

The contrasting effects of local environmental conditions on tree growth between  
populations at different latitudes

by

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## **Abstract**

To forecast future forest productivity and function it is critical to account for forests' responses to current environmental conditions. Current widely used climate envelope approaches, i.e., correlations between climatic variables and the presence of a species, simulate responses for the whole species and predict future range based solely on climatic suitability. However, most tree species will not be able to migrate to environmentally suitable locations fast enough to cope with climate change. Furthermore, short-term tree responses to climate change will take place within current populations, and these populations, acclimated to their local environments, are not likely to respond similarly to climate change. Thus, to develop reliable forecasts of forest responses to climate change, we need to consider this variability among populations. In this study, we tested the effect of environmental conditions on the growth of two common maples species (*Acer rubrum* L. and *Acer saccharum* Marshall) at two different latitudes within their northern distributional range. We collected tree growth data, i.e., increment cores, and analyzed year to year variability in tree growth as a function of temperature and precipitation. We identified the times of the year with a stronger association with tree growth, indicating phenological differences between the two latitudes, and quantified growth as a function of those variables. Results showed divergent responses between species and between populations of the same species. *Acer rubrum* had a positive response to increasing summer temperature and precipitation in the north, but a negative association to increasing summer temperature in the south. *Acer saccharum* only showed significant responses in the south, negative to summer temperature increases and positive to higher precipitation. Predicted growth under difference climate scenarios predicted for the region, showed that northern populations and southern populations

did not significantly differ from current range of growth variability but, still, reflected future trends of decreased growth under a forecasted climate, i.e., higher temperatures and lower precipitation. These results document population level responses to environmental conditions of these two species providing latitude-specific guidance for future forest management.

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## Introduction

Global climate patterns have rapidly changed in the past century with increasing temperatures, more intense precipitation events and higher frequency of extreme drought (IPCC 2014). These changes will shape forest ecosystems worldwide, as their composition, structure and function are strongly influenced by local environmental conditions (Cramer *et al.*, 2001; Wang *et al.*, 2017). Shifts in environmental variables will likely result in the alteration of tree physiology, population demography, community assemblage and species distributional ranges (Ackerly, 2003; Chaves *et al.*, 2002; Clark *et al.*, 2011; Hatfield *et al.*, 2015). However, the effects of these changes will be heterogeneous across the distributional range of a species (Sáenz-Romero *et al.*, 2017); with populations at higher latitudes likely benefiting from warming and populations at lower latitudes mostly being negatively affected (Davis & Shaw, 2001). Within these broad patterns of climate change, it is not clear which populations will be most affected. Thus, to understand how individual populations are coping with current environmental trends we need to assess the impact of climate change across a species distributional range.

Climate envelope approaches are the most common methods used to predict future changes in the distributional ranges of tree species, they use correlations between occurrence of a species and environmental conditions at those sites (Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Watling *et al.*, 2013). These predictions work well to assess dynamics that may take place on the order of centuries. However, to make predictions at finer time scales i.e., decades, information about performance at the population level is needed, and these responses are likely to differ across the distributional range of a species. Increases in temperature at higher latitudes will result in a longer growing season which might benefit the growth of local tree populations since they could be operating below their temperature optimum (Tucker *et al.*, 2001,

Way & Oren, 2010); however, for populations of the same tree species at lower latitudes, an increase in temperature might result in a shift beyond their optimal temperature range and affect growth negatively (Feeley *et al.*, 2007). As a result, it is reasonable to expect that similar environmental shifts will shape tree populations differently in the future. In this context, multi-site demographic studies can help us to understand the variability among populations responses to climate change.

The two most important climatic variables affecting tree growth are growing season temperature and precipitation (Babst *et al.*, 2013; Niinemets, 2010). Temperature affects growth by conditioning cell division, photosynthesis, and respiration (Ludlow, 1997). Temperatures from late winter to spring can also affect the initiation of cambial cell division and xylem differentiation which are closely related to tree growth (Oribe *et al.*, 2001; Oribe & Kubo, 1997). Cumulative elevated temperatures from late winter to spring can extend the growth period by advancing cambial reactivation and xylem differentiation and then facilitate more growth (Begum *et al.*, 2012). Temperature also regulates photosynthesis by affecting the related apparatus as well as the raw materials intake (Mathur *et al.*, 2014). High temperatures exceeding photosynthetic temperature optimum will deactivate Rubisco and inhibit the activity of stromal enzymes (Law & Crafts-Brandner, 1999). At the same time, increasing temperature will exacerbate water stress through increasing soil deficits and atmosphere deficits which will induce water loss via soil-plant-atmosphere continuum causing increasing evaporation (Bréda *et al.*, 2006). As a result, there will be the closure of stomata in order to avoid water loss which at the same time decreases the carbon dioxide intake (Heath & Meidner, 1957). All these combined factors result in an overall decrease in photosynthesis as temperature increases. Temperature can also have an immediate effect on respiration. Increasing temperatures can simulate enzyme



activity result on an exponential increase in respiration rate (Heskel *et al.*, 2016; Hofstra & Hesketh, 1969). In contrast to photosynthesis, respiration also has a higher ability to acclimate to increases in temperature (Smith & Dukes, 2017) which means plants can adjust their respiratory rate to temperature increases.

Besides temperature, precipitation is another important climatic variable affecting tree growth. Forests lose water via the soil-plant-atmosphere continuum, and insufficient precipitation can increase water deficit especially when temperature is high (Brady *et al.*, 2008; Bréda *et al.*, 2006). Water scarcity during the growing season can cause hydraulic failure which is the inability of plants to move water from roots to other parts (McDowell *et al.*, 2008). Meanwhile, as leaves are under water stress, they respond to this stress by closing their pores which will cause carbon starvation within the plant cell (Adams *et al.*, 2009).

When studying the effect of temperature as well as precipitation on tree growth and legacy effects are also relevant (Peltier *et al.*, 2016). Legacy effect, which has been widely documented in the literature, shows that climatic events that occur in the previous year can have a large influence on tree growth in the current year (Peltier *et al.*, 2016, Ibáñez *et al.* 2018, Ding *et al.*, 2020). When there are drought events, trees can operate anatomical and physiological adjustments and the growth in following years will then be affected (Pasho *et al.*, 2011). Also, the continuous gain of resources from previous year can also be allocated to growth in following year (McCollum & Ibáñez, 2020). Thus, this factor needs to be considered in any environment related analysis of tree growth response to climate change.

Even though some studies have shown that the climatic factors discussed above are critical in controlling tree growth, tree species with wide distributions are likely to show physiological acclimation at the population level, with photosynthesis and respiration rates

determined by the particular environmental conditions of the site (Smith & Dukes, 2013). As a result, each population's susceptibility to warmer and drier conditions is likely going to be different and a function of both the population's acclimation ability (Repo *et al.*, 2008) and the direction of the change with respect to the population optimum (Ibanez *et al.*, 2017), thus environment-induced growth responses are likely location-specific (Gaillard *et al.*, 2013).

To investigate how current trends in temperature and precipitation may differently affect future tree growth across populations, we studied the growth patterns of two tree species over the last 21 years (from 1997 to 2017) at two different geographic locations that differ in growing season length by more than 50 days. We analyzed tree growth as a function of spring temperature, summer temperature and summer precipitation. Spring temperature is a good proxy for the beginning of the growing season and determining its length. Summer temperature and precipitation are good proxies for water demand and water availability since both temperature and water availability (Tardif *et al.*, 2001, Schulze *et al.*, 1973). The objective of this study was to evaluate the effect of year-to-year variability in environmental conditions on the annual growth of these two species and assess how these effects may vary between latitudes. We aimed at answering the following questions: 1) How do temperature and precipitation affect the growth of these two species? 2) How do these effects differ for the same species located at different latitudes? 3) If these tree species respond differently, how could future climate change in this region affect these tree species? Answers to these questions will help us to assess possible forest changes under anticipated changes in the future and these inform local forest management.

## **Methods**

Due to its complexity, the study of climate change effects on plant performance needs data collected over time at a relatively fine resolution (Pugh *et al.*, 2018). In long-lived species like

trees, we can study their growth records from tree cores to learn about their growth patterns over years of varying environmental conditions to then infer about their future performance under climate change.

- Study Area

We collected tree core samples from forest stands located at two different latitudes in Michigan's Lower Peninsula, USA (Fig. 1). This region encompasses two different Eco Provinces, the northern part is categorized as Laurentian Mixed Forest and the southern part as Midwest Broadleaf Forest (McNab *et al.*, 2007). At the southern location, the climate is usually continental with warm to hot summers and frequent growing season water deficits. The average growing season length here is around 173 days. In the northern site winters are moderately long, and snow usually stays on the ground throughout the winter. The average growing season is relatively short which is about 122 days (Hatfield *et al.*, 2015; McNab *et al.*, 2007). The northern stands used in this study were located on the properties of University of Michigan Biological Station, Pellston, MI (Table 1). The average minimum temperature in January is -12.1°C, the average maximum temperature in July is 26.2 °C, and the annual precipitation is 735.076 mm. The southern stands are located around Ann Arbor, MI (Table 1). The average minimum temperature in January is -7.4 °C, the average maximum temperature in July is 28.8 °C, the annual average precipitation is 981.202 mm (NOAA, 2019).

All trees for this study were identified within a 100 m<sup>2</sup> plot at each site. In the southern sites, the overstory species are dominated by maple (*Acer*), oak (*Quercus*), hickory (*Carya*) and cherry (*Prunus*) while the understory is mainly dominated by maple (*Acer*) and American hophornbeam (*Ostrya virginiana*). In the northern sites, the overstory species are dominated by maple (*Acer*),

beech (*Fagus*) and aspen (*Populus*), while the understory is mainly dominated by beech (*Fagus*) and maple (*Acer*).

- Studied species

The two target species chosen for this study were red maple (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marshall), these are common tree species widely distributed across eastern North America (Fig. 1). The sampled populations are located within the northern range of both species (Fig. 1). *Acer rubrum* is a mid-canopy species with moderately long-life span (Barnes & Wagner, 2004), it grows at a medium to fast rate. It is tolerant of both saturated and well-drained soil. *Acer saccharum* is a large tree with a long-life span, it grows slowly especially in shaded conditions. It grows in well-drained, fertile soils, is intolerant to flooding during the growing season and is drought intolerant (Barnes & Wagner, 2004). Research has shown that *A. rubrum* and *A. saccharum* respond differently to environmental conditions at different life stages because of their physiology differences. For example, Edwards and Norby (1999) found that the coarse root respiration and root mass of *A. rubrum* seedlings responded negatively to increasing temperature while this negative effect was not significant for *A. saccharum* seedlings. Bishop *et al.*, (2015) found that the effect of temperature on adult *A. saccharum* growth can vary depending on the factors such as soil moisture, acidic deposition and the age of the population. Zhang *et al.*, (2015) showed that compared to environmental variability, site history such as logging events or other natural disasters have a bigger impact on the growth of *A. rubrum* which means we might not expect to see a big effect of climatic variables on their growth. These studies provide evidence that these two species might respond to environmental variability differently.

- Field and Laboratory Methods

Field sample collection took place in May and July of 2019. At each stand all *A. rubrum* and *A. saccharum* trees with a diameter at breast height (DBH) greater than 10 centimeters (cm) were sampled. Two increment cores were extracted from the east and west side of each tree using a 4.3 millimeter (mm) Haglof increment borer. All tree cores were stored in paper straws and air dried by spreading the cores out on a table for 24-48 hours before processing (Phipps, 1985).

The preparation of the tree cores followed standard protocols (Stokes & Smiley, 1968; Phipps, 1985; Speer, 2010). All air-dried tree cores were placed on wooden mounts prior to being sanded with P220 sandpaper to provide a flat core surface. The samples were then sanded with increasingly finer grit sandpaper (P320, P600, and for *A. saccharum*, up to P1500) until the individual growth rings of the cross-sectional view could be viewed clearly under a microscope. Among all of the collected samples, only those increment cores containing distinct growth rings were selected for further scanning and analysis.

The cores were scanned using a flatbed scanner at 1200 dpi resolution. The width of each growth ring in the tree core was measured using the software program CooRecorder (version 9.3.1). Growth ring measurements were taken along a predetermined radius in a straight line, and generally perpendicular to the growth ring boundaries. All the tree cores collected from the same site were cross dated using the software program CDendro (Version 9.3.1). After the cross-dating process, growth ring width measurements of the two tree cores that had been collected from the same individual tree were averaged to calculate the annual radial growth. The subsequent analysis only utilized the tree core samples that could be correctly cross-dated for at least 10 years.

- Climate Data

All the climate data used in this study was retrieved from the National Oceanic and Atmospheric Administration (NOAA) national weather station database (NOAA, 2019). The climate data obtained included the average monthly temperature and monthly precipitation from 1997 to 2017. The climate data used for northern sites was retrieved from the Pellston regional airport (GHCND: USW00014841) weather station (45°55'N 84°78'W; Fig. 1). The climate data used for southern sites was retrieved from the University of Michigan (GHCND: USC00200230) weather station located in Ann Arbor, Michigan (42°17'N 83°39'W; Fig. 1).

- Analysis

We did extensive exploratory data analysis to determine which monthly climate variables showed the strongest association with tree growth. The climate variables which displayed the highest correlation with growth were selected for the final analyses of tree growth, we used spring temperature, summer temperature and summer precipitation.

To account for growth variation as a function of tree size, detrending, the natural log of DBH was included in the model (Speer, 2010). To account for the previous years' effect on current growth, the previous years' growth ( $G$ ) was included as a lag effect (Ogle et al. 2015, Peltier et al. 2016, Ibanez *et al.*, 2018).

The likelihood of the growth increment for tree  $i$  in year  $y$ :

$$Growth_{i,y} \sim Normal(G_{i,y}, \sigma_{i,y}^2)$$

The process model is:

$$Growth_{i,y} = \alpha + \beta_1 \times \ln \ln (DBH_{i,y}) + \beta_2 \times Springtemp_y + \beta_3 \times Summertemp_y + \beta_4 \times Precipitation_y + \beta_5 \times (\omega_1 \times G_{i,y-1} + \omega_2 \times G_{i,y-2})$$

Parameters  $\omega$  represent the weight of each year's effect,  $\sum \omega_* = 1$ . To account for increases in growth variability with tree size (Lines *et al.*, 2012) we estimated the variance as a function of DBH:

$$\sigma_{i,y}^2 = a + b \times \ln \ln (DBH_{i,y})$$

In the southern sites, there were some individuals with missing growth data in certain years that precluded us from directly estimating DBH those years. We treated these missing DBH as latent variables to be estimated as:

$$DBH_{i,y} \sim Normal(D_{i,y}, \sigma_d^2); D_{i,y} = DBH_{i,y-1} - d \times (21 - y)$$

Parameter  $d$  represents the average increase in diameter each year. Parameters were estimated from non-informative prior,  $\alpha \sim Normal(2, 0.01)$ , since  $\alpha$  as the growth without environmental effects should be a positive value, while using mean of 0 and 1 gave us negative results.  $\beta, b, d \sim Normal(0, 0.0001)$ ,  $a \sim LogNormal(1, 0.001)$ ,  $\frac{1}{\sigma_d^2} \sim Gamma(0.0001, 0.001)$ , and  $\omega_G \sim Dirichlet(1)$ . Each species and latitude were analyzed independently.

The results obtained from this model were used to estimate future tree growth under three different climate change scenarios: 1) increasing temperatures (S1), 2) lower precipitation (S2) and 3) a combination of increasing temperatures and lower precipitation (S3). These forecasts were generated for the Geophysical Fluid Dynamics Laboratory An emphasis on fossil-fuels emission scenario (GFDL A1FI, Handler *et al.*, 2014), business as usual, which is the most fossil-fuel intensive scenario and for this region it predicts that spring temperatures will increase by 3.3 °C, summer temperatures will increase by 6.2 °C and precipitation will decline by 39% by the end of this century (Handler *et al.*, 2014). To estimate the effects of this scenario we ran three simulations: S1, an increase in both spring and summer temperature; S2, a decrease in summer

precipitation; and S3, an increase in spring and summer temperature as well as a decrease in summer precipitation.

Analysis and simulations were conducted using OpenBUGS (version 3.2.3; Thomas *et al.*, 2006; see Supplement 1 for analysis code); for the analysis we ran three chains of a Markov Chain Monte Carlo simulation for 10,000 iterations until convergence was reached. The posterior parameter means, standard deviations, and 95% credible intervals were then estimated at 20,000 iterations.

## Results

we ended up with data from 20 *A. saccharum* individuals and 19 *A. rubrum* individuals from the northern stands, and 26 *A. saccharum* as well as 22 *A. rubrum* individuals from the southern sites. The DBH range of *A. rubrum* samples collected from the southern and northern sites were 13.9-37.6 cm and 11.6-30.6 cm, respectively. The DBH range of *A. saccharum* samples collected from the southern and northern sites were 10.9-52.8 cm and 18.4-39.3 cm, respectively. The average growth rate for *A. saccharum* in the southern sites was  $1.518 \pm 0.983$  mm/yr and  $0.999 \pm 0.405$  mm/yr in the north. The average growth rate for *A. rubrum* in southern sites was  $1.273 \pm 0.761$  mm/yr and  $0.938 \pm 0.446$  mm/yr in the north.

### *Model selection and model fit*

Exploratory data analysis indicated that using April mean temperature as spring temperature, August mean temperature as summer temperature and July total precipitation as summer precipitation had the highest association with tree growth in the southern sites. For the northern sites, we used May mean temperature as spring temperature, July mean temperature as summer temperature, and June total precipitation as summer precipitation. The goodness of fit



(predicted vs observed;  $R^2$ ) was 0.60 and 0.69 for *A. rubrum* at the southern and northern sites; and 0.50 and 0.47 for *A. saccharum* at the southern and northern site.

Increasing DBH displayed a positive relationship with tree ring growth for almost all of the sample groups with the exception of *A. saccharum* located in the southern site (S2). For both species at both latitudes, previous years' growth had a significantly positive influence on the current year's growth (S2), and this effect was mainly attributed to growth at y-1 (S2). All parameter values can be found in the supplemental materials located in Supplement 2 (S2).

#### *Effect of climate variables*

For *A. rubrum* in the southern population, August temperature (summer temperature) was negatively associated with tree growth, while for the northern population both July temperature (summer temperature) and June precipitation were positively associated with growth (Fig. 2).

For *A. saccharum* only in the southern population we found a negative association with August temperature (summer temperature) and a positive association with July precipitation (Fig. 2).

#### *Simulations under future climate scenarios*

For both species, trees growing in the south sample area were predicted to likely be negatively influenced by changing climate variables compared to northern individuals (Fig. 3). Although not statistically different, predicted growth in the north slightly increases for both species under all changing climate scenarios. For *A. rubrum* located in the northern area, the predicted growth under current climate condition is 0.957 ( $\pm 0.06$ ) mm/yr, the predicted growth rates under S1, S2, S3 are: 1.047 ( $\pm 0.087$ ) mm/yr, 0.9615 ( $\pm 0.06157$ ) mm/yr and 1.051 ( $\pm 0.08987$ ) mm/yr respectively, indicating an increase of 9.4% under S1 and 9.8% under S3, while remains almost the same under S2. For *A. saccharum* located in the northern area, the

predicted growth under current condition is 0.9824 ( $\pm 0.0655$ ) mm/yr, while predicted growth rates under S1, S2, S3 are: 1.096 ( $\pm 0.1015$ ) mm/yr, 0.9784 ( $\pm 0.06563$ ) mm/yr and 1.092 ( $\pm 0.1052$ ) mm/yr, indicating an increase of 11.6% under S1 and 11.2% under S3 respectively, while remains almost the same under S2 compared to growth under current climate condition. In contrast, predicted growth in the south decreases for both species under all changing climate scenarios. For *A. rubrum*, the predicted growth under current climate condition is 1.355 ( $\pm 0.1193$ ) mm/yr, the predicted growth under S1, S2, S3 were: 1.228 ( $\pm 0.1471$ ) mm/yr, 1.339 ( $\pm 0.115$ ) mm/yr and 1.2 ( $\pm 0.1504$ ) mm/yr, a decrease of 10.1%, 2.1%, 12.2% under S1, S2 and S3 respectively compared to current climate condition. For *A. saccharum*, the predicted growth under current climate condition is 1.448 ( $\pm 0.1219$ ) mm/yr, the predicted growth rates under S1, S2 and S3 were: 0.7095 ( $\pm 0.2608$ ) mm/yr, 1.372 ( $\pm 0.1263$ ) mm/yr and 0.6318 ( $\pm 0.268$ ) mm/yr, indicating a decrease of 51%, 5.2%, 56.4% under S1, S2 and S3 respectively compared to current climate condition.

## **Discussion**

With gradually increasing changes in climate around the world (IPCC, 2014), it is critical to understand how forests might respond to these new environmental conditions. However, across their distributional ranges, tree species are likely to respond differently to environmental change due to both genetic differences or acclimation to local environments. Furthermore, specific population responses will likely vary as a function of the direction of climate change with respect to the species optimum. In this study, we identified how spring and summer temperature and summer precipitation affected the growth of two common maple species in eastern North America. We analyzed tree growth patterns at two latitudes to assess what climatic

clues each tree species and population responded to; we then used these results to forecast how each species might respond to future climate conditions. Our results showed that, within each species, the climatic variables influencing tree growth differed between latitudes. In general, in the northern locations, tree growth was not affected by changes in temperature, while in the southern location, tree growth decreased as temperatures increased. Precipitation had a positive effect on tree growth for both species at both latitudes but to different extents. These results confirm that there exist variations among populations in their responses to changing climate, even if both populations are located within the same general area of the distribution range of the species (Fig 1.). We found that the southern populations in this study will likely be negatively affected by global warming in the future while the northern populations, 400 km apart, may not.

The general expectation within the climate change literature is that forests at higher latitudes operate at growing season temperatures below their optimum thus they will respond positively to warming (Way & Oren, 2010; Zeng, Jia & Epstein, 2011). In this study, we observed that the trees growing in these two locations, within the higher latitudes of their ranges (Fig. 1), varied in physiological acclimation to temperature and did not always respond positively to higher temperatures. Neither species, or population, responded to variability in spring temperature, our proxy for longer growing seasons (Fig. 2) which indicate an extent growing season for their early growth might not benefit them significantly. In the southern populations, summer temperature had a negative effect on tree growth for both species, while in the north the effect was positive but only significant for *A. rubrum*, which indicates that current temperature might have already exceeded the temperature optimum for individuals of southern populations. plants tend to close their stomata in response to high temperatures exceeding their

temperature optimum to reduce water loss which then induces a reduction in photosynthetic activity (Heath & Meidner, 1957).

Previous studies have found contrasting relationships between climate and growth of *A. saccharum*. Tardif et al. (2001) showed that climatic variables have little effect on *A. saccharum* growth, while Bishop et al. (2015) reported that growth was positively correlated with precipitation and negatively correlated with summer temperature. However, Oswald et al. (2018) found that the impact of extreme climate events and the frequency of thaw-freeze cycles can be more critical to the growth change in different years. *Acer saccharum* has a broad temperature range for optimal photosynthetic performance and the temperature optimum does not vary a lot among populations (Gunderson et al., 2000). However, the acclimation ability of respiration to changing climatic conditions can vary across tree species (Gunderson et al., 2000). Thus, the different response towards increasing temperature for the northern and southern populations might be caused by their different acclimation of respiration. *Acer rubrum* has a great tolerance of wide environmental conditions (Abrams, 1998), warming in general may directly enhance photosynthesis, but it may indirectly reduce tree growth by exacerbating abiotic and biotic stresses such as drought and herbivory (Lahr et al., 2018). In our case, the negative effect of increasing temperature on southern *A. rubrum* population might be caused by insufficient water availability and consequent closure of the stomata. Since the annual growth of trees is closely related to the differences between products of photosynthesis and loss of carbon in- respiration (Bourdeau, 1957), decreasing photosynthetic activity due to stomata closure could adversely affect tree growth and (McDowell et al., 2008). *Acer rubrum* and *Acer saccharum* are both shade-tolerant species, and this characteristic further shapes their hydraulic conductivity in the root system since shade tolerant species lack the root traits associated with more plasticity in conduit numbers as well as root-specific hydraulic conductance among growth rings which allow them to

perform in environment with fluctuating and uncertain water status (Maherali *et al.*, 1997; Zadworny *et al.*, 2018). Both *A. rubrum* and *A. saccharum* are tree species associated with mesic environments (Barnes & Wagner, 2004), thus our results corroborate their dependence to moist conditions. This is confirmed at the southern sites, where we document a positive growth response to higher water availability. The fact that precipitation was only significant at the southern site likely indicates a higher water demand with higher temperature (Schulze *et al.*, 1973). Even though the southern populations we sampled were also at the relatively northern distributional range of both species (Fig. 1), the results of this study showed these individuals are already water limited since they respond positively to increasing precipitation, which makes them sensitive to both precipitation decline and global warming.

The lag effect of previous growth was positive in this study. This positive effect indicated a continuous gain in resources from previous years that can be allocated to growth in the following year. The significant effect showed that lag effect needs to be included when we were looking at the relationship between growth and environmental conditions (Ibáñez *et al.* 2018).

Our scenario simulations show that southern tree populations will be negatively affected under all three potential climate change conditions: only hotter (S1), only drier (S2) as well as hotter and drier (S3) (Fig. 3). This might indicate that these populations, even if located in the northern part of their distributional ranges (Fig. 1), are at risk of being negatively affected by warming. Any increase in temperature and/or decrease in precipitation will cause a decline in their growth. For *A. saccharum*, the effects of increasing temperature and decreasing precipitation will be considerably negative in the southern population (Fig. 3). Predicted growth decreased by more than 50% under the only warming scenario, and under the harsher conditions brought up by both warming and drought the decrease will be close to 56.4%. In recent years, the decline of *A. saccharum*, mainly characterized as reduced radial increment and loss of crown

vigor, has been recorded broadly across Ontario and Quebec, Wisconsin, Vermont, New York, and Pennsylvania (Horsley *et al.*, 2002). Our predicted growth of northern populations showed that their growth would increase under the three simulated climate scenarios, this indicates that low temperatures during the growing season are still a limiting factor in this area while summers are still moist enough to provide optimal growth conditions.

For both species, the northern populations might be able to maintain or increase their growth rates, but the southern populations are likely to experience lower growth rates. Moreover, *Acer rubrum* might be more successful than *Acer saccharum* in the south, which means the population of *A. saccharum* is likely to shrink in the future. These predicted results are consistent with the future species distribution changes forecast by USDA, which indicates that populations in these two areas are going to decline in the future for both species under warmer and drier conditions (Prasad *et al.*, 2014).

### **Future Research**

According to the acceptable R<sup>2</sup> standard proposed by Henseler *et al.* (2009), R<sup>2</sup> with 0.75, 0.5 and 0.25 are described as substantial, moderate and weak. In this case, models for *A. rubrum* were moderately predictive while models for *A. saccharum* were weakly predictive. These results indicated that environmental variables can only partially explain tree growth, to better predict their performance under changing environments, we also need to include other biotic and abiotic components in our model specifically for each species.

In this study, we only included spring temperature and summer temperature in the models. However, literature also showed that winter temperature has great influence on these two species, since increasing winter temperature is closely related to snow cover and thaw-freeze

cycle (Leites *et al.*, 2019). To account for the effect of these important factors, it might be better to consider winter temperature in further study.

## **Conclusion**

Our study presents evidence of performance variation among populations in responding to temperature and precipitation change. Although located in the northern range of their distribution, with a latitudinal difference between two sites relatively small, these populations showed varying responses to climate variables. Even if we expected individuals from these two populations to benefit from the longer growing seasons associated with warming, we found that it might not be the case at least for southern populations in this study. We found that the most northern population is not expected to experience big changes in growth while the southern population will likely decline. Incorporating these differences in vegetation models will be critical to ensure accurate predictions of future forest composition, structure and productivity.

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Site	Coordinate	Dominant species	Soil	Landform
South: Radrick Forest	42°17'N, 83°48'W	<i>Quercus rubra</i> , <i>Quercus alba</i> <i>Acer nigrum</i> , <i>Acer saccharum</i>	Fine-textured, well-drained	Recessional moraine
South: Stinchfield Wood	42°24'N, 83°55'W	<i>Quercus alba</i> , <i>Quercus velutina</i> , <i>Acer saccharum</i> , <i>Acer rubrum</i>	Coarse-textured, Well-drained	Kame
North: Northern hardwood	45°34'N, 84°41'W	<i>Acer saccharum</i> , <i>Fagus grandifolia</i> , <i>Populus</i> <i>grandidentata</i>	Coarse-textured, Well-drained	Outwash plain
North: Aspen	45°33'N, 84°42'W	<i>Acer rubrum</i> , <i>Acer saccharum</i> , <i>Fagus grandifolia</i>	Coarse-textured, Well-drained	Outwash plain

Table 1: Information about sampling sites at the two latitudes species, location, vegetation and physical characteristics.

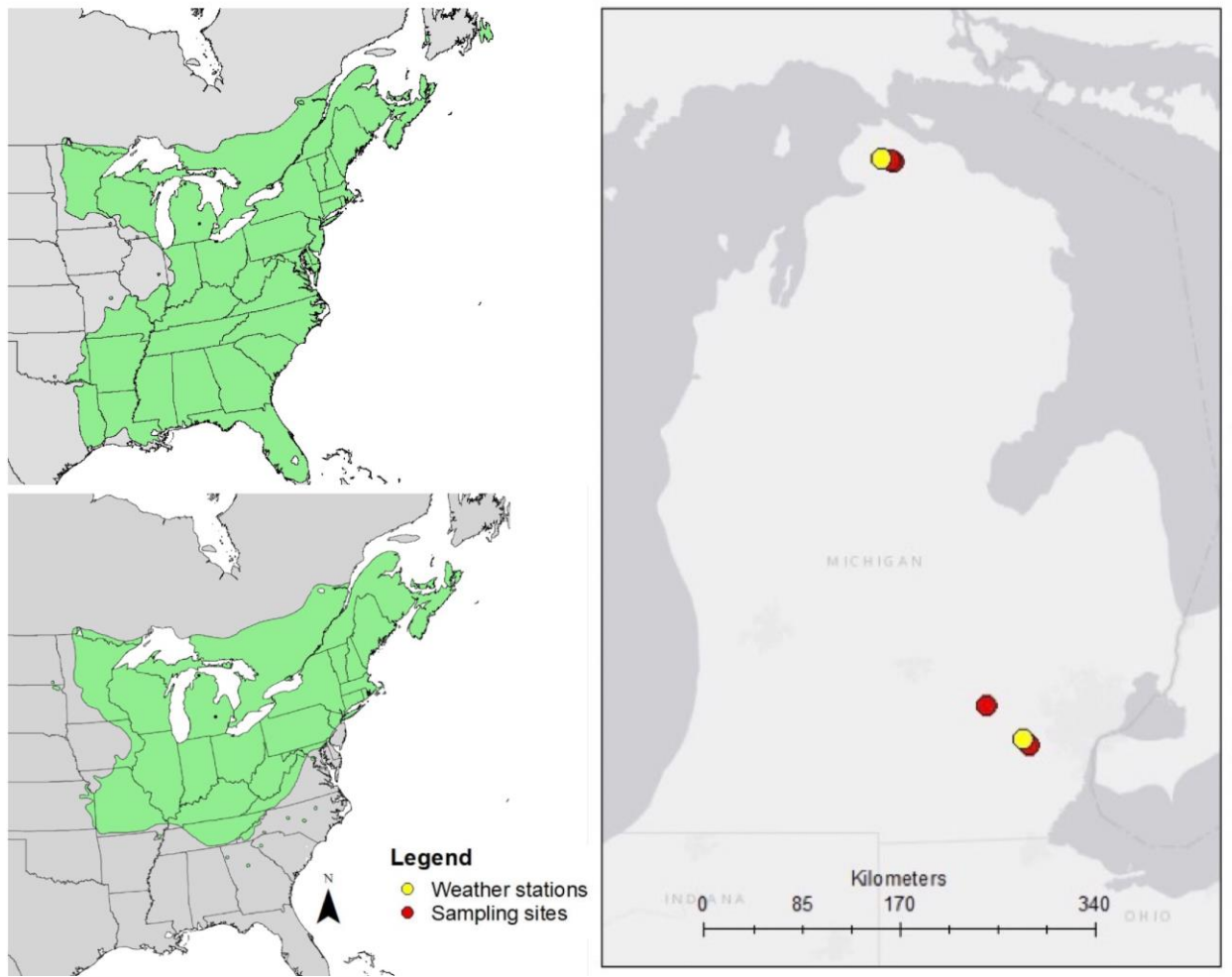
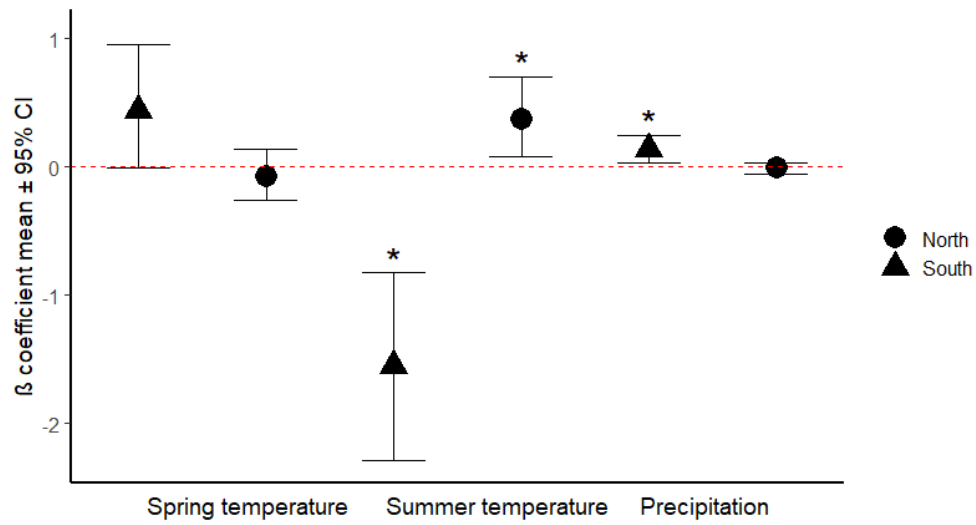
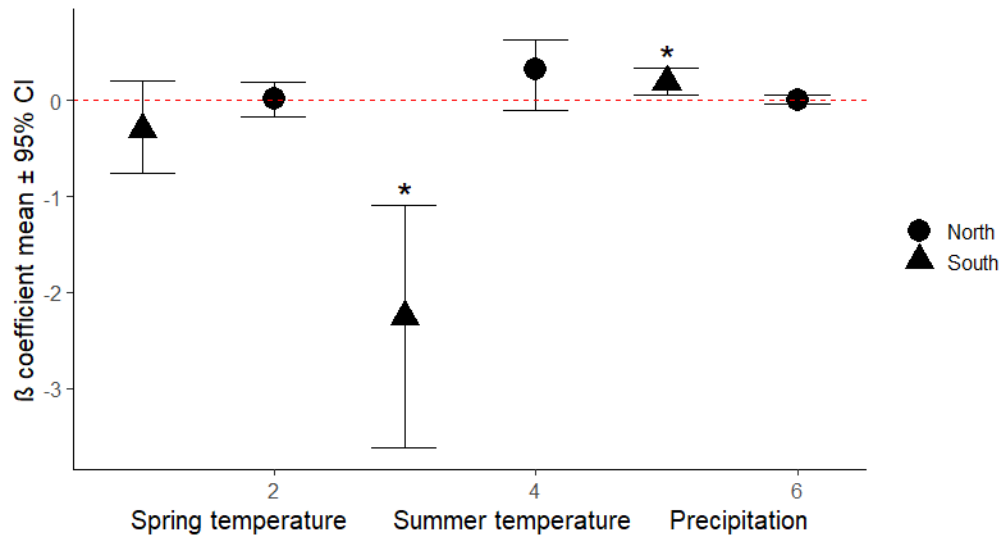


Figure 1: Distributional range of *Acer rubrum* (Left top) and *Acer saccharum* (Left bottom) and locations of study sites as well as weather stations at two latitudes in Lower peninsula, Michigan (Right). (Map retrieved from USGS on 2020.)

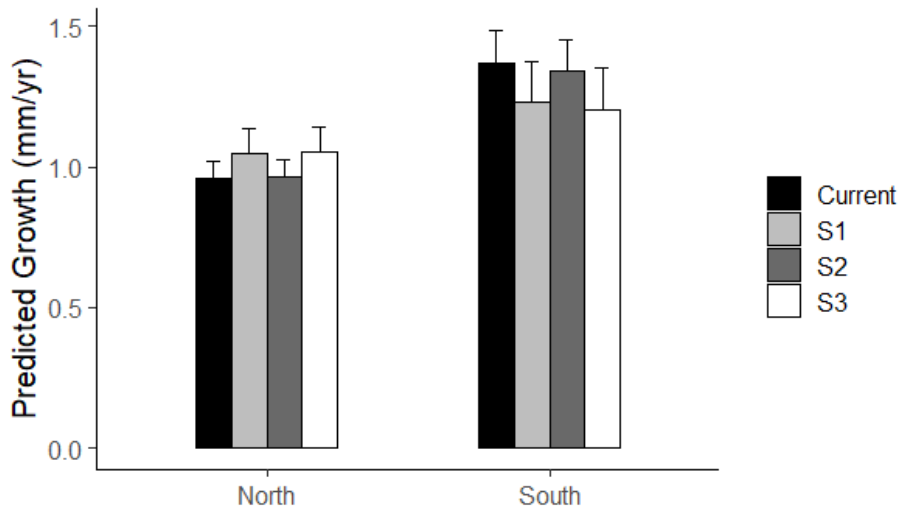


(a)

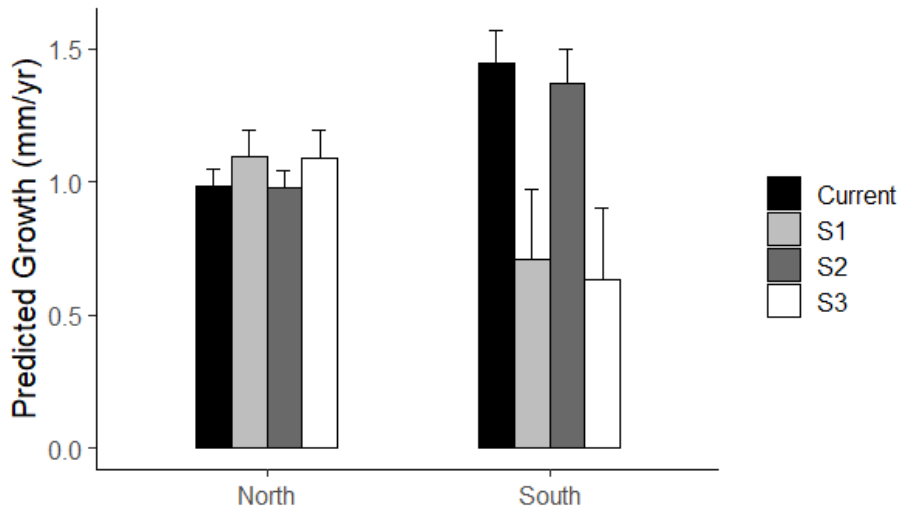


(b)

Figure 2: Parameter estimates (mean  $\pm$  95% CI) showing the effects of spring temperature (April for south and May for north), summer temperature (June for south and July for north) and summer precipitation (July for southern sites, August for northern sites) on the growth of (a) *Acer rubrum* and (b) *Acer saccharum*. Parameters were standardized by multiplying each one by the covariate mean.



(a)



(b)

Figure 3. Simulated growth under current condition, Scenario 1 with only increased temperature (S1), Scenario 2 with only decreased precipitation (S2) and Scenario 3 with both increased temperature as well as decreased precipitation (S3) in north and south for (a) *Acer rubrum* (b) *Acer saccharum*. Predicted mean+SD.

## Supplement Information

### Supplement 1:

#### OpenBUGS code:

```
model{
for(i in 1:no. of trees){
  for(y in 3:21){
    rg[i,y]~dnorm(R[i,y],tau[i,y])#likelihood
    rg.h[i,y]~dnorm(R[i,y],tau[i,y])#predictions
    R[i,y]<-alpha+beta[1]*log(dbh[i,y])+beta[2]*Springtemp[y]+beta[3]*Summertemp[y]
    beta[4]*(Summerprecip[y]) beta[5]*(wG[1]*rg[i,y-1]+wG[2]*rg[i,y-2])

tau[i,y]<-1/var[i,y]
var[i,y]<-a+b*log(dbh[i,y]) #variance is estimated as a function of the dbh (tree size)
}}
#priors
alpha~dnorm(2,0.01)
for(k in 1:5){beta[k]~dnorm(0,0.0001) }
a~dlnorm(1,0.001)
b~dnorm(0,0.0001)
wG[1:2]~ddirich(wGm[])
for(k in 1:2){ wGm[k]<-1}
}#end model
```

**Supplement 2:** Posterior parameter estimates at two latitudes for *A. rubrum* and *A. saccharum*, mean  $\pm$  SD and 95% CI. Bold indicate statistically significant coefficients, 95%CI does not include zero.

<b>Parameters for <i>A. rubrum</i></b>	<b>Southern sites</b>	<b>Northern sites</b>
$\alpha_1$ : intercept	1.0610 $\pm$ 0.5074(0.1578,1.9870)	-0.3244 $\pm$ 0.1739(-0.7209,-0.0260)
$\beta_{1,1}$ : effect of tree size on growth (natural log)	<b>0.1210<math>\pm</math>0.0556(0.0113,0.2284)</b>	0.0454 $\pm$ 0.0351(-0.0256,0.1078)
$\beta_{1,2}$ : effect of spring temperature	0.0450 $\pm$ 0.0254(-0.0012,0.0970)	-0.0067 $\pm$ 0.0083(-0.0230,0.0124)
$\beta_{1,3}$ : effect of summer temperature	<b>-0.0709<math>\pm</math>0.0184(-0.1048,-0.0379)</b>	<b>0.0196<math>\pm</math>0.0085(0.0043,0.0367)</b>
$\beta_{1,4}$ : effect of summer precipitation	<b>0.0015<math>\pm</math>5.91E-04(3.48E-04,0.0027)</b>	-1.58E-04 $\pm$ 3.06E-04(-7.41E-04, 4.54E-04)
$\beta_{1,5}$ : lag effects	<b>0.6997<math>\pm</math>0.0350(0.6301,0.7682)</b>	<b>0.9090<math>\pm</math>0.0438(0.8419,0.9753)</b>
$a_1$ : intercept of standard deviation model	0.0081 $\pm$ 0.0186(3.60E-06,0.0663)	0.0113 $\pm$ 0.0460(4.08E-07, 0.1101)
$b_1$ : effect of tree size (natural log) on SD	<b>0.1009<math>\pm</math>0.0096(0.0822,0.1225)</b>	<b>0.0167<math>\pm</math>0.0092(-0.0126,0.0226)</b>
$\omega_{G1,1}$ : weighted lag effect of growth in (y-1)	0.8232 $\pm$ 0.0652(0.6939,0.9532)	0.6490 $\pm$ 0.0563(0.5414,0.7582)
$\omega_{G1,2}$ : weighted lag effect of growth in (y-2)	0.1768 $\pm$ 0.0652(0.0468,0.3061)	0.3510 $\pm$ 0.0563(0.2418,0.4586)
<b>Parameters for <i>A. saccharum</i></b>	<b>Southern sites</b>	<b>Northern sites</b>
$\alpha_2$ : intercept	2.7510 $\pm$ 0.8274(1.3100,4.6660)	-0.4925 $\pm$ 0.2443(-0.9780,-0.0353)
$\beta_{2,1}$ : effect of tree size (natural log) on growth	-0.0308 $\pm$ 0.0897(-0.2113,0.1547)	<b>0.1379<math>\pm</math>0.0473(0.0426,0.2271)</b>
$\beta_{2,2}$ : effect of spring temperature	-0.0307 $\pm$ 0.0250(-0.0764,0.0214)	0.0018 $\pm$ 0.0081(-0.0144,0.0167)
$\beta_{2,3}$ : effect of summer temperature	<b>-0.1030<math>\pm</math>0.0310(-0.1656,-0.0500)</b>	0.0169 $\pm$ 0.0098(-0.0052,0.0331)
$\beta_{2,4}$ : effect of summer precipitation	<b>0.0021<math>\pm</math>7.741E-4(5.611E-4, 0.0036)</b>	1.25E-04 $\pm$ 3.49E-04(-5.50E-04,8.19E-04)

$\beta_{2,5}$ : lag effects	<b>0.7705±0.0422(0.6904,0.8492)</b>	0.6657±0.0417(0.5902,0.7368)
$a_2$ : intercept of standard deviation model	0.5222±0.2542(1.56E-03,0.9928)	0.0107±0.0364(2.86E-05,0.0909)
$b_2$ : effect of tree size (natural log) on SD	-0.0713±0.0843(-0.2232,0.0998)	0.0205±0.0077(-0.0055,0.0254)
$\omega G_{2,1}$ : weighted lag effect of growth in (y-1)	0.8362±0.0553(0.7281,0.9459)	0.8176±0.0703(0.6804,0.9555)
$\omega G_{2,2}$ : weighted lag effect of growth in (y-2)	0.1638±0.0553(0.0541,0.2719)	0.1824±0.0703(0.0445,0.3198)

---