Divergent Water Use Strategies of Temperate Tree Species Estimated from Continuous Sap Flow Measurements

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ABSTRACT

Due to a changing climate, droughts are becoming more frequent. As such, it is important to understand how trees will respond to droughts since forests play a key role in water and carbon cycling on Earth. Isohydricity is a continuum of tree hydraulic behavior used to describe a tree's water use strategy. Trees with more isohydric tendency will close their stomata in order to avoid excessive water loss through transpiration. However, prolonged stomatal closure during drought might ultimately lead to these trees dying of carbon starvation due to the lack of photosynthesis. Meanwhile, trees with strong anisohydric tendency will leave their stomata open in order to assimilate more carbon, but lose water through transpiration. Anisohydric trees, which may run out of water, are subject to hydraulic failure and subsequent xylem cavitation. Therefore, it is important to understand species-specific response to water stress in order to understand the resilience of a forest ecosystem as a whole. To address this question, sap flow sensors were installed on four different tree species to monitor tree water uptake over the course of a growing season. The sap flow (transpiration) data for each tree was plotted with vapor pressure deficit (approximated using meteorological tower data) in order to quantitatively interpret isohydric or anisohydric tendencies of each tree and tree species across changing seasons and soil moisture conditions. For *Acer rubrum, Quercus alba*, and *Pinus virginiana* species, larger trees were more likely to exhibit isohydric behavior. It was unclear whether *Fagus grandifolia* trees were more likely to exhibit different isohydricity. The species exhibiting isohydric behavior the most was *Pinus virginiana*, followed by *Acer rubrum*. The species exhibiting anisohydric behavior the most was *Quercus alba*, followed by *Fagus grandifolia*. While many factors affect a tree's water use strategy, this study provides an example of how sap flow analysis can be used to classify such strategies.

ACKNOWLEDGEMENTS

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INTRODUCTION

Trees play an important role in the water and carbon cycles on Earth through the processes of transpiration and photosynthesis, respectively. Their regulation of water and carbon allow for precipitation far from oceans and the storage of over 45% of terrestrial carbon (Luo et al., 2016). Trees exchange both water and carbon dioxide through open stomata on their leaves. The ratio of this water exchange to carbon exchange is known as water-use efficiency (Medlyn & De Kauwe, 2013). This ratio is critical for understanding how trees respond to drought conditions, which are becoming more and more frequent around the world, especially in temperate regions (Zhu et al., 2017). Drought conditions have an immense impact on tree physiology and the global ecosystem as a whole (Bhusal et al., 2019). How trees respond to drought can result in radical shifts of forest ecosystem structure and can cause more frequent and severe droughts in the future (Novick et al., 2016). It is therefore critical to understand different water use strategies that a tree can employ.

All trees have to optimize stomatal closure to minimize water loss and maximize carbon gain (Konings & Gentine, 2017). As such, a tree's response to drought conditions can be categorized along a continuum of isohydricity that describes how quickly the tree closes its stomata in response to decreased soil moisture conditions (Yi et al., 2019). Isohydric species decrease stomatal conductance quickly in order to maintain internal water potential and lose less water through transpiration (Skelton et al., 2015). The term isohydric comes from Greek, where "iso" is equal and "hydric" is water; hence isohydric trees maintain equal water potential (Scanlon, 2019). This is contrary to anisohydric ("an" means not in Greek) species, which do not decrease stomatal conductance quickly, and as such have lower internal water potential and lose more water through transpiration (Skelton et al., 2015). As a result of the two water use strategies, isohydric trees are prone to death through carbon starvation (due to limitation of carbon uptake caused by earlier stomata closure), whereas anisohydric trees are prone to death through cavitation (due to interference of water transport) under prolonged and severe drought (McDowell, 2008; Meinzer et al., 2016). Furthermore, because carbon starvation takes a while to kill a tree, long-duration and low-intensity droughts are especially damaging to isohydric species (McDowell, 2008). On the other hand, cavitation occurs rapidly if water potentials become too low. Therefore, anisohydric species tend to die during short-duration, high-intensity droughts (Scanlon, 2019). Long and intense droughts make both isohydric and anisohydric species vulnerable to death (see Figure 1).

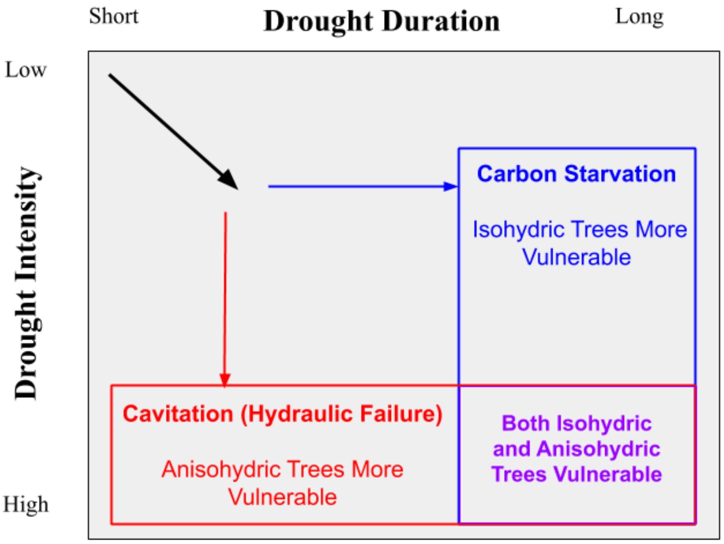

Figure 1. The likely cause of a tree's death during different drought scenarios depends largely on the tree's water use strategy (figure derived from McDowell, 2008).

It is important to note that a tree's water use strategy is not always fixed through time and it is not exclusively linked to the tree's inherent physiology. It can change depending on a variety of environmental factors such as hydraulic conductivity, maximum possible transpiration, soil conductance, and vapor pressure deficit (Hochberg et al., 2018). As such, the same tree species can have a very different water use strategy depending on the current environment in which it is growing. This makes classifying species as isohydric and anisohydric less of a dichotomy and more of a sliding scale, dependent on current environmental conditions (Meinzer et al., 2016).

Accordingly, isohydric and anisohydric status of a tree can be defined using many different quantitative or qualitative techniques (Feng et al., 2019). One such qualitative technique is to plot the sap flow and vapor pressure deficit (VPD) of a tree over time. Sap flow sensors allow for the continuous and automatic measurement of water and sap movement through the woody tissues of the tree located between the cambium and heartwood, known as sapwood (Burgess et al., 2001). Sap flow is a continuous and direct measurement of a tree’s transpiration rate and consequently can be used as an indicator of plant water stress (Nadezhdina, 1999). VPD is a way to measure air humidity. It is an important force of tree water loss through transpiration since dry air (large VPD value) creates a strong natural gradient for water movement from trees to the air (Wollaeger & Runkle, n.d.). Therefore, VPD is an indication of how much trees could transpire if no stomatal regulation occurred. Subsequently, if sap flow for a tree and VPD are plotted over time, a quick decrease in sap flow following an increase in VPD suggests isohydric tendencies (tree quickly closed its stomata), whereas a stable sap flow following an increase in VPD suggests anisohydric tendencies (tree did not quickly close its stomata) (Feng et al., 2019). The disparity between how quickly isohydric and anisohydric trees react to close their stomata during a large VPD is also dependent on soil moisture, where drier conditions should increase the disparity (Yi et al., 2019).

Despite the tenuous definition of isohydricity, attempting to clarify isohydric or anisohydric status of different tree species will become increasingly important as our climate continues to change and droughts become more severe. The purpose of this study is to examine water use strategies of four major temperate tree species as soil moisture conditions change during the course of a growing season in central Virginia.

METHODS

The study site was the Virginia Forest Research Facility (VFRF) in Fluvanna County, Virginia (37°55’22” N, 78°, 16’26” W, 140 m above sea level). The VFRF is part of the Pace/Steger teaching and research site owned by the University of Virginia Alumni Association and operated by the University of Virginia. It is characterized by a humid subtropical climate with a mean annual precipitation of 1092 mm and a mean annual temperature of 14° C. The field site contains a secondary growth, mixed deciduous forest in the Piedmont of central Virginia. It also has a 40-m meteorological tower for measuring trace gas exchanges. The data used was collected from three main sources: sap flow measurements (for transpiration), meteorological flux tower measurements (for vapor pressure deficit), and soil moisture measurements (for indication of drought conditions).

Between October 2018 and March 2019, twenty-two sap flow sensors (HRM30 variant, ICT International Pty Ltd., Australia) were installed at the site. Sensors were installed in trees surrounding the site’s meteorological tower (see Figure 2). The sap flow sensors require

Figure 2. An image from the installation of 22 sap flow sensors on 22 different trees (4 different species) surrounding the Pace flux tower.

electrical power, which limited the range of trees in which sap flow sensors could be installed. A variety of deciduous species and one coniferous species was selected. Red maple (*Acer rubrum*), white oak (*Quercus alba*), American beech (*Fagus grandifolia*), and Virginia pine (*Pinus virginiana*) were chosen for this study. For each tree, the diameter at breast height (DBH) was recorded when the sensor was installed (see Table 1).

The sap flow sensors utilize the heat ratio method (HRM), which is a variation of the compensation heat pulse method (CHPM) that is often used in older instruments. The HRM method is able to detect direction of sap flow and can measure low rates of flow accurately (Burgess et al., 2001). Both methods, however, work to measure sap flow using the same principle of heat conduction. A heater probe is inserted into the sapwood of the tree, along with two temperature probes. As heat is released by the heater probe, it is detected by the temperature probes (one upstream and one downstream) a certain time (t) interval later. The CHPM method uses a simple rate equation,

$$\mathrm{V_h} = \frac{\mathrm{x_1} + \mathrm{x_2}}{2\mathrm{t}}\, 3600 \tag{1}$$

where V_h is the heat pulse velocity (cm/h), and x_1 and x_2 are the distances (cm) between the heater and downstream and upstream temperature probes, respectively. The HRM method, on the other hand, measures the ratio of the increase in temperature from the heater using the equation

$$\mathrm{V_h} = \frac{\mathrm{k}}{\mathrm{x}} \ln\left(\frac{\mathrm{v_1}}{\mathrm{v_2}}\right) 3600 \tag{2}$$

where x is the distance (cm) between the heater and either temperature probe, v1 and v2 are increases in temperature (°C) from the initial temperatures at equidistant points (at distance x) downstream and upstream from the heater, and k is thermal diffusivity of fresh wood (assume

Table 1. DBH Values and Associated Sap Flow Sensors for Each Tree Species

Species	DBH (cm)	Sensor Address
Red Maple (AR)	5.5	w
	11.9	2
	17.4	O
	20	s
White Oak (QA)	11.7	S
	14.1	Q
	19.6	g
	22.9	C
	35.7	q
	45.9	a
American Beech (FG)	4.9	Y
	14.9	c
	18.2	E
	24.4	A
	30.1	U
	30.1	k
	37.9	i
Virginia Pine (PV)	10.6	I
	22.5	W
	23.2	K
	31.7	e
	40.5	6

$2.5 * 10^{-3}$ cm^2/s) (Burgess et al., 2001). Effectively, sap flow sensors work by using the conduction of heat as a representation of the rate of sap moving through the sapwood of a tree. Sap velocity was recorded continuously for all trees by the datalogger (SL5 Smart Logger) every 10 minutes. Diurnal curves of sap flow become evident as data is collected over many days (see Figure 3).

Tree cores were sampled for every tree in order to accurately determine the sapwood area. This ensures that each temperature probe was inserted to the required depth, with one thermistor in the inner sapwood and the second in the outer sapwood (see Figure 4). Measuring inner and outer sapwood lengths, and thus estimating sapwood area, also allows for the calculation of total volumetric sap flow (Phillips et al., 1996). The insertion of the heater and temperature probes decrease the flow of sap in the xylem by damaging conducting

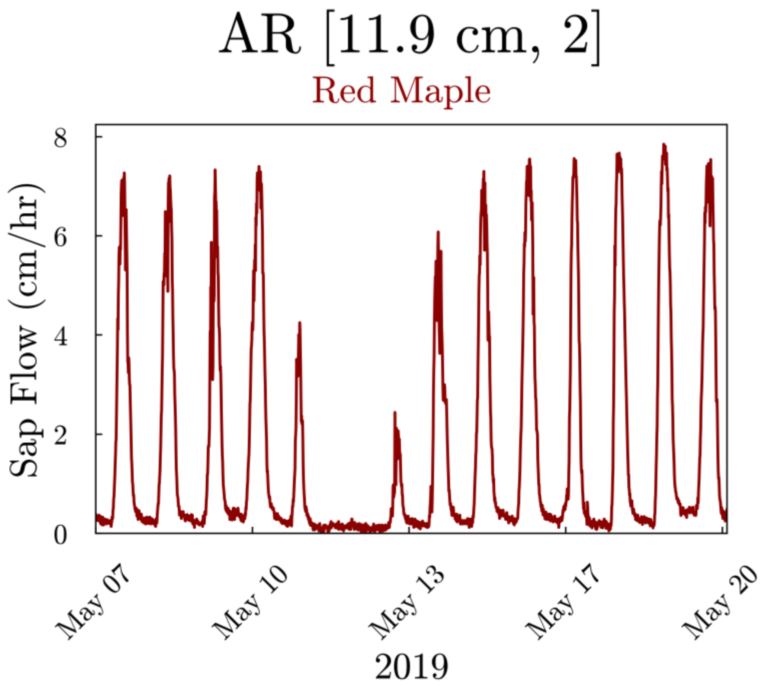

Figure 3. An example of a diurnal curve of sap flow (cm/hr) plotted over time (data is collected every 10 minutes). Diurnal patterns are very clear in this data, where water uptake increases during the day and drops back down at night. *Note.* AR stands for *Acer rubrum* (red maple), 11.9 cm is the DBH, and 2 is the sap flow sensor address (see Table 1 for species abbreviations). All subsequent figures will follow this notation convention.

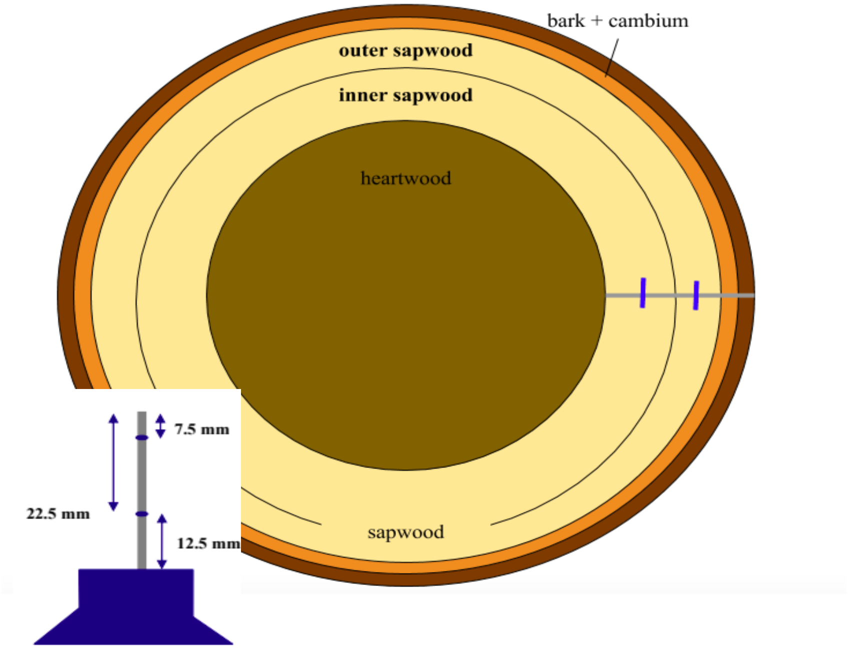

Figure 4. A cross section of a tree trunk showing the various layers. The inset image shows a sap flow sensor probe, with the two thermistors marked in dark blue. The sensor is also drawn over the tree cross section as an example of how the proper sensor depth is required for the thermistors to be within the sapwood.

vessels that are replaced by nonconducting wood as the tree heals itself (Burgess et al., 2001). Accordingly, wounding corrections were made to the sap flow measurements

$$V_c = aV_h + bV_h^2 + cV_h^3 \tag{3}$$

where V_c is the corrected heat pulse velocity (cm/hr), and a, b, c, are wounding coefficients (for wound widths of 1.35 mm for each probe) (Burgess et al., 2001). These corrections were made to the data automatically by the datalogger.

In order to determine the vapor pressure deficit (VPD), measurements were taken on the meteorological flux tower every 30 minutes. VPD could be found using the equation

$$\mathrm{VPD} = e_s - e_a \tag{4}$$

where e_s is saturation vapor pressure (kPa) and e_a is vapor pressure of air (kPa). Saturation vapor pressure (e_s) is found as a function of temperature (known as the Clausius–Clapeyron relation), which can be approximated as

$$e_s = 610.7 * 10^{\left(\frac{7.5 * T_a}{237.3 + T_a}\right)} \tag{5}$$

where T_a is air temperature (°C) measured by the flux tower (Kučera et al., 2017; National Weather Service, n.d.; Valiantzas, 2006). The vapor pressure of air (e_a) can be found using relative humidity (RH) measured directly by the flux tower in the equation

$$e_a = e_s * \frac{RH}{100} \tag{6}$$

Lastly, in order to determine the soil conditions (dry vs. wet) over the course of the data collection, two soil moisture probes were used in the footprint of the flux tower to measure soil water content, s_w (m^3/m^3). If s_w was less than or equal to the average s_w measured for the growing season of 2019 (May 1-October 31), conditions were considered to be dry. If s_w was greater than the average s_w, conditions were considered to be wet.

Data Analysis

Data was collected for the majority of the growing season in 2019 (May 1-October 31). In order to determine the isohydricity or anisohydricity of each tree species across seasons, the data was analyzed and interpreted using a range of approaches.

First, sap flow and daily max sap flow were analyzed over time in order to determine the effect of seasonality on transpiration for each species and any relation to soil moisture. Next, averaged diurnal curves were plotted to examine any differences in diurnal shapes between tree species and between wet and dry conditions. For each soil condition, the average sap flow rate during every 10-minute interval time period was plotted. For example, the sap flow rate during each wet day at 12:10:00 was averaged and plotted at 12:10:00 on the averaged diurnal curve for wet conditions.

The wet and dry averaged diurnal curves provide a preliminary examination of isohydricity, by visually showcasing the difference between sap flow during wet and dry conditions. Diurnal curves also showcase any unique features that may stand out for some species.

In order to further diagnose isohydric behavior, sap flow for each tree was plotted with VPD measurements in two ways. Analyzing the relationship between sap flow and VPD was key to understanding the isohydricity of a tree. Sap flow and VPD were first plotted together over time to provide a visual indication of how a tree's transpiration rate responds to a changing VPD. The less sap flow and VPD followed one another during dry conditions, the more isohydric a tree was behaving. Isohydric trees choose to close stomata quickly in response to increased VPD in order to decrease transpiration and keep water potential consistent. As a result, the difference between sap flow during dry and wet conditions is large. If max VPD and max sap flow follow each other closely during dry conditions, the more anisohydric a tree was behaving. Anisohydric trees choose not to close stomata regulation in response to increased VPD and instead allow the water potential to change. As a result, the difference between sap flow during dry and wet conditions is minimal.

In order to quantify this, sap flow and VPD were then compared to one another using a linear regression for each tree during wet and dry conditions. While the relationship between sap flow and VPD is not truly linear due to other confounding factors (VPD is just one of many variables that can affect sap flow), it was assumed to be linear during this analysis.

Regression slopes were found for each sensor during dry and wet conditions across the entire growing season. Isohydricity was ultimately determined using the equation

$$\Delta\text{Slope} = \frac{\text{Wet Slope} - \text{Dry Slope}}{\text{Wet Slope}} \tag{7}$$

where ΔSlope is the difference between a tree's regression slope during wet conditions and during dry conditions (normalized). ΔSlope was found for each tree during the growing period.

By quantitatively comparing how much the sap flow and VPD relationship differs between wet and dry conditions (size of ΔSlope), isohydric tendencies can be interpreted (Hochberg et al., 2018; Meinzer et al., 2016; Yi et al., 2017, 2019). If ΔSlope is large, isohydric behavior is occurring since sap flow was not naturally following VPD during dry conditions as much as it was during wet conditions (stomata must be actively closing) (Yi et al., 2019). If ΔSlope is small (near zero), anisohydric behavior is occurring since sap flow was naturally following VPD during both dry and wet conditions (Yi et al., 2019). ΔSlope values were compared within the same tree species across different DBHs in order to observe how isohydric behavior may change with tree size. Average ΔSlope values for each species were also compared to see which species had the greatest isohydric tendencies.

RESULTS

The growing season for 2019 was chosen to be May 1 to October 31. The mean soil water content (s_w) for the growing season of 2019 was 0.35 m_3/m_3. Therefore, data taken when s_w was measured by the soil moisture probes to be at or below 0.35 m_3/m_3 were considered to be dry conditions and data taken when s_w was above 0.35 m_3/m_3 were considered to be wet conditions.

I. Sap Flow Seasonality

The overall trend of decreasing sap flow throughout the growing season was expected (see Figure 5). All species tended to follow the same up and down patterns of maximum daily sap flow across the time period analyzed. Unexpectedly, American beech trees, not Virginia pine trees (the only evergreen species in this study), maintained the highest sap flow throughout the growing season.

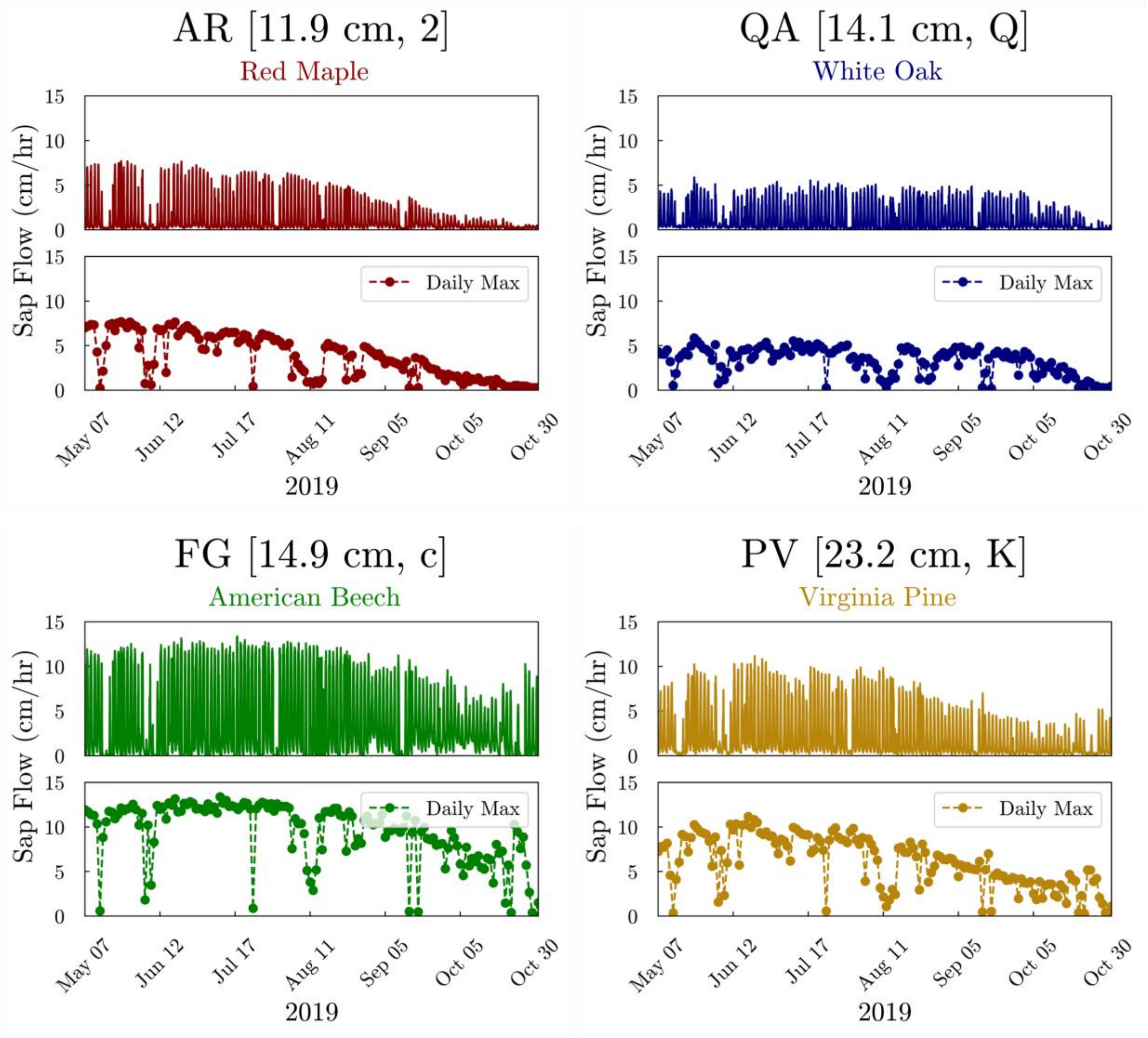

Figure 5. Sap flow (*top*) and daily max sap flow (*bottom*) over time, showcasing species seasonality.

II. Diurnal Patterns of Sap Flow

This largely visual interpretation provides a unique look at how diurnal patterns differ between species and how they differ between wet and dry conditions during the growing season (see Figure 6). All species exhibited the expected bell-shape curve for their diurnal patterns.

American beech had the highest average daily sap flow rate and white oak had the lowest. Within a species, sap flow rates increased with increasing tree DBH.

Sap flow values were all higher during wet conditions than during dry conditions as expected. Red maple had the largest difference in sap flow rate during wet and dry conditions, while white oak experienced almost no difference at all. While the minimal change in white oak's diurnal curve was a possible sign of anisohydric behavior, it was necessary to provide a more quantitative diagnosis using VPD.

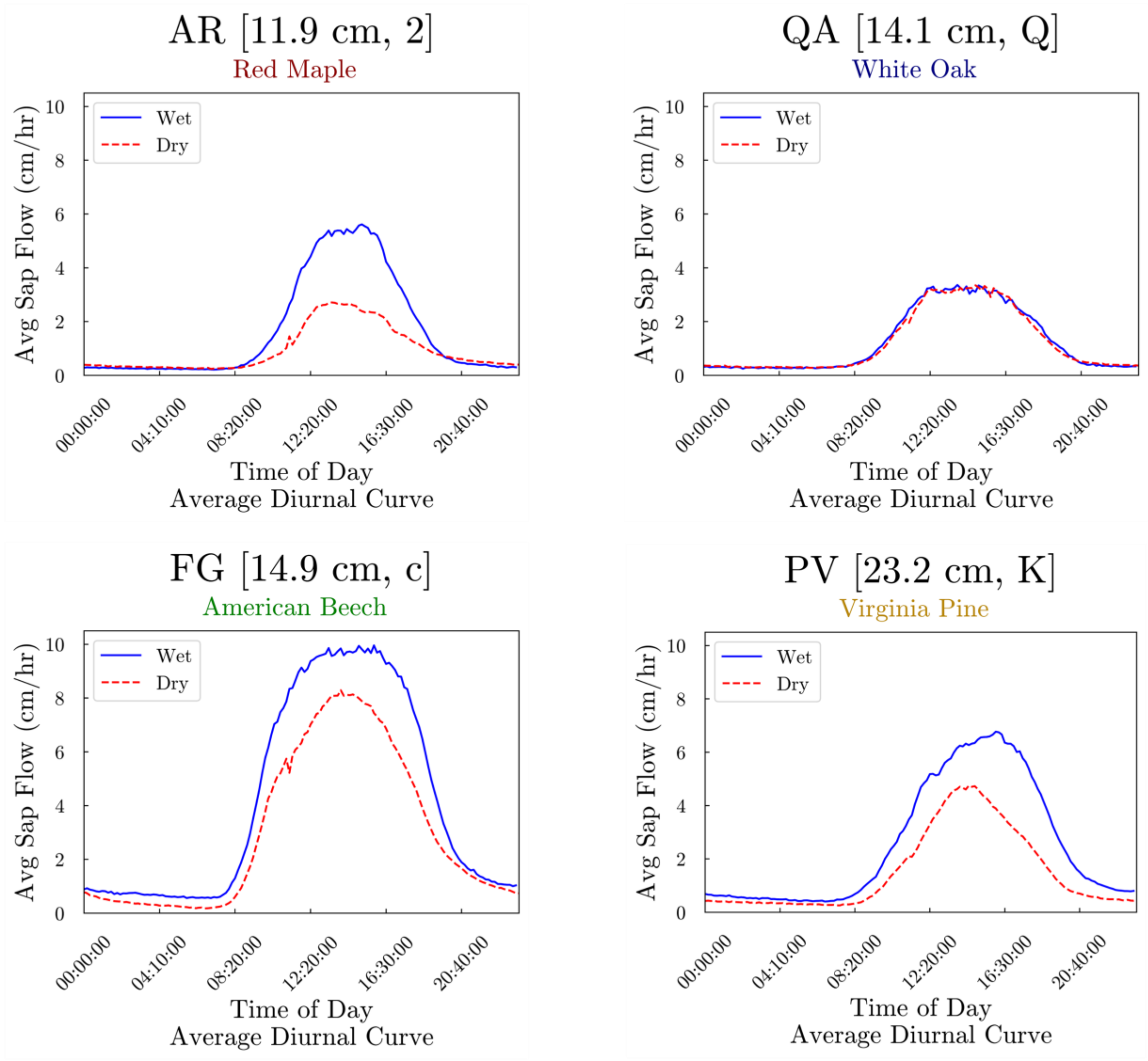

Figure 6. Average diurnal curves during wet and dry conditions.

III. Determining Isohydricity

Plotting the relationships between sap flow and soil moisture and sap flow and VPD produced expected results (see Figure 7). Soil moisture content appeared to have very little effect on sap flow on daily time scales. For all species, soil content would sometimes increase while sap flow would decrease and vice-versa. On the other hand, VPD appeared to have a strong effect on sap flow. For all species, there was a strong pattern of sap flow following VPD, indicating a relationship. The scatter plots and linear regressions of sap flow and VPD provided a clearer sense of this relationship (see Figure 8). All species exhibited an expected positive correlation, returning p-values below the set alpha of 0.05 for the linear regressions.

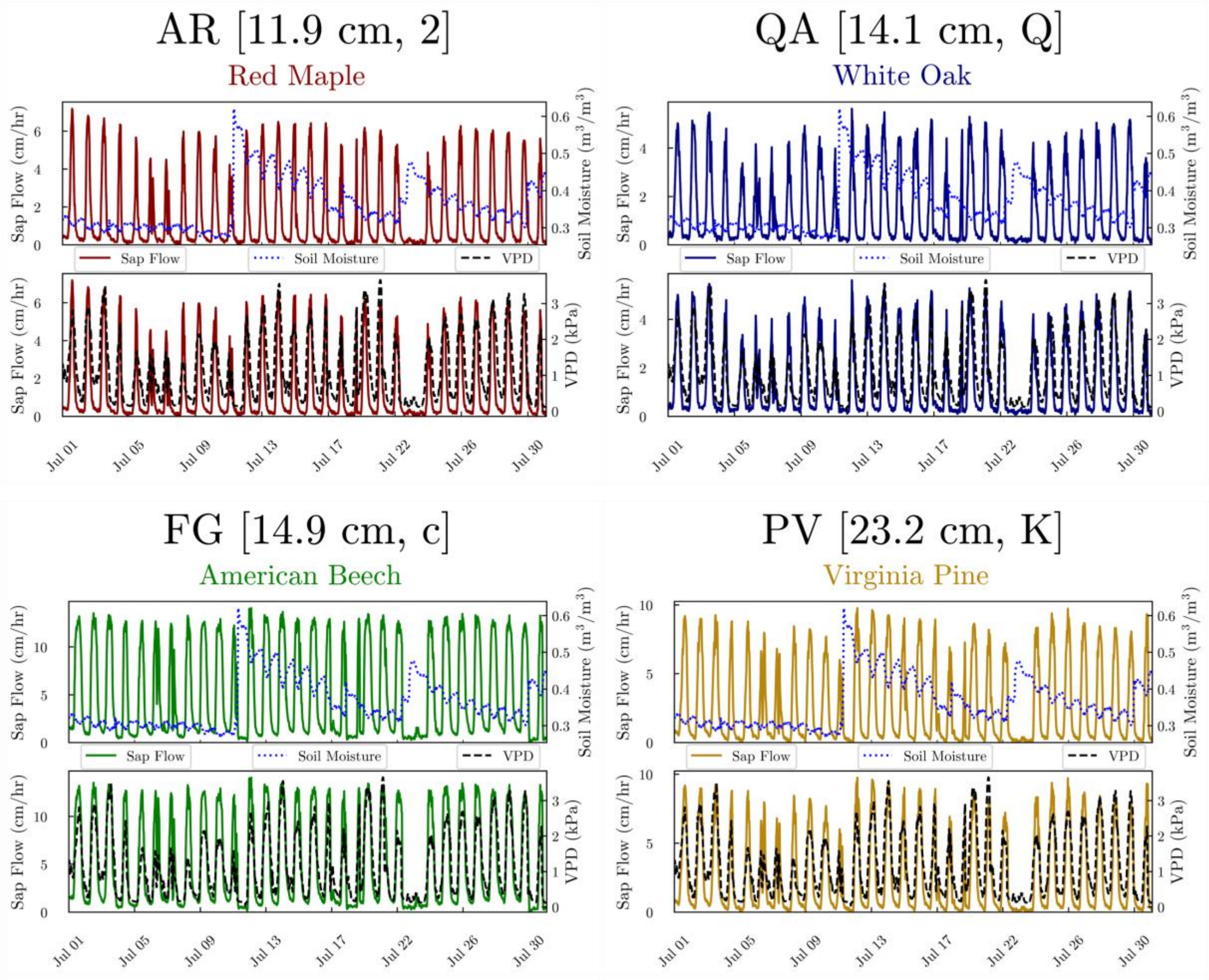

Figure 7. Daily sap flow was not responsive to changing soil moisture (*top*), but was very responsive to changing VPD (*bottom*). This observation was true for all trees and species.

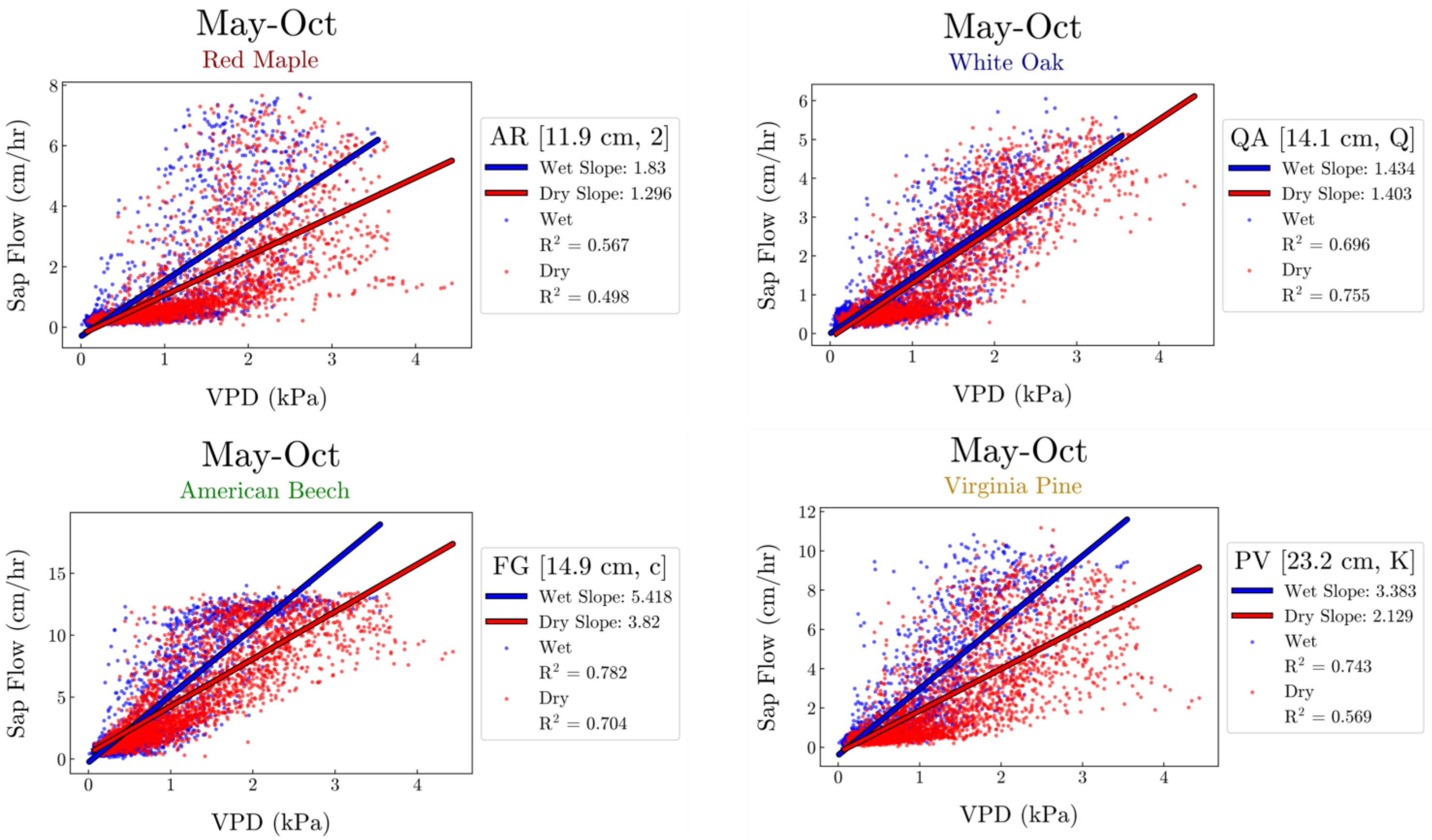

Figure 8. Sap flow and VPD were plotted for each tree using a scatter plot. The data was divided into dry and wet conditions based on soil moisture. For both dry and wet conditions, positive slopes were calculated during the linear regressions. This was true for all trees and species.

For individual species, the slope values during wet and dry conditions, as well as ΔSlope values (wet minus dry), indicated interesting relationships between isohydric behavior and DBH (see Figure 9). Except for American beech, an increase in DBH was associated with an increase in ΔSlope values also increased along increasing DBH, though not dramatically. ΔSlope increased the most along increasing DBH with white oak trees. ΔSlope was relatively stagnant among differently-sized American beech trees.

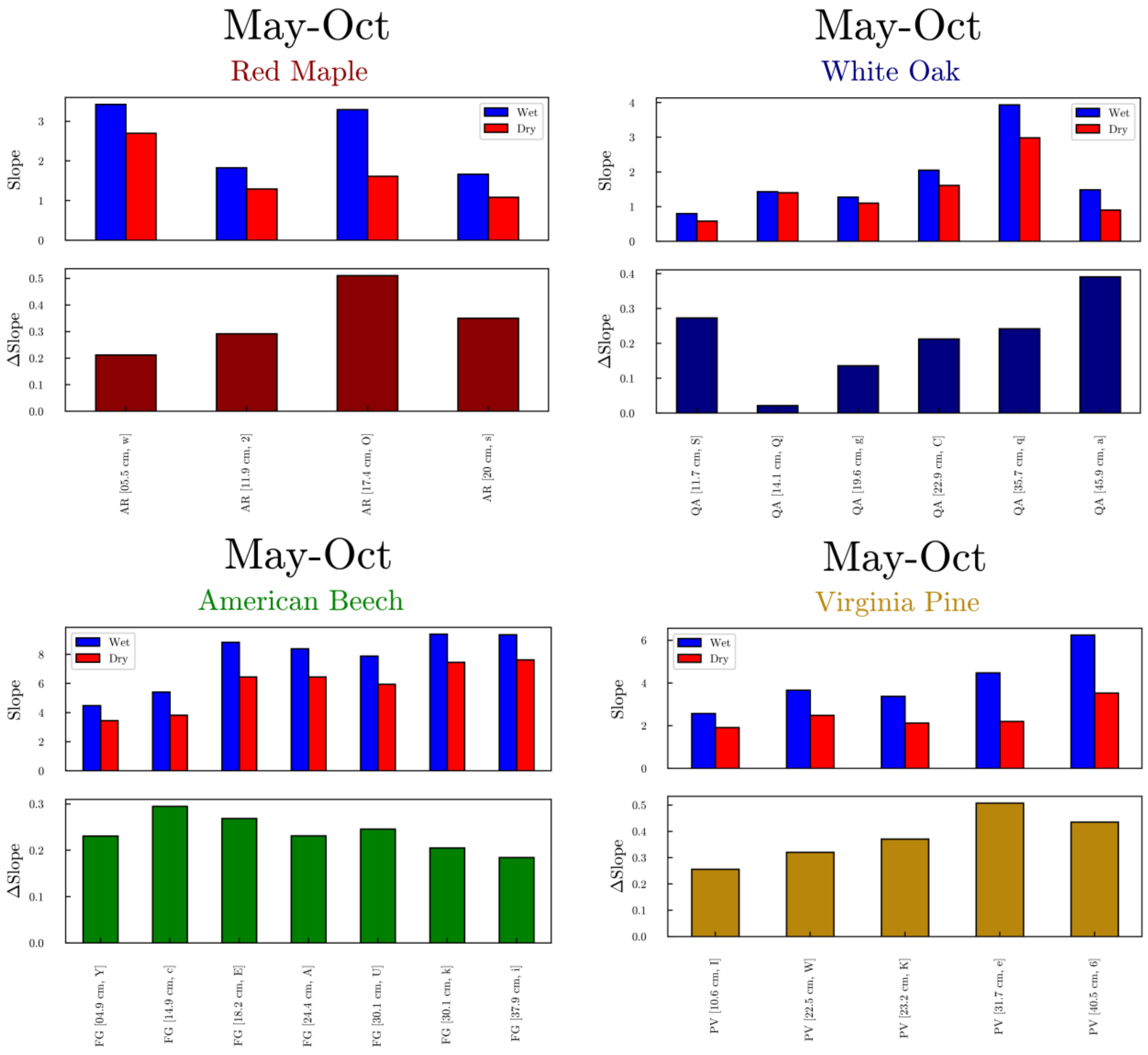

Figure 9. Using the slopes from the linear regressions, differently-sized trees were compared in order to determine isohydric tendencies within species. DBH is increasing along the x-axis. The greater the difference between wet and dry slopes (Wet-Dry, or ΔSlope), the more isohydric the tree behaved.

The species with the largest average ΔSlope value was Virginia pine (see Figure 10). Following closely behind was red maple. White oak had the smallest average ΔSlope value by far, followed by American beech.

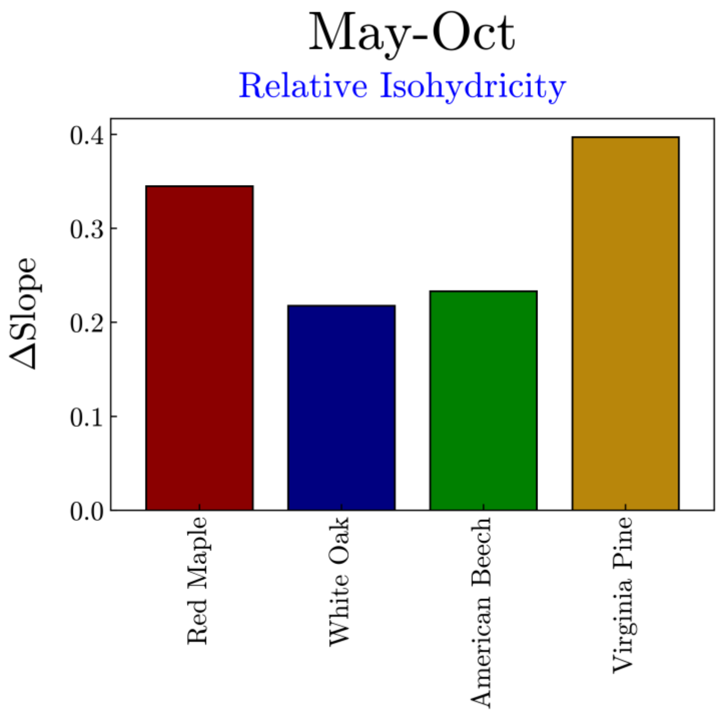

Figure 10. The average ΔSlope values for all species during the entire growing season. The larger the ΔSlope value, the more isohydric the species behaved.

DISCUSSION AND CONCLUSIONS

While the overall trend of decreasing sap flow throughout the growing season was expected, it was surprising that the Virginia pine trees, an evergreen species, decreased in sap flow significantly during the growing season. It was expected that Virginia pine trees would maintain their sap flow at higher levels than the rest of the species. While photosynthesis in pine trees does decline in the late fall months, it does not decline as much as deciduous trees do. Therefore, sap flow should also decrease proportionally at a lesser rate. But American beech trees actually maintained the highest sap flow throughout the growing season. In future work, the dataset should be expanded to include an entire year’s worth of data (January to December). This would allow for better observation of the expected differences in the “green up” and senescence periods of deciduous and evergreen species.

While there were some patterns present of the diurnal curves among the different species of trees, there were really no obvious shapes that differentiate the species. The diurnal curves between trees of the same species were largely consistent, with no obvious deviations observed due to differences in DBH. Red maple, American beech, and Virginia pine appeared to provide the “cleanest” curves within the data, while white oak curves appeared noisier than the other species.

Interestingly, there was evidence of mid-day depressions in the diurnal curves. When leaves get too warm, the stomata naturally close. This leads to a decrease in photosynthesis from less incoming CO_2 and a decrease in transpiration from less outgoing water vapor (Roessler & Monson, 1985). As a result, the rate of sap flow measurably decreases slightly. These mid-day depressions were especially prevalent in the red maple trees.

The inability to observe any unique patterns among species is likely because diurnal curve shape is not solely dependent upon species type. Rather, it depends on many different factors, such as a tree’s hydraulic conductivity, maximum possible transpiration, soil conductance, and VPD, with no easy way to differentiate the multivariate effects (Hochberg et al., 2018). It would be interesting to see if any obvious patterns do occur when other confounding variables could be isolated in a more extensive study.

Soil moisture content appeared to have very little effect on sap flow on daily time scales as compared to VPD. This was evident by the fact that soil content would increase while sap flow would decrease (and vice-versa) for all species. This was expected as soil moisture is a minor factor of how much transpiration occurs, especially on short, daily time scales. However, immediately upon plotting sap flow and VPD, it was evident that these two variables are inexorably linked. For all species, sap flow and VPD followed one another closely. As the growing season progressed, sap flow and VPD followed each other less and less. As photosynthesis rates decline in trees, stomata will close down since less CO_2 is needed. Therefore, less transpiration naturally occurs, regardless of VPD.

In order to determine isohydricity, the strength of the relationship between sap flow and VPD needed to be analyzed during wet and dry periods. The regression slope values during wet conditions were higher than during dry conditions as expected, since all tree species will leave stomata open when not water-stressed, allowing the transpiration sap flow gradient to naturally follow VPD. The key to understanding isohydric behavior, however, was determining how the trees regulate their stomata during dry conditions (i.e. drought). If the regression slope decreased significantly during dry conditions, this suggested that the tree was closing its stomata, preventing sap flow from naturally following VPD. This greater stomatal regulation (greater isohydric behavior) during dry conditions is evident from a larger difference between regression slopes during wet and dry conditions (larger ΔSlope) that was observed with some species.

The bar plots from the sap flow vs. VPD linear regressions provided clearer evidence of isohydric tendencies for the tree species. An increase in DBH was associated with an increase in ΔSlope for all species except American beech. This implied that the larger a red maple, white oak, or Virginia pine was, the more likely it exhibited isohydric behavior. Whereas, the larger an American beech was, the more likely it exhibited anisohydric behavior, though this wasn’t particularly clear. Interestingly, this result held when examining only one month (July) or the entire dataset (May-October).

The species with the largest average ΔSlope values was Virginia pine, with red maple following not far behind. Because their sap flow response was quite different between dry and wet conditions, indicating an active response when conditions became drier (i.e. drought), these species were most likely to exhibit isohydric behavior. White oak and American beech had significantly smaller average ΔSlope values. Therefore, these trees were most likely to exhibit anisohydric behavior since they did not actively change their sap flow response (via stomatal regulation) during dry periods.

Interestingly, all species except white oak had increased tendencies towards their overall water use strategy with increasing DBH. White oak was more anisohydric as a species overall, but the larger a white oak was, the more isohydric it became.

There is a lot of disparity in classifying trees as isohydric or anisohydric, mainly because the definition of these terms is not standardized (Novick et al., 2019). As a result, out of the four tree species being analyzed, only oak has been confirmed multiple times to be anisohydric (Novick et al., 2019; Roman et al., 2015; Scanlon, 2019; Yi et al., 2017, 2019). While this study also found that white oak tends to exhibit anisohydric behavior, a small sample size for each species limits the scope of conclusions that can be drawn. In future work, sensors should be installed on more of these trees, as well as more species such as mockernut hickory and tulip poplar, in order to paint a clearer picture of many species' water use strategies. The limited sample size and time period (data from only a single growing season) of this study also made it difficult to classify species along a more accurate sliding scale of isohydricity.

There remain several unanswered questions about why and how trees develop water use strategies to cope with droughts. While only barely tapping into the potential of sap flow research, the results from this experiment allow for an increased awareness of drought response across different temperate tree species at different times of the year. Continuously bettering our understanding of water use strategies will become important as droughts occur more frequently and forest ecosystem health is challenged by an increasingly changing climate.

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