Investigating Short-term Stem Circumference Fluctuations in Coast Redwood (*Sequoia sempervirens*) on Jackson Demonstration State Forest

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ABSTRACT

Many trees species have been found to have periods of temporary, reversible shrinkage in diameter, but this phenomenon has not been studied in the unique coastal climate of California. As California undergoes a changing climate, it becomes increasingly important to study growth processes such as these. In this study I use dendrometer band data to look at growth patterns in *S. sempervirens* in Mendocino County, CA and correlate them with vapor pressure deficit levels. I examine specifically the periods of shrinkage in circumference and compare it to annual growth as well as tree size. I found a significant negative correlation between VPD and stem circumference changes in three out of four plots, as well as in all trees combined. Maximum shrinkage magnitudes ranged from 0.243% to 0.389% of tree size across plots and averaged between 18% and 24% of annual tree growth, increasing with distance from the coast. I found potential for isolating the effect of the outer bark on these reversible fluctuations, but my results were inconclusive due to lack of data. The large shrinkage events suggest that they need to be accounted for when measuring annual growth in *S. sempervirens*, and the VPD correlation suggests that we may be able to use VPD levels to predict shrinkage events and periods of slow growth.

KEYWORDS

shrinkage, vapor pressure deficit, bark, reversible circumference change, fog

INTRODUCTION

Ecophysiology is vital to studying the concept of climate change, and one of the main foci of these studies is the changing phenology of plant species across the world. For example, many plants have been flowering or growing their first leaves of the season 1.2 days earlier with each decade in the Northern Hemisphere temperate areas since 1961 (Schwartz et al. 2006, Cleland et al. 2007). In Europe, 78% of all leaving, flowering and fruiting records indicate an earlier spring, with an average of these events occurring 2.5 days earlier with every decade (Menzel et al. 2006). This earlier start of season results in drastic effects, ranging from altering the amount of CO_2 extracted from the atmosphere annually (Cleland et al. 2007) to causing some herbivores and pollinators to die off from increasing interspecific competition as a result of these phenological differences (Gezon et al. 2016). Butterfly weed in Wisconsin bloomed 0.3 days earlier per year from 1936 to 1998 (Bradley et al. 1999). Some plant species, however, such as *Sequoia sempervirens* (coast redwood), require more unique climates than other species and therefore are more threatened by a warming planet and potentially more intensely affected by phenological changes (Dawson 1998).

Sequoia sempervirens, one of the oldest living and arguably the most fascinating tree species in existence because of various unique traits such as its disease resistance and its rare hexaploid genetics, has a limited range of habitat resulting from its dependence on the coastal fog bank of California. Its only native habitat is along the coast of Northern California, ranging from Monterey County, CA north slightly past the southern border of Oregon, and from 5 to 35 kilometers inland (Johnstone and Dawson 2010). The persistence of this species is becoming of greater concern, however, as climatic conditions continue to change and the fog belt declines (Johnstone and Dawson 2010). Summer fog, which occurs only in these ranges, can contribute over 30% of *S. sempervirens* annual hydration through foliar uptake and canopy drip (Burgess and Dawson 2004). When the trees become inundated in fog, the Vapor Pressure Deficit (VPD) decreases dramatically and the pressure gradient that causes transpiration decreases, potentially reversing in direction (Burgess and Dawson 2004, Chan et al. 2016). This allows the tree to retain water and can even increase its hydration. This increase in hydration comes from absorption of moisture through the bark, some of which can potentially be transferred into the xylem (Mason Earles et al. 2016). The heavily fog-inundated climate in California has decreased by roughly 33% over the past century, which is likely due to increasing average temperatures (Johnstone and Dawson 2010). To study how this decrease in fog is specifically affecting *S. sempervirens* requires an understanding of the circumference changes of the species over time to determine the response to a decrease in fog frequency.

Tree growth is sometimes measured annually to determine the amount of growth over one year, but growth is not evenly distributed throughout the year. There are irreversible overall intra-annual changes in tree circumference as part of stem growth, but there are also intra-annual changes that are reversible and many introduce variability into tree measurements (Herrmann et al. 2016). In southern Washington, these reversible changes occurred on the timescales of days and months (Zweifel et al. 2001, Herrmann et al. 2016), however conifers had the smallest fluctuations compared to the broad-leafed sites of the same study (Herrmann et al. 2016). Sap flow and bark hydration seem to be the two main contributors to this swelling and shrinking of stem circumference in most trees (Sevanto et al. 2008, Mason Earles et al. 2016), both of which are greatly affected by atmospheric moisture availability in an ecosystem like that of the coast redwoods. Quantifying this phenomenon is essential to studying the tree's phenology; it indicates what type of growth the tree undergoes at different points of the year, and if it is significantly affected by fog frequency. Ultimately, changes in growth of these important forest species could potentially reveal drastic implications for redwood growth estimates and the ecology of these coastal forests.

In this study I investigate if intra-annual fluctuations in coast redwood stem circumference, measured every two weeks, affect annual stem circumference growth measurements. To obtain a better overall understanding of seasonal redwood growth, I also compare these fluctuations to measurements of VPD, as an indicator of tree water intake. I hypothesize a negative correlation between VPD and redwood circumference fluctuations because an increase in VPD means a decrease in water availability to the trees and an increase in water loss, resulting in a hypothetical decrease in growth rate. Next, I determine what proportion of the tree's annual growth constitutes the magnitudes of these fluctuations to find how much the shrinkages affect annual growth measurements. I hypothesize that the magnitudes of the fluctuations will make up a small and insignificant proportion of the trees' annual growth. Lastly, I examine the specific contribution of the outer bark on these fluctuations to isolate the magnitude of circumference changes resulting from bark moisture intake.

METHODS

Study site description

Jackson Demonstration State Forest, in Fort Bragg, CA, has a Mediterranean climate and a coastal fog bank that decreases inland from the coast. The forest ranges in elevation from 24 – 671 meters, precipitation averages 99cm per year along the coast and 178cm per year inland, and the temperatures range from -4°C to 38°C. Precipitation mainly occurs in the winter months, and summers are dry except for a frequent fog belt. Coastal fog tends to be most frequent from about 180 – 400m in elevation, below which the fog becomes overcast cloud stratus events, and above which it decreases in frequency (Fischer et al. 2009). HOBO U23 Pro v2 Temperature/Relative Humidity Data Loggers were installed at each of three sites (Figure 1) to measure relative humidity and temperature every two hours. However, the mid plot weather station malfunctioned after one year, so I obtained data for the other two years from a Forest Service weather station located nearby. The RAWS data from the nearby USFS station did not match the HOBO measurements exactly when they were both functioning, but they produced similar patterns. Hence, although I am not measuring fog events, I have a continuous dataset of relative humidity, which should give a relatively accurate estimate of fog event occurrences.

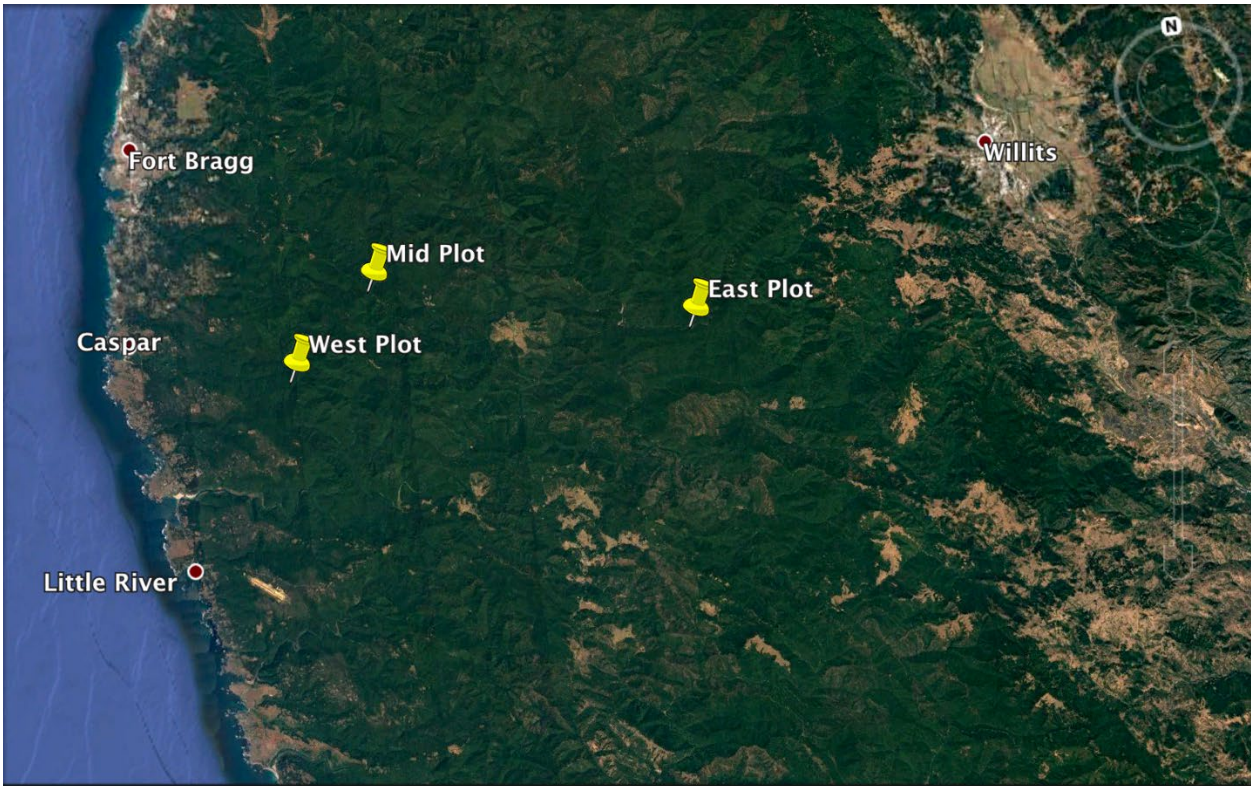

Figure 1. Map of plot locations. Data was downloaded from google earth.

This study includes three different sites (Figure 1) located in Jackson Demonstration State Forest and measures 27 coast redwoods distributed across the three sites, all similar stand composition and age. The sites are named West, Mid, and East, moving from most coastal to most inland respectively. The East plot is located at 39° 20' 51.13" N, 123°31'20.21"W. Its elevation is 164.6 meters, and it is 26.4 kilometers from the coast. The mid-plot is located at 39° 22’ 35.73” N, 123° 41’ 15.12” W. Its elevation is 292.6 meters, and it lies 11.6 kilometers from the coast. The West plot is located at 39° 20’ 35.45” N, 123° 43’ 55.83” W. Its elevation is 198.7 meters, and it is 6.8 kilometers from the coast. These plots were installed for a larger study organized by Dr. Kevin O’Hara (University of California, Berkeley) and Lynn Webb (Forester II, Cal Fire), in partnership for data collection by Cal Fire. The broader study replicates a similar study done from 1958 to 1961 in Jackson Demonstration State Forest and uses very similar sites, but not the exact same sites or trees (Bawcom et al. 1961). Identifying the period of winter dormancy was the intent of the original 1960’s study (Bawcom et al. 1961) that this study attempted to duplicate.

Stem Circumference Measurements

To obtain data on seasonal growth, Cal Fire measured bi-weekly stem circumference changes in coast redwood using dendrometer bands from August 2013 to November 2017. Measurements were taken every two weeks, with some short periods of absence due to complications, and I participated in these repeated measurements for June of 2017. A measured amount of bark of about one inch in depth, ranging from 0.3 inches to 2.9 inches, was stripped in a ring around each tree at breast height (1.3 m), and dendrometer bands were installed on the trimmed section, which attach at springs that maintain tension as the tree expands (Figure 2). Although the scale on the dendrometers goes up to 30mm, the set screw prohibits the scale from exceeding 25mm. Additionally, the dendrometers were initially set at 5mm to allow for potential shrinkage. This leaves only 20mm of circumference growth before the scale maxes out, which can occur in less than a year depending on the size of the tree. Therefore, they are reset to 5mm at or before they reach 20mm to ensure that they do not reach that critical threshold on the scale. Stripping the bark accounted for the high variability in bark thickness and the sponginess of the bark, as well as allowing the dendrometer bands to be more securely fastened to the trees. There were dendrometer bands left on unstripped parts of five trees to allow me to compare the two methods.

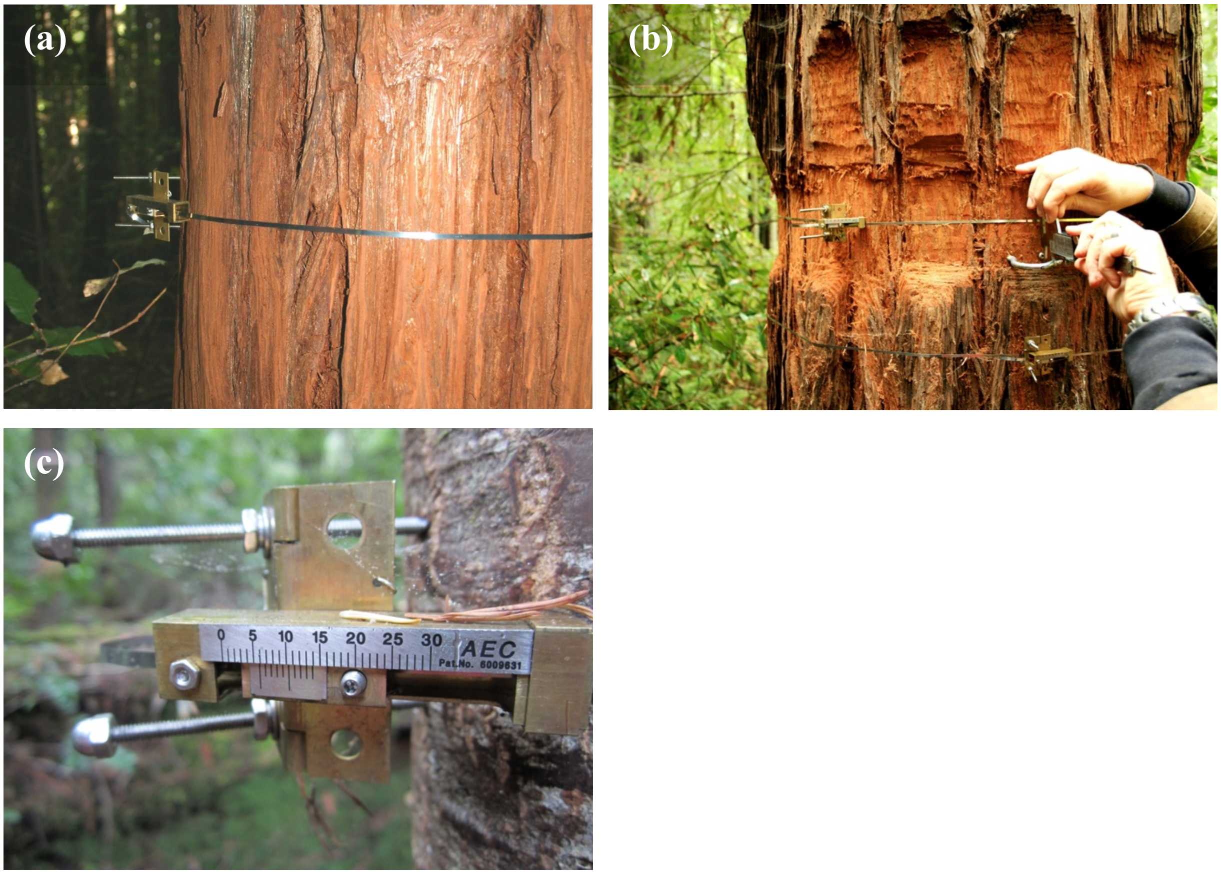

Figure 2: Dendrometer band installations. (a) minimal bark furrowing that did not need trimming. (b) Significant bark trimming. (c) Micrometer reading on the dendrometer.

Data Analysis

Vapor Pressure Deficit

To separate the climatic conditions of each site, I characterized vapor pressure deficit (VPD) patterns at each site as it is a more accurate measurement of the ability of trees to absorb and retain atmospheric moisture than relative humidity is (Burgess and Dawson 2004). I used relative humidity and temperature measurements to find average VPD at two-week intervals at each site, graphed these data and performed an ANOVA test comparing the three plots over time. This analysis helped me determine if there is a significant difference in VPD patterns between plots.

To evaluate the correlation between VPD and change in circumference, I graphed VPD averages for the week before each circumference measurement was taken against the proportional circumference change for that measurement averaged across each plot (Fosberg et al. 1981). To find the proportional circumference change I divided each change by the individual tree size at the time of measurement before that change to account for differences in tree size. This comparison would show a positive correlation if an increase in VPD coincided with a positive change in tree size for a plot, and a negative correlation if it coincided with a negative change in tree size. This gave me the overall correlation of each plot between circumference and VPD. I also performed a correlation test between these two factors for each plot to find the significance of the correlation.

Annual Growth Analysis

From looking at the graph of average growth of each plot over the full study I decided to use the 12-month period beginning April 2015 for my annual growth analysis because it was both the only time of year that had continuous data for a year following and seemed to be the most stable in circumference fluctuations. To determine this stability, I visualized on the graph of plot growth across the complete study the periods of time when the slope was closest to zero. I then found the circumference changes in proportion to individual tree size at the start of the year to account for differences in initial stem circumferences between trees. I made a graph of these proportional changes over time to show the fluctuations in circumference when in proportion to tree size.

I found the proportion of the largest measured shrinkage event (a decrease in circumference) to the tree's annual growth of that year. This proportion helped me determine how large the shrinkage events were compared to the annual growth. I was also able to average all the shrinkages for each tree, and average those for each plot and compare the significance of average shrinkage events to annual tree growth between plots. I made a graph of the circumference changes in proportion to annual tree growth over time to show how large the fluctuations in circumference were.

I also averaged the amount of shrinkages per tree in each plot over one year to find the average number of shrinkages per tree per plot per year. I made a box plot of this and performed an ANOVA test to determine significant differences in annual shrinkage counts. Mason Earles et al. (2016) found that over 30 times per year the bark of coast redwoods remains constantly moist for enough time to allow the tree to transport the moisture to the xylem and use the water for hydraulic recovery. Additionally, I separated the 'untrimmed' measurements from this analysis and performed the same processes – both the analysis of annual growth and the annual shrinkage counts – on these so that I could compare the shrinkages between untrimmed and trimmed measurements on the same trees. I made a graph of circumference changes in trimmed and untrimmed measurements over time to show the effect of the outer bark on the fluctuations. It is difficult to know what depth of the tree from the outer bark is contributing to the shrinkages without more advanced measurements, which makes it impossible to determine the exact amount of shrinkage the outer bark layer contributes. However, I can use the bark depth trimmed and the difference in shrinkage magnitudes between trimmed and untrimmed measurements to determine the amount of shrinkage per millimeter of outer bark depth.

RESULTS

Comparing vapor pressure deficit to circumference growth

The average VPD for the west plot over the course of the study was 332.40 Pa, for the mid plot it was 199.02 Pa, and for the east plot it was 301.56 Pa (Figure 3). For two-week proportional change in tree circumference as it relates to VPD averaged across a week before the circumference measurement (Fosberg et al. 1981), the mid plot was the only one that did not have a significant negative correlation. The west plot had a relatively strong negative correlation and the east plot and untrimmed trees had relatively weak correlations (Table 1). The analysis of all trees against VPD showed a significant, but weak negative correlation. The point at which the trendline crosses zero, meaning a higher VPD causes shrinkage for each of the significant plots, was 266.7 Pa for the west plot, 666.7 Pa for the east plot, and 714.3 Pa for the untrimmed trees (Figure 4).

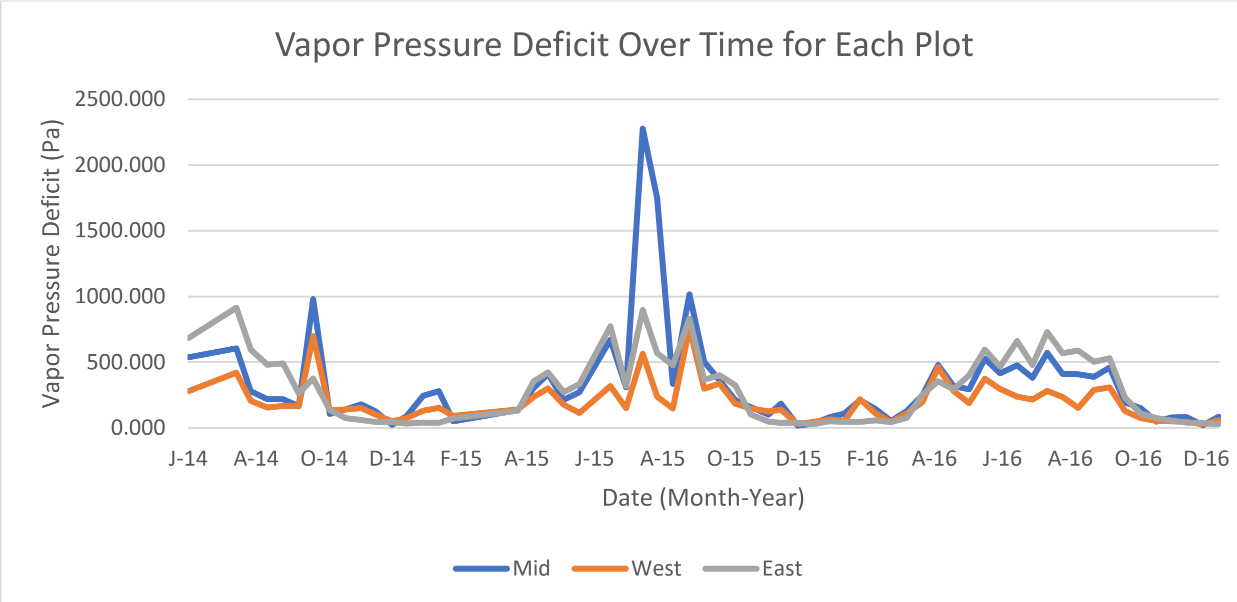

Figure 3: VPD over time for each plot. Measurements over 2.5 years.

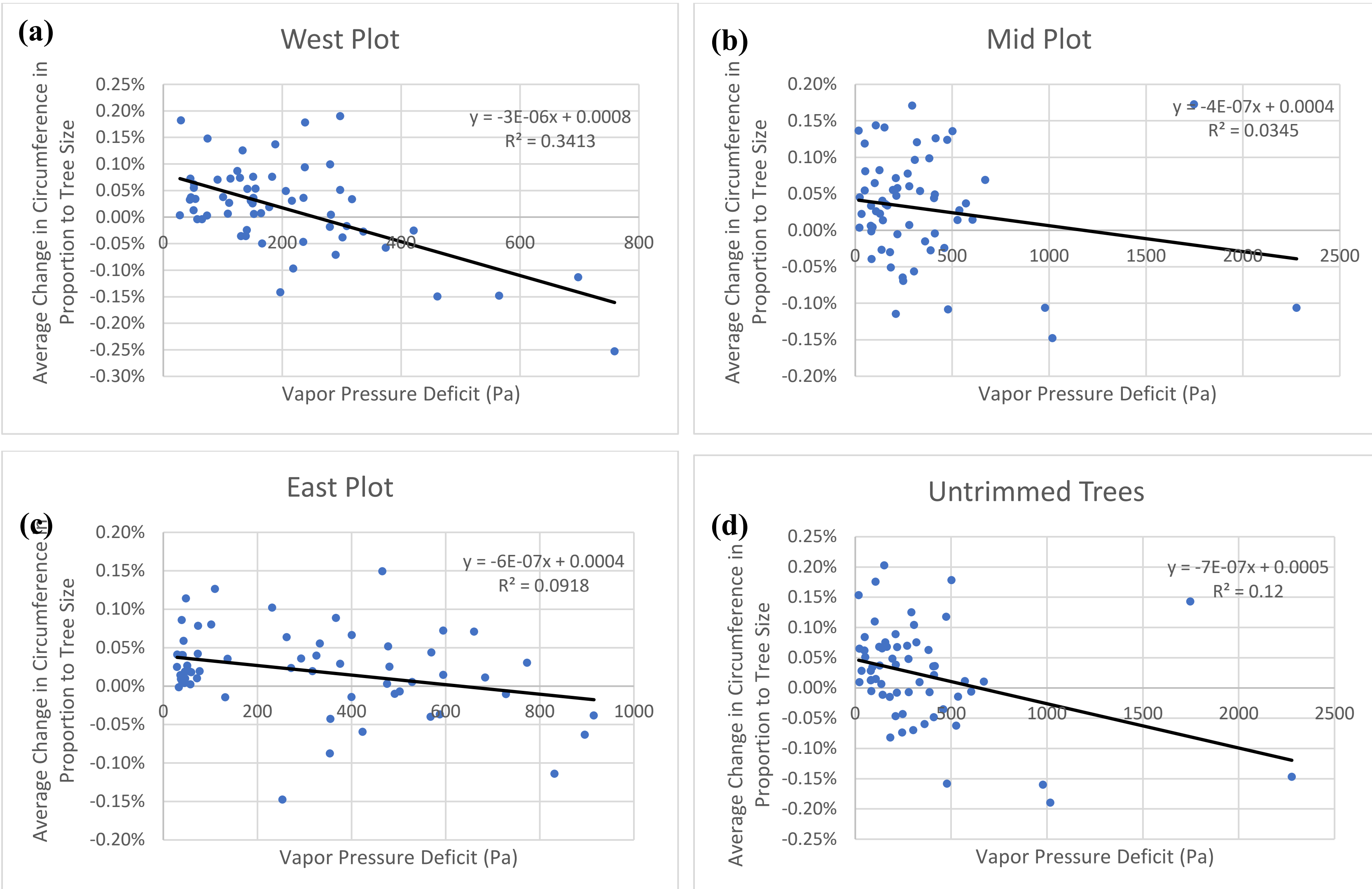

Figure 4: Graphs of circumference proportioned according to individual tree size compared to vapor pressure deficit. (a) west plot. (b) Mid plot. (c) East plot. (d) Untrimmed measurements.

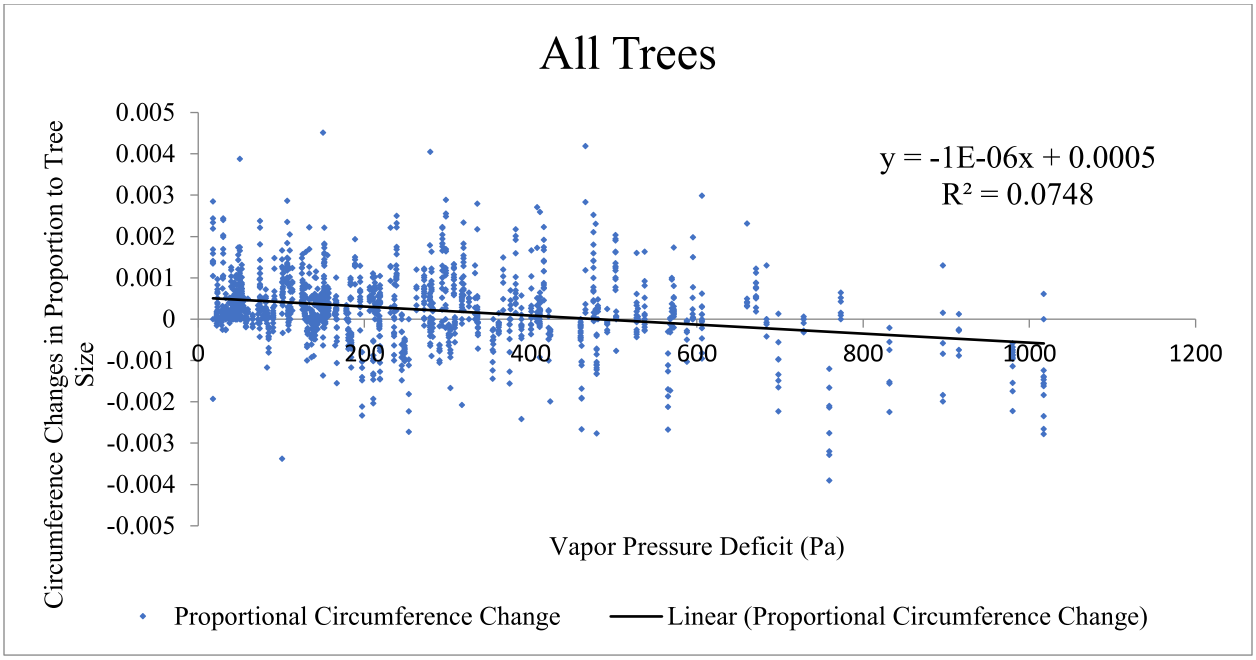

Figure 5: Graph of circumference against vapor pressure deficit for every tree in study. Circumference proportioned according to tree size.

Table 1: Significance of negative correlation between circumference changes and VPD.

Plot name	R-value	P-value
West	0.584	$7.55*10^{-7}$
Mid	0.186	0.151
East	0.303	0.0175
Untrimmed	0.347	0.00621
All Trees	0.274	$3.23*10^{-29}$

Significance of Shrinkage events

The maximum shrinkage magnitudes ranged from 2.4mm to 4.4mm in circumference in the west plot, 1.7mm to 13.5mm in the mid plot, 1mm to 3.2mm in the east plot, and 4.8mm to 6.4 mm for the untrimmed trees. The graph of circumference growth of each plot over the full study shows that most of the shrinkage events occurred at the same time across plots (Figure 6). There were an average of 10.6 shrinkage events per tree per year in the west plot (significantly different from mid and east, p=0.0047, p=0.0088), 8.9 in the mid plot, 7.8 in the east plot (significantly different from untrimmed, p=0.020), and 10.2 in the untrimmed trees (Figure 7). In proportion to tree size, these shrinkages were as large as 0.389% in the West plot, 0.281% in the Mid plot, 0.276% in the East plot, and 0.243% in the untrimmed trees (Figure 8).

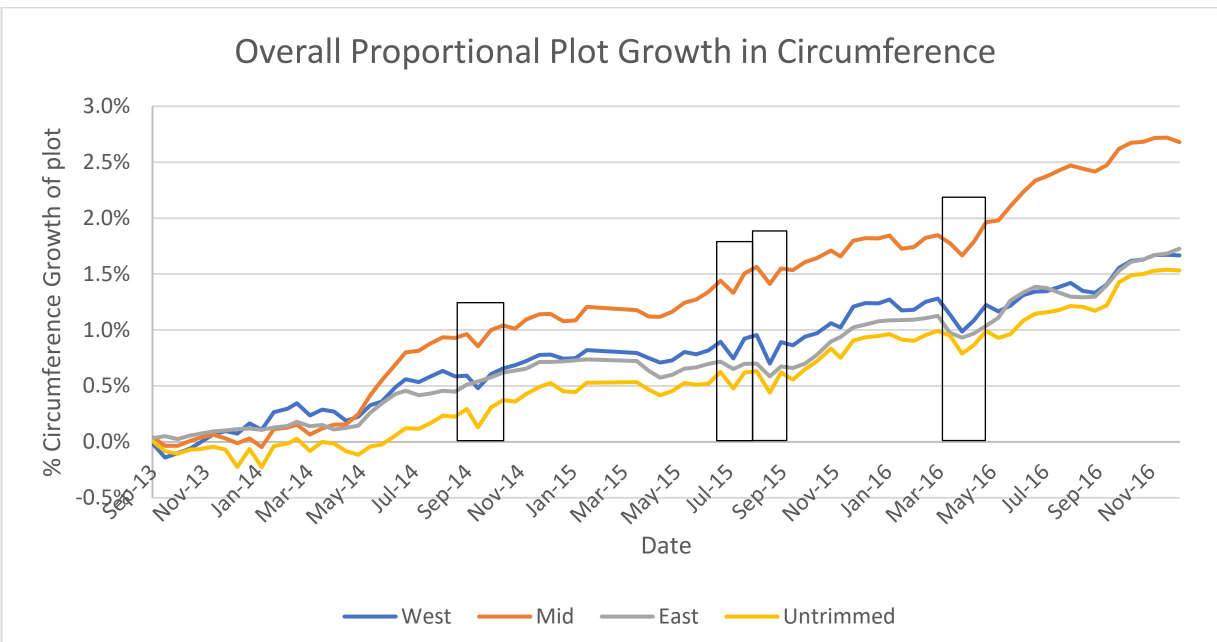

Figure 6: Plot growth over full study. Circumference changes proportioned by tree size at start of measurements. Boxes drawn to show large shrinkage events across plots.

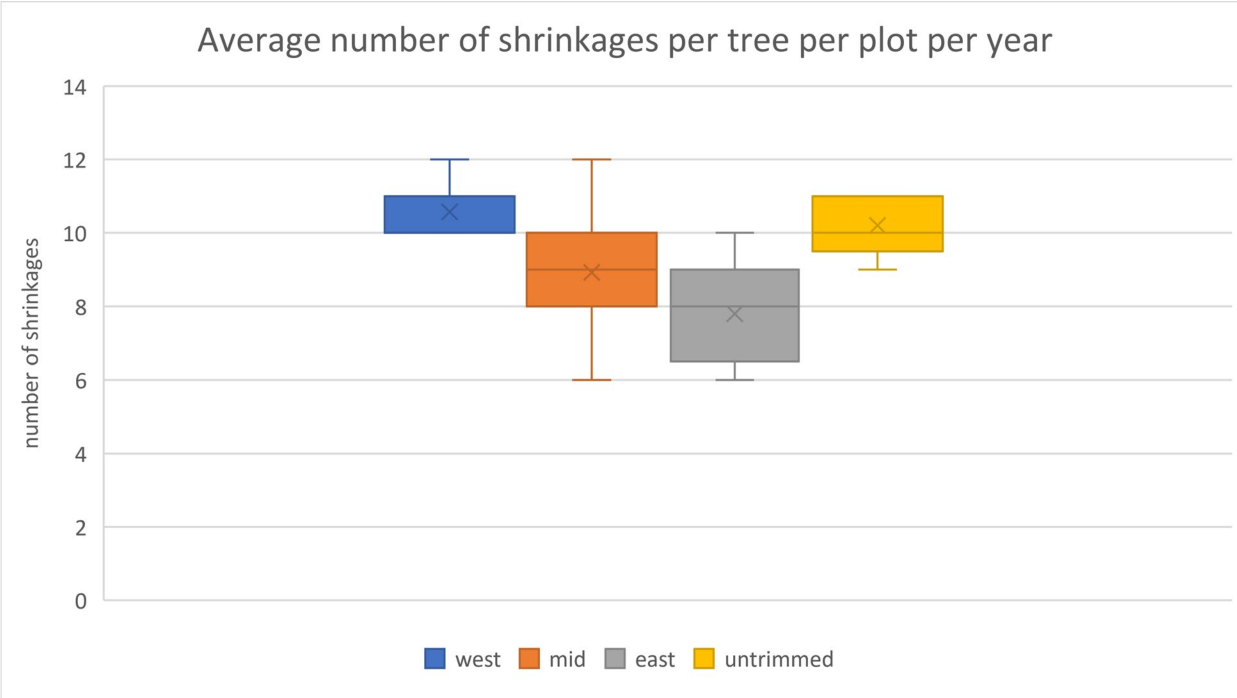

Figure 7: Average number of shrinkages per tree per year in each plot.

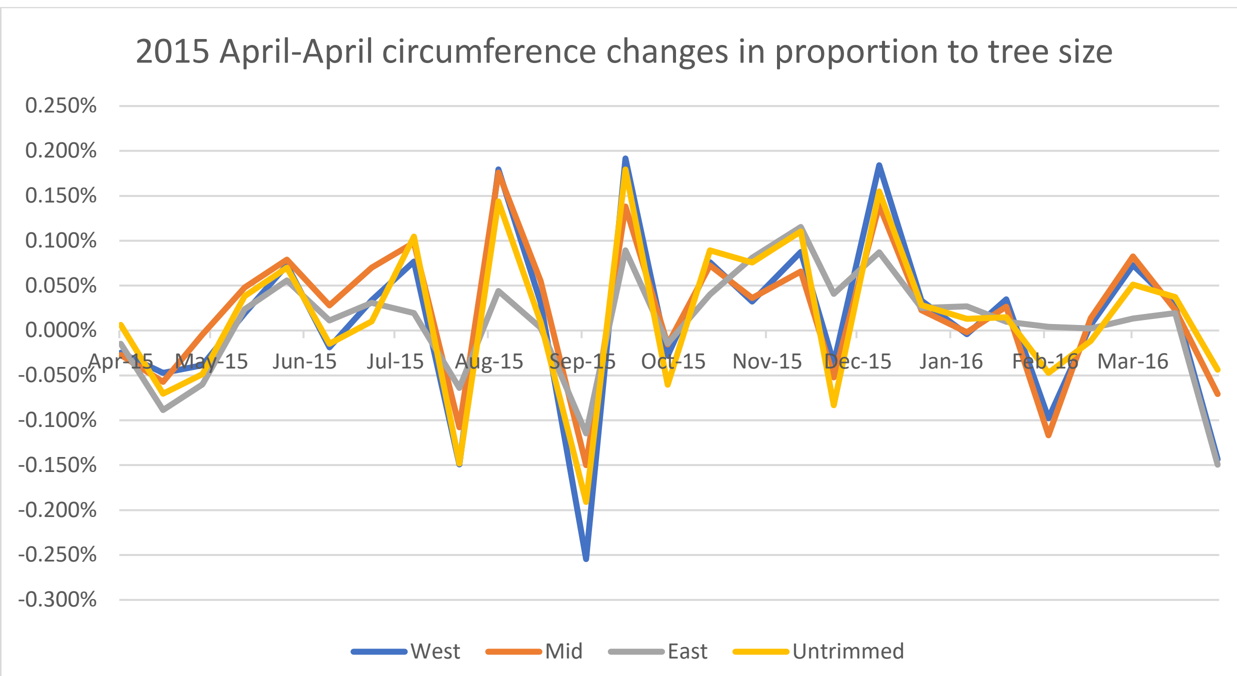

Figure 8: Circumference changes across plots in proportion to tree size over one year. West plot shows some of the largest amplitudes in fluctuations, and the East plot shows the smallest

For comparing shrinkages to annual growth, the average shrinkage magnitude was 18% of the annual growth for the west plot, 20% for the mid plot, 24% for the East plot, and 20% for the untrimmed trees (Figure 9). The largest individual shrinkage events ranged from 107% of annual growth to 9% of annual growth, with two outliers at 650% and 227% in the west and mid plots, respectively.

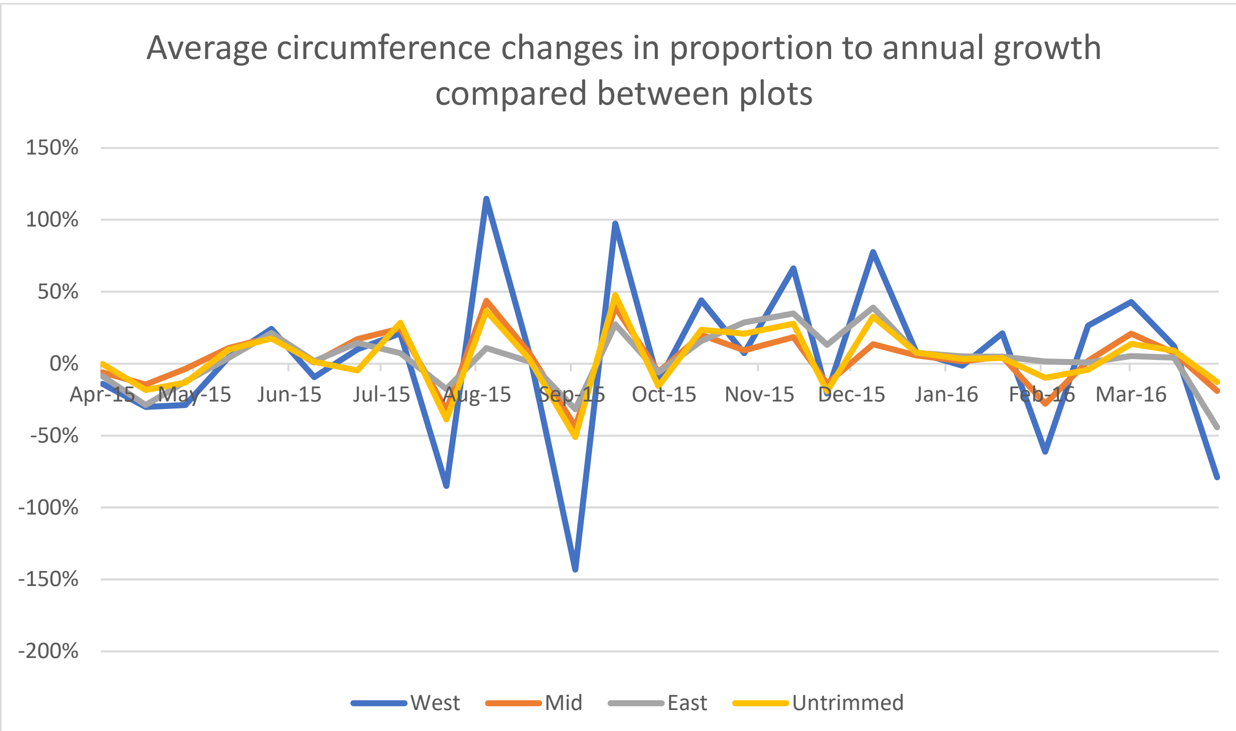

Figure 9: Circumference changes in proportion to annual growth for each plot. Again, the west showing the most variation and the east showing the least.

Effect of outer bark on stem fluctuations

Most of the shrinkages occurred at the same time in both the trimmed and untrimmed measurements, however there were some weeks when one measurement had a shrinkage and the other did not. The average untrimmed shrinkage was larger in every tree than the average trimmed shrinkage. Across all trees with untrimmed measurements, there was an average of 0.0145mm of circumference shrinkage per millimeter of bark depth. The average of the circumference changes, both growth and shrinkage, was about the same between trimmed and untrimmed measurements

(0.365 and 0.375mm respectively), but the untrimmed measurements had a variance of 4.60 whereas the trimmed measurements had a variance of 1.93 (Figure 10).

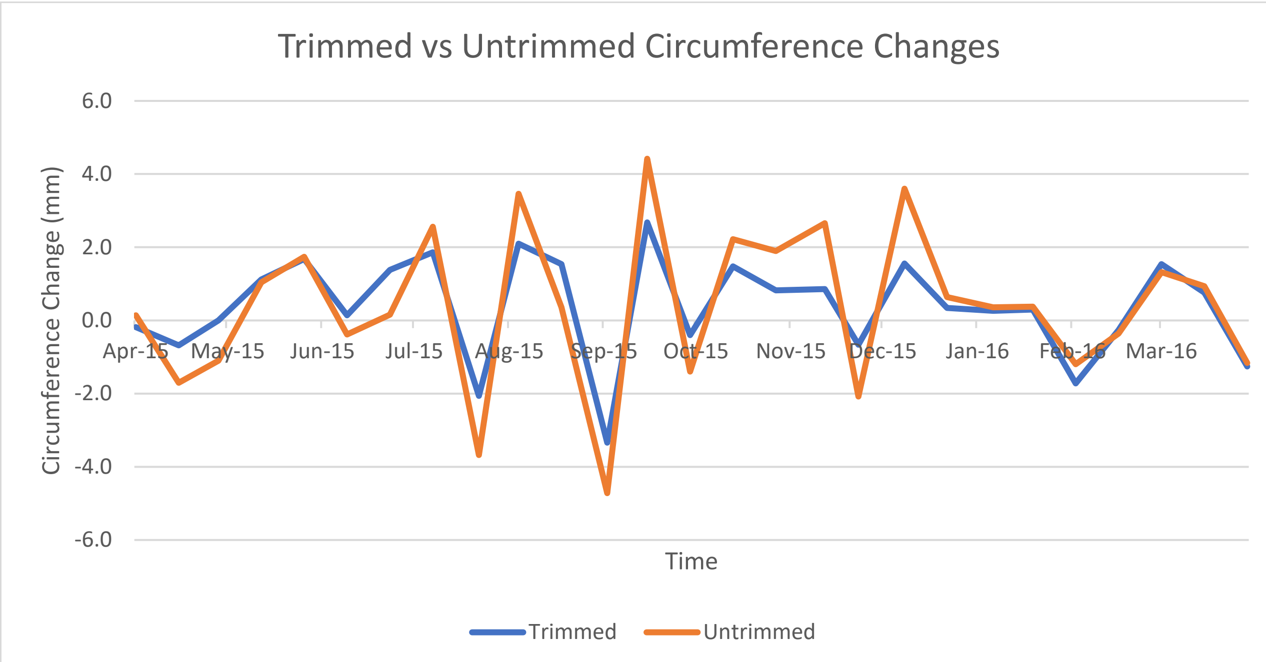

Figure 10: circumference changes across one year comparing trimmed and untrimmed measurements.

DISCUSSION

I found a significant negative correlation between vapor pressure deficit and circumference changes corrected for their tree size. I also found numerous large shrinkage events, with the largest being in the plot closest to the coast and at one of the lower elevations. The fluctuations in stem circumference were generally larger in amplitude for the untrimmed measurements that included the outer bark than the trimmed measurements that excluded a portion of the outer bark. All these findings indicate these fluctuations should be considered in growth measurements in redwood forests because there is a lot more variation than generally assumed.

VPD Correlation

The negative correlation between VPD and stem circumference fluctuations suggests that we could potentially use atmospheric conditions to predict a shrinkage or other reversible change.

Stem circumference changes have been significantly correlated with VPD in multiple forest types (Herrmann et al. 2016), and though I looked at a larger time scale, I found the same results in redwoods. My findings also agree with Stahl et al.'s findings on a correlation between relative humidity and stem circumference changes in tropical rainforests on the time scale that I used (Stahl et al. 2010). The west plot, which is closest to the coast, had the strongest correlation, which is to be expected because it is likely the most affected by atmospheric moisture content. The mid plot, which is only about 5 km farther from the coast than the west plot, did not have a significant correlation. However, the mid plot is nearly 100m higher in elevation than the west plot, and although it is still within the band of the fog belt it is likely less affected by fog than the west plot. The mid plot weather data was also likely not as accurate as the other two plots because of the substitution of the missing HOBO data with the nearby RAWS dataset. There was an extremely dry and hot period in August 2015, where the VPD increased in all plots, but the RAWS data had a much more drastic increase than the others, which likely affected the correlation results. The east plot had surprisingly low VPD levels considering it is over 26 km from the coast and closer to the edge of the fog belt. The low strength of correlation across all trees between circumference changes and VPD indicates the circumference changes are not caused by VPD alone, and that there are other factors affecting them. The stronger correlation in the west plot suggests VPD may have a stronger influence on circumference fluctuations in more coastal environments. The large differences between plots in the point at which a higher VPD correlates with a circumference shrinkage indicates we are unable to use VPD levels to predict shrinkages across plots.

Shrinkage Magnitudes

The magnitudes of the shrinkages in all the plots compared to annual growth suggest that timing should be considered when taking annual growth measurements of *S. sempervirens.* I used different metrics than other studies on the same phenomenon, but woody growth has been found to stop or is very minimal during periods of stem shrinkage in Norway spruce, European ash, European beech, and scots pine, and there was significant bias related to shrinkage in multiple trees from a study in India, both studies showing that temporal variation should be taken into account (Chitra-Tarak et al. 2015, Zweifel et al. 2016). The fact that multiple trees had two-week shrinkage events of magnitudes greater than their annual growth was unexpected.

Outer Bark Effect

The greater shrinkage magnitude and greater circumference change variance in the untrimmed measurements suggests that the outer bark contributes to the stem circumference swelling and shrinking. Mason Earles et al. found that it takes at least 24 hours of consistent moisture for bark-assisted hydraulic recovery to occur and caused a volume increase of the bark, and that only a small fraction of the moisture absorbed by the bark is then transported to the xylem of the tree, the rest being released back into the atmosphere (Mason Earles et al. 2016). The greater variance in untrimmed measurements agrees with this, however, I expected to find a larger difference in shrinkage magnitudes between trimmed and untrimmed measurements due to this temporary moisture absorption by the bark.

Limitations

The experimental design adequately addressed my hypotheses, however, there are many factors that I did not look at that have potential for future studies. Although I focused only on coast redwoods in Jackson Demonstration State Forest, there are other tree species in the forest, and other similar studies have looked at all tree species in a forest rather than only one. This would likely produce a better estimate of the correlation between atmospheric moisture and circumference changes. Using VPD to find a correlation between atmospheric conditions and stem circumference fluctuations successfully addressed my hypothesis, however, there are many other climatic factors that could be studied when examining this phenomenon. The shrinkage analysis only looked at one year and did not include a full statistical analysis of the significance of the shrinkages, but it adequately answered my research question. And the untrimmed analysis was not a complete analysis, unfortunately. It was lacking data on the complete depth of the outer bark and would need a larger dataset than five trees to make any conclusion on the effect. Hence, while it did address my hypothesis and answers it to the extent that was possible from my data, it is not statistically sound and would need another study focused on the process of outer bark shrinkage to produce a significant result. The results of this work may also not be generally representative of normal growth conditions for coast redwood. The entire period of study, and the one year used in this analysis, occurred during an unprecedented and severe drought in California. However, general short-term trends and reactions to changes in VPD provide valuable information on stem reactions to changes in moisture.

Future Directions

This study will hopefully inspire more studies on the significance of the circumference fluctuations in coast redwood and other species that live in the coastal fog belt of Northern California. As indicated by the relatively low correlation between VPD and circumference changes, there are other factors affecting these circumference fluctuations. I would like to see a study that looks for a correlation with other environmental factors such as precipitation, observed fog events, elevation, etc. as similar studies on other forests have done. As mentioned above, it is important to do more research on the effect of the outer bark on the fluctuations. It would also help to look at the contribution of the inner bark, the sap flow rates, as Chan et al. did in their study (Chan et al. 2016), and consequently the transpiration rates. Another thing to consider is the vertical variation in the circumference changes. My study only looked at the variation at diameter at breast height, or 1.3m above the ground, because it concerned the effect of the circumference fluctuations on annual growth measurements, which are standardly taken at breast height. However, as Dawson and Burgess found, there is variation in the transpiration and moisture uptake rates at different heights on the trees, so to find out more about the swelling and shrinking phenomenon throughout the tree we would need to repeat the measurements at different tree heights (Burgess and Dawson 2004).

My findings were successful in answering questions about fluctuations in stem circumference growth, specifically a factor causing them and how much they can affect growth measurements in coast redwood. The VPD correlation shows that we can use vapor pressure deficit levels to potentially predict a shrinkage event or a period of slow growth, and this can help us determine when growth measurements of trees on a plot will most accurately reflect the trees' annual growth. The large proportion of shrinkage to annual growth magnitudes shows that to obtain reliable and precise measurements of annual growth in redwoods, multiple measurements throughout the year need to be taken to account for potential shrinkage in some measurements. However, these measurements were completed with very precise tools that are not normally used in the field; the standard measurement tool for measuring tree size is a diameter tape, which only measures changes in diameter of a tree, not circumference, and therefore would only detect changes over 100% of annual growth in most trees. So, although my results indicated relatively large fluctuations in circumference, they only apply to detailed measurements usually taken for research projects rather than the typical forest measurements for inventory and management. As for the effect of the outer bark, I was able to measure it and perform an analysis of its effect on the shrinkages, which was my goal. But from my results I am unable to conclude anything about the extent of the bark's contribution to tree hydration.

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