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Impact of Drought Stress on Oak Stomatal Size and Density at Thompson Farm, NH

Emily Chen

University of New Hampshire, Durham

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Impact of Drought Stress on Oak Stomatal Size and Density at
Thompson Farm, NH

Emily Chen

Advisors: Heidi Asbjornsen, Michael Simmons

Department of Natural Resources and the Environment

University of New Hampshire, Durham, NH, USA

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Abstract

Global climate change is likely to affect northeastern U.S. forests by increasing the frequency and severity of drought events. Historically, droughts rarely occurred in this region, so native tree species are not well-adapted to extreme moisture stress. In the future, the changing climate will likely cause unprecedented levels of low water availability which may have implications on future forest composition. It is hypothesized that trees can respond to these environmental changes by altering their functional traits, also referred to as phenotypic plasticity; for example, by producing leaves with fewer and smaller stomata.

To determine the capacity to which oak trees adjust their functional leaf traits in response to water stress, stomatal size and density were measured in northern red oak (*Quercus rubra*), black oak (*Q. velutina*), and white oak (*Q. alba*) using leaves collected in 2020 and 2021 from the UNH Thompson Farm DroughtNet experiment. Imprints of the lower surface of each leaf were made with clear nail polish, mounted on slides, and examined under a light microscope. Images taken from these slides were then counted and measured using ImageJ software. Preliminary results show that both stomatal size and density values were lower in 2021 than 2020. No significant differences were found between drought and control treatments. Variation existed between individual trees of the same species and within different leaves of the same tree.

Introduction

It is predicted that global climate change will cause temperatures to increase during this century, especially in North America where the annual mean warming is predicted to exceed global mean warming in most areas (Christensen et al., 2007). Although it is predicted that total annual precipitation will increase in northeastern U.S., an increase in temperature, earlier snowmelt, and longer leaf-on seasons will all contribute to increases in soil evaporation and leaf

transpiration, resulting in potential water stress in plants by the end of the growing season (Contosta et al., 2019). With increasing interannual variability, extreme climate events such as drought will also become more frequent and severe (Swain and Hayhoe, 2014). Historically, the late twentieth century was a wet period with drought events typically lasting between one to three months from 1961 to 1990 (Coble et al., 2017). Medium- and long-term droughts were historically rare. Because of this, tree species native to northeastern U.S. are adapted to mesic climates, not to extreme moisture stress. Additionally, European settlement has caused a shift in fire regimes which ultimately contributed to mesic species replacing xeric species across the eastern U.S. (Nowacki and Abrams, 2008). With climate change causing unprecedented levels of low water availability, there will likely be serious consequences for northeastern forests.

One strategy for trees to adapt to environmental changes is altering their anatomical features to reflect new conditions. This is also referred to as phenotypic plasticity. This is a climate change resilience strategy that can promote change in a forest. Without adaptation, future forest composition in northeastern U.S. will likely change and stand types may be lost. In addition to creating novel communities, this process of shifting species composition may likely be disruptive to ecosystem processes, as trees will die and be replaced. Climate projections show that in New England, there will be a significant decline in suitable habitat for spruce-fir forests and expansion of suitable habitat for oak dominated forests in a high emission CO₂ scenario and more maple, birch, and beech habitat in a low emission scenario (Rustad et al., 2012). This demonstrates that the implications of climate change will be significant to future forests.

Given the potential impacts of global climate change on forests, it is important to study the effects of climate change at the individual tree level. Even if these changes are not directly impacting the function of a forest, there will be indirect effects that can lead to tree stress and

ultimately, mortality. For example, predisposing factors such as climate change and low soil moisture holding capacity combined with an inciting factor like drought may cause trees to be more susceptible to defoliators and wood and bark boring insects that could lead to mortality.

One anatomical feature that trees can manipulate to adapt to drought are their stomata. Stomata are small leaf pores controlling gas and water exchange through guard cells that open and close (Hetherington and Woodward, 2003). Leaves with large stomata or a high density of stomata can uptake more CO₂ for photosynthesis, but at the expense of greater water loss (Franks et al., 2009). A tradeoff between CO₂ uptake and water loss is fundamental to all plants, but different species can differ widely in the suites of traits related to carbon fixation, water uptake, water transport, and water loss (Blackman et al., 2019). Species that tolerate more negative water potentials for greater C uptake are at risk for hydraulic failure, so it is advantageous for species to adapt their leaf traits in response to drought (Asbjornsen et al., 2021).

Research Question

Given the implications of climate change on future forest composition in northeastern U.S. and lack of research on drought in this region, the guiding research question of this study is how will trees alter their functional leaf traits to environmental change such as drought? I hypothesized that water stressed trees in the treatment plots will produce leaves with fewer and smaller stomata to limit water loss than control trees. I also hypothesized that 2021 samples would show greater stomatal adaptation to drought than 2020 due to the severe or extreme drought experienced the previous year from August to December (NOAA, 2022).

Methods

This experiment was conducted at the DroughtNet experiment at the University of New Hampshire Thompson Farm in Durham, NH. DroughtNet is a global, highly coordinated, multi-site drought experiment network that researches how and why terrestrial ecosystems will be impacted by drought (DroughtNet, 2022). The experiment at Thompson Farm has been running since 2016 (Asbjornsen et al., 2021). There are four 30m by 30m plots present with two control and two treatment plots (Figure 1). The control plots are unmanipulated mature forest plots whereas the treatment plots have a manmade structure built over them. This structure is a wooden platform built around mature trees that ranges from 1 to 3m high, with reinforced polyethylene sheeting covering the surface (Figure 2). There is about 55% areal coverage of plastic resulting in about a 50% precipitation exclusion during the growing season from mid-May to at least mid-October. This throughfall removal experiment simulates a once in a century drought in New Hampshire, U.S. (Asbjornsen et al., 2021). Each plot includes at least three mature oaks and three mature pines with a mix of birches, maples, and other species.

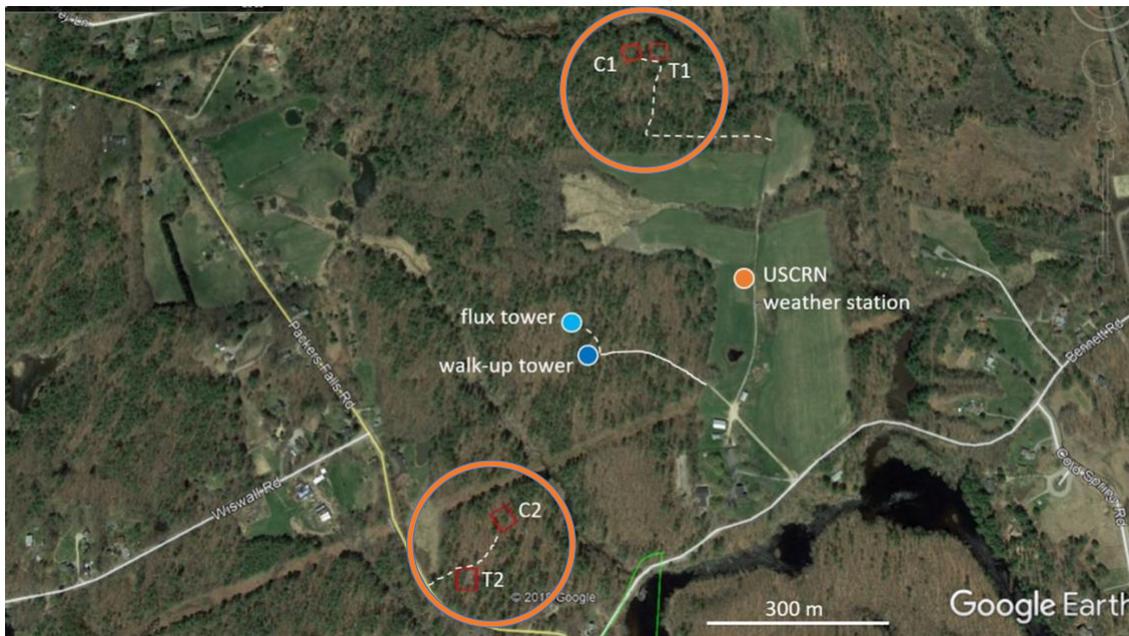


Figure 1. Aerial photograph of Thompson Farm with treatment (T) and control (C) plots labeled.



Figure 2. Aerial (left) and ground (right) view of throughfall removal structure simulating once in a century drought on mature trees at Thompson Farm, NH, U.S.

Leaves were collected from the canopies of mature northern red oaks, black oaks, and white oak trees in each of the four plots in August 2020 and 2021. Across all plots, there were 3 white oaks, 14 northern red oaks, and 9 black oaks. In 2020, leaves were obtained using a 90-foot DinoRXT boomlift (plot T1 and nearby control trees) and shotgun (all other plots) whereas 2021 leaves were obtained using only shotgun. Three leaves were collected from each individual tree from sun-exposed branches in the upper third of each tree's canopy. Clear nail polish was applied to the center of each fresh leaf, avoiding major veins, to create an imprint of the stomata. These imprints were peeled off and mounted on glass slides. Each slide was examined and photographed under a light microscope at 40x magnification with a camera attached (Figure 3). If multiple pictures were taken for each slide, the clearest and most densely packed picture was chosen for analysis.

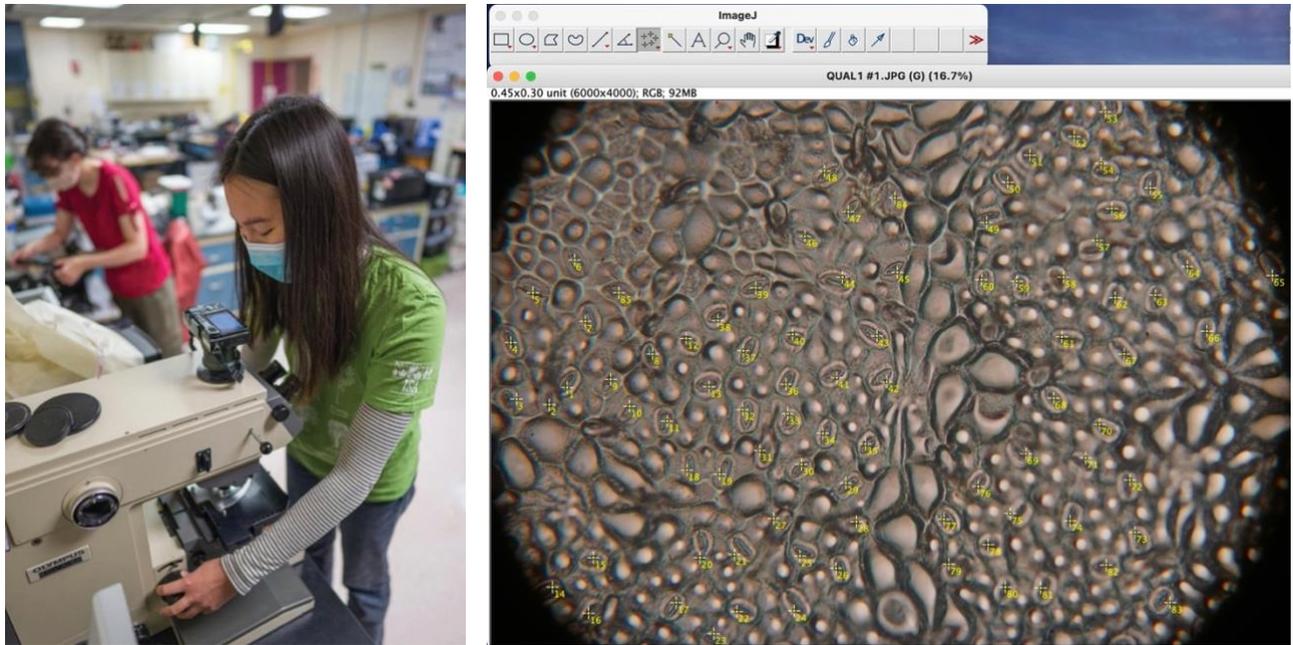


Figure 3. Data processing of stomatal slides under a light microscope (left) and measuring images using ImageJ software (right).

Each image was examined using ImageJ software to measure size (area in mm^2) and density (number of stomata per mm^2) (Figure 3). Stomatal size was calculated by taking the product of the length and width of the guard cell opening. To obtain density, the number of stomata present in the view were counted. The count divided by the area of the visible field resulted in the density measurement. The values of the three replicates for each individual tree were averaged to obtain one size and one density measurement for each tree.

This experiment is unbalanced as there were significantly more red and black oak species than white oak. Within the *Quercus* genus phylogenetic tree, northern red oak and black oak are genetically very similar and have been known to interbreed (Hipp et al., 2017). They are both in the Lobatae clade of the *Quercus* genus whereas white oak is in the *Quercus* clade (Hipp et al., 2017). Due to this genetic difference from the other two species, white oak was removed from the data pool for statistical analysis and values from northern red oak and black oak were combined. Therefore, a treatment and year effect were analyzed, but the species effect was not.

One-way ANOVAs were conducted to look at the statistical significance of treatment and year for both stomatal size and density while individual trees represented pseudo-replicates (Absjornsen et al., 2021). A regression analysis was also performed between stomatal size and density to see if there was a relationship between changes in multiple leaf traits.

Results

Between each oak species studied, average stomatal sizes and densities varied. White oak stomata tended to be smaller in size, but at a higher density than red and black oak (Table 1). Red and black oak had similar values, with red oaks averaging slightly larger stomatal size and higher density (Table 1).

Table 1. Comparison of average stomatal size (mm²) and average stomatal density (number of cells/mm²) for study species. All individuals of the same species were combined due to variance.

Species	Sample Size	Average size (mm ²)	Average density (#/mm ²)
white oak	3	0.021	496
northern red oak	14	0.054	414
black oak	9	0.051	351

No significant treatment effect was detected for either stomatal size or density. The *p* values for treatment effects on size and density were *p* = 0.420 and *p* = 0.595, respectively. The strongest differences were seen between years with values higher in 2020 than 2021 for both parameters and in both treatment and control plots (Figures 4 and 5). The mean stomatal size was 0.05 mm² in 2020 for both treatments and for 2021 control trees. For the 2021 drought treatment, the mean stomatal size was 0.04 mm² (Figure 4).

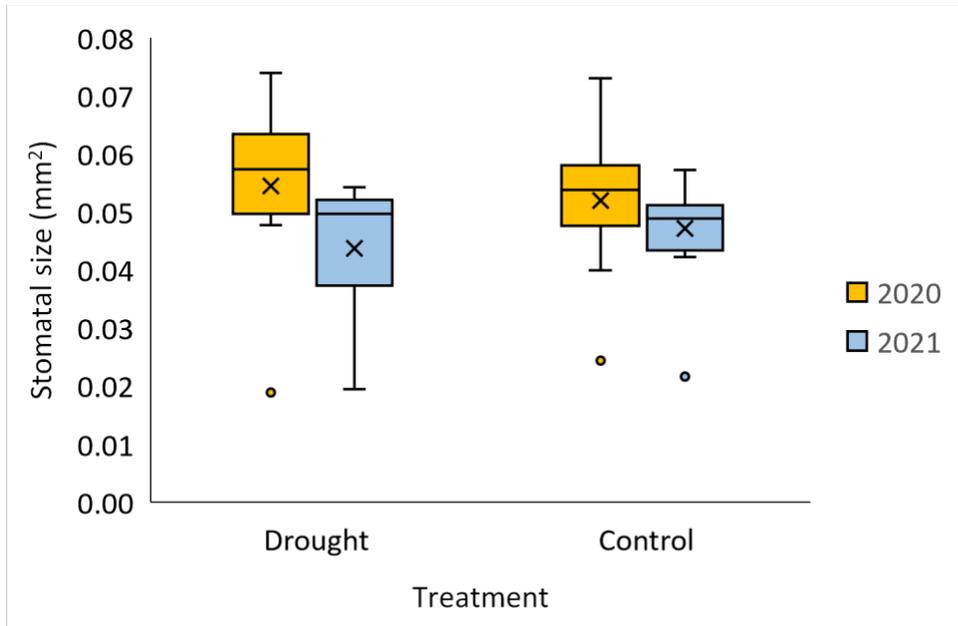


Figure 4. Stomatal size (mm^2) of all study species between drought ($n=19$) and control ($n=23$) treatments at Thompson Farm in 2020 ($n=18$) and 2021 ($n=24$).

The average 2020 values were also higher than 2021 in stomatal density too. In 2020, the mean stomatal density values for drought and control trees were 462 and 499 stomates per mm^2 of leaf area, respectively (Figure 5). In 2021, the mean stomatal density was 336 for drought trees and 339 stomata per mm^2 in control trees (Figure 5). For both stomatal size and density, $p < 0.001$ between years. There was a wide range in values obtained, especially in the drought treatment of stomatal size and the control treatment of stomatal density (Figures 4 and 5). Outliers were found in the 2020 drought treatment for stomatal density and in all the stomatal size plots except 2021 drought treatment (Figures 4 and 5).

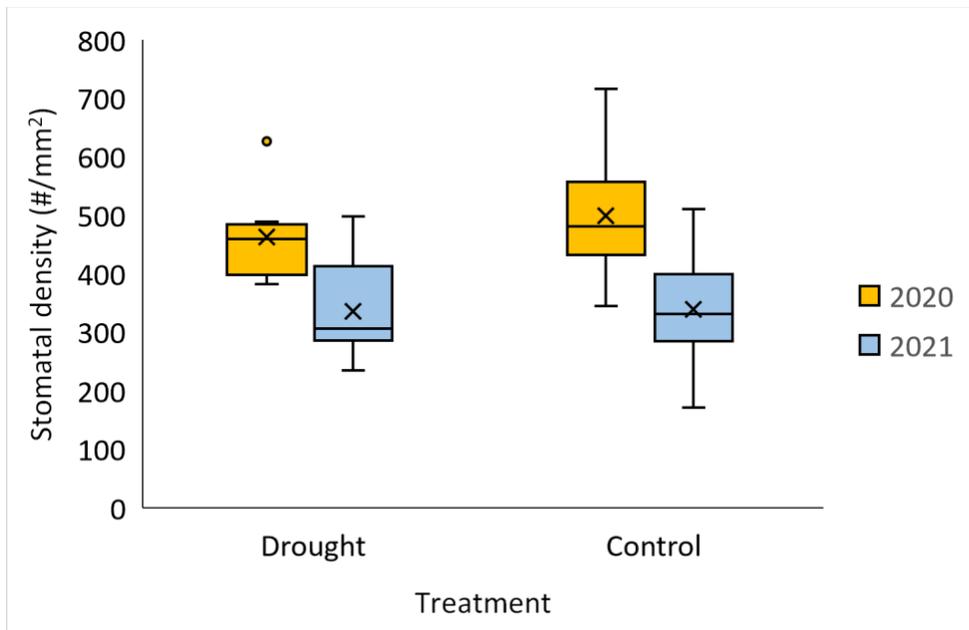


Figure 5. Stomatal density (cells/mm²) of all study species between drought (n=19) and control (n=23) treatments at Thompson Farm in 2020 (n=18) and 2021 (n=24).

A very weak negative correlation was found between stomatal size and density as $R^2 = 0.032$, though this relationship is not significant ($p = 0.259$). In general, leaves with smaller stomata had a higher density than leaves with larger stomata (Figure 6).

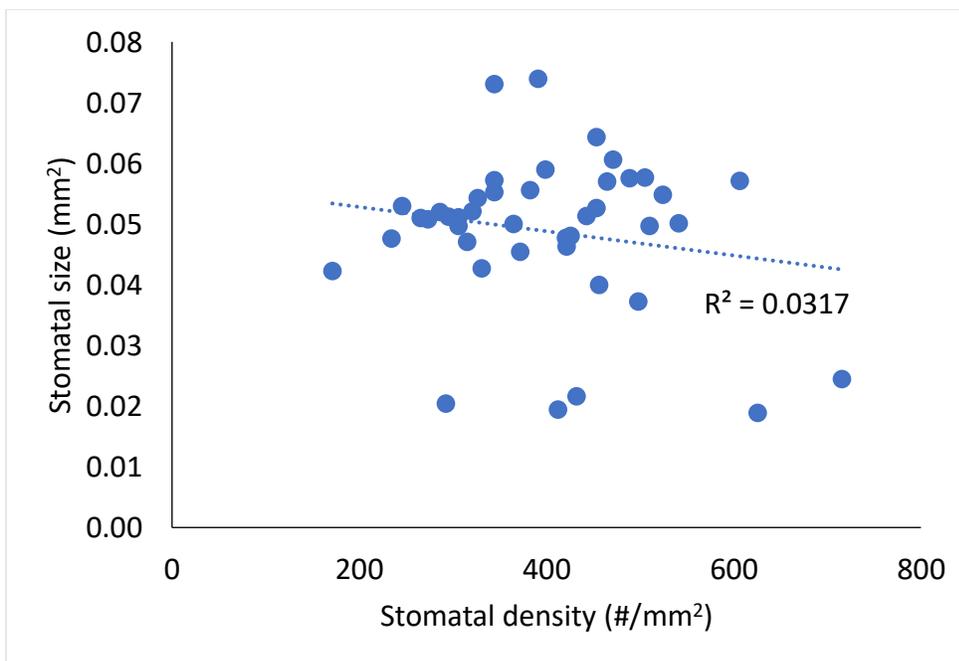


Figure 6. Relationship between stomatal size (mm²) and stomatal density (number of cells/mm²).

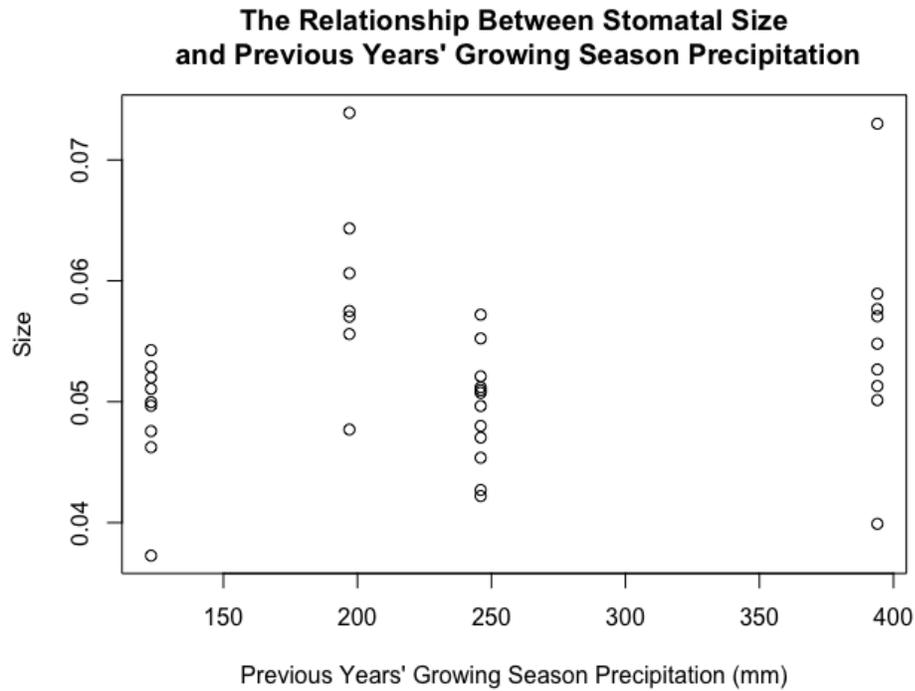


Figure 7. Relationship between stomatal size (mm^2) and previous years' growing season precipitation (mm).

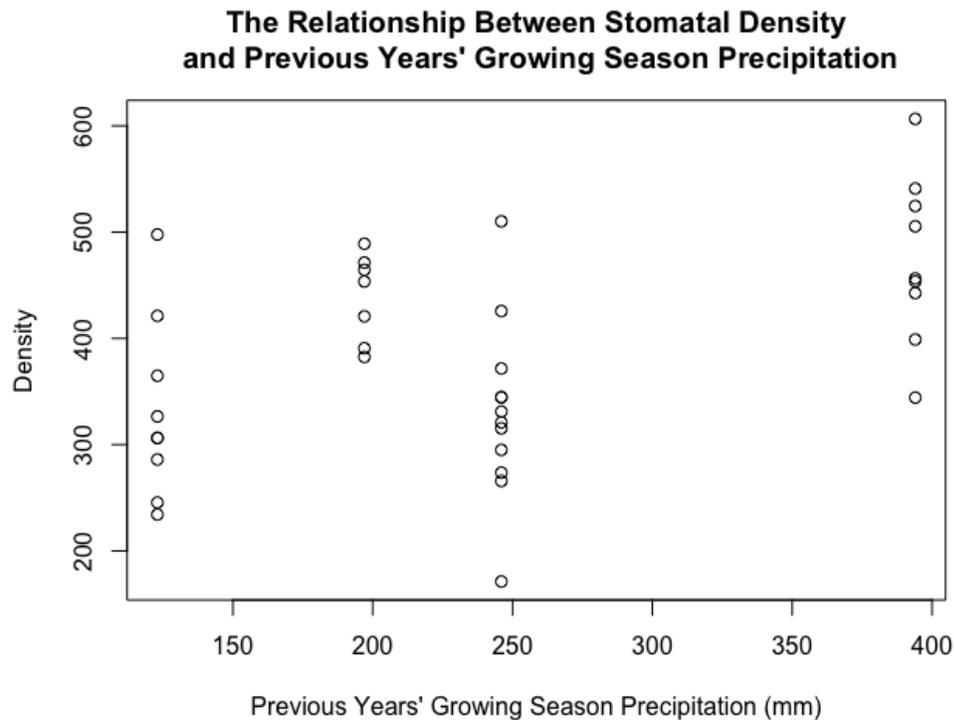


Figure 8. Relationship between stomatal density (count of stomata/ mm^2) and previous years' growing season precipitation (mm).

Through the National Oceanic Atmospheric Administration's Air Resources Laboratory, there is a climate reference network site at Thompson Farm. From these data, precipitation at Thompson Farm can be compared to the stomatal measurements obtained. When plotting stomatal size to the previous year of growing season precipitation for both treatments, the slope was not significant. The stomatal size correlation coefficient is 0.181 (Figure 7). However, the stomatal density relationship to precipitation is stronger than stomatal size. Both the slope and intercept are significant, and the correlation coefficient is 0.458 (Figure 8).

Discussion

The hypothesis that water stressed trees will produce leaves with fewer and smaller stomata to limit water loss was not supported because no treatment effect was detected for either stomatal size or density. Potentially, the experiment has not reached the threshold to cause anatomical change as the Thompson Farm DroughtNet experiment was established in 2016 (Asbjornsen, 2021). It is possible that the current drought adaptations are short-term responses like guard cell signaling to close stomata during temperature changes or dry periods (Wu et al., 2018). Long-term environmental changes occur on an annual to decadal scale, so perhaps the threshold of moisture stress has not been reached at Thompson Farm yet. It is also possible that the tree roots are growing outside the drought structure or rooting deeper than the growing-season exclusion can influence as oaks are known to root deeper compared to other species (Novick et al., 2022). Other leaf traits were not examined in this study, so perhaps the leaf size, leaf shape, leaf thickness, leaf number, and vein density adapted to drought instead of stomatal size and density.

While there was no treatment effect detected, there were changes observed between years. Both stomatal size and density values were higher in 2020 than 2021 in both treatment

effects. These differences were compared to the precipitation patterns observed at Thompson Farm as it is theorized that trees form their leaves from previous years' weather patterns (Wilczynski, 2018). In theory, a growing season (June-September) with little precipitation and prolonged drought should cause the next years' leaves to be adapted to dry conditions by producing smaller and lower density stomata (Hetherington and Woodward, 2003). No correlation was found with previous years' growing season precipitation and stomatal size (Figure 7), although a longer study would have greater power to detect these differences. The correlation coefficient between the previous years' growing season precipitation and stomatal density was reasonably high, so a relationship may be present (Figure 8). Changes in sampling procedure could have also caused differences in stomatal size and density between years. Because 2020 leaves were collected using both the boom lift and shotgun, it can be ensured that the leaves came from the top of the canopy. With shotgun, it is possible that the leaves collected were slightly less sun-lit.

To put the data found in this study in a larger ecological context, other studies found similar numbers in oak stomatal density. A 2003 study based in Harvard Forest in Petersham, Massachusetts, U.S. found an average of 494 stomata/mm² in sunlit red oak leaves (Sack et al., 2003). This is comparable to the range of 336 to 499 stomata/mm² found at Thompson Farm between both treatments and years (Figure 5). In the Sack et al. (2003) study, other species were studied in addition to northern red oak (*Quercus rubra*) including red maple (*Acer rubrum*), sugar maple (*A. saccharum*), and white birch (*Betula papyrifera*). Red oak had the highest density of stomata while birch shade trees had the lowest density at 82 stomata/mm² with both maple species falling between these values (Sack et al., 2003). These traits are highly relevant to

leaf drought tolerance, so differences between species may indicate different drought adaptation strategies.

Ashton and Berlyn (1994) also found differences between stomatal density and Stomate Area Index (SAI), the product of the mean stomate length and stomate density per unit area, between red oak and black oak. SAI may be used to approximate stomate area per unit area of leaf, and thus predict drought tolerance of species (Ashton and Berlyn, 1994). Red oak had a higher stomatal density and SAI than black oak (Ashton and Berlyn, 1994). The authors hypothesized that this may be due to different drought and shade tolerances between species. The SAI suggests that red oak is less drought intolerant compared to black oak (Ashton and Berlyn, 1994). The SAI results are also consistent with light tolerance as black oak had the lowest SAI and is light demanding, whereas red oak had the highest SAI and is shade tolerant (Ashton and Berlyn, 1994).

Oaks are widely viewed as drought tolerant compared to other species due to their anisohydric strategy in which they continue to have high gas exchange and growth in drought conditions at the expense of potential hydraulic failure (Novick et al., 2022). Because of this, the midday leaf water potential of oaks becomes more negative during droughts compared to co-occurring species. Oak stem xylem are therefore more vulnerable to embolism, which makes them just as or more likely to die during drought compared to neighboring species (Novick et al., 2022). It has also been found that oak stomata are less sensitive to increased vapor pressure deficit (VPD) compared to other species as they remain open even when soil moisture decreases and VPD increases (Novick et al., 2022). This gives them a slight immediate advantage as oaks experience smaller reductions in growth during drought than co-occurring neighboring species. This water handling strategy may not be advantageous in the long term as their lack of adaptation

ultimately causes more mortality from drought compared to other species. It is important to note that the baseline mortality for oaks is higher than other species due to their susceptibility to inciting factors such as pests and diseases (Novick et al., 2022). Discrepancy between mortality in oak species also exists as the red oak *Quercus* group were found to be more prone to mortality after drought than non-oak species and white oak groups (Novick et al., 2022).

Although it was not observed in this study, there are advantages to a negative correlation between stomatal size and density. It offers plasticity in water conductance without change in allocation of stomata in the epidermal area of the leaf (Franks et al., 2009). However, the Franks et al. (2009) study was conducted on *Eucalyptus globulus*, an evergreen tree endemic to Australia (Franks et al., 2009). Most drought studies are conducted in tropical environments, so it is probable that little information currently exists on oak species. Very few precipitation manipulation experiments are also conducted in mature forests such as Thompson Farm (Asbjornsen et al., 2018). In the case of the Franks et al. (2009) study, it was conducted on second rotation plantation trees that were replanted in 2006 (Franks et al., 2009). It is possible that these young plantation trees showed a stronger response to the drought treatments than a naturally regenerated, mature forest due to underdeveloped tolerance mechanisms (i.e., acclimation to metabolism at a low water potential) (Polle et al., 2019). Future drought exclusion studies could include a greater sample size, more replicates, and/or more species as leaf anatomy has been shown to be species dependent (Wu et al., 2018).

Conclusion

Due to climate change, northeastern U.S. forests will be subject to more frequent, short-term droughts. It is poorly understood how mesic temperate forests will respond to these droughts. A throughfall removal design was used in this study to research how leaf traits will

adapt to extreme moisture stress at Thompson Farm in Durham, NH. While the results did not support a drought treatment effect, the lack of anatomical change in leaf stomatal size and density suggests that trees at Thompson Farm are potentially resilient to climate change. There was little evidence of long-term stomatal adjustments so perhaps the sampled trees were able to adapt to low water availability using other methods. These could include guard cell signaling, extracting water from outside of the treatment plots via their roots, and altering other leaf traits. A yearly effect was found between all treatments and species, with 2020 values higher than 2021. However, correlation between weather patterns at Thompson Farm and the observed stomatal effects were only present in density and not size so it possible that this result is due to sampling differences.

These findings are only limited to a couple oak species native to northeastern U.S. As such, it is unknown how northeastern forests will respond to drought in general. Previous studies have shown that tree adaptations to drought are species specific, so it is possible that oak species will not follow the expected pattern or that oaks may take a longer time to adapt than the two-year time frame evaluated in this study. In general, oak species are accepted as more drought tolerant than other neighboring species due to high gas exchange and growth, but these traits are also associated with hydraulic failure and thus higher mortality during extreme drought (Novick et al., 2022).

Oak species provide tangible value to northeastern forests including but not limited to high quality timber, water cycle regulation, and providing a keystone forest food resource (i.e., acorns) that many wildlife species rely on (Novick et al., 2022). Understanding how oak species will respond to a threat as pervasive and global as climate change is critical to maintaining these species in future northeastern U.S. forests. This topic is extremely nuanced as it has been shown

that adaptations vary on a species, site, and time scale. Further work is therefore necessary to fully understand the implications of drought on oak species in mesic temperate forests.

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