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Physiology and Community Assembly in Mendocino’s Pygmy Forest

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PHYSIOLOGY AND COMMUNITY ASSEMBLY IN MENDOCINO'S PYGMY FOREST

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by

Katharine L. Cary

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Abstract

Physiology and Community Assembly in Mendocino's Pygmy Forest

Katharine L. Cary

This dissertation examines the effects of nutrient limitation on plant physiology and community assembly through the lens of Mendocino's iconic pygmy forest, a plant community in California, USA, that is severely stunted by acidic, low-nutrient, and high aluminum soils, but that experiences negligible water stress year-round.

Chapter 1 examines physiological mechanisms that lead to stunted growth by comparing 12 leaf functional traits between conspecific plants growing in the pygmy forest and nearby tall conifer forests. Pygmy plants did not have depressed leaf photosynthetic rates, which I had hypothesized were the mechanism of stunting. Instead, they grew fewer leaves, but their leaves were thicker and tougher, indicating they allocate fewer resources toward new leaves and growth, but instead increase investment in defense from mechanical damage and herbivory. This resource-conservative strategy increases their survival rate but decreases their growth rate.

Chapter 2 examines xylem physiology by comparing 13 anatomical and hydraulic traits between pygmy and conspecific control plants. Pygmy plants had smaller conduits, but could transport more water to each leaf than controls, due to their reduced leaf production. Pygmy plants had divergent responses in cavitation resistance, a critical predictor for drought survival: in a vessel-bearing angiosperm, pygmy plants were more vulnerable to cavitation, while in a conifer, pygmy plants were more resistant. Overall, changes in water transport due to nutrient limitation were profound, despite the absence of water stress.

Chapter 3 examines community assembly in the pygmy forest using a series of 100 m^2 plots. Pygmy forest plots had more species than adjacent tall conifer forests, but these species were more closely related to each other, indicating that fewer taxonomic groups can survive in the pygmy forest. Within the pygmy forest, higher soil aluminum levels, which stunt root growth, predicted lower phylogenetic diversity. Taxa with high water transport efficiency, a resource-acquisitive strategy, were rare at these low diversity sites, indicating that water transport is a key predictor for which species survive on the most stressful soils.

Overall, this dissertation reveals the critical role resource conservation plays in plant response to nutrient limitation across scales.

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Introduction

For plants, nutrient limitation is almost universal (Elser et al., 2007; Lambers, Chapin, et al., 2008; Fisher et al., 2012). Most mineral nutrients begin their lifecycle as rock, inaccessible to plants, before the rock weathers into soil and provides the nutrients plants need to grow. Over time, these nutrients are lost as they are washed away with water or irreversibly bound to other soil components. Without an adequate supply of macro- and micronutrients, plant growth is slowed or stunted, with cascading effects on the rest of the ecosystem.

This process is exemplified in several locations along the coast of northern California where sandstone that was originally low in mineral nutrients has weathered into soil that is even lower in nutrients (Jenny et al., 1969; Fox, 1976). As a result, plant growth on these soils is severely stunted, and trees that are several decades old may reach only chest-height (Jenny et al., 1969). The resulting patches of small, bonsai-like trees form a plant community commonly referred to as the pygmy forest. Pygmy forest occurs as far south as Monterey Bay, but is most commonly found in Mendocino County (McMillan, 1956).

The Mendocino pygmy forest presents an excellent opportunity to study the effects of nutrient limitation on plant growth in a natural context, because nutrient-depauperate soils that host pygmy forest occur side-by-side with more fertile soils, which host tall coniferous forests. Plants growing on both types of soil experience similar climatic and ecological conditions, minimizing differences between plant communities, which can confound research on nutrient limitation in other systems (Santiago, 2015). Furthermore, water limitation is negligible in both locations (Sholars, 1979), eliminating another extraneous factor that could affect plant growth. Thus, this dissertation focuses on the Mendocino pygmy forest as a model system for understanding the effects of nutrient limitation on plant physiology, both at an organismal and a community level.

In **Chapter 1**, I begin with the foundational question of how plants survive on these stressful soils at all. To begin to answer this, I examined the leaf physiology of pygmy plants, compared with conspecific controls from nearby. In theory, low nutrient availability may constrain plant growth by limiting photosynthetic rates, because photosynthesis relies on enzymes and pigments that are nutritionally expensive for plants to build (Sage and Pearcy, 1987). Photosynthetic rates too low to sustain plant metabolism would prohibit plants from growing on these soils. However, I found that most species had the same photosynthetic rates when growing in the pygmy forest as when growing on more fertile soil. Instead, the pygmy plants adopted a resource-conservative growth strategy: they grew fewer leaves, but their leaves had lower specific leaf area (leaf area divided by dry mass) and lower nitrogen content, meaning they were thicker, tougher, and less likely to be consumed by herbivores or physically damaged. This resource-conservative strategy explains the stunted growth of the pygmy forest: pygmy plants with fewer leaves have lower whole-plant photosynthetic rates, even if the photosynthetic rate of each individual leaf is comparable to controls. Furthermore, each leaf required more carbon to build, given the leaves' low specific leaf area and high carbon: nitrogen ratio. This investment in building thicker leaves, instead of building more leaves, causes slower growth rates, but may increase the plants' chances of survival. On such low-nutrient soils, any loss of leaves, and the nutrients they contain, due to physical damage or herbivory, could have a much larger impact on survival (see Coley et al., 1985).

In **Chapter 2**, I ask how nutrient limitation and stunted growth affect plant water transport, as well as xylem function during drought stress. Although changes in water transport are generally thought to be a result of water availability, I hypothesized that the nutrient limitation and altered growth patterns of the pygmy plants would alter water transport. Xylem supplies water to leaves, and I predicted the changes in leaf physiology and overall carbon balance would have downstream consequences on xylem form and function. I confirmed that the pygmy forest and the nearby tall coniferous forests used in this study experience minimal water stress, even at the end of the dry season of a drought year. Despite the lack of water stress, xylem anatomy and water transport differed between pygmy and control plants of the same species. Pygmy plants typically had smaller xylem conduits than conspecifics growing on more fertile soils, and in one species this decrease in conduit diameter reduced water transport efficiency, i.e., the xylem was less conductive to water. However, due to the pygmy plants' strategy of producing fewer leaves, some pygmy plants were able to transport more water to each leaf under the tested conditions. When drought was simulated in the lab, pygmy plants of one species were more vulnerable to drought stress, while in another species, pygmy plants were more resistant to drought stress. Taken together, these results indicate that pygmy plants shift toward a more resource-conservative strategy, with smaller conduits and less efficient water transport per unit xylem, despite minimal water stress.

In Chapters 1 and 2, one species stood out as an outlier in terms of physiological response to pygmy forest soils. *Sequoia sempervirens*, the tallest tree species in the world, is common in the tall coniferous forests surrounding the pygmy forest, but rare within the pygmy forest itself. Pygmy *S. sempervirens* had greatly reduced photosynthetic rates and leaf area compared to tall conspecifics, and they showed greater changes in stem-level drought resistance than other species. This disparity between a species rare in the pygmy forest and the other examined species, which are common in the pygmy forest, hinted that physiology drives which species can survive in the pygmy forest.

In **Chapter 3**, I examine community composition in terms of species diversity and functional traits. Compared to adjacent tall coniferous forests, patches of pygmy forest typically had more species. However, those species had more closely related evolutionary histories than species in the tall conifer forests. The pygmy forest was dominated by plants from the Ericaceae, Pinaceae, and Cupressaceae families, which are known for being stress-tolerators, while the tall conifer forests had a greater variety, including some species from the Berberidaceae and Rosaceae. Within the pygmy forest, as soil became less fertile, plants became more closely related to each other as the difficult environmental conditions restricted community composition to fewer and fewer taxa. These plots with more restricted taxa also had plants with a more resource-conservative growth pattern, indicating that the strategies seen within species in Chapters 1 and 2 are also seen at the community-wide level.

Overall, this dissertation informs our understanding of the impacts of nutrient limitation on physiology at the organismal and community level, using a model system with minimal water stress.

Chapter 1

Small trees, big problems:

Comparative leaf function under extreme edaphic stress

Abstract

The pygmy forest, a plant community of severely stunted conifers and ericaceous angiosperms, occurs on patches of highly acidic, nutrient-poor soils along the coast of Northern California, USA. This system is an excellent opportunity to study the effect of severe nutrient deficiency on leaf physiology in a naturally-occurring ecosystem. In this study, we seek to understand the physiological mechanisms stunting the plants' growth and their implications for whole plant function. We measured 14 traits pertaining to leaf photosynthetic function or physical structure on seven species. Samples were taken from the pygmy forest community and from conspecifics growing on higher-nutrient soils, where trees may grow over 30 m tall. Pygmy plants of most species maintained similar area-based photosynthetic and stomatal conductance rates to conspecific controls, but had lower specific leaf area (leaf area divided by dry weight), lower percent nitrogen, and less leaf area relative to xylem growth. *Sequoia sempervirens*, a species rare in the pygmy forest, had a categorically different response from the more common plants and had remarkably low photosynthetic rates. Pygmy plants were not stunted by low photosynthetic rates on a leaf-area basis; instead, several species had restricted whole-plant photosynthesis due to low leaf area production. Pygmy plants of all species

showed signs of greater carbon investment in their leaves and higher production of nonphotosynthetic leaf tissue, further contributing to slow growth rates.

Introduction

Nutrient availability is a critical environmental variable that sets the upper bounds of plant productivity and alters plant physiological function, which in turn has cascading effects on ecosystem nutrient cycling (Vitousek, 1998; Cornwell et al., 2008). Broad trends in plant physiological response to nutrient limitation have been observed: nutrient-limited plants worldwide are typically characterized by low growth rates, low photosynthetic rates, and an increase in allocation toward defense from herbivory and mechanical damage (Coley et al., 1985; Wright et al., 2004). Cases of extreme nutrient limitation, however, do not universally follow these general trends. Pioneer species on young, N-limited soils can be nitrogen-fixers with high growth rates (e.g., Kurten et al., 2008), desert annuals similarly may have high photosynthetic rates (Mooney et al., 1981; Ehleringer, 1983), and plants on ancient, severely P-limited soils may have cluster roots that allow them to take up enough phosphorus to thrive (Lambers, Raven, et al., 2008). Extreme nutrient limitation on soils of intermediate age—long past primary succession but not yet hosting a suite of plants that have specifically adapted to them for millennia—is more rare, but provides a conceptually interesting variation on better understood examples of nutrient deficiency. These systems may allow us to get a glimpse of the processes that have shaped selection and community assembly on nutrient-depauperate soils across the globe.

Where nutrient-poor soils naturally occur, it can be difficult to separate edaphic effects on plant physiology from the effects of climate, species composition, and ecological interactions. The marine terraces in Mendocino County, California, however, form an ideal natural experiment for studying the effects of extreme nutrient deficiency on plant physiology. Here, marine terraces rise from the ocean, increasing in age and nutrient deficiency farther from the coastline (Jenny et al., 1969). The result is nutrient-depauperate soils juxtaposed with less weathered, relatively more fertile soils within the space of a kilometer, maintaining similar climactic and ecological conditions across soil types. Soils on the older marine terraces have low levels of N and especially P (Northup et al., 1998; Izquierdo et al., 2013). The elements Ca, Mg, and K are also in low supply (Jenny et al., 1969). These soils are particularly nutrient-poor for their age, because their primary parent material, greywacke sandstone, is especially high in quartz content, which offers no plant-available nutrition as it weathers (Jenny et al., 1969; Fox, 1976). Furthermore, average soil pH is roughly 4, but can reach as low as 2.2, and high levels of aluminum may stunt root growth (Westman, 1975; Northup et al., 1998). Compounding these stressors, a shallow hardpan, only about 30 cm from the surface, limits space for root growth in many locations (Westman, 1975; Fig. 1). These stressful soils support a unique plant community aptly named the “pygmy forest.”

Plants in the pygmy forest peak at a few meters tall, despite reaching 30–100 years old (Jenny et al., 1969). Many patches of pygmy conifers remain only knee height and achieve a distinct, bonsai-like appearance (Fig. 1). Although most species found in the pygmy forest are found on adjacent soils, species composition of plants, lichens, and bacteria vary with soil type, and several species or subspecies are endemic to the pygmy forest (Westman, 1975; Eckert et al., 2012; Uroz et al., 2014). Earlier studies suggested that due to the limitation of root depth, plants on these soils faced extreme drought during the summer months, but further work revealed that soil moisture remains high throughout the year (Sholars, 1979). Thus, water limitation is not a contributor to the slow growth rate of the pygmy forest plants.

The diminutive heights of plants in the pygmy forests are clearly linked to soil type: when planted on more fertile soils, pygmy forest conifers rapidly increase in growth rate, and tall conspecifics are commonly found outside of the pygmy forest (McMillan, 1956). However, the physiological mechanisms that link soil type to stunting remain unknown. We seek to understand the mechanisms by which pygmy plants tolerate severe nutrient deficiency by studying a number of leaf physiological characteristics and coupling them to overall plant function. Specifically, we hypothesized that in pygmy plants, nutrient limitation would lead to decreased photosynthetic rates via limited synthesis of nutrient-expensive photosynthetic enzymes (Sage and Pearcy, 1987); this limitation could explain their exceptionally slow growth rates. We further hypothesized that older leaves in pygmy plants would have even further reduced photosynthetic capacity, because nutrients may be resorbed at higher rates on nutrient-poor soils, to provide nutrients for production of new leaves (Wright and Westoby, 2003). Overall, the goal of this study is to thoroughly investigate the functional consequences of severe nutrient limitation to understand how plants survive on these stressful soils and why they are stunted.

Methods

Main study area and species

The main survey area was in Mendocino County, California, where the most stunted pygmy forest occurs (McMillan, 1956). This temperate region experiences coastal fog much of the year, with an average yearly rainfall of 96.4 cm, an average daily high of 15°C, and an average low of 7°C in the past decade (California Climate Data Archive 2017). Pygmy plants were sampled from Van Damme State Park (at latitude 39°15′48″N, 123°44′12″W) for six species: *Gaultheria shallon* Pursh (Ericaceae), *Hesperocyparis pygmaea* (Lemmon) Bartel (Cupressaceae), *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae), *Pinus contorta* Loudon ssp. *bolanderi* (Parl.) Critchf. (Pinaceae), *Rhododendron columbianum* (Piper) Harmaja (Ericaceae), and *Rhododendron macrophyllum* D. Don (Ericaceae). Conspecific control individuals of most of the species were sampled near Gibney Lane, a country road, in Jug Handle State Reserve, on the second marine terrace from the ocean (39°22′41″N, 123°48′19″W). This site is considered, paradoxically, tall hydric pygmy, because it supports the same species as the pygmy forest, including the endemic subspecies *P. contorta* ssp. *bolanderi*, but these species grow tens of meters tall at the site

(Westman, 1975). Our final species, *Sequoia sempervirens* (D. Don) Endl. (Cupressaceae), which is rare in the pygmy forest, could not be found near the other species and was sampled from Jug Handle State Reserve Ecological Staircase (39°22′22″N, 123°47′26″W) for pygmy individuals, and in Van Damme State Park (39°16′43″N, 123°47′09″W) for control plants (see Table 1 for comparison of soil composition from the literature). Sites ranged 1–3 km from the coast and were all within 9 km of each other.

Heights and diameters

Mature, fully sun exposed, and healthy-looking plants were selected, and diameters were measured at ground level instead of breast height because of the diminutive stature of the pygmy trees. Height was measured with a measuring tape for shorter plants, and with a clinometer for taller trees.

Photosynthesis and leaf gas exchange

Light-saturated photosynthetic rate (standardized by leaf area or leaf mass), stomatal conductance (rate of water loss from leaves), and dark respiration (rate of CO_2 production during dark conditions) were measured at the Mendocino sites between mid-June and mid-August 2014. These dates comprise the early-to-mid growing season in the pygmy forest, which ends in November (Sholars, 1979). Healthy-looking, mature study plants ($n = 8$) were selected for full sun exposure, and samples were collected at approximately 0.5–1.5 m above the ground. To ensure equivalent water potentials, environmental conditions, and time of day in pygmy and control samples, we rehydrated stems before gas exchange measurements (Pérez-Harguindeguy et al., 2013). In a pilot study in August 2015, we verified that the rehydration method caused no artifacts or other substantial changes to gas exchange measurements for any of the seven sampled species.

To rehydrate samples, we bagged 40–60 cm stems (*n* = 8 for all species) for 15–30 min in the late evening to relax xylem tension, then cut them and immediately placed them in water, before transporting them and cutting them back by 15–20 cm underwater. The samples were then left overnight to rehydrate with their cut ends in water, such that water potentials relaxed to an average of –0.2 MPa. Between 10 am and 3 pm the next day, we measured leaf gas exchange with a LiCor-6400XT (LiCor, Lincoln, Nebraska, USA). Within each species, we mixed pygmy and control samples and haphazardly selected stems for gas exchange to control for effects of time of day. Measurements were made on the most recently expanded fully mature leaf of each sample, as well as the most recent leaf produced the previous year for species where leaf age was readily identified. For light-saturated photosynthetic rates and stomatal conductance measurements, light levels were slowly increased to 2000 $\mu mol \cdot m^2 \cdot s^{-1}$ before recording results. Light levels were then decreased to zero, and dark respiration measurements were taken. Reference [CO_2] was held at 400 ppm, chamber relative humidity was kept at approximately 60%, and leaf temperature was held at 20°C ± 1°. Intrinsic water-use efficiency was calculated as the photosynthetic rate divided by stomatal conductance.

F_v/F_m, the ratio between variable fluorescence (F_v) and maximum fluorescence (F_m), was measured on the same or adjacent, same-age leaves as gas exchange measurements using a pulse amplitude modulated fluorometer (OS1p, Opti-Sciences, Hudson, New Hampshire, USA) after 35 min of dark adaption. F_v/F_m is a fluorescence-based measurement of the efficiency of the light reactions of photosynthesis and is a proxy for stress levels. Care was taken not to stress photosystems by making a fluorescence-based measurement on a leaf before using the leaf for gas exchange measures.

Leaf construction measures

Chlorophyll content was measured on the same or adjacent leaves as gas exchange and F_v/F_m measurements using a fluorescence-based chlorophyll meter (CCM-300, Opti-Sciences, Hudson, New Hampshire, USA). After field measurements, leaves were dried at 60°C and stored before being ground into a fine powder and analyzed for leaf C and N stable isotopes and total content using an elemental analyzer (Carlo Erba 1108 elemental analyzer coupled to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer; Stable Isotope Laboratory, University of California, Santa Cruz, California, USA). The standardized ratio of heavy-to-light carbon, $\delta^{13}C$, is an indicator of integrated stomatal conductance, because stomatal closure limits internal CO_2 and decreases Rubisco discrimination against ^{13}C (Dawson et al., 2002). Photosynthetic nitrogen-use efficiency was calculated as the ratio of light-saturated photosynthetic rate to leaf N content.

Leaf area of freshly collected leaves was measured using a leaf area meter (LiCor-3100, Lincoln, Nebraska, USA), and leaves were then dried at 60°C to a constant weight and weighed. Specific leaf area (SLA) was then calculated as leaf area divided by leaf dry mass.

To assess whether pygmy plants were producing fewer leaves, annual leaf vs. wood production was assessed. Total leaf area produced in the 2015 spring/summer growing season was measured using a leaf area meter (LiCor-3100, Lincoln, Nebraska, USA) using stems collected in late September 2015. The stem was then cross-sectioned at the base of the oldest leaf from that growing season, and the growth ring width was measured using Image J analysis software (Schneider et al., 2012). This produced a measurement of how much leaf area a stem produced, relative to wood production, in a single growing season.

To estimate leaf longevity, we recorded the age of the oldest cohort of leaves with more than 50% of its leaves remaining (Pérez-Harguindeguy et al., 2013). This method of measuring leaf longevity works best for species with easily identifiable leaf age that form leaf scars and experience low rates of herbivory on young leaf cohorts, so we measured leaf longevity on four species.

Other sites

To assess the generality of our findings in the Mendocino pygmy forest, we selected two more survey areas for a subset of physiological measures. Pygmy and control samples were taken from Salt Point State Park in Sonoma County, CA (38°34′46″N, 123°18′28″W for pygmy; 38°34′26″N, 123°18′00″W for control) as well as the SFB Morse Botanical Preserve, Monterey County, California (36°35′23″N, 121°56′10″W for pygmy; 36°35′18″N, 121°55′52″W for control). Both of these areas occur on marine terraces and have pygmy forests formed by similar conditions to the Mendocino pygmy forest (McMillan, 1956; Millar, 1989; Jones and Stokes Associates, 1994). Species sampled at these sites were *Gaultheria shallon, Pteridium aquilinum*, *Hesperocyparis goveniana* (Gordon) Bartel (Cupressaceae), and *Vaccinium ovatum* Pursh (Ericaceae). Samples for SLA and isotope measurements (see above for methods) were collected in April 2017.

Statistics

We used *t*-tests to analyze our data, because of the pairwise nature of our questions. Most trait measures were normally distributed. The SLA data were log transformed before analysis. One-sided *t*-tests were used to compare leaf functional traits of conspecific pygmy and control plants in the statistical software package R (R Core Team, 2016); two-sided *t*-tests were used when we had no single-sided hypothesis (for stomatal conductance, water-use efficiency, $\delta^{13}C$, and photosynthetic nitrogen use efficiency). Student's *t*-tests were used when variances were equal;

otherwise, Welch's *t*-tests were used. The relationship between log-transformed height and diameter, as well as the relationship between chlorophyll content and percent N, were assessed using linear regressions. Sequential Bonferroni corrections to adjust the critical *p*-values (Holm, 1979) were applied separately for each physiological variable, treating each one as a separate hypothesis to decrease family-wise type I error risk without unduly decreasing power. Graphs were produced using ggplot2 (Wickham, 2009).

Results

Heights and diameters

Mendocino pygmy plants of all species averaged 4 m or shorter, but Mendocino control trees reached up to 30 m tall (Fig. 2A). Control plants were significantly taller in three species ($P < 0.001$ for all) and marginally significant in *G. shallon* ($t = 2.3$, df = 11.3, $P = 0.02$; see Appendix 1, Table S1, for data and full statistical results). Log-transformed height and diameter remained positively correlated across species and soil type (Fig. 2B).

Photosynthesis and leaf gas exchange

In the Mendocino pygmy forest, results for light-saturated photosynthetic rate differed when standardized on a per-mass basis compared to a per-area basis. Light-saturated photosynthetic rate per unit leaf area was significantly lower only in pygmy *Sequoia sempervirens* ($t = 6.64$, df = 14, $P < 0.001$; Fig. 3) and marginally significant, but not substantially lower in *Hesperocyparis pygmaea* and *Rhododendron columbianum* (P <0.05 for both; Fig. 3; see Appendix 1, Table S1, for summary table and detailed statistical results). However, photosynthetic rate per unit leaf mass was lower in pygmy plants in four species: *H. pygmaea*, *R. columbianum*, *R. macrophyllum*, and *S. sempervirens* (P <0.005 for all; Fig. 4A). Furthermore, the difference in mass-based photosynthesis was marginally significant in *Gaultheria shallon* (t = 2.4, df = 14, P = 0.02) and *Pteridium aquilinum* (t = 1.95, df = 14, P = 0.036) after the Bonferroni correction. This decrease in mass-based photosynthesis reflects a greater allocation toward nonphotosynthetic tissues in pygmy plants.

Other gas exchange measurements rarely differed between pygmy and control plants, with the exception of *S. sempervirens*. Stomatal conductance did not differ within any of the 7 species, although pygmy *S. sempervirens* had dramatically lower intrinsic water-use efficiency than conspecific controls due to its low photosynthetic rates (t = 7.3, df = 10.7, P <0.00005; see Fig. 3). Dark respiration, an indicator of metabolic activity of leaves, was significantly lower only in pygmy *R. columbianum* (t = 3.4, df = 14, P = 0.002). The F_v/F_m ratios were in the healthy range for all species, indicating that chloroplast photosystems were operating at normal, nonstressed efficiency levels in pygmy and control plants (see Ritchie, 2006).

We had hypothesized that pygmy plants would have a greater drop in photosynthetic rates of old leaves. Such a pattern would indicate increased nutrient resorption rates from old to young foliage, as can occur on nutrient-limited soils (Vitousek, 1998; Wright and Westoby, 2003). Decreased rates of photosynthesis in older leaves would also lead to lower whole-plant photosynthetic rates and could contribute to the pygmy plants' slow growth rates. However, the drop in photosynthesis in older leaves was the same in conspecific control and pygmy plants for all species, except for *S. sempervirens*. In pygmy *S. sempervirens*, area-based photosynthesis did not change from young leaves to old leaves, but in control plants, area-based photosynthesis decreased slightly in older leaves ($t = 3.34$, $df = 13.4$, $P = 0.005$, see Appendix 1, Table S2, for data). This may indicate that control *S. sempervirens* begins to senesce old leaves sooner than pygmy plants; however, the effect size was small and may not be physiologically relevant.

Leaf construction measures

SLA was significantly lower in pygmy plants for all measured species, indicating thicker, denser leaves ($P < 0.01$ for all; Fig. 4B; see Table S1 for data and full statistical results). Pygmy plant leaf C:N ratio was higher in *P. contorta* ssp. *bolanderi, R. columbianum*, and *S. sempervirens*, where it ranged from 25% higher in *P. contorta* ssp. *bolanderi* to 150% higher in *S. sempervirens* ($P < 0.001$ for all; Fig. 4C). Percent N was lower in pygmy plants of four species ($P < 0.01$ for all). Chlorophyll content per unit leaf area was significantly lower only in pygmy *H. pygmaea* and *S. sempervirens* ($P < 0.001$ for all) and marginally significant, but not substantial, in *G. shallon* and *P. contorta* ssp. *bolanderi* ($P < 0.05$; see Table S1 for full statistical results). There was a positive relationship between chlorophyll content and percent N (Fig. 5).

Standardized leaf carbon isotope ratios ($\delta^{13}C$) ranged from –26‰ to –31‰, indicating neither water stress nor internal CO_2 limitation in either group. Both pygmy and control *H. pygmaea* had less negative $\delta^{13}C$ values than other species, denoting higher integrated water-use efficiency, which is consistent with previous characterizations of drought-resistant taxa of the Cupressaceae (Pittermann et al., 2012; Larter et al., 2017).

Photosynthetic nitrogen-use efficiency, the ratio of photosynthetic rate to leaf N content, is typically higher in nutrient-limited plants. However, it was significantly lower in pygmy *P. aquilinum* and *P. contorta* ssp. *bolanderi* than in controls ($P < 0.01$ for all, see Figure S1 for barplot and Table S1 for data) and marginally significant in *G. shallon* and *R. columbianum* ($P < 0.05$ for both).

Leaf area standardized by xylem area was significantly lower in pygmy plants in two species, and marginally significant for two additional species after the Bonferroni critical *p*-value adjustment ($P < 0.02$ for all; see Fig. 6 and Table S1). For these pygmy plants, leaf production was decreased relative to wood production at the stem level.

Leaves of the three ericaceous species examined were short-lived in both the pygmy forest and control site, averaging between 2–3 years of age before dropping. *Sequoia sempervirens* leaves averaged around 6 years before dropping. Of the examined four species, pygmy and control plant leaf longevity differed only in *G. shallon*, where control plant leaves lasted 2.5 years on average, and pygmy leaves lasted 1.75 years ($t = 3.02$, df = 13.7, $P < 0.01$). It is possible that there are small differences in leaf longevity, on the order of a few months, which our method was not able to detect.

Other sites

Other pygmy forests showed similar trends to the Mendocino pygmy forest in SLA, C:N ratio, and percent N, but results were less universal. At Salt Point State Park in Sonoma County, SLA was lower in pygmy individuals of two out of three species, and C:N ratio and percent N were lower only in *Vaccinium ovatum* ($P < 0.01$ for all, see Appendix 1, Table S3, for species averages and full statistical results). In the SFB Morse Botanical Preserve in Monterey County, farther south, only *P. aquilinum* out of the three species had lower SLA, C:N ratio, and percent N in pygmy individuals ($P < 0.01$ for all).

Discussion

The pygmy forest is a unique plant community filled with decades-old trees that continue to persist in their nutrient-poor habitat despite being severely stunted. We hypothesized that this stunting was caused by low photosynthetic rates due to severely restricted nutrient availability, which impedes chlorophyll and enzyme synthesis (e.g., Sage and Pearcy, 1987). Instead, we found that area-based photosynthesis was substantially lower only in *S. sempervirens*, and chlorophyll content per unit area lower only in *S. sempervirens* and *H. pygmaea* (Fig. 3 and 4D). Neither did we find evidence for lower assimilation rates in older leaves in pygmy plants compared to control plants. Thus, our initial hypothesis for the physiological cause of stunting was not supported. On a per-area basis, both old and young leaves of pygmy plants function just as leaves of conspecific control plants do, with very few exceptions. Instead, leaves differed in mass-based traits and pygmy plants of some species produced far fewer leaves.

Some pygmy plants had half the leaf area of conspecific controls (Fig. 6). On a whole-plant level, this loss of potential leaf area results in greatly decreased photosynthetic rates, despite the pygmy plants maintaining carbon acquisition rates on a leaf-area basis. This drop in whole-plant photosynthesis is likely a major contributor to low growth rates and stunted height in these species. The restriction in new leaf area may be purposeful: plants generally decrease leaf mass relative to stem or root mass when under nutrient limitation (Poorter and Nagel, 2000). Leaves have a higher cost in nutrients than stems and roots, and thus new leaf production may be limited when nutrition is limiting.

Although pygmy plants generally produced fewer leaves, they invested more carbon into their leaves. Pygmy plants invariably had lower SLA, which results from thicker leaves, denser leaf tissue, or both. Low SLA is associated with greater robustness, allowing leaves to weather mechanical damage or deter herbivory, although it comes at a carbon cost. As a result of their low SLA, pygmy plants of almost all species had lower mass-based photosynthetic rates. This drop in mass-based photosynthesis reflects a lower proportion of leaf tissue allocated to photosynthesis, relative to schlerenchyma and other support tissues that contribute to low SLA. Pygmy plants of several species also had higher C:N ratios and lower percent N, similarly reflecting a lower proportion of leaf mass dedicated to N-intensive photosynthetic machinery. Northup et al. (1998) found that pygmy plants of several species produced higher concentrations of polyphenols, which are carbon compounds that can deter herbivory and decrease soil decomposition (see also Kraus et al., 2004). These polyphenols may account for part of the high leaf carbon concentration in pygmy plants, along with support tissues.

Pygmy plants may even invest a smaller proportion of leaf N into photosynthetic proteins than control plants, because photosynthetic N-use efficiency was lower in pygmy plants of a few species (see Appendix 1 for barplot and data). It may be that P is the most limiting nutrient in the pygmy forest (Izquierdo et al., 2013), and therefore the total amount of photosynthetic proteins and pigments is constrained by the amount of P, not N. Fertilizing with P alone does not increase pygmy plant growth rates, while either the addition of N or N and P does (McMillan, 1956); however, N addition may increase P uptake (Westman, 1975).

Shifts in pygmy plant functional traits broadly follow the worldwide leaf economics spectrum (Wright et al., 2004) and the resource availability hypothesis (Coley et al., 1985; Endara and Coley, 2011). The worldwide leaf economics spectrum describes the correlation of a number of leaf functional traits on an axis ranging from a slow-return, resource-retention strategy to a fast-return, fast-growth strategy. According to this theory, plants tend to adopt a more slow-return strategy on lower-nutrient soils, with lower SLA, longer leaf lifespan, lower photosynthetic rates (especially mass-based photosynthesis), and lower concentrations of leaf N and P. The more nutrient-limited plants in our study did show evidence of this slow-return strategy, with lower SLA, mass-based photosynthesis, and leaf N, although the pygmy plants did not have longer leaf lifespan. Most of the species in our study are evergreen, which may constrain their range of response. We might expect greater variation if the pygmy forest had more annual and deciduous taxa. The resource availability hypothesis also describes a slow-return strategy on resource-poor soils, because of increased investment in herbivory defense being favored on these soils. Plants in the pygmy forest do have more polyphenols (Northup et al., 1998) and lower SLA, which are both constitutive defenses. The pygmy plants' C:N ratio also contributes to defense: high leaf C:N makes leaves less attractive or nutritious for herbivores (Pérez-Harguindeguy et al., 2003). It is likely that low production of new leaf area aids pygmy plants in adopting these defensive strategies: instead of producing many cheaply-built leaves with low photosynthetic rates, pygmy plants produce fewer leaves, but are able to invest more carbon into them. Overall, this tactic slows growth rates, but is likely the reason that these plants are able to survive on highly acidic, nutrient-depauperate soils.

Plants of the two other examined pygmy forests also followed this general strategy, although the effect was less pronounced across species. Unlike the universal decrease in SLA across species in the Mendocino pygmy forest, only one or two out of three species adopted the strategy in the two pygmy forest sites south of Mendocino. The pygmy forest soils farther south are less developed and thus more nutrient-rich than the Mendocino soils (McMillan, 1956; Millar, 1989), possibly reflecting slower weathering rates due to decreased precipitation farther south. While our study covers three pygmy forests that are found on acidic, weathered marine terraces, it is plausible that the same slow-return, carbon-reallocation strategy is the physiological cause of stunting in other pygmy forests for which the cause has not yet been identified. For example, Reich and Hinckley (1980) examined a pygmy oak ecosystem in Missouri, USA, and ruled out water stress as the dominant cause of stunting; they speculated that nutrient limitation was a factor. Fang et al. (2006) determined that genetics were not the main cause of stunting in dwarf pines in New York, USA, and Vanderklein et al. (2012) similarly ruled out hydraulic limitations for the site.

Not all dwarf or pygmy forests are stunted by nutrient limitation. The soils of the New Jersey Pine Plains, USA, a region of stunted pines and oaks, are little different from the soils found under taller trees (Andresen, 1959). Instead, the dwarfism observed in the Pine Plains is a genetic adaptation to high fire frequency, allowing plants to allocate resources to early reproductive maturity (Ledig et al., 2013). In high-altitude elfin cloud forests, high winds can alter resource allocation patterns, decrease photosynthetic rates, and limit tree height (Cordero, 1999).

Within our study, there was one species that was an outlier, despite the generally consistent functional trait responses in other species. Pygmy *S. sempervirens* had dramatically lower chlorophyll content, area-based photosynthesis, and water-use efficiency than control plants (Fig. 3, Fig. 5). *Sequoia sempervirens* is rare in the pygmy forest: it is not always included in pygmy forest species lists (Westman, 1975) and cannot produce viable seeds when growing in the pygmy forest (Northup et al., 1998). Pygmy *S. sempervirens* can display old-growth characteristics on unusually small plants, but will also form small, multi-stemmed shrubs (Russell and Woolhouse, 1999; Lambert, 2012). *Sequoia sempervirens*, while the dominant plant of adjacent redwood forests, is only marginally able to survive in the pygmy forest, perhaps because of an inability to maintain area-based photosynthesis like more common species. *Sequoia sempervirens* did show all the signs of carbon reallocation observed in other species: lower SLA, higher C:N ratio, and lower leaf area. However, it appears that *S. sempervirens* does not constrain leaf area production enough to maintain leaf photosynthetic rates.

Belowground processes may also play a key role in determining which species are successful in the pygmy forest. Most of the common pygmy forest species belong to the Pinaceae or Ericaceae, which associate with ectomycorrhizae and ericoid mycorrhizae, respectively. Wurzburger and Bledsoe (2001) confirmed ericoid or ectomycorrhizal associations for six pygmy forest species, including *P. contorta* ssp. *bolanderi*, *R. macrophyllum,* and *R. columbianum*. They found arbuscular mycorrhizal association in one species, *Arctostaphylos nummularia*. Ericoid and ectomycorrhizae are more effective at taking up nutrients bound to other soil components than arbuscular mycorrhizae, and they are more abundant on older, more nutrient-limited soils (Lambers, Raven, et al., 2008). *Sequoia sempervirens* may not be able to extract as much nutrients from the soil as the more common pygmy forest species, because of its association with arbuscular mycorrhizae (Mejstrik and Kelley, 1979). Alternatively, the hardpan present in much of the pygmy forest or toxic aluminum concentrations may restrict root growth more than *S. sempervirens* can tolerate.

Plant community composition has been described as being determined by a historical filter (what species can disperse to the site), a physiological filter (what species can survive and reproduce in that environment), and an ecological filter (what species are competitive and defend themselves; see (Lambers, Chapin, et al., 2008). It is probable that the nutrient-poor soils of the pygmy forests exert a strong physiological filter and is only hospitable to plants capable of both helpful mycorrhizal associations and the plasticity needed to alter carbon allocation. Multiple studies have observed limited species richness, or increased phylogenetic relatedness, on nutrient-poor soils (e.g., Aplet et al., 1998; Fine and Kembel, 2011). Other stressors, too, including periodic flooding due to poor drainage through the soil hardpan, likely filter species composition in the pygmy forest (Jenny et al., 1969). The pygmy forest is old enough to have some endemics or subspecies in the process of speciation (including *P. contorta* ssp. *bolanderi*), but is a relatively young system for the level of nutrient deficiency it experiences.

An interesting counterpoint to our study is the sandplains of Southwest Australia. Here, soils reach several million years old, becoming severely depleted in P (Pidgeon et al., 2004; Fisher et al., 2006; Laliberte et al., 2012). *Banksia* plants common in these soils have low specific leaf area and maintain moderately high photosynthetic rates, similar to pygmy forest plants in our study, but these species also increase their P residence time via long leaf lifespan and remobilizing much of their P from leaves before senescence (Denton et al., 2007). Over the course of millennia of natural selection, plants in this region have developed some highly adaptive traits. Some Proteaceae species have the ability to replace many of their phospholipids with lipids that do not contain P, conserving their P for photosynthetic machinery and dramatically raising their photosynthetic P-use efficiency (Lambers et al., 2012). Cluster roots, a type of high-surface-area root that releases compounds to make soil P more available, are common on these soils (Lambers, Raven, et al., 2008). Species diversity along a chronosequence in this region was found to be primarily determined by soil pH and to increase with soil age, suggesting physiology plays a large role in filtering species composition in this region (Laliberte et al., 2014). The Mendocino pygmy forest may similarly experience environmental filtering via soil chemical composition (Westman, 1975), but the process is likely to be dramatically different given the soils' relatively rapid progression from nutrient-rich enough to support 30 m tall trees to so nutrient-poor that trees remain less than a few meters tall.

The pygmy forest is an example of a stable, post-successional ecosystem in which plants have evolved to tolerate the extremely poor soils they grow on. Plants do not thrive here, but they persist, with a few species dominating the landscape, and some such as *S. sempervirens* hanging on in this marginal habitat. They survive here by producing tough, low-SLA leaves—a physiological strategy that is effective on low-nutrient soils around the globe (Wright et al., 2004), and they maintain area-based photosynthetic rates by producing fewer leaves, instead of producing greater leaf area with lower photosynthetic rate. Furthermore, allocation away from new leaf area and toward thicker leaves, higher leaf C:N, and higher polyphenol production also reduces growth rates and possibly reproductive output, but nonetheless, in the high-light, open woodlands of the pygmy forest ecosystem, plants have managed to eke out an existence.

Table 1. Soil data reported from literature. Citations were chosen to match terrace, soil type, and general location.

	Data Source	Control Sites	Pygmy Redwood Site	Main Pygmy Site
Terrace	Jenny 1973 (map and heights of terraces)	2	3	5
Estimated Age (years)	Merritts et al. 1991	200,000	>200,000; <330,000	>400,000
pH (H_20)	Northup et al. 1998	5.12	4.49	4.8
C (g/kg)	Northup et al. 1998	51.5	49.5	42.6
N (g/kg)	Northup et al. 1998	1.7	1.3	1
Labile P (g/m^2)	Izquierdo et al. 2013	1.62	1.87	0.49
Organic P (g/m^2)	Izquierdo et al. 2013	80.21	59.24	46.25
Ca (mg/kg)	Northup et al. 1998	1.2	0.3	0.6
Mg (cmol/kg)	Northup et al. 1998	0.8	0.2	0.4
Al (cmol/kg)	Northup et al. 1998	2.9	2.8	2.8
Depth to hardpan (cm)	Northup et al. 1998	N/A	43	53

Note: data are reported from O, A, E, and B horizons, weighted by horizon depth

Figure 1. Photo panel. A.) Pygmy forest at Van Damme State Park, California, exhibiting 30 cm tall *Hesperocyparis pygmaea* (foreground) and 1.5 m tall *Pinus contorta* ssp. *bolanderi* (midground), as well as the whitish soil characteristic of much of the pygmy forest. In the distance, the peaks of tall trees can be seen, signaling the edge of the pygmy forest. B.) Pygmy (right) and control (left) *Sequoia sempervirens* leaves. C.) Light-colored soil in pygmy forest at Jug Handle State Reserve, CA. Erosion has exposed the reddish hardpan layer.

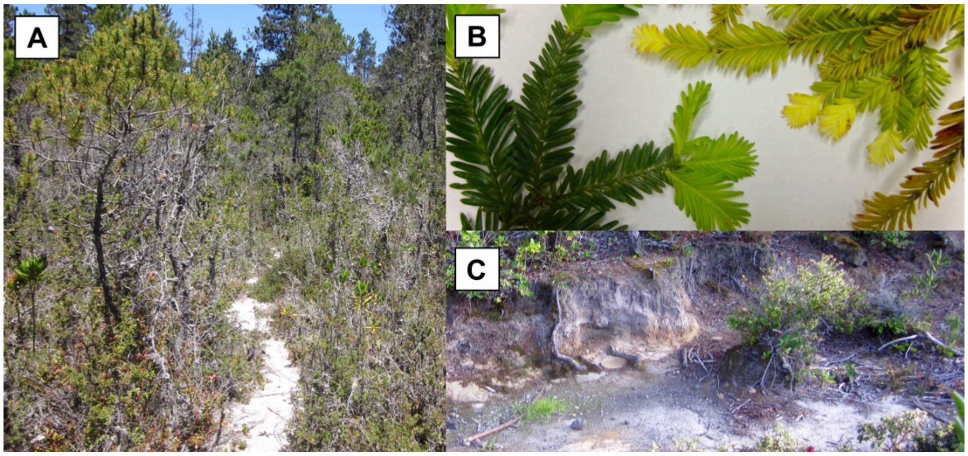


Figure 2. A.) Heights of pygmy (dark gray) and nearby control (light gray) plants from Mendocino County, California, with standard error and asterisks indicating significance (one asterisk signifies $p<0.05$; two, $p<0.01$; three, $p<0.001$). B.) Relationship of height versus diameter (df=109, $p<0.0001$). Both parameters have been transformed by $\log_{10}$; equation and R^2 value refer to transformed data. Each point represents an individual plant.

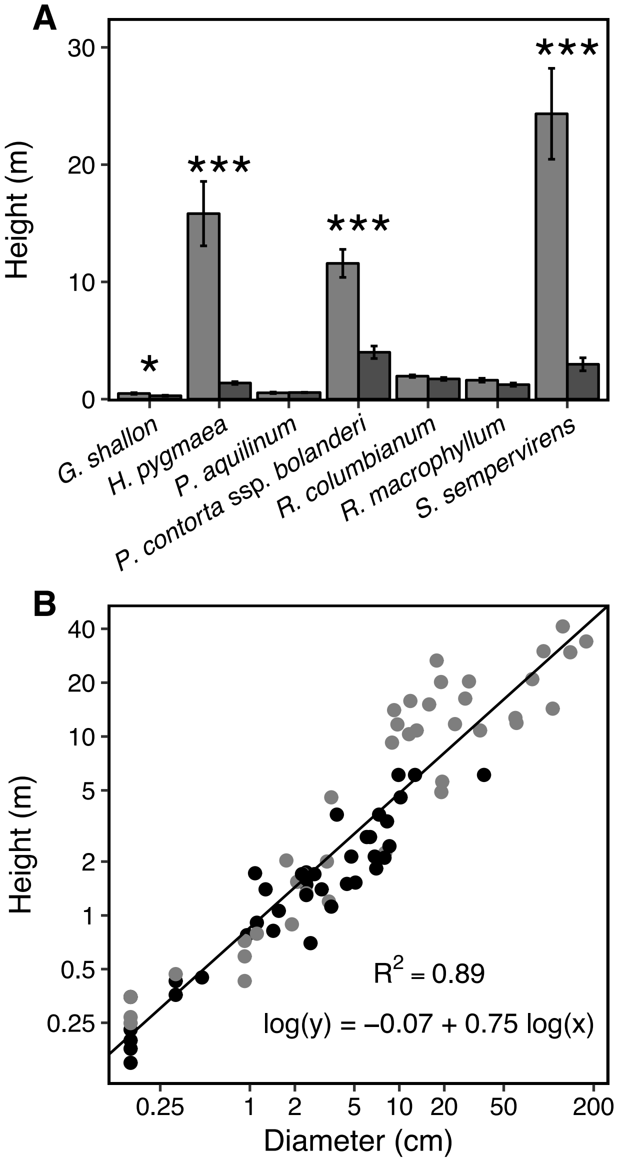


Figure 3. Mean stomatal conductance and photosynthetic rate standardized by leaf area of pygmy (black) and control plants (light gray; n=8) for each species. Points are average values, with standard error, and are represented by species initials (e.g., Pa represents *Pteridium aquilinum*). Note how pygmy and control plants of most species fall along the same line of increasing photosynthetic rate with increasing stomatal conductance, while pygmy *S. sempervirens* instead gains very little CO_2 for the same amount of water loss (i.e., has lower intrinsic water-use efficiency) compared to other samples.

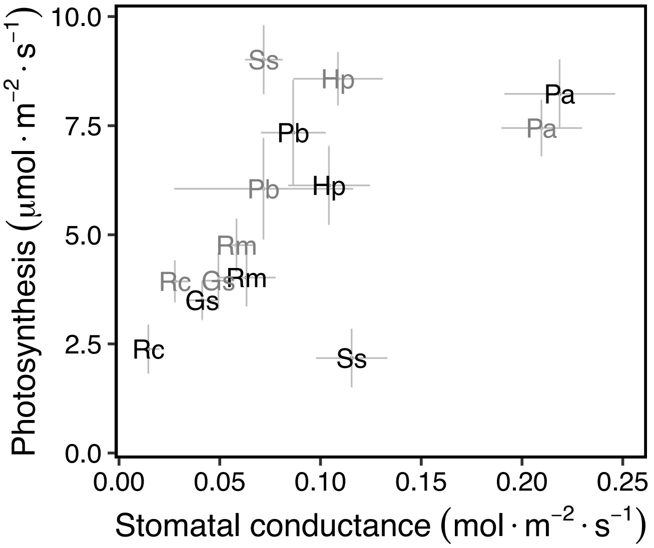


Figure 4. A.) Light-saturated photosynthetic rate per unit leaf mass for pygmy (dark gray) and control (light gray) plants. B.) Specific leaf area (leaf area divided by leaf dry weight) of the same plants. C.) Carbon to Nitrogen ratio of leaves, by mass. Bars represent standard error and n=8 for all.

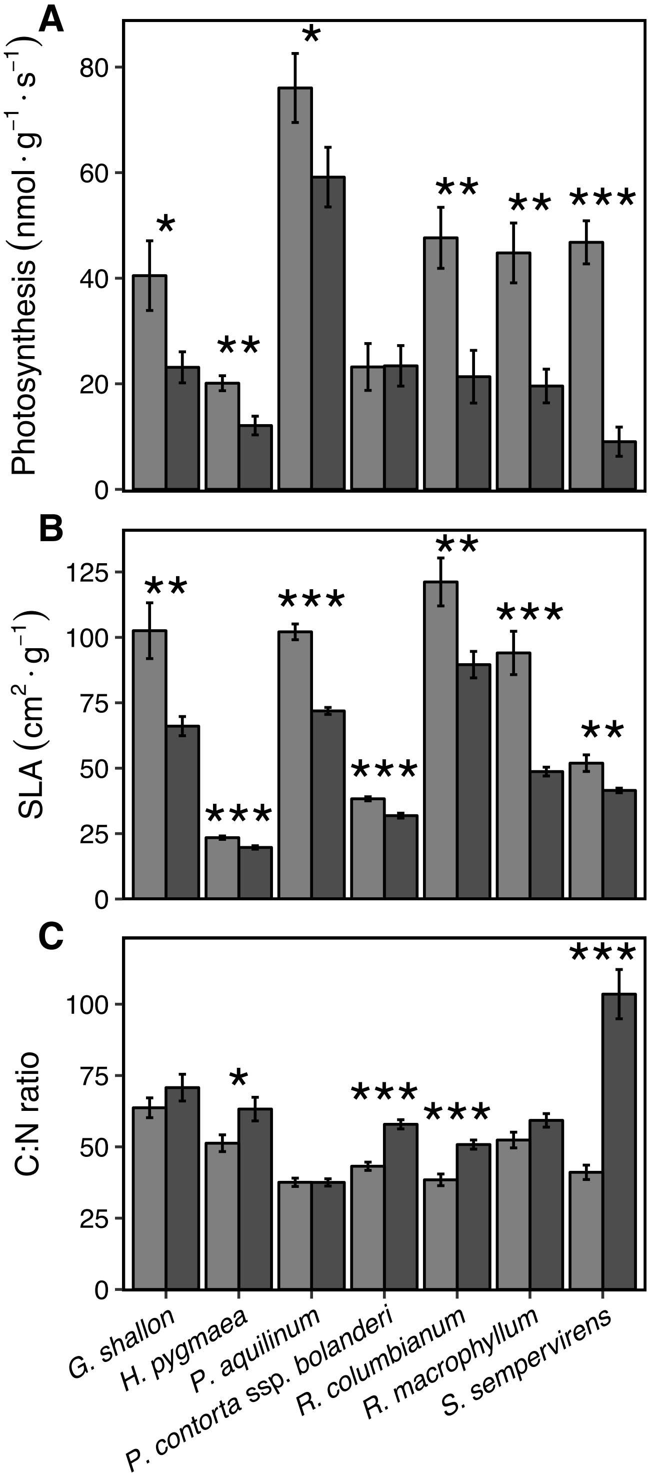

A
Photosynthesis (nmol · g^{-1} · s^{-1})
0
20
40
60
80
*
**
*
**
**
***
B
SLA (cm^{2} · g^{-1})
0
25
50
75
100
125
**
***
***
***
**
***
**
C
C:N ratio
0
25
50
75
100
*
***
***
***
G. shallon
H. pygmaea
P. aquilinum
P. contorta ssp. bolanderi
R. columbianum
R. macrophyllum
S. sempervirens

Figure 5. Relationship of leaf chlorophyll content versus percent nitrogen content (df=12, p=0.003) in both pygmy (black) and control (light gray) plants. Points are average values, with standard error. Note position of pygmy *Sequoia sempervirens* relative to conspecific control.

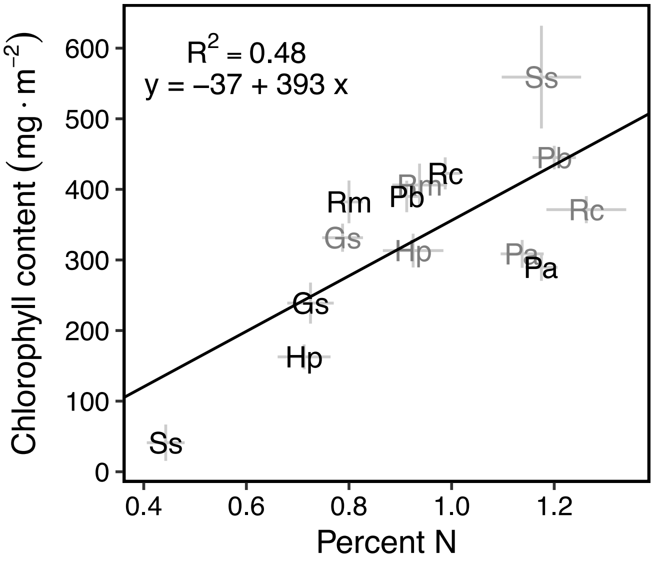
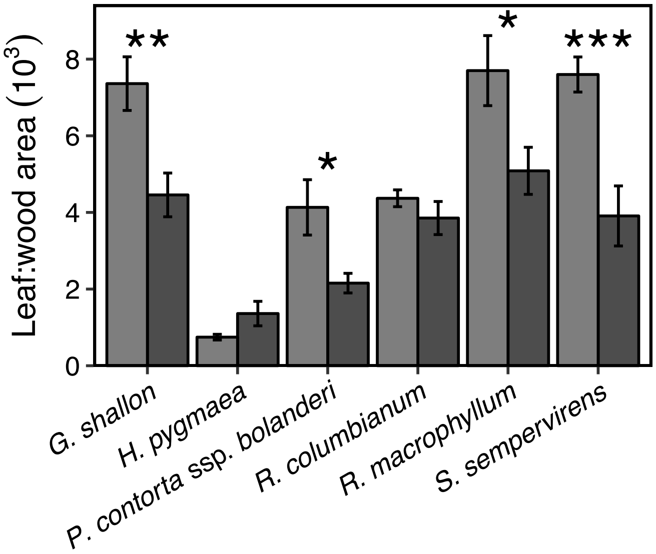


Figure 6. New leaf area produced in a single year, relative to new xylem area produced in the same year, for pygmy (dark gray) and control (light gray) stems (n=8).



Chapter 2

Divergent responses in cavitation resistance to nutrient limitation in the absence of water stress

Abstract

Xylem anatomy and function have large implications for plant growth as well as survival during drought, but the impact of nutrient limitation on xylem is not fully understood. This study uses the pygmy forest in northern California, a plant community that experiences negligible water stress but is severely stunted by low-nutrient and acidic soil, to examine how nutrient limitation affects xylem function in a natural ecosystem. Thirteen key anatomical and hydraulic traits of stems of four species were compared between pygmy forest plants and nearby conspecifics growing on richer soil. In some species, pygmy plants had smaller xylem conduits, higher leaf-specific conductivity (K_L), and lower xylem-specific conductivity (K_S) than conspecific controls. Resistance to cavitation (P_{50}) was higher in pygmy plants of one species, but lower in another. All species had large hydraulic safety margins and low native embolism levels. Compared to conspecific controls, pygmy plants showed species-specific adjustments in xylem form and function. Edaphic stress, even in the near absence of water stress, had large and varied impacts on water transport, with downstream implications for plant growth and survival.

Introduction

The threat of increased drought frequency and severity across many ecosystems worldwide has drawn interest toward predicting plant survival using an understanding of how plant vascular systems function under water stress (Choat et al., 2018). Little is known, however, about how nutrient limitation affects plant water transport, although recent research has been making advances (e.g., Gessler *et al.*, 2017; Zhang *et al.*, 2018). Nutrient limitation is an almost universal phenomenon across plant communities (Elser et al., 2007; Fisher et al., 2012), making the combined effect of nutrient limitation and drought a critical factor in predicting plant survival.

Most commonly, the interaction between nutrient availability and plant water transport is studied in potted plants or via nutrient addition to forest plots, because climate can confound results when plant functioning is measured along naturally-occurring edaphic gradients (Santiago, 2015). Soil nutrient addition generally causes plants to produce larger diameter xylem conduits, if it has any effect on conduit size (Goldstein et al., 2013; Zhang et al., 2018). Larger conduits transport water more efficiently, so soil nutrient addition can also cause an increase in xylem-specific conductivity (K_S), the rate of water transport standardized by xylem area (Zhang et al., 2018). High K_S can allow plants to supply water to a larger canopy of leaves, further supporting high growth rate under high nutrient availability (Goldstein et al., 2013).

Larger diameter conduits also tend to increase xylem vulnerability to cavitation, a process in which air embolisms form and block water transport to leaves (Hacke et al., 2001; Lens et al., 2011). Cavitation resistance is a critical trait that contributes to plant survival during dry conditions: for example, Brodribb and Cochard (2009) found that four conifers species were not able to recover after xylem conductivity was reduced by 50% from cavitation. Zhang *et al.* (2018)'s recent meta-analysis of N deposition experiments showed an overall 20% decrease in resistance to cavitation with higher N availability, in line with predictions based on conduit diameter increases. However, large variability in cavitation resistance responses has been observed, and results vary greatly by species and environment (Goldstein et al., 2013; Santiago, 2015). In hybrid poplar, fertilization with N decreased cavitation resistance, fertilization with P increased resistance, and K addition did not affect cavitation (Harvey and Van Den Driessche, 1997, 1999). In another experiment on five Brazilian savannah species, N addition increased cavitation resistance by up to 50 percent (Bucci et al., 2006). Information about the effects of nutrient limitation on cavitation resistance is currently sparse and contradictory, with different species and experiments showing widely differing responses (Goldstein et al., 2013; Zhang et al., 2018).

Few studies have examined the interaction between nutrient availability and water transport using naturally-occurring nutrient gradients, instead of fertilization or greenhouse experiments. However, some observational studies have still yielded valuable results. When controlling for temperature and precipitation in a meta-analysis of 21 tree species, Borghetti *et al.* (2017) found that higher estimated N deposition rates were associated with larger growth ring width and conduit size, as well as increased conduit density. Coomes *et al.* (2007) found that *Pinus sylvestris* growing on more nutrient-depleted islands in Swedish lakes were shorter and had smaller maximum conduit diameters, but scaling between tree height and conduit size did not vary among islands. Southern hemisphere conifers that are nutrient-limited but not water-limited have smaller conduits than Northern hemisphere conifers at similar degrees of cavitation resistance, and overall they have low cavitation resistance and xylem-specific conductivity compared to the Pinaceae and Cupressaceae (Pittermann et al., 2006).

This study seeks to expand our understanding of the effects of nutrient limitation on water transport by examining a system where nutrient-poor soils occur closely adjacent to more fertile soils. The pygmy forest in Mendocino County, California, is a plant community that occurs in patches within a few kilometers of the coast. It has earned its name due to the extreme stunting of its trees caused by low-nutrient and acidic soils: trees in the pygmy forest may remain only a few meters tall, even after decades of growth (McMillan, 1956; Jenny et al., 1969; Westman, 1975). When pygmy forest plants are grown in soil from nearby, less nutrient-limited sites, their growth rate is much higher than on pygmy forest soil (McMillan, 1956). Conversely, when planted within the pygmy forest, closely related plants from less nutrient-limited communities gain less than 1 cm in height per year (McMillan, 1964). In the space of a few hundred meters, the edges of pygmy forest patches transition to tall *Pseudotsuga menziesii*, *Pinus muricata*, and *Sequoia sempervirens* forests as soil composition changes, while climatic variables remain unchanged (Northup et al., 1998; Izquierdo et al., 2013).

Occurring within a few kilometers of the coast, the pygmy forest receives dense summer fog and experiences mild, rainy winters. Soil moisture remains high throughout the year, and flooding is common in the pygmy forest throughout the winter, due to the shallow hardpan (Sholars, 1979). This seasonal flooding may have an additional impact on plant growth and function on these low-nutrient, acidic soils.

This study compares xylem anatomy, hydraulic function, and cavitation resistance in four woody species, from the pygmy forest and nearby tall coniferous forests. Pygmy plants were predicted to have smaller diameter conduits and lower xylem-specific conductivity compared to conspecific controls, in line with prior research on other systems (Pittermann et al., 2006; Goldstein et al., 2013; Borghetti et al., 2017; Zhang et al., 2018). Although there is a trade-off between conduit size and cavitation resistance (Pratt et al., 2007; Gleason et al., 2015; Jacobsen et al., 2016), it was hypothesized that pygmy plants would have lower cavitation resistance than control plants despite having smaller conduits, because of other aspects of xylem anatomy (Goldstein et al., 2013). Nutrient limitation in the pygmy forest is severe enough to impede growth, and this system offers a rare opportunity to examine the degree to which the stunting modifies xylem structure and function.

Methods

Survey areas and species:

Four species were chosen for analyses based on abundance in the Mendocino pygmy forest and nearby plant communities. *Rhododendron columbianum* (Piper) Harmaja (Ericaceae) is a flowering species in the same genus as a number of other common flowering species in the pygmy forest (Westman, 1975). It is a shrub that grows 1-2 m tall, both inside and outside the pygmy forest (Cary and Pittermann, 2018). *Pinus contorta* Loudon ssp. *bolanderi* (Parl.) Critchf. (Pinaceae), a pine subspecies endemic to the pygmy forest, and *Hesperocyparis pygmaea* (Lemmon) Bartel (Cupressaceae) are two of the most characteristic species in the pygmy forest (McMillan, 1956; Jenny et al., 1969). *Sequoia sempervirens* (D. Don) Endl. (Cupressaceae), the tallest tree species in the world, dominates nearby tall forests, but occurs rarely in the pygmy forest and is not thought to produce viable seeds on pygmy forest soil (Northup et al., 1998). These three conifer species remain only a few meters tall in the pygmy forest, but can reach tens of meters tall on more fertile soil (Cary & Pittermann, 2018; Fig 1).

Three sites were selected for sampling, two from stunted pygmy forest areas and one from a nearby tall coniferous forest. Plants sampled from the tall forest site are referred to here as controls, in order to distinguish them from pygmy plants. Pygmy individuals of all species except *S. sempervirens* were sampled from Van Damme State Park (latitude 39.263383, longitude -123.736765, elevation 195 m). Control individuals of all species were sampled from coniferous forests inside Jug

Handle State Reserve (39.378074, -123.805218, 56m), and pygmy *S. sempervirens* were sampled from the edge of the pygmy forest in Jug Handle State Reserve (39.372800, -123.790533, 84m). All sites were within 13 km of each other and 2-4 km of the coast.

Soil fertility is measurably greater in the control site than either pygmy site. Previous research found higher N, P, Ca, Mg, organic matter, and pH on the second marine terrace, where this study's control site is located, than the pygmy forest sites on terraces three and five, where this study's pygmy forest sites are located (Northup *et al.*, 1998; Izquierdo *et al.*, 2013; Uroz *et al.*, 2014; see Cary & Pittermann, 2018, for table).

All samples were collected from mature, healthy-looking plants, and only full-sun branches were selected. Branches (n = 7 or 8) were sampled from 0.5 m to 1.5 m above the ground to control for effect of gravity on water potential. Sampling and analyses on fresh samples occurred in late June through early August 2015, the early to mid growing season in the pygmy forest (Sholars, 1979).

Hydraulic Conductivity and Vulnerability Curves:

Selected stems were first bagged in the morning for at least 30 minutes to relax xylem tension (Wheeler et al., 2013) before being cut underwater at least 30 cm away from the section desired for analyses. Stem sections used for analyses were roughly 8 mm in diameter. Stems were transported back to the lab in bags with wet paper towels, before being refrigerated overnight. The next day, stems were cut back by 30 cm underwater, and stem conductivity was measured using a hydraulic apparatus (Sperry et al., 1988) with a pressure head of 5 kPa and a stem length of 16.2 cm, to produce K_{native} (hydraulic conductivity in the field). Stems were then degassed underwater overnight in a vacuum at 5 kPa to remove embolism (McCulloh et al., 2014; Pittermann et al., 2018), and stem conductivity was re-measured to produce K_{max} (hydraulic conductivity after embolism removal). Resin ducts in *P. c. bolanderi* were plugged by refrigerating stems until resin hardened, then trimming the ends of the stems to remove any resin clogging conduits at the end.

Within 5 days of collection, stems were used to generate vulnerability curves via the centrifugation method (Alder et al., 1997). No effect of storage (e.g., a drop in conductivity from K_{native}) was observed during this time range. Stems were trimmed to 14.2 cm to fit rotor size and remove any possibly clogged conduits just before beginning vulnerability curves. Stems were then spun at intervals of 1 MPa or 2 MPa, depending on the species, for 4 minutes at each interval. Hydraulic conductivity was measured between spins, with measurements starting less than 2 minutes after removal from centrifuge to prevent xylem refilling. P_{50}, the water potential at which 50% of conductivity is lost, was calculated for each stem by fitting data points to a Weibull function (Neufeld et al., 1992; Pammenter and Willigen, 1998).

An approximately 5 cm section of each stem, basal to the portion used for centrifuge curves, was used for dye perfusion to measure functional xylem (Sperry and Tyree, 1988; Jacobsen, 2005). These stems were stored in water in a refrigerator, but not degassed. Within 7 days of collection, acid fuchsin (Sigma-Aldrich, St. Louis, MO, USA) was perfused through these stems at 10 kPa, until the dye began to show through the other side of the stem. Stems were then immediately frozen and later cut in increments of 1 cm. A section 1-2 cm from the end of the stem the dye entered was used for cross-sectional functional xylem area, depending on branching patterns and clarity of dye pattern. The cross-sectional area dyed by fuchsin was then measured using the software Fiji (Schindelin et al., 2012). K_S, xylem specific conductivity, was calculated as K_{max} divided by the cross-sectional area dyed by fuchsin. K_L, leaf specific conductivity, was calculated as K_{max} divided by downstream leaf area. Huber values were calculated as downstream leaf area divided by functional xylem area (Huber, 1928). Native embolism levels were calculated as $(K_{max}-K_{native})/K_{max}$.

Field water potentials were measured using a Scholander pressure chamber (PMS Instrument Co., St Albany, OR, USA) on a hot sunny day in September 2014, near the end of the dry season of an exceptional drought year (Griffin and Anchukaitis, 2014). This water potential was assumed to be close to the minimum field water potential experienced by these plants. Hydraulic safety margin was calculated for each species as minimum water potential measured in that species minus P_{50}.

Xylem anatomy:

After stems were used to generate vulnerability curves, they were frozen and stored, before being slowly thawed in cold water. *Sequoia sempervirens*, *H. pygmaea,* and *P. c. bolanderi* stems were boiled for 15 minutes to soften them before being cross sectioned. All species were hand sectioned, dyed for 5-7 minutes in Toluidine Blue O (EMD Chemicals Inc., Darmstadt, Germany), washed in water, and mounted for microscopy (see Fig 1 for example photos). Three sectors of the functional xylem, typically spanning 5 to 20 growth rings, were photographed using a Motic BA400 compound microscope (JH Technologies, San Jose, CA). Care was taken to avoid compression wood.

The diameter of conduits in 1-2 files for each radial sector were measured, for an average of 217 conduits diameters per stem, across all functional growth rings. Files measured for each growth ring were selected using a random number generator and were re-selected every growth ring. Diameters were calculated by measuring the area inside of a conduit in Fiji and then calculating diameter with the assumption that the conduit is circular (Scholz et al., 2013). Mean hydraulic diameter was calculated as $\Sigma(b^5/b^4)$, where b = lumen diameter (Sperry et al., 1994). Double wall thickness was measured at two locations on conduits that were within 10% of the mean hydraulic diameter (averaging n=36 for each stem). Only wall shared by two water-conducting xylem conduits were measured. Thickness: span ratio, $(t/b)^2$, was calculated, where t = double wall thickness and b = conduit lumen diameter (Hacke et al., 2001). $(t/b)^2$ was also measured for randomly selected fibers or vasicentric tracheids adjacent to vessels in *R. columbianum* (n=30 per stem). In *R. columbianum*, vessel grouping index was measured by counting the number of groups of vessels and dividing the total number of vessels by the number of groups (Carlquist 2001). The width of all functional growth rings was measured in 2-3 locations per stem in all four species.

Statistics:

Cavitation vulnerability curves were fit to a Weibull function (Neufeld et al., 1992; Pammenter and Willigen, 1998) using the statistical software package R (R Core Team 2017). Traits were compared using Welch's t-tests, after confirming normality. Relationships between traits were compared using ordinary least squares linear regressions. Graphs were produced in the R packages ggplot2 (Wickham 2009) and cowplot (Wilke 2019). All reported errors are standard error, indicating confidence interval for population mean, with each population defined as one species at one site.

Results:

Hydraulic conductivity and Vulnerability Curves:

Hydraulic traits differed between conspecific pygmy and control plants in most species. Huber values were lower in pygmy *R. columbianum* and *S. sempervirens* plants compared to control plants ($P<0.0001$), indicating that pygmy plants had less leaf area relative to xylem area (Fig 2a). Leaf-specific conductivity (K_L) was higher in pygmy *H. pygmaea* and *S. sempervirens*, suggesting that pygmy plants of these species can supply more water to each leaf than control plants, under identical conditions ($P<0.05$; Fig 2b). Xylem-specific conductivity (K_S) differed only in *R. columbianum*, where pygmy plants had lower water transport efficiency per cross-sectional xylem area ($P<0.05$; Fig 2c). No measured hydraulic parameters differed between pygmy and control *P. c. bolanderi*.

Cavitation resistance also varied between pygmy and control plants. Pygmy *R. columbianum* were more vulnerable to cavitation than controls: pygmy plants reached 50% loss of water transport efficiency (P_{50}) at 1 MPa less water stress than control plants (Fig 3a). Pygmy and control *H. pygmaea* had similar P_{50} (Fig 3b). Pygmy and control *P. c. bolanderi* also did not significantly differ (Fig 3c). *Sequoia sempervirens* showed the greatest differences: pygmy *S. sempervirens* had an average P_{50} over 2 MPa more negative than controls (Fig 3d).

Midday water potential of pygmy and control plants of the five species near the end of the dry season averaged -0.5 MPa, with a minimum water potential of -1.2 MPa, observed in a pygmy *H. pygmaea* stem (see species averages presented in Table 1). Pygmy *P. c. bolanderi* had slightly less negative water potentials than control plants, but water potential did not differ between pygmy and control plants in any of the other species. These results agree with past extensive sampling that has shown that water potentials of pygmy forest plants near our study sites remain more hydrated than -1.8 MPa (Sholars, 1979).

Native embolism, the percentage of water transport blocked by embolism in the field, did not differ significantly from zero in *P. c. bolanderi* and *R. columbianum* ($P>0.10$). Native embolism was significantly greater than zero in pygmy and control

H. pygmaea and *S. sempervirens* ($P<0.02$), but averaged less than 8% loss of conductivity for each.

Hydraulic safety margin, the difference between minimum water potential experienced in the field and P_{50}, was large in all species. Hydraulic safety margin was slightly lower in pygmy *R. columbianum* compared to controls (2.8 MPa in pygmy vs. 3.7 in control plants). Pygmy and control *P. c. bolanderi* hydraulic safety margins were 2.8 MPa and 3.1 MPa, respectively, while *H. pygmaea* safety margins were 7.1 MPa in pygmy plants, and 6.3 MPa in controls. Pygmy *S. sempervirens* had a 6.0 MPa safety margin, compared to 3.3 MPa in controls.

Xylem anatomy:

Xylem anatomy differed between pygmy and control plants. Pygmy plant growth rings were significantly smaller than controls in three out of the four species ($P<0.04$ for all three; Fig 4). Pygmy *H. pygmaea* and *S. sempervirens* had significantly smaller diameter conduits ($P<0.02$; Fig 5a), while pygmy *H. pygmaea*, *S. sempervirens*, and *R. columbianum* conduits had a smaller hydraulic mean diameter than controls ($P<0.04$; Fig 5b). Double wall thickness did not vary significantly in any species (Fig 5c), but $(t/b)^2$, an estimate of resistance to implosion (Hacke et al., 2001), was higher in pygmy *H. pygmaea* ($P=0.03$; Fig 5d). Vessel grouping index, a measure of how connected vessels are to each other (Carlquist, 2001), did not vary in *R. columbianum*, the only angiosperm examined, and it was approximately 1.45 for both pygmy and control plants ($P=0.45$). $(t/b)^2$ of fibers adjacent to vessels in *R.*

columbianum and averaged 0.49 in pygmy plants and 0.56 in controls and did not differ significantly (P=0.52).

Across individuals of all four species, xylem conduit diameter was a significant predictor of P_{50} ($F_{1,62}$=15.8, P=0.0002), although adjusted R^2 was 0.19. Conifers and angiosperms differ in their relationship between anatomy and P_{50} (Hacke et al., 2001), so the relationship was also analyzed using only the three conifer species. Conduit size was not a predictor of cavitation resistance in conifers ($F_{1,46}$=1.5, P=0.23, R^2=0.01, Fig 6a). Similarly, when the vessel-bearing angiosperm species was included, $(t/b)^2$ was a significant predictor of P_{50} ($F_{1,62}$=9.8, P=0.002), but explained even less of the variance in P_{50} with an adjusted R^2 of 0.12. When only the conifer species were included, $(t/b)^2$ did not predict P_{50} ($F_{1,46}$=0.24, P=0.63, R^2=-0.02, Fig 6b). Within each species, conduit size did not predict P_{50} ($F_{1,14}$<1.2, P>0.30, R^2<0.02 for all four species; see Fig 6c for *R. columbianum*). Neither did $(t/b)^2$ predict P_{50} within any of the four species ($F_{1,14}$<0.6, P>0.45, R^2<0.01 for all; see Fig 6d for *R. columbianum*).

Discussion

The pygmy forest presents an interesting combination of stressors. Plant growth in the pygmy forest is greatly stunted by nutrient limitation; at the same time, water stress is negligible, even at the end of the dry season of an exceptional drought year (Table 1). The large hydraulic safety margins and low native embolism levels support the conclusion that both control and pygmy sites experience no meaningful water stress. Despite the lack of water stress, pygmy plants of all species showed substantial reductions in conduit diameter or growth ring thickness, and these shifts have implications for carbon allocation. In some cases, pygmy plants had a third or even a quarter of the Huber values of conspecific controls (Fig 2a), indicating much lower investment in leaf tissue relative to xylem tissue. Leaves are plants' main photosynthetic organ, so a reduction in leaf area is correlated with a decrease in growth rate (Poorter and Remkes, 1990; Cary and Pittermann, 2018). In *R. columbianum*, pygmy plants had lower K_S (Fig 2c) but compensated by building fewer leaves for the same xylem area (Fig 2a) to keep K_L constant (Fig 2b). Cavitation resistance is a critical predictor for survival during drought (Choat et al., 2018), and pygmy plants of two species showed large (25-50%) shifts in cavitation resistance, although resistance increased in one species and decreased in another (Fig 3).

Across species, responses in functional traits, such as K_L, K_S, and P_{50}, were less consistent than those of anatomical traits. This disparity is likely because K_L, K_S, and P_{50} are all affected by a number of anatomical traits, some of which varied consistently between pygmy and control plants, such as hydraulic mean diameter; some of which consistently did not vary, such as wall thickness; and some of which could not be measured for this study, such as xylem sap content, calcium content of xylem walls and pits, and pit membrane porosity (Rockwell et al., 2014). Neither conduit diameter nor $(t/b)^2$ explained the variation in P_{50} (Fig 6), even though these traits are classically considered good predictors of P_{50} (Hacke et al., 2001), further backing the conclusion that responses in anatomical traits did not necessarily translate to responses in related functional traits.

Cavitation resistance was the only trait where stunting caused directly contrasting responses in different species. In the one angiosperm species examined, *R. columbianum*, pygmy plants were more vulnerable, while in *S. sempervirens*, one of the two Cupressaceae species, pygmy plants were more resistant (Fig 3). Angiosperm xylem typically includes both vessels, which conduct water, and fibers, which provide mechanical strength and contribute to cavitation resistance (Jacobsen, 2005), while conifer conduits comprise only tracheids, which conduct water and provide support simultaneously (Pittermann et al., 2006; Sperry et al., 2006). Given the fundamentally different nature of angiosperm and conifer xylem, it is possible that the two taxonomic groups have generally divergent responses to nutrient limitation, in that angiosperms may respond to high nutrient availability by reinforcing xylem, but gymnosperms may respond to low nutrient availability by reinforcing xylem. However, more research would be needed to elucidate taxa-specific responses to nutrient availability.

Sequoia sempervirens, the tallest tree in the world, struggles to survive on pygmy forest soils in a way that the other species examined do not. Other species maintain similar photosynthetic rates between pygmy and control plants, but pygmy *S. sempervirens* have negligible photosynthetic rates and water-use efficiency compared to controls (Cary and Pittermann, 2018). *Sequoia sempervirens* is not thought to produce viable seeds when growing on pygmy forest soil (Northup et al., 1998), and it is rare in the pygmy forest, although it is the dominant species nearby forests. However, despite the species' struggle to photosynthesize and grow in the pygmy forest, pygmy *S. sempervirens* cavitation resistance was substantially greater than controls (Fig 3d). It appears that tracheid wall strength and pit membrane attributes, such as margo strength and torus overlap (Pittermann, 2010), were not compromised by nutrient limitation. Pygmy *S. sempervirens* did have smaller conduits than controls (Fig 5a). Typically, smaller conduits are more resistant to cavitation (Hacke et al., 2000; Pittermann et al., 2006; Pratt et al., 2007; Gleason et al., 2015; Jacobsen et al., 2016). Pygmy *S. sempervirens* had smaller diameter conduits and more negative P_{50} than conspecific controls, in line with the trade-off between conduit size and cavitation resistance and also in line with average response to nutrient limitation in N deposition experiments (Zhang et al., 2018).

Rhododendron columbianum, however, did not follow the trade-off between conduit size and cavitation resistance. Pygmy *R. columbianum* had smaller mean hydraulic diameters than controls, but also was more vulnerable to cavitation (Fig 3a, Fig 5b). Neither vessel grouping index nor fiber $(t/b)^2$ can explain the difference in cavitation resistance between pygmy and control *R. columbianum*. It may be that pygmy *R. columbianum* have lower cavitation resistance because their vessel and fiber walls are structurally weaker due to nutrient limitation. Pygmy forest soil is depleted in calcium, an important component of cell walls (Northup et al., 1998). Low calcium availability may limit lignin production during xylem development (Lautner et al., 2007), and disruption of calcium bonds in xylem increases cavitation vulnerability (Herbette and Cochard, 2010). Alternatively, pit membrane density, aperture size, and depth, which affect cavitation resistance (Lens et al., 2011), may be impacted by nutrient limitation.

Flooding, which is common in the pygmy forest due to its shallow hardpan (Jenny et al., 1969; Sholars, 1979), may also contribute to smaller conduit size and greater cavitation vulnerability, which was observed in pygmy *R. columbianum*. Venturas *et al.* (2013) found that *Ulmus laevis*, an elm species that grows in waterlogged soils, had smaller conduits, but a less negative P_{50}, than *Ulmus glabra*. Greater vulnerability to formation of air embolism may even be a benefit to plants growing on flooded soils without aerenchyma: higher air content in stems allows greater infiltration of much-needed oxygen (Sorz and Hietz, 2006).

There were no differences between control and pygmy *P. c. bolanderi* in any measured trait, except for growth ring width. *Pinus contorta* ssp. *bolanderi* is edaphically specialized and has difficulty surviving when grown in more fertile soils (McMillan, 1956). It is likely that this pygmy forest endemic has specialized to the point where it does not have the plasticity or genetic variability to alter its xylem architecture and take advantage of higher-nutrient soils. Plants that have adapted to infertile soils are often less capable of responding to nutrient addition than plants from more fertile systems (Mattson, 1980; Chapin III et al., 1986).

Even in the virtual absence of water stress, nutrient limitation had large and varied impacts on the xylem anatomy and function of pygmy plants, with potential implications for whole-plant growth and survival. The pygmy forest might never experience a drought severe enough for the plants’ altered cavitation resistance to affect their survival, given their water status during the 2014 drought. However, there are many plant communities across the globe that are both nutrient-limited and water-limited, where shifts in cavitation resistance could affect survival. The pygmy forest, while unusually stunted, grows on soils no more nutrient-depauperate than soils in a number of tropical and subtropical regions (Anderson, 1981; Foulds, 1993; Oliveira et al., 2015). Therefore, nutrient limitation could be a large factor on xylem structure and function in these regions as well. This appears to be the case in Southern Hemisphere conifers growing on nutrient-limited but not water-limited soils (Pittermann et al., 2006). The impact of nutrient limitation on xylem form and function appears complex and variable, changing with location, environment, and taxa, but a mechanistic understanding of the processes underlying these responses has the potential to improve knowledge of nutrient-limited plant communities and guide predictions about plant survival during drought.

Table 1: Midday water potentials, in MPa with standard error, for the five study species, measured in September 2014 (n=7 or 8 for all).

Species	Pygmy	Control	*P*-value
Hesperocyparis pygmaea	-0.64 ± 0.13	-0.80 ± 0.09	0.351
Pinus contorta ssp. *bolanderi*	-0.48 ± 0.14	-0.96 ± 0.04	0.012
Rhododendron columbianum	-0.20 ± 0.03	-0.29 ± 0.06	0.210
Sequoia sempervirens	-0.41 ± 0.01	-0.49 ± 0.08	0.345

Figure 1: Control (a) and pygmy (b) *Rhododendron columbianum* leaves, exemplifying the variation in leaf area supported by control and pygmy plants. Control (c) and pygmy (d) *R. columbianum* xylem photos taken at 400x magnification, after staining in toluidine blue. Control (e) and pygmy (f) *Sequoia sempervirens* xylem; note small growth rings on pygmy individual. Control (g) and pygmy (h) *S. sempervirens* trees. The control plant was measured at 34 m, and the pygmy plant at 1.8 m.

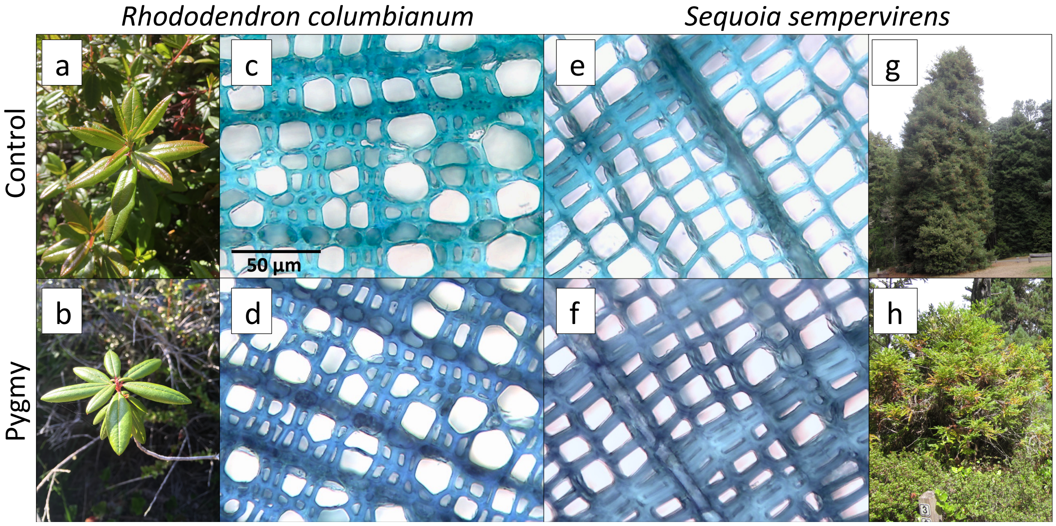


Figure 2: Boxplots of hydraulic traits in control (white) and pygmy (grey) plants of four species. (a) Huber values (leaf area divided by functional xylem area that supports it). (b) Leaf-specific conductivity (K_L), water transport efficiency divided by downstream leaf area, for control and pygmy plants. (c) Xylem-specific conductivity (K_S), water transport efficiency divided by functional xylem area. Significance of Welch's t-test comparing pygmy and control plants of the same species denoted by asterisks: *, P <0.05; **, P <0.01; ***, P <0.001.

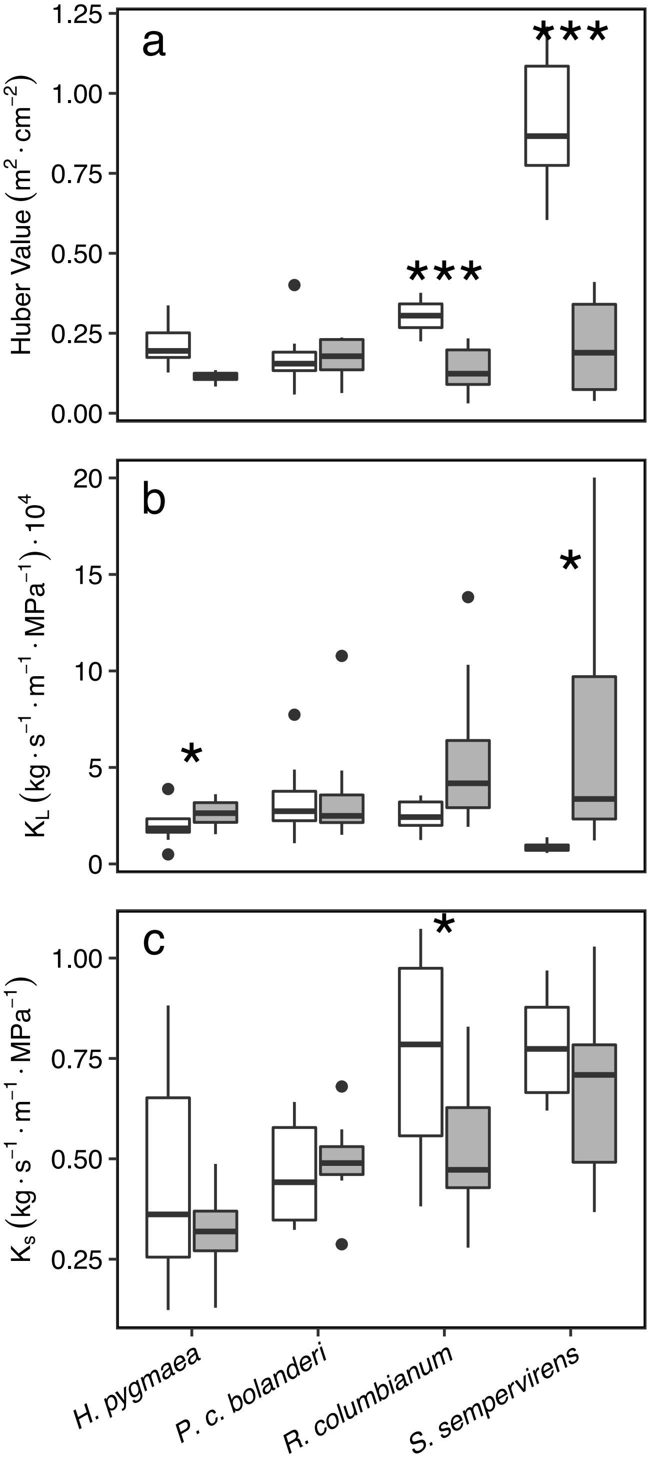

a
***
***
Huber Value ($m^2 \cdot cm^{-2}$)
1.25
1.00
0.75
0.50
0.25
0.00
b
*
*
K_L ($kg \cdot s^{-1} \cdot m^{-1} \cdot MPa^{-1}$) $\cdot 10^4$
20
15
10
5
0
c
*
K_s ($kg \cdot s^{-1} \cdot m^{-1} \cdot MPa^{-1}$)
1.00
0.75
0.50
0.25
H. pygmaea
P. c. bolanderi
R. columbianum
S. sempervirens

Figure 3: Vulnerability curves of pygmy (black triangles and solid lines) and control (grey circles and dashed lines) plants, showing resistance to cavitation in (a) *Rhododendron columbianum*, (b) *Hesperocyparis pygmaea*, (c) *Pinus contorta* ssp. *bolanderi*, and (d) *Sequoia sempervirens*.

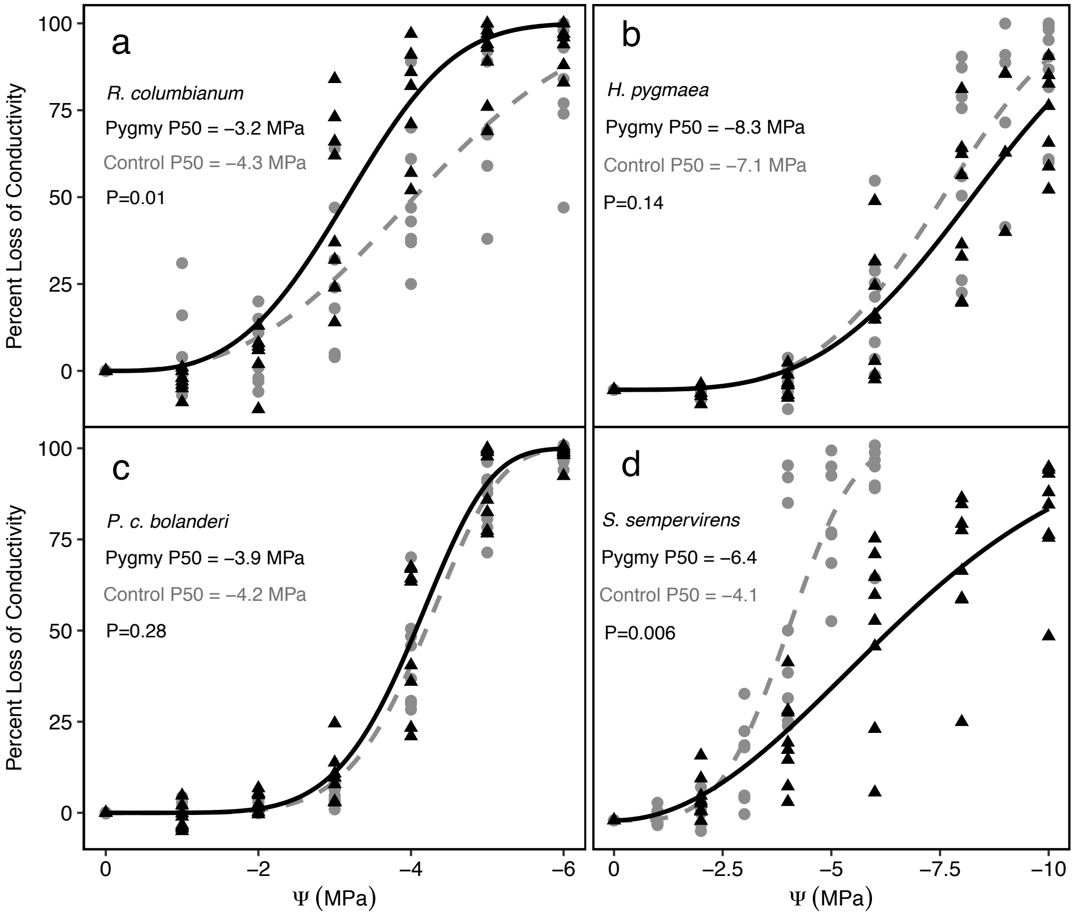


Figure 4: Width of functional growth rings in control (white) and pygmy (grey) plants. Significance of Welch's t-test comparing pygmy and control plants of the same species denoted by asterisks: *, P <0.05; **, P <0.01; ***, P <0.001.

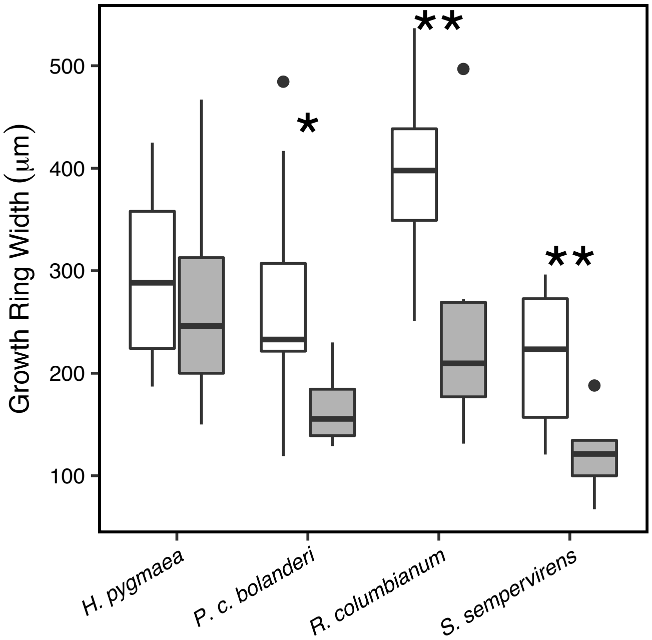


Figure 5: Boxplots of xylem anatomical traits in control (white) and pygmy (grey) plants. (a) conduit diameter. (b) Hydraulic mean diameter, calculated as $\Sigma(b^5/b^4)$, where b = conduit diameter. This statistic is weighted toward larger conduits, which contribute more to water transport. (c) Double wall thickness, measured on walls between two water-conducting conduits that were within 10% of the hydraulic mean diameter. (d) Thickness-to-span ratio, $(t/b)^2$, where t = double wall thickness, and b = conduit diameter. This metric approximates conduit resistance to implosion during water transport.

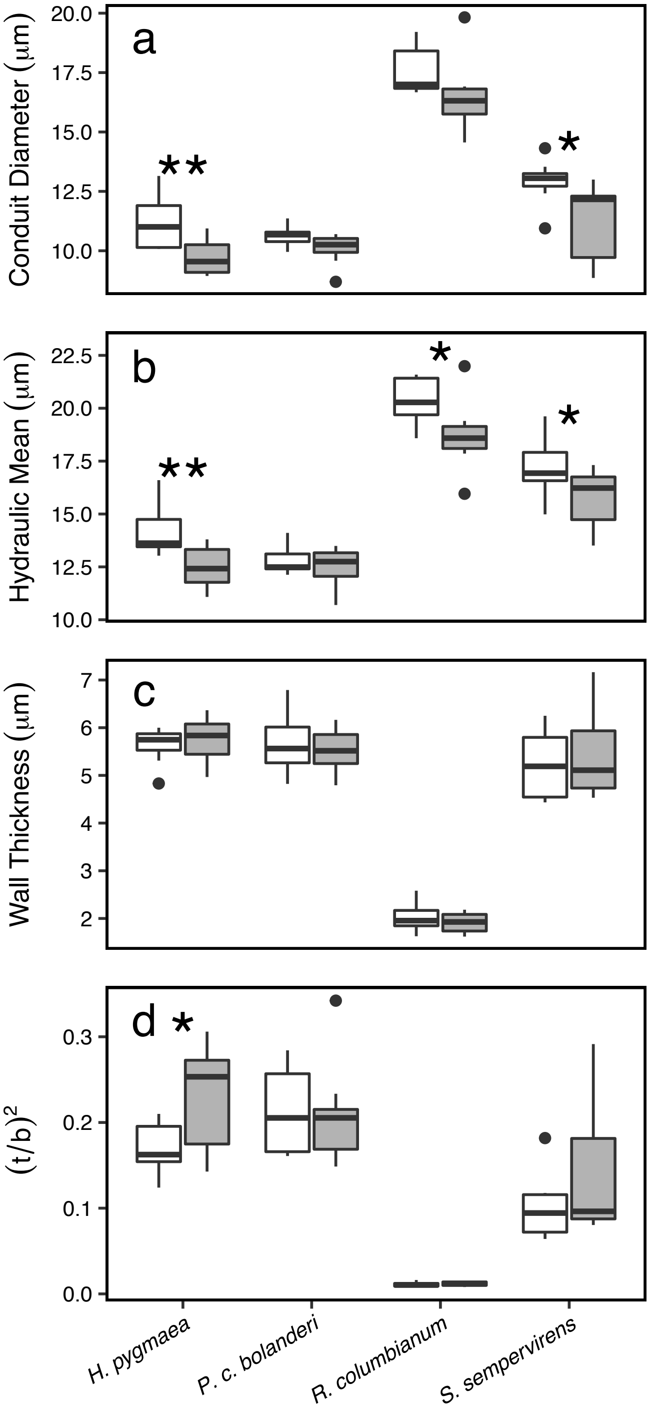
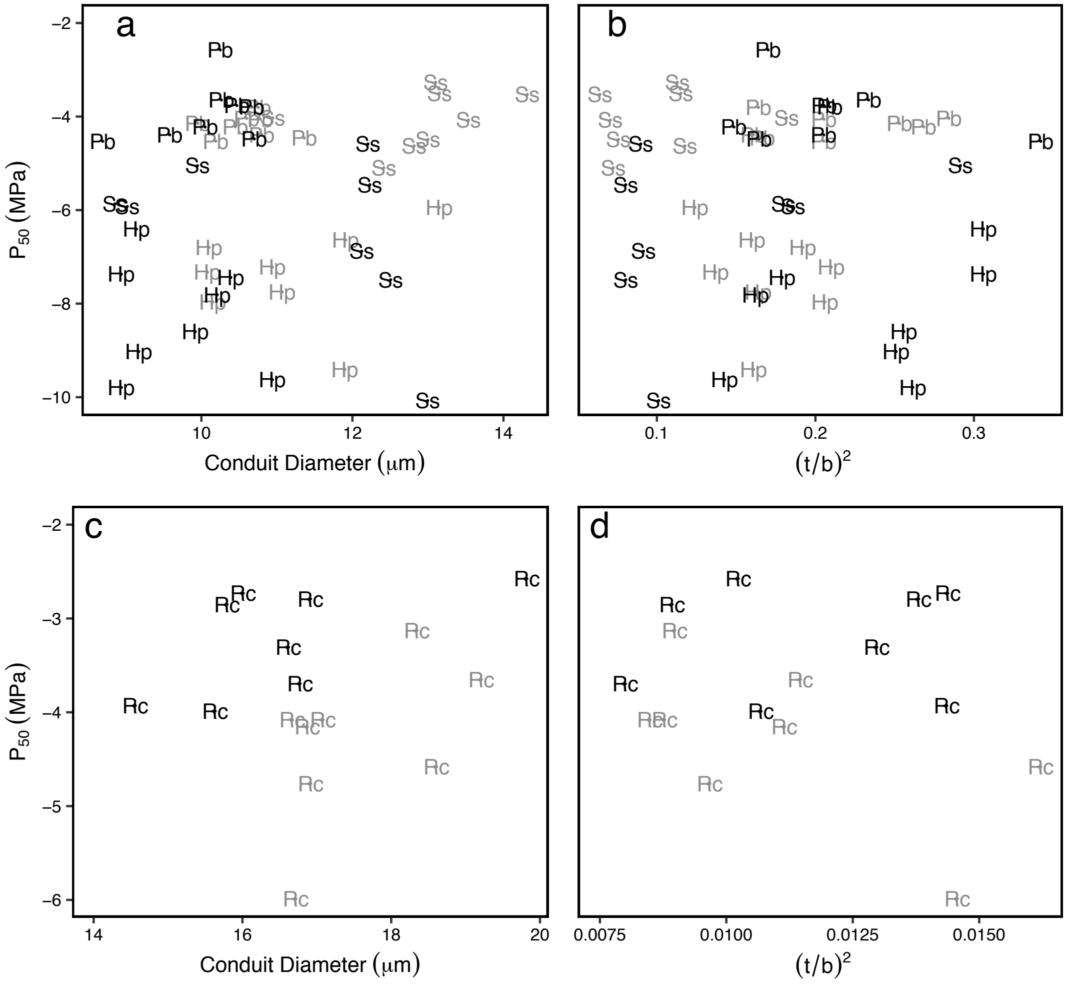

a
b
c
d
Conduit Diameter (μm)
Hydraulic Mean (μm)
Wall Thickness (μm)
$(t/b)^2$
20.0
17.5
15.0
12.5
10.0
22.5
7
6
5
4
3
2
0.3
0.2
0.1
0.0
**
*
H. pygmaea
P. c. bolanderi
R. columbianum
S. sempervirens

Figure 6: Scatterplot comparisons between P_{50} and anatomical traits, including pygmy (black) and control (grey) individuals of four species. Hp = *Hesperocyparis pygmaea*, Pc = *Pinus contorta* ssp. *bolanderi*, Rc = *Rhododendron columbianum*, and Ss = *Sequoia sempervirens*. (a) Relationship between P_{50} and xylem conduit diameter in tracheid-bearing conifer stems. (b) Relationship between P_{50} and $(t/b)^2$ in conifers. (c) Relationship between P_{50} and xylem conduit diameter in vessel-bearing *Rhododendron columbianum* stems. (d) Relationship between P_{50} and $(t/b)^2$ in *R. columbianum*.



Chapter 3

Community composition and physiology along an edaphic gradient in California's pygmy forest

Abstract

The pygmy forest in coastal northern California and the nearby plant communities present a unique opportunity to study environmental filtering along an edaphic gradient, due to large shifts in soil fertility and vegetation type within a small geographic range, with negligible water limitation throughout. At 15 100m^2 plots in the pygmy forest, we examined phylogenetic relatedness, soil nutrient availability, pH, and aluminum toxicity, as well as four physiological traits that are key to describing where species fall along a resource-conservative to resource-acquisitive spectrum. We also assessed phylogenetic relatedness at 15 plots in closely adjacent tall forests. Plants in the pygmy forest were more closely related to each other than plants in the tall conifer forests. Within the pygmy forest, phylogenetic diversity decreased as soils became more stressful, and plots with lower phylogenetic diversity had more resource-conservative trait values. Results suggest that low soil fertility imposes an environmental filter on which species can grow and survive in the pygmy forest, and the strength of this filter increases with increasing aluminum toxicity and decreasing soil organic matter.

Introduction

Cases of severe nutrient limitation are widespread throughout the world, from the newest volcanic soils, low in organically-derived N, to ancient, P-depauperate soils that were formed before Pangaea and have never been scoured by glaciers (see Walker and Syers 1976). These soils can direct the evolutionary trajectory of the plants that grow on them (Fine et al. 2013), alter plant community composition (Fine and Kembel, 2011), and shape entire ecosystems (Orians and Milewski, 2007).

Edaphic chronosequences, sequences of soil that vary along a gradient of age, are an excellent way to study shifts in plant communities with changing soil fertility. The Hawaiian islands form an over 4 million year chronosequence, stretching from N-depleted to P-depleted (Treseder and Vitousek, 2001). Community composition shows large shifts with increasing soil age on the younger soils (Aplet et al., 1998), and fertilization of older soils dramatically increases epiphytic species richness (Benner and Vitousek, 2007). An over 2 million year chronosequence in southwestern Australia also shows large changes in community composition: there, older, more acidic soils have greater species richness (Laliberte et al., 2014).

The coast of Mendocino County, California, contains an edaphic chronosequence with a twist: on the older soils, plant growth is severely stunted by the acidic, nutrient-poor soil (McMillan, 1956; Jenny et al., 1969). Conifers can grow for decades and only reach a meter tall, creating a bonsai-like appearance and earning the plant community its name: the pygmy forest (Jenny et al., 1969; Fig 1). The chronosequence is short. Near the town of Mendocino, five marine terraces rise from the ocean, increasing in age with greater distance from the ocean (Jenny et al., 1969). The youngest two terraces have no pygmy forest, but the older three, ranging in age from roughly 200,000 years old to over 330,000 years old (Merritts et al., 1991), contain patches of pygmy forest. Wherever soil has been disturbed, commonly by increased weathering rates on sloped surfaces (Jenny et al., 1969), soil fertility increases and trees grow tall. The pygmy forest, although it cannot be older than the marine terraces it is found on, is considered a stable, post-successional ecosystem (Jenny et al., 1969). Few species specialize on its harsh soils: the pygmy forest has only two endemic subspecies, *Arctostaphylos nummularia* ssp. *mendocinoensis* and *Pinus contorta* ssp. *bolanderi* (Westman, 1975; Aitken and Libby, 1994; Parker et al., 2007). Many species that grow in the nearby tall conifer forests do not occur within the pygmy forest. Acidity has previously been reported to be a critical predictor for whether or not soil supports a pygmy forest community (Westman, 1975). Additionally, differences observed between common and rare species have hinted that physiological limitations may prevent more species from becoming common in the pygmy forest (Cary and Pittermann, 2018).

Community assembly may be described as resulting from three filters: a historical filter due to limitations in which species can disperse to a site, a physiological filter due to which species have the adaptations necessary to survive in an environment, and an ecological filter due to interactions with other organisms present at the site ((Lambers, Chapin, et al., 2008). The last two interact with each other, because herbivory and pathogen defense are affected by physiological response to environmental conditions (e.g., Dohmen et al. 1984, Plaut et al. 2012) and competition interactions can have different outcomes on different soils (Fynn et al., 2005). Restriction of community composition mediated by environmental conditions, via both physiological and ecological processes, is referred to as environmental or habitat filtering. The presence of an environmental filter is presumed when species in a given community have phylogenetic histories more similar to each other than would happen by chance alone.

Environmental filters may be driven by selection for phylogenetically conserved traits, in which case, sites will have more closely related species and a smaller range in trait values across species (Kraft et al., 2007). However, trait ranges may be reduced without a change in phylogenetic relatedness if traits important for survival and competitive ability at that site do not show a phylogenetic signal, either due to high levels of plasticity or convergent evolution (Kraft et al., 2007; Cavender-Bares et al., 2009). Furthermore, identifying the traits selection is acting upon and interpreting patterns may be difficult due to complex biotic interactions and evolution of differing phylogenetic strategies to achieve the same goal (Cavender-Bares et al., 2009; Adler et al., 2013). Results may be further complicated by spatial or temporal variation in traits or selection, and interactions may vary idiosyncratically by community (Adler et al., 2013).

In this study, we examine functional trait patterns in woody plants along a soil fertility gradient in the Mendocino pygmy forest, in order to examine their relationship with community composition. We selected four traits that were found to vary between plants growing in the pygmy forest and tall conspecifics (Chapter 1; Chapter 2). Specific leaf area (SLA), leaf area divided by leaf dry mass, is a key part of the worldwide leaf economics spectrum, which describes a gradient between resource conservative and acquisitive strategies (Wright et al., 2004). Low SLA arises from thicker leaves, denser leaf tissue, or both, and may protect leaves from damage at the cost of slower growth rates. In other words, low SLA is a resource-conservative strategy. Huber value, the ratio of leaf area to xylem area that supports it, indicates the relative investment in leaves vs. wood. Low Huber values may constrain growth rates, because leaf area is positively correlated with growth rate (Poorter and Remkes, 1990), or they may reflect decreased allocation to nutrient-expensive leaf tissue (Poorter and Nagel, 2000). Xylem-specific conductivity is water transport efficiency standardized by xylem area, and it is weakly negatively correlated with resistance to drought-induced xylem dysfunction (Hacke et al., 2001; Pratt et al., 2007; Gleason et al., 2015; Jacobsen et al., 2016). Leaf-specific conductivity, water transport efficiency standardized by leaf area, reflects the amount of water a plant can transport to each leaf under certain conditions. Plants with high SLA, high Huber values, and high water transport efficiency are more resource-acquisitive and will likely have higher growth rates and competitive ability (Poorter and Remkes, 1990; Fan et al., 2012; Kunstler et al., 2016). However, plants with those traits may perform poorly on nutrient-poor soils, which generally favor a resource-conservative strategy (Coley et al., 1985; Wright et al., 2004).

We hypothesized that the pygmy forest would exhibit environmental filtering when compared to adjacent tall forests, and that within the pygmy forest, there would be strong associations between phylogenetic relatedness, soil variables, and physiological trait values. Specifically, we hypothesized that (1) plants in the pygmy forest would be more closely related to each other than plants in nearby tall conifer forests, reflecting environmental filtering due to the low-nutrient, acidic soils of the pygmy forest. We also hypothesized that (2) within the pygmy forest, phylogenetic relatedness would increase as soils became more stressful, due to environmental filtering increasing in strength and restricting the plant community to only a few taxa. We predicted that (3) functional diversity would be positively correlated with phylogenetic diversity, and that sites with high phylogenetic relatedness would have resource conservative traits. Finally, we predicted that (4) plants would be increasingly resource conservative at plots with more stressful soils.

Methods

Study Site and Species Surveys

The coastal region of northern California where the pygmy forest occurs experiences frequent fog and mild temperatures throughout the year. Plants in the pygmy forest and nearby experience low levels of water stress, even at the end of the dry season (Sholars, 1979; Chapter 2), although much of the pygmy forest experiences winter flooding (Jenny et al., 1969). All sites were within 1-6 km of the coast and within 14 km of each other. Sampling took place between late June and early August 2018.

Fifteen 100 m^2 square plots were chosen within the pygmy forest and fifteen 100 m^2 plots were chosen in nearby tall forests, as closely adjacent to the pygmy forest plots as possible. All plots were on level ground with minimal human disturbance, not directly adjacent to roads or paths. In each plot, five or more line transects were selected using a random number generator. Each line transect was continued until it crossed 20 woody plants or reached the edge of the plot, and new line transects were selected until exactly 100 woody plants were identified for the plot. We chose to standardize sampling by plant number instead of transect length to avoid inflating species diversity measures in sites with more stunted, smaller plants. Each woody plant was identified, and the distance it covered along the line transect recorded to assess percent cover. Herbaceous plants averaged 1% of the plant cover and were not included in the analyses.

At each pygmy forest plot, the height of each tree was measured using either a meter stick or an electronic clinometer (EC II-D, Haglof Inc., Järfälla, Sweden). If a tree species was abundant at that plot, we haphazardly subsampled selected individuals of that species for height measurement (n=10). Average tree height for each plot was weighted by abundance of each tree species.

Soil Analyses

Soil variables were chosen based on results and speculation from previous literature. Acidity has previously been identified as a predictor for community composition (Westman, 1975), and both N and P have been implicated in the stunted growth rates of the pygmy plants (McMillan, 1956; Izquierdo et al., 2013). Cations and organic matter are lower in pygmy forest soils than soils on other marine terraces in the chronosequence (Westman, 1975; Northup et al., 1998; Uroz et al., 2014). Al, which is toxic to plants and can stunt root growth, has been reported at high concentrations in pygmy forest soil (Westman, 1975). No single soil variable has yet been identified as the main stressor for the pygmy forest, and it is possible that soil variables have different effects on community assembly and physiology. For example, it could be that acidity primarily affects species composition, while N levels affect leaf traits. Thus, we chose a wide range of soil variables to assess.

30 cm deep soil samples were taken from five evenly spaced locations at each pygmy forest plot using a 3.8 cm diameter soil auger (AMS, Inc., American Falls, Idaho, USA). Samples from within a plot were homogenized to form one mixed sample per plot. The mixed samples were sent to the University of California Davis Analytical Lab (Davis, California, USA), where they were ground and analyzed for pH and extractable nitrate, P, K, Mg, Ca, Na, Al, and organic matter (OM) content. Cation exchange capacity (CEC) was estimated as the sum of K, Ca, Mg, and Na; P was measured using the Bray method (Diamond 1995). When nutrients were below

the detection limits of the tests used, we used the value of the detection limit for analysis.

Functional traits

Stems were subsampled for functional trait analyses. For each of the fifteen pygmy forest plots, a species list was compiled from the 100 woody plants found along the line transects. For rare species (defined as fewer than 8 plants present in the 100 m^2 plot), each individual plant in the plot was sampled. For more common species, plants were subsampled (n=8). Although common procedure is to select only healthy-looking plants for sampling (Pérez-Harguindeguy et al., 2013), we did not filter by health, because many of the plants appeared unhealthy, e.g., chlorotic or necrotic leaves. Only fully sun-exposed stems less than 2 m above the ground were selected.

To collect the stems in preparation for hydraulic efficiency measurements, stems were first covered by opaque plastic bags for >15 minutes to relax xylem tension (Wheeler et al., 2013), before being cut underwater and transported to the lab. Stems were then placed underwater and vacuumed at -5 kPa overnight to remove air embolisms, which are blockages that can form under water stress (McCulloh et al., 2014; Pittermann et al., 2018). Next, stems were cut back underwater, and conductivity was measured using a hydraulic apparatus (Sperry et al., 1988) with a pressure head of 5 kPa. K_{max}, the hydraulic conductivity after embolism removal, was calculated as water flow rate standardized by gravitational driving gradient and stem length (Sperry et al., 1988). All K_{max} measurements were made within one week of sampling; no effects of storage were seen in this time.

Functional xylem area, downstream leaf area, specific leaf area, and Huber values were also measured on the stems. Functional xylem was measured on each stem after determining K_{max}, by flowing acid fuchsin (Sigma-Aldrich, St. Louis, MO, USA) through the stems at 10 kPa, until the distal end of the stem began to show the stain. Stems were frozen and later sectioned at the distal end to measure cross-sectional area stained by the fuchsin, which represents area of xylem actively transporting water. Xylem-specific conductivity (K_S) was calculated as K_{max} divided by functional xylem area. Downstream leaf area was measured for each stem using a leaf area meter (Li-3011C; LiCor, Lincoln, Nebraska, USA). Leaf specific conductivity (K_L) was calculated as K_{max} divided by downstream leaf area. Huber values were calculated as downstream leaf area divided by functional xylem area (Huber, 1928). After leaf area was measured, leaves were dried in an oven at 60°C until they reached a constant weight, and then weighed. Specific leaf area (SLA) was calculated as leaf area divided by dry leaf mass.

Statistics

Community-wide functional traits were quantified in two ways: range and abundance-weighted average. First, means were calculated for each species at each plot, preserving intraspecific variation in trait values. Range in functional trait within a plot was then calculated as the maximum species value minus minimum species value, considering only species found at that plot. Community-weighted mean was calculated for each trait at each plot by multiplying each species average by the abundance of that species at that plot (Garnier et al., 2004). To assess overlap of functional traits across plots, we plotted the trait positions of all measured stems from all plots using a principle components analysis (PCA) in R (R Core Team 2019), after log-transforming trait data for normality.

We quantified phylogenetic relatedness using the metrics mean pairwise distance (MPD), mean nearest taxon distance (MNTD), and tenth quantile distance. The MPD of a plot is the mean of the phylogenetic distance between every possible pair of species found at that plot, and MNTD is the mean distance from each species to its nearest phylogenetic neighbor found within the plot (Webb, 2000). Tenth quantile distance is similar to MPD in that it considers all pairwise distances within a plot, but instead of averaging all distances, it describes the 10% quantile (Parker et al., 2015). MPD is more sensitive to long phylogenetic branches (describing species distantly related to each other), while MNTD is most sensitive to patterns at the tips of the phylogeny, especially within genera. Tenth quantile distance describes relatedness without being especially sensitive to long branches or nearest neighbor taxa. In all measures, smaller values than would be predicted by chance alone (i.e. greater phylogenetic relatedness) indicate environmental filtering.

Metrics of phylogenetic relatedness were calculated using the dated megaphylogeny of Qian and Jin (2016), with added resolution in the *Rhododendron* and *Hesperocyparis* genera (Terry et al., 2016; Hart et al., 2017). The megaphylogeny was pruned using the R package “picante” (Kembel et al 2010) in R (Fig 2). Mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) were calculated for each of the 30 plots using the R package “phylocomr,” which includes Phylocom (Webb et al., 2008; Ooms and Chamberlain, 2018). Tenth quantile distance was calculated for each plot in R using the ‘quantile’ function (Parker et al., 2015), using the default type 7 quantile. Measures of phylogenetic relatedness presented here are not weighted by abundance; analyses with relatedness weighted by species count and percent cover are presented in Table S1. Overall, weighted MPD and MNTD produced similar results to unweighted measures. Weighting MPD and MNTD did strengthen their relationship with community-weighted functional trait means, however.

Hypotheses were tested using t-tests and multiple linear regressions. Species count and phylogenetic diversity of pygmy and tall conifer forest plots were compared using Welch’s t-tests in R. One pygmy forest plot was removed from all analyses because it was an outlier in terms of soil pH, number of plant species, and complete absence of trees. It is possible that this site experienced logging or other disturbance and that signs of this were obscured by dense shrub growth. Relationships between soil nutrients, phylogenetic diversity, and functional traits were assessed using multiple linear regressions in R. K, Ca, Mg, and Na were removed as soil variables because they each had high collinearity with estimated cation exchange capacity (CEC; calculated as the sum of K, Ca, Mg, and Na), as well as multicollinearity with each other, with calculated tolerances below 0.15. Thus, estimated CEC was included in lieu of these four cations. One plot had unusually high CEC, although this plot was not an outlier in any other variable; when this plot had leverage above 0.8, the model was reanalyzed without this plot. Explanatory variables were selected using AIC model selection in the R package "MASS" (Venables and Ripley 2002). All reported R^2 are adjusted R^2. Graphs were produced using ggplot2 (Wickham 2009), cowplot (Wilke 2019), and ggbiplot (Vu 2011) in R. To reduce type I error, all critical P-values were adjusted using a Bonferroni correction, within each hypothesis (Bonferroni 1936). Thus, for all hypotheses where species richness and three measures of phylogenetic relatedness were response variables, critical P-value was 0.0125. All reported errors are standard deviation.

Results

Soil and Functional Traits in the Pygmy Forest

Across pygmy forest plots, soils were acidic and low in many nutrients (Table 1). For comparison, crop plants will likely respond to fertilizer when nitrate is below 10 ppm, P is below 37.5 ppm, and K is below 80 ppm (Hartz 2007). Al can reduce plant growth at only 1 or 2 ppm in acidic soils in sensitive plants (Vlamis, 1953; Jaskowiak et al., 2018).

Plant families were characterized by different functional trait values. Members of the Fagaceae and Myricaceae had higher xylem-specific conductivity (K_S) than all other families, and also had higher specific leaf area (SLA) and Huber values than the Cupressaceae and Pinaceae (Table 1; Fig 3). Higher values in all three of these traits are linked with faster growth rate due to a more resource acquisitive physiological strategy (Poorter and Remkes, 1990; Fan et al., 2012; Kunstler et al., 2016).

Diversity in Pygmy versus Nearby Coniferous Forests

Pygmy forest plots had higher species richness but higher phylogenetic relatedness than adjacent tall forest plots. Pygmy forest plots averaged 7.4 ± 2.1 species, higher than the tall conifer forest plots, which averaged 5.8 ± 1.5 species per 100 plants (P=0.038). Pygmy plots had lower MPD than tall conifer plots (P=0.002), lower MNTD (P=0.0005), and lower tenth quantile distance (P=0.008; Fig 4), indicating a greater degree of phylogenetic clustering in pygmy forest plots for all examined measures of phylogenetic relatedness. Long phylogenetic distances were common in both pygmy and tall conifer plots, because most plots had both angiosperms and conifers, which diverged many millions of years ago (Fig 2). MPD and MNTD were strongly affected by the large phylogenetic distances between angiosperms and conifers, while tenth quantile distance was less affected by these deep branches. As a result, mean tenth quantile distances were smaller than even MNTD (Fig 4).

Effect of Soil Nutrient Levels on Diversity and Physiology in the Pygmy Forest

Soil variables did not predict species richness, MNTD, tenth quantile distance, tree height, or percent bare ground, after Bonferroni correction of critical P-value (Table 3). However, higher Al and lower OM were associated with lower MPD (more phylogenetic relatedness), indicating that plots with more stressful soil had more related species (Table 3). Decreased tree height, i.e. a greater degree of stunting, predicted lower species richness, as well as more phylogenetic clustering, as assessed by tenth quantile distance (Fig 5). The positive relationship between tree height and tenth quantile distance suggests that higher overall stress level predicts greater phylogenetic relatedness.

Measured soil variables were rarely good predictors of trait ranges (Table 3). Higher soil nutrients or pH predicted higher community-wide mean SLA, Huber, K_L, and K_S, indicating a shift toward a more resource-acquisitive strategy on more fertile soils, but these relationships were almost all marginally significant, with low R^2 (Table 3).

Diversity and Functional Traits

Greater range in SLA and K_S at a plot predicted higher species richness at that plot (Table 3). We had hypothesized that trait range would have a positive relationship with phylogenetic relatedness as well, under the reasoning that less stressful sites would contain species with a larger range of physiological strategies and with a larger range of phylogenetic histories. The marginally significant positive relationship between range in SLA and MPD followed our hypothesis. However, greater range in xylem-specific conductivity (K_S) predicted lower MNTD, and was a marginally significant predictor of lower MPD, contrary to our hypothesis. Tenth quantile distance had no significant relationships with trait ranges.

Higher community-wide mean K_S, consistent with a more resource-acquisitive strategy, predicted greater tenth quantile distance and higher species richness (Table 3). However, higher mean K_L, which indicates potential water supply to each leaf, predicted lower MPD and species richness. K_L may be higher in more stressed pygmy forest plants, because these plants may grow fewer leaves, as leaf tissue is nutrient-expensive (Chapter 2).

Discussion

Habitat filtering limits the taxa that can survive and successfully compete in the pygmy forest: although pygmy forest plots had greater species richness on average compared to adjacent tall conifer plots, the pygmy forest plots had more closely related species, by all three measures of phylogenetic diversity examined (Fig 4). Even within the pygmy forest, habitat filtering increased in strength along an edaphic gradient. Higher Al concentration in soil predicted greater phylogenetic relatedness, while higher organic matter (OM) predicted greater phylogenetic diversity (Table 3)—these results are in line with our hypothesis that more stressful soils (i.e., higher Al toxicity and less OM) result in species being more related to each other. At plots with lower phylogenetic diversity, plants generally displayed a more resource-conservative physiological strategy, with less efficient water transport. Overall, our results show that soil fertility impacts plant physiology and constrains species at the most nutrient-depauperate sites to a few taxonomic groups with the physiological adaptations that allow them to survive at these low-biomass sites.

On average, pygmy forest plots had greater species richness than tall conifer forest plots, despite having more closely related species (Fig 4). The higher species richness in the pygmy forest was driven by the taller pygmy forest plots (Fig 5a), which occur along the transitional zone between the more extreme pygmy forest and the tall conifer forest; these plots host species found in both types of forest.

We had also predicted that plots with species that varied more in traits would also have a more varied phylogenetic history. There were no significant relationships between ranges in Huber values or K_L and phylogenetic diversity, but there was a marginally significant positive relationship between range in SLA and MPD. However, plots with greater K_S range had more closely related species. This disconnect between trait range and phylogenetic history is likely driven by convergent evolution. Species from the distantly related Ericaceae, Cupressaceae, and Pinaceae generally had less efficient water transport, while Fagaceae and Myricaceae species, more closely related to the Ericaceae than the conifer taxa, had greater transport efficiency (Table 2, Fig 3). Furthermore, only MPD and MNTD showed this negative relationship with trait range. MPD and MNTD are more affected by long phylogenetic distances than tenth quantile distance, so plots that contained mostly Ericaceae and Cupressaceae had high MPD and MNTD, because those two families are nearly as distantly related to each other as vascular plants can be (Fig 2).

Unexpectedly, tree height was not predicted by soil variables (Table 3). It is possible that some unmeasured soil variables, such as seasonal nitrate-ammonia dynamics, anoxia, or small-scale soil heterogeneity not captured by the five soil samples per plot, drive variation in tree height. Alternatively, biotic interactions could play a large role. Soil microbial community has been shown to differ on soils of different ages in this system (Uroz et al., 2014), and unexplained pygmy forest plant responses to soil N addition have been attributed to unmeasured changes in the mycorrhizal community (McMillan, 1956). Within the pygmy forest, tree height may be a more integrated proxy for plant stress levels than soil nutrients. Decreased tree height predicted both reduced species richness and phylogenetic diversity (Fig 5), which supports our hypothesis that greater stress levels within the pygmy forest would lead to greater phylogenetic relatedness.

The pygmy forest presents an interesting case study of community assembly. Other equally stressful soils can be found around the globe (Anderson, 1981; Foulds, 1993; Oliveira et al., 2015). However, the pygmy forest system is distinctive in that it experiences negligible water stress year-round (Sholars, 1979; Chapter 2), yet plant growth is severely stunted by acidic, nutrient-depauperate, high aluminum soils. Furthermore, given that the marine terraces on which the pygmy forest is found are only a few hundred thousand years old (Merritts et al., 1991), plants have had relatively little time to adapt to pygmy forest soils, and thus the pygmy forest has only two endemic subspecies of plants. Furthermore, with more fertile sites producing seeds nearby, local adaptation is likely limited by gene flow from the fertile sites. As such, the pygmy forest grants us insight into processes of community assembly in the context of edaphic stress, in a case where plants have not accumulated the physiological adaptations found in ecosystems such as Western Australia, where

Proteaceae species produce specialized roots that mine soil for nutrients more effectively than mycorrhizae, along with a number of other strategies for increasing growth rate on low P soils (Denton et al., 2007; Lambers, Raven, et al., 2008). Without that degree of edaphic specialization, the pygmy forest demonstrates progressive limitation in the number of taxa that can survive and successfully compete as soils become more stressful and plant physiology shifts towards more resource-conservative strategies. These resource-conservative growth patterns, including having fewer, yet thicker and tougher leaves, combined with less efficient water transport, result in the slow growth rates and short stature of the pygmy plants (see Chapter 1 and Chapter 2). A positive feedback mechanism may also perpetuate the state of the soil: slow-growing plants with low SLA contribute fewer nutrients to the soil as leaves senesce, and pygmy plants also produce more polyphenols, which occlude nutrients in the soil (Northup et al., 1998). The pygmy forest is a stable, post-successional ecosystem shaped by edaphic stress, where a limited number of plant taxa that disperse from nearby forests can maintain a foothold and grow, albeit at glacially slow rates.

Table 1: Average soil variables across pygmy forest plots, with standard deviation (n=15).

pH	4.35	±	0.36
nitrate (ppm)	0.24	±	0.09
P (ppm)	1.13	±	0.96
K (ppm)	29.87	±	13.15
Na (ppm)	7.80	±	4.28
Ca (meq/100g)	0.22	±	0.22
Mg (meq/100g)	0.19	±	0.12
CEC (meq/100g)	0.52	±	0.37
OM (%)	3.74	±	1.21
Al (ppm)	111.83	±	74.66

Table 2: Physiological traits of species found in the pygmy forest plots, with averages and standard deviation across plots, and average percent abundance on especially stressful soils.

						Relative Abundance		
Family	Species	SLA ($cm^2 g^{-1}$)	Huber Value (m^2m^{-2})	K_L ($kg\ s^{-1}\ m^{-1}\ MPa^{-1}$) $*10^4$	K_S ($kg\ s^{-1}\ m^{-1}\ MPa^{-1}$)	Al > 150 ppm	pH < 4	Nitrate < 0.20 ppm
Ericaceae	*Arctostaphylos columbiana*	53.3 ± 4.4	0.34 ± 0.09	3.1 ± 1.0	1.02 ± 0.23	0%	0%	0%
Ericaceae	*Arctostaphylos nummularia*	45.9 ± 6.4	0.23 ± 0.15	5.5 ± 3.3	1.04 ± 0.58	5%	3%	9%
Ericaceae	*Gaultheria shallon*	60.0 ± 13.6	0.55 ± 0.34	0.8 ± 0.4	0.38 ± 0.26	34%	39%	33%
Ericaceae	*Rhododendron columbianum*	69.4 ± 11.2	0.13 ± 0.15	3.2 ± 1.8	0.30 ± 0.20	14%	8%	11%
Ericaceae	*Rhododendron macrophyllum*	48.0 ± 12.5	0.26 ± 0.18	2.2 ± 1.5	0.46 ± 0.27	5%	8%	6%
Ericaceae	*Vaccinium ovatum*	45.5 ± 8.2	0.24 ± 0.16	2.2 ± 1.4	0.43 ± 0.23	18%	15%	15%
Myricaceae	*Myrica californica*	68.7 ± 18.4	0.34 ± 0.20	11.4 ± 20.4	1.40 ± 0.44	0%	0%	0%
Fagaceae	*Chrysolepis chrysophylla*	47.7 ± 7.9	0.34 ± 0.16	8.6 ± 6.2	2.52 ± 1.58	0%	0%	0%
Fagaceae	*Notholithocarpus densiflorus*	49.0 ± 6.0	0.62 ± 0.42	5.1 ± 3.1	2.63 ± 1.77	0%	2%	2%
Cupressaceae	*Hesperocyparis pygmaea*	17.2 ± 1.9	0.13 ± 0.06	2.7 ± 2.2	0.31 ± 0.12	21%	20%	19%
Pinaceae	*Pinus contorta* ssp *bolanderi*	29.8 ± 3.8	0.16 ± 0.07	4.8 ± 5.6	0.55 ± 0.20	4%	3%	3%
Pinaceae	*Pinus muricata*	24.1 ± 2.5	0.22 ± 0.11	1.9 ± 0.7	0.41 ± 0.20	0%	2%	1%
Pinaceae	*Pseudotsuga menziesii*	50.6 ± 7.9	0.35 ± 0.15	2.3 ± 2.2	0.58 ± 0.15	0%	0%	0%
Pinaceae	*Tsuga heterophylla*	53.0 ± 4.1	0.45 ± 0.08	1.9 ± 0.7	0.82 ± 0.26	0%	1%	0%

Table 3: Results of multiple linear regressions examining relationships between soil variables, tree height, species richness, phylogenetic relatedness, and functional traits. Pluses or minuses next to predictor variables indicate whether their relationship with the response variable was positive or negative, followed by significance level after a Bonferroni correction, resulting in a critical P-value of 0.0125. Significance of both entire model and of predictors indicated by asterisk (No asterisk or m = $P<0.05$; * = $P<0.0125$; ** = $P< 0.0025$; ***= $P<0.00025$). All R^2 are adjusted.

Response Variable	Explanatory Variable Group	AIC selected predictors	DF	F	R^2	P	
Species richness	Soil	Al	1, 12	3.70	0.17	0.0788	
MPD	Soil	nitrate, pH, Al (-)*, OM (+)**	4, 8	7.88	0.70	0.0070	**
MNTD	Soil	nitrate, pH	2, 11	4.78	0.37	0.0320	m
Tenth Quantile	Soil	Al (-)	1, 12	6.96	0.31	0.0216	m
Tree height	Soil	Al	1, 12	2.60	0.11	0.1309	
Bare Ground	Soil	nitrate (-)	1, 12	5.50	0.26	0.0364	m
Species richness	Tree height	height (+)*	1, 12	11.43	0.45	0.0055	*
MPD	Tree height	height	1, 12	0.13	-0.07	0.7205	
MNTD	Tree height	height	1, 12	3.86	0.18	0.0732	
Tenth Quantile	Tree height	height (+)*	1, 12	9.57	0.40	0.0093	*
Species richness	Trait Ranges	SLA (+), K_L, K_S (+)**	3, 10	8.70	0.64	0.0038	*
MPD	Trait Ranges	SLA (+), K_L, K_S (-)	3, 10	4.85	0.47	0.0247	m
MNTD	Trait Ranges	K_L, K_S (-)*	2, 11	8.51	0.54	0.0058	*
Tenth Quantile	Trait Ranges	K_S	1, 12	3.97	0.19	0.0695	
Species richness	Trait Averages	Huber, K_L (-)***, K_S (+)***	3, 10	21.40	0.84	0.0001	***
MPD	Trait Averages	K_L (+)	1, 12	4.77	0.22	0.0495	m
MNTD	Trait Averages	SLA, Huber, K_L, K_S	4, 9	2.88	0.37	0.0867	
Tenth Quantile	Trait Averages	K_L, K_S (+)*	2, 11	6.90	0.48	0.0114	*
SLA Range	Soil	nitrate	1, 12	2.10	0.08	0.1710	
SLA Average	Soil	nitrate (+), P, OM	3, 10	1.94	0.18	0.1874	
Huber Range	Soil	all poor predictors; none selected					
Huber Average	Soil	nitrate (+)	1, 12	6.17	0.28	0.0288	m
K_L Range	Soil	nitrate	1, 12	2.12	0.08	0.1700	
K_L Average	Soil	nitrate, P, pH, CEC(+)*	4, 9	3.52	0.44	0.0540	
K_S Range	Soil	pH, CEC, OM	3, 9	2.69	0.30	0.1092	
K_S Average	Soil	P (+), pH (+), CEC (+)	3, 9	5.93	0.55	0.0162	m

Figure 1: Photo panel showing plots with an average tree height of a.) 1.2 m, b.) 3 m, and c.) 5.5 m. All three plots would be classified as pygmy forest plant community, and are located within 1.6 km of each other.

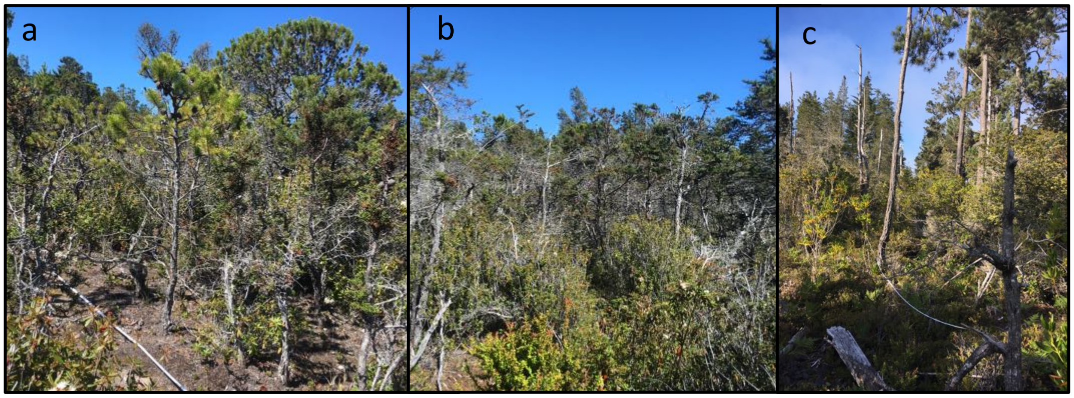


Figure 2: Pruned phylogeny of plants found at pygmy or control plots. Closed black circles indicate species are found at plots where average tree height is less than 2 m, grey circles indicate species are found at plots where tree height averages over 2 m, and open circles indicate species are found at plots with tree height averages 4.5 m and above. Absence of circles indicates that species were not found in pygmy forest plots.

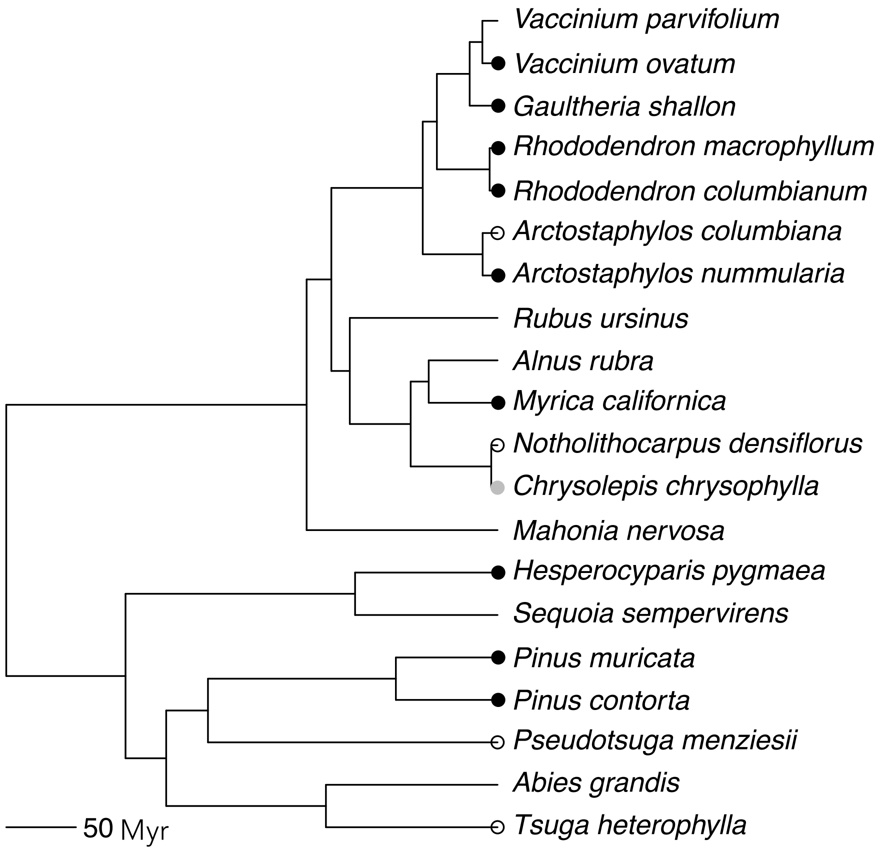


Figure 3: First two principle components of log-transformed functional trait data from pygmy forest plots, explaining 84% of total variation. Traits are SLA, which is specific leaf area; Huber value, leaf area divided by supporting functional xylem area; K_S, xylem-specific conductivity, a measure of water transport efficiency; and K_L, leaf-specific conductivity. Concentration ellipses include 68% of the data for each plant family, assuming normal distributions. Numbers indicate average tree height at the plot each stem was sampled from, in m.

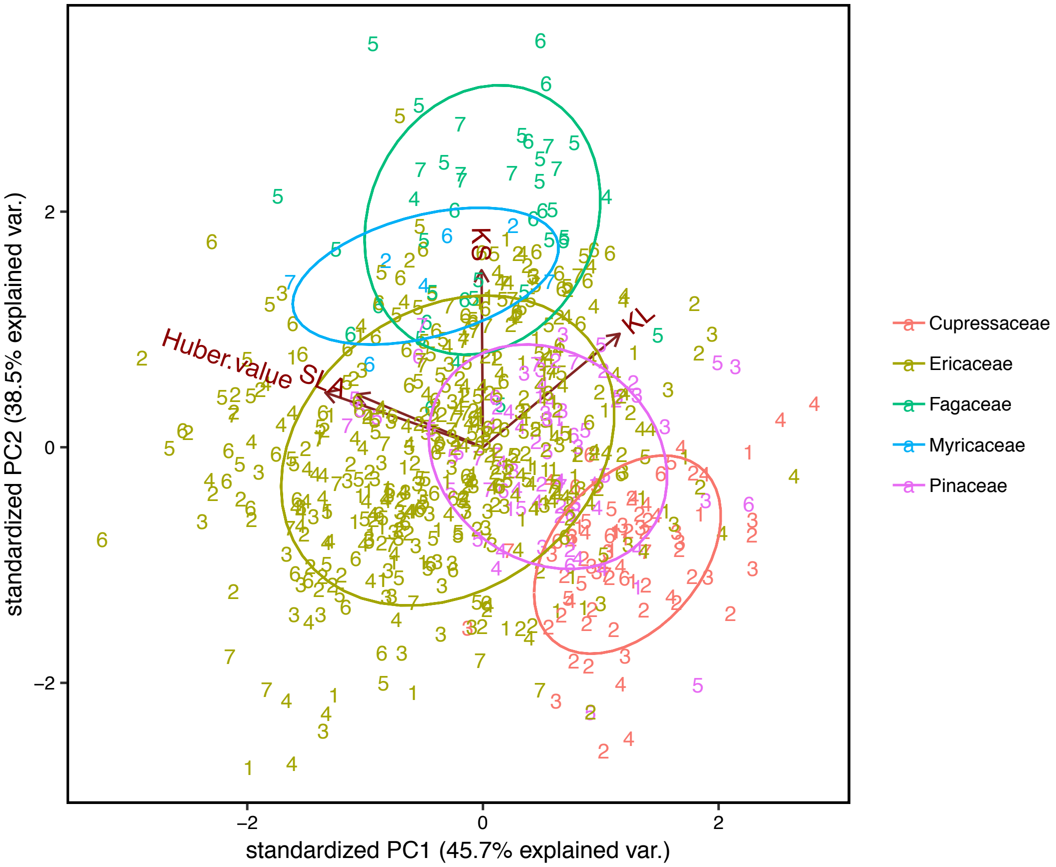


Figure 4: Boxplot of three measures of phylogenetic relatedness at tall conifer forest (white) and pygmy forest (grey) plots. MPD is the mean of all phylogenetic pairwise distances between plants within a plot. MNTD is the mean phylogenetic distance between each plant found at a plot and its nearest neighbor. Tenth quantile distance is the tenth quantile of all phylogenetic pairwise distances between plants within a plot. Significance level of t-test between tall and pygmy plots indicated by asterisk (* = P<0.05; ** = P<0.01; *** = P<0.001).

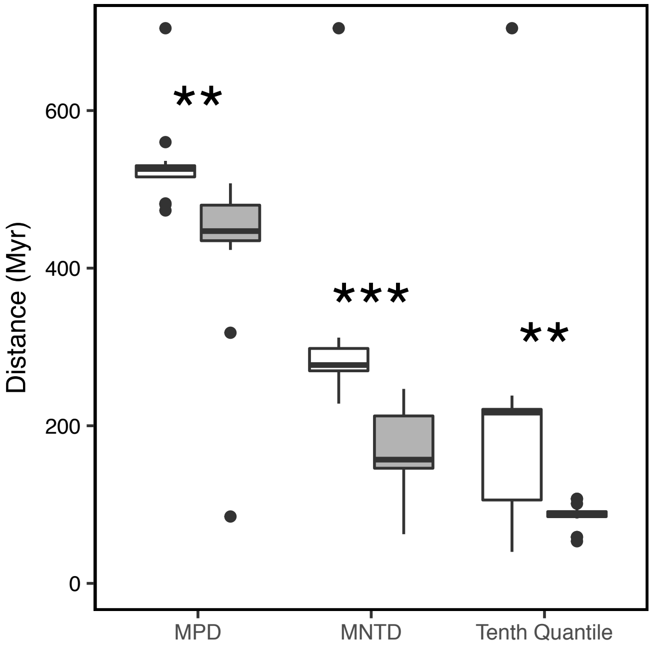
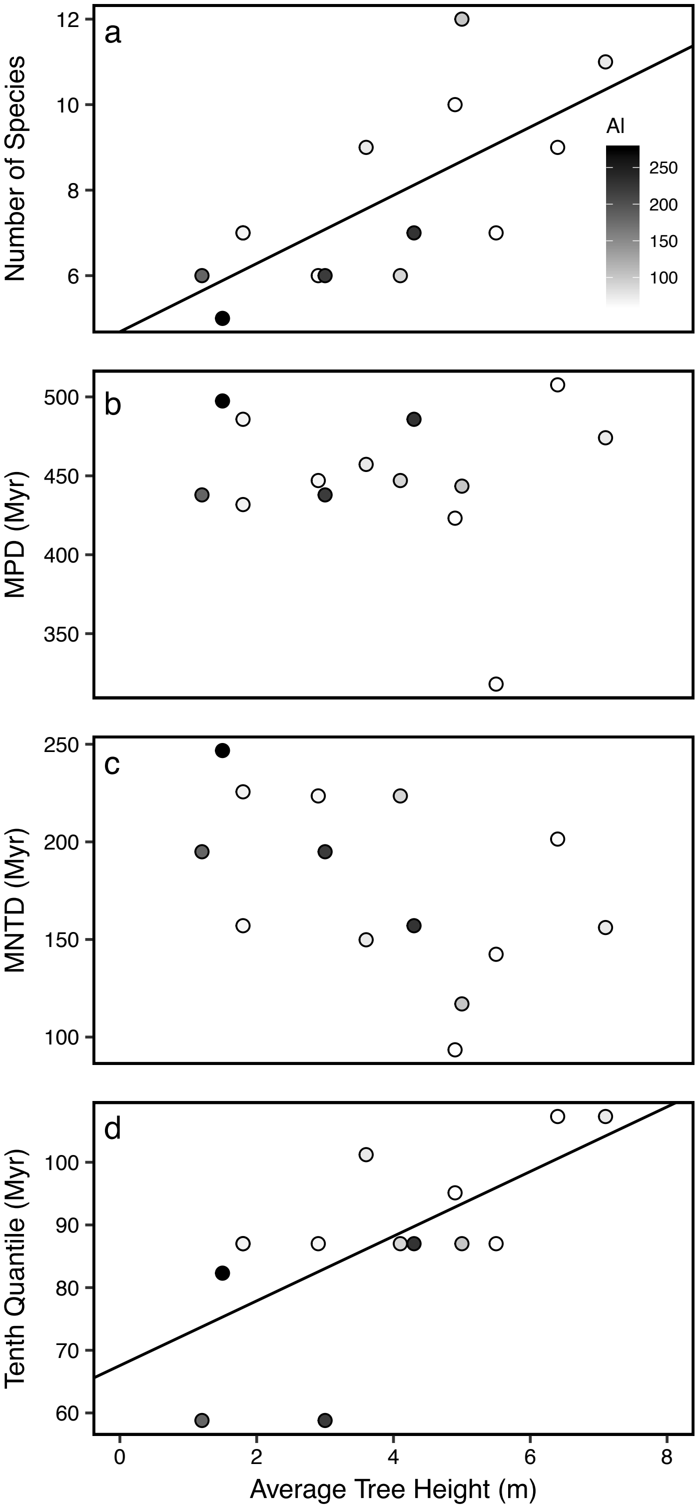


Figure 5: Relationships between tree height and four measures of diversity within pygmy forest plots. Point shade indicates soil Al level in ppm at each plot, with darker fill indicating higher levels of Al. (a) Number of species found by sampling 100 plants at each plot. (b) MPD, the mean of all phylogenetic pairwise distances between plants within a plot. (c) MNTD, the mean phylogenetic distance between each plant found at a plot and its nearest neighbor. (d) Tenth quantile distance, the tenth quantile of all phylogenetic pairwise distances between plants within a plot.


a
Number of Species
12
10
8
6
AI
250
200
150
100
b
MPD (Myr)
500
450
400
350
c
MNTD (Myr)
250
200
150
100
d
Tenth Quantile (Myr)
100
90
80
70
60
0
2
4
6
8
Average Tree Height (m)

Conclusion

This dissertation uses Mendocino's pygmy forest as a model system for understanding how nutrient limitation and stunted growth impact leaf physiology, water transport, and community assembly. The nutrient-depleted, acidic soils of the pygmy forest have pushed plants toward more resource-conservative physiological strategies, both within species and at the community level. As soils become more stressful and tree height decreases within the pygmy forest, the effects of nutrient limitation manifest across different scales. Taken together, the chapters of my dissertation reveal the critical role resource conservation strategies have at the organismal level, where they affect growth rate and drought response, as well as the community level, where the ability to grow slowly and conserve resources determines which species can survive on nutrient-depauperate soil.

In **Chapter 1**, I sought to understand how plants survive in the Mendocino pygmy forest, as well as ascertain the physiological mechanism of stunting. The stunting of the pygmy forest is not, as I had initially predicted, a rarity caused by an inability to maintain leaf photosynthetic rates. Instead, it is an extreme case of a global phenomenon described in the worldwide leaf economics spectrum (Wright et al., 2004) and the resource availability hypothesis (Coley et al., 1985), whereby nutrient-limited plants shift toward a more resource-conservative physiology, with lower specific leaf area and lower nitrogen content, to limit herbivory and physical damage. Pygmy plants also produced fewer leaves, allowing them to invest more resources into each leaf, but decreasing whole-plant photosynthetic rates. This shift in physiology and carbon allocation is responsible for both the pygmy plants' slow growth rates and for their survival. Other pygmy or dwarf forests exist where the cause of stunting has not been determined, but resource conservation is plausible (Reich and Hinckley, 1980; Fang et al., 2006; Vanderklein et al., 2012). Further research could also elucidate carbon balances and physiology in other nutrient-limited systems that have not been examined.

Despite having no need to conserve water, pygmy plants also showed a shift toward a resource-conservative strategy in their water transport, examined in **Chapter 2**. Compared to conspecific controls, pygmy plants had smaller conduits and less efficient water transport per unit xylem, both traits that slow growth rate (Fan et al., 2012), but are generally thought to be caused by water stress, not nutrient limitation. However, xylem supplies the water lost during leaf gas exchange, so alterations in number of leaves or in leaf physiology have downstream effects on water transport. In *Sequoia sempervirens*, small conduits caused increased cavitation resistance in pygmy plants compared to controls, indicating that stem xylem of pygmy plants will stay functional under increased water stress. This increase in cavitation resistance is another instance of a resource-conservative strategy: plants with high cavitation resistance typically have low growth rates, because traits that increase cavitation resistance are resource-expensive and decrease water transport efficiency, but also improve survival during drought.

Information about the effects of nutrient limitation on cavitation resistance is currently sparse (Santiago, 2015) and contradictory (e.g., Goldstein et al., 2013; Zhang et al., 2018). The contrasting responses in cavitation resistance I observed in pygmy forest species agree with the divide in the literature, confirming that it is not simply an effect of different researchers using different experimental designs in different systems. Some species improve cavitation resistance under nutrient limitation, while other decrease resistance, even within the same study on the same pygmy forest system. The changes I observed were substantial enough to make the difference between surviving or dying during drought, because drops in P_{50} decrease hydraulic safety margin, resulting in plants living closer to the edge of mortality from runaway cavitation (Brodribb and Cochard, 2009; Choat et al., 2018).

At the community level, examined in **Chapter 3**, the pygmy forest also showed a shift toward resource-conservation as soil fertility restricted taxa. Resource conservation was evident in decreased water transport. Plots on soils with higher aluminum levels and lower organic matter content had more closely related species, and more stunted sites similarly exhibited higher phylogenetic relatedness. Plots with more closely related species had lower xylem transport efficiency, falling on the resource-conservative side of the spectrum compared to plots with more diverse species. This drop in water transport efficiency is likely due to xylem responding to upstream demands, because xylem supplies water lost in leaf gas exchange.

The field of phylogenetic community ecology has been growing rapidly in the last several years. However, patterns in phylogenetic relatedness can be hard to accurately interpret without also examining organismal-level processes, including physiology and competition. This study represents a novel contribution to bridging the gap between organismal-level and community-level dynamics.

I began my dissertation with the hypothesis that the plants of the pygmy forest are struggling to survive, unable to maintain leaf function and vulnerable to water stress. Instead, I found that their slow growth rate is part of a resource-conservative strategy that prioritizes safety over growth, and that pygmy plants can survive water deficits many times greater than what they experienced at the end of the dry season of a drought year. The plants of the pygmy forest have converged on a physiological strategy that minimizes risk, and they represent a select few taxa that are able to survive and even thrive on these stressful soils.

Viewing physiology as a gradient from resource conservation to resource acquisition, as presented in the worldwide leaf economics spectrum (Wright et al., 2004), is a more powerful lens to use to examine plant physiology than previously thought. Resource conservation can explain extreme phenomenon such as Mendocino's pygmy forest, which alters plant growth and whole communities in visible and dramatic ways. Resource conservation affects not only leaves, but necessarily affects xylem, which supplies water to leaves. These downstream consequences change xylem form and function and affect drought response in unpredictable yet consequential ways. These responses to nutrient limitation are likely global and pervasive; for example, a resource conservative growth strategy may explain the small conduits and inefficient water transport of tropical Southern

Hemisphere conifers (Pittermann et al., 2006). These changes are felt all the way up to the community level. Only species that can adopt a physiology that is resource conservative enough can survive on the most stressful soils. Based on my results from Chapter 3, xylem transport efficiency is a better descriptor for where a species falls on the gradient from resource conservation to resource acquisition than specific leaf area, which is more developmentally plastic. Thus, xylem traits appear to be a more limiting factor for which species can survive on nutrient-depauperate soils, even in the absence of water stress. This result is entirely unexpected: across the field of plant physiology, the interest in how nutrient limitation affects leaf physiology vastly outweighs the interest in how nutrient limitation affects xylem physiology, and studies on community assembly rarely examine xylem traits. However, xylem physiology is greatly affected by nutrient limitation, and stressful soils filter out species with resource-acquisitive xylem physiology, resulting in greater phylogenetic relatedness on these soils.

Appendix 1

Supplementary Tables and Figures for Chapter 1

Table S1: Summary of physiological measurements of the most recently fully mature leaves of pygmy and control plants from Mendocino County, California, USA, with standard error.

Trait	Species	Pygmy	*n*	Control	*n*	*t*	df	*P*-value
Height (m)	*Gaultheria shallon*	0.29 ± 0.04	8	0.48 ± 0.07	8	2.31	11.3	0.0204
	Hesperocyparis pygmaea	1.38 ± 0.12	8	15.82 ± 2.75	7	5.25	6.0	0.0009*
	Pteridium aquilinum	0.57 ± 0.02	8	0.54 ± 0.07	8	0.38	8.5	0.6445
	Pinus contorta ssp. *bolanderi*	4.00 ± 0.53	8	11.58 ± 1.19	8	5.80	9.7	0.0001*
	Rhododendron columbianum	1.73 ± 0.12	8	1.96 ± 0.11	8	1.44	13.8	0.0855
	Rhododendron macrophyllum	1.24 ± 0.14	8	1.62 ± 0.16	8	1.75	13.7	0.0515
	Sequoia sempervirens	2.97 ± 0.56	8	24.34 ± 3.88	8	5.45	7.3	0.0004*
Area-based photosynthesis (μmol m^{-2} s^{-1})	*G. shallon*	3.5 ± 0.4	8	3.9 ± 0.6	8	0.575	14.0	0.2873
	H. pygmaea	6.1 ± 0.9	8	8.6 ± 0.6	8	2.251	14.0	0.0205
	P. aquilinum	8.2 ± 0.8	8	7.5 ± 0.6	8	0.77	14.0	0.7735
	P. contorta ssp. *bolanderi*	7.3 ± 1.2	8	6.1 ± 1.2	8	0.77	14.0	0.7729
	R. columbianum	2.4 ± 0.6	8	3.9 ± 0.5	8	2.11	14.0	0.0265
	R. macrophyllum	4.0 ± 0.7	8	4.8 ± 0.6	8	0.83	14.0	0.2094
	S. sempervirens	2.2 ± 0.7	8	9.0 ± 0.8	8	6.64	14.0	5.6E-6*
Mass-based photosynthesis (nmol g^{-1} s^{-1})	*G. shallon*	23.1 ± 2.9	8	40.5 ± 6.6	8	2.41	9.7	0.0189
	H. pygmaea	12.1 ± 1.8	8	20.1 ± 1.4	8	3.53	14.0	0.0017*
	P. aquilinum	59.2 ± 5.6	8	76.0 ± 6.5	8	1.95	14.0	0.0355
	P. contorta ssp. *bolanderi*	23.4 ± 3.8	8	23.2 ± 4.4	8	0.03	14.0	0.5136
	R. columbianum	21.3 ± 5.0	8	47.6 ± 5.8	8	3.45	14.0	0.0020*
	R. macrophyllum	19.6 ± 3.2	8	44.8 ± 5.7	8	3.87	14.0	0.0013*
	S. sempervirens	9.0 ± 2.8	8	46.8 ± 4.1	8	7.66	14.0	2.5E-6*
Stomatal conductance (mol m^{-2} s^{-1})	*G. shallon*	0.04 ± 0.01	8	0.05 ± 0.01	8	0.73	14.0	0.4760
	H. pygmaea	0.10 ± 0.02	8	0.11 ± 0.02	8	0.15	14.0	0.8829
	P. aquilinum	0.22 ± 0.03	8	0.21 ± 0.02	8	0.27	14.0	0.7939
	P. contorta ssp. *bolanderi*	0.11 ± 0.02	7	0.07 ± 0.04	8	1.11	12.5	0.2870
	R. columbianum	0.01 ± 0.01	7	0.03 ± 0.01	8	1.52	14.0	0.1518
	R. macrophyllum	0.06 ± 0.01	8	0.06 ± 0.01	8	0.30	14.0	0.7678
	S. sempervirens	0.12 ± 0.02	8	0.07 ± 0.01	8	2.20	10.5	0.0511
Intrinsic water-use efficiency (μmol mol^{-1})	*G. shallon*	118.0 ± 31.2	8	83.7 ± 12.7	8	1.0	9.3	0.3338
	H. pygmaea	67.7 ± 12.4	8	100.9 ± 22.0	8	1.3	11.0	0.2157
	P. aquilinum	39.6 ± 3.2	8	35.9 ± 1.7	8	1.0	10.7	0.3470
	P. contorta ssp. *bolanderi*	80.7 ± 10.2	7	74.0 ± 13.0	8	0.4	12.7	0.6900
	R. columbianum	225.6 ± 77.4	6	177.9 ± 32.0	8	0.6	6.7	0.5877
	R. macrophyllum	77.2 ± 12.9	8	85.1 ± 4.7	8	0.6	8.9	0.5797
	S. sempervirens	21.4 ± 7.3	8	134.1 ± 13.7	8	7.3	10.7	1.9E-5*

Trait	Species	Pygmy	n	Control	n	t	df	P-value
Dark respiration (μmol m^{-2} s^{-1})	*G. shallon*	-0.70 ± 0.15	8	-1.21 ± 0.14	8	2.50	14.0	0.0127
	H. pygmaea	-2.57 ± 0.24	8	-2.49 ± 0.34	8	0.18	12.4	0.5684
	P. aquilinum	-0.54 ± 0.04	8	-0.58 ± 0.19	8	0.22	7.5	0.4169
	P. contorta ssp. *bolanderi*	-1.67 ± 0.24	7	-1.59 ± 0.36	8	0.19	11.8	0.5729
	R. columbianum	-0.49 ± 0.07	8	-0.84 ± 0.07	8	3.44	14.0	0.0020*
	R. macrophyllum	-0.87 ± 0.18	8	-0.63 ± 0.16	8	1.01	14.0	0.8357
	S. sempervirens	-1.19 ± 0.21	8	-1.09 ± 0.08	8	0.46	9.0	0.6728
Fv/Fm	*G. shallon*	0.73 ± 0.01	8	0.69 ± 0.04	8	0.858	7.9	0.7918
	H. pygmaea	0.74 ± 0.02	8	0.74 ± 0.02	8	0.117	14.0	0.4544
	P. aquilinum	0.80 ± 0.01	8	0.80 ± 0.00	8	0.150	11.9	0.4418
	P. contorta ssp. *bolanderi*	0.80 ± 0.01	8	0.80 ± 0.01	8	0.516	14.0	0.6930
	R. columbianum	0.74 ± 0.02	8	0.69 ± 0.02	8	1.895	14.0	0.9606
	R. macrophyllum	0.80 ± 0.01	8	0.78 ± 0.01	8	1.501	14.0	0.9158
	S. sempervirens	0.77 ± 0.01	8	0.83 ± 0.00	8	5.726	10.4	0.0001*
Specific leaf area (cm^{2} g^{-1})	*G. shallon*	66.1 ± 3.7	8	102.6 ± 10.7	8	3.24	8.6	0.0054*
	H. pygmaea	19.7 ± 0.7	8	23.5 ± 0.7	8	4.09	14.0	0.0005*
	P. aquilinum	71.9 ± 1.3	8	102.1 ± 3.0	8	10.16	9.6	1.8E-7*
	P. contorta ssp. *bolanderi*	31.9 ± 0.9	8	38.3 ± 0.8	8	4.96	13.5	0.0002*
	R. columbianum	89.6 ± 5.1	8	121.2 ± 9.2	8	3.09	10.9	0.0040*
	R. macrophyllum	48.7 ± 1.7	8	94.0 ± 8.3	7	6.56	6.5	0.0001*
	S. sempervirens	41.5 ± 0.9	8	51.9 ± 3.2	8	3.11	8.1	0.0067*
Chlorophyll content (mg m^{-2})	*G. shallon*	239 ± 29	8	332 ± 20	8	2.6	12.4	0.0108
	H. pygmaea	163 ± 18	8	313 ± 24	8	5.1	12.9	0.0001*
	P. aquilinum	290 ± 19	8	309 ± 20	8	0.7	14.0	0.2491
	P. contorta ssp. *bolanderi*	390 ± 22	8	445 ± 17	8	2.0	13.0	0.0348
	R. columbianum	423 ± 23	8	371 ± 19	8	1.7	13.6	0.9470
	R. macrophyllum	382 ± 30	8	406 ± 30	8	0.6	14.0	0.2930
	S. sempervirens	41 ± 26	8	559 ± 73	8	6.7	8.7	0.0001*
C:N ratio	*G. shallon*	70.8 ± 4.7	8	63.7 ± 3.5	8	1.21	12.9	0.1238
	H. pygmaea	63.2 ± 4.1	8	51.3 ± 2.9	8	2.36	12.6	0.0177
	P. aquilinum	37.5 ± 1.3	8	37.6 ± 1.5	8	0.02	14.0	0.5076
	P. contorta ssp. *bolanderi*	57.9 ± 1.6	8	43.2 ± 1.4	8	6.79	14.0	4.4E-6*
	R. columbianum	50.8 ± 1.6	8	38.4 ± 2.1	8	4.75	13.2	0.0002*
	R. macrophyllum	59.3 ± 2.4	8	52.4 ± 2.7	8	1.90	14.0	0.0393
	S. sempervirens	103.5 ± 8.6	7	41.1 ± 2.5	8	6.94	7.0	0.0001*
Percent N (% by mass)	*G. shallon*	0.73 ± 0.05	8	0.79 ± 0.04	8	1.04	14.0	0.1588
	H. pygmaea	0.71 ± 0.05	8	0.93 ± 0.06	8	2.71	14.0	0.0084*
	P. aquilinum	1.18 ± 0.03	8	1.14 ± 0.04	8	0.72	14.0	0.7570
	P. contorta ssp. *bolanderi*	0.91 ± 0.02	8	1.20 ± 0.04	8	6.00	10.7	5.0E-5*
	R. columbianum	0.99 ± 0.03	8	1.26 ± 0.08	8	3.31	9.0	0.0046*
	R. macrophyllum	0.80 ± 0.03	8	0.94 ± 0.05	8	2.31	10.3	0.0215
	S. sempervirens	0.44 ± 0.04	7	1.18 ± 0.08	8	8.54	9.9	3.4E-6*

Trait	Species	Pygmy	*n*	Control	*n*	*t*	df	*P*-value
δ^{13}C (‰)	*G. shallon*	-30.1 ± 0.5	8	-29.5 ± 0.3	8	0.96	10.4	0.3602
	H. pygmaea	-25.9 ± 0.3	8	-26.5 ± 0.4	8	1.21	12.5	0.2488
	P. aquilinum	-29.1 ± 0.1	8	-28.6 ± 0.3	8	1.62	8.2	0.1427
	P. contorta ssp. *bolanderi*	-30.1 ± 0.3	8	-30.8 ± 0.3	8	1.46	14.0	0.1673
	R. columbianum	-30.0 ± 0.4	8	-27.5 ± 0.3	8	4.70	14.0	0.0003*
	R. macrophyllum	-28.5 ± 0.2	8	-30.5 ± 0.5	8	3.50	9.1	0.0067*
	S. sempervirens	-31.3 ± 0.5	7	-28.4 ± 0.7	8	3.39	12.3	0.0052*
Photosynthetic nitrogen-use efficiency (μmol mol^{-1} s^{-1})	*G. shallon*	44.2 ± 4.1	8	71.2 ± 10.0	8	2.49	9.3	0.0336
	H. pygmaea	24.7 ± 3.8	8	30.9 ± 2.4	8	1.39	11.7	0.1897
	P. aquilinum	71.5 ± 7.9	8	95.8 ± 11.0	8	1.80	12.7	0.0962
	P. contorta ssp. *bolanderi*	36.6 ± 6.4	8	27.3 ± 5.3	8	1.13	14.0	0.2785
	R. columbianum	29.8 ± 6.8	8	53.0 ± 6.1	8	2.54	14.0	0.0237
	R. macrophyllum	34.5 ± 5.7	8	66.2 ± 6.5	8	3.68	13.7	0.0025*
	S. sempervirens	23.0 ± 6.2	7	57.0 ± 5.4	8	4.14	14.0	0.0012*
Leaf production vs. wood production (cm^2 cm^{-2})	*G. shallon*	4457 ± 571	8	7361 ± 700	8	3.21	13.5	0.0033*
	H. pygmaea	1361 ± 320	8	746 ± 75	8	1.87	7.8	0.9506
	P. contorta ssp. *bolanderi*	2155 ± 256	8	4132 ± 722	8	2.58	8.7	0.0152
	R. columbianum	3853 ± 432	8	4369 ± 220	8	1.06	10.4	0.1557
	R. macrophyllum	5086 ± 614	8	7700 ± 914	8	2.37	12.3	0.0174
	S. sempervirens	3908 ± 784	8	7599 ± 458	8	4.07	11.3	0.0009*
Leaf longevity (years)	*G. shallon*	1.78 ± 0.15	9	2.50 ± 0.19	8	3.02	13.7	0.0095*
	R. columbianum	2.60 ± 0.16	10	2.88 ± 0.13	8	1.34	15.7	0.2002
	R. macrophyllum	2.42 ± 0.19	12	2.63 ± 0.18	8	0.78	17.5	0.4439
	S. sempervirens	6.18 ± 0.35	11	5.75 ± 0.45	8	0.75	14.3	0.4639

Notes: *P*-values are from *t*-tests. Starred *P*-values indicate significance after sequential Bonferrroni correction (Holm 1979). Statistics for SLA were performed on log-transformed data.

Table S2: Summary of physiological measurements on new and old leaves of pygmy and control plants, with standard error (n=8). New leaves were the most recently fully mature leaves at the time of sampling, while old leaves were from the oldest identifiable cohort (the previous year's cohort for all species except *H. pygmaea*, where the cohort was two years old at the time of sampling). Old leaves were not measured for *P. acquilinum*, which is summer deciduous, and *P. contorta* ssp. *bolanderii*, where leaf cohort was not identifiable on pygmy plants. "Decrease" column was calculated as the mean of old leaves subtracted from the mean of new leaves; negative values indicate trait values were higher in older leaves than new leaves. Statistical resluts are from paired t-tests. Asterisks indicate significance after critical *P*-value was adjusted using a sequential Bonferrroni correction (Holm 1979).

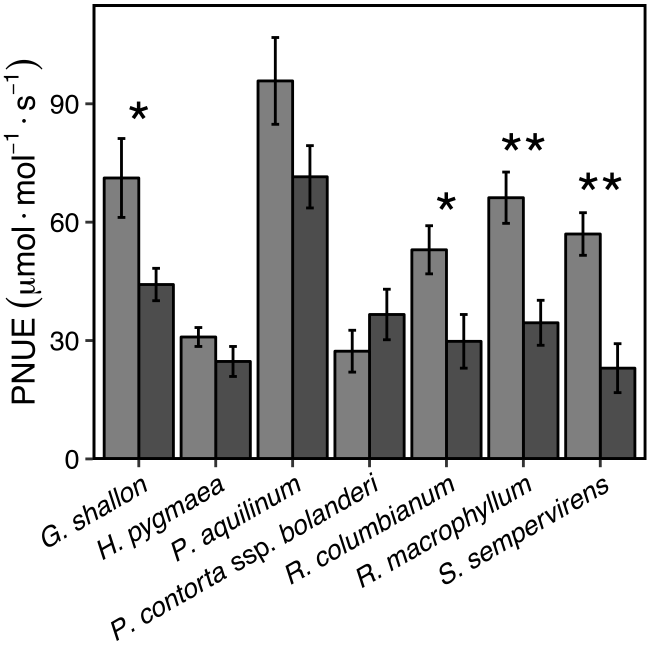
Trait	Species	Pygmy New		Pygmy Old			Control New		Control Old			*t*	df	*P*
		Mean	S.E.	Mean	S.E.	Decrease	Mean	S.E.	Mean	S.E.	Decrease			
Area-based photosynthesis (μmol m^{-2} s^{-1})	*Gaultheria shallon*	3.50	± 0.45	2.31	± 0.61	1.18	3.95	± 0.64	3.42	± 0.77	0.53	1.06	13.65	0.307
	Hesperocyparis pygmaea	6.13	± 0.90	8.84	± 0.79	-2.70	8.57	± 0.61	8.72	± 1.13	-0.15	1.67	13.77	0.117
	Rhododendron columbianum	2.38	± 0.56	2.59	± 0.75	-0.21	3.93	± 0.48	2.05	± 0.81	1.88	1.85	13.52	0.087
	Rhododendron macrophyllum	4.02	± 0.66	2.84	± 0.76	1.18	4.76	± 0.60	2.35	± 0.43	2.41	1.35	10.63	0.206
	Sequoia sempervirens	2.18	± 0.67	2.97	± 0.77	-0.80	9.01	± 0.79	7.22	± 0.94	1.79	3.34	13.43	0.005*
Stomatal conductance (mol m^{-2} s^{-1})	*G. shallon*	0.04	± 0.01	0.03	± 0.01	0.02	0.05	± 0.01	0.03	± 0.01	0.02	1.00	12.04	0.336
	H. pygmaea	0.10	± 0.02	0.10	± 0.02	0.01	0.11	± 0.02	0.11	± 0.02	0.00	0.17	13.58	0.866
	R. columbianum	0.01	± 0.01	0.03	± 0.01	-0.02	0.03	± 0.01	0.14	± 0.13	-0.12	0.79	6.08	0.460
	R. macrophyllum	0.06	± 0.01	0.05	± 0.01	0.01	0.06	± 0.01	0.02	± 0.01	0.04	1.63	12.70	0.128
	S. sempervirens	0.12	± 0.02	0.09	± 0.02	0.02	0.07	± 0.01	0.16	± 0.07	-0.09	1.55	8.52	0.157
Dark respiration (μmol m^{-2} s^{-1})	*G. shallon*	-0.70	± 0.15	-0.65	± 0.14	-0.05	-1.21	± 0.14	-0.93	± 0.12	-0.28	1.33	11.66	0.209
	H. pygmaea	-2.57	± 0.24	-2.12	± 0.29	-0.45	-2.49	± 0.34	-1.92	± 0.23	-0.57	0.31	11.52	0.765
	R. columbianum	-0.49	± 0.07	-0.41	± 0.06	-0.08	-0.84	± 0.07	-0.77	± 0.24	-0.07	0.04	7.66	0.971
	R. macrophyllum	-0.87	± 0.18	-0.46	± 0.10	-0.41	-0.63	± 0.16	-0.57	± 0.17	-0.06	1.40	13.73	0.184
	S. sempervirens	-1.19	± 0.21	-0.96	± 0.12	-0.23	-1.09	± 0.08	-1.05	± 0.11	-0.04	0.68	9.10	0.511
Intrinsic water-use efficiency (μmol mol^{-1})	*G. shallon*	118.0	± 31.2	82.4	± 7.7	35.7	83.7	± 12.7	121.2	± 28.9	-37.5	2.07	9.85	0.065
	H. pygmaea	67.7	± 12.4	143.2	± 41.7	-75.4	100.9	± 22.0	92.6	± 11.9	8.2	1.50	10.93	0.162
	R. columbianum	267.4	± 126.6	35.9	± 37.6	286.2	177.9	± 32.0	28.5	± 29.8	155.2	0.90	5.74	0.402
	R. macrophyllum	77.2	± 12.9	111.1	± 52.3	-33.9	85.1	± 4.7	132.5	± 29.9	-47.4	0.21	10.98	0.835
	S. sempervirens	21.4	± 7.3	31.8	± 7.8	-10.4	134.1	± 13.7	86.9	± 21.2	47.1	2.79	11.37	0.017
Chlorophyll content (mg m^{-2})	*G. shallon*	238.9	± 29.1	145.4	± 30.9	93.5	331.5	± 19.9	419.6	± 29.3	-88.1	4.04	13.92	0.001
	H. pygmaea	162.8	± 17.6	251.5	± 28.7	-88.8	313.3	± 23.9	328.1	± 22.4	-14.9	1.91	12.98	0.078
	R. columbianum	422.6	± 22.7	308.6	± 20.3	114.0	371.3	± 19.2	202.3	± 27.8	169.0	1.8	13.29	0.098
	R. macrophyllum	382.3	± 30.3	312.6	± 59.3	69.6	406.1	± 30.3	387.9	± 32.0	18.3	0.69	10.35	0.504
	S. sempervirens	41.1	± 25.8	124.5	± 25.1	-83.4	559.0	± 72.7	581.3	± 61.0	-22.3	1.45	12.51	0.173

Table S3: Averages, standard errors, and *t*-test results of physiological trait measurements on pygmy and control plants sampled from Salt Point State Park in Sonoma County, CA, the SFB Morse Botanical Preserve in Monterey County, CA, and Humboldt Redwoods State Park in Humboldt County, CA (*n*=8 for all).

Location and Trait	Species	Pygmy	Control	*t*	df	*P*-value
Sonoma County Specific Leaf Area (cm^2 g^{-1})	*Gaultheria shallon*	46.70 ± 2.00	67.39 ± 2.11	7.13	13.96	5.2E-6*
	Pteridium aquilinum	101.38 ± 6.53	112.12 ± 2.63	1.53	9.22	0.1606
	Vaccinium ovatum	33.54 ± 3.07	47.21 ± 2.75	3.32	13.83	0.0051*
Monterey County Specific Leaf Area (cm^2 g^{-1})	*Hesperocyparis goveniana*	22.1 ± 0.8	21.6 ± 0.9	0.35	13.95	0.7281
	P. aquilinum	71.67 ± 3.88	105.4 ± 7.3	4.09	10.68	0.0019*
	V. ovatum	42.3 ± 1.1	52.6 ± 3.7	2.67	8.10	0.02811
Sonoma County C:N ratio	*G. shallon*	53.6 ± 3.0	47.8 ± 2.1	1.60	12.30	0.1339
	P. aquilinum	26.1 ± 1.5	28.3 ± 1.4	1.11	13.91	0.2872
	V. ovatum	92.6 ± 4.3	76.7 ± 1.3	3.50	8.22	0.0077*
Monterey County C:N ratio	*H. goveniana*	59.1 ± 3.6	50.9 ± 3.8	1.59	13.96	0.1351
	P. aquilinum	33.0 ± 1.0	26.2 ± 1.4	3.99	12.97	0.0016*
	V. ovatum	66.7 ± 3.5	60.1 ± 2.4	1.57	12.30	0.1428
Sonoma County Percent N	*G. shallon*	0.9 ± 0.1	1.0 ± 0.1	0.95	13.96	0.3596
	P. aquilinum	1.8 ± 0.1	1.6 ± 0.1	1.11	13.94	0.2869
	V. ovatum	0.5 ± 0.0	0.7 ± 0.0	4.44	12.83	0.0007*
Monterey County Percent N	*H. goveniana*	0.9 ± 0.1	1.0 ± 0.1	1.73	11.83	0.1092
	P. aquilinum	1.4 ± 0.1	1.8 ± 0.1	3.89	11.19	0.0024*
	V. ovatum	0.8 ± 0.0	0.8 ± 0.0	1.69	12.23	0.1157
Sonoma County δ^{13}C (‰)	*G. shallon*	-29.5 ± 0.2	-31.4 ± 0.2	7.60	13.33	3.3E-6*
	P. aquilinum	-27.8 ± 0.2	-29.2 ± 0.1	6.11	10.91	0.0001*
	V. ovatum	-30.0 ± 0.3	-31.1 ± 0.3	2.52	13.42	0.0251*
Monterey County δ^{13}C (‰)	*H. goveniana*	-28.5 ± 0.3	-28.0 ± 0.3	1.42	13.58	0.1775
	P. aquilinum	-28.5 ± 0.3	-27.5 ± 0.3	2.27	13.98	0.0398
	V. ovatum	-30.1 ± 0.4	-30.2 ± 0.3	0.38	13.11	0.7082

Notes: *P*-values are from *t*-tests. Starred *P*-values indicate significance after sequential Bonferrroni correction (Holm 1979).

Figure S1: Photosynthetic nitrogen-use efficiency (PNUE) as μmol CO_2 gained per mol leaf N per sec in pygmy (dark grey) and control (light grey) plants from Mendocino County, CA, USA. Error bars are standard error, and asterisks indicate significance (one asterisk signifies $P<0.05$; two, $P<0.01$; three, $P<0.001$). Please see Appendix S1 for full statistics.



Appendix 2

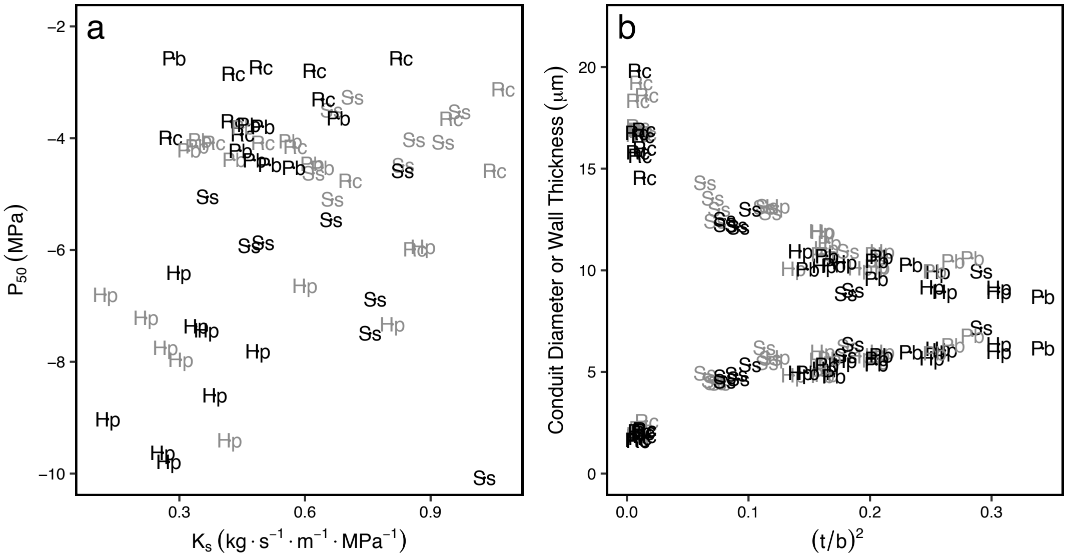
Supplementary Tables and Figures for Chapter 2

Table S1 Data with results from Welch's t-tests comparing pygmy and control plants within species. Reported error is standard error. Continues onto next page.

Trait	Species	Pygmy	*n*	Control	*n*	*t*	df	*P*-value
Conduit Diameter (µm)	*Hesperocyparis pygmaea*	9.7 ± 0.3	8	11.2 ± 0.4	8	3.08	12.5	0.0091
	Pinus contorta ssp. *bolanderi*	10.1 ± 0.2	8	10.6 ± 0.2	8	1.88	11.9	0.0844
	Rhododendron columbianum	16.5 ± 0.5	8	17.6 ± 0.4	8	1.60	12.0	0.1359
	Sequoia sempervirens	11.2 ± 0.6	8	12.9 ± 0.3	8	2.45	11.2	0.0160
Hydraulic mean diameter (µm)	*H. pygmaea*	12.5 ± 0.4	8	14.2 ± 0.4	8	3.01	13.5	0.0096
	P. c. bolanderi	12.5 ± 0.3	8	12.8 ± 0.2	8	0.66	12.6	0.5202
	R. columbianum	18.7 ± 0.6	8	20.4 ± 0.4	8	2.34	12.0	0.0375
	S. sempervirens	15.7 ± 0.5	8	17.2 ± 0.5	8	2.10	14.0	0.0273
Wall thickness (µm)	*H. pygmaea*	5.7 ± 0.2	8	5.6 ± 0.1	8	0.46	13.3	0.6500
	P. c. bolanderi	5.5 ± 0.2	8	5.7 ± 0.2	8	0.49	12.6	0.6317
	R. columbianum	1.9 ± 0.1	8	2.0 ± 0.1	8	0.87	12.8	0.3988
	S. sempervirens	5.4 ± 0.3	8	5.2 ± 0.3	8	0.45	13.3	0.6605
$(t/b)^2$	*H. pygmaea*	0.23 ± 0.02	8	0.17 ± 0.01	8	2.54	10.2	0.0288
	P. c. bolanderi	0.21 ± 0.02	8	0.21 ± 0.02	8	0.13	13.5	0.8979
	R. columbianum	0.01 ± 0.00	8	0.01 ± 0.00	8	0.38	13.8	0.7131
	S. sempervirens	0.14 ± 0.03	8	0.10 ± 0.01	8	1.20	10.5	0.2559
Growth ring width (µm)	*H. pygmaea*	272 ± 38	8	295 ± 32	8	0.48	13.5	0.6403
	P. c. bolanderi	166 ± 13	8	275 ± 42	8	2.49	8.3	0.0366
	R. columbianum	240 ± 41	8	395 ± 30	8	3.04	12.9	0.0096
	S. sempervirens	119 ± 13	8	214 ± 25	8	3.33	10.5	0.0071
Fiber wall $(t/b)^2$	*R. columbianum*	0.49 ± 0.05	8	0.57 ± 0.11	8	0.66	9.8	0.5228
Vessel Grouping Index	*R. columbianum*	1.44 ± 0.03	8	1.49 ± 0.05	8	0.78	10.7	0.4504

Trait	Species	Pygmy	*n*	Control	*n*	*t*	df	*P*-value
K_L (kg s^{-1} m^{-1} MPa^{-1}) $*10^4$	*H. pygmaea*	3.01 ± 0.37	8	1.98 ± 0.32	8	2.14	14.1	0.0499
	P. c. bolanderi	3.69 ± 1.07	8	3.36 ± 0.74	8	0.25	12.4	0.8070
	R. columbianum	5.61 ± 1.49	8	2.53 ± 0.29	8	2.03	7.5	0.0796
	S. sempervirens	6.72 ± 2.39	8	0.90 ± 0.10	8	2.43	7.0	0.0454
K_S (kg s^{-1} m^{-1} MPa^{-1})	*H. pygmaea*	0.32 ± 0.04	8	0.45 ± 0.10	8	1.28	8.9	0.2332
	P. c. bolanderi	0.49 ± 0.04	8	0.47 ± 0.05	8	0.47	13.8	0.6455
	R. columbianum	0.52 ± 0.06	8	0.76 ± 0.09	8	2.19	12.0	0.0491
	S. sempervirens	0.67 ± 0.08	8	0.78 ± 0.05	8	1.21	11.6	0.2509
Huber Value (m^2 m^{-2})	*H. pygmaea*	0.12 ± 0.01	8	0.26 ± 0.07	8	2.00	7.3	0.0837
	P. c. bolanderi	0.17 ± 0.02	8	0.18 ± 0.04	8	0.13	11.6	0.9017
	R. columbianum	0.13 ± 0.03	8	0.30 ± 0.02	8	5.33	12.7	0.0002
	S. sempervirens	0.21 ± 0.06	8	0.91 ± 0.08	8	7.45	12.8	0.0000
P_{50} (MPa)	*H. pygmaea*	-8.3 ± 0.4	8	-7.4 ± 0.4	8	1.56	13.7	0.1405
	P. c. bolanderi	-3.9 ± 0.2	8	-4.2 ± 0.1	8	1.15	8.9	0.2805
	R. columbianum	-3.2 ± 0.2	8	-4.3 ± 0.3	8	2.95	12.3	0.0119
	S. sempervirens	-6.4 ± 0.6	8	-4.1 ± 0.2	8	3.58	8.8	0.0061
Native Percent Loss of Conductivity	*H. pygmaea*	8% ± 2%	8	3% ± 1%	9	1.93	10.6	0.0804
	P. c. bolanderi	0% ± 1%	8	1% ± 2%	8	0.73	11.1	0.4786
	R. columbianum	12% ± 7%	8	3% ± 6%	8	1.01	13.4	0.3316
	S. sempervirens	7% ± 1%	8	5% ± 1%	8	1.56	13.8	0.1424
Midday Water Potential (MPa)	*H. pygmaea*	-0.64 ± 0.13	8	-0.80 ± 0.09	8	0.97	12.5	0.3508
	P. aquilinum	-0.28 ± 0.10	8	-0.30 ± 0.08	8	0.17	13.3	0.8659
	P. c. bolanderi	-0.48 ± 0.14	7	-0.96 ± 0.04	8	3.41	6.9	0.0117
	R. columbianum	-0.20 ± 0.03	8	-0.29 ± 0.06	8	1.33	10.8	0.2097
	S. sempervirens	-0.41 ± 0.01	8	-0.49 ± 0.08	8	1.01	7.3	0.3451

Fig. S1 a.) Weak or non-existent relationship between cavitation resistance (P_{50}) and xylem-specific conductivity (K_S) for pygmy (black) and control (gray) plants of four species. Hp = *Hesperocyparis pygmaea*, Pc = *Pinus contorta* ssp. *bolanderi*, Rc = *Rhododendron columbianum*, and Ss = *Sequoia sempervirens*. Linear regression showed that K_S was a significant predictor of P_{50} across individuals of all four species ($F_{1,62}$=4.8, P=0.03) with an adjusted R^2 of 0.06. However, when only the three conifer species were considered, K_S was a marginally non-significant predictor of P_{50} ($F_{1,46}$=3.5, P=0.07, R^2=0.05). b.) Scatterplot of $(t/b)^2$ and its two components, double wall thickness (t) and conduit diameter (b). Points above the horizontal dashed line are average conduit diameter, while points below the dashed line are average double wall thickness for the same stems. A linear regression revealed that wall thickness was a significant predictor of $(t/b)^2$ within conifers ($F_{1,46}$=92.3, P <0.00001), indicating that variation in $(t/b)^2$ was driven by variation in both conduit diameter and wall thickness, although diameter varied more across individuals.


a
P_{50} (MPa)
−2
−4
−6
−8
−10
K_s (kg · s^{-1} · m^{-1} · MPa^{-1})
0.3
0.6
0.9
Pb
Rc
Ss
Hp
b
Conduit Diameter or Wall Thickness (μm)
20
15
10
5
0
$(t/b)^2$
0.0
0.1
0.2
0.3

Appendix 3

Supplementary Tables and Figures for Chapter 3

Table S1: Results of multiple linear regressions, with MPD and MNTD weighted by species abundance, as quantified by either species count or percent cover. Pluses or minuses next to predictor variables indicate whether their relationship with the response variable was positive or negative, followed by significance level after a Bonferonni correction.

Weighted by Species Count

Response Variable	Explanatory Variable Group	AIC selected predictors	DF	F	R^2	P	
MPD	Soil	nitrate, P, pH, OM	4, 8	2.4	0.32	0.13	
MNTD	Soil	nitrate	1,12	5.9	0.27	0.03	
MPD	Tree height	height	1,12	6.953	0.3141	0.022	
MNTD	Tree height	height (-)**	1,12	18.8	0.578	1E-03	**
MPD	Trait Range	SLA , KS (-)*	2,11	8.6	0.53	0.006	*
MNTD	Trait Range	KL, KS (-)*	2,11	6.5	0.46	0.014	
MPD	Trait Average	SLA (-)**, KL (-)*	2,11	11	0.6	0.002	**
MNTD	Trait Average	SLA (-)**, Huber, KS (-)*	3,10	17	0.79	3E-04	**

Weighted by Percent Cover

Response Variable	Explanatory Variable Group	AIC selected predictors	DF	F	R^2	P	
MPD	Soil	nitrate, pH, Al, CEC, OM	5, 8	3.884	0.5259	0.044	
MNTD	Soil	pH (-)*, CEC	2, 11	7.615	0.5044	0.008	*
MPD	Tree height	height	1, 12	0.423	-0.046	0.528	
MNTD	Tree height	height (-)	1, 12	7.414	0.3304	0.019	
MPD	Trait Range	SLA (+)*, Huber, KS (-)*	3, 9	9.284	0.6744	0.004	*
MNTD	Trait Range	SLA, KL, Huber, KS (-)**	4, 8	8.578	0.7164	0.005	*
MPD	Trait Average	SLA, Huber, KS (-)*	3, 10	9.724	0.6681	0.003	*
MNTD	Trait Average	SLA, KL, KS (-)*	3, 10	11.18	0.7014	0.002	**

Table S2: Plot locations, species richness, within-community phylogenetic relatedness, average tree height, and soil variables for pygmy forest plots, as well as plots from nearby tall conifer forests.

Plot Type	GPS	Number of Species	MPD (Myr)	MNTD (Myr)	Tenth Quantile (Myr)	Average Tree Height (m)	pH	nitrate (ppm)	P (ppm)	K (ppm)	Na (ppm)	Ca (meq/ 100g)	Mg (meq/ 100g)	CEC (meq/ 100g)	OM (%)	Al (ppm)
Pygmy Forest	39.314571 -123.760501	6	447.0	223.5	87.0	2.9	3.88	0.30	0.8	15	6	0.04	0.12	0.22	2.83	66.8
Pygmy Forest	39.312919 -123.760087	6	437.9	194.9	58.8	3	4.00	0.18	1.5	20	10	0.07	0.22	0.39	3.72	220.3
Pygmy Forest	39.313171 -123.760309	6	437.9	194.9	58.8	1.2	3.93	<0.10	1.9	14	8	0.04	0.13	0.24	2.96	182.8
Pygmy Forest	39.312631 -123.744279	10	423.1	93.5	95.1	4.9	4.73	0.35	0.8	36	4	0.28	0.14	0.53	2.58	59.1
Pygmy Forest	39.311518 -123.743768	3	84.9	62.4	53.5	0	5.00	0.34	<0.5	39	4	0.39	0.17	0.67	3.71	48.4
Pygmy Forest	39.311674 -123.748601	7	485.8	157.0	87.0	4.3	4.52	0.27	4	39	10	0.13	0.27	0.55	6.14	228.6
Pygmy Forest	39.317528 -123.750185	7	485.8	157.0	87.0	1.8	4.57	0.24	1.2	20	6	0.07	0.13	0.28	3.94	65.7
Pygmy Forest	39.319303 -123.752282	9	457.2	149.8	101.2	3.6	4.75	0.30	<0.5	35	5	0.18	0.15	0.44	3.53	74.9
Pygmy Forest	39.313913 -123.742058	7	318.0	142.4	87.0	5.5	4.23	0.40	1.7	66	19	0.9	0.56	1.71	6.06	60.9
Pygmy Forest	39.321240 -123.752558	12	443.5	117.0	87.0	5	4.63	0.21	0.8	20	4	0.04	0.07	0.18	3.14	102.3
Pygmy Forest	39.371710 -123.777167	9	507.6	201.4	107.3	6.4	4.31	0.26	<0.5	21	7	0.19	0.14	0.41	3.32	61.6
Pygmy Forest	39.372358 -123.778666	11	474.1	156.1	107.3	7.1	3.93	0.19	1.5	33	8	0.34	0.26	0.73	3.07	74.7

Plot Type	GPS	Number of Species	MPD (Myr)	MNTD (Myr)	Tenth Quantile (Myr)	Average Tree Height (m)	pH	nitrate (ppm)	P (ppm)	K (ppm)	Na (ppm)	Ca (meq/ 100g)	Mg (meq/ 100g)	CEC (meq/ 100g)	OM (%)	Al (ppm)
Pygmy Forest	39.373543 -123.783845	6	447.0	223.5	87.0	4.1	4.48	0.15	0.8	34	5	0.27	0.11	0.48	2.69	89.7
Pygmy Forest	39.372542 -123.779275	7	431.8	225.6	87.0	1.8	4.34	0.25	0.6	30	6	0.29	0.17	0.56	2.8	67.8
Pygmy Forest	39.313300 -123.760609	5	497.4	246.8	82.3	1.5	3.91	<0.10	2.6	26	15	0.07	0.24	0.45	5.6	273.9
Tall Forest	39.318868 -123.761437	6	559.9	300.3	238.3											
Tall Forest	39.320361 -123.764393	5	532.4	295.8	223.2											
Tall Forest	39.267918 -123.739089	7	520.2	269.9	87.0											
Tall Forest	39.268147 -123.740033	5	525.9	269.8	216.7											
Tall Forest	39.268966 -123.739919	6	473.2	245.4	87.0											
Tall Forest	39.272106 -123.742782	5	525.9	269.8	216.7											
Tall Forest	39.269983 -123.741753	7	514.9	257.9	40.0											
Tall Forest	39.271394 -123.731025	5	527.7	277.0	218.5											
Tall Forest	39.27082 -123.732028	5	527.7	277.0	218.5											
Tall Forest	39.374858 -123.80142	8	516.7	307.1	230.4											
Tall Forest	39.374775 -123.800466	7	536.1	311.9	211.9											

Plot Type	GPS	Number of Species	MPD (Myr)	MNTD (Myr)	Tenth Quantile (Myr)	Average Tree Height (m)	pH	nitrate (ppm)	P (ppm)	K (ppm)	Na (ppm)	Ca (meq/ 100g)	Mg (meq/ 100g)	CEC (meq/ 100g)	OM (%)	Al (ppm)
Tall Forest	39.374722 -123.797243	6	482.1	271.2	124.6											
Tall Forest	39.374761 -123.796484	8	480.8	228.1	87.0											
Tall Forest	39.269087 -123.732387	2	704.5	704.5	704.5											
Tall Forest	39.270131 -123.731916	5	527.7	277.0	218.5											

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