

RESEARCH ARTICLE

Familiar soil conditions help *Pinus ponderosa* seedlings cope with warming and drying climate

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Changes in temperature and moisture as a result of climate forcing can impact performance of planted trees. Tree performance may also be sensitive to new soil conditions, for example, brought about by seeds germinating in soils different from those colonized by ancestral populations. Such “edaphic constraint” may occur with natural migration or human-assisted movement. *Pinus ponderosa* seedlings, sourced from one location (“home” site), were grown across a field environmental gradient in either their original home soil or in soils from two different “away” sites. Seedlings were inoculated with site-specific soil organisms by germinating seeds in living soil. After 6 months, the inoculated seedlings were transplanted into sterilized soils from the home or away sites. This experimental design allowed us to uncouple the importance of abiotic and biotic soil properties and test (1) how biotic and abiotic soil properties interact with climate to influence plant growth and stress tolerance, and (2) the role of soil biota in facilitating growth in novel environments. Seedlings grew least in hotter and drier away sites with away soil biota. Home soil biota ameliorated negative impacts on growth of hotter and drier away sites. Measurements of photosynthetic rate, stomatal conductance, and chlorophyll fluorescence (Fv/Fm) suggest that edaphic constraint reduced growth by increasing tree water stress. Results suggest that success of *Ponderosa pine* plantings into warming environments will be enhanced by pre-inoculation with native soil biota of the seed source.

Key words: bio-inoculant, conifer, edaphic constraint, mycorrhizal fungi, simulated climate change, stomatal conductance, water stress

Implications for Practice

- *Pinus ponderosa* seedlings grown with soil biota from their site of origin grew more during simulated warming and drying than seedlings grown with unfamiliar soil biotic communities.
- This “sympatric advantage” is likely linked to reduced water stress.
- Preinoculation of nursery-grown seedlings with sympatric soil biota should be considered in plantings to improve establishment.
- Exposure of seedlings to soils with abiotic characteristics distinct from the seed source—edaphic mismatch—may diminish seedling performance.
- Practitioners may benefit from reducing edaphic mismatch experienced by seedlings, by taking soils into account when planting.

Introduction

Tree populations are experiencing widespread mortality as a result of climate change, drought, and heightened pressure by native and non-native pathogens and insects (Adams et al. 2009; Breshears et al. 2009; Allen et al. 2010; Anderegg et al. 2012b, 2012c, 2015). Trees have a variety of physiological and adaptive strategies for coping with novel environments that are emerging due to climate forcing. Some of these strategies

occur over many generations and result in the evolution of traits such as the ability to regulate stomatal conductance to maintain water status, known as isohydry (McDowell et al. 2008). The ability to regulate stomata may result in the immediate survival of a short-term drought because it allows plants to conserve water during a drought event; however, by also reducing photosynthetic rate this response may also result in reduced growth or possibly carbon starvation in extreme cases, and may not be beneficial during long-term drought or prolonged warming-drying trends (McDowell et al. 2008; Adams et al. 2009; Breshears et al. 2009).

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Because tree populations can migrate via seed dispersal, or intentional movement of nursery stock and seed by humans, they can also be said to experience edaphic constraint in addition to climate forcing when they must grow in soil conditions different (away) from those of the seed source (home). Both abiotic and biotic characteristics of soils influence tree growth and physiological processes (Bowker et al. 2012; Laliberté et al. 2013; Laliberté 2016; Bjorkman et al. 2017). Soils vary in composition of mineral nutrients with nutrient-rich soils generally facilitating higher photosynthetic rates and greater plant growth (Bailey et al. 2004; Pasquini & Santiago 2012). In addition, soil texture may also have a strong influence on plant growth and physiological processes by influencing water availability and root morphology (Pregitzer et al. 2010; Bowker et al. 2012; Looney et al. 2012; Smith et al. 2012). Thus, trees living in different soil environments may respond differently to an environmental change, such as drought, with soil properties either mitigating or exacerbating the effects of drought (Bowker et al. 2012).

Soil biota may contribute positively or negatively to plant performance and are highly responsive to variation in soil characteristics (Näsholm et al. 2013; Pizano et al. 2014). Soil biota include a complex suite of microorganisms including pathogens, saprotrophs, and mutualists such as mycorrhizal fungi. The accumulation of species-specific pathogens in soil can hinder plant growth, whereas specific species of ectomycorrhizal fungi can increase drought resistance (Mangan et al. 2010a, 2010b; Rúa et al. 2016; Gehring et al. 2017). Fungal symbionts may even facilitate widespread biological invasions of the genus *Pinus* in what is known as coinvasion (Dickie et al. 2010, 2017). These diverse examples of the influence of soil biota on plant growth are likely dependent on the environmental context (David et al. 2018). David et al. (2018) coined the idea that in stressful, resource-poor environments microbes may mitigate the effect of stressful environments, while in benign, resource-rich environments they may exacerbate stress (the microbial mitigation–exacerbation hypothesis). This complements well-supported ideas that facilitative plant–plant interactions are more common in stressful environments and competitive plant–plant interactions tend to dominate benign environments (the stress gradient hypothesis) (Callaway & Aschehoug 2000; Revillini et al. 2016; van der Putten et al. 2016; Lekberg et al. 2018). Many studies have suggested that plant–microbe relationships are more beneficial when they are comprised of potentially coadapted plant hosts and soil biota community that have shared an evolutionary environment (home pairings), as opposed to recently assembled plant–microbial consortia (away pairings) (the sympatric advantage hypothesis; Hoeksema 2010; Hoeksema et al. 2010, 2018; Johnson et al. 2010, 2013; Peters et al. 2013; van der Heijden et al. 2015).

To test how tree growth and physiological processes respond to changes in climate, soil, and soil biota, we designed a field experiment in northern Arizona using the Southwest Experimental Garden Array (SEGA, <https://sega.nau.edu/home>). We grew *Pinus ponderosa* from seeds collected at a home site near Flagstaff, Arizona, and out-planted them to two “away” sites:

one warmer and drier than the home site, and another cooler and wetter. This environmental gradient simulates changes that may be encountered by establishing trees as a result of global change or plant migration (including restoration plantings and migration assisted by humans), while also creating a natural gradient to examine how physiology changes across an environmental gradient. We grew trees in either home or away soil to better understand how soil influences plant growth. To test how soil biota influences plant growth, prior to transplant, we inoculated treatments with either a home or away soil biotic community. We tested the following nonmutually exclusive hypotheses:

- (1) *Local preference*: Local preference suggests that plant growth will be highest at the home site. We also expected net photosynthetic rates to be highest at home, and greater plant growth at away sites when plants are grown in their home edaphic conditions.
- (2) *Coadapted microbial mitigation*: Our predictions follow from synthesizing the microbial mitigation–exacerbation hypothesis and the sympatric advantage hypothesis. We predicted that coadapted home soil microbes would be more beneficial for trees than away soil microbes at the warm dry site (more stressful) and thus ameliorate stress induced by warming. At the cooler-wetter site (less stressful), we predict that home microbes would be less important to plant growth relative to away-soil microbes.

Evaluation of these hypotheses will bolster understanding of how trees will respond to warming environments, and exposure to other climatic and edaphic novelties as a result of migration. This information will help inform tree planting projects in silviculture, assisted migration, and ecological restoration in an increasingly warmer world.

Methods

Plant and Soil Source Sites

We conducted our study using Northern Arizona University’s Southwest Experimental Garden Array (SEGA), which is a collection of experimental sites situated on a climate gradient spanning 4°C in long-term air temperature records. Seeds were collected from 10 mature trees at the home site in August of 2013. Pole pruners were used to clip cones that were then air dried and seeds were extracted and stored at –4°C. Seeds used in this study came from the same maternal tree and thus are the most genetically similar offspring possible. Soil was collected in the summer of 2014 from the same home site plus two additional away sites, creating a total of three sites. Table 1 provides detailed information about each site.

Preparation of Experimental Units

We focused on one natal population of *P. ponderosa* from the Arboretum SEGA site (ARB), and used the ARB as the home out-planting site, White Pockets Canyon (WPC) as a warm/dry out-planting site, and Bear Springs (BS) as a cool/moist out-

Table 1. Site characteristics for each study site. Precipitation and climate data are derived from 1981 to 2010 averages from PRISM (PRISM Climate Group, Oregon State University). Soil characteristics are derived from on site NRCS soil surveys (Soil Survey Staff, Natural Resources Conservation Service, U.S. Department of Agriculture).

	BS	ARB	WPC
Latitude	36.37	35.16	36.11
Longitude	-112.18	-111.73	-112.41
Precipitation (mm)	773	556	443
Average mean temp (°C)	5.6	7.9	9.5
Dominant tree species	<i>Pseudotsuga menziesii</i> , <i>Pinus ponderosa</i> , <i>Abies concolor</i>	<i>Pinus Ponderosa</i>	<i>Pinus edulis</i> , <i>Juniperus osteosperma</i>
Soil taxonomy (suborder)	Ustalfs	Ustolls	Agrids
Soil texture	Loam to clay loam	Sandy clay loam	Gravelly loam to cobbly loam
Soil pH	7.6	7.2	8.0
Soil parent material	Kaibab Limestone	Basalt	Kaibab Limestone

planting site. To prepare our experimental units, we first made soil collections in the summer of 2014. Inoculum soil was collected from all sites by picking a random starting point and collecting soil every five meters for 90 m in each cardinal direction. We collected inoculum soil from the rhizosphere of target trees and later homogenized it. We justify homogenizing inoculum because we were interested in seedling responses to average soil conditions across three sites, rather than within a single site or extrapolating to a broader geography than our sampling sites (a “type C” design; Gundale et al. 2017, 2019). Target plants were *P. ponderosa* at the home site and overstory dominant trees (Table 1), including but not limited to *P. ponderosa*, at away sites. This soil was stored refrigerated until it could be used within 60 days. To inoculate seedlings with soil biotic communities, we placed four *P. ponderosa* seeds from the home population into Steuwe & Sons RL200 containers filled with 50 mL live soil inoculum, filling the containers to just below the rim, collected from each site, creating one home treatment that represents trees from the ARB grown with soil biota from the ARB and two different away treatment combinations, one with soil biota from BS and one with soil biota from WPC. As seeds germinated, they were thinned to one seedling per container, always keeping the largest seedling.

Seedlings were grown in the NAU Research Greenhouse until roots occupied most of the container or about 6 months, at which

point the seedlings were transplanted into Steuwe & Sons TP1124R tree pots filled with 30 L of sterilized background soil. Background soil was previously collected from each site by locating patches of unvegetated soil and digging up to 1.5 m deep to collect bulk soil away from the rhizosphere of living plants. Soil was then homogenized by mixing soil with shovels into one well-mixed pile per site. Prior to use, this background soil was steam sterilized at 125°C for 24 hours twice. In transplanting containers into tree pots, we were able to create custom treatments of the soil biota and soil. We created nine combinations varying in degree of environmental novelty for the ARB-sourced plants: plants inoculated with home soil biota in home, away (WPC), or away (BS) soil, plants inoculated with away (WPC) soil biota in either home or away (WPC) soil, and plants inoculated with away (BS) soil biota in either home (BS) or away (BS) soil (Table 2). We then grew trees in the greenhouse in the large pots for an additional 4 months. This gave time for trees to establish roots into the background soil and proliferate with the inoculated soil biota, before exposure to additional soil organism colonizers in the field. Plants were hardened outside under a shade cloth for an additional month before transplanting to the field sites.

Field Planting

To simulate climate change, we out-planted experimental units to the field by excavating planting holes and inserting the plants, still in pots, into the holes so that the soil levels inside and outside of pots were similar. We retained the pots as a method to maximize exposure to the manipulated abiotic and biotic soil environments and decrease and delay influences from the surrounding soil. The 30 L volume and 61 cm depth of our pots was adequate to accommodate seedling growth in initial growing seasons, simulating the crucial establishment phase. Plants were planted in the large pots in the greenhouse in February of 2015 and then planted at field sites in May of 2015.

As an “all home” frame of reference, we out-planted a set of experimental units with ARB soil biota and ARB soil back into the ARB site. The rest of the plants were planted into sites that are approximately 3°C (WPC) warmer, or 2°C (BS) cooler than

Table 2. Treatment combinations in relation to ARB sourced plants. A, away; H, home.

Background Soil	Inoculum	Out-planting Site
ARB (H)	ARB (H)	ARB
ARB (H)	ARB (H)	BS
ARB (H)	ARB (H)	WPC
ARB (H)	BS (A)	BS
ARB (H)	WPC(A)	WPC
BS (A)	ARB (H)	BS
BS (A)	BS (A)	BS
WPC (A)	WPC (A)	WPC
WPC (A)	ARB (H)	WPC

the ARB home site. BS was planted with experimental units featuring all four combinations of BS and ARB soil and soil biota. Likewise, WPC was planted with experimental units featuring all four combinations of WPC and ARB soil and soil biota. The full design creates situations where ARB plants are exposed to a new climate, either warmer-drier or cooler-wetter, while varying the novelty of the soil and soil biota. Each treatment combination had 10 replicates creating a total of 90 experimental units, including the 10 reference units at ARB. Climate data was recorded using the SEGA weather instrumentation at the site level. Climate data for this study do not exist at individual experimental units and thus climate metrics are only used to assess how effective the environmental gradient was in simulating warming and cooling and to make general observations about weather patterns during the duration of the experiment. Climate was not used as a predictor to plant responses due to the lack of experimental unit level information and thus the categorical predictor of “site” was used as a representative variable for climate manipulations.

Plant Performance

We measured plant height, diameter at root collar, and the number of branches on all trees three times, in spring, summer, and fall. This allowed us to estimate biomass with allometric equations. We destructively harvested seedlings grown in the Arboretum Research Greenhouse adjacent to our field site to construct allometric equations based on field measurements of root collar diameter, number of branches, tree height, and canopy diameter. We used a multiple linear regression to fit an allometric equation to estimate biomass.

To ensure that measurements could be taken on the same day, we conducted physiological measurements on only a subset of trees, focusing on expected maximal contrasts: plants growing with both home soil and soil biota at all sites including the home site, and plants growing with both away soil and soil biota at each of the away sites. We used an Integrated Fluorometer (ADC BioScientific Ltd., Hoddesdon, United Kingdom) to measure stomatal conductance, net photosynthetic rate, and fluorescence ratios (Fv/Fm) of dark-adapted leaves. Stomatal conductance and net photosynthetic rate were measured along light response curves. These datasets were collected on 10 trees for each treatment combination and on four leaf sets for each tree (two sun leaves near the meristem and two shade leaves on the lowest branches). These data were collected during the summer monsoon season of 2016 at approximately noon, repeated with multiple PAR values ranging from 0 to 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at a CO_2 level of 400 ppm, temperature of 25°C, and relative humidity of 30%.

Statistical Analysis

To compare the effects of climate, soil, and soil biota on seedling allometric biomass, we calculated Cohen’s *d* effect sizes and 95% confidence intervals (Hedges & Olkin 1985). These effect sizes and associated confidence intervals provide alternative inference than the traditional *p* values associated with ANOVA

in that a confidence interval that overlaps 0 is considered a non-significant effect and a confidence interval that does not overlap 0 is considered a significant effect (Rhea 2004; Lee 2016). Seedlings that were grown at ARB with home soil and home soil biota was considered group one and compared to each other group, thus making a positive effect size represent seedlings that are bigger than those grown at the arboretum and a negative effect size would represent plants that are smaller. This method was chosen because our study does not have a full factorial design, in that the home site lacks all possible treatment combinations. The more common two-way ANOVA approach would have necessitated removing the home site from our analysis, thus we preferred the use of Cohen’s *d* and 95% confidence intervals so that all treatment groups could be included. We also used Cohen’s *d* effect size to compare Fv/Fm ratios for the same reason.

We used repeated measure ANOVAs to compare photosynthetic rates and stomatal conductance values. Repeated measure ANOVAs were used to understand the categorical effect of soil biota, soil, and site on tree responses rather than the continuous effect of photosynthetic active radiation (PAR) on the response variable. PAR was analyzed as the repeated measure so each individual PAR value was compared for categorical predictors of soil, soil biota, and site (Meredith & Stehman 1991). Analysis was conducted in R (R Core Team 2014) and figures were produced using the package *ggplot2* (Wickham 2009).

Results

Climate Data

During the time period of this study, BS was approximately 2.3°C cooler than the Arboretum. White Pockets was 3°C warmer than the Arboretum. All three sites received slightly below the 1981–2010 average precipitation (Fig. 1)

Tree Growth

We were able to successfully build allometric biomass equations using multiple linear regression models based on our destructive harvest ($F = 81.67$), $p = 0.0001$, $r^2 = 0.9167$). Canopy diameter was not a useful predictor for seedling biomass in these measurements and is thus not included in our model. The best fitting allometric model is written below where *B* is the aboveground biomass, *h* is the height, *d* is the diameter at root collar, and *b* is the number of branches. In this allometric model, –151.38 is the y intercept, and 1.97, 4.5221, and 2.90 are slopes.

$$B = -151.38 + 1.97h + 4.5221d + 2.90b.$$

Quadratic formulas and other variants of linear models with more or less terms were also fit, however, the model with the highest r^2 was used to model biomass for this article. Using a linear model as opposed to quadratic models has been supported for seedlings and parameters for other tree seedling species and was the most appropriate choice given our data (Kebede & Soromessa 2018).

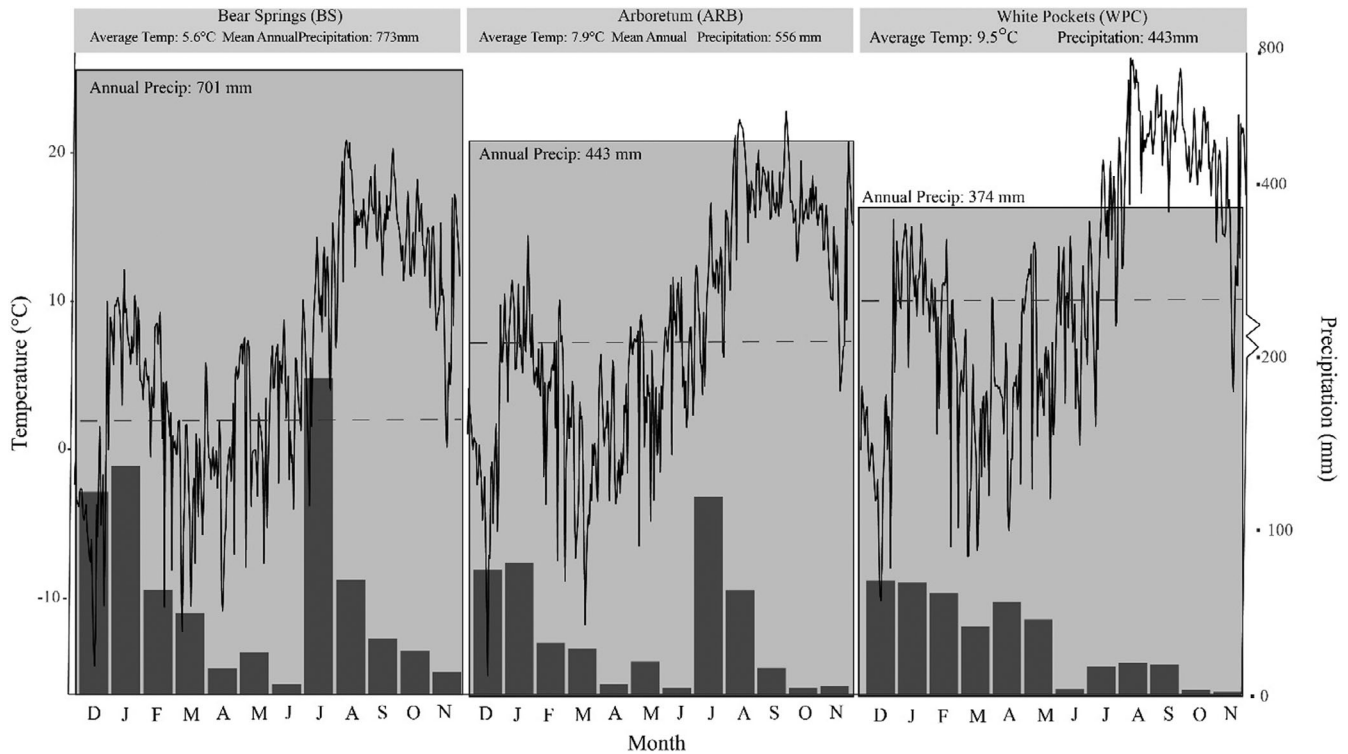


Figure 1. Daily temperature in degrees centigrade (line and points) and monthly precipitation in mm (dark gray bars) as well as total annual precipitation (light gray bars) observed for the months prior to planting and following planting. Red dashed line represents the observed average annual temperature. PRISM 30 year averages are printed at the top of each facet for comparison. Data are only presented for a time period in which we have a complete data record for all sites. Data are summarized in the facet of each graph. Horizontal dashed line represents 0° centigrade, vertical dashed line represents the date trees were planted at the field sites.

In May, the spring after planting, there were no differences in tree biomass across sites, or inoculum sources. By July, there were no differences among treatments at the cooler-wetter BS site, and between BS and the Arboretum (Fig. 2). However, at the warmer-drier White Pockets site, plants grown in home soil and inoculated with their home soil biota were 150% larger than plants grown in soil and inoculum from the Arboretum ($F = 5.8$, $p = 0.001$). This pattern is perpetuated in the September sampling with all plants about 20% larger than they were in July (Fig. 2; $F = 2.8$, $p = 0.04$).

Aboveground tree biomass after 1 year was influenced by site in that BS differed from the Arboretum ($d = -0.83$, $\text{min} = -1.57$, $\text{max} = -0.13$); however, plants at White Pockets did not differ overall from those at Arboretum ($d = -0.24$, $\text{min} = -0.90$, $\text{max} = 0.42$). Soil source was more influential. At BS there was a negative effect of the home soil ($d = -0.86$, $\text{min} = -2.03$, $\text{max} = -0.65$) and a neutral effect of away soil ($d = -0.05$, $\text{min} = -1.1$, $\text{max} = 1.7$). At White Pockets there was a negative effect of away soil ($d = -3.63$, $\text{min} = -4.38$, $\text{max} = -2.94$) and a neutral effect of home soil ($d = 0.28$, $\text{min} = -1.1$, $\text{max} = 1.24$). At BS there was a negative effect of away soil biota ($d = -1.26$, $\text{min} = -2.1$, $\text{max} = -0.76$). At White Pockets there was a negative effect of away soil biota ($d = -1.38$, $\text{min} = -2.1$, $\text{max} = -0.71$) and a positive effect of home soil biota ($d = 1.73$, $\text{min} = 0.56$, $\text{max} = 2.7$). The various combinations of home and away soils and soil biota produced different results at BS and

White Pockets, indicative of a site \times soil \times soil biota interaction. At BS, plants grown with away inoculum but in home soil were 50% smaller than any other treatment combination, suggesting an interaction effect between away inoculum and home soil, and site ($d = -4.5$, $\text{min} = 7.6$, $\text{max} = -1.8$). At White Pockets plants grown with home soil and home soil biota were 10% larger than plants grown at the Arboretum, and plants grown with both away soil and away inoculum (originating from White Pockets) were 100% smaller than all other treatments (Fig. 3; $d = -3.4$, $\text{min} = -5.05$, $\text{max} = -2.4$; $d = 0.8$, $\text{min} = 0.23$, $\text{max} = 1.4$).

Physiology

Similar photosynthetic rates occurred at all sites in the all home treatments, but away soils and inoculum affected photosynthetic rate at the warmer and cooler sites (Fig. 4). At the warm-dry White Pockets site there was a significant difference in light saturation point and net photosynthetic rate at any light level greater than $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ with home soils and soil biota combinations having 40% greater net photosynthetic rates than away soils and soil biota ($F = 24.6$, $p < 0.001$). Home treatment combinations also had 20% higher dark respiration rates ($F = 8.76$, $p = 0.002$). At the cool-wet BS site there was no statistical difference in photosynthetic rate at any light level among soil treatments (Fig. 4).

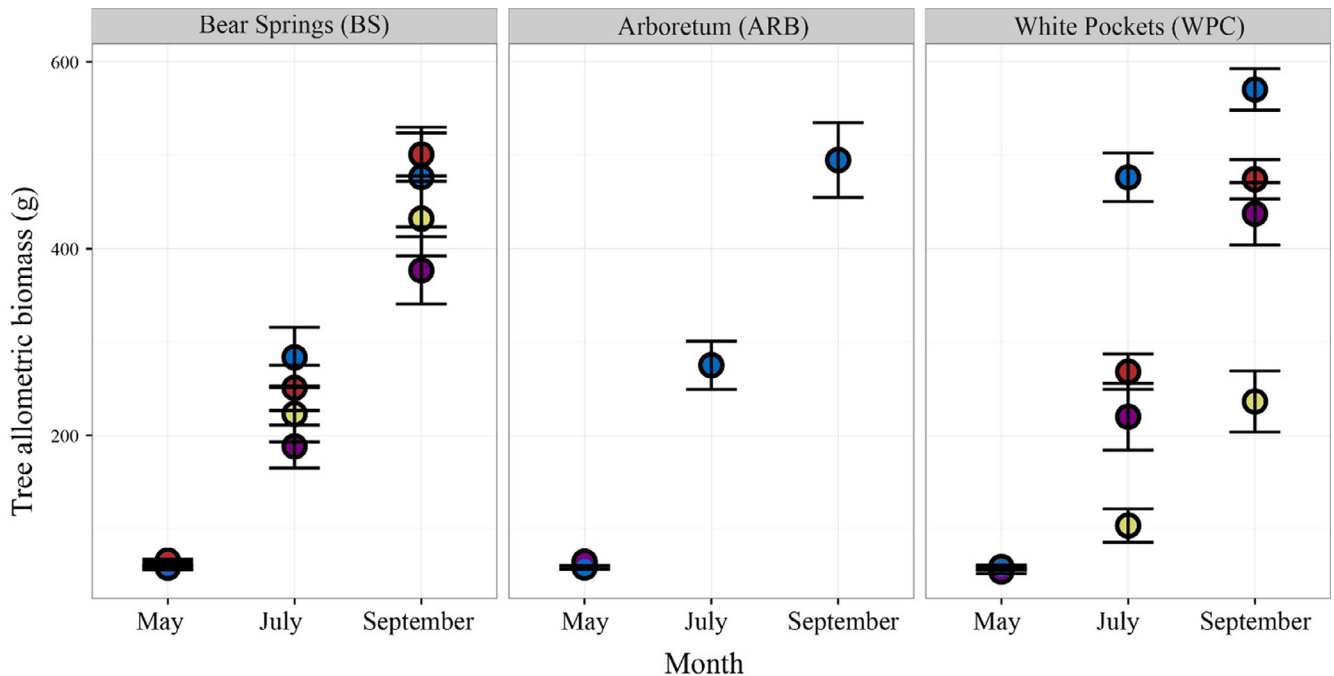


Figure 2. Aboveground allometric tree biomass for *Pinus ponderosa* for each sampling period in the field. Colors refer to the provenance of the soil and inoculum relative to the out-planting sites. Yellow dots represent plants grown in away soil and away inoculum, purple represent home soil, away inoculum, red represents away soil, home inoculum and blue represents home soil and home inoculum. Error bars are \pm SE.

Stomatal conductance was similarly influenced by soil treatments under contrasting warming and cooling scenarios (Fig. 5). At the warm-dry White Pockets site, stomatal conductance was up to 100% higher for the home soil and inoculum treatment at light levels less than $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ and more than $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$, compared to away soil and inoculum ($F = 18.4$, $p < 0.001$). It is also notable that at White Pockets, home soil and inoculum exhibited stomatal conductance values 10% higher than those at the Arboretum ($F = 3.4$, $p = 0.01$). In contrast, the away soil and inoculum treatment had stomatal conductance well below that of the home site ($F = 12.6$, $p < 0.001$). Stomatal conductance in home and away soil and inoculum treatments was nearly identical at the cool-wet site ($F = 0.48$, $p = 0.54$). Lastly, Fv/Fm ratios at the White Pockets site were 20% lower than at the Arboretum ($d = -0.28$, $\text{min} = -0.46$, $\text{max} = -0.10$) (Fig. 6). But Fv/Fm ratios at BS did not differ from the Arboretum ($d = 0.15$, $\text{min} = -0.08$, $\text{max} = 0.32$). Within both BS and White Pockets, Fv/Fm ratios were about the same regardless of provenance of soils and soil biota.

Discussion

Our study shows a stronger effect of edaphic constraint than climate on growth of planted *P. ponderosa* seedlings. Soil biota was an important influence on growth regardless of climate or soil type. We documented some clear differences in final seedling biomass after 6 months of growth in the nursery and a full growing season in the field, such that under warmer, drier climates, seedlings grew larger with home soil conditions. Soil

conditions were much less influential under wetter, cooler conditions. We demonstrate that in part these differences are likely due to differences in physiological performance and water stress experienced by the seedlings. Importantly, our study documents that edaphic boundaries are important factors in determining growth rate of *P. ponderosa* seedlings and soil biota may effectively mitigate some environmental stress. While our study was conducted at only three study sites and many confounding variables beyond climate and soil may exist, we attempted to control these variables as best as possible by utilizing pots and manipulating soils across the study site. Additionally, all three study sites were in openings, thus limiting influence of canopy cover or adjacent vegetation on our experimental units.

Local Preference

Interestingly, our study documents little evidence of local preference with respect to climate because seedlings grew to approximately the same biomass across all sites along the elevation gradient when averaged across all soil and inoculum treatments. A likely explanation for the lack of local preference observed in our study is the unusual weather patterns experienced during the field portion of our study. Compared to long-term modeled averages, during our study period, all of our sites experienced unusually high temperatures and an unusually wet spring (PRISM Climate Group, Oregon State University). This likely facilitated plant growth at all three sites (Dreesen et al. 2012).

In contrast, our study provides evidence for local preference with respect to soil and soil biota that appears to be modulated

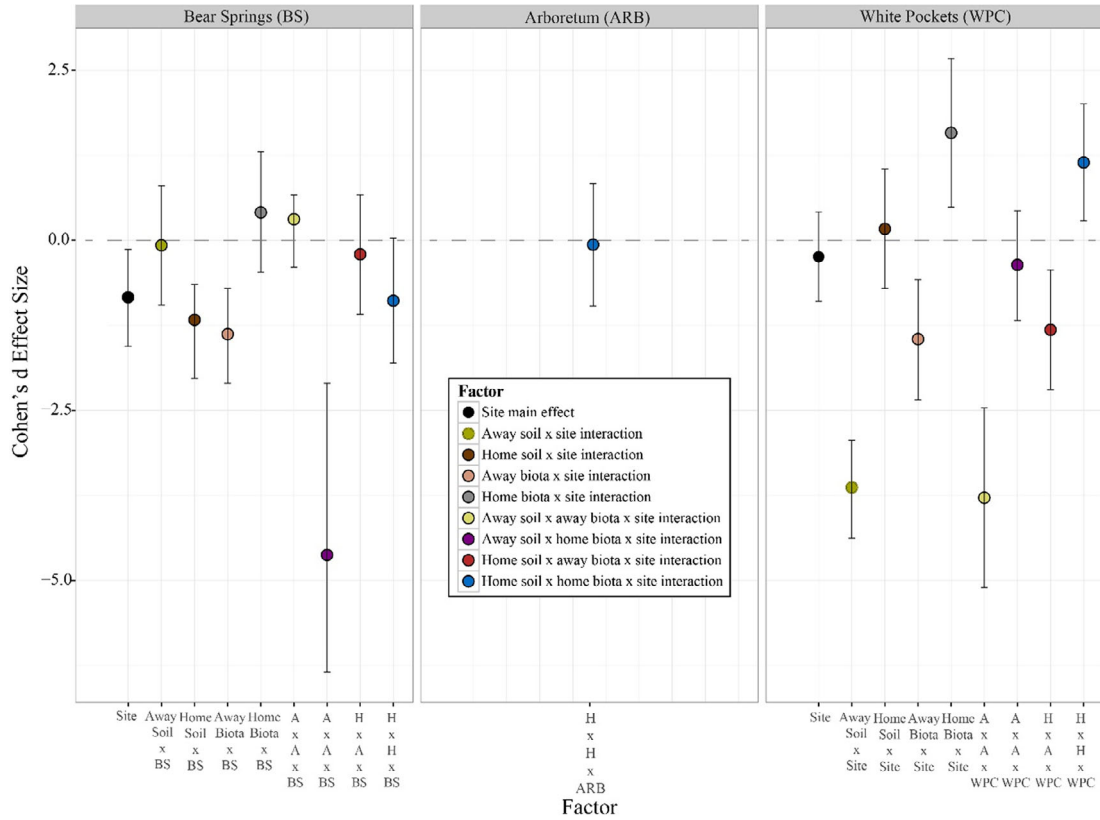


Figure 3. Aboveground allometric biomass represented as Cohen's *d* effect sizes for plants grown at the Arboretum compared to each experimental combination for *Pinus ponderosa* after 1 year of growth in the field. Error bars are the ± 95% CI for the effect size. Factors represent main effect or interaction effects between factors where "x" indicates an interaction between factors. Letter combinations on the X-axis represent the soil source and the soil biota source relative, in that order, where "A" means away and "H" means home. Thus, A x A represents away soil by away soil biota interaction, A x A x BS represents away soil x away soil biota x BS interaction effect.

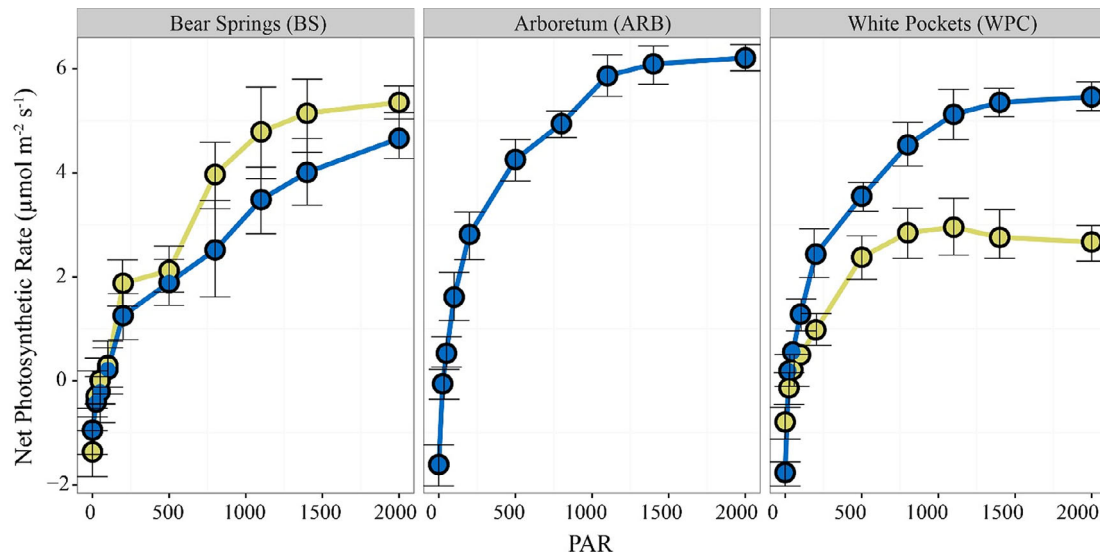


Figure 4. Net photosynthetic rate for *Pinus ponderosa* at varying levels of PAR. Colors refer to the provenance of the soil and inoculum relative to the out-planting sites. Blue dots represent trees grown in their home soil with home inoculum, yellow dots represent trees grown in away soil with away inoculum. Error bars are ± SE.

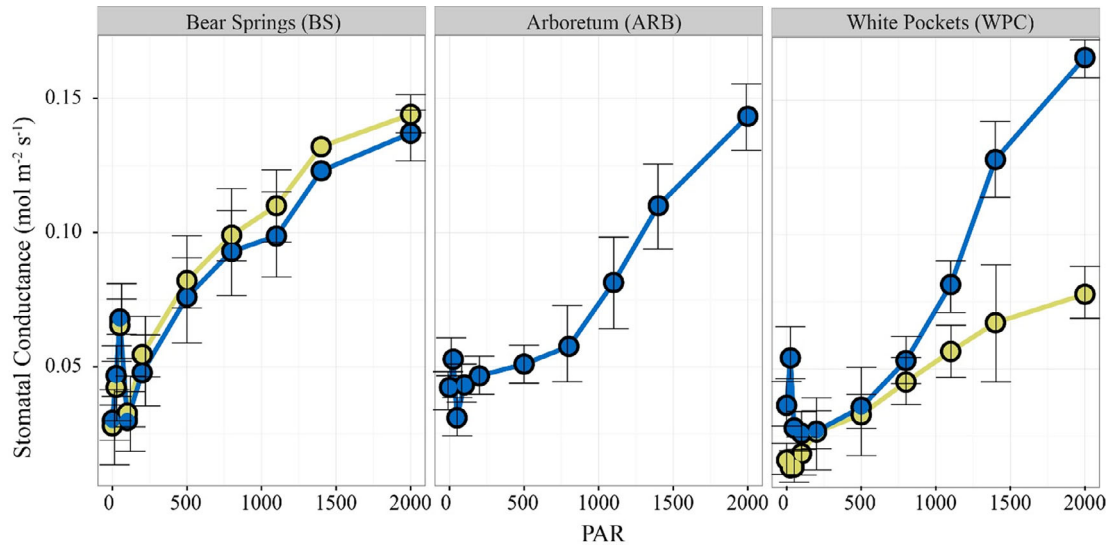


Figure 5. Stomatal conductance for *Pinus ponderosa* at varying levels of PAR ($\text{mol m}^{-2} \text{s}^{-1}$). Colors refer to the provenance of the soil and inoculum relative to the out-planting sites. Blue dots represent trees grown in their home soil with home inoculum, yellow dots represent trees grown in away soil and away inoculum. Error bars are \pm SE.

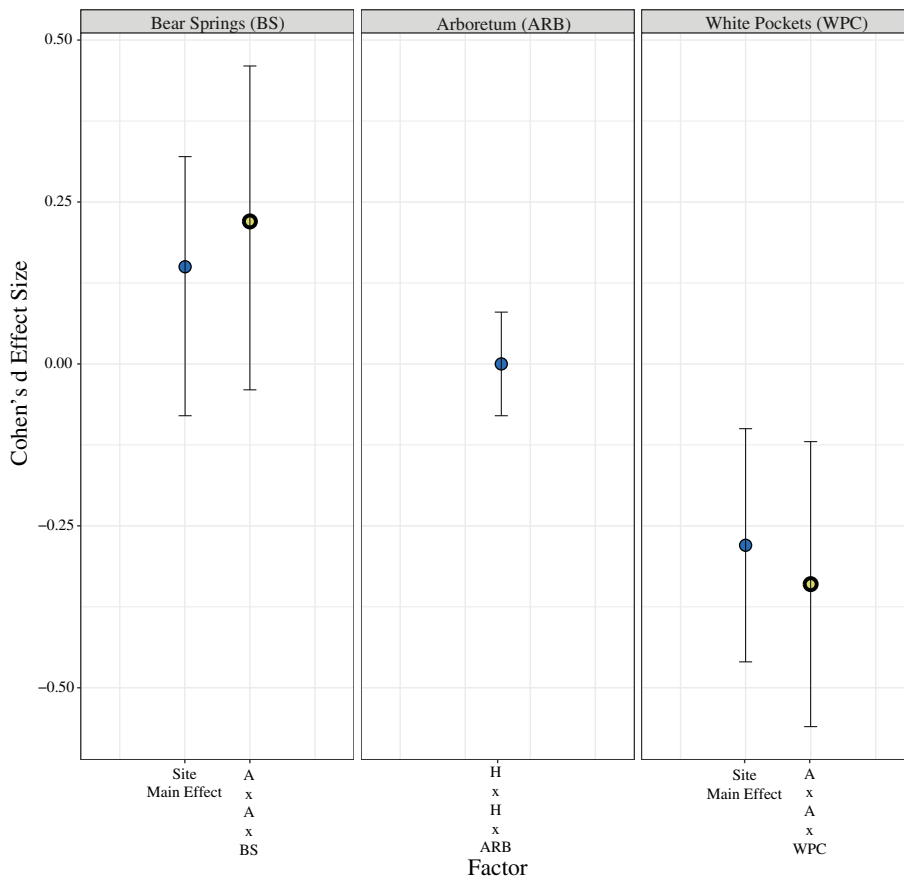


Figure 6. F_v/F_m ratio represented as Cohen's d effect size for *Pinus ponderosa* during the July sampling period. Colors refer to the provenance of the soil and inoculum relative to the out-planting sites. Blue bars represent trees grown in their home soil with home inoculum, yellow dots represent trees grown in away soil and away inoculum. Error bars represent the \pm 95% CI for Cohen's d effect size. $H \times H \times ARB$ = home soil biota and home soil and Arboretum, $A \times A \times BS$ = away soil biota and away soil and BS interaction effect.

by climate. Possibly the best overall indicator of preference for home or away inoculum is the final seedling biomass after the entire growing season. These results indicated better plant performance with either home soil, home inoculum, or both in the warmest site. In contrast, there was no such preference for home soil or inoculum in the coolest site. Local adaptation to soil has been demonstrated before in tree species with soil chemical and physical properties being principal drivers of adaptation (Pregitzer et al. 2010; Bucharova et al. 2017). Interestingly, in our study the home soil type is not the most fertile soil, suggesting that a simple preference for greater fertility is not a complete explanation of the patterns. Possibly, the effect of home soil biota resulted in the greatest plant growth because the combination of individuals from the plant population and the soil biota with which they shared an evolutionary history was the most efficient in gathering soil resources, and the result was heightened mutualistic function (Johnson et al. 2010; Rúa et al. 2016; Bjorkman et al. 2017). These findings demonstrate the importance of soil properties and soil biota in determining local adaptation of a species to a specific geography and environment (Gibson et al. 2016; Bjorkman et al. 2017; Bucharova 2017; Bucharova et al. 2017).

Synthesizing Microbial Mitigation–Exacerbation and the Sympatric Advantage

Why are the positive effects of home soil biota most clearly observed at the warmer-drier site? We must synthesize two hypotheses to develop a new working hypothesis that explains these results. The microbial mitigation–exacerbation hypothesis proposes that in response to a stressor, soil microbes may either mitigate or exacerbate stress. The net effects of soil biota are predicted to shift in the direction of mitigation as stress increases, and in the direction of exacerbation in benign, low-stress sites (David et al. 2018). This prediction is based upon comparing the effect of live soil biota to sterile soils. Possibly, the sympatric advantage hypothesis follows a similar dynamic in that locally adapted soil biota are likely to be more effective in mitigating environmental stresses than novel soil biota, with this difference becoming more pronounced under increasing stress. Our study supports this assertion, *but only with regard* to the home soil biota. Along the SEGA gradient and in the region, suboptimal soil moisture is the most common source of plant stress and mortality (Anderegg et al. 2015; Gitlin et al. 2006). Although water stress may have been somewhat dampened in this wet year, precipitation was clearly lower at White Pockets than at the other sites.

At the wetter end of the environmental gradient, home inoculum did not appear to mitigate stress more than away inoculum, there was neither evidence for a mitigating nor exacerbating one. This suggests that perhaps because the environment was unlikely to be water-limited, that plants growing there were less dependent on mutualisms and beneficial soil microbes. Had our gradient been broader, extending into even more benign climates, we could plausibly have observed microbial exacerbation by home soil biota, but we would posit that in order for this to happen our study system would had to have been richer in

antagonistic interactions (Revillini et al. 2016; van der Putten et al. 2016).

How Might Home Soil Biota Mitigate Stress?

Some work has shown that specific phenotypes of trees are associated with specific groups of ectomycorrhizas which confer resistance to drought stress (Gehring et al. 2017). Other studies have shown that the mutualistic function of such associations is higher in coevolved partnerships, suggesting that microbial mitigation of environmental stress is dependent on intact coevolved partnerships (Johnson et al. 2010; Rúa et al. 2016). While our study did not control for host tree genetics, we only observed microbial mitigation in home partnerships, where seedlings and soil microbes were sourced from the same site, though we cannot determine whether this was the result of microbial community composition as opposed to shared evolutionary history of the plant–microbe relationship, or both. We also demonstrate that the effect of the home soil biota was most effective in home soil, particularly at the warm-dry site suggesting the plant–microbe relationship is perhaps locally adapted to soil type (Rúa et al. 2016). In either case, we do have evidence that superior performance of plants growing with home soil biota is linked to water limitation and its effect on photosynthesis in this isohydric species.

Overall, our physiological data support the interpretation that stomatal closure and lower photosynthetic rates are the result of a reduction in water availability (Frey-Klett et al. 2005; Warren et al. 2008; Lehto & Zwiazek 2011; Goltsev et al. 2012), which may in turn be influenced by soil biota (Warren et al. 2008; Lehto & Zwiazek 2011). At White Pockets, the most water-limited site, plants grown with home soil and soil biota clearly exhibited higher photosynthetic rates than plants grown in away soil and soil biota. Given that Fv/Fm ratios were similar among home and away soil treatments under warmer, drier conditions, differences in photosynthetic rate are unlikely to be explained by light harvesting efficiency in photosystem II. Instead, they mirror differences in stomatal conductance. Because isohydric plants regulate water loss through stomatal conductance, higher stomatal conductance strongly indicates greater relative water availability, which is likely influenced by soil microbial communities. Because restriction in stomatal conductance also restricts gas exchange, we believe this is the key reason why photosynthetic rate was higher in plants grown with home soil and soil biota and lower with away soil and soil biota. Gradients in water availability could be the result of different soil types holding water differently, or ectomycorrhizas could be influencing tree water relations by hydraulic redistribution, albeit only within the confines of our pots (Warren et al. 2008; Lehto & Zwiazek 2011; Bowker et al. 2012). Ectomycorrhizas are well known to redistribute water in the soil profile making it more available in the rhizosphere (Warren et al. 2008; Lehto & Zwiazek 2011). If water limitation was mitigated by home soil biota, trees may have been able to maintain their hydration status under the home soil and soil biota condition with a lesser degree of stomatal closure, and therefore higher photosynthetic rate and ultimately biomass than plants grown under the away soil and soil

biota treatment. We did not measure leaf nitrogen concentration, therefore we cannot rule out that photosynthetic rates were reduced under joint warming and edaphic constraints partially due to lower RuBisCO levels brought about by nitrogen limitation. Because one of the primary outcomes of ectomycorrhizal fungi for plants is greater access to soil nitrogen, this may represent an additional means by which restraining edaphic constraint by pairing plants with the appropriate soil biota or planting plants in similar soil conditions to those in which seeds came from can bolster photosynthesis.

Restoration Implications

These findings have utility for restoration ecology because they suggest that reducing edaphic mismatch may play a critical role in facilitating growth of planted *P. ponderosa*, and plausibly other plants. This can be accomplished by prior inoculation of seedlings with sympatric soil biota from the plant seed source, and potentially by using plant stock in soils similar to those of the plant seed source. Furthermore, our study provides environmental context as to when mitigation of edaphic mismatch should be a priority in restoration. In particular, we demonstrate that locally adapted soils and soil biota were more beneficial to their plant host in warmer, drier environments than cooler, wetter environments. This suggests that minimization of edaphic mismatch is best applied when the current or future environment of the planting site is warmer and/or drier than that experienced by adult reproductive trees at the seed source site when they established. We note that this condition often occurs, even when plant seeds are being locally sourced for local planting, a common practice. Our study does not suggest that minimizing edaphic mismatch is beneficial in assisted migration to cooler and/or wetter environments. In our study system, it is likely that soil water is a major limiting factor of tree establishment, and thus limitation is likely to become stronger as climates warm and dry. In warmer, drier scenarios, we provide physiological evidence linking improved moisture status to familiar soil conditions. Plant moisture status can be influenced either by soil physical characteristics or soil biota, and our results suggest that when water is limiting, reduction of edaphic mismatch might enhance water status in restoration plantings.

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