Hub trees, mycorrhizae, and the early life stages of *Quercus buckleyi*

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Introduction

Mycorrhizae are an ancient symbiosis between plants and fungi. The first clear fossilized evidence of mycorrhized rhizomes dates to 407 million years ago in the Devonian period, however there is some indication these relationships originated earlier, perhaps even arriving with plants to land (Brundrett and Tedersoo 2018). Though quite diverse and understudied, the simplest description of this interaction is one of mutualistic reciprocity: plants provide photosynthetic sugars to fungi and fungi relay soil resources to plants. Soil resources commonly include low-mobility nutrients such as phosphorus, which some plants receive entirely from their mycobiont (Santander et al, 2017). Mycorrhizal fungi can also alleviate plant water stress through a variety of mechanisms including direct uptake and transfer of soil water (Püschel et al. 2020; Marulanda et al., 2003; Egerton-Warburton et al., 2003), regulation of the phytohormone ABA (Ouledali et al., 2019) and aquaporin expression (Bárzana et al., 2014; He et al., 2015), protection from oxidative damage (Lehto and Zwaizek 2011; Santander et al., 2017), enhanced nutrition (Augé 2001; Li et al., 2021) and photosynthetic efficiency (Porcel and Ruiz-Lozano 2004; Augé et al., 2016), and improved soil physical properties (Bitterlich et al., 2018; Augé 2004). This benefit of symbiotic association may be particularly important to germinants in water-limited environments, where fungal partners may help seedlings survive the most vulnerable first weeks of life (Pereira et al., 2021; Atala et al., 2012).

Mycorrhizae also connect plants of similar and diverse phylogenies through a Common Mycorrhizal Network (Southworth et al, 2005; Fodor, 2013; Toju et al, 2018). Larger mature trees can serve as "hubs" in these networks; this role in network topology has been shown to increase at more xeric sites (Beiler et al 2015). It has been argued, though direct evidence is scarce, that the mycorrhizal inoculum of mature "hub" trees is required to forge connections with the most beneficial mycorrhizal species (Tatsumi et al., 2021; Simard, 2009), thus proximity to large trees with shared mycobionts may impact growth and survivorship outcomes for seedlings.

For decades the field of mycorrhizal research has largely oriented around how to improve agricultural productivity; most studies were (and continue to be) conducted on herbaceous plants in greenhouse settings using commercial inoculum (Hoeksema et al, 2010). However, in recent years, scientists have increasingly begun to investigate the impact of endogenous mycorrhizae on native plants and restorationists are beginning to apply this knowledge. Examples in which the incorporation of native fungal partners have enhanced restoration success include Koziol et al., 2022; Allen et al., 2005; Davidson et al., 2016. Not surprisingly, this work remains limited to particular ecoregions and species; little is known about the role of mycorrhizal communities to species of conservation priority in Texas.

Texas red oak (*Quercus buckleyi*) is an iconic tree endemic to the limestone hills spanning the Balcones Escarpment from southcentral Texas into northcentral Oklahoma. For roughly the last 80 years it has failed to recruit (Fowler and Russell 2004). The growth of new generations is impinged upon by overabundant white-tailed deer, extreme drought, and oak wilt fungus (*Ceratocystis fagacearum*), among other threats. For central Texas oaks, the seedling

stage is particularly vulnerable. Though abiotic stressors can be mitigated by canopy cover (O'Donnell et al. 2020), it remains unclear what role the belowground biotic influence of mature trees might be. Is the available mycorrhizal community a significant factor for promoting success in the seedling stage? Does the community differ in proximity to adult conspecifics and to mature codominant *Juniperus ashei*? Does growth and survival in early life stages differ with proximity to hub trees?

Mycorrhizal associations are thought to be highly phylogenetically conserved within plant families or genera; oaks are one of the rare groups of trees capable of dual mycorrhization (Teste et al. 2019). They partner with both arbuscular mycorrhizal fungi (AM) and ectomycorrhizal fungi (EM). Adults maintain predominantly EM relationships, though it has been suggested that the AM and EM mutualism types may complement one another (Teste et al, 2019) and their prevalence can correspond to abiotic factors such as soil moisture (Quereteja et al, 2009). The evolutionarily more primitive lineage of AM are obligate symbionts, which form specialized structures within the root cortical cells of more than 70% of all vascular plant species (Brundrett and Tedersoo 2018). By contrast, the more diverse group of EM, which evolved independently at least 60 times (Raven and Andrews 2010), remain external to the root cells and form hyphal mantels around plant root tips. The prominent morphological and physiological differences between AM and EM confer different benefits to the plant, for instance AM require less carbon to maintain (they do not produce fruiting bodies), scavenge inorganic nutrients, and are more resilient to environmental extremes (Wipf 2019); there is also more evidence supporting their role as mitigators of drought stress (Augé, 2004; Lehto and Zwaizek, 2011). EM possess saprophytic abilities, enabling mineralization of N and P from soil organic compounds and offer more protection from pathogens by physically enveloping root tips (Bennett et al, 2017). Increasing evidence indicates that microbial taxa, including mycorrhizal and pathogenic fungi play major roles in neighborhood interactions and structure (Liang et al 2020; Toju et al 2018). Studies from multiple climate regions demonstrated positive plant-soil feedback and density dependence for EM seedlings and the opposite trend for AM seedlings (Liang et al, 2020).

We do not know with which general types (AM, EM) or which specific taxonomic groups *Q. buckleyi* seedlings associate and whether these associations vary with proximity to conspecific and heterospecific hub trees. Given that we know little to nothing about the mycorrhizal relationships of Texas red oak, anything we learn will be of interest to conservationists and land managers. *Quercus buckleyi* seedlings may or may not associate with both EM and AM; they may or may not associate with the same taxa of AM fungi as the *Juniperus ashei* with whom they commonly cohabitate. In mixed oak-juniper woodlands spatial variability in mycorrhization may significantly impact seedlings growth and survival in early life stages. We interrogate the impact of mature Ashe juniper and Texas red oak hub trees on oak seedlings in this semi-arid ecological community as a pilot study for a subsequent greenhouse experiment analyzing effects of source inocula on mycorrhization and drought stress. In this study we collect data on emergence, growth, and survival of seedlings over a two year period to see whether these parameters differ between treatment groups situated beneath and removed from large conspecific and codominant heterospecific trees.

Methods

Experimental Design

In the fall of 2020 several hundred *Quercus buckleyi* acorns were collected from the Balcones Canyonlands Preserve (BCP) at Reicher Ranch. All acorns were inspected for weevil damage and stored under refrigeration for up to one month in a paper bag. Before sowing, we submerged acorns to test viability and selected only acorns that sank for planting.

Seeds were sown on 15 November 2020 onto a shelf above the Colorado River on the Reicher Ranch tract of the BCP around 30.330312 N, -97.936771 W (See Figure 1). On the southeast-facing portion of the shelf the canopy is primarily comprised of oak and juniper with a relatively high abundance of *Q. buckleyi* ("Oak Zone"), whereas the canopy of the east-facing area is almost entirely juniper ("Juniper Zone").

Twenty circular plots with 1 m circumference were installed, each surrounded with 1-m tall wire mesh to discourage granivores and herbivores. Ten plots were set up in the "oak zone" and ten in the "juniper zone" (See Figure 1). In each zone, five plots were established immediately adjacent to (about 50 cm to the south of) a hub tree (either *Quercus buckleyi* or *Juniperus ashei* with a circumference at ground level greater than 100 cm) and five plots were situated at a minimum distance of 7.5 m away from the nearest large oak tree and 2.75 m from the nearest large juniper tree, though the spacing was typically further. Paired "Near" and "Far" plots were set up relatively close to each other. Soil depth measurements were taken for each plot quadrant prior to sowing. Each plot was seeded with 24 acorns and individual acorns were tracked through their position in the plot.

Seedling monitoring

From the time of first emergence, in the first week of March 2021, plots were visited weekly until mid-August, then bimonthly through September and once in October followed by a final visit on 20 November 2021. Observations consisted of seedling status (emergence and mortality), height from ground to tallest point of chlorophyllic leaf tissue, leaf number, and estimated percent leaf area damage from pathogens or herbivores. Monitoring recommenced in 2022 in the first week of March and continued at irregular intervals through the spring into fall and included measurements of stem basal diameter. We also took gas exchange measurements with Licor to document potential differences in plant water status or leaf photosynthetic capacity.

Plot characterization

In 2022, we conducted additional observations to improve plot characterization. In June, we measured soil water content with a soil moisture probe. Additionally, we characterized plots by litter type and conducted a neighborhood census of woody plant species. Up to a distance of 2.5 m from the plot perimeter, we recorded the presence all woody species with at least one member above 50 cm and counted each juniper and oak tree by size class categories (<50 cm, 50-100 cm, and >100 cm circumference at ground level). Lastly, we measured the distance to

nearest oak and juniper neighbors and their size, as well as distance to nearest large juniper and oak tree.

Mycorrhization sampling

October 2022, we destructively harvested a small random subsample (n=3) of each treatment. The samples are stored frozen pending microscopy work to identify fungal morphotypes. This work will be conducted in conjunction with the Gehring Lab at Northern Arizona University.

Preliminary Results

Seedling emergence differed significantly by zone (Wald Chi-Square p-value = 0) and distance (Wald Chi-Square p-value = 0.007); however, the interaction was not significant ($p = 0.449$). Forty three percent (43%) of Near Oak seedlings emerged whereas in the Juniper Far treatment, emergence was less than 7%. Survival of emerged seedlings, however, was not significantly impacted by treatment and was $\geq 73\%$ for all groups. End of season height in the first year was significantly greater in the oak zone ($p = 0.021$) and near treatments ($p = 0.017$), and the interaction was significant (0.014). Leaf count was also significantly higher in the oak zone ($p = 0.031$), with seedlings producing one more leaf on average. Damage to leaves from herbivory and disease was also greater in the oak zone ($p = 0.023$).

By the end of the end of their second spring, seedlings' leaf count did not differ significantly between treatments. Seedlings in the Near Oak treatment group were taller than all other treatment groups (see Figure 2), though the contrast with Juniper Far (with an n of 5) was not statistically significant (Tukey's test p-value = 0.0852). Stem diameters were larger in the oak zone, though all treatments were within one standard deviation. Licor measurements showed higher photosynthetic rates in the Oak Zone. Soil moisture was significantly higher in the oak zone than juniper zone, however soil depth did not differ between zones (see Table 1).

Neighborhoods differed substantially among treatment (see Tables 2 and 3). Species richness was higher in the Juniper Zone and highest in the Near Juniper neighborhoods. Near Juniper plots had the smallest number of sapling and midsize juniper neighbors of any treatment; they averaged 1.6 oak sapling neighbors and the mean distance for nearest oak was 1.5 m. The Juniper Far plots had more oak sapling neighbors than any other treatment with an average nearest oak distance of 2.08 meters; they also had the most midsize juniper neighbors. Both treatments in the Oak Zone had an average 0.8 midsize juniper neighbors; the average size of the nearest juniper neighbor was about 40 cm circumference at ground height, however Oak Far plots had the closest juniper neighbors (aside from Near Juniper) and Near Oak had the furthest juniper neighbor. Oak Far plots had the most juniper sapling neighbors of any treatment and more oak sapling neighbors than the Near Oak plots; the average distance to nearest oak in the Far plots was 1.7 m. Besides the Near Oak plots, for all other treatments mean distance to nearest oak neighbor exceeded 1.5 meters and mean size of nearest oak was ≤ 10 cm.

	FINAL N	EMERGE	SURVIVAL	HEIGHT	STEM DIAMETER	PMAX (N=5)	SOIL DEPTH	SWC	WOODY SP. N
NEAR O	40	0.433	0.7692	9.56 ± SE 0.404	1.02 ± SE 0.054	3.166 ± SE 0.564	17.6 ± SE 2.478	18.01 ± SE 1.342	8
O FAR	20	0.217	0.7692	6.62 ± SE 0.309	0.94 ± SE 0.068	4.126 ± SE 0.582	19.7 ± SE 4.186	14.61 ± SE 2.912	8
NEAR J	11	0.125	0.7333	7.05 ± SE 0.933	0.82 ± SE 0.100	2.308 ± SE 0.676	19.5 ± SE 2.522	8.39 ± SE 0.778	13
J FAR	5	0.067	0.625	7.52 ± SE 0.763	0.83 ± SE 0.125	1.856 ± SE 0.432	15.95 ± SE 1.632	8.54 ± SE 0.604	8

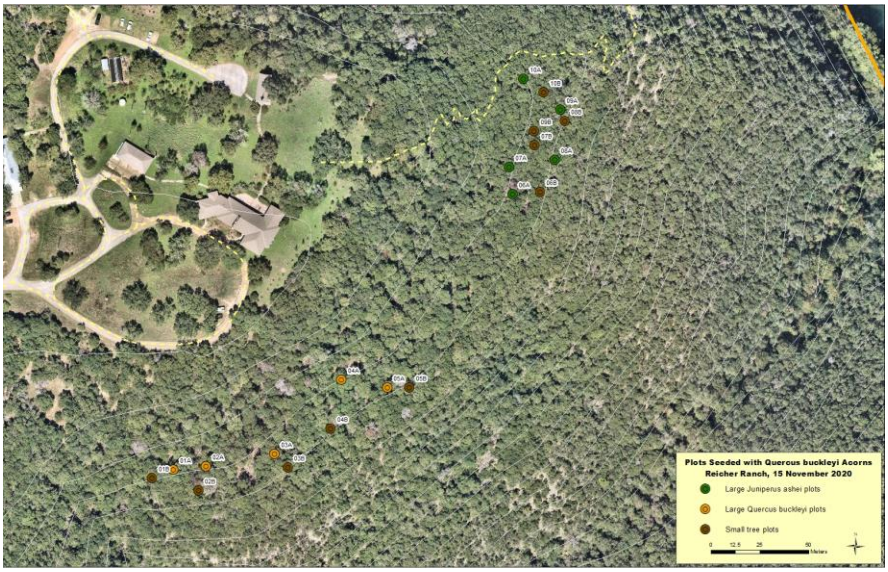
Table 1.
Each treatment's final seedling count, % emergence in year one, % survival of emerged in year two, mean height in year two, mean stem diameter in year two, maximum photosynthetic rate, mean soil depth, mean soil moisture content, and count of woody neighbor species.

TREATMENT	DIST. TO J (M)	SIZE J (CM)	DIST. TO O (M)	SIZE O (CM)
OZ	0.92	40.25	1.17	91.74
NEAR O	1.25	40.7	0.64	181.4
O FAR	0.60	39.8	1.71	2.07
JZ	0.74	103.1	1.81	9.17
NEAR J	0.48	148.8	1.54	8.3
J FAR	0.99	57.4	2.08	10.04

Table 2.
Nearest oak and juniper neighbor: average distance from plot perimeter and circumference at ground height

TREATMENT	JUNIPER SMALL	JUNIPER MIDSIZE	OAK SMALL	OAK MIDSIZE
OZ	3	0.8	0.7	0
NEAR O	1.6	0.8	0.2	0
O FAR	4.4	0.8	1.2	0
JZ	2.3	1.3	2	0
NEAR J	1.4	0.2	1.6	0
J FAR	3.2	2.4	2.4	0

Table 3.
Average number of juniper and oak neighbors by size class. Small < 50 cm; midsize ≥ 50 cm, <100 cm circumference at ground level



Map by Lisa O'Donnell
Figure 1.
Map of study site, Reicher Ranch

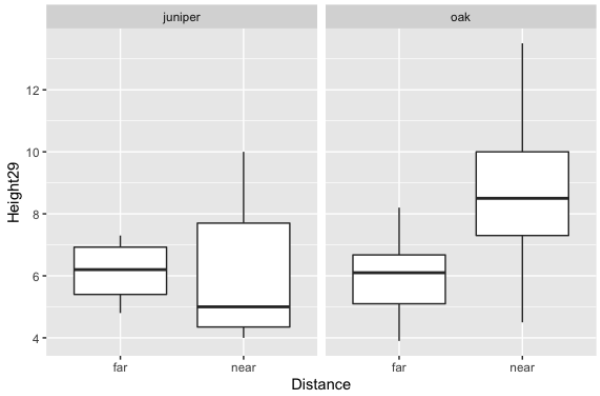


Figure 2. Height in second season

Discussion/Conclusion

This study was hampered to some extent by both small sample sizes due to low emergence in the Juniper Zone, and the complications of setting up distinct treatments in such a mixed woodland with prominent microsite differences, especially in soil moisture. We confirmed our suspicions that granivores absconded with most acorns in the Juniper Zone by excavating two of the plots in which nothing emerged, only to find 1-4 acorns. Small rodents could easily breach the caging we established and may have been more motivated to do so in an area without abundant oak trees. There was obvious evidence of digging in most of the plots away from oak trees.

The preliminary results of this study indicate that access to EM networks proximate to mature oak trees may impact growth, however biotic and abiotic influences are inextricable in this context. Of all differences between treatments, the greatest was in soil moisture, which was higher in the Oak Zone and highest in the Near Oak treatment plots. More access to water especially during such a severe drought season in 2022, undoubtedly contributed to increased growth and higher photosynthetic rates. It may also be that deeper shade at the base of mature oaks promoted etiolation. However, a correlation between height and EM colonization has been demonstrated in *Quercus ilex* (de Jalón et al, 2020). EM tend to be more concentrated around adult conspecifics compared with AM (Koga et al, 2020) and percent colonization corresponds to soil moisture potential (Querejeta et al 2009), so we can reasonably assume that seedings in the Near Oak treatments were more frequently colonized by EM. We will investigate this further in the microscopy analysis. Because midsize adult junipers were proximate to all treatment plots, it is likely that if there is overlap in fungal partners, all plots would have been within range to access that CMN. In another oak study trying to compare EM and AM hub trees, Dickie et al. 2002 situated AM plots at least nine meters from any EM vegetation. We did not achieve that degree of spacing for conspecifics, and even less so for junipers.

Interestingly although soil moisture was higher in the oak zone, survivorship was not. Koga et al 2020 demonstrated that Quercus did not succumb to Conspecific Density Dependence induced mortality, however in this study seedlings did seem marginally more affected by pests and disease in the Oak Zone. At least ¾ of all emerged seedlings survived the first year in all treatments; in the second year the already small sample size in Juniper Far dwindled to 5. Because mycorrhizal dependence in oaks has been shown to be inversely correlated to seed size (de Jalón et al, 2020), and larger seeded plants such as oak tend to live on cotyledon reserves in early life stages, it is more likely that any differences in growth and survivorship in the second year are related to mycorrhization.

These numbers are based on data collected from all 20 plots, however not all plots were well-chosen. For instance, one Near Juniper plot was very close to an adult shin oak tree (*Quercus sinuata* var. *breviloba*); another Near Juniper plot was situated under a massive tree with a dead canopy. Probably at least the latter plot should be removed, and analyses rerun for more accurate results. Other limitations included a very small sample size (n = 5) for the Licor data, and only one-time readings for Licor and for soil moisture.

Due to the complications of parsing drivers in a field study, we cannot draw many conclusions about the relationship between mycorrhization and oak seedling development, however it is clear that seedlings near mature conspecifics grew taller than all other treatment groups. Microscopy analysis of a small subsample may give us a rough idea of the prevalence of AM and EM colonization in the different treatments. Future research will further this line of questioning in the simplified context of a greenhouse. By introducing seedlings soil inoculum from similar sites (beneath conspecific, beneath juniper), we hope to determine whether source inoculum affects which partnerships develop, and whether mycorrhization by different partners alters seedling response to drought.

Literature Cited

Allen, M.F., Allen, E.B., Gómez-Pompa, A. (2005). Effects of mycorrhizae and nontarget organisms on restoration of a seasonal forest in Quintana Roo, Mexico: factors limiting tree establishment. *Restoration Ecology,* 13(2): 325-333.

Atala, C., Muñoz-Capponi, E., Pereira, G., Navarrette, E., Oses, R., and Molina-Montenegro, M. (2012). Impacto de la inoculación con micorrizas y el riego en la sobrevivencia de plántulas de *Pinnus radiata* D. Don sometidas a sequía. *Gayana Bot,* 69(2): 209162-304.

Augé, R.M. (2001). Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza,* 11: 3-42.2004

Augé, R.M. (2004). Arbuscular mycorrhiza and soil/plant water relations. *Canadian Journal of Soil Science,* 84:373-381.

Augé, R.M., Toler, H.D., and Saxton, A.M. (2016). Mycorrhizal stimulation of leaf gas exchange in relation to root colonization, shoot size, leaf phosphorus and nitrogen: a quantitative analysis of the literature using meta-regression. *Frontiers in Plant Science,* 7:1084.

Bárzana, G., Aroca, R., Bienert, G.P., Chaumont, F., and Ruiz-Lozano, J.M. (2014). New insights into the regulation of aquaporins by the arbuscular mycorrhizal symbiosis in maize plants under drought stress and possible implications for plant performance. *Molecular Plant-Microbe Interactions,* 27(4):349-363.

Beiler, K., Simard, S., Durall, D., and Heijden, M. (2015). Topology of tree-mycorrhizal fungus interaction networks in xeric and mesic Douglas-fir forests. *Journal of Ecology* 103(3):616-623.

Bennett JA, Maherali H, Reinhart KO, Lekberg Y, Hard MM, Klironomos J (2017). Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. Science 355:181-184.

Bitterlich, M., Sandmann, M., and Graefe, J. (2018). Arbuscular mycorrhiza alleviates restrictions to substrate water flow and delays transpiration limitation to stronger drought in tomato. *Frontiers in Plant Science,* 9:154.

Brundrett, M.C., and Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist,* 220:1108-1115.

Davidson, B.E., Novak, S.J., and Serpe, M.D. (2016). Consequences of inoculation with native arbuscular mycorrhizal fungi for root colonization and survival of *Artemisia tridentata* ssp. *wyomingensis* seedlings after transplanting. *Mycorrhiza,* 26:595-608.

de Jalón, LG, Limousin J-m, Richard, F, Gessler, A, Peter, M, Hattenschwiler, S, and Milcu, A. (2020). Microhabitat and ectomycorrhizal effects on the establishment, growth, and survival of *Quercus ilex* L. seedlings under drought. *PLoS ONE,* 15(6)

Dickie, I.A., Koide, R.T., and Steiner, K.C. (2002). Influences of established trees on mycorrhizas, nutrition, and growth of *Quercus rubra* seedlings. *Ecological Monographs,* 72(4):505-521.

Egerton-Warburton, L.M., Graham, R.C., and Hubbert, K.R. (2003). Spatial variability in mycorrhizal hyphae and nutrient and water availability in a soil-weathered bedrock profile. *Plant Soil,* 249:331-342.

Fodor, E. (2013). Linking biodiversity to mutualistic networks – woody species and ectomycorrhizal fungi. *Annals of Forest Research* 56(1): 53-78.

Fowler, NL and Russell FL (2004). Effects of white-tailed deer on the population dynamcis of acorns, seedlings and small saplings of *Quercus buckleyi. Plant Ecology* 173(1):59-72.

He, F., Zhang, H., and Tang, M. (2016). Aquaporin gene expression and physiological responses of *Robina pseudoacacia* L. to the mycorrhizal fungus *Rhizophagus irregularis* and drought stress. *Mycorrhiza,* 26:311-323.

Hoeksema, J.D., Chaudhary, V.B., Gehring, C.A., Johnson, N.C., Karst, J., Koide, R.T., Pringle, A., Zabinski, C., Bever, J.D., Moore, J.C., Wilson, G.W.T, Klironomos, J.N., and Umbanhowar, J. (2010). A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters,* 13:394-407.

Koga, W., Suzuki, A., Masaka, K., and Seiwa, K. (2020). Conspecific distance-dependent seedling performance, and replacement of conspecific seedlings by heterospecifics in five hardwood, temperate forest species. *Oecologia,* 193(4):937.

Koziol, L., Bauer, J.T., Duell, E.B., Hickman, K., House, G.L., Schultz, P.A., Tipton, A.G., Wilson, G.W.T., Bever, J.D. (2022). Manipulating plant microbiomes in the field: Native mycorrhizae advance plant succession and improve native plant restoration. *Journal of Applied Ecology,* 59:1976-1985.

Lehto, T. and Zwiazek, J.J. (2011). Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza,* 21:71-90.

Li, Y., Zhang, T., Zhou, Y., Zou, X., Yin, Y., Li, H., Liu, L., and Zhang, S. (2021). Ectomycorrhizal symbioses increase soil calcium availability and water use efficiency of *Quercus acutissima* seedings under drought stress. *European Journal of Forest Research,* 140(5):1039-1048.

Liang, M., Johnson, D., Burslem, D.F.R.P., Yu, S., Fang, M., Taylor, J.D., Taylor, A.F.S., Helgason, T., and Liu, X. (2020). Soil fungal networks maintain local dominance of ectomycorrhizal trees. *Nature Communications* 11(2636).

Marulanda, A., Azcón, R., and Ruiz-Lozano, J.M. (2003). Contribution of six arbuscular mycorrhizal fungal isolates to water uptake by *Lactuca sativa* plants under drought stress. *Physiologia Plantarum,* 119(4):526-533.

O'Donnell, L., Pickles, B.J., Campbell, C.M., Moulton, L.L., Hauwert, N.M., Gorzelak, M.A. (2020). Native tree and shrub canopy facilitates oak seedling regeneration in semiarid woodland. *Ecosphere,* 11(2).

Ouledali, S., Ennajeh, M., Ferrandino, A., Khemira H., Schubert, A., and Secchi, F. (2019). Influence of arbuscular mycorrhizal fungi inoculation on the control of stomata functioning by abscisic acid (ABA) in drought-stressed olive plants. *South African Journal of Botany,* 121:152-158.

Pereira, S., Santos, M., Leal, I., Tabarelli, M., Santos, M.G. (2021). Arbuscular mycorrhizal inoculation increases drought tolerance and survival of *Cenostigma microphyllum* seedlings in a seasonally dry tropical forest. *Forest Ecology and Management,* 492:119213.

Porcel R. and Ruiz-Lozano, J.M. (2004). Arbuscular mycorrhizal influence on leaf water potential, solute accumulation, and oxidative stress in soybean plants subjected to drought stress. *Journal of Experimental Botany,* 55(403):1743-1750.

Püschel, D., Bitterlich, M., Rydlová, J., and Jansa, J. (2021). Drought accentuates the role of mycorrhiza in phosphorus uptake. *Soil Biology and Biochemistry, 157:108243.*

Querejeta, J.I., Egerton-Warburton, L.M, and Allen, M.F. (2009). Topographic position modulates the mycorrhizal response of oak trees to interannual rainfall variability. *Ecology*, 90(3):649-662.

Raven, J.A., and Andrews, M. (2010). Evolution of tree nutrition. *Tree physiology,* 30(9):1050:1071.

Santander, C., Aroca, R., Ruiz-Lozano, J.M., Olave, J., Cartes, P., Borie, F., and Cornejo, P. (2017). Arbuscular mycorrhiza effects on plant performance under osmotic stress. *Mycorrhiza,* 27: 639-657.

Simard, S.W. (2009). The foundational role of mycorrhizal networks in self-organization of interior Douglas-fir forests. *Forest Ecology and Management*, 258 Supplement:S95-S107.

Southworth, D., He, X.H., Swensosn, W., Bledsoe, C.S., Horwath, W.R. (2005). Application of network theory to potential mycorrhizal networks. *Mycorrhiza*,15(8):589-595.

Tatsumi, C., Taniguchi, T., Hyodo, F., Du, S., Yamanaka, N., Tateno, R. (2021). Survival Rate, Chemical and Microbial Properties of Oak Seedlings Planted with or without Oak Forest Soils in a Black Locust Forest of a Dryland. *Forests, 12*:669.

Teste, F.P., Jones, M.D., Dickie, I.A. (2019). Dual-mycorrhizal plants: their ecology and relevance. *New Phytologist,* 225: 1835-1851.

Toju, H., Tanabe, A.S., and Sato, H. (2018). Network hubs in root-associated fungal metacommunities. *Microbiome,* 6:116.

Wipf, D., Krajinski, F., van Tuinen, D., Recorbet, G., and Courty, P-E. (2019). Trading on the arbuscular mycorrhiza market: from arbuscules to common mycorrhizal networks. *New Phytologist,* 223(3):1127-1142.