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Drought in Temperate Mesic Regions Leads to Micro-density Anomalies in White Pine

AN ALL COLLEGE THESIS

College of St. Benedict/St. John's University

by

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April, 2020

Abstract

Wood density and wood volume determine the amount of carbon fixed by trees; however, while we are beginning to understand normal seasonal variation in wood density, anomalies are common, and their drivers are poorly understood. In conifers, wood density normally increases continuously throughout the season, but intra-annual fluctuations in wood density can occur and have been linked to climatic events. The causes of these fluctuations in density at the micro-scale (hereafter micro-density anomalies) are still debated.

Mesic regions are experiencing more droughts, but micro-density anomalies are rarely studied in these ecosystems. This study examined micro-density anomaly distribution within the boles of white pines (Pinus strobus) in central Massachusetts and its relationship with climate. We cored 41 white pines at (i) breast height (1.5m), (ii) near branches, (iii) and from the 2010 growth section. To determine if the timing of climatic variables impacted anomaly formation, we broke the growing season apart into early, mid, and late growing season. All of the trees had at least two micro-density anomalies. There was not a higher occurrence of micro-density anomalies near branches or in the 2010 growth section. Even in this temperate mesic ecosystem, anomaly formation was related to particular drought events. Micro-density anomalies coincided with low soil moisture in the early, mid, and late growing season as well as higher mid-season air temperature. It is unclear why the anomalies are uniformly distributed throughout the bole. Micro-density anomalies may be a physiological response to drought and may prevent embolisms from forming. Thus, with a better understanding of micro-density anomaly drivers we can anticipate how trees in mesic areas may react to drought.

Keywords: false rings, intra-annual density fluctuations, drought, soil moisture, climate change, wood density, carbon.

Introduction

Afforestation has been suggested as an important solution in combating climate change due to forests' important role in the carbon cycle (Vieira et al., 2020). In fact, trees can sequester carbon for centuries in their woody biomass, and wood is the main carbon pool of living terrestrial biomass (Rathgeber et al., 2016; Vieira et al., 2020). However, the drivers of carbon allocation in trees are not fully understood. In particular, more studies are needed to understand carbon allocation in woody growth. Wood, or secondary xylem, formation occurs in five stages: cell division, cell enlargement, secondary wall formation, cell wall lignification, and programmed cell death (Plomion et al., 2001; Rathgeber, 2017). When the volume of the ring is equal, the density of wood determines how much carbon is stored in the ring, with denser wood sequestering more carbon (Pompa-García & Venegas-González, 2016). Wood density is often assumed to be constant when estimating woody biomass, which creates errors in forest carbon inventories (Babst et al., 2014; Chave et al., 2006). Through better understanding the drivers of wood density and formation in general, we can generate more accurate tree allometric equations and obtain better estimates of future carbon sequestration by trees.

Trees that experience seasonal growth constraints form growth rings. These seasonal growth rings change inter-annually in width, wood density, and xylem anatomy due to resource availability and climate (Rathgeber, 2017). In conifers, these rings form as cells transition throughout the growing season between earlywood cells and latewood cells (Cartenì et al., 2018). Earlywood cells, which have comparatively large diameters and thin cell walls are composed of less dense wood than latewood cells, which have smaller diameters and thicker cell walls (De Micco et al., 2016; Plomion et al., 2001). During earlywood cell formation, the period of cell enlargement is comparatively longer while cell wall thickening is shorter (Rathgeber, 2017). This produces the large yet thin-walled earlywood cells. Later in the growing season, cell division slows, cell enlargement is less pronounced, but cell walls are thicker, resulting in narrower latewood cells with thicker cell walls. This differentiation between thinner-walled earlywood cells and thicker-walled latewood cells creates clear annual growth rings (Hartmann et al., 2017). Earlywood tracheids have wider conduits than latewood tracheids, so they conduct water more efficiently as water-conduction is proportional to the fourth power of the radius of xylem conduits. However, conduits that have higher conductivity may be more vulnerable to embolism, meaning they may be more likely to have air bubbles form in them, which disrupt the water flow, and can damage the tree (Hargrave et al., 1994; Schulte & Gibson, 1988; Sperry & Saliendra, 1994). Under dry conditions latewood may be less likely to embolize than earlywood (Domec, 2002). This indicates that the earlywood to latewood transition could be driven by a trade-off between water-conduction efficiency and security.

The amount of earlywood and latewood within a growth ring can vary, which impacts the overall density of the ring, and thus the amount of carbon sequestered, but the mechanisms of this variation are still being researched (e.g., Cartení et al., 2018). Some studies argue that development and genetics control the earlywood to latewood transition (Hargrave et al., 1994; Schulte & Gibson, 1988; Sperry & Saliendra, 1994). Environmental factors, such as extreme droughts, may also impact this transition, but in general they play a less important role than developmental and genetic controls (Rathgeber, 2017). In a typical conifer growth ring, there is usually a continuous increase in density as the cells transition from earlywood to latewood (Fig. 1). The density of annual growth rings in white pine (*Pinus strobus* L.) increases from around 200 kg/m^3 in the earlywood to 750 kg/m^3 in the latewood (Patrick Fonti, private communication, 2018). Since the density of growth rings varies seasonally more than threefold, it can be difficult to accurately estimate the amount of carbon a tree may sequester in its woody biomass.

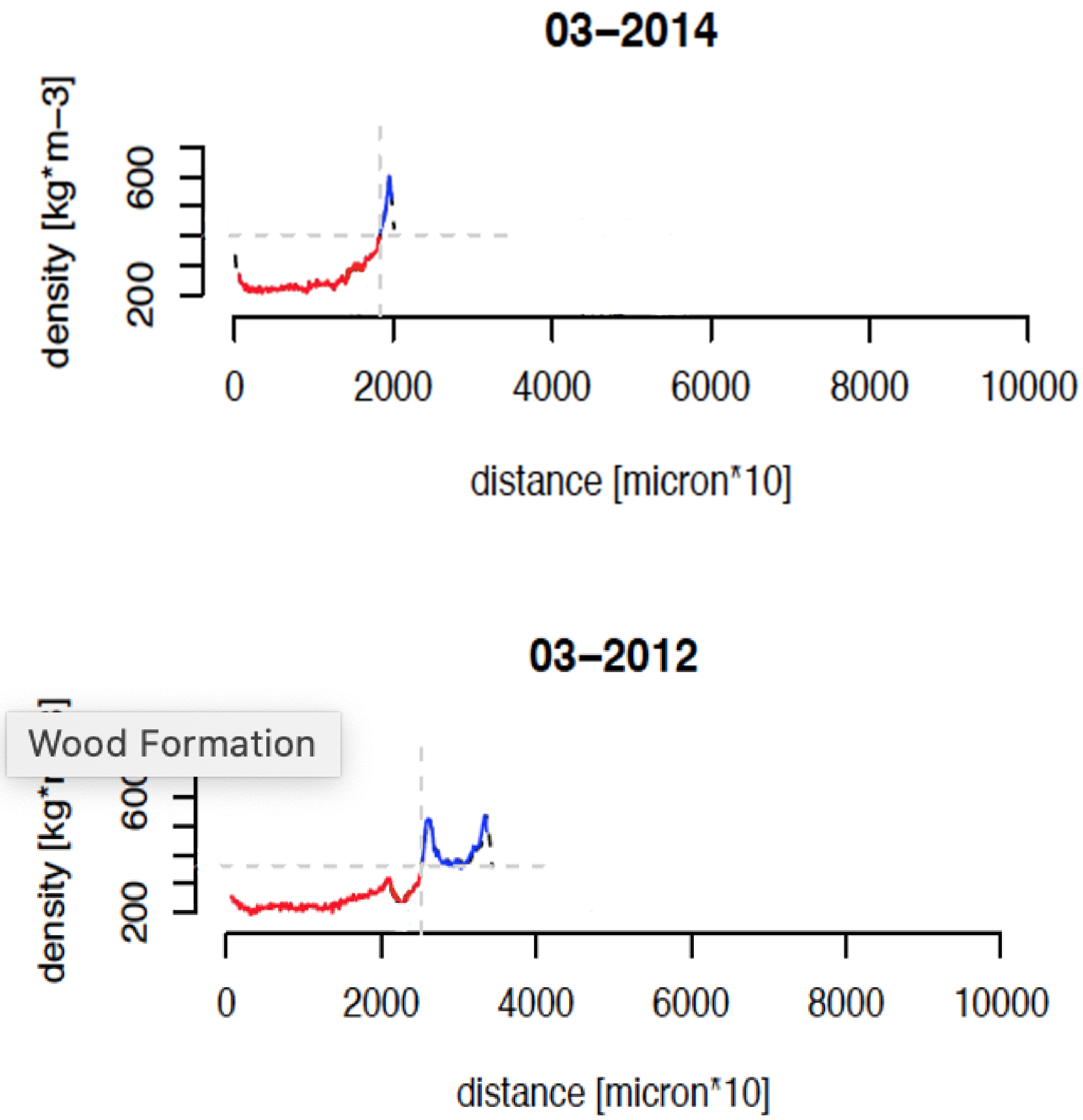

Figure 1. Density graphs of annual growth rings from *Pinus strobus*. The top graph represents the density and width of the 2014 annual growth ring. The 2014 ring illustrates the normal annual increase in density in a ring. The bottom graph is the 2012 ring, which represents a micro-density anomaly in a ring. The red lines are earlywood, and the blue line is latewood (Fonti, personal communication, 2018).

Besides the inter-annual changes in density, which is caused by varying amounts of earlywood and latewood in the rings, there are also intra-annual changes. These intra-annual changes are commonly referred to as intra-annual density fluctuations, false rings, or micro-density anomalies. We use the latter term hereafter. Micro-density anomalies occur when cambial activity slows during the growing season to produce cells with latewood characteristics, but then resumes within that same growing season to produce cells with earlywood characteristics (De Micco et al., 2016). Micro-density anomalies begin like normal growth rings with a continuous gradual increase in density, but the density suddenly decreases before increasing again (Fig. 1). Micro-density anomalies may vary in their ring position as well as their distinctiveness (Hoffer & Tardif, 2009).

Micro-density anomalies are hypothesized to be an alteration to the regular process of ring formation caused by unusual disturbing factors. They may, for example, reflect patterns of stomatal conductance and photosynthetic water-use efficiency (Battipaglia et al., 2014). It is hypothesized they develop due to droughts, air pollution, floods, extreme temperatures, sudden frosts or defoliation (Marchand & Filion, 2012). Some suggest that the climate at the end of the growing season must allow enough time for radial growth in order to differentiate the micro-density anomalies from latewood (Babst et al., 2016).

Few studies have examined micro-density anomaly distribution, so it is unknown whether their formation varies along the bole of a tree. It has been argued that micro-density anomalies do not occur uniformly throughout the tree because the chemical signal for latewood formation originates from active, lateral meristem. Accordingly, areas of increased cambial activity such as near branches are more likely to produce micro-density anomalies (Fritts, 1976). One study found that the circumferential distribution of micro-density anomalies is also not uniform (Battipaglia et al., 2010). This suggests that the drivers of micro-density anomalies affect various parts of the tree disproportionately.

Others observed that micro-density anomalies in conifers are more likely to occur in younger rings (Vogel et al., 2001, Copenheaver et al., 2006, Zalloni et al., 2016, Marchand & Filion, 2012) and wider rings of fast-growing trees (Vogel et al., 2001, Campelo et al., 2013, Zalloni et al., 2016). However, we were unable to find any studies that examined the distribution of micro-density anomaly formation throughout the stem in trees. While environmental factors may lead to micro-density anomaly formation, natural factors related to the tree itself such as development and vigor may predispose anomaly formation.

The majority of micro-density anomaly studies on conifers have been conducted in regions that commonly experience droughts such as dry boreal or Mediterranean forests (De Micco et al., 2016). Studies conducted in these drier ecosystems found that micro-density anomalies are driven by drought or low precipitation during the growing season. When moister conditions return later in the growing season, trees respond by forming earlywood-like cells again (Campelo et al., 2013; Copenheaver et al., 2006; De Micco et al., 2016; Marchand & Filion, 2012; Zalloni et al., 2016). There are few micro-density anomaly studies in temperate mesic areas, and the relationship between climate and wood density varies from region to region (Chave et al., 2006). In fact, a previous study in Massachusetts conducted on climatic impacts on white pine found no evidence of micro-density anomalies (Abrams et al., 2000; Marchand & Filion, 2012). Thus, trees in mesic areas may not respond to variations in water availability by forming micro-density anomalies. However, as the climate changes, droughts may become more common in these areas, so it is important to understand what impact, if any, water has on wood formation (Thibeault & Seth, 2014). To better understand carbon allocation in mesic forests, more research is necessary, especially as climate change threatens these regions with more frequent drought.

Using Eastern white pine as our study organism, we examined the within-tree distribution of micro-density anomalies and the climatic drivers of these anomalies in a temperate mesic mixed forest. White pine is a convenient and important species to use in researching micro-density anomalies for several reasons: (i) it is a valuable economic and ecological species in regions such as the North-Eastern United States (Leak et al., 1995) and (ii) white pine is a conifer, which tend to have more visible micro-density anomalies than hardwoods (De Micco et al., 2016).

This study aimed to determine the distribution and drivers of micro-density anomalies in white pine trees. We hypothesized that (i) the sampled trees would have a similar expression of micro-density anomalies, (ii) micro-density anomalies would be differently distributed near branches and breast height, (iii) micro-density anomaly formation would be similar throughout the stem of the tree, and (iv) wider rings would be more likely to have micro-density anomalies. We also hypothesized that (i) lower than average water supply (e.g., precipitation and soil moisture) and (ii) higher than average water demand (e.g. vapor pressure deficit) and temperature in the middle of the growing season are the main drivers of micro-density anomaly formation.

Materials and Methods

Sampling site

To study the formation of micro-density anomalies, 41 young white pines were sampled in Tom Swamp, a tract of Harvard Forest in Petersham, Massachusetts (42.5°N Latitude; 72°W Longitude). The site is a temperate mesic environment, with an annual mean precipitation of 1100 mm that is evenly spread across the seasons, and a mean annual temperature of 8.4 °C with temperatures ranging from a mean July temperature of 20 °C to -7 °C in January. The elevation is 220m to 410m above sea level (*Physical and Biological Characteristics of the Harvard Forest | Harvard Forest*, n.d.).

The white pines naturally regenerated on stony loam soil that was moderately to well-draining after a clear-cut in 1990. All of the trees ranged from 15 to 26 years of cambial age at breast height, had a single straight bole for at least 4 m above the root collar, and had no obvious large scars or recent damage. The trees chosen for the study occupied a codominant canopy position and their surroundings did not show signs of recent disturbance.

Sample preparation

We collected increment cores from the 41 trees at breast height (ca. 1.5m) using a 5.1mm three-threaded Haglöf standard increment borer at the start of the growing season in 2019. Seven of the trees died in 2018 as they were part of a previous girdling study. These seven trees were cut down in July and August of 2019. For the cut trees, (i) we measured the length of each growth section, which is the yearly apical growth of a conifer, and was designated by the branch whorl above and below the growth section, and (ii) we recorded the number and width of the branches at each branch whorl. Cross-sections were cut with a chainsaw from the middle of each growth section, and the 2010 growth section was used to analyze if micro-density anomaly distribution was equal throughout the height of the tree (Fig 2). After gluing all the samples into the core mounts, we sanded the cores and cross-sections with incrementally finer sandpaper (80 to 8000). Using an Epson Perfection V600 Photo scanner at 2400 dpi, we then scanned the cores and cross-sections. To examine if micro-density anomalies occurred more frequently near areas of actively growing lateral meristem, we took additional cores from ten trees above breast height near branches (Fig 2). All of the increment cores went through the pith of the tree, which gave us two sets of rings in each tree for the majority of the tree's growth history.

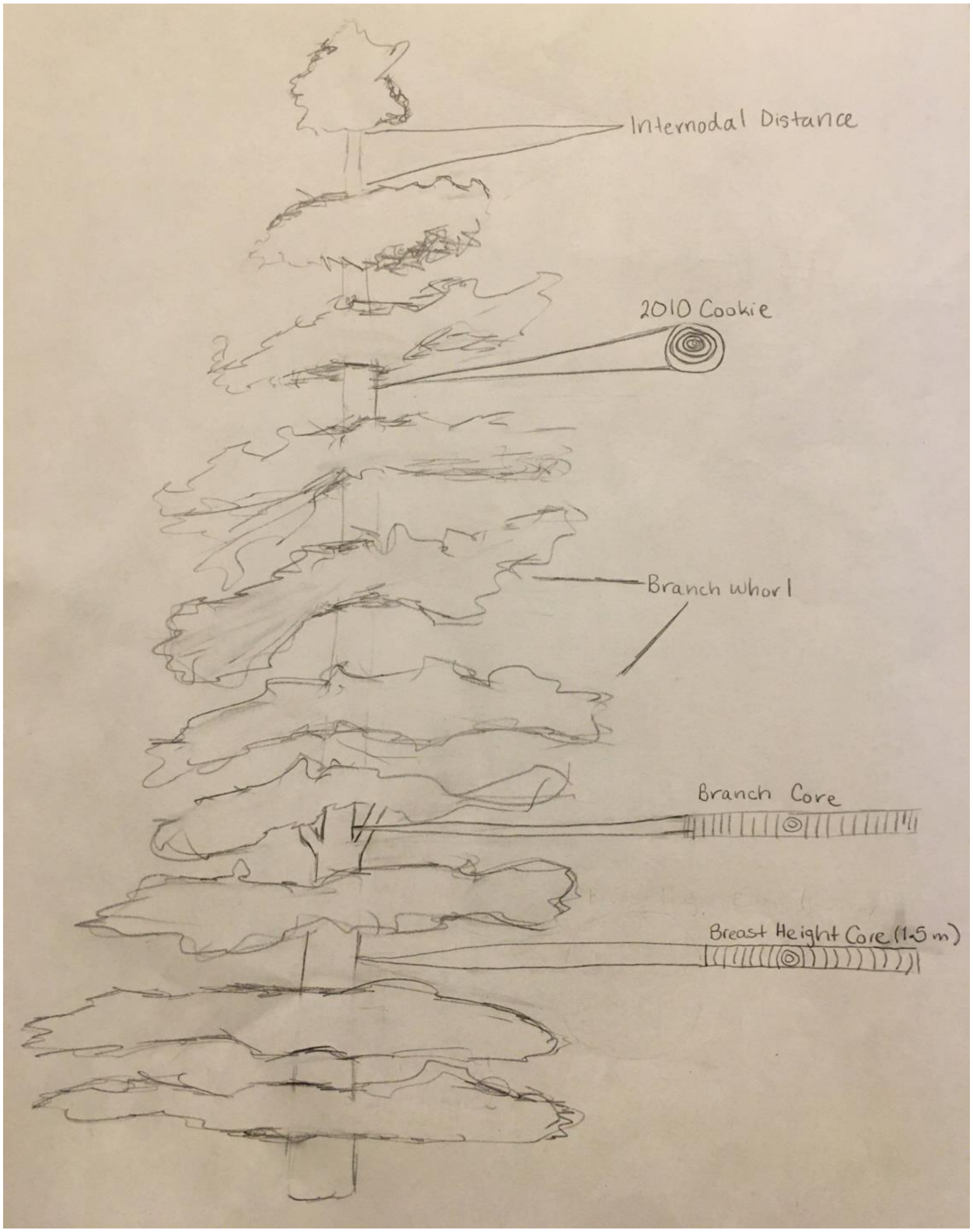

Figure 2. Graphic illustrating the internodal distance and the different sampling locations (i) breast height, (ii), above branches, and (iii) 2010 growth section (where radial growth is put on beginning in 2010).

Analysis

Tree Ring Image Analysis and Database (TRIAD), an online repository for images of tree cores and a ring width measuring tool, allowed us to analyze the scans. We then measured tree ring width of (i) the breast height increment cores, (ii) the branch increment cores, and (iii) the 2010 cross-section (Fig 2). After visually cross dating the increment cores and stem disks, we recorded the presence of micro-density anomalies in each growth ring. Micro-density anomalies were counted when a continuous band of intra-annual latewood-like cells interrupted the middle of an earlywood growth section (Fig 3). Another expert checked any questionable micro-density anomalies.

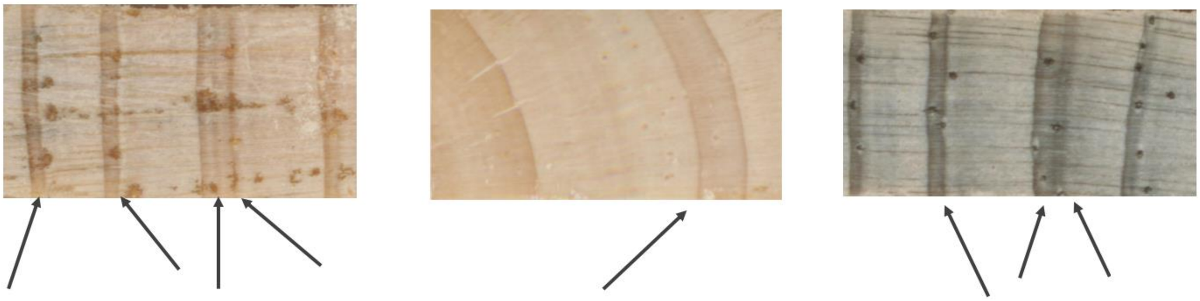

Figure 3. Micro-density anomalies (arrows) found in three cores taken from different *Pinus strobus* samples at breast height. These micro-density anomalies were formed by latewood like cells interrupting the earlywood growth section.

Meteorological data

We gathered the climatic data from Fisher Meteorological Station, the weather station at Harvard Forest. The station was around 1.2 kilometers away from the sampling site. Soil moisture was assembled from various data sets available through the Harvard Forest Data Archives which cover the period from 1998 to 2018 (Hadley, 2007; Melillo et al., 2017). PhenoCam Network, which is a North American scale phenological observatory that uses digital cameras to track vegetation phenology, allowed us to identify the photosynthetically-active season of white pine at Harvard Forest (Hufkens et al., 2018). This data allowed us to break apart the year into various stages of the growing season. We defined the start of the season as the 50% green up of the 90th percentile and the end of the season as the 50% green-down of the 90th percentile. The green-up is a phenophase event that occurs in the early spring before the growing season begins whereas green-down is the phenophase event that occurs in the fall and signifies the plant preparing for winter dormancy (*U2_MonitoringPhenology_Background_Final.pdf*, 2016). We defined the early-growing season as two weeks before and after the 50% green-up, mid-season is between the two weeks after 50% green-up and two weeks before 50% green-down, and late-season is two weeks before and after 50% green-down.

Statistical Analyses

All statistical analyses were performed in R (R Core Team, 2019). We used a simple linear regression to compare micro-density anomaly occurrence with precipitation, soil moisture, vapor pressure deficit, and air temperature for each part of the growing season (early, mid, and late growing season). After examining the climatic graphs, several years of interest, 1999, 2002, 2012, and 2016, which had lower precipitation and soil moisture than average, were classified as drought events. We calculated partial correlations of precipitation and air temperature with micro-density anomalies occurrence as well as soil moisture and vapor pressure deficit with micro-density anomalies on all of the years. We grouped these variables together in order to separate out general environmental variables, as in precipitation, versus variables that are commonly used to assess drought such as soil moisture and vapor pressure deficit. T-tests were conducted to test ring width the year before, during, and after one of the years with a drought event. The frequency of micro-density anomalies near branches as opposed to at breast height was also tested using a t-test. All code and data is available on github (https://github.com/E1Miller/Micro-density-Project).

Results

Micro-density anomaly occurrence

In the 41 trees, we found 210 annual rings with micro-density anomalies in white pine in a temperate mesic ecosystem. All sampled trees exhibited micro-density anomalies in at least one year. Five trees were at least one standard deviation above the mean micro-density anomaly occurrence while three trees were at least 1 standard deviation away from the mean micro-density anomaly occurrence ($\sigma = 9.67$) (Fig. 4). The number of annual growth rings that had anomalies for any individual tree ranged between 2 and 11.

Micro-density anomaly occurrence exhibited a clear temporal pattern (Fig. 5). In 1999, 18 trees ($n = 19$) showed micro-density anomalies, 31 trees in 2002 ($n = 36$), 35 trees in 2012 ($n = 41$), and 30 trees in 2016 ($n = 41$) compared to an average of 5 trees for all other years. The strong temporal clustering of micro-density anomalies prompted us to further investigate the climate of years with high frequency of micro-density anomaly occurrence (Table 1). These years (1999, 2002, 2012, and 2016) were comparatively dry and in particular had lower May-July precipitation (Fig. 8). However, by August precipitation began to increase again (Fig. 8). This suggests that the trees experienced water stress during their peak-growing season, which was then alleviated in August.

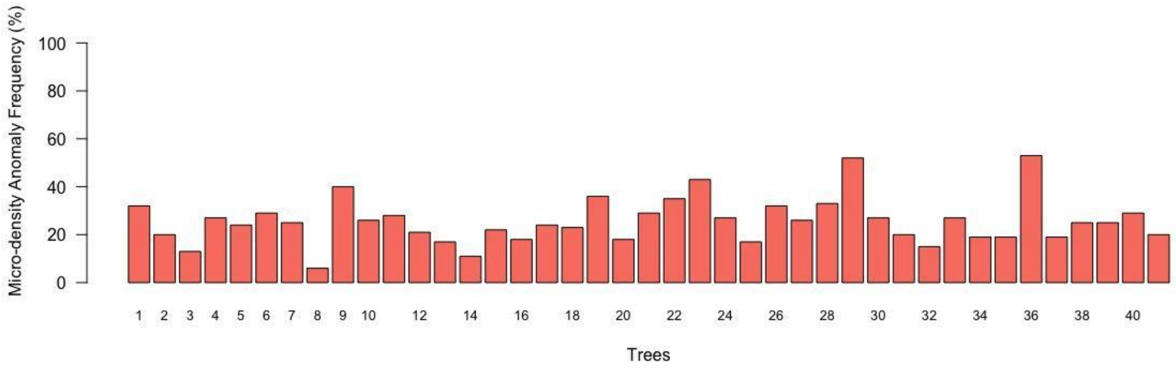

Figure 4. The percentage of annual growth rings with micro-density anomalies from increment cores taken at breast height for 41 sampled trees.

Distribution of micro-density anomalies

Unlike our hypothesis, micro-density anomaly occurrence was homogeneous along the bole. The occurrence of micro-density anomalies in cores taken from branches and those taken at breast height did not differ (t-test, p-value = 0.9917). There was also no difference in micro-density anomaly occurrence in 2010 cross-sections of the tree versus from increment cores at breast height (t-test, p-value = 0.2068) (Fig. 5).

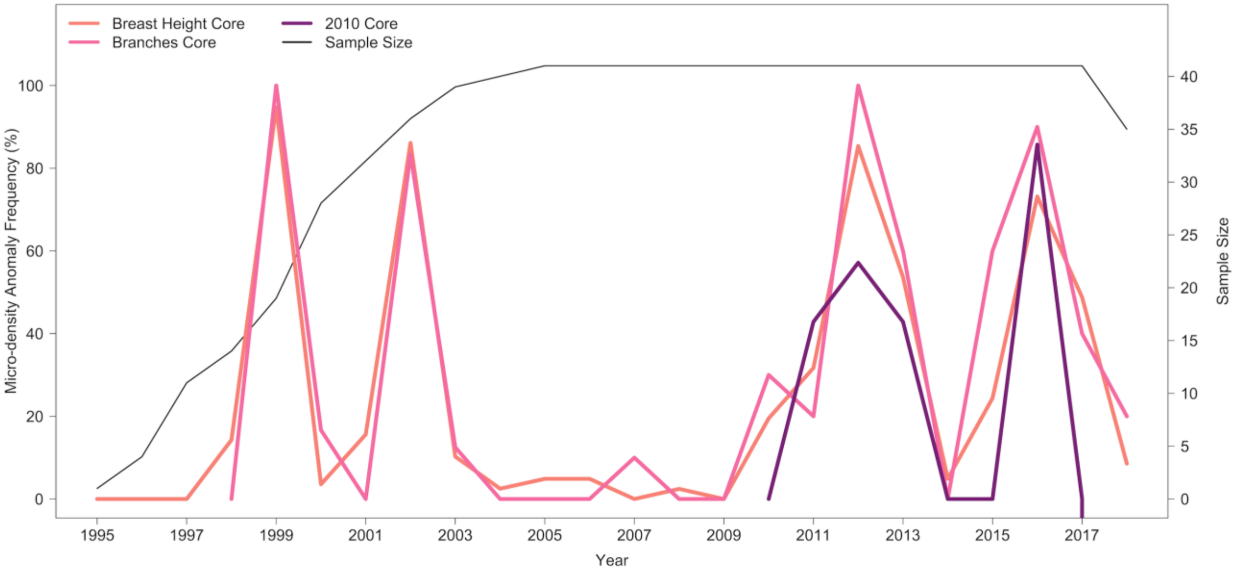

Figure 5. The micro-density anomaly frequency (%) found in increment cores taken at (i) breast height, (ii) near branches, and (iii) from the 2010 growth section. The gray line shows the number of increment cores taken at breast height that have a growth ring for that specific year.

Table 1. Climate data for 1999, 2002, 2012, 2016, and the average year (Boose & Gould, 2019; Hadley, 2007; Melillo et al., 2017)

	1999	2002	2012	2016	Average Year
Mean Air Temperature (℃)	8.42	8.41	9.49	8.97	7.61
Total Precipitation (mm)	1033	1540	841	981	1268
Mean Soil Moisture	0.271	0.243	0.251	0.237	0.285
Average VPD (kPa)	NA	0.309	0.387	0.397	0.332

Ring width before, during, and after drought events

We compared ring widths for years before, during, and after a year of interest (1999, 2002, 2012, and 2016) for trees that showed a micro-density anomaly for the particular year versus those that did not (Fig. 9). Annual growth increments were wider for trees with micro-density anomalies as opposed to those without for years before (t-test, p-value = 0.000219), during (t-test, p-value = 4.79×10^{-5}), and after the years examined (t-test, p-value = 0.000280). The annual growth rings for trees with micro-density anomalies were on average 1.18 mm wider than those without, indicating that micro-density anomalies predominantly occurred in fast growing individuals.

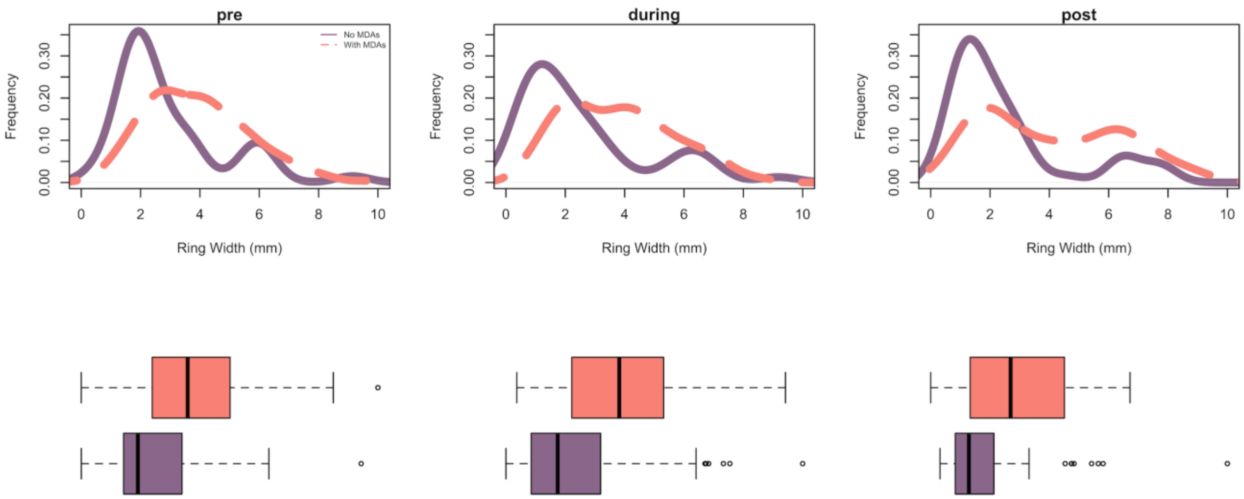

Figure 9. Density plot comparing the ring width of rings with micro-density anomalies (With MDAs) and those without micro-density anomalies (No MDAs). The years were grouped together into the years before, during, and after a drought event (1999, 2002, 2012, 2016). The box and whisker plots illustrate the difference in average ring width.

Climate and micro-density anomaly occurrence

The four climate variables were examined: precipitation, air temperature, soil moisture, and vapor pressure deficit. All of these variables interact and impact one another, and clear patterns emerged in the simple regressions. Soil moisture and mid-season air temperature were clearly related to micro-density anomaly occurrence. Soil moisture in the early (simple regression, p value = 0.005466, R^2 = 0.3205), mid (simple regression, p value = 0.00499, R^2 = 0.334), and late growing season (simple regression, p value = 0.0138, R^2 = 0.2973) explained around 30% of the variation in micro-density anomalies (Fig. 6). Mid-season air temperature was also related with micro-density anomaly formation and explained around 30% of the variation in the formation (simple regression, p-value = 0.003012, R^2 = 0.324) (Fig. 7). No strong relationships were found between the remaining climate variables and micro-density anomalies (Table 2).

Table 2. Simple linear regression results for climate variables and micro-density anomaly occurrence

	Early season	Mid-season	Late-season
Precipitation			
p-value	0.3927	0.825	0.1737
R^2	-0.01096	-0.04512	0.04279
Soil moisture			
p-value	0.005466	0.004499	0.0138
R^2	0.3205	0.334	0.2973
Vapor pressure deficit			
p-value	0.3471	0.07872	0.7351
R^2	-0.003567	0.1379	-0.05829
Temperature			
p-value	0.4862	0.003012	0.5002
R^2	-0.02314	0.3177	-0.02582

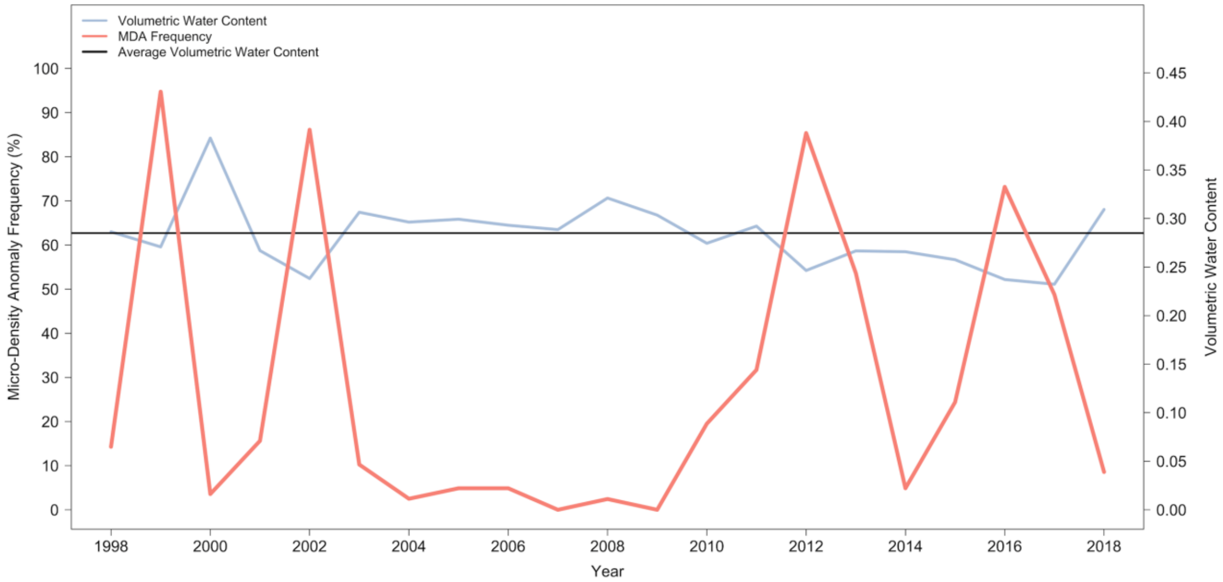

Figure 6. Micro-density anomaly frequency (%) compared with average annual volumetric water content (soil moisture) and mean volumetric water content from 1998 to 2018.

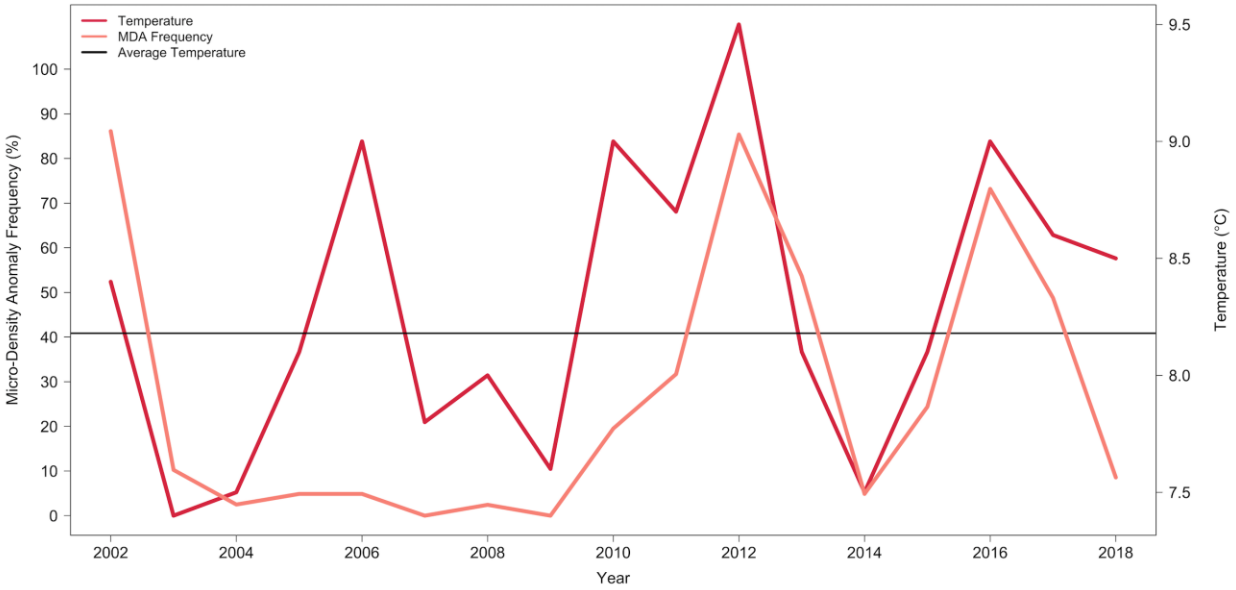

Figure 7. Micro-density anomaly frequency (%) compared with average annual temperature and mean temperature from 2002 to 2018.

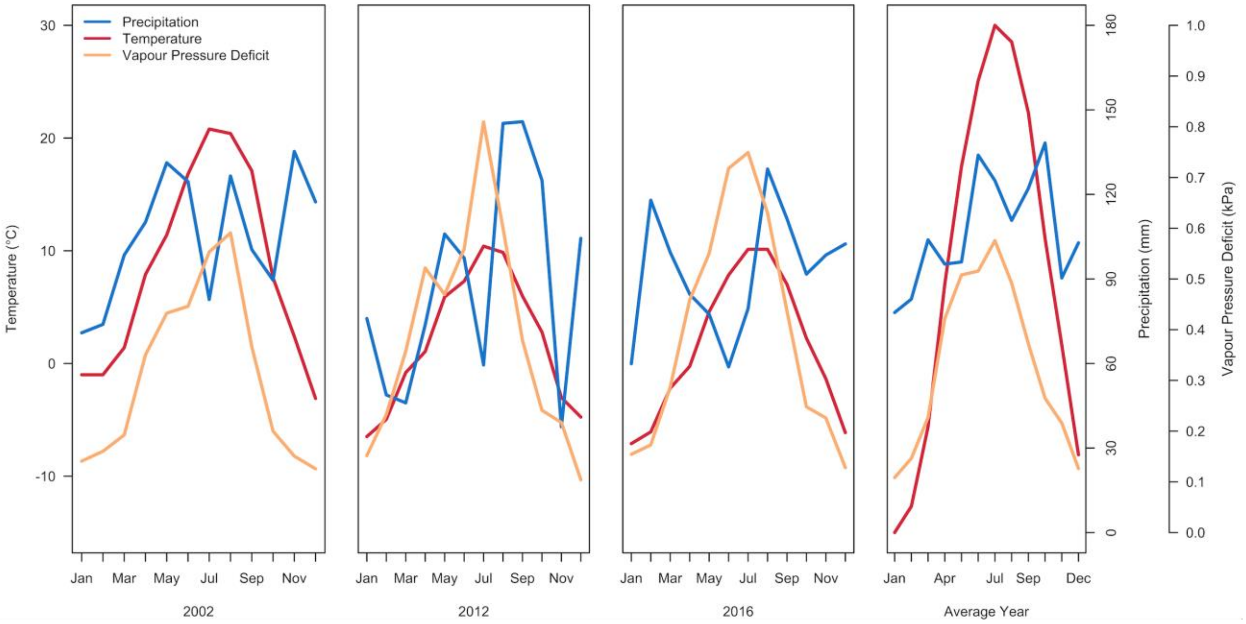

Figure 8. Comparison of average monthly precipitation, temperature, and vapor pressure deficit (VPD) for 2002, 2012, 2016, and the average of all other years. The years 2002, 2012, and 2016 showed high occurrence of micro-density anomalies. There meteorological data captured prior to 2002 was not sufficient to calculate vapor pressure deficit for 1999, which also coincided with high micro-density anomalies (Boose, 2019).

Discussion

Distribution of micro-density anomaly formation

For the first time, we found evidence of micro-density anomalies in temperate mesic regions that corresponded to specific drought events. Unlike previous research, our results illustrated that there was no clear difference between micro-density anomaly formation at breast height compared to wood forming near branches. There was also no difference in micro-density anomaly formation at breast height compared to wood forming higher up the stem. Since the formation of micro-density anomalies throughout the bole was consistent, this suggests that the drivers for latewood formation are less dependent on chemical signals from the lateral meristem, such as auxin concentrations, than previously assumed (Fritts, 1976). Thus, these chemical signals seem less important in latewood, and in turn micro-density anomaly formation. Indeed, other studies have found that the transition to latewood is not caused by a reduction in auxin supply (Uggla et al., 2001).

Since micro-density anomalies in these trees formed uniformly throughout the bole, the driver of the transition to latewood cells must also be distributed equally in the tree. However, many of the proposed mechanisms for this transition from earlywood cells to latewood cells are height dependent. Others hypothesize that cell turgor pressure impacts cell enlargement (Wilkinson et al., 2015), which varies along the bole due to gravity (Woodruff et al., 2004). When there are periods of low water availability, the lower cell turgor pressure limits cell enlargement, leading to smaller lumens, and which forms latewood like cells. Gravity impacts the turgor pressure of cells, so cells higher up the tree experience a lower turgor pressure than those at the base of the tree (Woodruff et al., 2004). The trees in our study were relatively short and ranged from 7.6 to 13.53 m, which is half the height of the trees in the Woodruff et al. (2004) study, so there may have been a smaller gradient in turgor pressure in our trees. In tall trees during a drought the relative change in xylem water potential due to declining soil moisture is already lower due to gravity (Hölttä et al., 2010).

We found that trees with wider rings were more likely to have micro-density anomalies, which agrees with previous findings. Trees with narrower rings may be less likely to have micro-density anomalies because they lack the reserves necessary to resume cambial activity after climate conditions are favorable again (Zalloni et al., 2016). Similarly, wider rings may be formed due to either a higher rate of cambium cell production (Rathgeber et al., 2011) or due to a longer growing season (Rossi et al., 2008). Higher rates of cambium cell production allow for the formation of more cells after conditions improve. A longer growing season allows for a longer period of recovery after conditions have alleviated. Furthermore, in smaller trees the cambial activity starts later and finishes earlier, so there is a shorter time period to record climate variability, and potentially even a less plastic response to environmental changes (Campelo et al., 2013).

All of the trees had micro-density anomalies, however there were five trees that had more micro-density anomalies than average while three trees had fewer micro-density anomalies than average. This difference may be due to variations in the microhabitat of the trees. Within the sampling area, there was a small rocky hill with several of the trees on it. One study found that drainage conditions predisposed the formation of micro-density anomalies. Micro-density anomalies were more common among the trees growing on rocky outcrop sites compared to those in shallow soil. Superficial soil deposits form a buffer that reduces the chance of a water deficit due to low precipitation and may reduce the amount of water lost due to runoff (Marchand & Filion, 2012). In our study, the trees with a higher occurrence of micro-density anomalies may have been experiencing more drainage or less access to water. Conversely, the trees that had fewer micro-density anomalies may have been in some of the lower and poor draining areas of the sampling area. Thus, the location of the trees may impact their propensity to form micro-density anomalies.

Drivers of micro-density anomaly formation

The driving factor of micro-density anomaly formation in this selection of white pines was low soil moisture, which has been found by other studies (Fig. 7) (Hoffer & Tardif, 2009). Vapor pressure deficit (VPD) and precipitation did not have a direct role in micro-density anomaly formation. During a drought, trees may be experiencing a lower supply of water from soils and a higher demand of water from the atmosphere. Our results indicate that the lack of a supply of water from the soil is what causes the observed micro-density anomalies in white pines. White pine has a shallow root system, which means that in times of low soil moisture, it may be unable to take advantage of deeper water reserves (Farrar, 2001). The amount of precipitation was never significantly lower during the drought years (1999, 2002, 2012, 2016), but soil moisture had a relationship with micro-density anomaly formation. Though the amount of precipitation in the drought years may have been similar to the average year, there may have been more extreme precipitation events which had more runoff or were unable to penetrate the soil as well.

Similar to other research, the mid-growing season air temperature was also found to have a relationship with micro-density anomaly formation. Other studies found that temperature drives the rate of wall material deposition and latewood cells have thicker cell walls than earlywood cells (Rathgeber, 2017). Thus, a variety of factors may contribute to the transition to latewood formation in conifers such as drought or elevated summer temperatures (Begum et al., 2016). Our results indicated that micro-density anomalies were triggered by cambial growth resuming after environmental conditions are favorable again such as August precipitation, which other studies have found (Zalloni et al., 2016). During droughts that extend throughout the growing season, the trees may not produce any new growth because they are saving their reserves to survive.

Water may often be a limiting factor in tree growth. A hypothesized method of water transport in trees is the cohesion-tension theory, which argues that water in trees travels upward due to tension, or when xylem pressure is more negative than the vapor pressure of water (Tyree, 1997). The tree may shift to producing latewood-like cells during a period of low soil moisture as a method of water-conduction security (Rathgeber, 2017). It has been hypothesized that compression wood, or reaction wood formed due to gravity, which is composed of a greater proportion of latewood, may be more resistant to drought due to the latewood's higher resistance to embolism at low water potentials (Domec, 2002; Plomion et al., 2001). The cells may become more like latewood in the tree when there is a low water supply in the soil to prevent embolisms from forming. When the water supply in the soil is again sufficient, the cells will transition back to earlywood so that the tree can continue to put on more wood to increase their water uptake efficiency. Thus, trees that can transition to latewood like cells during water stress may be more likely to survive a drought. In temperate mesic regions, trees usually do not experience long periods of drought, so one would suspect that trees in mesic ecosystems respond slower to water stress. Since all of the trees in our study formed micro-density anomalies, they clearly vary wood density as a physiological response to supply-driven drought. However, the white pines we examined were young trees, and older trees may be less likely to have as immediate of a response to limited water.

Conclusion

Even in temperate mesic regions, trees form micro-density anomalies in response to low soil moisture. There have been few studies conducted on micro-density anomalies in mesic regions or on micro-density anomaly distribution throughout the bole. However, it is important to understand how trees in mesic areas will react to low water availability. Trees that are unable to quickly adjust their wood properties due to climatic variabilities may be more vulnerable to drought (Martinez-Meier et al., 2008). Further studies will also allow us to learn how carbon sequestration may be impacted. Since a higher proportion of latewood is often associated with higher wood density, micro-density anomaly fluctuations may change the amount of carbon stored in annual growth rings (Zobel & Buijtenen, 1989). Future research is needed to better determine at what soil moisture levels micro-density anomalies form. There should also be further analysis that examines how rain fell during the years with micro-density events. For example, the years may have had similar total precipitation, but the years that formed micro-density anomalies may have had a few extreme precipitation events that led to higher run-off. By increasing our understanding of tree responses to water stress in mesic regions, we can decide which species may be best suited for these areas in the future, create more accurate wood allometric equations, and predictions of carbon sequestration.

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