

The Pennsylvania State University

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**SENSITIVITY OF ANNUAL DIAMETER INCREMENT AND ITS RELATIONSHIP
WITH CLIMATE: A COMPARATIVE ANALYSIS OF FIVE BROADLEAF
DECIDUOUS FOREST TREE SPECIES**

A Thesis in

Forest Resources

by

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ABSTRACT

Climate modifies tree growing environment, potentially impacting their annual diameter growth. Trees of different species may have different diameter growth response to climate because they have different physiological, morphological, genetic and adaptive characteristics. For example, trees from species with a ring-porous xylem structure start diameter growth earlier in the growing season than trees from species with a diffuse porous xylem structure. As a results, climate conditions at different times during the growing cycle may affect differently. In addition, trees with different competitive status in the forest may have differential diameter growth response to climate because they access different levels of resources potentially modified by climate.

This thesis investigates tree diameter growth-climate relationships among five broadleaf deciduous tree species at four mixed hardwood forested sites in Southeastern Pennsylvania. These species are: black walnut (*Juglans nigra* L.), red maple (*Acer rubrum*), tree-of-heaven (*Ailanthus altissima* Mill. Swingle), tulip poplar (*Liriodendron tulipifera* L.) , and white oak (*Quercus alba* L.). I combine dendrochronological and annual/seasonal climate data with statistical analyses and modeling to understand: 1) potential differences in diameter growth sensitivity among the focus species, 2) potential differences in diameter growth sensitivity among trees of different competitive status in red maple and tulip poplar, 3) relationship between diameter growth sensitivity and climate variability, and 4) relationships between growth and climate.

Diffuse-porous red maple and tulip poplar displayed higher diameter growth sensitivity, while ring-porous white oak and tree-of-heaven displayed lower diameter growth sensitivity, and

black walnut displayed intermediate sensitivity. Further study should incorporate more tree species to investigate this relationship. We did not detect differences in diameter growth sensitivity among trees of different competitive statuses in red maple and tulip poplar. The variability of many climate variables was associated with diameter growth sensitivity in tulip poplar, and few associations were detected in black walnut. We used linear mixed effects models and random forests to model relationships between diameter growth, estimated as ring width index, and climate predictors for the current and previous year. Models explained the most variance in ring width index in tulip poplar, white oak, and tree-of-heaven. Models did not explain variation in red maple and explained little variation (2.3%) in black walnut. Previous year climate across seasons and current year climate in the growing season (May-September) appear important to current year growth.

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Chapter 1: Introduction

Annual tree diameter growth has been used as an indicator of the health and productivity of forests and of forests' capacity to provide essential ecosystem services (Gamfeldt et al 2012, Chamagne et al 2017, Xu et al 2017). Diameter growth for a given year is a product of both the environment surrounding the tree and the characteristics of the tree itself (Fritts 1971). The growing environment is modified by intra- and interannual climate (Douglas 1919, Sheppard 2010). Trees of the same species share a combination of morphological, physiological, genetic, reproductive, and/or adaptive characteristics (Gurevitch et al 2002), and thus their annual diameter growth responses to the environment and to climate are likely more similar than to the responses of trees of other species. Comparative studies of diameter growth responses to climate among different species (Pederson et al 2004, Rollinson et al 2016, D'Orangeville 2018) highlight the need to consider species responses separately and to increase understanding of differences across more tree species (e.g., Rollinson et al. 2016), especially in the eastern US, which is characterized by multispecies forests (Braun 1951). In addition to differences among species, tree diameter growth response to climate may also differ based on the competitive status of the tree, and this in turn may interact with species, because of differences in life history strategies and/or occupied niches with distinct annual and seasonal characteristics (Aranda et al 2005, Cavin et al 2013). Interactive effects of climate and competition on tree diameter growth have been studied during extreme events such as late spring frost and drought (i.e., Kramer 1994, D'Amato et al. 2013), and overall (Benito et al. 2008, Rollinson et al. 2016, Leblanc et al. 2020), but to improve projections of future forest dynamics and productivity as climate becomes increasingly volatile, we need to better understand diameter growth and climate relations in

individual trees of different species and different competitive status (McDowell 2020, Rollinson et al 2021).

Differences in diameter growth patterns may be present in trees with different xylem structure (Fritts 1976). Some trees species have xylem with a diffuse porous structure, others have ring porous structure, while yet others have a semi-diffuse porous structure. Ring porous structure is characterized by an earlywood with large distinct xylem vessels formed before or during budburst (García-González et al. 2016, Takahashi et al. 2013). These vessels typically transport water for only one year, and new vessels are grown each year (García-González et al. 2016). The size and structure of these water-efficient vessels have been shown to vary with tree size and age (Perez de lis et al 2018), and some evidence suggests that vessels formed in ring-porous earlywood are responsible for a large proportion of water transport throughout the growing season (García-González et al 2016). This indicates that early spring conditions, when these cells are formed and frost damage is possible, are critically important for these trees' diameter growth. Additionally, previous-year growing season may have increased importance in the formation of earlywood for ring porous species because stored starches and sugars are used to produce a large proportion of their earlywood xylem (Garcia-González et al 2016, Barboroux and Breda 2002). In diffuse-porous species, consistently sized vessels form throughout the season, and unlike ring porous species, these vessels form and lignify as the photosynthetic capacity of leaves increases during their expansion (Takahashi et al 2013), which indicates that conditions later in spring may be more important and that there may be less reliance on previous-year carbohydrate storage. Semi-diffuse porous species form larger vessels in earlywood, though the time-lag between budburst, leaf formation, and diameter growth initiation is unclear (Takahashi and Takahashi 2021).

During the growing season and post-leaf formation, tree radial growth is indeterminate and largely tied to sugars produced during the growing season as well as moisture availability (Fritts 1976). However, the levels and allocation of sugars and starches (also referred to as non-structural carbon) in tree storage organs can play a role in day-to-day metabolic activity as well (Furze et al 2020). These storage mechanisms retain starch reserves from previous growing years and can be used to supplement tree metabolism during the growing season when recent sugars are unavailable (Loescher et al 1990, Richardson et al 2013). A study in *Acer rubrum* (red maple) showed that vigorous trees store more than less vigorous ones, and nonstructural carbon stored in a given year is consistently present in the following years' growth (Carbone et al 2014). Additionally, overall nonstructural carbon storage varies between tree species and wood porosity, with ring porous trees storing more compared to diffuse porous trees (Furze et al 2018, Furze et al 2020).

The beginning of diameter growth very early in the growing season, especially in ring-porous species, and tree storage dynamics highlight the potential importance of carryover effects in the size of ring width increment from one year to another and indicate that previous year climate conditions may be as relevant as climate conditions when diameter growth is occurring. Other year-to-year carry-over effects on diameter growth can occur during masting events and during drought periods (Lloret et al 2011, Hacket-Pain et al 2015). Masting events are years where trees of a given species produce large quantities of seed. While the possible explanations for the life history strategies for these masting years is debated (Gurevitch et al 2006), a departure in diameter growth from average growth has been detected in years with masting events, and these years have been linked to previous growing seasons with warm temperatures in European beech (*Fagus sylvatica*) (Hacket-Pain et al 2015). This departure appears to be due to a

shift in nutrient allocation from the formation of radial cells to increased formation in reproductive structures (flowers, seeds). Another carry-over effect is related to water stress. Water stress impedes metabolic functions such as cell division, leaf function, and nutrient transport. Water stress can lead to embolism in xylem cells and is often caused by drought. Effects from drought and water stress on growth can carry over for greater than one year and response to drought effects vary between species, tree size, and in stands under different silvicultural treatments (Lloret et al 2011, D'Amato et al 2013, Keyser and Brown 2016).

Other factors that affect annual diameter growth include inter-tree competition, age, and size. A complex forest structure comprising trees of different competitive status may be a good indicator of ecosystem resilience, but at an individual level, trees access a limited pool of light, water, and soil resources. Trees in dominant crown positions have greater access to resources due to their size and rooting depth (Looney et al 2016), but over time may grow slower than in their youth because they require more resources to maintain their size and competitive status (Fritts 1976, Peters et al 2015). Trees in lower canopy positions can be strained for light and nutrient resources and have reduced growth relative to their taller competitors but have been shown to be shielded from variable climate by their competitors possibly due to a more stable microclimate in the understory (Martin-Benito et al. 2008). However, Rollinson et al. (2021) found reduced diameter growth in understory trees relative to overstory ones in four northeastern tree species under warmer temperatures. Additionally, in three of the four species studied by Rollinson et al. (2021) (*Quercus rubra*, *Acer rubrum*, *Tsuga canadensis*, *Fagus grandifolia*), diameter growth in overstory trees was sensitive to vapor pressure deficit, while growth in understory trees was not. It is important to disentangle how competition level modifies diameter growth-climate relationships given differences in microclimate in the lower canopy and the resources that are

accessible to different trees. Disentangling these relationships will allow us to better quantify the growth and productivity across forests with different growing conditions and under a changing climate (Rollinson et al. 2021).

In this study we focus on and compare the annual diameter growth - climate relationships of five broadleaf deciduous species of eastern North America forests: black walnut (*Juglans nigra* L.), red maple (*Acer rubrum* L.), white oak (*Quercus alba* L.), tree-of-heaven (*Ailanthus altissima* Mill. Swingle), and tulip poplar (*Liriodendron tulipifera* L.). These species were selected to capture a diversity of biological and ecological traits including differences in xylem anatomy (Table 1.1).

Table 1.1. Species characteristics (adapted from Burns 1990 and Fischer 1987).

	Black Walnut	Red Maple	Tree-of-heaven	White Oak	Tulip Poplar
Shade Tolerance	Intolerant	Tolerant	Intolerant	Moderate	Intolerant
Native	Yes	Yes	No	Yes	Yes
Wood Type	Semi-diffuse porous	Diffuse-porous	Ring-porous	Ring-porous	Diffuse-porous
Latitude of native range	30-40°N	25-50°N	22-34°N	30-45°N	30-40°N
Successional Stage	Mid	Mid	Early	Mid-Late	Early

A few important characteristics related to these species responses to climate follows. Black walnut and other members of genus *Juglans* are very susceptible to frost injury during spring freezing and thawing cycles. In fact, this is a factor limiting the northern range of its

distribution (Gauthier and Jacobs 2011). This may translate into a high sensitivity to spring climate conditions and less diameter growth in years with more variable spring temperatures.

Red maple has, in the past century, become ubiquitous to forest types across the east coast and midwestern US, co-occurring with a multitude of tree species. Red maple can exhibit a variety of forms and canopy positions based on its growing environment and soil moisture conditions (Abrams 1998). Its ability to thrive under moderate to poor conditions is a driver of its widespread abundance (Abrams 2003). Tolerance of diverse growing conditions may mean that red maple is tolerant to a variety of climate conditions as well compared to other species it is commonly associated with. In a 2016 study, Rollinson and others found increases in red maple diameter growth as annual temperature increased, and this increase was dependent on precipitation levels in that year; years with minimal precipitation and high temperature had lower growth rates than years with high temperature and high precipitation (Rollinson 2014, Rollinson et al 2016).

White oak is found in a similar range to that of red maple, though in the past its dominance in forests benefitted from additional growing space (both in light and soil conditions) provided by low-mid severity fire damaging or killing its competitors (Abrams 2003, Thompson et al 2013). White oak growth has been previously shown to be both slow and associated with moisture balance during the early growing season but is moderately drought-tolerant during the growing season (Abrams 2003, Tardif et al 2006).

Tree-of-heaven is a non-native shade intolerant tree whose success against native competitors in both the US and worldwide could be due to its drought resistance through strong stomatal closure mechanisms and root water conductance reduction when soil moisture conditions are suboptimal (Trifilio et al 2004). Tree-of-heaven is an important species of interest

in the eastern US because it is a known host of the spotted lanternfly (*Lycorma delictula*), which is a newly introduced non-native leafhopper that could net substantial losses in agricultural production in the eastern US if it is not appropriately managed (Harper et al 2019). Tree-of-heaven is both fast-growing and spreads prolifically, especially in previously disturbed sites (Sladonja and Sušek 2015). It is important to learn more about its growth-climate relations compared to native trees to best manage it.

In contrast, tulip poplar is a shade intolerant that grows quickly when found on mesic sites (McConathy and McLaughlin 1978) and is sensitive to drought and frost (Leblanc 2020). As a result, climate during spring when trees are susceptible to frost, and summer when they are susceptible to drought may be especially important to tulip poplar diameter growth.

A tree's annual diameter increment is sensitive when it varies greatly from one year to the next and is insensitive when it does not (Fritts 1971). In this study we estimate a tree's sensitivity in annual diameter growth by calculating the standard deviation or the coefficient of variation of the ring width indices (RWI) for a given tree and period of time. RWIs are ring widths that have been detrended to remove age and stand dynamics related growth patterns (Cook 1985). Using RWIs, we quantify sensitivity in annual diameter growth without prevailing trends such as size or autocorrelation caused by a short-term disturbance event. This way, high sensitivity in an individual is not overwhelmingly caused by, for example, a canopy gap opening at age 30. We hypothesize that trees of different species and of different competitive status have different sensitivity in annual diameter growth. Furthermore, we hypothesize that tree species differ in their diameter growth-climate relationships. In this research, we aim to answer the following questions:

1. Are there differences in sensitivity of annual diameter growth (measured through ring width index) of individual trees across tree species?
2. Does the competitive status of a tree affect its sensitivity of annual diameter growth?
3. What is the relationship between annual diameter growth sensitivity and climate variability across species?
4. What are the relationships between annual diameter growth and climate in different species?

Answers to these questions are important to our understanding of tree growth in species with different life history strategies and physiology. A better understanding of these growth-climate relationships can inform potential tree range dynamics under climate change and benefit future adaptive management. To address these questions, we sampled the five species focus of this study across four sites in southeastern Pennsylvania. For each we quantify and comparatively assess past annual diameter growth sensitivity via dendrochronological methods, compare the variability in annual growth with temporal climate variability, and model growth relationships with climate at the species-level using a variety of statistical modelling techniques.

Chapter 2: Methods

Study Sites

We selected four mixed hardwood forest sites in southeastern Pennsylvania (Figure 2.1): 1) Musser Scout Reservation (“M” hereafter) of the Boy Scouts of America, 2) Texter Mountain Preserve (“T” hereafter) of the Lancaster Conservancy, 3) Crow’s Nest Preserve (“CN” hereafter) of the Natural Lands, and 4) Blue Marsh National Recreation Area (“BM” hereafter) of the US Army Corp of Engineers. These sites represent a sample of mature mixed-hardwood forests; their main characteristics are highlighted in Tables 2.1 and 2.2, and their geographic location is presented in Figure 2.1.

Table 2.1. Mean basal area per acre and mean trees per acre with corresponding 95% confidence intervals (in parenthesis) at each of the study sites.

	Total	<i>Carya/Quercus</i> spp.	<i>Acer rubrum</i>	<i>Liriodendron tulipifera</i>
	Basal Area (ft ² /ac)			
CN	123.9 (94.0-153.8)	28.8 (8.5-49.1)	20.4 (7.3-33.4)	35.8 (14.3-57.4)
M	119.3 (99.9-138.8)	16.9 (2.9-30.8)	7.5 (0.1-14.9)	45.8 (21.2-70.5)
T	89.4 (67.3-111.6)	21.1 (3.2-39.0)	2.4 (0.5-4.2)	26.1 (3.3-48.9)
BM	87.9 (51.9-123.9)	41.8 (1.4-82.2)	1.3 (0-2.7)	4.8 (0-12.3)
	Trees per acre			
CN	117 (92-143)	17 (7-29)	38 (19-57)	27 (13-41)
M	118 (97-139)	13 (3-22)	13 (0-28)	26 (6-46)
T	91 (69-114)	8 (2-14)	6 (2-10)	27 (4-50)
BM	112 (72-153)	30 (5-55)	5 (0-10)	2 (0-4)

Table 2.2. Environmental characteristics of the study sites (sources: Wang et al 2016 and Fortner et al 2006).

	Mean annual temperature, °C	Mean annual precipitation, mm	Elevation, ft	Soil type
CN	11.2	1166	499	Silt loam
M	11.4	1193	341	Silt loam, gravelly silt loam
T	10.4	1205	958	Stony silt loam
BM	11.0	1142	370	Channery silt loam, channery loam

Field data collection

At each site, we delineated 10-acre sampling areas (Figure 2.2). Within these areas, we established 10 fixed-area plots 0.124 acres (500 m²) in size using systematic sampling (Figure 2.2). Within plots, we obtained tree cores for all trees ≥ 5 inches in diameter at breast height (DBH, measured at 4.5 ft from the ground), using Swedish-type increment borers (Maeglin 1979). We collected one core per tree at 4.5ft on the north face of trees, except where tree defect or damage prevented cores from being properly collected. On trees with damage or defect on the north face, we used the closest available face. We sampled cores during late September of 2019 at CN and M, and during early October of 2020 at BM and T. In addition, at the M and CN sites we established two transects (one in each site) to increase the number of red maple trees in the sample, and we identified 2 additional black walnut groves (one in each site) to increase the number of black walnut trees in the sample. Both transects and groves were located near each site's 10-acre mixed-hardwood forest area. In each transect, we identified 10 additional red maple trees at regular intervals for a total of 20 additional red maple trees. In each grove, we identified five black walnut trees for a total of 10 additional trees. At Blue Marsh we identified

an additional area where we collected cores from nine additional red maple trees, and two areas where we collected cores from 6 additional tree-of-heaven trees (Table 2.1). For each tree sampled, we recorded DBH and crown class. Crown classes followed Helms (1998, description in Appendix B) and were: dominant, codominant, intermediate, or overtopped. These classes were later grouped into trees that had dominant or codominant crowns (DCD class hereafter), and trees that had intermediate or overtopped crowns (IO class hereafter). We also recorded height to the tree crown base and total tree height to calculate crown ratio, except at sites where interference from vines and understory vegetation did not allow us to accurately take these measurements.

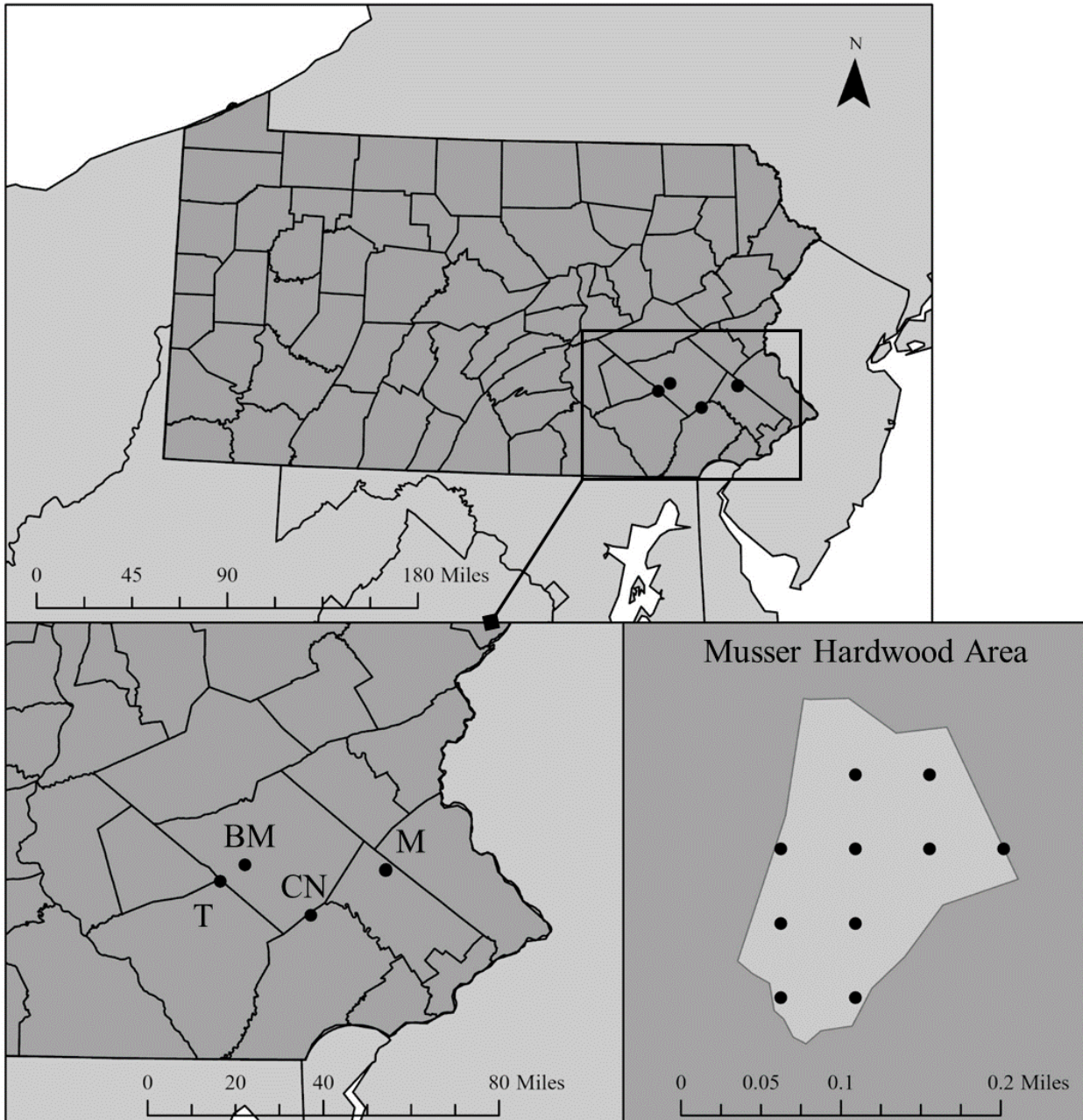


Figure 2.1. Site locations in southeastern Pennsylvania (upper and lower left frames) and an example of plot locations in a 10-acre mixed-hardwood forest area following systematic sampling (lower right frame).

Table 2.3. Summary of number of trees by sampling locations at each study site.

	Mixed-hardwood Area	Red Maple Transect	Black Walnut Transect	Tree-of-heaven Area
CN	60	10	5	
M	36	10	4	
T	25			
BM	17	9		6

Dendrochronological Methods

Tree cores from the four sites were dried for a week or more, then oriented, glued, and progressively sanded using a belt sander and sandpaper in cross-section of each tree. Afterwards tree cores were scanned using a 2400 dots per inch (dpi) scanner (Epson America Inc n.d.). We measured annual ring increments in tree cores using a combination of two methods. Using the scans, we measured rings using Cdendro and Coorecorder software (Larsson 2017). We then validated our measurements using a variable magnification stereo microscope (Amscope n.d.) and Velmex measurement system (Velmex Inc n.d.) by selecting a subset of tree cores from each species, measuring them under the microscope and comparing with measurements made on the scans. Coorecorder measures within 1/100th of a millimeter, while the Velmex measurement system measures within 1/1000th of a millimeter (or 1 μm). Cores with fainter rings were measured directly and only using a microscope and Velmex measurement system. We removed cores from our analysis when we could not ensure that all rings were formed in annual increments. Cores collected and measured but not included in this analysis had prevalent false rings, were warped, or in diffuse porous species, some rings did not display distinct boundaries between latewood – earlywood in consecutive years. Attempts to crossdate cores or portions of cores with these characteristics were unsuccessful.

We used both visual and statistical crossdating with the R package `dplR` to ensure that measured rings were formed in the correct year (Bunn 2010, R Core Team 2021). Ring porous species statistically crossdated well, while diffuse-porous species did not (Appendix A). To supplement statistical crossdating, we identified marker years that were present in a majority of trees within a species at a site and checked trees that did not align with marker years.

We used detrending to remove long growth trends in tree ring series such as the age/size relationship and short growth trends such as rapid changes in growing environment to produce individual RWIs for each year of growth (Galvan et al 2014, Primicia et al 2015). The tree-level RWIs were then used to calculate response variables in all analyses. A summary of the final sample used in this study is presented in Table 2.3. To detrend we used a cubic spline with a frequency response of one half and a frequency cutoff $2/3$ times the length of the ring width series. When the cubic spline did not remove the prevailing trends in ring width series, we used the “Friedman super smoother” method in `dplR` (Bunn 2010). Of the 182 tree cores used in this analysis, 16 cores were detrended using Friedman super smoother, and 166 using the cubic spline method.

Table 2.4. Summary statistics of tree cores sampled by species. * Number of trees by crown class: CDC = dominant/codominant, IO = intermediate/overtopped crown classes.

Species	No. Trees	Mean No. Rings/tree	SD No. Rings/tree	Mean DBH (in)	No. trees per crown class (DCD/IO)*
Black Walnut	22	37	19	13.5	18/4
Red Maple	67	54	17	10.5	43/24
Tree-of-Heaven	13	25	9	9.1	9/4
White Oak	21	101	10	19.0	20/1
Tulip Poplar	59	61	32	15.9	45/14

Climate Data

For each of the study sites, we obtained annual and seasonal climate variables for the period 1901 to 2019 from the gridded climate data product ClimateNA version 6.40 (Wang et al 2016). ClimateNA uses PRISM and weather station data in combination with elevation (Daly et al 2008) to create datasets that balance accuracy and high resolution. We selected a sample of the available directly calculated and derived variables based on their biological relevance (Table 2.4).

Table 2.5. Annual and seasonal climate variables from ClimateNA (Wang 2016) used this study.

Temperature	Precipitation	Moisture balance
Annual		
<ul style="list-style-type: none"> • Mean Annual Temperature, °C (MAT) • Mean Warmest Month Temperature, °C (MWMT) • Mean Coldest Month Temperature, °C (MCMT) • Difference between MWMT and MCMT (TD) • Degree-days below 0°C (DD0) • Degree-days above 5°C (DD5) • Degree-days below 18°C (DD_18) • Degree-days above 18°C (DD18) • Length Frost-free period, number of days (FFP) • Beginning of Frost-free Period, Julian date (bFFP) • End of Frost-free period, Julian date (eFFP) • Degree-days greater than 10 °C and below 40 °C (DD1040) 	<ul style="list-style-type: none"> • Mean Annual Precipitation, mm (MAP) • May to September Precipitation, mm (MSP) • Precipitation as Snow, mm (PAS) 	<ul style="list-style-type: none"> • Hargreaves Reference Evaporation, mm (eREF) • Climate Moisture Index, mm (CMI) • Annual Heat-moisture Index (AHM) • Summer Heat-moisture index (SHM) • Average Relative Humidity, % (RH)
Seasonal (Spring = _sp, Summer = _sm, Autumn = _at, Winter = _wt)		
<ul style="list-style-type: none"> • Mean Seasonal Temperature, °C (Tave_xx) 	<ul style="list-style-type: none"> • Total Seasonal Precipitation, mm (PPT_xx) 	<ul style="list-style-type: none"> • Seasonal Climate Moisture Index, mm (CMI_xx) • Seasonal Average Relative Humidity (RH_xx)

Statistical Analysis

Comparison of RWI sensitivity among species

For all analyses we use the RWI of individual trees within species as an estimate of the annual diameter growth (although we do not multiply it by two). This methodology is distinct from dendrochronological studies that average chronologies over some space or across trees with a given set of characteristics (Briffa and Melvin 2011). Averaging tree chronologies mutes growth patterns in individual trees and emphasizes the patterns that are present in most trees or in trees with large growth relative to the group being summarized (Primicia et al 2015). Methods using averages may emphasize an underlying climate signal found in some trees in a sample against that found in trees with an uncommon size or competitive characteristic (Peters et al 2015).

To estimate the sensitivity in RWI, we calculated the coefficient of variation (CV) of RWI for each tree. We utilized RWI from 1989-2019 in all species (past 30 years) because the number of rings per tree measured varied widely across the species (Table 2.2), and this recent period ensured an overlapping period for all trees and species. In addition, information in older rings may not be directly comparable to newer ones even once detrended if their growing environment and climate was drastically different (Breinen et al 2017). To compare the sensitivity in RWI among species (research question 1), we tested the difference in mean CV of RWI between the five tree species, using a two-way ANOVA ($\alpha = 0.1$) accounting for species and site with the hypotheses:

$$H_0: \mu_1 = \mu_2 = \mu_3 = \mu_4 = \mu_5$$

H_a : at least one population mean CV is not equal

We used Tukey's Honestly Significant Difference test (HSD) to identify which species differ in their CV of RWI if the alternative hypothesis was chosen. To address question 2 and test differences in sensitivity between trees of different competitive status, we used two of the five species, red maple, and tulip poplar, because the other species had a small number of intermediate or suppressed trees (Table 2.1). These species differ in competitive strategies; red maple is a shade-tolerant generalist that can take many forms and hold different canopy positions, and tulip poplar is shade intolerant and regarded as highly competitive when site conditions are ideal (Burns et al 1990, Abrams 2003). For each of these species, we tested the difference in sensitivity (CV of RWI) between trees with crowns in the upper canopy (DCD class) against those with crowns forming the lower canopy (IO class) (Helms 1998). We tested differences using a Welch's t-test, which accounts for unequal sample sizes.

Relationship between RWI sensitivity and temporal climate variability

To address question 3, and to evaluate potential associations between RWI sensitivity and climate variability, we fit linear models of the standard deviation of RWI as a function of the standard deviation of a climate variable and site, doing this for all climate variables in Table 2.3. We graphically summarized all models where climate variables had a slope significantly different from zero at $\alpha = 0.1$.

Individual Tree Modelling

To model relationships between tree RWI and climate (research question 4) we used two modeling approaches: 1) mixed effects linear models, and 2) random forests, using tree RWI as the response variable and current and previous year climate variables as predictors. We fitted models using all available RWIs, and models using only data for the 1989-2019 period. To select

climate variables to include as predictors in each species model, we used a two-step correlation analysis: 1) we evaluated correlations between RWI and climate variables, 2) we evaluated correlations between climate variables. In step one, we selected climate variables with a Spearman correlation coefficient (r_s) $\geq |0.05|$ with RWI across all trees (independent of site), or with an $r_s \geq |0.05|$ in at least 75% sites that had at least 2 trees of the species under consideration. In step two, we compared r_s among the selected climate variables. If climate variables were correlated among themselves with an $r_s \geq 0.5$, we retained the one that had the highest r_s with RWI. Using this methodology, we attempted to maximize the amount of information potentially explained by climate variables while avoiding multicollinearity and potential overfitting. In both mixed-effects linear and random forests models, we tested site, DBH, and crown class as covariates. In the linear mixed effects models, we tested site, plot, and tree as random effects (affecting the intercept), when appropriate, using the lme4 package in R (R Core Team 2021, Bates et al 2014). To fit random forests models, we used the randomForest package in R (Breiman 2001), and tested different numbers of trees (ntree), and number of variables tried at each node in trees (mtry). We used randomForest functions to evaluate the importance of predictor variables and used partial dependency plots to understand relationships between response and predictors.

Chapter 3: Results

Comparison of RWI sensitivity among species

The mean sensitivity (measured as mean CV of tree-level RWI) differed among species as well ($\alpha = 0.1$), with white oak and tree-of-heaven having the lowest sensitivity, while red maple, black walnut, and tulip poplar had higher mean sensitivity (Figure 3.2). The mean CV of white oak was significantly lower than all other species except for tree-of-heaven. Mean CV of tree-of-heaven was significantly lower than mean CV of red maple and tulip poplar. The mean CV of black walnut was intermediate, and only differed from white oak.

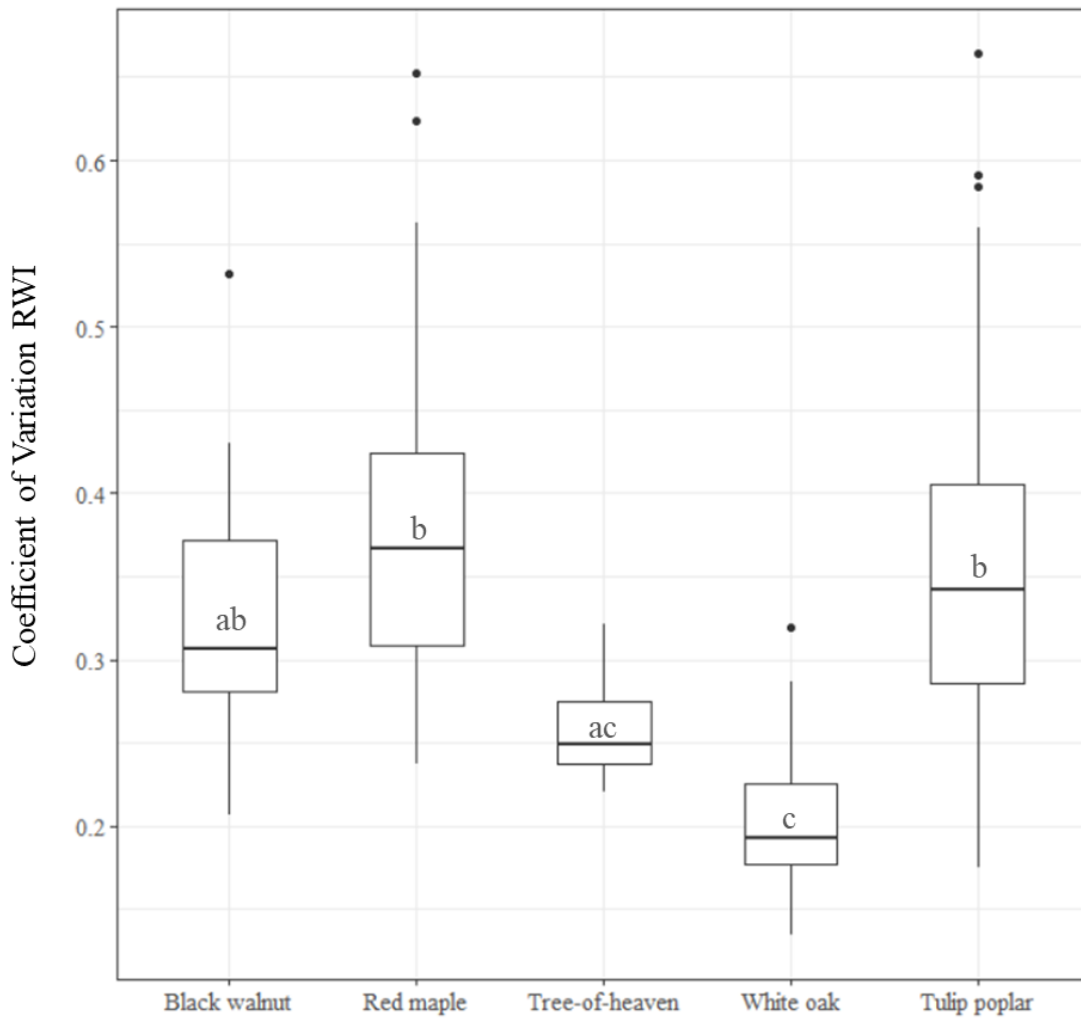


Figure 3.1. Tree-level coefficient of variation of RWI in five tree species. Same letters indicate absence of statistical difference while different letters indicate statistical differences at $\alpha = 0.1$. Number of trees use for each species (i.e., n) is as presented in Table 2.4.

Comparison of RWI sensitivity among crown classes

We found no significant differences in sensitivity (RWI CV) between crown classes in tulip poplar and red maple. ($\alpha = 0.1$, Figure 3.2).

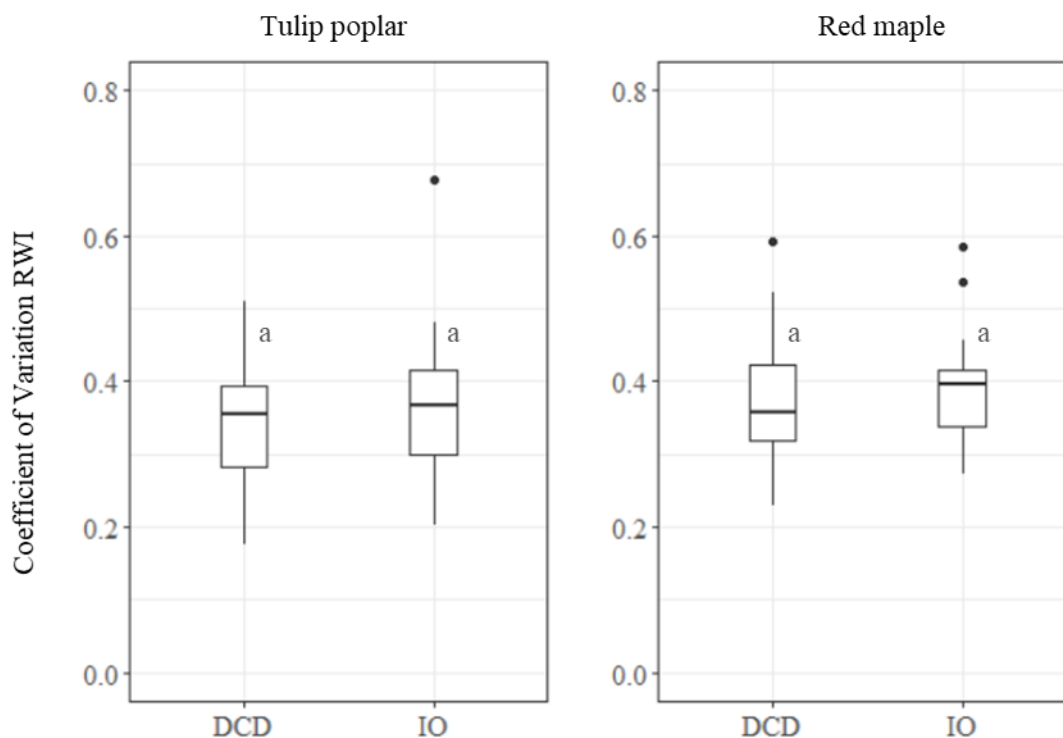


Figure 3.2. Boxplot of coefficient of variation of tree-level RWI by crown class in tulip poplar and red maple. DCD = dominant/codominant trees, IO = intermediate/overtopped trees. Same letters indicate absence of statistical difference while different letters indicate statistical differences at $\alpha = 0.1$. Number of trees use for each species and crown class (i.e., n) is as presented in Table 2.4.

Relationship between RWI sensitivity and temporal climate variability

Standard deviation (SD) of several climate variables was linearly related to the standard deviation of RWI (Figure 3.4, Appendix C). The variability of a larger number of climate variables was associated with the RWI sensitivity of tulip poplar, while the variability of a very small number of climate variables was associated with the RWI sensitivity of black walnut (Figure 3.4). Variability in moisture balance variables was associated with RWI sensitivity more

often or at the same rate as temperature-related variables across species, while variability in precipitation-related variables was less often associated with RWI sensitivity (Figure 3.4).

Interestingly, variability in a climate variable did not always show a positive relationship with RWI sensitivity, and in many cases a larger climate variability corresponded to lower RWI sensitivity.

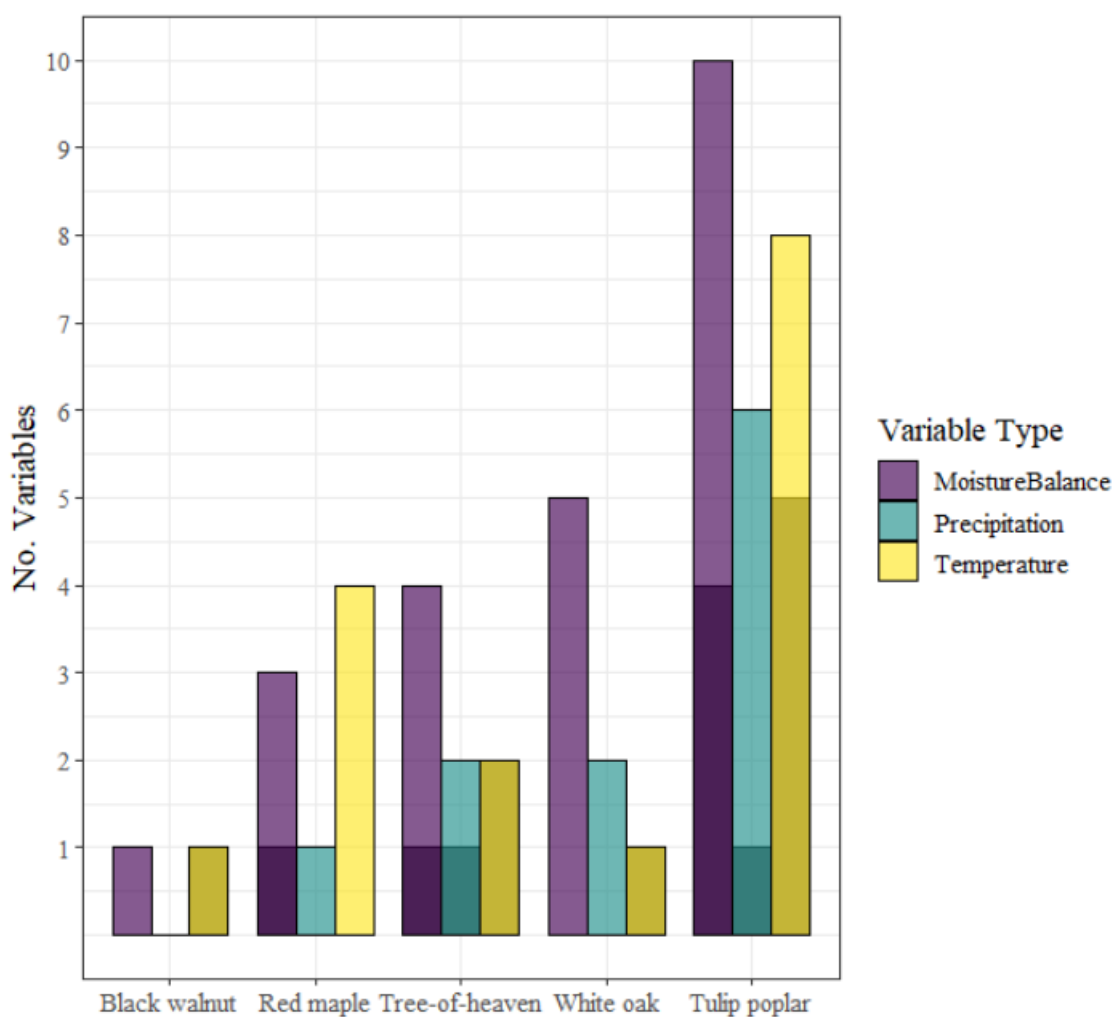


Figure 3.3. Number of significant linear relationships between standard deviation of RWI and standard deviation of a climate variable ($\alpha = 0.1$) by climate variable classes. Dark shaded areas within columns indicate number of variables with positive linear relationships while light shaded columns indicate number of variables with negative linear relationships. For each species, the total number of climate variables and models tested in moisture balance, precipitation, and temperature categories were 13, 7, and 16 respectively (Table 2.3).

Models of RWI as a function of climate

For each species, we develop models using two approaches: mixed-effects linear models and Random Forests. We present here the best overall model for each species, using percent of explained variation as the model selection criterion. Best overall models were for the 30-year period, from 1989-2019. Models that explained the largest proportion of variation were Random Forests models for tulip poplar (11%), tree-of-heaven (20%), and white oak (20%). A mixed effects linear model was the best for black walnut using all rings, but this model only explained 2.3% of the variation in RWI (Appendix C). None of the evaluated models explained any variation in the RWI of red maple trees.

Table 3.1. Percent variance explained by climate variables in individual species models, and model type.

Species	Model Type	% Variance Explained
Tree-of-heaven	Random Forest	20.0
White oak	Random Forest	20.4
Tulip poplar	Random Forest	11.0
Black walnut	Linear Model	2.3
Red maple	-	-

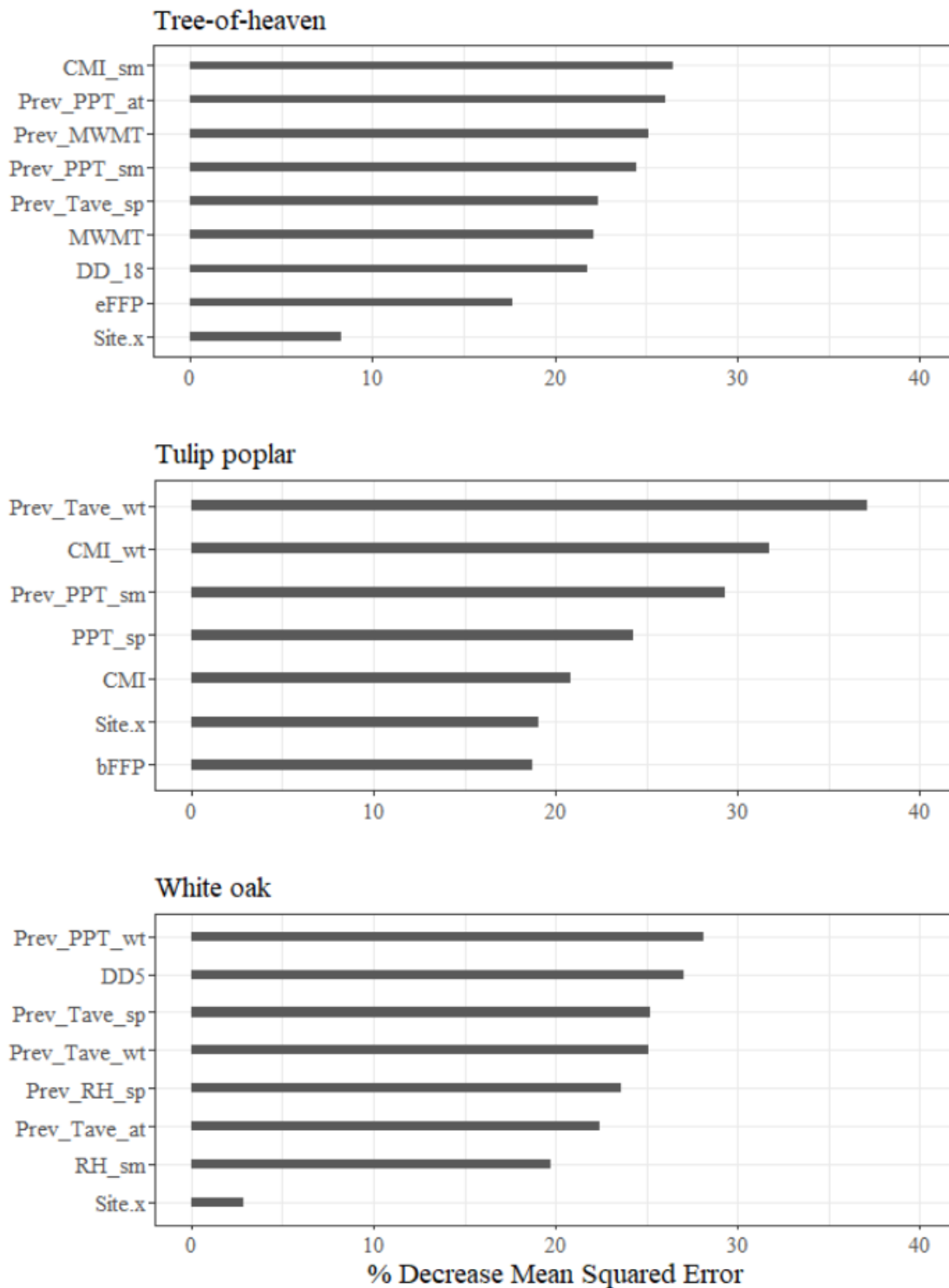


Figure 3.4. Variable importance plots for the random forest models for tree-of-heaven, tulip poplar, and white oak. Prev_ indicates previous year climate, other variable acronyms are as in Table 2.4.

Variable importance plots show that half or more of the climate variables associated with RWI were those describing previous year climate for tree-of-heaven and white oak, while only two of them were important in tulip poplar. Interestingly, previous year autumn conditions are important in two of the three species. Previous year winter conditions, i.e. conditions in the winter preceding the previous year growing season, appear in two of three species as well: tulip poplar, and white oak. Climate conditions in all seasons during the previous year appear as important, while climate conditions during the growing season appear important in the current year in all species. In addition, in the three random forest models all climate predictor variables were important with percent decrease mean square error larger than 15%. In tree-of-heaven, summer CMI is narrowly the most important variable, followed by previous year climate variables describing conditions in spring, summer, and autumn. In tulip poplar, previous year winter conditions seem to be important and related to current year RWI (the two most important variables) followed by precipitation in the previous spring and current summer. In white oak, previous year precipitation during winter and spring temperature were the most important, followed by current year degree days above 5° C. Overall, the variables down-selected and included as predictors, as well as their importance ranking, indicate that climate variables related to moisture and precipitation during the growing season are more important for tree-of-heaven while the coldness of winter may be more important for tulip poplar and white oak. Further summarizing the important variables in the final models for the five species, we highlight the importance of weather conditions during the winter, spring, and summer of the previous year, while summer and annual climate variables appear more influential during the year growth occurred (Table 3.2).

Table 3.2. Current and previous year temperature, precipitation, and moisture balance variables important in random forests among tree species. *Black walnut variables are from a linear model (Appendix C).

	Winter	Spring	Summer	Autumn	Annual
	Previous Year				
Black walnut*	Temperature	Moisture Balance			
Tree-of-heaven		Temperature	Temperature, Precipitation	Precipitation	
White oak	Temperature, Precipitation	Temperature, Moisture Balance		Temperature	
Tulip poplar	Temperature, Moisture Balance		Precipitation		
	Current Year				
Black walnut*			Temperature	Moisture Balance	Temperature
Tree-of-heaven			Temperature, Moisture Balance		
White oak			Moisture Balance		Temperature
Tulip poplar		Precipitation			Moisture Balance, Temperature

The RWI response to climate variables that appear in the model of more than one species indicate similarities of response between species.

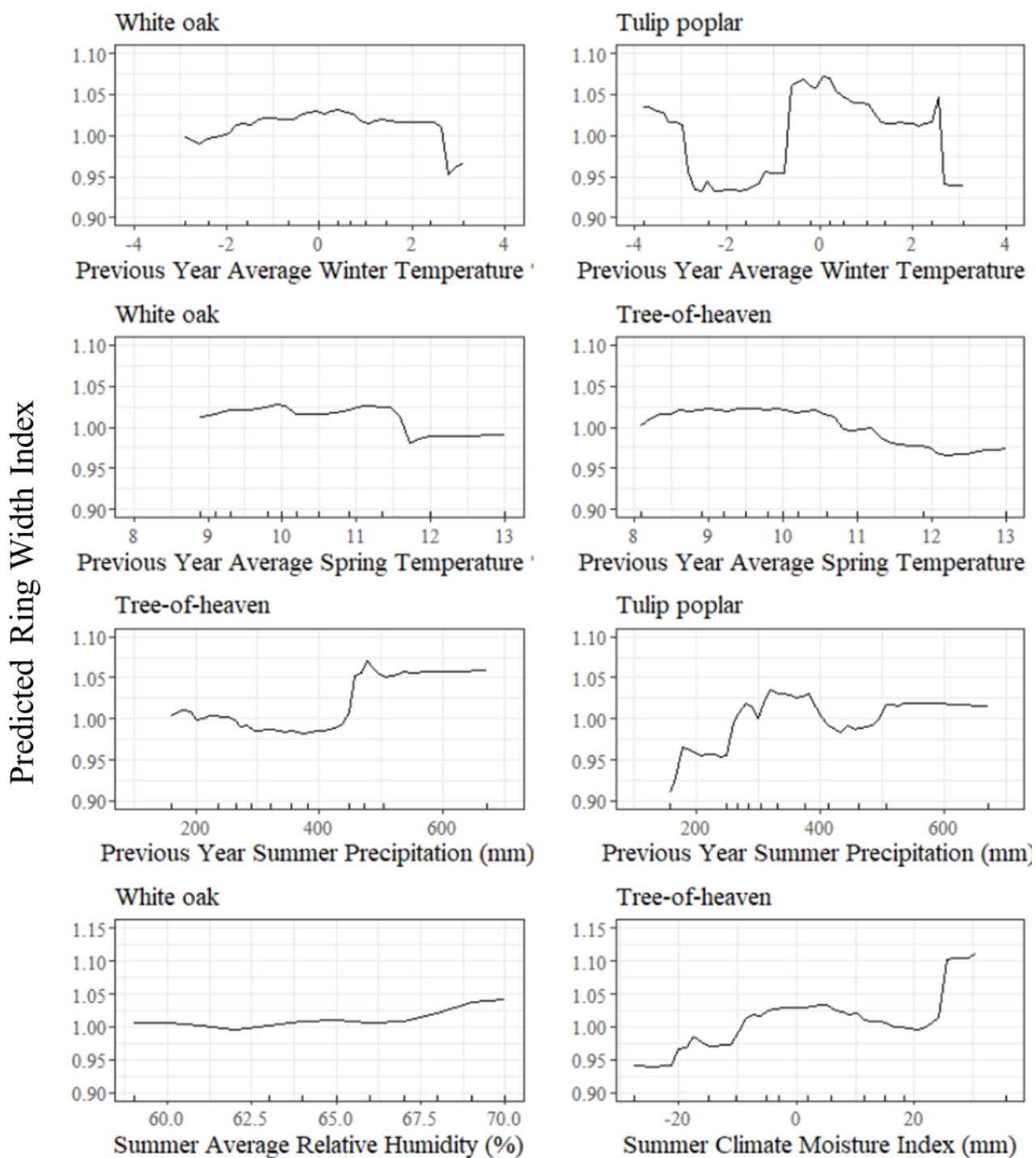


Figure 3.5. Partial dependency plots illustrating the relationship between climate variables and RWI for common climate variables among species level random forest models.

Both white oak and tulip poplar RWI are associated with previous year winter temperature and their RWI response to changes in this variable are similar. As previous year average winter temperature increases, RWI in white oak remains stable, but is predicted to decrease in years where temperature is above approximately 2.5°C (Figure 3.5 row 1). In tulip poplar, RWI is predicted to be high when previous year average winter temperature is between approximately -1.5°C and 2.5°C . A threshold of 2.5°C in winter temperature seem to exist in both species above which RWI is negatively affected. In both white oak and tree-of-heaven, predicted RWI decreases as previous year average spring temperature increases, also pointing to a threshold at approximately 11.5°C after which RWI decreases (Figure 3.5 row 2). The decrease in white oak is notably steeper at approximately 11.5°C whereas tree-of-heaven RWI declines gradually. Predicted RWI increases as previous year summer precipitation increases in both tree-of-heaven and tulip poplar, and in tulip poplar RWI is predicted to be lower than that of tree-of-heaven in previous year summers with less precipitation (Figure 3.5 row 3). As current year moisture balance increases in white oak (% Summer average relative humidity) and tree-of-heaven (summer climate moisture index), RWI increases, although the increase is small for white oak, while non-linear for tree-of-heaven (Figure 3.5 row 4).

Chapter 4: Discussion

Comparison of RWI sensitivity among species

Sensitivity of RWI differed among species. Tulip poplar and red maple showed high RWI sensitivity, while tree-of-heaven and white oak displayed low RWI sensitivity, and black walnut had intermediate RWI sensitivity (Figure 3.2). These patterns coincide with differences in ring formation present between these groups (Martin-Benito and Pederson 2015). Most active vessel elements in ring porous species form in earlywood early in spring before budbreak (García-González et al 2016, Barbaroux and Breda 2002), while diffuse-porous species form active vessel elements throughout the season beginning later in spring post-budburst (Takahashi et al 2013). As a result, diffuse porous diameter growth is subject to a longer period where variable environmental conditions can affect growth, likely leading to higher sensitivity in diameter growth in Tulip poplar and red maple compared to tree-of-heaven and white oak. Semi-diffuse porous black walnut, intermediate in the characteristics of these ring anatomies is also intermediate in growth sensitivity (Takahashi and Takahashi 2021).

Comparison of RWI sensitivity among crown classes

We expected differences in sensitivity between trees in the upper canopy compared to those in the lower canopy because previous research has indicated that trees of different competitive statuses have differential growth responses to climate (Martin-Benito et al 2008, Primicia et al 2015, Rollinson et al 2016). However, we did not find differences in RWI CV in either of the two evaluated species. A potential explanation is that current crown class may not explain well the variation in tree competition throughout time because current canopy position

may not reflect past competitive status and growth. This is a limitation of most dendrochronology studies as estimating a tree's past competition status is usually not feasible. Another possible explanation is that studies that do find differences in RWI sensitivity between trees of different competitive status (e.g., Rollison et al. 2021) compare average chronologies and this could reveal larger patterns related to competition while reducing variance provided by individual tree comparisons (Galvan et al 2014, Peters et al 2015). If this were the case, our results indicate that tree-level variability in sensitivity is large, so much so that it can obscure competitive status patterns.

Relationship between RWI sensitivity and temporal climate variability

Tulip poplar RWI sensitivity had the most relationships with different climate variables (Figure 3.4), while black walnut had the least. Positive relationships with temperature variables in tulip poplar were related to the frost-free period (Appendix C), and variability in RWI increased as variability in the frost-free period increased for this species. This relationship could be due to temperature mediated leaf phenology (Donnelly et al 2017, Singh et al 2016). Annual, growing season, and winter relative humidity variability in tulip poplar was positively related to variability in RWI. This could be governed by the high susceptibility to drought previously observed in tulip poplar (Martin-Benito and Pederson 2015, Leblanc 2020).

In tree-of-heaven, variability in spring temperature, winter temperature, spring precipitation, precipitation as snow, and winter climate moisture index increases as variability in RWI increases (Appendix C). Tree-of-heaven is sensitive to winter injury in juvenile stages as well as in the upper newer shoots of new growth, and winter conditions are harsher in north

America compared to its hypothesized native range (Kowarik and Saumel 2007, Sladonja and Susek 2015), so this relationship in variability to tree-of-heaven growth sensitivity may be related to winter injury as well frost sensitivity during earlywood formation.

Variability in white oak RWI declines as variability in moisture balance and precipitation variables increase (Appendix C). Previous studies indicate strong relationships between white oak radial growth and precipitation variables (Tardif et al 2006), and sensitivity to water balance during the early growing season (Leblanc and Terrell 2001), followed by insensitivity to water balance during the remainder of the growing season (Leblanc and Terrell 2001, Abrams 1990). The negative relationship between RWI sensitivity and moisture related variables we found, suggests a conservative phenotypically plastic response with trees subjected to larger interannual variability having stable growth across years (lower sensitivity).

In both tulip poplar and red maple, increased variability in spring relative humidity was positively related to variability in RWI, while in tree-of-heaven, variability in spring temperature was also positively related to increased RWI (Appendix C). During spring, trees release from dormancy, and xylem sap flows upward in newly formed cells. Variable temperature and moisture balance during these months may translate to springs with more freezing and thawing events, which could be causing damage and embolism in xylem cells, creating ring widths that depart from the average negatively (Kramer 1994, Améglio et al 2002, Pederson et al 2004, Fadon et al 2020). Spring temperature is a mediator of dormancy release and bud burst (Hanninen and Tanino 2011, Singh et al 2016), and the timing of spring events advances as temperatures become warmer (Monahan et al 2016). Early leafing caused by winter and spring temperatures that depart from the average may create longer growing seasons, resulting in growth that departs from the average positively.

Models of RWI as a function of climate

In models using RWI as a function of climate, more previous year climate variables than current year climate variables are important across the tree species evaluated. This supports the hypothesis that carry-over effects in consecutive growing seasons affect tree radial growth (Hackett-Pain et al 2014). Results of the correlation analysis reveal that RWI in trees in many of the species evaluated are associated with previous-year spring and winter conditions, and individual species models also indicate that species are sensitive to climate during one or both of these seasons in previous years. Sugars and starches allocated toward consecutive year diameter growth fluctuate as climate during photosynthetic production, storage, and dormancy fluctuates in the previous year (Barbaroux and Breda 2002, Hanninen and Tanino 2011), while in the current year the window of impacts on current year diameter is found during the period of ring formation in the growing season.

Current year annual and summer moisture balance and temperature are important among tree species. Changes in water potential drives a plant's ability to acquire, transport, and lose water as it performs metabolic functions such as cell division, and photosynthetic production (Gurevitch et al 2002). At the same time a plant's water potential is linked to surrounding environmental conditions. Moisture deficits and low relative humidity during the growing season negatively impact water potential and metabolic functions, which results in decreased growth. Moisture and precipitation climate variables are important in tree-of-heaven. This is unexpected because of its documented drought resistance (Trifilo 2004). Previous winter climate is important for white oak and tulip poplar (Table 3.2). In white oak and tulip poplar, the importance of winter variables to RWI could be related to temperature mediated phenology (Singh et al 2016, Pederson et al 2004), and future studies should investigate relationships between leaf phenology,

diameter growth phenology, and climate to understand the relationships between these characteristics. Partial dependency plots further highlight the differences in strategies between species related to highly important climate variables.

Partial dependency plots show some interesting differences between species (Figure 3.5). In previous year average winter temperature, tulip poplar shows greater changes in RWI as winter temperature increases than white oak. Timing of phenological events may be more tied to previous year winter temperature in tulip poplar than in white oak, resulting in different levels of growth and subsequent storage carryover (Monahan et al 2016, Barbaroux and Breda 2002). , Precipitation and moisture balance are also important for white oak and tulip poplar during previous spring, so winter climate may be related to spring moisture through snowpack dynamics and subsequent groundwater recharge (Coulthard et al 2021). White oak has a sharper decline in growth as previous year average spring temperature increases, while tree-of-heaven growth declines more steadily, but tree-of-heaven does reach a lower predicted RWI than white oak. Tree-of-heaven maintains higher growth under less precipitation than in tulip poplar. We hypothesize that both responses here in tree-of-heaven are related to its highly efficient vessels, and this result supports that tree-of-heaven better tolerates extreme conditions than native trees (Sladonia and Sušek 2015). Further experimental studies should compare growth in this species under variable moisture conditions with native trees.

CHAPTER 5: Conclusion

We detected differences in sensitivity of annual diameter growth across five broadleaf deciduous tree species, and these differences coincide with their differing wood anatomies. The northeastern US is diverse in tree species, and further study using more tree species could confirm patterns of higher sensitivity in diffuse-porous species and lower sensitivity in ring porous species. We did not find differences in sensitivity in trees of different competitive status. RWI variability of trees from different species responded differently to variability in climate variables, indicating that tree growth in different species is affected in different ways by climate conditions. Sensitivity in RWI did not necessarily translate into sensitivity to a variety of climate conditions. The clear prevalence and importance of previous year climate variables in radial growth found in this study provides further evidence of a carry-over effect from year-year tree diameter growth in trees, supporting that storage and allocation are important components of tree diameter growth. Overall, for the species we modelled, previous-year climate throughout all seasons affects growth in the current year, while current-year climate during early spring through the growing season is important to current-year growth. Tree growth-climate studies using random forests in combination with partial dependency plots may benefit from the way that these tools make non-linear growth-climate relationships easier to understand.

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APPENDICES

Appendix A. Number of trees, mean inter-series Pearson correlation coefficients at individual sites and altogether among study species. Correlations calculated between individual trees and a master chronology built from other series at the site and for all trees in the species (using a leave-one-out principle). Correlations between individual trees and master chronology summarized by site and altogether (Bunn 2010)

Site	# Trees	Mean Inter-series correlation
Black Walnut		
CN Walnut Grove	5	0.14
M Walnut Grove	4	0.19
T	3	0.09
BM	10	0.01
All	22	0.003
Red maple		
CN Hardwood Area	18	0.18
CN Transect	10	0.04
M Hardwood Area	7	0.16
M Transect	10	0.23
T	7	0.06
BM	15	0.20
All	67	0.14
Tulip poplar		
CN	24	0.25
M	25	0.28
T	9	0.30
BM	1	
All	59	0.23
Tree-of-heaven		
M	1	
T	6	0.51
BM	6	0.63
All	13	0.55
White oak		
CN	18	0.38
M	3	0.05
All	21	0.32

Appendix B. Crown class descriptions from Helms (1998)

crown class a category of tree based on its crown position relative to those of adjacent trees —*see stem class, thinning grade, wolf tree*; types of crown class are the following:

- codominant** a tree whose crown helps to form the general level of the main canopy in even-aged stands or, in uneven-aged stands, the main canopy of the tree's immediate neighbors, receiving full light from above and comparatively little from the sides
- dominant** a tree whose crown extends above the general level of the main canopy of even-aged stands or, in uneven-aged stands, above the crowns of the tree's immediate neighbors and receiving full light from above and partial light from the sides
- emergent** a tree whose crown is completely above the general level of the main canopy, receiving full light from above and from all sides
- intermediate** a tree whose crown extends into the lower portion of the main canopy of even-aged stands or, in uneven-aged stands, into the lower portion of the canopy formed by the tree's immediate neighbors, but shorter in height than the codominants and receiving little direct light from above and none from the sides
- overtopped (suppressed)** a tree whose crown is completely overtopped by the crowns of one or more neighboring trees —*note* the vigor of over-

Appendix C. Summary of linear models of the standard deviation of ring width index as a function of the standard deviation of climate variables for the same period in which annual rings in individuals were formed. ‘+’ indicates a positive slope, ‘-’ indicates a negative slope.

		Tulip Poplar	Red Maple	Tree of Heaven	White Oak	Black Walnut
	Temperature					
MAT_SD	Mean Annual Temperature °C					
MWMT_SD	Mean Warmest Month Temperature °C	-				
MCMT_SD	Mean Coldest Month Temperature °C					
TD_SD	Temperature difference between MWMT and MCMT	+				
DD_0_SD	Degree-days below 0°C	-			+	
DD5_SD	Degree-days above 5°C		-			
DD_18_SD	Degree-days below 18°C					
DD18_SD	Degree-days above 18°C		-			
FFP_SD	Length Frost-free period (days)	+	-			+
bFFP_SD	Beginning of Frost-free period (day)	+				
eFFP_SD	End of Frost-free period (day)	+				
DD1040_SD	Degree Days greater than 10 °C and below 40 °C		-			
Tave_wt_SD	Average Winter Temperature °C			+		
Tave_sp_SD	Average Spring Temperature °C	-		+		
Tave_sm_SD	Average Summer Temperature °C					
Tave_at_SD	Average Autumn Temperature °C	+				
		Tulip Poplar	Red Maple	Tree of Heaven	White Oak	Black Walnut
	Precipitation					
MAP_SD	Mean Annual Precipitation mm	-			-	
MSP_SD	May to September Precipitation mm	-			-	
PAS_SD	Precipitation as Snow mm	-		+		
PPT_wt_SD	Winter Precipitation mm	+				
PPT_sp_SD	Spring Precipitation mm					
PPT_sm_SD	Summer Precipitation mm	-		-		
PPT_at_SD	Autumn Precipitation mm	-	-			
		Tulip Poplar	Red Maple	Tree of Heaven	White Oak	Black Walnut
	Moisture Balance					
Eref_SD	Hargreaves Reference Evaporation mm	-		-		
RH_SD	Relative Humidity %	-			-	
CMI_SD	Climate Moisture Index mm	-			-	
AHM_SD	Annual Heat-moisture Index	+			-	
SHM_SD	Summer Heat-moisture index			-	-	
RH_wt_SD	Winter Relative Humidity %	+			-	
RH_sp_SD	Spring Relative Humidity %	+	+			-
RH_sm_SD	Summer Relative Humidity %	+				
RH_at_SD	Autumn Relative Humidity %	-	-			
CMI_wt_SD	Winter Climate Moisture Index mm		-	+		
CMI_sp_SD	Spring Climate Moisture Index mm					
CMI_sm_SD	Summer Climate Moisture Index mm	-		-		
CMI_at_SD	Autumn Climate Moisture Index mm	-				

Appendix D. Summary of the black walnut linear model using RWI as response variable.

Black Walnut	Estimate	R ²	P-value
		0.02345	<0.001
Temperature			
Tave_sm	0.0002		<.05
DD5	0.0025		<.05
Prev_MCMT	0.0137		<.05
Moisture Balance			
CMI_at	-0.0025		<.01
Prev_CMI_sp	0.0041		<.01
$\sigma^2_{Residual}$	0.2907		