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The Graduate School

**ADAPTATION TO CLIMATE IN *JUGLANS NIGRA*: EXPLORING HOW HOME
CLIMATE SHAPES GROWTH PATTERNS OF NATURAL POPULATIONS**

A Thesis in

Ecology

by

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ABSTRACT

Many autochthonous tree species are distributed across extensive geographic ranges. To survive, tree populations must adapt to both spatial and temporal climate heterogeneity through evolutionary processes, such as natural selection, which act on genetic variation. Most tree species combine adaptation to the local climate (i.e. specialization) with phenotypic plasticity. Adaptation to local climate is common in wide ranging tree species and fitness clines driven by climate have been documented for many tree species. This thesis focuses on adaptation to climate in black walnut (*Juglans nigra L.*) and explores how home climate shapes growth patterns of natural populations. Chapter 1 evaluates population differentiation in adaptation to spatial and temporal climate variability using average annual scaled growth, annual ring width increment, and the coefficient of variation in average annual scaled growth. We found evidence of specialization, and thus adaptation to spatial climate variability, in populations' average scaled radial growth as a function of climate transfer distance. We also found that temporal variability of populations' home climate was linked to phenotypic plasticity and populations from more temporally variable climates exhibited less interannual growth variability. Chapter 2 evaluates height growth up to age 10 from planting of black walnut populations to elucidate differences in early growth patterns. We found that populations from warmer climates had the highest cumulative growth and reached maximum absolute growth earlier in time. Populations from colder climates had a smaller size (cumulative growth), reached maximum absolute growth later in time, and had higher relative growth rates at any given age within our study's age range. The results from this thesis highlight the role natural selection and temporal/spatial climate variability may play in driving growth patterns among black walnut populations.

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CHAPTER 1

Spatial and temporal variability of home climate shape genetic differences in diameter growth responses of *Juglans nigra* populations

ABSTRACT

Many tree species are distributed across extensive ranges of spatial and temporal climate heterogeneity. To accommodate this heterogeneity, most species combine adaptation to the local climate (i.e. specialization) with phenotypic plasticity. Therefore, genetic differences among populations within a species range are shaped by both spatial and temporal climate variability. In this study, we evaluate the effect of spatial and temporal climate variability in determining differentiation in growth responses of 33 black walnut (*Juglans nigra*) natural populations growing in a common garden (provenance tests) for 40 years. Common gardens provide evidence of local adaptation to climate when associations between fitness traits and the populations' home climates are observed. We evaluate population differentiation in average annual scaled diameter increment to assess local adaptation to climate. We also use the coefficient of variation in average annual scaled growth to assess population differentiation in phenotypic plasticity. We found that genetic differences among populations and the resulting growth patterns are shaped by both spatial and temporal climate variability. We found evidence of specialization, and thus adaptation to spatial climate variability, in populations' average scaled radial growth as a function of climate transfer distance. We also found that temporal variability of populations' home climate was linked to phenotypic plasticity and populations from more temporally variable climates exhibited less interannual growth variability. These findings indicate that both spatial and temporal climate variability are critical in understanding genetic differences among populations.

INTRODUCTION

Many tree species are distributed across extensive ranges of spatial and temporal climate heterogeneity. Spatial climate variability is defined as climate gradients in space while temporal climate variability involves annual, seasonal, or daily climate fluctuations in a given location. To survive, tree populations must adapt to both spatial and temporal climate heterogeneity through evolutionary processes, such as natural selection, which act on genetic variation (Morgenstern 1996). Most tree species combine adaptation to the local climate (i.e. specialization) with phenotypic plasticity (Alfaro et al 2014). Adaptation to local climate can occur when spatial climate variability influences natural selection, which results in populations adapted to a segment of climate within the species range (Rehfeldt 1984; Alberto et al 2013; Aitken and Bemmels 2016). Phenotypic plasticity is an evolutionary strategy that allows a single genotype to modify its expression under different environmental stimuli and thus allows long-lived and sessile organisms to accommodate temporal variability (Via 1993; Via et al 1995; Sultan and Spencer 2007)

Adaptation to local climate is common in wide ranging tree species and fitness clines driven by climate have been documented for many tree species (Langlet, 1971; Campbell 1974; Rehfeldt 1999; St Clair et al 2005; Rehfeldt et al 2014; Aitken and Bemmels 2016; Leites et al 2019). Common garden studies (provenance testing) demonstrate that, in general, populations growing close to their home climate achieve maximum values in several quantitative traits, and decrease growth as the climate becomes more dissimilar to home climate (Matyas 1994; Carter 1996; Rehfeldt et al 1999; Wang et al 2006; Thompson and Parker 2008; Leites et al 2012ab; Saenz-Romero et al 2017). It is important to recognize that adaptation to climate does not necessarily indicate that populations exhibit local adaptation. Only populations that achieve

highest fitness in their home climate are considered to exhibit local adaptation. However, in several tree species, populations from the edge of the species range have been found to improve fitness when moved a small distance from their home climate (Namkoong 1969; Rehfeldt et al 1999, 2018; Wang et al 2010; Leites et al 2012ab; Saenz-Romero et al 2017). Populations' fitness in different climates can be evaluated when they are tested in several common gardens. Their response to departures from home climate can be modeled by calculating a climate transfer distance between the population home climate and the common garden climate (hereafter climate transfer distance). There is evidence of adaptation to local climate when maximum growth is achieved at or near transfer distance zero.

Phenotypic plasticity is ample in tree species that withstand centuries of climate variation (Berg and Ellers 2010; Nicotra et al 2010; Richter et al 2012). However, not all phenotypic plasticity enhances fitness; when it does, the term adaptive plasticity is used (Sultan 1995). When organisms are only passively responding to a stressful environment and fitness is not enhanced, the term inevitable plasticity is used (Sultan 1995, Ghalambor et al 2007). For this reason, all of the phenotypic change associated with different environmental conditions cannot be assumed to represent adaptive plasticity (Stearns 1982; Taylor and Aarssen 1988). Phenotypic plasticity is trait specific and phenotypic plasticity in one or several traits could result in homeostasis in another trait (Bradshaw 1965; Van Tienderen 1991). Adaptive phenotypic plasticity is an important strategy in environments with significant temporal heterogeneity over the course of an organism's lifetime (Van Tienderen 1991; Balaguer et al 2001; Valladares et al 2007, Valladares et al 2014). Conversely, specialization by adapting to local climate is an advantageous strategy in temporally stable and spatially variable climates (Rehfeldt, 1984). This is because phenotypic plasticity is costly, more plastic genotypes have lower average fitness

regardless of their expressed phenotype (Van Tienderen 1991; Dewitt et al 1998; Van Buskirk and Steiner 2009; Chevin et al 2013).

Genetic differences among populations and the resulting growth patterns are then shaped by both temporal and spatial variability. In this study, we evaluate their effects in determining differentiation in average and annual radial growth responses of 33 black walnut (*Juglans nigra*) natural populations growing in a common garden for 40 years. First, we test for evidence of specialization, i.e. adaptation to spatial climate variability, by modeling populations' average scaled radial growth as a function of climate transfer distance. Then, we evaluate the relationship between temporal home climate variability and phenotypic plasticity by modeling the coefficient of variation of scaled annual radial growth as a function of the variability of home climate variables. We also evaluate the contributions of home climate characteristics and weather experienced at the test site to annual scaled radial growth. We use black walnut as a study organism because it is a species with strong intraspecific genetic differentiation related to climate (Wright and Lemmien, 1972; Bey, 1973; Bey, 1979, Leites et al 2019).

We hypothesize the following:

1. Adaptation to local climate will be reflected in the maximum average annual growth occurring at, or close to, home climate (climate transfer distance = 0). Populations transferred farther from their home climate will exhibit less average annual growth.
2. Temporal variability of home climate will be linked to phenotypic plasticity, with populations from more temporally variable climates exhibiting less interannual growth variability.

3. Interacting characteristics of spatial and temporal home climate variability will be an important determinant of a population's annual radial growth.

METHODS

Data

We used data from a provenance test (common garden) established in 1980 in Pennsylvania, USA. This test site evaluated 33 natural populations from the black walnut range (Figure 1) using a randomized complete block design with 5 blocks. The common garden is set up with four-tree row plots within blocks (trees were planted 3 m apart). At the test site, the trees on the outside of the plot have reduced competition from other trees and the trees on the inner rows have competition from other trees in all sides (Figure 2). Therefore, we only used data from trees on the outside edge of a row (green arrow in Figure 2) to remove some of the impacts of inter-tree competition on the results. Inter-tree competition would obscure the expression of genetic differences and likely decrease existing differences among populations (e.g. Franklin 1979; Foster 1986; Rehfeldt et al 1991). In total, 144 trees were evaluated from the 33 populations. The maximum number of trees representing a population was 7 and the minimum was 2.

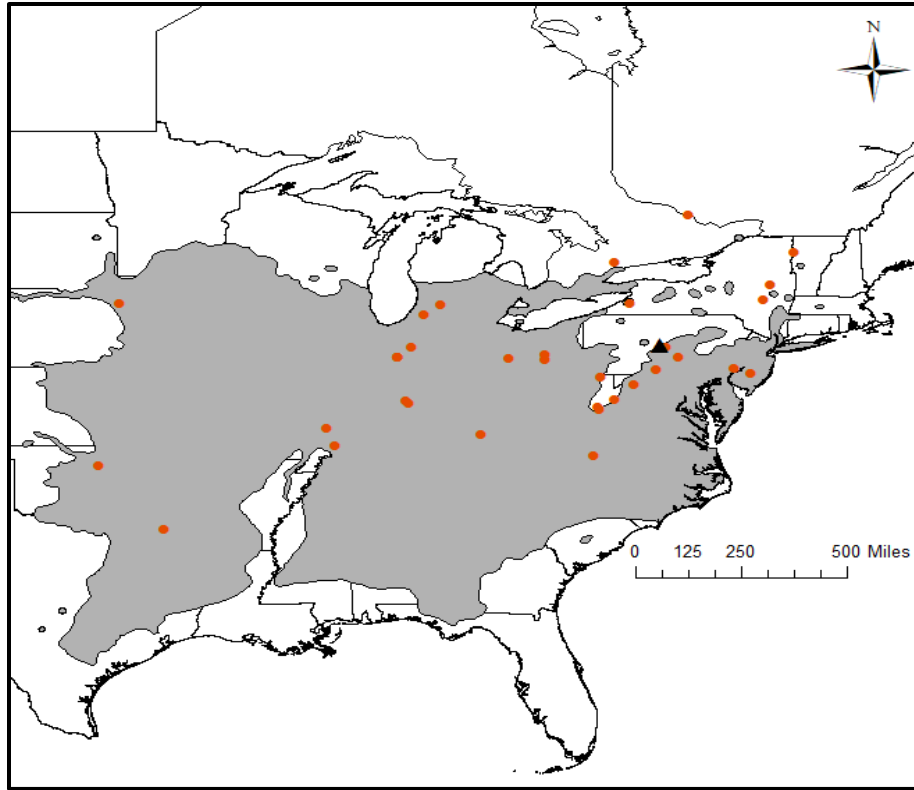


Figure 1. Populations (orange circles) planted at the test site (black triangle) in relation to the geographic range of black walnut (gray).



Figure 2. Image of one block in the test site that shows outer vs inner row trees. Trees in the same row as the green arrow are examples of outer row trees and are under reduced competition. Trees in the same row as the blue arrow are examples of inner row trees that were subjected to competition.

Annual radial growth

In the fall of 2018, one core (from bark to pith), 0.3 meters from the base of the east facing aspect of each tree was extracted using a 4.3 mm increment borer. All cores were dried, mounted and sanded following Stokes & Smiley, 1968. Next, cores were scanned to a resolution of 2400 dpi and ring widths were measured to a resolution of 0.01 mm using the software Coorecorder (Cybis, Saltsjobaden, Sweden). Trees with extremely faint and suppressed rings were

measured under a light microscope at 45x magnification using a Velmex tree-ring measuring system and the Telervo software. All cores were cross-dated and validated using 6-year segments with the “corr.rwl.seg” function from the ‘DPLR’ 1.6.3 package in R (Bunn 2008). Cores with a segment correlation of below 0.5 were flagged and raw ring-width measurement were re-evaluated to check for potential measurement errors. If no measurement mistakes were found, we kept the original reading. The age of each tree at the time it was cored was known; therefore, any segments with low correlations and no measurement errors were assumed to be due to growth differentiation among populations.

To test our hypothesis, we calculated scaled annual ring widths (SRW) instead of detrending with traditional methods. For each tree, each year’s raw ring width was scaled by dividing it by the test site’s mean raw ring width in that year. The test site’s mean raw ring width in a given year was calculated by averaging the raw ring width of all trees in that year. Scaling in this way removed the age trend without removing population or block effects because all trees were the same age. In addition, it helped identify whether the growth of a tree in a given year was above or below the test-site average. A SRW value ≥ 1 indicates the tree grew average or above average in that year; a value < 1 indicates the tree grew below average.

Climate Data

Annual and seasonal climate normals for the 1951–1980 period, and annual climate averages for the 1900-1980 period, were obtained using the latitude, longitude, and elevation of each population. Annual and seasonal climate data was obtained from the 1980 – 2018 at the test site. All climate data was obtained at an 800 m resolution from ClimateNA (Wang et al 2016). The time period for the climate normals represents the climate prior to seed collection. The climate transfer distance (clim.trds) for each population was calculated by subtracting the climate

normal of the population from the climate normal of the test site. The period used to calculate temporal variability of home climate was 1900 to 1980. The annual climate from 1890 to 2018 was used to characterize the weather experienced at the test site.

Analysis

To assess for evidence of adaptation to local climate the mean scaled ring width (SRW_{Mean}) for each tree was modeled as a function of the populations' clim.trds using a linear mixed effects model (Equation 1).

$$\overline{SRW}_{ij} = (\beta_0 + u_j) + \beta_1 * CLIM.trds_i + \beta_2 * CLIM.trds_i^2 + \varepsilon_{ij} \quad (1)$$

Where \overline{SRW}_{ij} is the SRW_{Mean} for tree i in block j , u_j is the random effect for block, β_1 and β_2 are fixed effects parameters, and ε_{ij} is the error term. If climate transfer distance was a significant predictor ($\alpha = 0.1$), and SRW_{Mean} was maximum at or near climate transfer distance = 0, we interpreted it as evidence of adaptation to local climate.

To evaluate whether populations from more temporally variable home climates differ in phenotypic plasticity of annual radial growth, we calculated the coefficient of variation of the SRW across all years for each tree (SRW_{cv}). To do this, we calculated the standard deviation of the SRW across all years for a given tree and divided it by the SRW_{Mean} for that same tree. We then model SRW_{cv} as a function of the standard deviation of the population home climate (clim.stdv) and of clim.trds as fixed effects, and block as a random effect (Equation 2).

$$SRW_{cv_{ij}} = (\beta_0 + u_j) + \beta_1 * CLIM.STDV_i * \beta_2 * CLIM.trds_i + \beta_3 * CLIM.trds_i^2 + \varepsilon_{ij} \quad (2)$$

Where $SRW_{cv_{ij}}$ is the coefficient of variation of the SRW for tree i in block j , u_j is the random effect for block, β_1 , β_2 and β_3 are fixed effects parameters, and ε_{ij} is the error term. If

climate.stdv was a statistically significant predictor of population's CV ($\alpha = 0.1$), we interpreted this as evidence of temporal home climate variability affecting phenotypic plasticity.

Each model was fit with one of 11 different climate variables that represented the mildness of climate (e.g. mean annual temperature), the coldness of winter (e.g. mean temperature of the coldest month), the moisture balance of summer (e.g. summer heat moisture index), and the length of the growing season (e.g. frost free period, Appendix A). To select the best univariate model, we chose the model with the lowest Akaike's Information Criterion (AIC; Akaike 1974) that also had fixed effect parameters different from zero (t-test, $\alpha = 0.1$). To fit mixed effects models, we used the package lme4 (Bates et al 2015).

Finally, to evaluate whether the characteristics of home climate are an important determinant of a population's annual radial growth, we model raw annual ring width increment. In this model, clim.trds, age, and the weather experienced at the site the year under consideration and the previous year were included. To determine what weather variables to include in the model (see Appendix B), we evaluated the Pearson correlation coefficient (r) between the mean raw annual ring width increment (calculated across all trees in the test for a given year) (\overline{RRWI}_{Test}), and the weather variables in that year, and the year before. If the weather variable had a $r \geq |0.25|$ with \overline{RRWI}_{Test} , it was kept for further consideration. The selected weather variables were then correlated amongst themselves and only those with $r < 0.7$ (between themselves) were included in the model. The final weather variables selected were: summer relative humidity, growing degree-days above 5⁰C, and Julian day of the beginning of the frost-free period of the current year. The variables selected to be analyzed in the previous year were: summer relative humidity, mean coldest month temperature, and the Julian day of the beginning of the frost-free period. We consider age, clim.trds, and weather variables as fixed effects, and

block and tree nested within block as a random effects (Equation 3). To remove heteroskedasticity, the variance was modeled as power function of the fitted values. This model was fit using the nlme package in R (Pinheiro et al 2013).

$$RAW_{ijk} = (\beta_0 + u_j + u_{i(j)}) + \beta_1 * Age_k + \beta_2 * CLIM.trds_i + \beta_3 * CLIM.trds_i^2 + \sum_4^6 \beta_i * PA.clim_k + \sum_7^9 \beta_i * PA.clim_{k-1} + \varepsilon_{ijk} \quad (3)$$

Where RAW_{ijk} is the raw growth for tree i in block j at year k , u_j is the random effect for block, $u_{i(j)}$ is the random effect for tree nested within block, $\beta_1 - \beta_9$ are fixed effects parameters, and ε_{ijk} is the error term.

RESULTS

Adaptation to local climate

Of the climate variables evaluated, mean annual temperature transfer distance (MAT.trds) resulted in the model with the lowest AIC. This model had a marginal R^2 of 3% and a conditional R^2 of 10%. The model illustrates that the maximum SRW_{Mean} is close to a transfer distance of 0 and that on average, populations grew more when close to home and less when transferred farther from home (Table 1 and Figure 3).

Table 1. Parameter estimates, standard errors, and 90% bootstrapped confidence intervals (C.I.) for the model predicting SRW_{Mean} from mean annual temperature transfer distance (MAT.trds, Equation 1).

Variable	Estimate	Standard error	C.I.
Intercept	1.15	0.049	1.066, 1.228
MAT.trds	-0.00082	0.012	-0.0223, 0.0194
MAT.trds ²	-0.0068	0.0036	-0.0127, -0.0010
σ Block	0.082		
σ Residual	0.29		

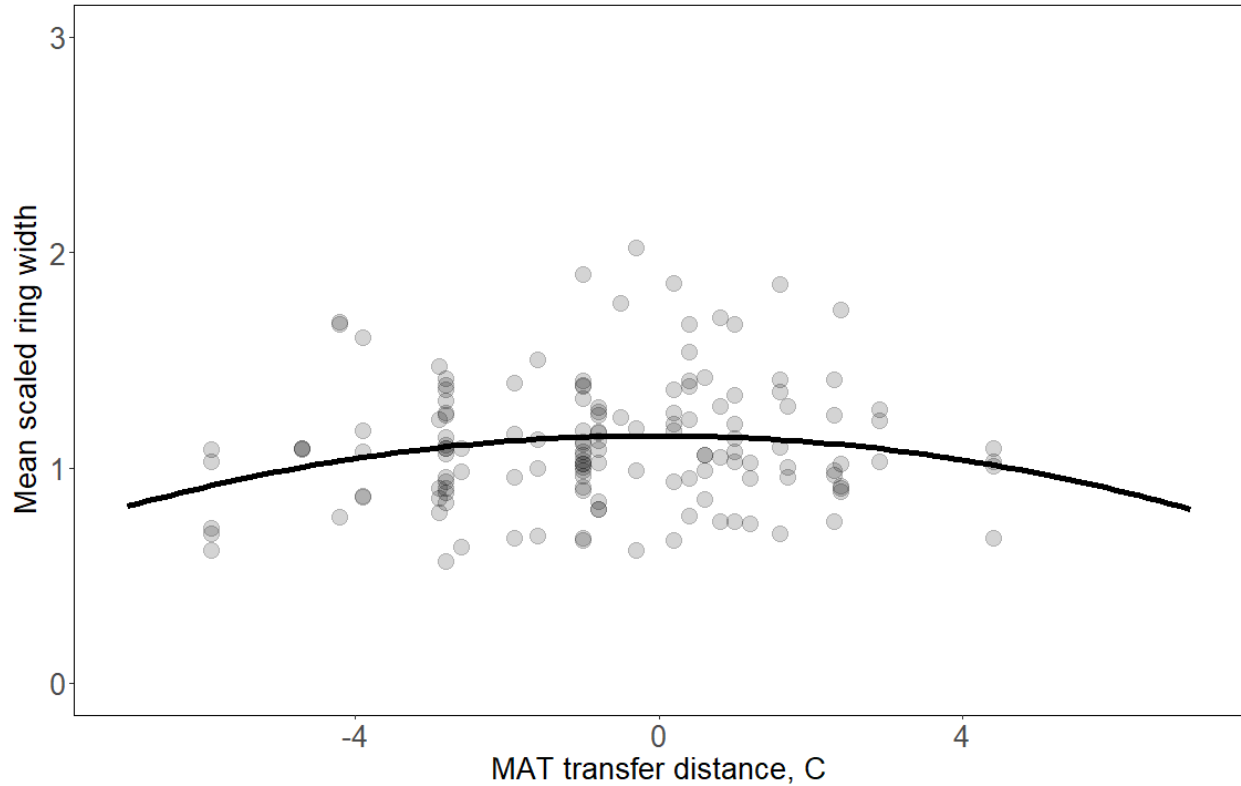


Figure 3. Marginal (fixed effects only) predictions of mean scaled ring width (SRW_{Mean}) as a function of mean annual temperature (MAT) transfer distance (black line, Table 1). Gray circles are observed SRW_{Mean} where the block effect have been removed using the block random effects estimates.

Phenotypic plasticity and temporal variability of home climate

Of the climate variables evaluated, the model including mean annual temperature had the lowest AIC. When predicting, SRW_{CV} , both the standard deviation of the mean annual temperature characterizing population home climate (MAT.stdev) and MAT.trds were statistically significant ($\alpha = 0.1$), including the interaction term. The quadric term for MAT.trds was not significantly different from 0 ($\alpha = 0.1$) and was removed from the final model. We note that in this model MAT.trds is confounded with population MAT because each population was

only tested in one site. The effects of transfer distance are apparent in this test site and show the characteristic quadratic relationship with growth (Figure 3); thus, we continue the discussion focusing on MAT.trds but the confounding effect with population MAT should be kept in mind. The block random effect was not necessary in the model and removed; as a result, the final model was fit using multiple linear regression (Table 2).

Table 2. Parameter estimates, standard errors, and 90% confidence intervals (C.I.) for the model predicting SRW_{CV} from the standard deviation of the mean annual temperature characterizing the populations' home climate (MAT.stdev) and mean annual temperature transfer distance (MAT.trds, Equation 2).

Variable	Estimate	Standard error	C.I.
Intercept	0.75	0.090	0.60, 0.90
MAT.trds	0.091	0.051	0.0056, 0.18
MAT.stdev	-0.48	0.13	-0.69, -0.27
MAT.trds x MAT.stdev	-0.13	0.074	-0.25, -0.0079

The parameter estimate for the population MAT.stdev was negative indicating that populations with less variability in their annual ring width increment originated from climates with larger temporal climate variability (Table 2, Figure 4 at MAT.trds = 0). Population MAT.stdev interacted with MAT.trds. In general, populations from more variable climates were more stable in their interannual ring width increment (Figure 4). The effects of MAT.stdev on the SRW_{CV} was small for populations with negative MAT.trds values. In general, populations with negative MAT.trds also have higher MAT's (Figure 1); therefore, an alternative explanation

is that the effect of MAT.stdev is smaller in populations from warmer climates. For populations with positive MAT.trds (moved to warmer climates), the MAT.stdev had a large impact on the SRW_{CV} . Again, the alternative interpretation is that MAT.stdev is more important in populations adapted to colder climates (which were in general transferred a warmer climate, Figure 10).

Each SRW_{CV} is a measure of the phenotypic plasticity in annual ring width increment; however, it does not indicate whether the phenotypic plasticity is adaptive or inevitable. To better distinguish between the two, Figure 5 illustrates the relationship between SRW_{CV} and SRW_{Mean} . Recall that if SRW_{Mean} is ≥ 1 , the annual ring width increments were at least as good as the average growth for the test in the corresponding year. Interestingly, the highest SRW_{CV} values were for populations either growing well above average (SRW_{Mean} much greater than 1 and thus higher fitness), or well below average (SRW_{Mean} much less than 1). Combining the information in Figures 4 and 5, the performance of populations transferred to much warmer climates (positive MAT.trds values), had the highest SRW_{CV} and both the highest and lowest values of SRW_{Mean} ; populations that had a $SRW_{Mean} \geq 1$ originated in climates with a slightly higher MAT.stdev. We would also like to note that we found no correlation between populations' home climate MAT and populations home climate MAT standard deviation ($r = -0.026$). This suggests that these results are not confounded with evidence for adaptation to spatial climate.

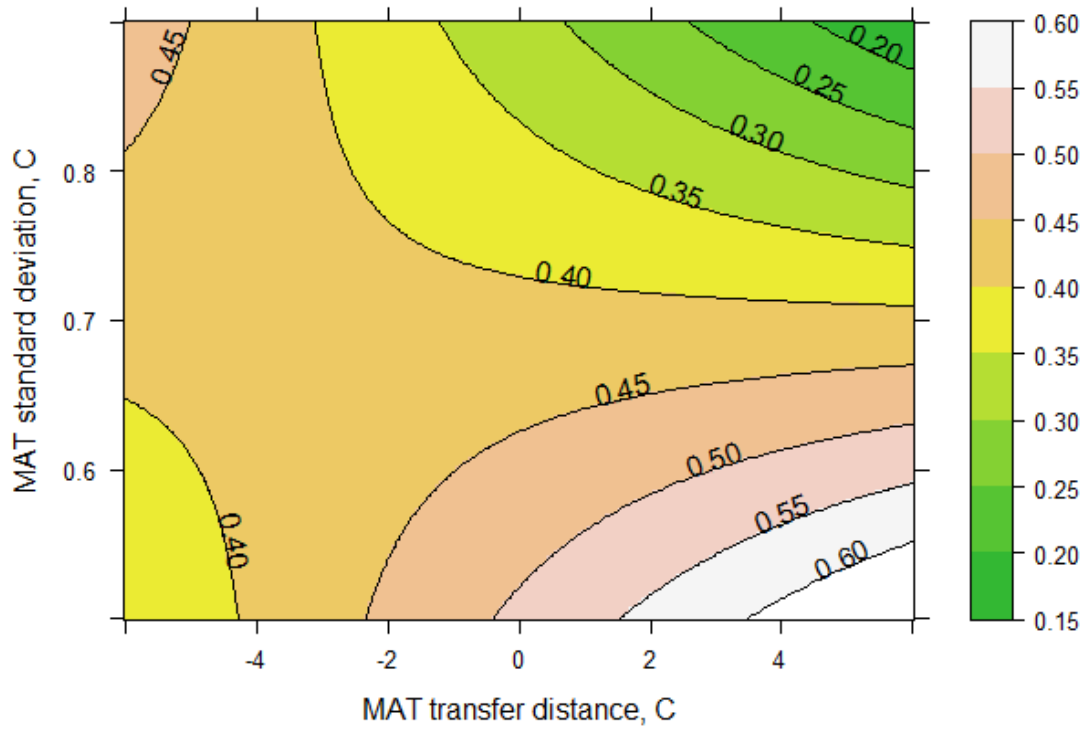


Figure 4. Contour plot for the model predicting SRW_{CV} from mean annual temperature transfer distance and mean annual temperature standard deviation (Table 2). The variation in color and labeled contour lines indicate the levels of SRW_{CV} .

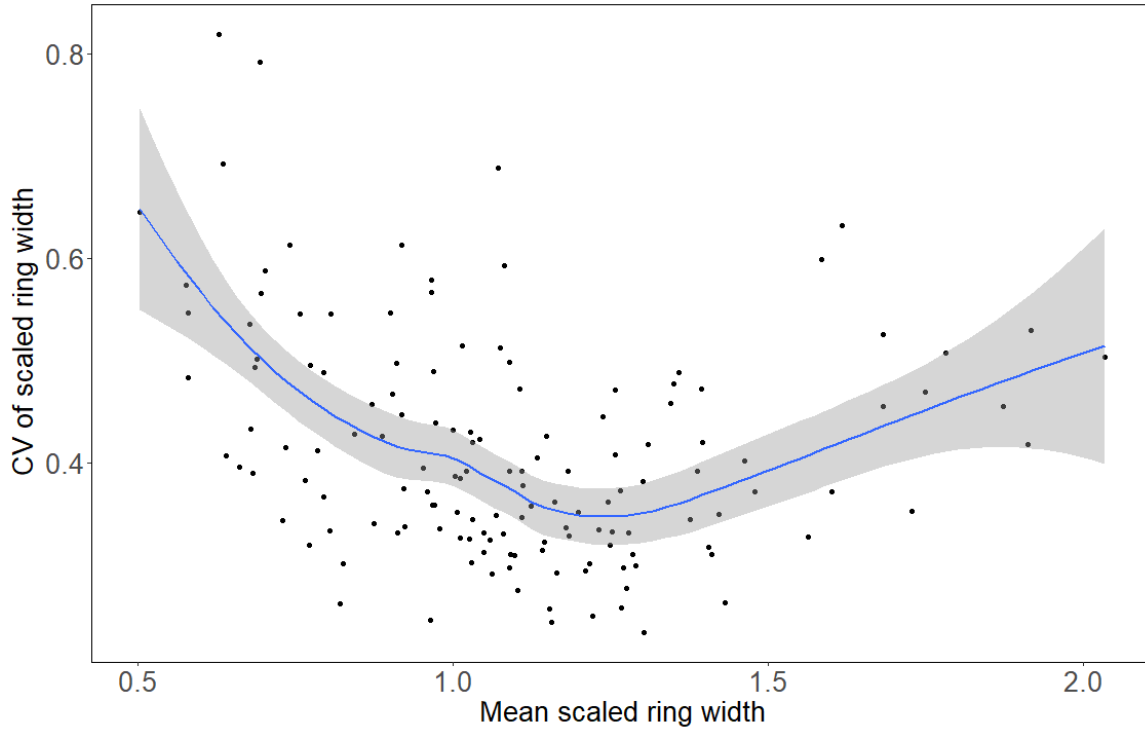


Figure 5. CV of the scaled ring width as a function of the raw average scaled ring width for each tree. The blue line is a polynomial regression line and the gray band is the 95% prediction interval.

Model of annual radial growth

The final model for the annual ring width increment (ARWI) had a marginal R^2 of 57% and a conditional R^2 of 91%. As expected, both MAT.trds and the experienced weather were important predictors of ARWI (Table 3). However, their effects were additive; the interaction terms between both types of variables were not statistically significant ($\alpha = 0.1$). Climate transfer distance had the same effect in ARWI as in SRW_{Mean} ; the maximum ARWI was achieved by the populations closest to home. The weather variables in the model are related to the beginning of the growing season in the current and previous year, and summer relative humidity of the current year. The positive coefficients for the beginning of the growing season indicate that later starts of

the growing season potentially avoided late spring frost injuries. Higher relative humidity in summer correlates with lower water stress and thus larger ring width increments. To evaluate the relative importance of home climate characteristics and weather variables, we predicted ARWI at age 9. Then, we varied each variable within its observed range while keeping the other fixed effects at their observed mean value (Figure 6). The range of MAT.trds produced the largest range of ARWI predictions. This range was the same as the range of marginal predictions, highlighting its relative importance in the model predictions.

Table 3. Parameter estimates, standard errors, and 90% confidence intervals (C.I.), for the model predicting annual ring width increment (Equation 3).

Variable	Estimate	Standard error	C.I.
Intercept	-2.22	1.01	-3.88, -0.56
Age	-0.93	0.0019	-0.096, -0.90
MAT.trds	0.0013	0.032	-0.052, 0.054
MAT.trds ²	-0.016	0.0093	-0.031, -0.00019
Summer relative humidity	0.039	0.069	0.028, 0.050
Start date of the frost-free period	0.023	0.0045	0.015, 0.031
Start date of the frost-free period of previous year	0.017	0.0048	0.0096, 0.025
σ Block	0.20		
σ Tree (Block)	0.73		
σ Residuals	0.39		

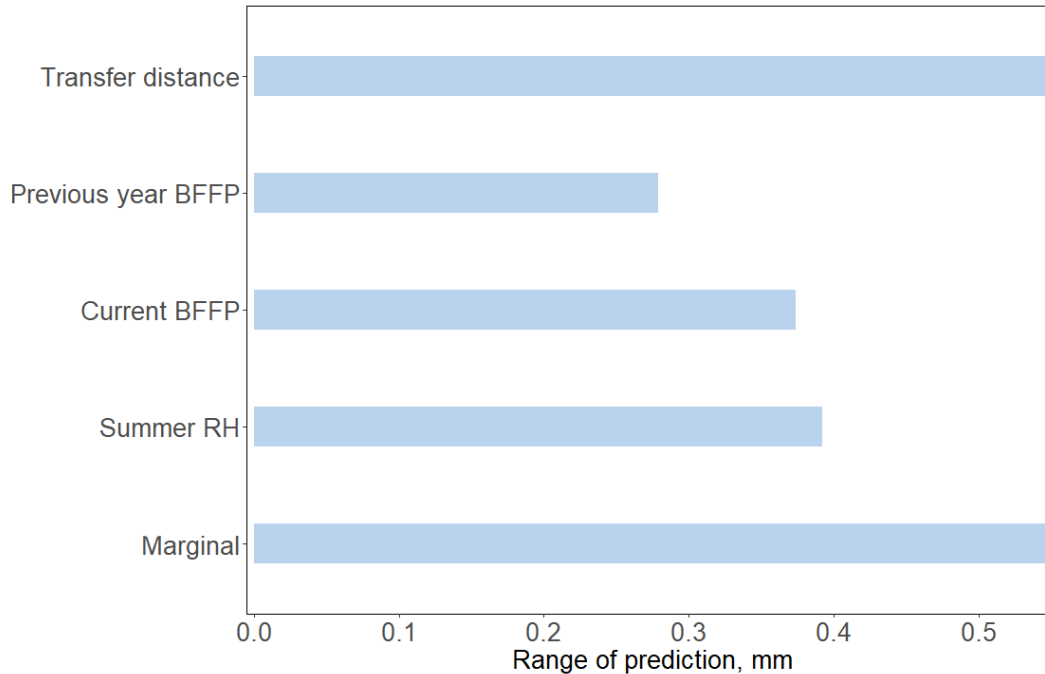


Figure 6. Range of predictions for the ARWI model calculated by varying each variable within its observed range, while keeping the others at their observed mean value and using the age 9.

DISCUSSION

We found evidence of adaptation to local climate among black walnut populations. Studies evaluating radial growth responses among populations also found evidence of genetic differentiation related to climate gradients in other tree species (Savva et al 2002, 2007; McLane et al 2011ab; Taeger et al 2013; Leland et al 2016; Chhin et al 2018; Housset et al 2019). Our models indicate that populations had the maximum SRW_{Mean} closer to home climate (climate transfer distance = 0) and decreased growth as the difference between test and home climate increased. For example, our model predicts that populations growing in their home climate grow 17% more per year compared to populations transferred 5 degrees warmer. Although this percent difference may seem small, it could result in a diameter at breast height difference of 30 versus

25 inches after many years of growth. These size differences are ecologically important because biomass and other allometric relationships with stem diameter are exponential. As expected, the marginal and conditional R^2 values for the model were low (3% and 10% respectively). This is likely because diameter growth is sensitive to interannual climate variability and competition dynamics (Alberto et al 2013). For this reason, tree height is typically used as a proxy for fitness in provenance tests to assess population differentiation in growth responses (e.g. Rehfeldt 1989, 1990, 1991; St Clair et al 2005; Thompson and Parker 2008; Rehfeldt et al 2014; Aitken and Bemmels 2016; Saenz-Romero et al 2017; Leites et al 2019). This was confirmed later in our results when we evaluated annual radial growth. These models had significantly higher R^2 values when climate experienced at the test site was included in the model.

Due to the limitations imposed by using data from only one test site, we were unable to model population-level responses to climate transfer. As a result, we could not test whether populations differ in their response to climate transfer distance and thus, whether there are differences in their adaptation to local climate (e.g. Rehfeldt et al 2018). Previous studies have demonstrated that in some species populations achieve maximum growth a short distance from the home climate and thus a lag in adaptation to climate exists, most commonly in populations from the colder front of the species range (e.g. Rehfeldt et al 1999; Savolainen et al 2007). On average, however, our results suggest that there is evidence of adaptation to local climate in these black walnut populations.

In our analyses, we found a relationship between temporal climate variability of home climate and phenotypic plasticity. We found that populations from more variable climates exhibit less phenotypic plasticity in annual radial growth. Phenotypic plasticity is trait specific, for diameter growth to be stable across years, other physiological and morphological traits need to

be more plastic (Bradshaw, 1965). We interpret this as evidence that in temporally variable climates, phenotypic plasticity in diameter growth may have adaptive value to ensure high fitness. A more stable diameter growth may confer higher fitness as larger black walnut trees compete better and produce seed earlier in time (Landt and Phares 1973). As previously highlighted, we found no correlation between populations' home climate MAT and populations home climate MAT standard deviation ($r = -0.026$), suggesting that these results are not confounded with evidence for adaptation to spatial climate.

The interaction between temporal home climate variability and climate transfer distance indicates that the effect of temporal home climate variability in SRW_{CV} when populations were moved to colder climates was less than its effect when populations were transferred to warmer climates. As populations were transferred farther from their home climate, and to warmer climates, the effect of temporal home climate variability in phenotypic plasticity becomes more important (Figure 4). In addition, when populations are moved to colder climates ($MAT.trds < -4$) the relationship between temporal home climate variability and phenotypic plasticity reverses. However, we note that only a few observations were available at that transfer distance ($MAT.trds < -4$) which makes the model less reliable in that region. The effects of temporal home climate variability on phenotypic plasticity when populations are moved to warmer climates, however, is clear and highlights the relevance of accounting for phenotypic plasticity when evaluating species and populations responses to climate change.

Phenotypic plasticity is beneficial if it results in better fitness (adaptive) and understanding results in that context is important. We found an inverse quadratic relationship between populations' SRW_{Mean} and its phenotypic plasticity (SRW_{CV}). The SRW_{Mean} serves as an indicator of fitness in black walnut because individuals that grow more per year typically reach

reproductive maturity earlier in time (Landt and Phares 1973). The highest and lowest SRW_{Mean} values were for populations with the highest phenotypic plasticity, indicating that there were two distinct types of phenotypic plasticity at play: adaptive leading to $SRW_{Mean} \geq 1$, and inevitable leading to $SRW_{Mean} < 1$. Populations with the highest SRW_{Mean} and SRW_{CV} occurred at transfer distance = 0 (Figures 3 and 5), those with the lowest SRW_{Mean} and highest SRW_{CV} occurred when transferred to warmer climates (Figures 3, 4, 5). A low SRW_{CV} was correlated with SRW_{Mean} of approximately 1 (Figure 5), and a low SRW_{CV} was correlated with higher temporal home climate variability (Table 2), which indicates that there is likely an adaptive value in a stable annual radial growth. However, our results also suggest that high phenotypic plasticity in annual radial growth may also be of adaptive value in some cases (e.g. $SRW_{Mean} > 1.5$ and $SRW_{CV} > 0.5$, Figure 5), while in others it just reflects inevitable plasticity (e.g. $SRW_{Mean} < 0.5$ and $SRW_{CV} > 0.6$, Figure 5). Within the context of a warming climate, populations from more variable climates may have an advantage in maintaining higher fitness as climate warms. At MAT.trds of greater than 3, populations originating in climates with high MAT.stdv's had low SRW_{CV} 's, which was related to a SRW_{Mean} close to 1 (Figures 4 and 5).

We also tested the effects of home climate characteristics in annual ring width increment (ARWI) and found that the maximum ARWI was achieved by the populations closest to home. The significant weather variables in the model were related to the beginning of the growing season in the current and previous year, and summer relative humidity of the current year. The positive coefficients for the beginning of the growing season indicate that later starts of the growing season potentially resulted in larger ARWI. A probable reason for this relationship is that later starts of the growing season avoided late spring frost injuries. Daily probabilities of frost at the test site location indicate that the earliest start of the frost-free period during the

experiment period was April 28th. The average 50-year probability of spring frost on April 28th is 27%. This percent drops dramatically (to 6%) after May 14th, the latest start of the frost-free period during the experiment period (Pennsylvania State Climatologist, 2020). The positive coefficient of summer relative humidity indicates that higher relative humidity resulted in larger ARWI. A high relative humidity during summer is indicative of lower water stress and higher carbon uptake by trees, resulting in increased growth. At the test site, summer relative humidity and summer precipitation were highly correlated ($r = 0.66$). Upon further analyses of the relative importance of home climate characteristics and experienced climate, we found that the range of MAT transfer distance produced the largest range of predictions. This range was the same as the range of marginal predictions, highlighting its relative importance in explaining variation among populations' annual growth.

In summary, the results suggest that genetic differences among populations and the resulting growth patterns are shaped by both spatial and temporal climate variability. We found evidence of specialization, and thus adaptation to spatial climate variability, in populations' average scaled radial growth as a function of climate transfer distance. We also found that temporal variability of populations' home climate was linked to phenotypic plasticity and populations from more temporally variable climates exhibited less interannual growth variability. These findings indicate that both spatial and temporal climate variability are critical in understanding genetic differences among populations. We also highlight the importance of assessing adaptive versus inevitable phenotypic plasticity among populations in future studies.

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CHAPTER TWO

Genetic differences in early growth patterns of black walnut populations: one size does not fit all

ABSTRACT

Many boreal and temperate forest tree species distributed across large geographic ranges are composed of genetically distinct populations that are adapted to the climate they inhabit. Forestry provenance studies and common gardens provide evidence of local adaptation to climate when associations between fitness traits and the populations' home climates are observed. Most studies that evaluate tree height as a fitness trait do so at a specific point in time (i.e. they focus on cumulative growth at a given age). In this study, we model height growth from planting to age 10 to elucidate differences in early growth patterns in *Juglans nigra* populations. The data comprised tree height measurements for 52 natural populations planted in one or more of 3 common gardens, totaling 342 observations. We use the Chapman-Richards growth model in a mixed-effects framework and test whether populations differ in growth patterns by incorporating populations' home climate into the model. We found that populations from warmer climates had the highest cumulative growth and reached maximum absolute growth earlier in time; populations from colder climates had a smaller size (cumulative growth), reached maximum absolute growth later in time, and had faster relative growth rates at any given age within our study's age range. Our results highlight the role natural selection may play in driving early growth patterns among populations within a tree species. They suggest that fast early growth rates are likely selected for in relatively mild environments that are presumably more competitive. Conversely, natural selection likely acts on cold tolerance rather than fast growth rates in harsh/cold sites.

INTRODUCTION

Boreal and temperate tree species with extensive geographic ranges encounter high spatial climatic variability; they accommodate this variability by forming genetically distinct populations that are adapted to a segment of the climate within the species range. Specifically, natural populations synchronize their annual growth cycle, defined as alternating periods of active growth and winter dormancy, with the frost-free period of their respective localities (Morgentsern 1996; Howe et al 2003; Bennie et al 2010). When grown in common gardens, populations exhibit differences in phenology that result in differences in the length of the growth period. Populations from colder climates, adapted to shorter frost-free periods, generally exhibit shorter growing seasons and are thus smaller. However, a shorter growing season in these environments confers them frost-hardiness and thus better cold tolerance. Conversely, populations from warmer climates, adapted to longer frost-free periods, are taller but more susceptible to late spring and early autumn frosts making them less cold tolerant (Campbell and Sorensen 1978; Rehfeldt et al 2004, 2018; Howe et al 2003; Aitken and Bemmels 2016).

Genetic differences along climatic gradients in cumulative growth at a given age have been well documented for populations in many tree species (e.g. Rehfeldt 1988, 1989, 1990, 1991; St Clair et al 2005; Thompson and Parker 2008; Rehfeldt et al 2014; Aitken and Bemmels 2016; Saenz-Romero et al 2017; Leites et al 2019); however, few studies have modeled or described the early growth patterns that lead to those differences among tree populations. For many tree species, early growth patterns are crucial in determining the likelihood of tree survival (Petit and Hampe 2006). In a regenerating forest, trees must compete not only with other tree seedlings but with herbaceous plants and woody shrubs; therefore, rapid juvenile growth is critical in early stages of forest regeneration. In addition, when trees arrive at the stem exclusion

stage (when canopy closure occurs and density dependent mortality begins) with a competitive advantage, they are more likely to survive subsequent competition and to occupy a dominant or co-dominant position in the new canopy (Oliver and Larson 1996); therefore, the taller a tree is by stem exclusion stage, the more likely it is to outcompete neighboring individuals (Weiner 1990; Oliver and Larson 1996).

Early growth rates are more important in climatically mild sites where competition with other vegetation is high and stem exclusion stage is reached earlier. Populations from climatically milder sites grow more per year due to their longer growing seasons; however, it is also likely that natural selection may favor faster early growth rates at these sites. Previous studies indicate that selection for growth rate in plants is related to environmental factors that influence productivity and competition dynamics (Rosielle and Hamblin 1981; Rose et al 2009; Dmitriew 2011). Slow growth rates are favored in climatically stressful environments, while fast growth rates are favored in resource-rich, or climatically-mild environments where competition is likely to be higher (Chapin et al 1993; Weis et al 2000; Kimball et al 2013). The combination of longer growing seasons with potentially higher growth rates would result in populations from mild climates displaying rapid growth early on, and reaching the inflection point on the sigmoidal curve that characterizes tree growth over time earlier than populations from colder environments.

In this study, we model differences in early growth patterns of natural black walnut (*Juglans nigra L.*) populations grown in common gardens. Previous studies have found that this species exhibits significant patterns of genetic variation in height growth along climatic gradients (Leites et al 2019), and strong differentiation among populations in several other fitness traits (Wright and Lemmien 1972; Bey 1973,1979). Additionally, early growth patterns are very

important for this shade intolerant species (Baker 1949). In mixed forest stands, trees must reach a dominant position by stem exclusion phase to survive (Burns and Honkala 1990).

To assess differences among populations' early growth patterns, we model cumulative height growth, absolute growth rate, and relative growth rates of 52 natural populations between ages 1 and 10 following classical growth analyses (e.g. Pienaar and Turnbull 1973; Paine et al 2012; Pommerening and Muszta 2016). Ultimately, these models will allow us to better understand tree species strategies to adapt to climate and their potential responses to climate change. We use data from provenance trials (common gardens), where differences among populations can be attributed to genetic differences (Davis et al 2005; Kremer et al 2014; Etterson et al 2016), and where clinal association between growth traits and the natural populations' home climate can be interpreted as evidence for genetic adaptation to climate (Campbell and Sorensen 1978, Rehfeldt 1984, Aitken et al 2008; Alberto et al 2013).

METHODS

Data

We used published and unpublished data from two provenance tests (common gardens) series, one established in 1967 (Bey 1973; Bey and Williams 1974) and another established in 1980 (Waite et al 1988). These experimental series comprised three test sites located in Indiana, Pennsylvania, and Vermont, USA, and evaluated a total of 92 natural populations from the black walnut range (Little 1971). Each test site followed a randomized complete block design (6 blocks in Indiana and Vermont, and 5 in Pennsylvania), with four-tree row plots. Trees were planted 3.7 meters (m) apart in Indiana, 3 m apart in Pennsylvania, and 2.5 m apart in Vermont. At each site,

total tree height was recorded at several ages between 1 to 10 years for all populations. We used the average tree height of each population at each age and test site. Climate normals for mean annual temperature for the period of 1961–1990 for all populations and test sites were obtained from Rehfeldt's climate surfaces for North America at 1 km resolution (Rehfeldt 2006; data available at <http://charcoal.cnre.vt.edu/climate/>); this time period represents the climate prior to seed collection, and thus is a good representation of the population's home climate as well as the climate during the test period. In this study, we used observations where populations were transferred to a test site within ± 2 °C of the population home climate to minimize the effect of transfer distance in the expression of innate growth potential for each population (Rehfeldt 1990; Rehfeldt et al 1999). Several studies have demonstrated the negative effect of transfer distance on growth potential, with maximum growth occurring close to home climate and decreasing as transfer distance increases in absolute terms (e.g. Carter, 1996, Rehfeldt et al 1999, Wang et al., 2006, Leites et al, 2012). Accounting for climatic transfer distance (difference between the climate of origin and test site) was not possible due to the number of observations available and the model complexity. In total, 52 natural populations and 342 observations were used in this study (Figure 7 and Table 4).

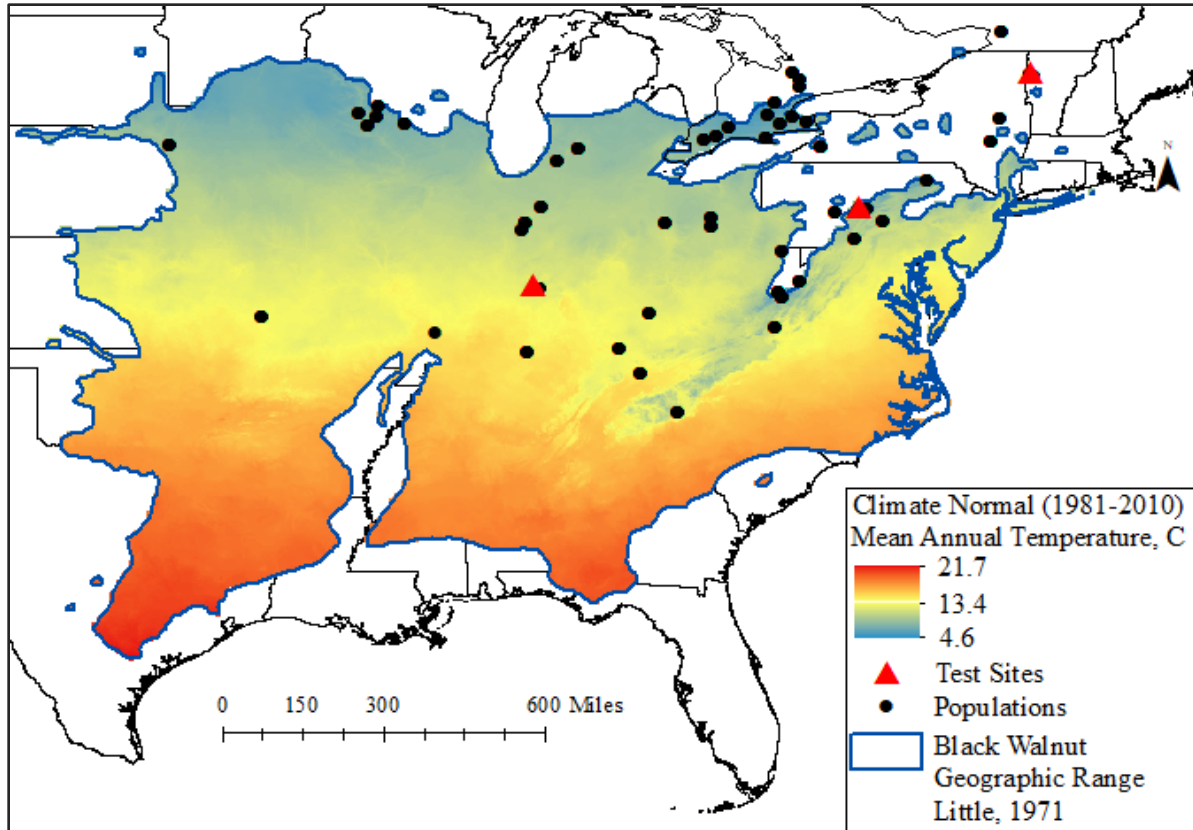


Figure 7. Distribution of evaluated populations and test sites in relation to the mean annual temperature of the species range.

Table 4. Test establishment year, number of populations tested, test site MAT, population MAT range, and ages measured at each test site.

Site	Year established	No. of populations	MAT ($^{\circ}\text{C}$)	Pop. MAT range ($^{\circ}\text{C}$)	Ages Measured (years)
Vermont	1980	29	7.1	5.4 – 8.9	1 – 6
Pennsylvania	1980	19	9.4	7.7 – 10.9	1 – 10
Indiana	1967	10	11.8	10.4 – 13.7	1 – 10

Analysis

To model populations non-linear height growth with age, we utilized the Chapman-Richards (Richards 1959) growth function in a mixed effects framework (Equation 1); we considered test site and population as random effects affecting the asymptote, and age as a fixed effect. We chose to incorporate the test site as a random effect on the asymptote (β_{00}) because site productivity is a strong determinant of maximum tree height (Oliver and Larson 1996). To test for population differences in growth patterns related to their adaptation to climate, we added mean annual temperature of the population’s home climate (MAT) as a fixed effect affecting the rate-related (β_{10}) and shape-related (β_{20}) parameters of Equation 1. In a common garden, observed clines in fitness traits along home climate gradients are interpreted as evidence for genetic differentiation in adaptation to climate (Campbell and Sorensen 1978; Rehfeldt 1984; Davis et al 2005; Etterson et al 2016). We use MAT because of previously observed clines with tree height in black walnut (Leites et al 2019), and in many tree species (reviewed by Aitken and Bremmels 2016). If populations’ MAT improved model fit and its parameter was statistically different from zero, we interpreted it as evidence that early growth patterns differ among populations and that such differentiation is likely driven by adaptation to climate. We did not

incorporate MAT affecting the asymptote parameter to avoid overparameterization and to reflect the aforementioned relationship between maximum height and site quality.

We evaluated models where population MAT affected either the rate-related (β_{10}) or the shape-related (β_{20}), and both simultaneously (full model presented in Equation 2). To evaluate the improvement to model fit, we used Akaike's Information Criterion (AIC; Akaike 1974) and to evaluate the statistical significance of the fixed effect parameters we used a t-test with an α -level of 0.05).

$$Ht_{ijk} = (\beta_{00} + u_j + u_{i(j)}) * (1 - e^{\beta_{10} * Age_k})^{\beta_{20}} + \varepsilon_{ijk} \quad (1)$$

$$Ht_{ijk} = (\beta_{00} + u_j + u_{i(j)}) * (1 - e^{(\beta_{10} + \beta_{11} * MAT_i) * Age_k})^{\beta_{20} + \beta_{21} * MAT_i} + \varepsilon_{ijk} \quad (2)$$

Where Equation 1 is the baseline model and Equation 2 is the model with MAT affecting both the rate-related (β_{10}) or the shape-related (β_{20}) parameters. Ht_{ijk} is the average height in decimeters (dm) of population i in site j at age k . β_{00} , $\beta_{10} + \beta_{11}$, and $\beta_{20} + \beta_{21}$ are parameters for the asymptote, rate related, and shape related, respectively. MAT_i is the mean annual temperature of population's home climate i , Age_k is the population age, u_j and $u_{i(j)}$ are the random effects for site and population nested within site, and ε_{ijk} is the error term.

We constructed bootstrapped 95% prediction confidence intervals for the final model by using the variance-covariance matrix of the parameter estimates and resampling (n=1000) parameter estimates from the multivariate normal distribution to produce a range of predictions. We then used the 2.5 and 97.5 percentiles of the resampled predictions to get the upper and lower bounds for the interval. The final model form was used to calculate absolute and relative growth rates through time (Appendix C; Pommerening and Muszta 2016). All analyses were

performed in the statistical environment R (v.1.2.1335 RStudio Team 2018). To fit mixed effects models, we used the package lme4 (Bates et al 2015).

RESULTS

The parameter estimates for the evaluated models are presented in Table 5. MAT was a statistically significant parameter and improved model fit when added to the rate-related parameter β_{10} (Table 5, model 2), to the shape-related parameter β_{20} (Table 5, model 3), and when added to both the shape-related parameter β_{20} and the rate-related parameter β_{10} (Table 5, model 4). However, model 3 had one of the lowest AIC and all parameters were significantly different from zero and was chosen as the final model (Figure 8, diagnostic plots and statistical summaries for the final model are presented in Appendix D and E).

Table 5. Parameter estimates, model AIC, and standard deviation (S) of the residuals for models tested. Parameter significance at $\alpha = 0.05$ is indicated by *. Final selected model is indicated by **.

Model Tested	Parameter					Model AIC	S Residuals
	β_{00}	β_{10}	β_{11}	β_{20}	β_{21}		
1) Base	96.16*	-0.17*		1.92*		1679	2.36
2) Rate Related	97.33*	-0.085*	-0.0093*	1.95*		1631	2.05
3) Shape Related**	103.36*	-0.16*		2.58*	-0.076*	1617	2.06
4) Rate and Shape Related	105.73*	-0.18*	0.0035	2.77*	-0.099*	1617	2.08

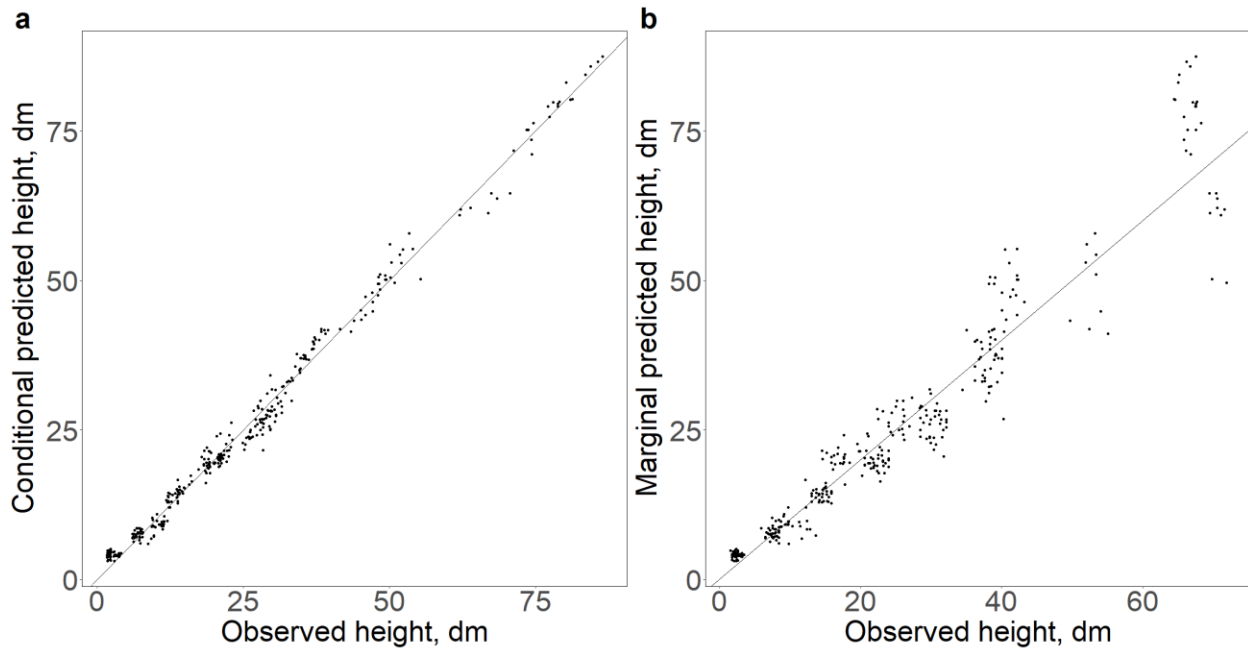


Figure 8. Final model plots, (a) conditional predicted heights (using fixed and random effects) vs observed heights, (b) marginal predicted heights (using only fixed effects) vs observed heights.

Site effects on the asymptote were accounted for in the random effect and were likely driven by differences in site quality and management, not climate (Figure 9). Although the Indiana test-site has the highest mean annual temperature (11.8 °C), it performed similarly to the Vermont test site that has a mean annual temperature of 7.1 °C, while the Pennsylvania performed best having a mean annual temperature of 9.4 °C. Additionally, because we only used observations where populations were transferred within +/-2 °C of the population home climate, the impact of test site climate was likely diminished.

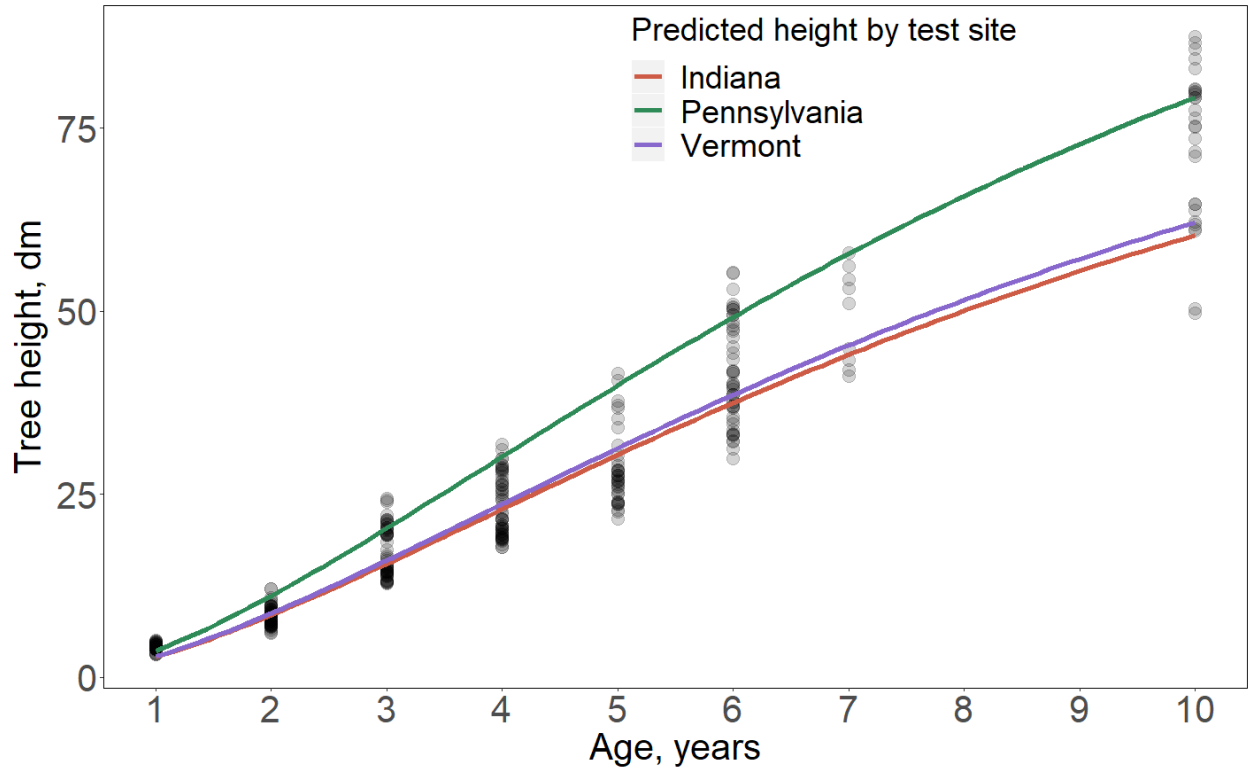


Figure 9. Differences in predicted height growth for each test site. Each line represents the predicted average height trajectory for each test site. Gray circles represent raw observations.

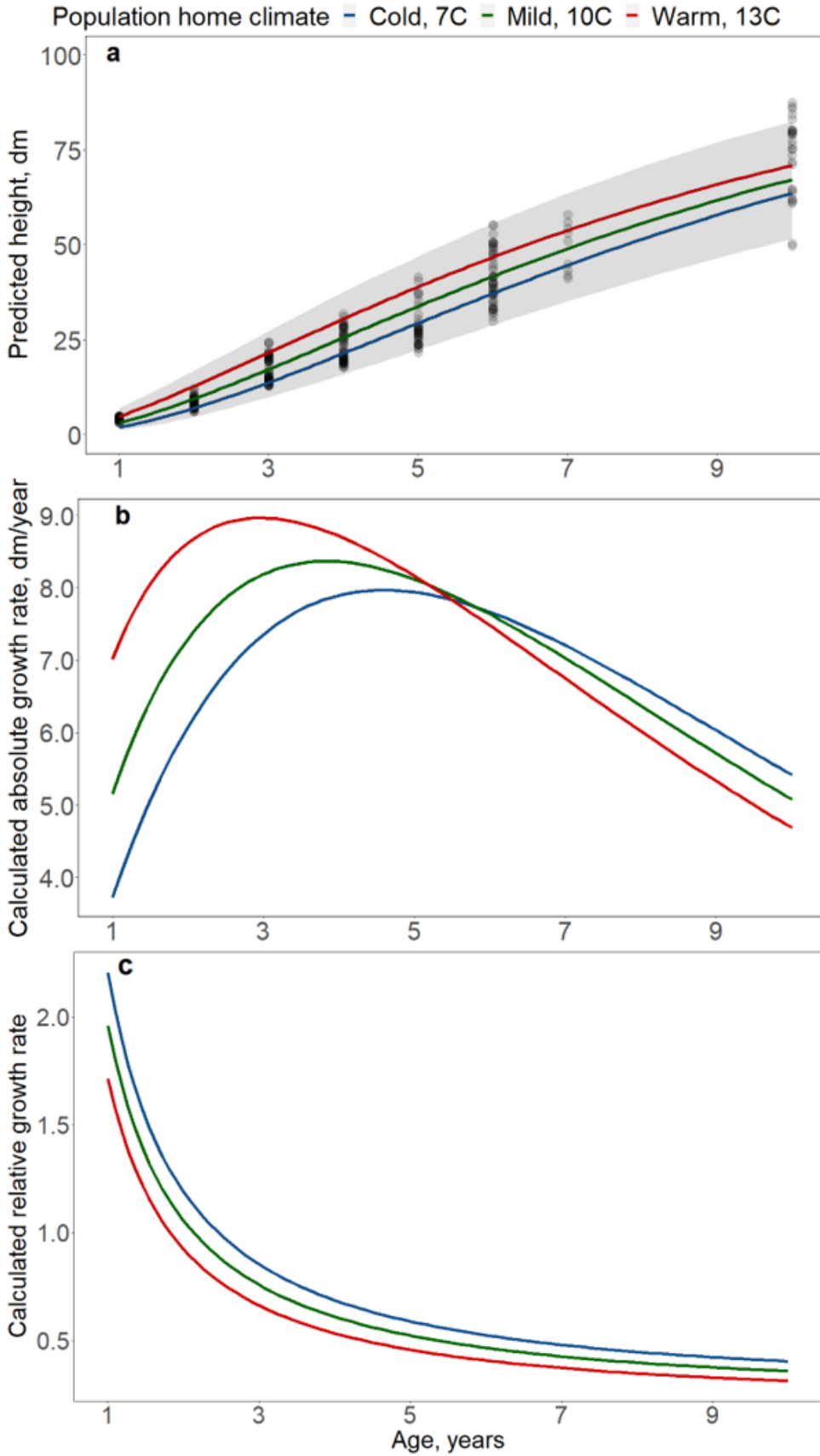


Figure 10. a) Predicted population tree height using the selected model for three hypothetical populations originating in cold (7 °C MAT), mild (10 °C MAT), and warm (13 °C MAT) climates. The 95% prediction confidence interval is represented by the gray band. Gray circles represent observations. (b) Calculated absolute, and (c) calculated relative growth rates for the same three hypothetical populations.

Cumulative growth. Compared to populations from cold climates, populations from warm climates exhibit faster growth from an early age; but, these relative differences among populations decrease through time. At age 2, populations with a MAT of 13 °C are predicted to be 83% taller than populations with a MAT of 7 °C, by age 5 they are predicted to be 33% taller, and by age 10 they are predicted to be 11% taller (Table 6 and Figure 10a).

Absolute growth rates (AGR). Populations from warm climates have higher maximum AGR and reach it much earlier in age compared to populations from cold climates. Populations with a MAT of 13 °C are predicted to reach their maximum AGR of 8.97 dm/year by age 3, whereas populations with a MAT of 7 °C will not reach their maximum AGR of 7.97 dm/year until age 4.6. The age of maximum AGR decreases by 0.27 years for each additional degree Celsius in MAT. The maximum AGR decreases by 0.17 dm/year for each decreased degree Celsius in MAT (Table 6 and Figure 10b). After age 5, the higher absolute growth rate of populations from cold climates is the result of their faster relative growth rates.

Relative growth rates. Given their larger size, populations from warm climates exhibit slightly slower relative growth rates per unit area through time. At age 2, populations with a MAT of 7 °C are predicted to grow 1.12 times their size while populations with a MAT of 13 °C grow 0.92 times their size. The difference in relative growth rate decreases with age and by age 5

the difference in relative growth rate between these populations is of 0.9 (Table 6 and Figure 10c).

Table 6. Predicted growth responses for hypothetical populations originating in cold (7 °C) and warm climates (13 °C). For mean height and absolute growth rate, percent change was calculated using the value at MAT 7 °C as the baseline ((the value at MAT of 13 °C – the value at MAT of 7 °C) / the value at MAT of 7 °C).

Predicted Response	Age	Hypothetical Home Climate		
		7 °C	13 °C	Percent Change (%)
Mean Height, dm	2	7.0	12.8	82.8
	5	29.3	38.9	32.5
	10	63.6	70.3	11.5
Absolute growth rate, dm/year	2	6.1	8.6	41.9
	5	8.0	8.2	2.9
	10	5.4	4.7	-13.5
Relative growth rate	2	1.19	0.92	
	5	0.59	0.46	
	10	0.40	0.31	
Age of Maximum Absolute Growth Rate (years)		4.6	3.0	

DISCUSSION

In this study we model the early growth patterns of natural black walnut populations and find evidence of genetic differentiation related to population home climate. We use data from three test sites and include populations with $MAT \leq |2|$ °C of the test site MAT to reduce the

effect of climate transfer distance. As a result, the tests and populations are not fully crossed (i.e. each population is not tested in each test site). However, there is a small overlap in the MAT among populations tested in the three sites (Table 4). Some populations adapted to colder climates were tested in both the Vermont (cold climate) and Pennsylvania (mild climate) test sites. Similarly, populations adapted to warm climates were tested in the Pennsylvania (mild climate) and Indiana (warm climate) test sites. In general, populations from warmer climates were tested in the warmer test site, while populations from the colder climates were tested in the coldest test site. This limitation presents the possibility that effects attributed to MAT could be partly confounded with the test effect. However, we believe that the confounded test effect may not be important for two reasons. First, the magnitude of the test effect on the overall growth does not correlate with the test MAT. If these differences were confounded with test site climate, we would expect populations to perform best at the warmest test site. Although the Indiana test site has the highest mean annual temperature (11.8 °C), it performed similarly to the coldest test site in Vermont (7.1 °C). The Pennsylvania site actually performed best with a mean annual temperature of 9.4 °C. Second, diagnostic plots (Appendix E) show that the model fits all tests and populations equally well, making the confounding effect less likely to exist. If it existed, differences in residual distribution by site would likely be observed.

Our models indicate that populations with the highest cumulative growth originate in warmer climates (as measured by MAT), while populations from colder climates are smaller. In fact, this difference is present at age 1, which is the start of the measurement period and the models we created. Yet surprisingly, populations from colder climates exhibit slightly faster relative growth rates at each observed age within the study's range; these differences decrease through time. One possible explanation is that populations differ in phenotypic plasticity and

acclimation. However, the populations from colder climates were not tested in environments different from their home climate so there would be no reason for acclimation. Another possible explanation is that populations adapted to colder climates may grow more per day compared to populations from warmer climates to account for their shorter window of favorable growing conditions (reviewed in Alberto et al 2013). In either case, this result warrants further investigation. Despite the higher relative growth rates in early growth, populations from cold climates do not compensate for the cumulative growth difference observed at age 1, where our models start.

We also find evidence of a cline between the age of maximum absolute growth and home climate, although the shape of the cline is not discernible from these models' predictions. In general, populations from warmer climates achieve maximum absolute growth earlier than those from colder climates (4.6 vs 3 years), which would provide a competitive advantage early on to populations from warmer climates. Additionally, part of the modeled differences in early growth patterns can be explained by the well-documented differences in phenology among populations of several tree species. These phenological differences, such as differences in bud break and bud set, translate partly into differences in growing season lengths and thus differences in cumulative growth (reviewed by Aitken et al 2016). The importance of competition during seedling and sapling stage, and differences in competition levels in climatically disparate sites are factors that also likely play a role in these early growth patterns. After a stand replacing disturbance, the rapid height growth of seedlings in a regenerating forest is critical for seedling survival as it competes for light with other vegetation; furthermore, the size of the sapling during the stem exclusion stage of forest development is a determinant of tree survival as density-dependent mortality occurs (Oliver and Larson 1996). Therefore, patterns of fast early height

growth rates lead to taller trees better able to capture light resources and survive competition.

Biophysical models of site productivity (e.g. Monserud 2006; Weiskittel et al 2011) indicate that climatically milder sites are on average more productive than climatically harsher sites.

Competition is thus higher in these sites and stem exclusion stage is likely reached earlier (Oliver and Larson 1996). In these sites, natural selection is likely driven, at least in part, by competition dynamics.

Conversely, it is likely that for populations adapted to cold climates, survival is more dependent on cold tolerance than overcoming competition (Hanninen 2016). A shorter growing season allows cold adapted populations to avoid late spring and early autumn frosts; therefore, they are more cold tolerant but exhibit less cumulative growth (Morgensten 1996). Natural selection may also favor slower early growth rates in harsh environments (Chapin et al 1993; Weis et al 2000; Kimball et al 2013). The trade-off between selection for cold tolerance and growth potential has been well documented in tree species (Rehfeldt 1991; Howe et al 2003; Aitken and Bemmels, 2016; Leites et al 2019) and more generally as an ecological strategy in all plant species (Grime 2006). For trees, the cline of the age of maximum absolute growth with home climate has received less attention (but see Rehfeldt et al 1991 for an example) and could provide insights on the tradeoff between competition and stress-tolerance driven selection. We also found that population differences in cumulative, absolute, and relative growth rates diminish through time. This is likely due to the initiation of competition among trees in the common gardens as they approached age 10. This competition would obscure the expression of genetic differences and likely decrease observed differences (e.g. Franklin 1979; Foster 1986; Rehfeldt et al 1991). Tree level mortality data, which could also explain decreased differences through time, is not available at all test sites. However, original testing at the Vermont and Indiana sites

indicate that mortality rates were distributed randomly across populations and likely does not impact observed differences among populations (Bey and Williams 1974; Waite et al 1988).

The differences we observed in early growth patterns support that intraspecific competition may be responsible for the displacement of populations from their optimal climate to colder climates within the species geographic range (Namkoong 1969; Matyas and Yeatman 1992; Rehfeldt et al 2004; Rehfeldt et al 2018). For many tree species, populations inhabit climates slightly colder than optimal, with populations adapted to colder climates having a larger lag between their ecological and physiological optima (Rehfeldt et al 2018). The large differences in size as well as the earlier age of maximum absolute growth for populations from warmer climates, could lead to populations from colder climates being competitively excluded by those with higher growth rates. The mechanism behind this is well explained in Rehfeldt et al 2004; in each new generation, the balance between competitive exclusiveness and stress tolerance needs to be re-established. At this point, asymmetric gene flow from the center of the distribution to the periphery, and competition-driven selection interact generating populations that do not inhabit their physiological climate optimum. Therefore, the distribution of populations within a species range, is the result of a balance between selection for competitive ability and for stress tolerance (e.g. Loehle 1998; Howe et al 2003; Rehfeldt, 2004; Bennie et al 2010).

In summary, populations originating in warmer climates exhibit faster cumulative growth rates through time compared to cold adapted populations (83% more at age 2). Populations originating in warm climates achieve maximum absolute height growth at an earlier age. Our results highlight the role that natural selection may play in driving differences in early height growth patterns among populations within a species. Competition driven selection is likely more

important in climatically mild environments and achieving a large size fast is critical. In climatically harsh environments, cold tolerance rather than large size is more important for survival. These results highlight that populations' distribution within their range is the result of a balance between competition ability and stress tolerance.

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APPENDIX A

List of population home climate variables evaluated in Equation 1, 2, and 3.

Climate variable	Acronym
Mean annual temperature, C	MAT
Mean annual warmest month temperature, C	MWMT
Mean annual coldest month temperature, C	MCMT
Frost free period	FFP
Degree-days below 0°C	DD0
Degree-days above 5°C	DD5
Summer heat moisture index	SHM
Hargreaves climatic moisture deficit, mm	CMD
Precipitation as snow, mm	PAS
Mean annual precipitation, mm	MAP
May to September precipitation, mm	MSP

APPENDIX B

List of annual weather variables at the test site evaluated to be used in Equation 3. Both the year evaluated and the year before were used in the correlation matrix for each weather variable.

Climate variable	Acronym
Mean annual temperature, C	MAT
Mean annual warmest month temperature, C	MWMT
Mean annual coldest month temperature, C	MCMT
Annual relative humidity	RH
Mean annual precipitation, mm	MAP
May to September precipitation, mm	MSP
Degree-days above 5°C	DD5
Degree-days below 0°C	DD0
Summer heat moisture index	SHM
Annual heat moisture index	AHM
Hargreaves climatic moisture deficit, mm	CMD
Temperature difference between MWMT and MCMT, C	TD
Frost free period	FFP
Beginning of the frost-free period	bFFP
End of the frost-free period	eFFP
Mean annual solar radiation, MJ m ⁻² d ⁻¹	MAR

Hargreaves reference evaporation, mm	EREF
Winter degree-days below 0°C	DD0_wt
Spring degree-days below 0°C	DD0_sp
Average winter temperature, C	Tave_wt
Average spring temperature, C	Tave_sp
Average summer temperature, C	Tave_sm
Summer relative humidity, %	RH_sm
Summer Hargreaves climatic moisture deficit, mm	CMD_sm
Spring Hargreaves climatic moisture deficit, mm	CMD_sp
Spring precipitation, mm	PPT_sp
Winter precipitation, mm	PPT_wt
Winter precipitation as snow, mm	PAS_wt
Spring precipitation as snow, mm	PAS_sp

APPENDIX C

Model forms used to calculate absolute (A) and relative (B) growth rates from Equation 3 (Pommerening and Muszta 2016).

$$Ht' = \beta_{00} * \beta_{10} * (\beta_{20} + (\beta_{21} * MAT)) * (e^{\beta_{10} * Age}) * (1 - e^{\beta_{10} * Age})^{((\beta_{20} + \beta_{21} * MAT) - 1)} \quad (\mathbf{A})$$

$$Ht'' = \beta_{10} * (\beta_{20} + \beta_{21} * MAT) * ((1 - e^{\beta_{10} * Age})^{-1}) \quad (\mathbf{B})$$

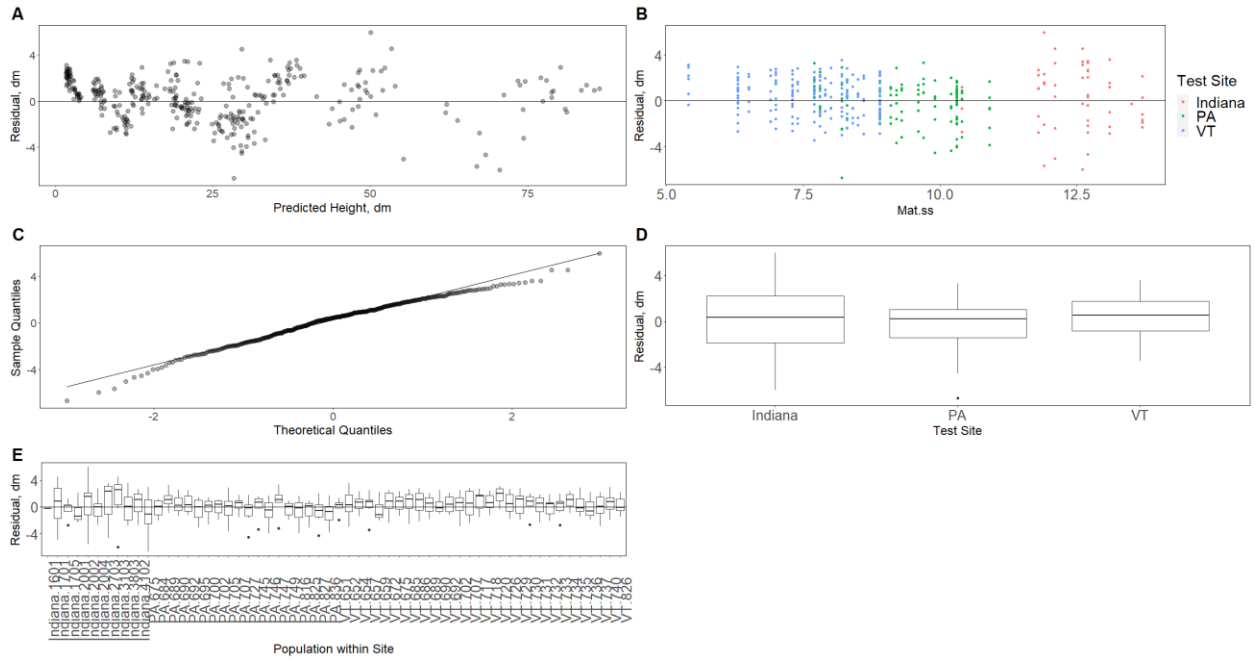
In Equation C, Ht' is the absolute growth rate in dm. In Equation b, Ht'' is the relative growth rate. β_{00} , β_{10} , and $\beta_{20} + \beta_{21}$ are parameters for the asymptote, rate related, and shape related, respectively. MAT is the mean annual temperature of the population, Age is the population age.

APPENDIX D

Statistical summary and diagnostic plots for the selected model (Table 5, Model 3).

Parameter	Estimate	SE	Sum of Squares	Proportion of Explained Variation
β_{00}	103.4	8.74		
β_{10}	-0.16	0.0098		
β_{20}	2.58	0.11		
β_{21}	-0.076	0.0089		
σ Site	13.26			
σ Population within Site	8.41			
σ Residual	2.06			
Observed			131826.99	
Predicted (Fixed Effects)			115637.00	0.88
Predicted (Complete Model)			128453.52	0.97

APPENDIX E



Diagnostic plots for final model, (a) residual vs predicted height, (b) residual vs population home climate colored by test site, (c) normal quantiles plot for the residuals, (d) residual variation by site, and (e) residual variation by population within site.