

**Coast redwoods (*Sequoia sempervirens*) and Climate Change:
Age Based Differences in Leaf Hydraulic Traits**

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ABSTRACT

Climate change is projected to increase the frequency and severity of droughts in many regions. However, there is not yet a consensus on how forests will respond in part because we lack understanding about how hydraulic traits that confer drought tolerance change as trees age. In this study, I aimed to determine if and how hydraulic traits differ with age in *Sequoia sempervirens* (*S. sempervirens*) growing in a secondary forest. I tested for a difference in hydraulic traits, dawn and midday leaf water potential (Ψ_{leaf}) and leaf turgor loss point (TLP), between *S. sempervirens* in different age groups. I also measured differences in the hydraulic traits of juveniles growing under nursery trees compared to those growing in more open locations to test for a nursery effect. Using diameter at breast height (DBH) as a proxy for age I separated coast redwoods within Redwood Regional Park in Oakland, California into 5 DBH size classes. To measure the nursery-tree effect on the hydraulic traits of recruits I had two groups within the smallest size class that were $\sim 0.3\text{m}$ and $>1.7\text{m}$ from a more mature *S. sempervirens*. Dawn Ψ_{leaf} had no trend across size-classes, however, both midday Ψ_{leaf} and TLP were negatively correlated with tree height. Additionally, juvenile trees growing in close proximity to a mature tree had considerably higher midday Ψ_{leaf} and TLP compared to the freestanding juvenile trees suggesting that they benefited from a nursery effect. These results provide a physiological mechanism for explaining how older and larger trees within a forest canopy tolerate higher levels of water-stress when compared to younger understory trees.

KEYWORDS

life history stage, ontological plasticity, forest ecology, Plant physiology, functional diversity

INTRODUCTION

Climate change is forecasted to alter the incidence and severity of extreme weather events such as drought (Rummukainen 2012). While the extent to which climate change has impacted current forest composition is unclear, evidence suggests that at least a portion of the world's forests is already responding to climate change (Allen et al. 2010). Despite the existing knowledge gaps, scientists predict that the longer and more severe droughts caused by climate change will increase the amount of stress forests experience which could lead to an increase in the background tree mortality rate (Allen et al. 2010, Allen et al. 2015). However, despite the recent focus on the impact of future droughts there is still not an agreement on what these climatic changes mean for forests on a regional scale (McDowell et al. 2008). This uncertainty for how climate change will impact forests is significant for places like California where a recent drought, only partially linked to climate change, led to progressive canopy water stress across the state and increased the tree mortality rate by an order of magnitude. (Mao et al. 2015, Asner et al. 2015, Young et al. 2017).

Part of this uncertainty can be traced back to a need for more information about how hydraulic traits vary within a species. Often used as a metric to predict drought tolerance, hydraulic traits characterize how a plant or species interact with and use the water in their ecosystem (McDowell et al. 2008, Bartlett et al. 2012, Bartlett et al. 2014). Studies have shown that the hydraulic traits of a tree species can change along precipitation gradients; however, relatively few studies have been focused on if these traits vary as a tree ages (Limousin et al. 2010, Martin-St. Paul et al. 2013, Baguskas et al. 2016). Water stress is increased for both young and old trees as younger trees have a less developed root system, which limits access to water in the soil, and older trees, when close to their maximum height, have to move water across an increased gradient (McDowell et al. 2008). Additionally, the recruitment of saplings can impact the degree of water stress these trees experience as the traits that are required for successful recruitment can be dictated by proximity to shelter by larger trees (Kobe et al. 1995). These structural and location differences between the life history stages of trees have been shown to lead to age-based differences in water status and, in extreme cases, different rates of drought induced mortality (Baguskas et al. 2016, Condit et al. 1995, Nepstad et al. 2007, Ogle et al. 2000, Douhovnikoff et al. 2004).

Hydraulic traits such as leaf water potential (Ψ_{leaf}), Turgor loss point (TLP), osmotic potential (π_o) and modulus of elasticity (ϵ) can be used to understand the physiological mechanisms

driving this age-based differences in water stress (Bartlett et al. 2016). Ψ_{leaf} is a metric that can be used to determine both the amount of water each tree has access to in the soil (dawn Ψ_{leaf}) as well as the maximum amount of water stress a tree experiences during the day (midday Ψ_{leaf}) (Bhasker and Ackerly 2006). TLP measures the Ψ_{leaf} at which the cells in a leaf lose function due to water stress (Bartlett et al. 2012). π_o is a measure of the concentration of solutes within a cell while ϵ is the ability of the cell wall to expand and contract as the amount of water changes (Bartlett et al. 2012).

Age-based differences in leaf hydraulic traits could have novel implications for the future of California's forest ecosystems as some native tree species play an important role in shaping the biophysical and ecological dynamics of their environment (Record et al. 2018). One such species is the coast redwood (*S. sempervirens*). *S. sempervirens* create unique microclimates within the forests they inhabit – supporting understory plants and changing the hydrology of the ecosystem through fog drip (Dawson 1998). They also provide numerous ecosystem services such as providing wildlife habitat and sequestering large amounts of CO₂, especially in old-growth stands (Sillett et al. 2015). One of two California state trees, *S. sempervirens* are an important source of timber as well as recreation within the state (Save the Redwoods League, California Department of Parks and Recreation). As a result, understanding how hydraulic traits vary with the age of a *S. sempervirens* has both ecological and social implications.

By conducting field research to determine the ways in which the age of a *S. sempervirens* affects its leaf hydraulic traits, this study will provide a physiological baseline that will help explain how droughts will impact *S. sempervirens* in the future. I will use diameter at breast as a proxy for age to answer the following questions: Is there a difference in hydraulic traits, dawn and midday leaf water potential (Ψ_{leaf}) and leaf turgor loss point (TLP), between *S. sempervirens* age groups? Do hydraulic traits differ in *S. sempervirens* juveniles growing under nursery trees compared to those growing in more open locations? I hypothesized that younger *S. sempervirens* would have more negative dawn Ψ_{leaf} than the older groups while these more mature age groups would experience high levels of water stress at midday (McDowell et al. 2008). Additionally, I predicted that TLP would decrease as the age of the group increases, reflecting midday Ψ_{leaf} . Finally, while I hypothesized Ψ_{leaf} to decrease as the distance of a juvenile increases from a more mature *S. sempervirens* I expected TLP to more closely reflect the age class of the juveniles and not their proximity to a nursery tree.

METHODS

Study Species

S. sempervirens are a fast-growing and long-lived conifer native to the coastal regions of southern Oregon to Central California. *S. sempervirens* can live for over 2,000 years and can reach heights of 116 meters (Save the Redwoods League). Additionally, *S. sempervirens* have multiple recruitment strategies including the ability to sprout new clones from the roots or trunk base of an older tree after a disturbance. This phenomenon is commonly seen after fires or logging. When compared to non-clonal seed-grown trees, clonal saplings can use resources from other trees and increasing their ability to survive in difficult environments (Douhovnikoff et al. 2004). *S. sempervirens* can also use fog to decouple their water status from the soil water availability (Simonin et al. 2009, Dawson 1998). This is done through the creation of fog drip and the uptake of fog directly through their leaves (Limm et al. 2009). *S. sempervirens* are most dependent on fog as a source of water was highest during years where precipitation was low, but fog was normal (Dawson 1998).

Study site

S. sempervirens were sampled from Redwood Regional Park (740 area ha), located in the Pacific Coast range on the eastern edge of Oakland, Ca (East Bay Regional Park District). Oakland receives on average 527 mm of rainfall annually with the majority falling between during the rainy season which lasts from November to May (Climate Data). Additionally, Oakland, Ca experiences a Mediterranean climate characterized by moderate winters and warm water-scarce summers with high frequencies of fog (Iacobellis et al. 2016). In the 1800s this area was extensively logged and, as a result, the *S. sempervirens* stands in this park are composed of secondary growth (East Bay Regional Park District).

Tree selection and age classification

To control for confounding variables that could impact my data I selected *S. sempervirens* trees that were exposed to similar environmental conditions. By doing this, each of the *S. sempervirens* I studied had similar soil moisture conditions, ground cover, proximity to creeks and streams, and sun exposures at different times of day. Additionally, all of the *S. sempervirens* I selected were located on the same slope face in areas with similar temperature and humidity. Finally, to minimize the effects of gravity on the hydraulic traits I measured, I collected samples from the same height on all individuals (~20 ft). Due to the fact that I was collecting samples from the understory none of the branches I collected samples from were in direct sunlight.

I used diameter at breast height (DBH ~1.37 meters) as a proxy for age and separated *S. sempervirens* into 5 DBH size classes: 3-13cm, 21-34cm, 76-86cm, 108-115cm, and 140-165cm (Waring and O'Hara 2006). To measure the nursery-tree effect on the hydraulic traits of recruits I had two groups within the smallest size class: one with juveniles located within ~0.3 m of a more mature *S. sempervirens* (age class 1) and another with juveniles growing >1.7m from the nearest mature tree (age class 0) (Table 1). I selected the cutoffs for each age class so that the ranges in girth were approximately the same for each age group. However, variability in the range of DBH for each age class arose based on trees I was able to collect samples from.

Table 1. Table with the diameter at breast height, number of individuals and number of samples per individual for each age class. Individuals in age class 0 are located >1.7m from a more mature *S. sempervirens* while individuals in age class 1 are growing within ~0.3m of these larger trees.

Age Class	DBH range (cm)	# of individuals	# of samples per measurement
			time per individual
0	3 -13	6	5
1	3-13	5	5
2	21 - 34	5	5
3	76 - 86	5	5
4	108 – 115	5	5
5	140-165	2	10

Leaf water potential

I used a Scholander pressure chamber (PMS model 1000) to measure the dawn and midday leaf water potential (Ψ_{leaf} , [MPa]) from *S. sempervirens* in each size class between September and November 2018 (Table 2). I collected Dawn Ψ_{leaf} measurements between 0630 and 0730 before daylight savings and between 0730 and 0830 after. I measured Midday Ψ_{leaf} between 1330 and 1430 and between 1430 and 1530 respectively. Once I had removed a branch from a *S. sempervirens*, I placed the branch directly into a black plastic bag in order to minimize transpiration losses from the leaves before I measured their Ψ_{leaf} . I sampled between 5 and 10 leaves from each individual for both dawn and midday, all of which were 2018's growth growing on new growth.

Leaf Turgor Loss Point

I used the bench drying method to construct pressure-volume curves (Ψ_{leaf} ([MPa] vs. volume of water in leaf [g, %]) to estimate the turgor loss point (TLP, [MPa]) (Bartlett et al. 2012, Sack et al. 2011) (Table 2). I measured TLP from November and March 2019 and collected all of the samples in the 20 minutes before first light to increase the accuracy of the estimated TLP for each leaf. Once I removed the branch from which I sampled leaves from, I immediately placed the branch in a black plastic bag and then into a bucket of water so that any transpiration losses that occurred when the branch was in the plastic bag would lead to the movement of a continuous water column in the xylem and not to the formation of embolisms. As with midday and dawn Ψ_{leaf} , the leaves I measured were 2018's growth growing off of new growth; however, for TLP all of the leaves I sampled were the one directly below the first leaf on each branchlet.

I also used the pressure volume curve to derive the osmotic potential (π_o) and the modulus of elasticity (ϵ) of each of the leaves I measured the TLP for (Sack et al. 2011). By calculating the π_o and the ϵ for each leaf I was able to determine how the different size classes controlled their TLP.

Table 2. Summary of the hydraulic traits that are measured or derived in this study.

Symbol	Definition	Units	Significance
Dawn Ψ_{leaf}	Dawn leaf water potential	MPa	Amount of water trees have access to (Lambers et al. 2008).
Midday Ψ_{leaf}	Midday leaf water potential	MPa	Maximum amount of water stress a tree experiences during the day (Bhasker and Ackerly 2006).
TLP	Turgor loss point	MPa	Leaf water potential at which the cells in a leaf start to lose function (Bartlett et al. 2012)
π_o	Osmotic potential	MPa	Concentration of solutes in cells (Bartlett et al 2012)
ε	Modulus of elasticity	MPa	Flexibility of cell walls (Bartlett et al. 2012)

Statistics

To determine statistical significance, I used R and the *lme4* package to run a linear mixed effects models to analyze the relationship between age and each hydraulic trait I measured (Ψ_{leaf} , TLP, π_o , and ε) (R core team 2012, Bates et al. 2012). The model I used to analyze the differences in Ψ_{leaf} had both age and time of day as fixed effects and week of sampling and individual where random effects. However, for TLP, π_o , and ε , week and individual where entered as random effects and age was entered as the only fixed effect for each of the 3 linear mixed effects models. I visually examined the residual plots for each of the 5 hydraulic traits and determined that there were no obvious outliers with regards to homoscedasticity or normality. To calculate the P-value for each of the 4 linear mixed effects model I used the likelihood ratio test that compared the complete model against the same model but without age as an effect.

RESULTS

Leaf Water Potential

Both time of day and age had an effect on the Ψ_{leaf} of each age group (Figure 1). For all age classes there was a significant difference between their dawn Ψ_{leaf} and midday Ψ_{leaf} ($P < 0.001$ and X^2). Additionally, I found that Dawn Ψ_{leaf} did not differ significantly between the age class with values ranging from -6.30 ± 0.01 MPa to $-.71 \pm 0.01$ MPa. However, at midday the differences in the Ψ_{leaf} between the age classes was significant with values decreasing from -0.94 ± 0.01 to -1.47 ± 0.02 MPa as the size of the class increased ($P < 0.001$).

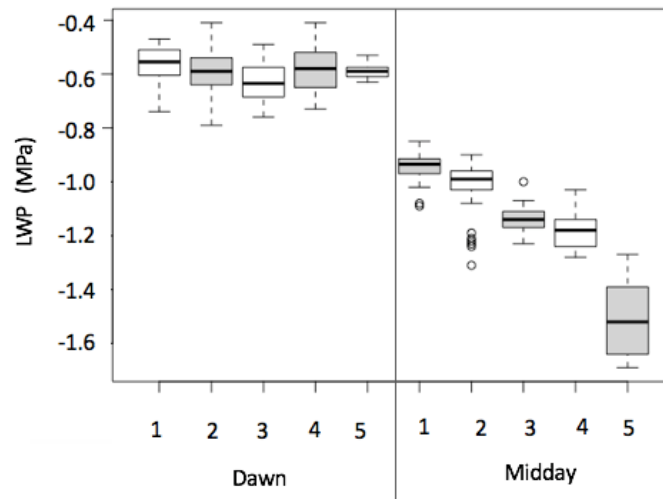


Figure 1. Dawn and midday leaf water potential (Ψ_{leaf}) for *S. sempervirens* age groups of increasing DBH. The center line represents the median LWP for the leaves I sampled for each age class. The box represents the interquartile range between 25% and 75% of the measured individuals or leaves. The whiskers define the “fence” = $[Q1, Q3] + 1.57 * IQR$, and the open circles are outliers beyond the fence. The grey and white are only to provide contrast between the boxes.

Turgor Loss Point

As the age of class increased the TLP and π_o for each group decreased (Figure 2). The differences in the TLP of each age class were statistically significant with the youngest group having an average TLP of -1.78 ± 0.01 while the average TLP of the cohort with the largest DBH was -2.14 ± 0.02 MPa ($P < 0.001$). There was no significant difference between the ϵ of each age class. However, the π_o also differed significantly as the age of the class increased ($P < 0.01$). I found that the π_o followed a similar trend to that of TLP and ranged from -1.55 ± 0.02 to -2.00 ± 0.04 MPa decreasing as the age of the group increased (Figure 3).

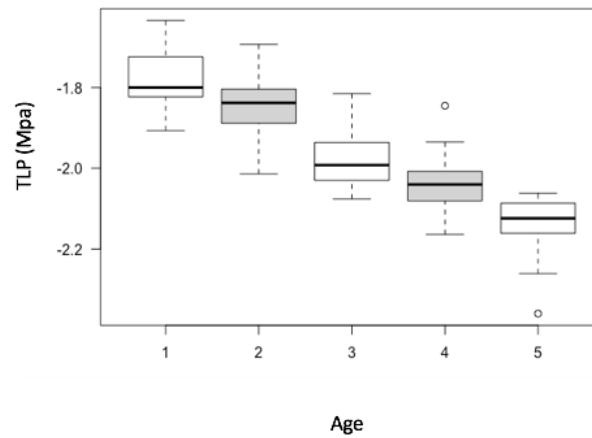


Figure 2. Turgor loss point (TLP) for *S. sempervirens* age groups of increasing DBH. The boxes are defined the same way as described in figure one.

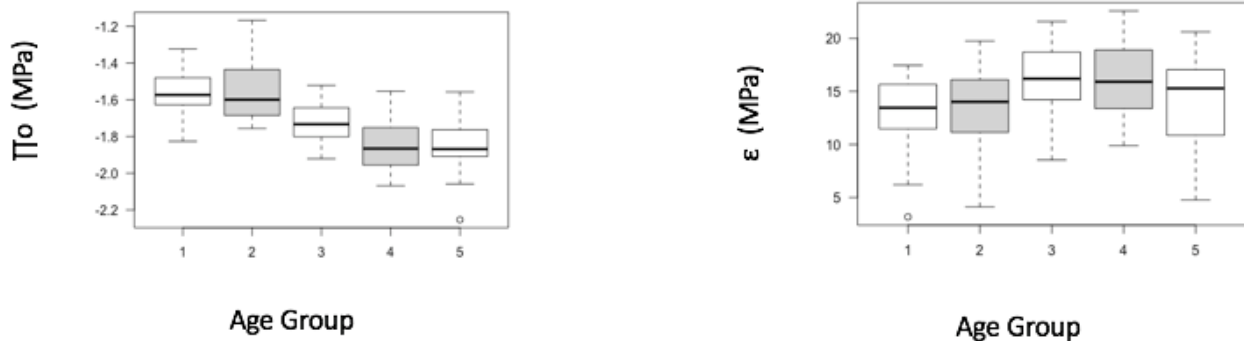


Figure 3. Osmotic potential (π_o) and modulus of elasticity (ϵ) for *S. sempervirens* age groups of increasing DBH. The boxes are defined the same way as described as figure one.

Nursery Effect

The juveniles growing in close proximity to a more mature *S. sempervirens* had lower midday Ψ_{leaf} , TLP, and π_o than their counterparts growing farther from a more mature tree (Figure 4, 5 and 6). I found that there was not significant difference in the dawn Ψ_{leaf} of each group. However, the midday Ψ_{leaf} of the juveniles growing $>1.7\text{m}$ away from a more mature *S. sempervirens* had a significantly more negative Ψ_{leaf} than their counterparts growing in close proximity to a larger tree, $-1.69 \pm 0.09 \text{ MPa}$ and $-0.94 \pm 0.01 \text{ MPa}$ respectively ($P < 0.001$). The TLP of these 2 classes of juveniles were significantly different with the group growing in close proximity to a more mature tree having an average TLP of $-1.78 \pm 0.01 \text{ MPa}$ and the juveniles growing in a more open location had an average TLP of $-2.06 \pm 0.01 \text{ MPa}$ ($P < 0.001$). While there was no significant difference between the ϵ of the two juvenile classes, π_o decreased significantly as the distance of the juvenile class from a more mature tree increased ($-1.55 \pm 0.02 \text{ MPa}$ and $-1.77 \pm 0.03 \text{ MPa}$, respectively) ($P < 0.01$).

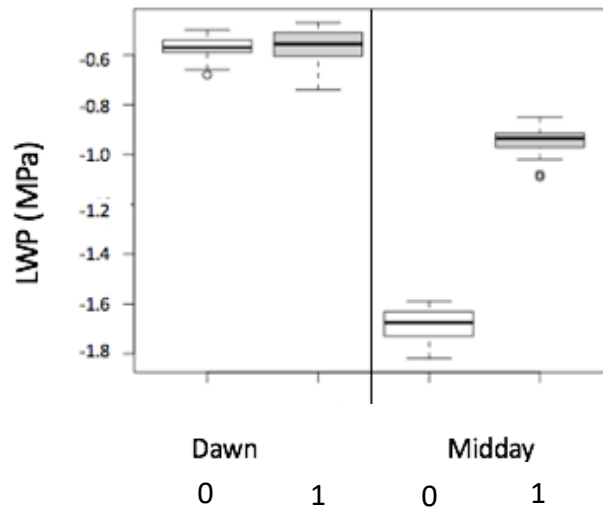


Figure 4. Dawn and midday leaf water potential (Ψ_{leaf}) for *S. sempervirens* juveniles $>1.7\text{m}$ (age class 0) and $\sim 0.3\text{m}$ (age class 1) from a mature *S. sempervirens*. The boxes are defined the same way as described as figure one.

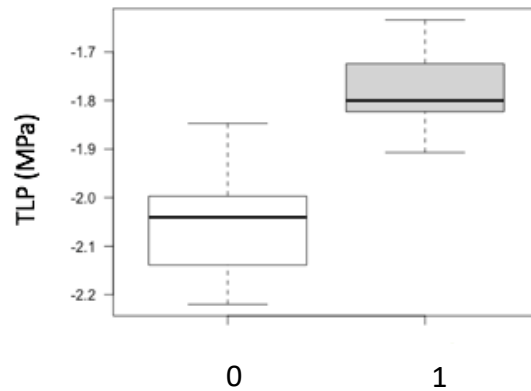


Figure 5. Turgor loss point (TLP) for *S. sempervirens* juveniles >1.7m (age class 0) and ~0.3m (age class 1) from a mature *S. sempervirens*. The boxes are defined the same way as described as figure one.

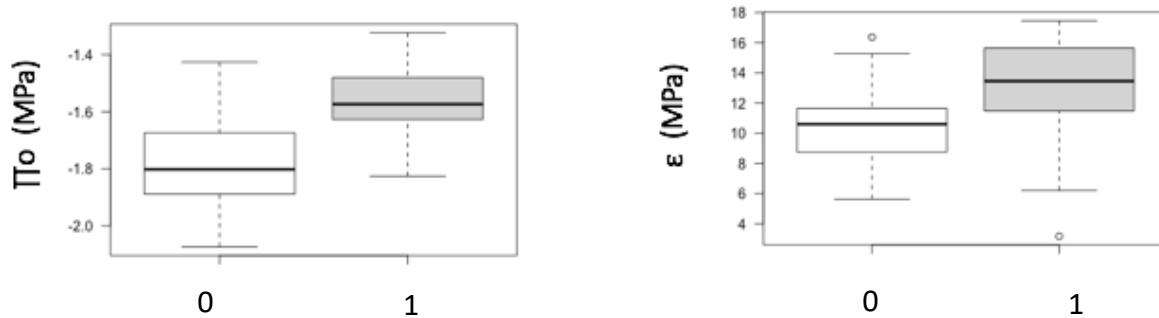


Figure 3. Osmotic potential (π_o) and modulus of elasticity (ϵ) for *S. sempervirens* juveniles >1.7m (age class 0) and ~0.3m (age class 1) from a mature *S. sempervirens*. The boxes are defined the same way as described as figure one.

DISCUSSION

My results provide evidence that age is an important determinant of leaf hydraulic traits in *S. sempervirens*. The hypothesis that midday Ψ_{leaf} varies significantly with age class is supported by the data from this study; however, these data do not support the hypothesis that dawn Ψ_{leaf} would differ with age as well (Figure 1). The higher midday Ψ_{leaf} that the older age classes experience is coupled with more negative TLP (Figures 1 and 2) allowing these more mature trees to experience a higher level of water stress during the day without their leaves starting to lose function. This study also demonstrates that juvenile trees growing under a nursery tree experience

less negative midday Ψ_{leaf} and TLP than their counterparts growing in a more open environment (Figures 4 and 5). The hypothesis that juvenile trees growing closer to a more mature *S. sempervirens* experience a nursery effect from these larger trees is supported by the data from this study. π_0 decreased both with the age of the cohort and distance of a juvenile tree from a mature *S. sempervirens* (Figure 3 and 6). However, ϵ did not differ between these groups. As a result, this study shows that π_0 , not ϵ , that is the primary trait driving the observed differences in TLP between the classes. My study is the first to quantify how leaf hydraulic traits vary along an age gradient in *S. sempervirens* growing in a secondary forest.

Leaf water potential and age

At dawn all of the age classes experienced a similar Ψ_{leaf} ; however, at midday the Ψ_{leaf} of each class diverged with Ψ_{leaf} decreasing as the size and therefore age of the cohort increased (Figure 1). The lack of a significant difference of dawn Ψ_{leaf} between the different age groups signifies that *S. sempervirens* of all ages have comparable baselines for Ψ_{leaf} as all age groups are able to access and take up enough water in the soil to increase their Ψ_{leaf} to a similar point (Lambers et al. 2008). However, at midday, the amount of water stress a size group experienced increased with age as midday Ψ_{leaf} decreases with age (Bhasker and Ackerly 2006). This study supports the growing consensus in the literature that taller (and older) trees experience higher levels of water stress when compared to their shorter and, in many cases, younger counterparts (Condit et al. 1995; Ogle 2004; Nepstad et al. 2007). The ability of the larger classes to experience more negative midday Ψ_{leaf} can be partly explained by age-based differences in the TLP of each group.

Variation of turgor loss point across an age gradient

My results show that older and therefore larger trees are able to experience more negative midday Ψ_{leaf} , in part, because TLP decreases with age as well (Figure 2). The TLP values I measured for the older classes were similar to the reported TLP values for *S. sempervirens* in the literature (-1.972 ± 0.038 MPa as compared to the TLP I measured for age class 3: -1.98 ± 0.02) (Ishii et al. 2014). I found that the differences of π_0 between age classes mirrored those of TLP but ϵ does not differ significantly between the classes (Figure 2 and 3). These findings agree with

recent studies that have found that π_o is the primary trait determining TLP (Bartlett et al. 2012). Additionally, global meta-analyses have linked both π_o and TLP to plant water availability and drought tolerance at the biome scale (Bartlett et al. 2012; Bartlett et al. 2014). As a result, the observed decrease in both TLP and π_o over the total increase in size class helps suggest that older *S. sempervirens* adjust their hydraulic traits because they are operating under higher levels of water stress compared to the younger age groups. The increased water-stress could be due to differences in root to shoot ratio, the ratio of crown volume to root volume or, differences in sun exposure, but these proposed drivers should be the focus of future research.

Nursery Effect on juvenile *S. sempervirens*

This study also demonstrates that mature *S. sempervirens* create a nursery effect for juveniles growing in close proximity to them as these juveniles experience higher midday Ψ_{leaf} and TLP than their counterparts growing in more open environments (Figure 4 and 5). I found that while juvenile *S. sempervirens* growing under a more mature tree had the lowest midday Ψ_{leaf} out of all of the age classes the juveniles growing >1.7 meters from a larger *S. sempervirens* midday Ψ_{leaf} was more negative than that of the largest age class measured in this study. The differences in the TLP of these two juvenile classes can also be explained by their different π_o and similar ϵ . Their similar values of ϵ showed that regardless of their distance from a more mature *S. sempervirens* juvenile *S. sempervirens* invest similar amounts of energy in the elasticity of their cell wall. However, the class of juveniles growing in more open locations invested more energy moving solutes into their cells to decrease their cell's π_o allowing them to have a more negative TLP than the juveniles growing under a nursery tree (Bartlett et al. 2014, Bartlett et al. 2016). Therefore, even though the juveniles growing under nursery trees do not experience as much water stress as the juveniles growing in more open locations they also lack the same physiological capacity as the juveniles growing in more open locations to experience as negative Ψ_{leaf} .

Limitations

To set up this study I used assumptions that could impact the accuracy of my findings. Instead of directly measuring the age of each *S. sempervirens* I used DBH as a proxy. While the

exact relationship between DBH and age is not known for the *S. sempervirens* in this site previous studies have shown that there is a linear relationship between these two allometric variables for *S. sempervirens* (Waring and O'Hara 2006). Additionally, I assumed that dawn Ψ_{leaf} would convey the same hydraulic information as predawn Ψ_{leaf} , which may not hold true if there is a statistically significant difference in the pre-dawn and dawn Ψ_{leaf} of *S. sempervirens*. Finally, the model I used to calculate the TLP, π_o , and ϵ held ϵ constant for the entire dehydration process. While this assumption has been used in previous metaanalyses of these hydraulic traits, ϵ does change as the water content of a leaf changes (Bartlett et al. 2016). However, regardless of the variation of ϵ during the dehydration process there was still a statistically significant difference in the TLP of the different age and juvenile groups.

Future Directions

Based on the scope of my study further research on how the life history stage of a tree impacts their hydraulic traits is needed. Even though traits such as TLP and π_o have been associated with drought response in the literature my study still only provides a baseline measurement for these leaf hydraulic traits (Bartlett et al. 2012; Bartlett et al. 2014). To better understand the ecological significance of these differences a study measuring these traits during a drought is needed. Additionally, while the age gradient I measured in this study is representative of secondary growth *S. sempervirens* it is not representative of the species as the whole. As a result, it is important to increase the range of ages hydraulic traits are measured across to quantify the plasticity of these traits across all life history stages of *S. sempervirens*.

Broader Implications

My study is the first to demonstrate that leaf hydraulic traits vary across an age gradient in a secondary *S. sempervirens* forest. These findings help to explain how older and more dominant trees in forest canopy can withstand more water stress than their younger and subdominant counterparts. Additionally, my results help demonstrate conditions under which juvenile trees can deviate from this trend (Condit et al. 1995; Ogle 2004; Nepstad et al. 2007, Kobe et al. 1995). The significant differences I found between age classes and the proximity of juveniles to a nursery tree

help also have important implications for dynamic vegetation models. These models often parameterize their species with one value per hydraulic variable. However, my data demonstrates that there can be significant variation in these traits based on the life history stage of the species.

While this variation of hydraulic traits by life history stage may not hold true for all tree species it is important to take into consideration when modeling *S. sempervirens*. Not only do *S. sempervirens* face an increased occurrence of drought due to climate change but the frequency of fog has decreased by approximately 33% over the last 100 years (Diffenbaugh et al. 2015, Johnstone & Dawson 2010). As a result, not only are these trees facing a future with an increased occurrence of drought but the meteorological event that this species depends on to mitigate water stress is decreasing. Therefore, it is important that future analysis of this species hydraulic reflect this ontological variation of leaf hydraulic traits.

ACKNOWLEDGEMENTS

I would like to thank Thomas Powell for his continued guidance and mentorship throughout this process. I would also like to thank my faculty sponsor, Lara Kueppers, for her support and help developing my methods. I am grateful for the help of the ESPM 100es and ESPM 175 teaching team especially John Battles, Tina Mendez and Leslie McGinnis who provided valued feedback throughout this process. I also need to thank my ESPM 175 peer review group, Soy Tree Huggers, who helped me improve all versions of my thesis. This experience would not have been the same without the presence of my friends and family who supported me every step of the way. Finally, I would like to thank the East Bay Regional Park District for allowing me to conduct this study in Redwood Regional Park.

REFERENCES

- Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest ecology and management* 259: 660-684.
- Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6: 1-55.

- Asner, G. P., P. G. Brodrick, C. B. Anderson, N. Vaughn, D. E. Knapp, and R. E. Martin. 2016. Progressive forest canopy water loss during the 2012–2015 California drought. *Proceedings of the National Academy of Sciences* 113: E249-E255.
- Baguskas, S. A., C. J. Still, D. T. Fisher, C.M. D’Antonio, and J. Y. King. 2016. Coastal fog during summer droughts improves the water status of sapling trees more than adult trees in a California pine forest. *Oecologia* 181:137-148.
- Bartlett, M.K., C. Scoffoni and L. Sack. 2012. The determinants of leaf turgor loss point and prediction of drought tolerances of species and biomes: a global meta- analysis. *Ecology Letters* 15: 393 – 405.
- Bartlett, M.K., T. Klein, S. Jansen, B. Choat, L. Sack. 2016. The correlations and sequence of plant stomatal, hydraulic and wilting responses to drought. *Proceedings of the National Academy of Sciences* 113: 13098 – 13103.
- Bartlett, M. K., Y. Zhang, N. Kreidler, S. Sun, R. Ardy, K. Cao, and L. Sack. 2014. Global analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecology letters* 17: 1580-1590.
- Bates, D.M., M. Maechler, and B. Bolker. 2008. Mixed- effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language* 59: 390-412.
- Bhaskar, R. And D. D. Ackerly. 2006. Ecological relevance of minimum seasonal water potentials. *Physiologia Plantarum* 127: 353-359.
- California Department of Parks and Recreation. 2019. California’s Redwood Parks. http://www.parks.ca.gov/?page_id=24723. (Accessed 3/06/2109).
- Climate Data. Climate Oakland. <https://en.climate-data.org/north-america/united-states-of-america/california/oakland-1491/>. (Accessed 3/13/2019).
- Condit, R. S. P. Hubbell, and R. B. Foster. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological monographs* 65: 419-439.
- Dawson, T. E..1998. Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia* 117: 476-485.
- Diffenbaugh, N.S., D. L. Swain and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Science of the United States of America* 112: 3931-3936.
- Douhovnikogg, V., A. M. Cheng, and R.S. Dodd. 2004. Incidence, size and spatial structure of clones in second -growth stands of coast redwoods *Sequoia semperviren* (Cipressaceae). *Journal of Botany*. 91:1140 – 1146.

- East Bay Regional Park District. 2018. Redwood Regional Park.
<http://www.ebparks.org/parks/redwood/default.htm#movie>. Accessed 04/17/2018.
- Iacobellis, S.F., D. R. Cayan, J. T. Abatzoglou, and H. Mooney. Climate. Pages 9-26 in H. Mooney and E. Zavaleta, editors. Ecosystems of California. University of California Press, Oakland, California, USA.
- Ishii, H.R., W. Azuma, K. Kuroda, S.C. Sillett. 2014. Pushing the limits to tree height: could foliar water storage compensate for hydraulic constraints in *Sequoia sempervirens*? Functional Ecology 28: 1087-1093.
- Johnstone, J.A. and T.E. Dawson. 2010. Climatic context of ecological implications of summer fog decline in the coast redwood region. Proceedings of the National Academy of Science of the United States of America 107: 4533-4538.
- Kobe, R.K. S.W. Pacala. J.A. Silander Jr., C.D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications 5: 517-532.
- Lambers, H., F. Stuart Chapin III, and T. L. Pons. 2008. Plant physiological ecology. Springer Science & Business Media
- Limm, E. B., K. A. Simonin, A. G. Bothman, and T.E. Dawson. 2009. Foliar water uptake: a common water acquisition strategy for plants of the redwood forest. Oecologia 161: 449-459.
- Limousin, J.-M., D. Longepierre, R. Huc, and S. Rambal. 2010. Change in hydraulic traits of Mediterranean *Quercus ilex* subjected to long-term throughfall exclusion. Tree Physiology 30: 1026-1036.
- Mao, Y., B. Nijssen, and D. P. Lettenmaier. 2015. Is climate change implicated in the 2013–2014 California drought? A hydrologic perspective, Geophysical Research Letter 42: 2805-2813.
- Martin-St. Paul, N. K., J.-M. Limousin, H. Vogt-Schilb, J. Rodríguez-Calcerrada, S. Rambal, D. Longepierre, and L. Misson. 2013. The temporal response to drought in a Mediterranean evergreen tree: comparing a regional precipitation gradient and a throughfall exclusion experiment. Global Change Biology 19: 2413-2426.
- McDowell N., W.T. Pockman, C. D. Allen, D. G. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D. G. Williams and E. A. Yepez. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while other succumb to drought?. The New Phytologist 178: 719- 739.
- Nepstad, D. C., I. M. Tohver, D. Ray, P. Moutinho, and G. Cardinot. 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. Ecology 88: 2259-2269.

- Ogle, K., T. G. Whitham, and N. S. Cobb. 2000. Tree-ring variation in pinyon predicts likelihood of death following severe drought. *Ecology* 81: 3237-3243.
- R Core Team. 2012. R: a language and environments for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
- Record, S., T. McCabe, B. Baiser, and A. M. Ellision. 2018. Identifying foundation species in North American forests using long term data on ant assemblage structure. *Ecosphere* 9: e02139.
- Rummukainen, R.. 2012. Changes in climate and weather extremes in the 21st century.2012. *WIREs Climate Change* 3:115–129.
- Sack, L., Pasquet-Kok, J., & PrometheusWiki Contributors (2011). Leaf pressure-volume curve parameters. PrometheusWiki, Retrieved from <http://www.publish.csiro.au/prometheuswiki/tiki-pagehistory.php?page= Leafpressure-volumecurveparameters&preview=16>.
- Save the Redwoods League. 2018. Coast Redwoods. <https://www.savetheredwoods.org/redwoods/coast-redwoods/>. Accessed 11/18/2018. (Version 11/18/2018).
- Sillett, S.C., R. V. Pelt, A. L. Carroll, R. D. Kramer, A. R. Ambrose, and D. Trask. 2015. How do tree structure and old age affect growth potential of California redwoods?. *Ecological Monographs* 85: 181 - 212.
- Simonin, K.A., L. S. Santiago and T.E. Dawson. 2009. Fog interception by *Sequoia sempervirens* (D. Don) crowns decouples physiology from soil water deficit. *Plant, Cell & Environment* 32: 882-892.
- Waring, K.M and K. L. O'Hara.2006. Estimating relative error in growth ring analysis of second- growth coast redwoods (*Sequoia sempervierens*). *Canadian journal of forest research* 36: 2216 -2222.
- Young, D.J.N., J.T. Stevens, J.M. Earles, J. Moore, A. Ellis, A.L. Jirka and A. M. Latimer. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecology Letters* 20: 70-86.

APPENDIX A

Table A1. Midday Ψ_{leaf} and TLP for *S. sempervirens* age groups of increasing DBH.

Hydraulic Trait	Age Class				
[MPa]	1	2	3	4	5
Midday Ψ_{leaf}	-0.94±0.01	-1.03±0.02	-1.14±0.01	-1.18±0.01	-1.47±0.02
TLP	-1.78±0.01	-1.85±0.02	-1.98±0.02	-2.04±0.01	-2.14±0.02

Table A2. Midday Ψ_{leaf} and TLP for juvenile classes. Age class 0 is juveniles growing in more open conditions while age class one is juveniles growing under a nursery tree.

Hydraulic Trait	Age	Class
[MPa]	0	1
Midday Ψ_{leaf}	-1.69±0.09	-0.094±-1.78
TLP	-2.06±0.01	-1.78±0.01