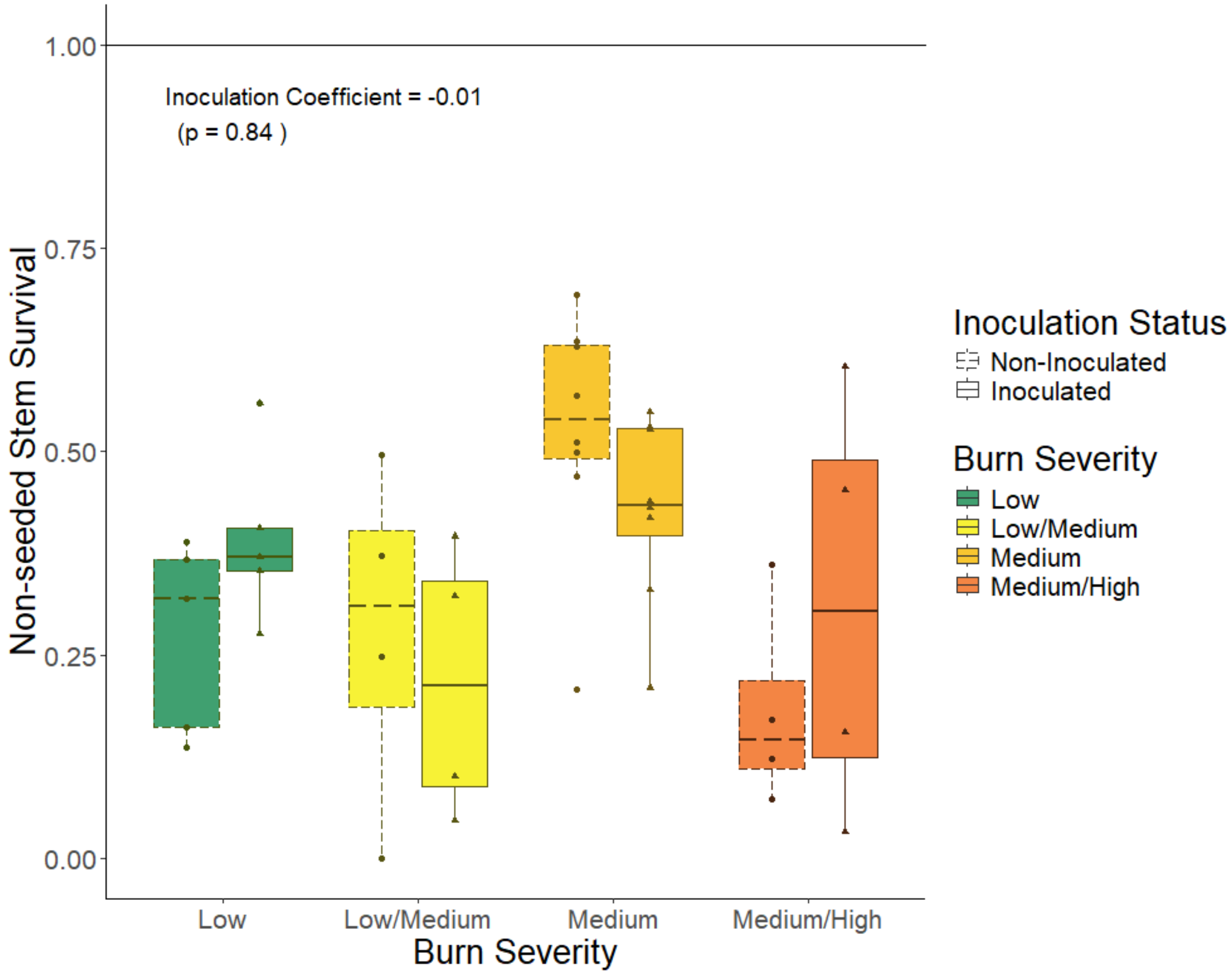
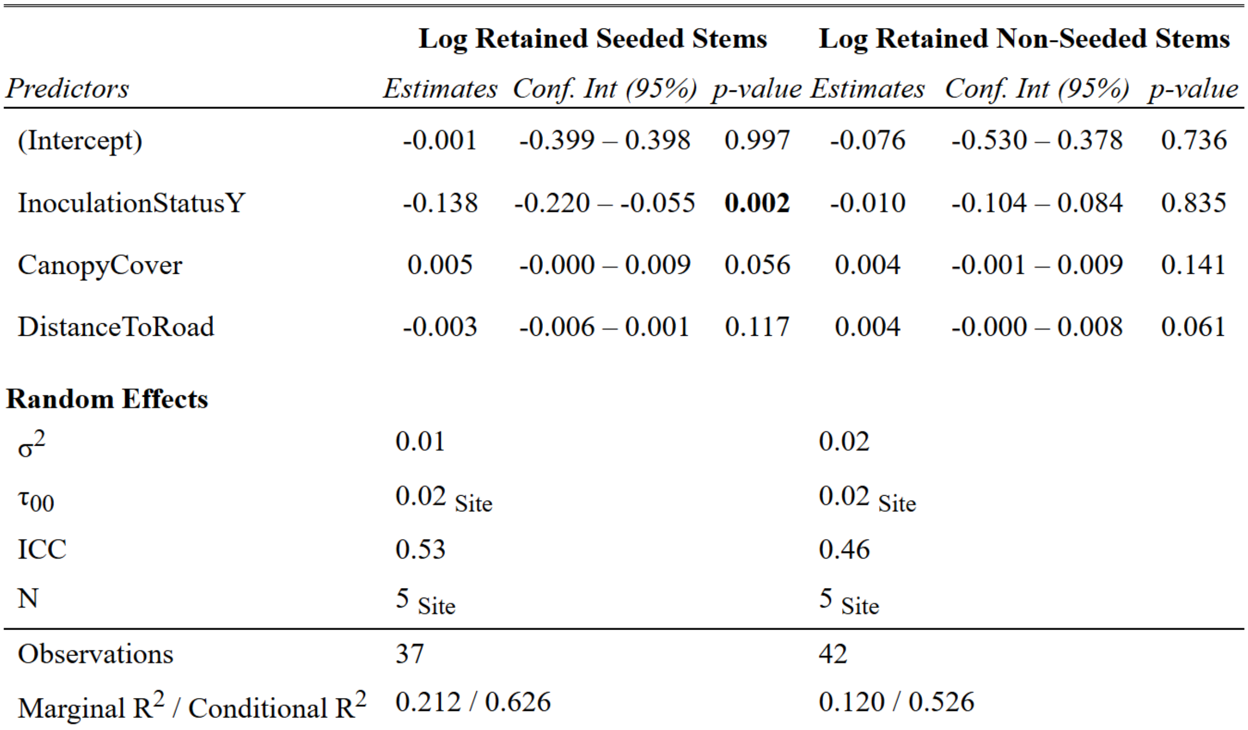


Figure 8: Effect of mycorrhizal inoculation on non-seeded species survival (calculated as stems remaining at final survey since peak abundance) at each site. Inoculated plots for each burn severity are denoted by solid lines, and non-inoculated plots are denoted with dashed lines. Model estimates of inoculation effects are listed in the upper left corner.

Survival of non-seeded native species did not respond to inoculation or site, except for the medium severity sites experiencing greater survival; instead, distance to the road had a near significant influence on the log survival of stems (Fig. 10; p = 0.06). Across all sites, native non-seeded species experienced nominally higher retention from peak abundance the deeper into the forest interior they were. Canopy cover had a non-significant effect on the log survival of stems (p = 0.141).

Shannon's diversity of all species at each burn severity did not respond to receiving crude root inoculum. The diversity of plots was, however, influenced by site (p = 0.013). Similarly to non-seeded species, sites categorized as medium burn severity appeared to retain the most diversity by the end of the first growing season (Fig. 13).



	Log Retained Seeded Stems			**Log Retained Non-Seeded Stems**		
Predictors	*Estimates*	*Conf. Int (95%)*	*p-value*	*Estimates*	*Conf. Int (95%)*	*p-value*
(Intercept)	-0.001	-0.399 – 0.398	0.997	-0.076	-0.530 – 0.378	0.736
InoculationStatusY	-0.138	-0.220 – -0.055	**0.002**	-0.010	-0.104 – 0.084	0.835
CanopyCover	0.005	-0.000 – 0.009	0.056	0.004	-0.001 – 0.009	0.141
DistanceToRoad	-0.003	-0.006 – 0.001	0.117	0.004	-0.000 – 0.008	0.061
Random Effects						
σ^2	0.01			0.02		
τ_{00}	0.02 $_{\text{Site}}$			0.02 $_{\text{Site}}$		
ICC	0.53			0.46		
N	5 $_{\text{Site}}$			5 $_{\text{Site}}$		
Observations	37			42		
Marginal R^2 / Conditional R^2	0.212 / 0.626			0.120 / 0.526		

Table 2: Model outputs estimating the effect of Inoculation, Canopy Cover, and Distance to Road on first-year seeded (left) and non-seeded (right) species survival. Site (burn severity) is included as a random effect in both models.

VI. DISCUSSION

In this thesis I tested the hypothesis that inoculating plant communities with native mycorrhizae would increase the performance and competitive ability of native plants post-fire. Results from both experiments yielded mixed support for my hypothesis. The greenhouse demonstrated mechanistic support for native mycorrhizal fungi increasing the performance of native species against invasives post-fire, while refuting the alternative hypothesis that invasive *Brachypodium sylvaticum* may benefit from pairing with native mycorrhizal fungi. However, the field experiment did not support my hypothesis and revealed the practical applications of this benefit are highly context specific; Inoculation of native arbuscular mycorrhizal fungi across all sites resulted in decreases in first-year germinate stem survival for seeded species, and no response from non-seeded species.

Inoculation of native plants with local arbuscular mycorrhizal fungi growing in high-severity burn soil in a greenhouse setting resulted in increased competitive ability of native species, while conferring no advantage to invasive false brome (Fig. 4). Increases in native plant competitive ability were apparent (although variable) through increases in plant biomass with inoculation. These results demonstrate support for my hypothesis, indicating that locally sourced mycorrhizal fungi can be effectively utilized in post-fire restoration settings where invasive competition is of concern.

Our three native plants experienced mostly positive responses to mycorrhizal inoculation (Fig. 4). While both *Elymus glaucus* and *Achillea millefolium* varied in their response to competition with *Brachypodium sylvaticum*, both still received significant increases in biomass from inoculation in competition situations. *Achillea millefolium* also received a significant increase in biomass from inoculation when growing alone. Conversely, *Bromus carinatus* received non-significant increases in biomass when growing alone and in competition. In addition to native/invasive status potentially driving inoculation responses, plant functional groups may also be a significant factor (Hoeksema et al. 2010, Grove et al. 2017). In particular, C3 grasses (of which *Elymus glaucus* and *Bromus carinatus* are included), often respond less positively to mycorrhizal inoculation than do forbs and woody plants (i.e. *Achillea millefolium* and all non-seeded species observed in the field experiment) (Hoeksema et al. 2010).

In assessing dried shoot biomass, invasive *Brachypodium sylvaticum* exhibited no significant response to inoculation- whether growing alone or in competition. While responses were not significant, *B. sylvaticum* responded negatively to inoculation when growing in competition and marginally so when growing alone (Fig. 4, Table 1). Other studies have also demonstrated similar results where false brome is capable of benefitting from native mycorrhizal networks when isolated from other plants, but are neutrally or negatively affected by mycorrhizal partnership when native plant species are able to interact (Workman & Cruzan 2016). The lack of a response to inoculation from false brome lends additional support for species specific effects of arbuscular mycorrhizal inoculation- reinforcing the need for mycorrhizal treatments in restoration contexts to be locally sourced (Hoeksema et al. 2010, Grove et al. 2017).

However, in an applied field setting, inoculation of native plants with native arbuscular mycorrhizal fungi led to negative responses in plant performance (Table 2, Fig. 13). Inoculation had no effect on final shannon's diversity of native species across all sites (Fig. 13). Contrary to my hypothesis, there is a significant decline in seeded stem first-year survival as a result of inoculation (Fig. 7, $p = 0.002$). A non-ecological explanation for this trend suggests that since seeding intensity and implementation was conducted by a restoration outfit focused on restoration outcomes, and not experimental design, seeding intensity may have been irregular within sites. Timeseries data in figure 5 depicts all sites except the medium/high burn severity site having higher initial seeded species abundances in the non-inoculated plots. Non-intentional bias via varying seeding intensity between inoculated and non-inoculated plots may have caused non-inoculated sites to have greater abundances and a longer germination period compared to inoculated sites. This can generate what appears to be a negative effect of inoculation, when in actuality may be driven by irregular seeding intensity and strict site limitations that disallowed for alternative site selections.

Despite refuting my hypothesis, the negative effect inoculation has on first-year seeded stem survival falls in line with several expectations of when mycorrhizae are parasitic according to the mutualism-parasitism continuum (Johnson et al. 1997). Soil nutrient availability is a leading hypothesis as to the behavior and prevalence of mycorrhizal fungi (Grove et al. 2017). High availability of soil nutrients such as nitrogen and phosphorus may lessen the dependence of plants on mycorrhizal partners, and in certain instances lead to parasitism of the host plant (Johnson et al. 1997, Hoeksema et al. 2010). This occurs as plants continue to give the fungus photosynthates while receiving trivial benefits in return when resources are abundant. Increased soil nitrogen availability may have been greater in lower burn severity sites, where organic matter and duff layers were retained, compared to higher burn severity sites that may have lost more organic matter (Verma and Jayakumar 2012). Nitrogen deposition from lower severity fire may then be contributing to negative responses to inoculation from seeded species. Greater retention of a duff layer may also assist in soil moisture retention, which in turn would further lessen plant dependence on mycorrhizal partners (Valette et al. 1994, Smith and Read 2008). Visibly smaller differences between inoculated and non-inoculated plots at the higher burn severities may then be attributable to more stressful environmental conditions where mycorrhizal partnership is more beneficial (Fig. 7).

While lower burn severities can offer fewer nutrient benefits to forming mycorrhizal partnerships, the availability and value of carbon for the plants is likely another large factor determining response to mycorrhizal inoculation in the field (Johnson 1997). Most of the seeded species in the field experiment were still small seedlings by the end of the summer; carbon investment from such young plants to establish mycorrhizal connections may come at a heavy cost. Giving carbon to mycorrhizae when young can lead to increased mortality that balances out with increased performance in the future for individuals who were able to afford forming mycorrhizal partnerships (Johnson 1997, Jones & Smith 2004). Repeat surveys in future years may then find results opposite to those presented here in the first-year post-fire. Carbon is also notably scarce for seedlings growing in the site with low burn severity; the high canopy cover at the low burn severity site makes photosynthesis for early seral species much more difficult. This lower light availability may thus make forming mycorrhizal partnerships extra costly (Jones & Smith 2004, Ibáñez & McCarthy-Neumann 2016).

Notably, the negative association with inoculation was not observed in non-seeded plant communities (Fig. 8); indicating that the effect inoculation has on native species may be more a factor of a species-specific response. Other drivers of observed responses to inoculation include plant functional groups and identity (Grove et al. 2017). Plant responses to mycorrhizal inoculation are broadly variable; in addition to soil nutrients, plant identity may also explain the negative response to inoculation across sites, particularly in our seeded species (Klironomos 2003, Hoeksema et al. 2010). As observed in the greenhouse experiment, *Elymus glaucus* and *Bromus carinatus*, as C3 grasses, may be responding less positively to the inoculum compared to forbs (Hoeksema et al. 2010). The lessened sensitivity and variable response to inoculation in the two most dominant seeded species in the field experiment may have contributed to worsened first-year germinate survival across sites. Support for this explanation may also be seen in non-seeded species, which are mostly forbs, often having neutral to positive reactions to inoculation, particularly at sites with higher burn severities (Fig. 8). However, many non-seeded species in higher burn severity sites were dominated by disturbance adapted species like *Chamaenerion angustifolium* (Fig. 14), which may contribute to positive responses to greater abiotic stress. These patterns are also observed in the greenhouse experiment, where *Achillea millefolium*, a forb, had consistent positive reactions to inoculation in all competition settings, compared to the other species (Fig. 4). While seeded species were negative in their response to inoculation, it was not the only factor driving their performance in post burn environments.

Across all metrics of performance (proportion of stems retained from peak abundance & shannon's diversity), native plants were impacted by distinct site level effects and canopy cover (Table 2, Fig. 13). Seeded species performed best at the site categorized as lower burn severity (Fig. 7). Increased stem retention at this site is likely driven by less abiotically stressful conditions compared to sites with higher burn severities. Higher burn severity sites saw lower canopy cover (Figs. 11, 12), which exposed germinates to full sun conditions for large portions of the day- leading to many individuals to desiccate as summer droughts continued on. Additionally, soils at higher burn severities often exhibit hydrophobic characteristics, reducing available soil moisture for germinates to use (MacDonald & Huffman 2004). Conversely, non-seeded species were unaffected by burn severity, except for an increase in retained stems at the medium severity sites (Fig. 8). Diversity of all native species experienced a similar pattern, where shannon's diversity at the end of the summer was highest at medium severity sites (Fig.

13). These patterns resemble other findings demonstrating greater diversity and performance in post-fire forests at intermediate disturbance levels (Miller and Safford 2020).

Seeded species performance was unaffected by distance to the road (p = 0.117). Varied performance near roadsides for seeded species may be attributable to variable seeding intensity. The Walama Restoration project undertook seeding operations throughout burned portions of the H.J. Andrews based on agreements between them, the U.S. Forest Service, H.J. Andrews personnel, and myself. To minimize impacts to interior forest communities that may be part of long-term research, the Walama Restoration project was limited to seeding only within 50ft of roadsides. This strict limitation may have inadvertently led to differential seeding closer to roadsides, which could allow for a larger seed-bank and more continuous germination throughout the growing season.

Roadsides often experience increased soil compaction, dust damage, and light availability, which may benefit more stress tolerant species such as those we seeded and invasives (Lázaro-Lobo & Ervin 2019). Conversely, non-seeded species performed marginally better further away from roadsides across all burn severities (figure 10, p = 0.061). Non-seeded understory species throughout the H.J. Andrews are more adapted to growing in dense shade with deep duff layers. These non-mycorrhizal factors of seeded plant performance indicate that seedings aren't necessarily more likely to remain close to roadsides post-burn, and may have potential of creeping into the forest interior at higher burn severity sites; however they don't appear to be inhibiting the establishment of non-seeded species in the first year.

Contrary to expectations, *Brachypodium sylvaticum* was not observed at any sites, despite ample opportunity for spread via vehicle traffic and burn disturbance through areas where it is already established. While results from the field experiment currently contradict the practical application component my hypothesis, the ability for *B. sylvaticum* to spread in the next few years, and for mycorrhizal partnerships to change, make repeat future surveys of particular need to further elucidate how results from the greenhouse may translate to the field.

VII. CONCLUSION / MANAGEMENT RECOMMENDATIONS

I found that using native arbuscular mycorrhizae to benefit native species in post-fire restoration settings was beneficial in higher burn severity soils, where forbs are the target species to be competing against invasives. I also found that when in direct competition, native pacific northwest arbuscular mycorrhizae confer a competitive advantage to native species while offering no benefit (and potential antagonism) to invasive *B. sylvaticum*, which is in mechanistic support of my hypothesis. Survival of first-year seeded germinates did not respond positively to arbuscular mycorrhizal inoculation in the first year post fire- particularly in lower burn severity sites where nutrient inputs, light availability, and growth stage may have shifted mycorrhizae to be more parasitic, running contrary to my applied hypothesis. However, repeat surveys across multiple years may provide greater clarity on whether inoculation effects are being confounded by fluctuating environmental factors.

I would recommend that mycorrhizal inoculation be utilized to supplement post-fire herbaceous plant restoration only in high burn severity sites where restoring forbs is the priority. Early seral species and C3 grasses are likely to respond less positively to inoculation, and in settings where nutrient inputs are high and light is low (i.e. low burn severity sites), mycorrhizal partnerships may be detrimental to plant performance in their first year (Johnson et al. 1997, Grove et al. 2017). As stated before, however, repeat surveys are needed to generate a clearer image of how mycorrhizal inoculation influences plant species demographics beyond their first year, especially if invasive species begin to establish. As fire returns to the pacific northwest landscape, caution is needed to avoid invasive species from taking advantage of disturbed landscapes (Brambila et al. 2023). Inoculation of seeded plant communities with native arbuscular mycorrhizae post-fire can assist native plant communities to better compete against invasive species; yet, as is customary in the field of community ecology, context is key.

VIII. SUPPLEMENTAL FIGURES

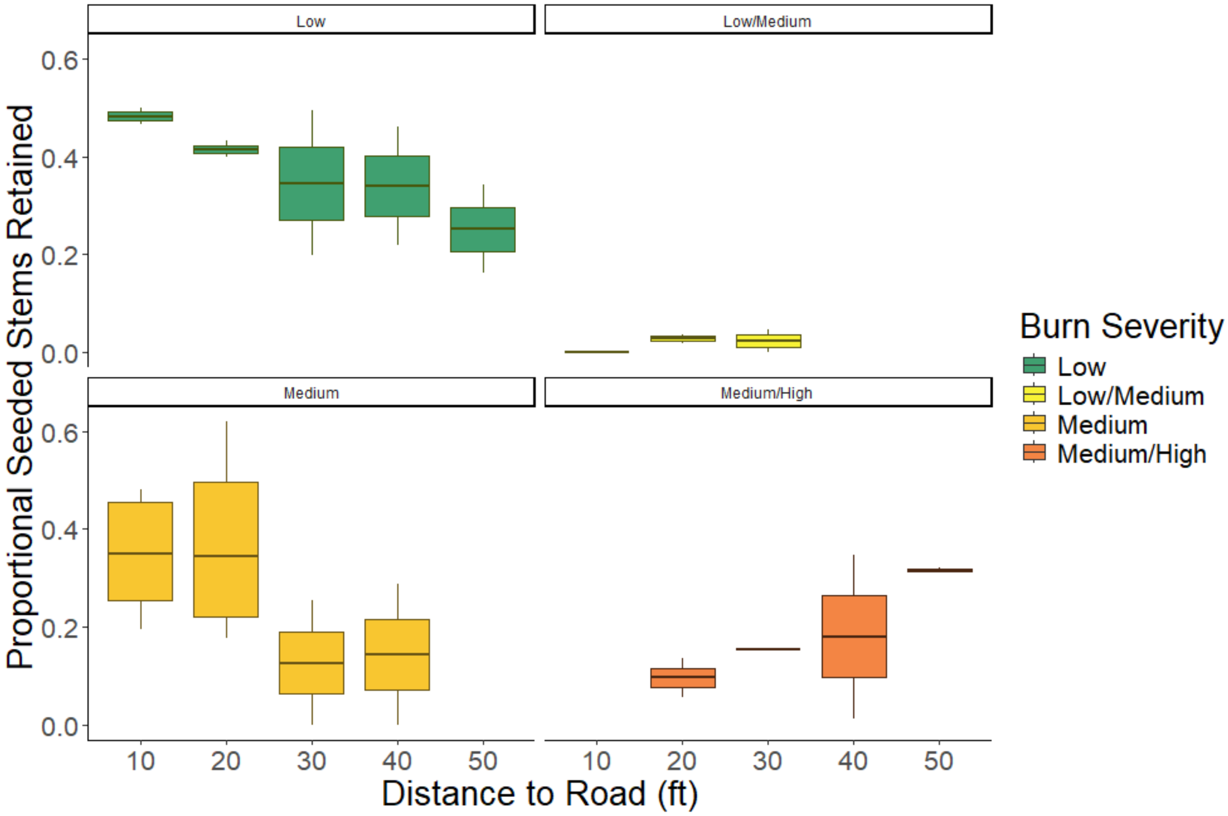


Figure 9: First-year germinate survival of seeded species at different distances from the road. Panels represent different sites.

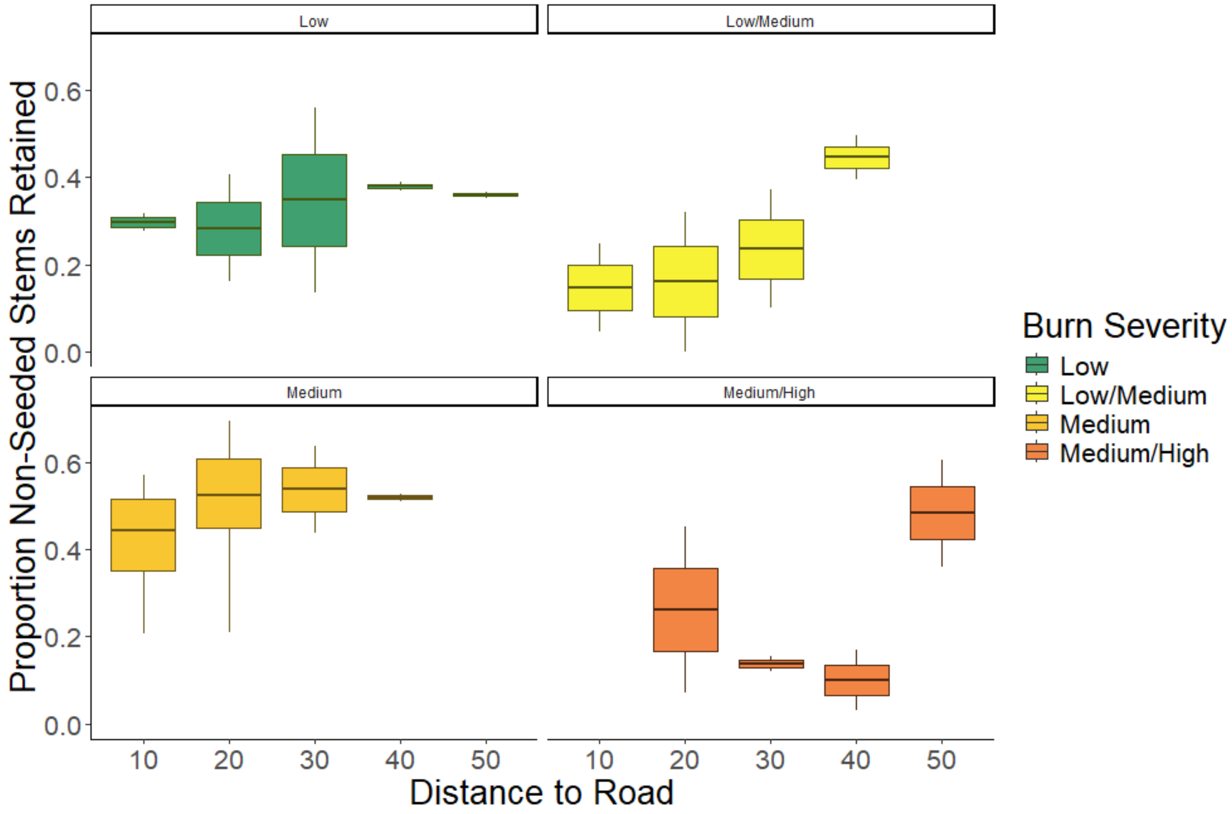


Figure 10: First-year survival of non-seeded species at different distances from the road. Panels represent different sites.

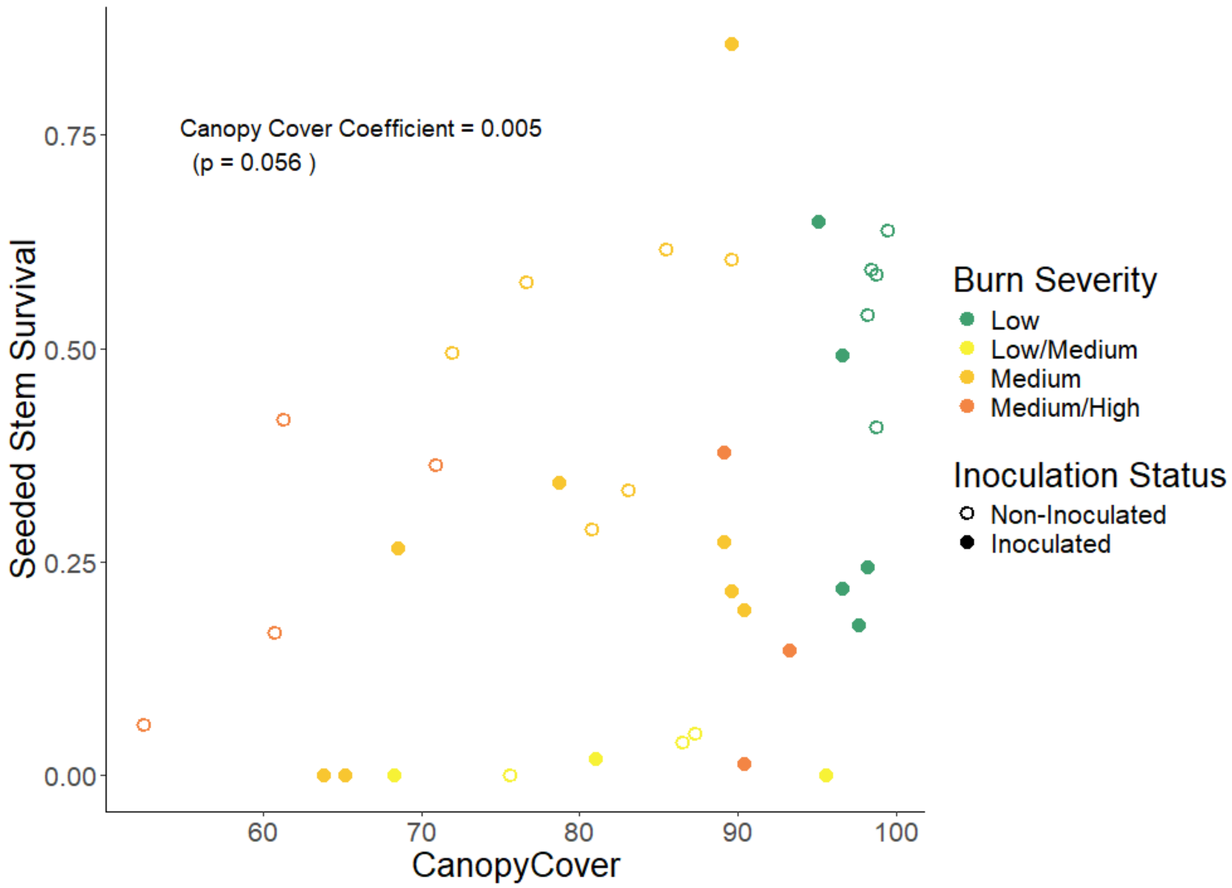


Figure 11: First-year germinate survival of seeded species in response to canopy cover. Model estimates of canopy cover effects are included in the top left (Table 2).

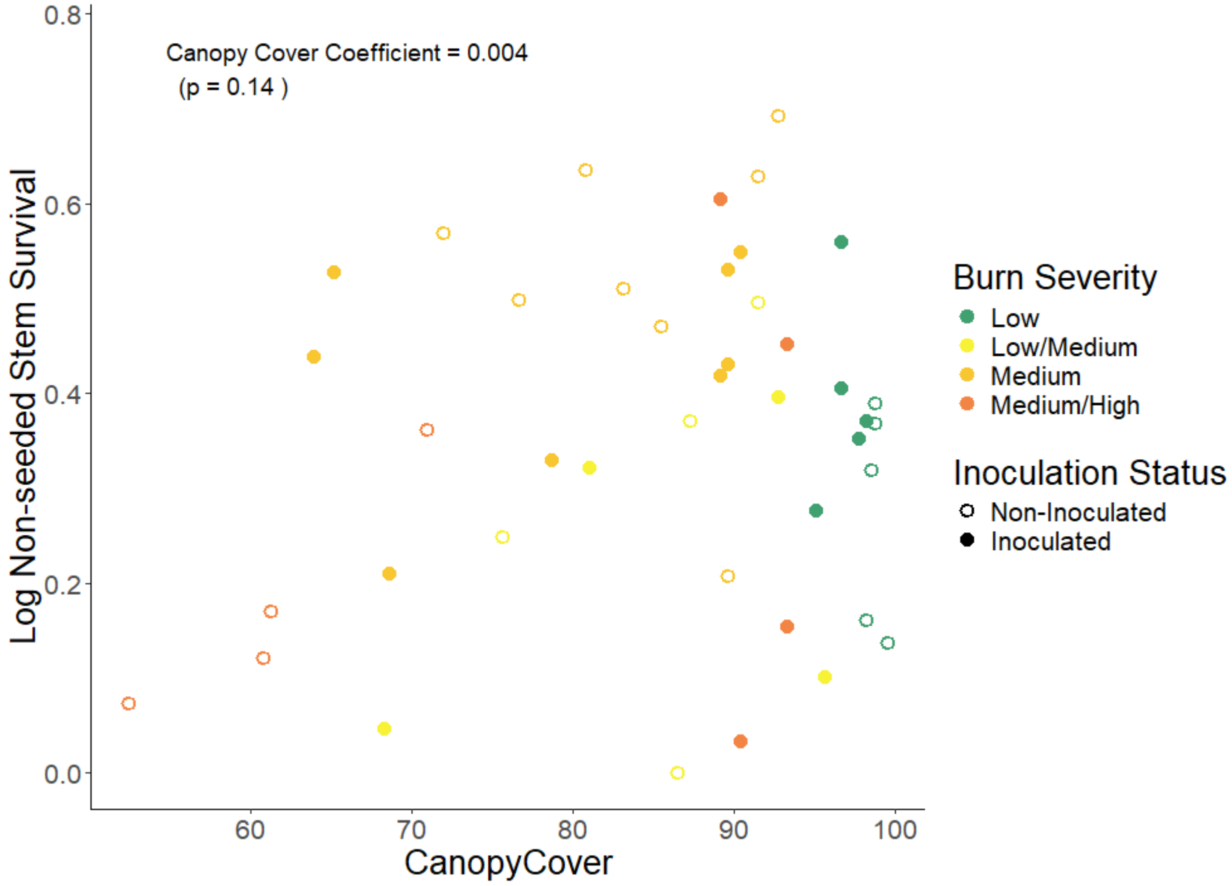
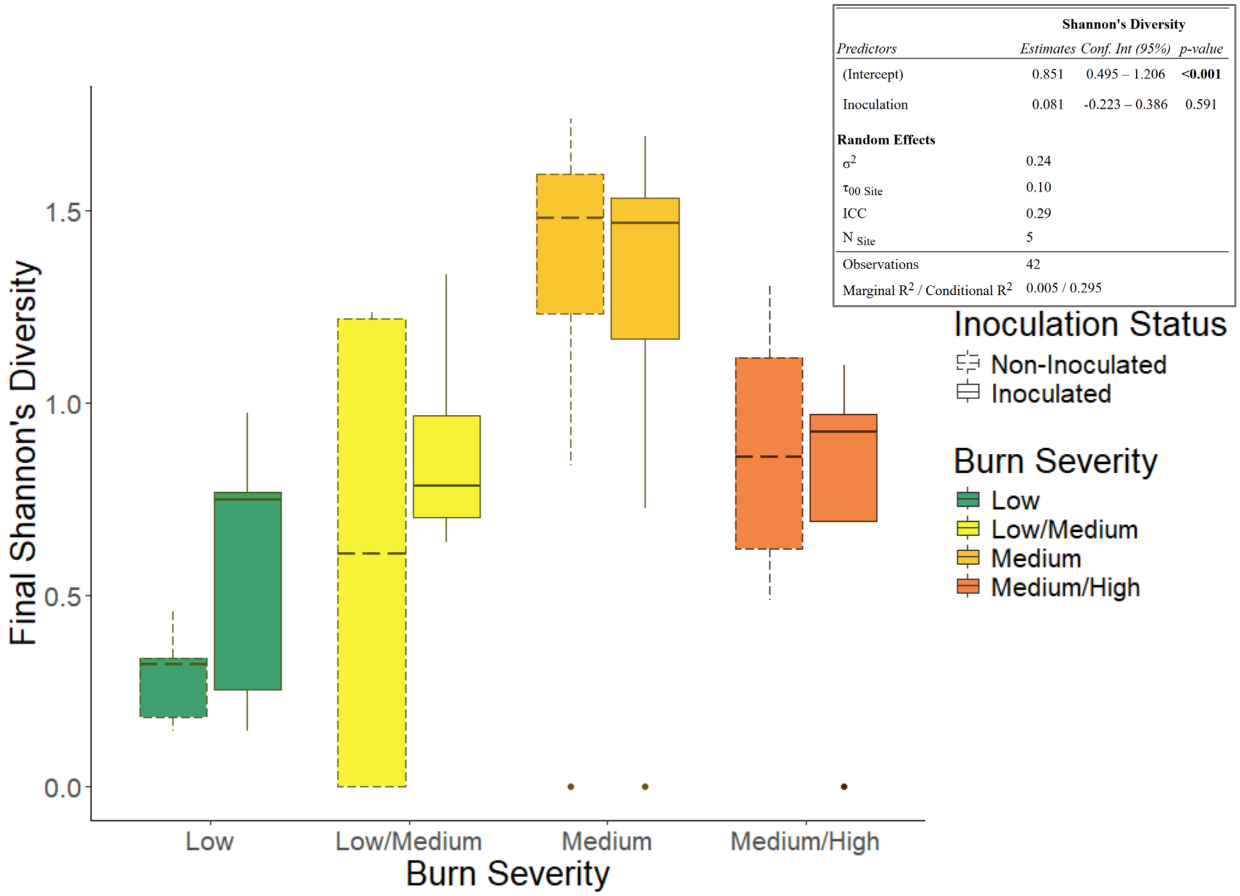


Figure 12: First-year survival of non-seeded species in response to canopy cover. Model estimates of canopy cover effects are included in the top left (Table 2).



	Shannon's Diversity		
Predictors	*Estimates*	*Conf. Int (95%)*	*p-value*
(Intercept)	0.851	0.495 – 1.206	**<0.001**
Inoculation	0.081	-0.223 – 0.386	0.591
Random Effects			
σ^2	0.24		
$\tau_{00\ Site}$	0.10		
ICC	0.29		
N_{Site}	5		
Observations	42		
Marginal R^2 / Conditional R^2	0.005 / 0.295		

Figure 13: Shannon's diversity of inoculated (solid) and non-inoculated (dashed) plots at each burn severity category at the final survey (August 23, 2024). Model output table for assessing the effect of inoculation on diversity is included in the upper right corner. Inoculation had no effect on diversity- however ANOVA comparison of models with and without site random effects indicate a significant site effect on final diversity

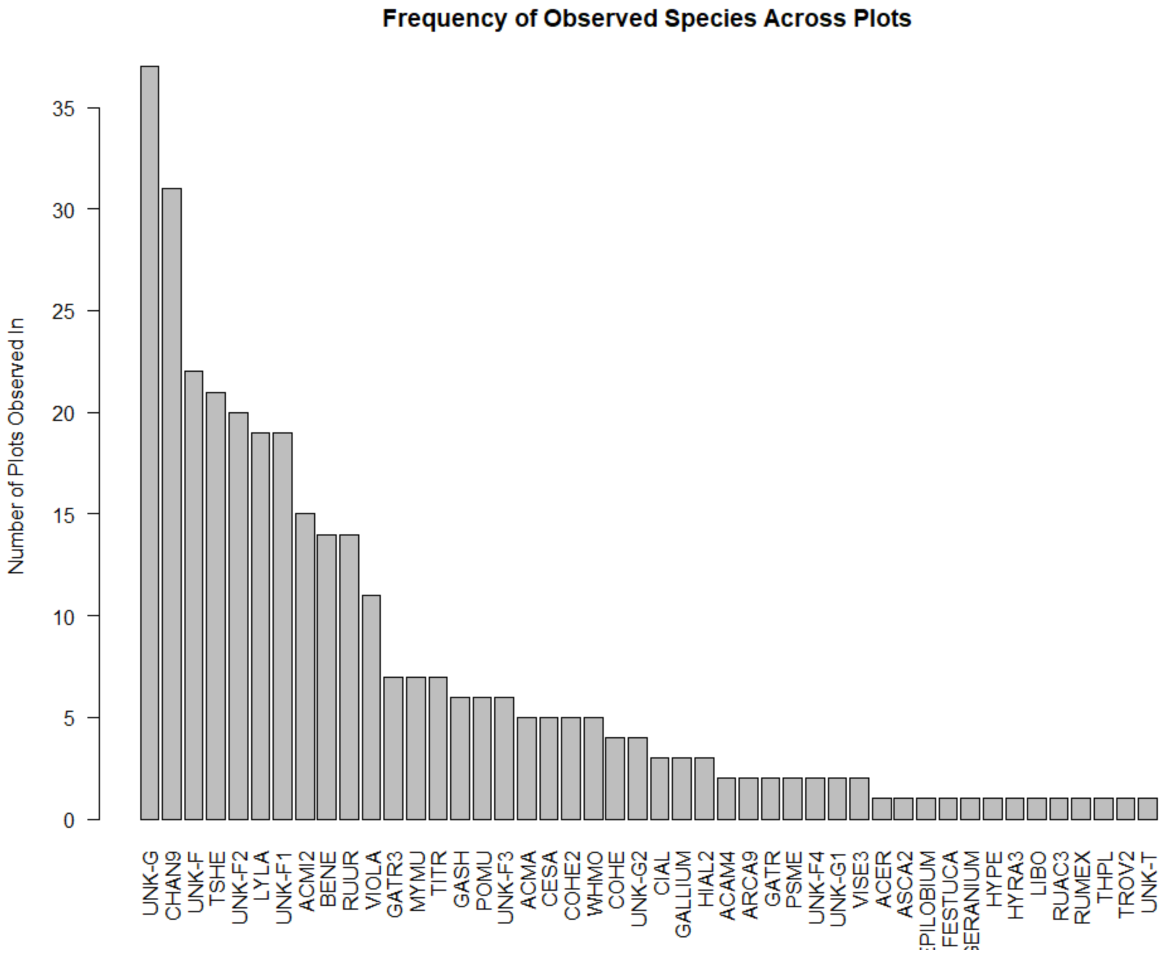


Figure 14: All species observed in the field experiment ranked by the number of different plots they occurred in. Species are listed here with conventional USDA alpha codes or complete genera names if only ID'd to genus.

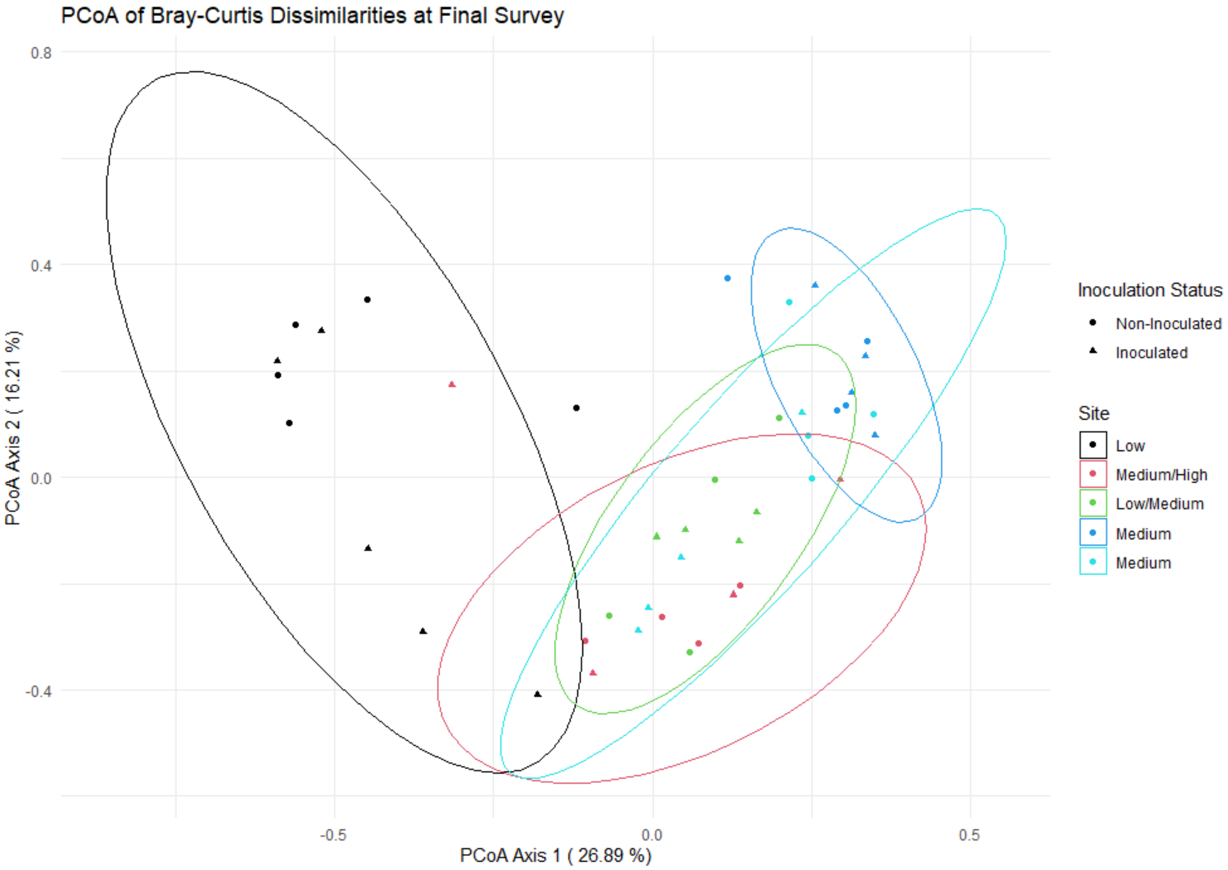


Figure 15: Principal Coordinate Analysis of plot Bray-Curtis dissimilarity at the end of the first growing season post-inoculation. Burn Severities are grouped by color, and inoculated plots are represented by triangles. By the final survey, plots across sites appeared to vary from low burn severity plots in their composition. Inoculated and non-inoculated plots within burn severities did not vary in a distinguishable way.

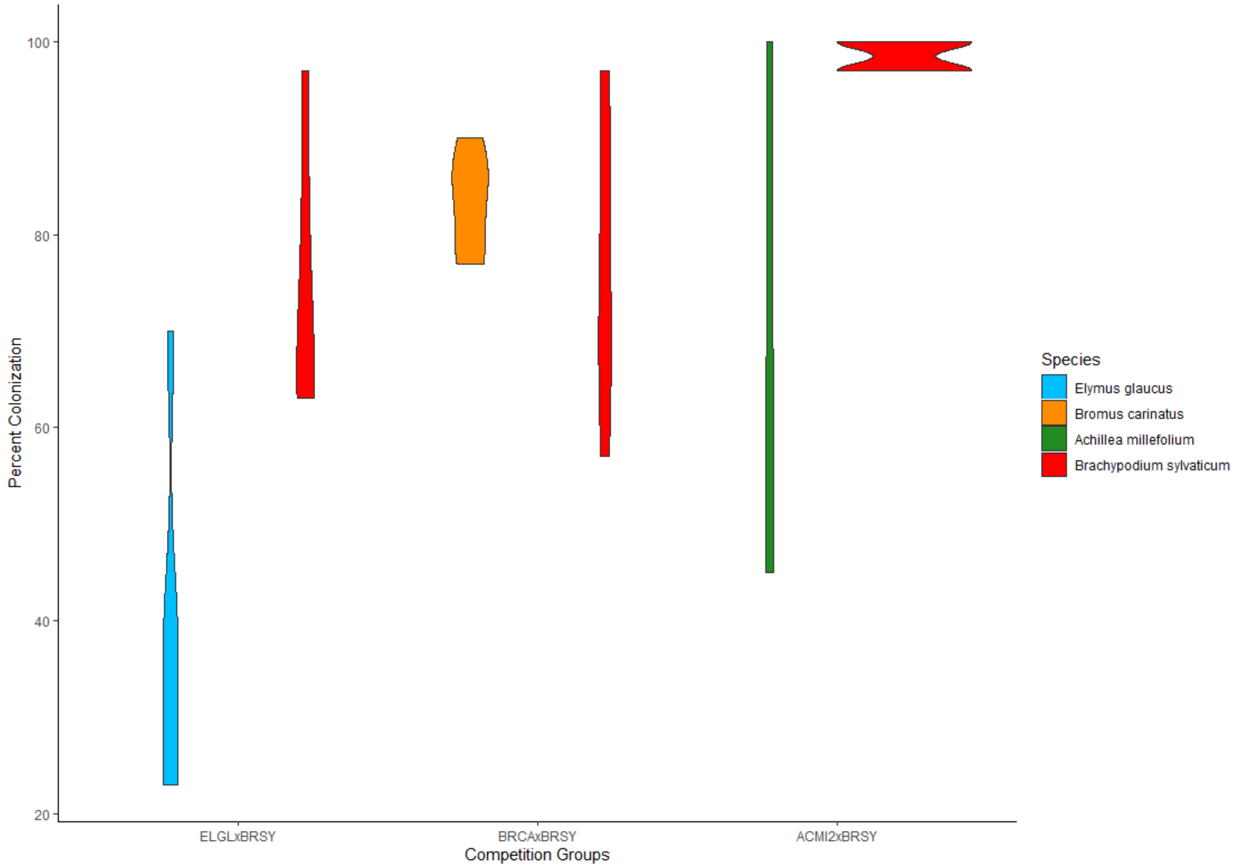


Figure 16: Preliminary results detailing the percent of plant roots colonized by mycorrhizal fungi in each inoculated competition grouping. Data is preliminary and exact percentages are subject to change, but it is evident that inoculation generated high colonization percentages in both the native and invasive plant species.

IX. CONFLICT OF INTEREST

I have no conflict of interest to declare.

X. LITERATURE CITED

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