

## **Influence of Climate on Oak Savanna Tree Species in the Midwestern United States**

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### **Authors' contributions**

*This work was carried out in collaboration between both authors. Authors SC and IH conceptualized the study. Authors IH and SC carried out the methodology of the study. Author IH wrote the first draft of the manuscript. Authors IH and SC contributed to revisions and editing of the manuscript. Both authors read and approved the final manuscript.*

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### **ABSTRACT**

**Aims:** The previously abundant high quality and open canopy oak savanna communities in the Midwest have been reduced by more than 98% of their pre-settlement (pre-1840) area because of changing land use and represent some of the most threatened ecosystems in North America. Prior knowledge of oak savanna communities' climatic resilience to potential impact of climate change and competition is critical to restoration success. This study examined sensitivity to climatic stress, and effects of competition, which are important considerations during oak savanna restoration.

**Methodology:** Dendrochronological methods were used to sample oak savanna communities located in MacCreedy Reserve (MR) situated in southern Michigan, U.S.A. The influence of climate (mainly temperature and precipitation) on white oak (*Quercus alba* L.), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh) were correlated using dendroclimatic techniques. The effect of competitor species (*A. rubrum* and *P. serotina*) on *Q. alba* were examined using competitor ratio chronologies and examining correlations with climatic variables.

**Results:** Findings indicate that precipitation in winter, spring, and summer is beneficial for radial

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growth of white oak. White oak is more resilient to drought stress than red maple and black cherry due to its ecophysiological adaptations but tends to grow rather slower when in competition with shade tolerant and fire sensitive competitor species.

**Conclusion:** Overall, this study has shown that temperature and precipitation play key roles in tree productivity and thus climatic sensitivity should be incorporated in the restoration of oak savanna ecosystems.

**Keywords:** Dendrochronology; climate; drought stress; ecology; oak savanna; restoration.

## 1. INTRODUCTION

Climate and competition have been recognized as important factors affecting forest productivity [1]. Climate change is largely responsible for observed changes in forest productivity, tree phenology, as well as a primary initiator of latitudinal and altitudinal species distribution. Current findings suggest an upward surge of climatic changing regimes and consequent adverse impact on forest resources [2,3].

Both above-and belowground competition have the potential to reduce the radial growth of trees due to limited resource availability, negative water potentials, and decreased stomatal conductance and photosynthetic rates [4]. Knowledge of the impact of competition on tree growth is critical to develop appropriate management practices to optimize the use of environmental resources, with the prospect to buffer residual trees from stressful climatic conditions [5]. Competition plays an influential role on how forests cope with climate and regulates species response to future climate projections [4].

The pristine, abundant, and high quality and open canopy oak savanna communities in the Midwest have been reduced by more than 98% of their presettlement (pre-1840) area because of changing land uses [6,7] and represent some of the most threatened ecosystems in North America [8]. Even where relict oak savannas remain, fire suppression-induced invasion of native and exotic species have altered vegetative structure, reduced understory light levels, restricted oak regeneration, and led to the death of many species that originally characterized oak savannas [9]. Oak savanna ecosystems are typically transitional communities (ecotones) found between forests and prairies, and ecotones are expected to be very sensitive to climate change and serve as important indicators of environmental change [10]. Current restoration efforts, however, have paid less attention

to the potential impact of climate and competition.

Long records of environmental conditions are very important for assessing scenarios of climate change and consequences for species and plant productivity. Instrumental records lack the sufficient length to provide a complete representation of dynamics in past climates, and thus need to be supplemented by proxy records. Trees are well known to record ecologically germane information in their annual rings and hence are important natural archives for the study of past environmental conditions [11,12]. Ring width is the anatomical property that is conventionally used in dendrochronology for studying forest dynamics and reconstructing past climate variations.

This study seeks to investigate the influence of climate (mainly temperature and precipitation) and competition on white oak (*Quercus alba* L.) productivity in the MacCreedy Reserve located in southern Michigan. To do this, we test the following hypotheses: (1) The competitors species red maple (*Acer rubrum* L) and black cherry (*Prunus serotina* Ehrh) will grow better when climatic conditions are favorable, whereas the focal oak trees will outgrow the competitors during stressful growing conditions (e.g. drought). (2) The oak growth decreases with late spring frost and summer drought.

## 2. MATERIALS AND METHODS

### 2.1 Study Area

The study was conducted in MacCreedy Reserve (Fig. 1) in the summer of 2010. The MR is located in Jackson County, Michigan (42°07'36" N, 84°23'38" W), is approximately 165ha and lies in the Jackson interlobate region, an area formed at the intersection of three separate glacial lobes (13,000–16,000 years ago) [9]. The reserve is comprised of glacial landscape features such as moraine and outwash plains, as well as ice-contact topography [13]. A diversity of natural

communities characterize the reserve and include oak savannas, hillside prairies, prairie fen wetlands, and southern wet meadows [9,14].

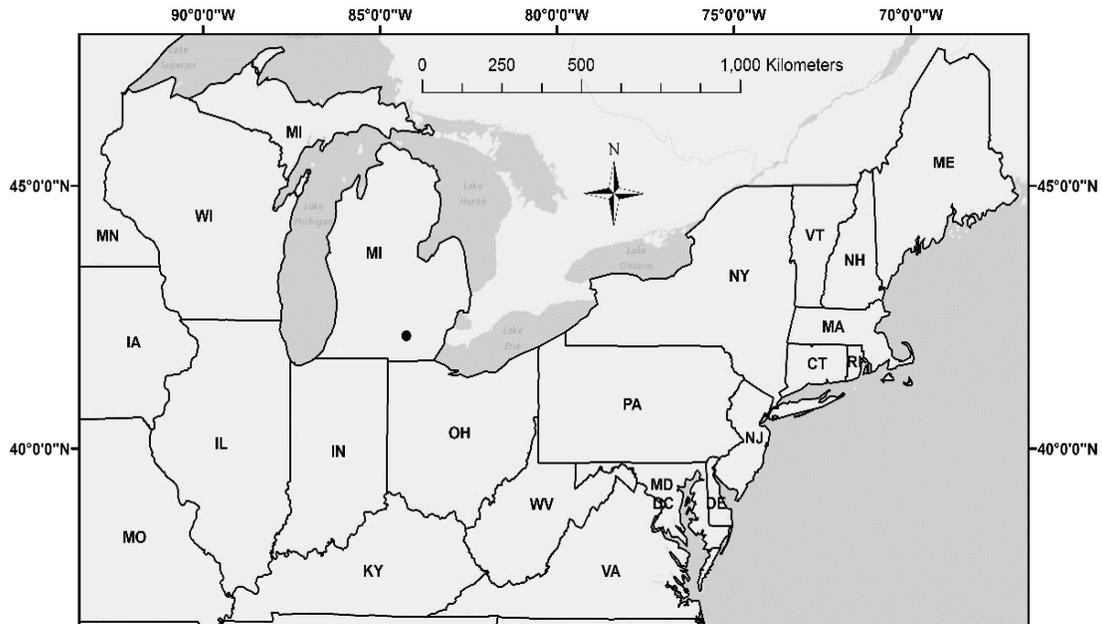
The once prevalent oak savanna has declined due to fire suppression and clearing for agriculture and urban development [13,14]. Mostly, the oak savannas in this study area have either been converted to farm land or have grown into closed-canopy oak forests as a result of fire suppression. The forest cover of the moraine landform is composed predominantly of white, black, red and northern pin oaks (*Quercus alba* L., *Quercus rubra* L., *Quercus ellipsoidalis* E.) as well as competitor species including red maple (*Acer rubrum* L.), black cherry (*Prunus serotina* Ehrh.), shellbark hickory (*Carya laciniosa* Michx), pignut hickory (*Carya glabra* Mill), and yellow birch (*Betula alleghaniensis* Britton).

The soil texture in the Jackson Interlobate region (where the MacCready Reserve is located) generally range from sand to clay: the most common soil texture being sandy loam found on moraine ridges and sand on the outwash plains. The moraines are formed from circumneutral glacial drift and many of the horizons of the moraine soils are clay-rich due to illuviation and thus provide better water-holding capacity than many of the outwash soils. The soils of the moraines are characteristically well and

excessively well-drained sandy loam. The average snowfall ranges between 1016 mm and 1270 mm with greatest amounts experienced in the extreme north and south. The highest annual precipitation occurs in the south and within the range 762 mm and 813 mm. The minimum temperature in the region is between -22°F and -28°F with the coldest value recorded in the north [13].

## 2.2 Field Sampling

Field sampling was carried out in the summer of 2010. Tree cores were extracted from nine (9) fire-suppressed forest stands of remnant oak savanna in the MR with an increment borer. Stands that showed no obvious recent history of disturbances (disease, fire, or insect damage) served as the major criterion for selection of the nine remnant oak savanna plots. Two cores were taken from the north and south faces of each tree with a diameter at breast height (DBH; 1.3 m above the ground) greater than 10 cm. Each plot had a 10 m × 10 m dimension. Within each plot, the diameter at breast height (DBH; 1.3 m above the ground) of stems with DBH >0.9 cm were measured. The stand basal area for each of the 9 plots was calculated for three groupings, namely oak and hickory combined, shade tolerant competitors combined, and all tree species combined.



**Fig. 1. Location of MacCready Reserve (●) located in southern Michigan (MI). The regional context includes midwestern and northeastern United States**

### 2.3 Increment Core Processing, Cross-Dating and Tree-Ring Measurements

All tree cores were processed using standardized dendrochronological techniques [5,16]. Tree cores were air dried, glued onto grooved wood strips to act as a stable base, and sanded with progressively finer grades of sandpaper to achieve clearly visible annual ring-width patterns. Sanded increment cores were scanned into a computer at an optical resolution of 2400dpi, which corresponds to a measurement accuracy of 0.01 mm. All samples were visually crossdated under a binocular microscope to identify any missing and/or false rings [17]. Ring widths were measured using the programs CooRecorder and CDendro. The visual crossdating and tree ring measurements were subsequently verified through statistical crossdating with the program COFECHA [18,19]. COFECHA is a computer software program that assesses the quality of crossdating and measurement accuracy of tree-ring series and thus identifies tree-ring series that ought to be rechecked for any dating and measurement errors.

### 2.4 Dendrochronological Analysis

The program ARSTAN was used to detrend the raw ring width measurements using a 50-year cubic spline, following crossdating and statistical quality control [20]. A 50-year cubic smoothing spline was used to remove low frequency variation associated with age and stand dynamics such as competition, suppression, and release [11,21]. Each measured series was converted into dimensionless ring width indices (with nearly stable mean and variance, allowing indices from the trees to be averaged into a site chronology) through standardization (i.e. dividing the observed values by the predicted values), which could then be compared to historical climate data. The purpose of the standardization was to preserve the climatic signal (inter-annual high-frequency variations) while removing the geometrical and ecological trends (low-frequency or long term variation) that are normally associated with non-climatic factors such as age-related trends and stand dynamics [11].

Chronology statistics such as mean sensitivity and standard deviation were estimated from program ARSTAN. Mean sensitivity is a measure of the relative intensity of year-to-year growth variability. It is an estimate of the difference between the increments of the current and preceding year divided by the mean of these

two increments [11]. Standard deviation represents the magnitude of long and medium term variation.

### 2.5 Dendroclimatic Analysis

Historical primary climate data was obtained from the PRISM Climate Group, which triangulates data from several weather stations and accounts for geographical and topographical disparities to give site-specific weather records that date back to 1895 [22]. The primary climate variables obtained included mean daily minimum and maximum temperature for each month, plus total monthly precipitation over the period 1895-2010. Mean monthly temperature (TAV) was estimated by averaging the mean daily minimum and maximum monthly temperatures. A Climate Moisture Index (CMI), which represents estimated net water availability to trees, was also calculated by subtracting monthly values of potential evapotranspiration (PET) from monthly precipitation (i.e. P-PET). Potential evapotranspiration was estimated based on mean, minimum, and maximum temperature as provided in Hogg [23].

The standard chronology and individual set of climate variables were run through the program DendroClim 2002 to identify significant monthly correlations between each climate variable and tree growth from April of the previous year to October of the current year [24]. Analysis begins in the April of the previous year because growing conditions of the previous year can affect the current year's growth by how much carbon they store and how many needle buds that are formed [25]. Pearson correlation coefficients were calculated between growth and monthly climate variables for every tree species. Dendroclim 2002 uses 1000 bootstrapped samples to compute response and correlation coefficients, and to test their significance at the 0.05 level [24].

### 2.6 Climate and Competition Interactions

The interactive effects of climate and competition on white oak and competitor trees productivity were assessed. To do this, competitive chronologies between the focal tree (in this study, white oak) and competitor tree species (red maple and black cherry) were estimated using the formula mentioned in Johnson et al. [26] and stated as follows:

$$\text{Competition ratio} = \frac{\text{Focal tree radial growth index}}{\text{Competitor radial growth index}}$$

A competition ratio  $> 1$  implies that conditions favored the growth of the focal tree more than the growth of the competitor species. However, a competition ratio  $< 1$  means that conditions were conducive for the growth of competitor species than white oak. Competitive chronologies were computed for red maple and black cherry separately for all the plots that had white oak and at least one of the competitor species co-existing. The competitive chronologies for the individual plots were subsequently averaged across the plots to arrive at a single competitive chronology for each competitor species. A competitive chronology for each competitor species was then related with climate data (precipitation, temperature and climate moisture index) using the same approach applied for the species specific chronologies.

### 3. RESULTS

#### 3.1 Stand Characteristics and Tree-Ring Chronologies

The DBH and stand basal area contribution for white oak, red maple, and black cherry are provided in Table 1. The mean sensitivity of the standard tree-ring chronology was highest for red maple (0.222) and smallest for white oak (0.214) (Table 2). The standard deviation of the standard tree-ring chronology was highest for red maple (0.264) and smallest for black cherry (0.236). White oak exhibited below average ring widths from longer term stressful growing conditions in mid 1970s to late 1980s; while ring widths were above average in early to mid 1970s, and mid 2000s to late 2000s (Fig. 2). Long term below average growth was also observed for red maple in mid 1970s to early 1980s, and mid 1990s to mid 2000s; while above average growth was seen in early 1980s to late 1980s. Black cherry on the other hand also portrayed below average radial growth in mid 1960s to mid 1970s, and early 1980s to mid 1980s; but the only long term above average growth was observed in mid 1980s to early 1990s. Besides these long-term growth rate variations, however, there were other short-term below and above average growth variations observed in all the three species, with mostly one or two species suppressing the growth of the other.

#### 3.2 Growth-Climate Relationships

White oak radial growth showed no response to temperature in the past and current year (Fig. 3A) (all  $P > 0.05$ ). The correlation analysis showed that the radial growth of red maple was

positively correlated with mean temperature for October of the previous year and May of the current year (Fig. 3B) (all  $P < 0.05$ ). Mean temperature of the previous July was also positively correlated with black cherry growth (Fig. 3C) ( $P < 0.05$ ).

Radial growth of white oak was positively correlated with January, March, May, and June precipitation of the current year (Fig. 4A) (all  $P < 0.05$ ). In addition, a positive correlation to precipitation was observed in August of the previous year for radial growth of black cherry (Fig. 4C) ( $P < 0.05$ ). The radial growth of red maple exhibited no positive correlation with precipitation (Fig. 4B) (all  $P > 0.05$ ). All negative precipitation correlations were found to be with the radial growth of red maple and black cherry (all  $P < 0.05$ ). Red maple had radial growth that was negatively correlated with precipitation in May of the previous year and current year (all  $P < 0.05$ ). The negative radial growth-precipitation correlation was observed in December of the previous year for black cherry ( $P < 0.05$ ).

Growth of white oak was positively associated with available moisture (CMI) in January, February, March, May, June, and July of the current year of ring formation (Fig. 5A) (all  $P < 0.05$ ). A positive growth relationship was also found with CMI for black cherry during August of the previous year (Fig. 5C) ( $P < 0.05$ ). Red maple (Fig. 5B) and black cherry had radial growth that were negatively correlated with CMI in May and December of the previous year, respectively (all  $P < 0.05$ ).

#### 3.3 Climate and Competition Interactions

Red maple competition ratio (for white oak-red maple interspecific) showed no response to temperature in the past and current year (Fig. 6A) (all  $P > 0.05$ ). Warm summer (July) temperatures of the current year favored the growth of black cherry over white oak whilst temperatures in September of the current year favored white oak growth over black cherry (Fig. 6B) (all  $P < 0.05$ ). Precipitation and climate moisture index in July and December of the previous year were conducive for white oak growth than red maple (Figs. 7 & 8) (all  $P < 0.05$ ). In addition, white oak grew better than black cherry in December of the previous year and January of the current year precipitation and climate moisture index (Figs. 7 & 8) (all  $P < 0.05$ ).

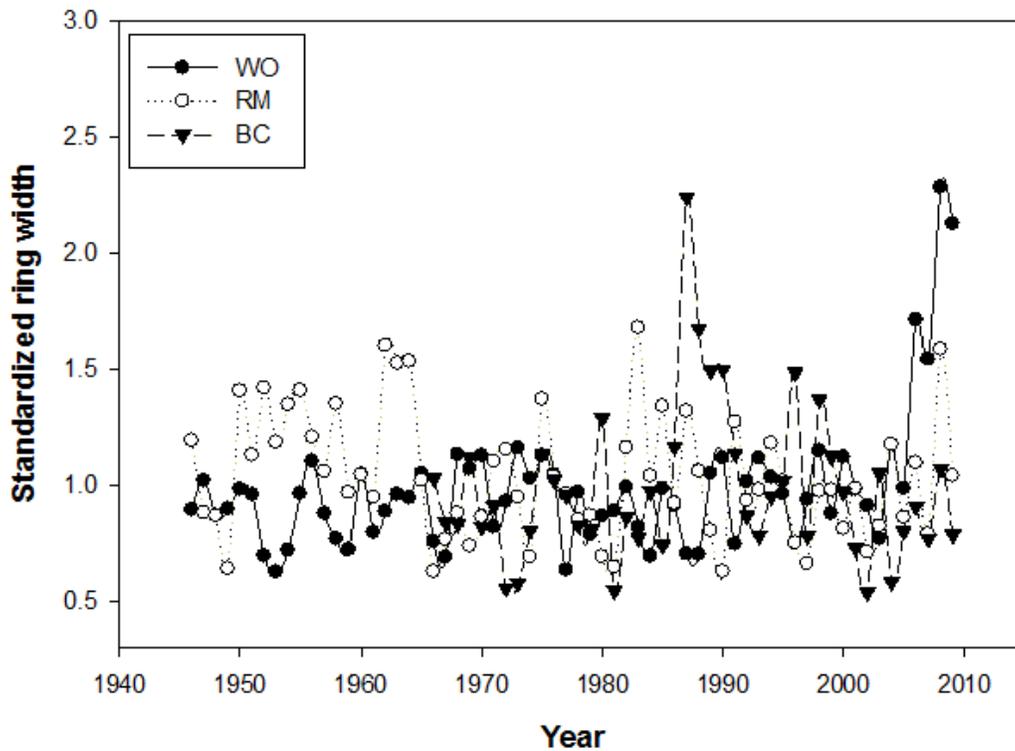
**Table 1. Mean stand level productivity parameters of a) white oak, b) red maple, and c) black cherry**

Species/Growth Parameter		Stand Number								
		2-1	3-1	4-1	5-1	5-2	6-2	7-1	8-1	10-1
<b>A) White oak</b>	<b>DBH (cm)</b>	5.3 (4.7)	-	27.0 (14.1)	-	36.0 (0)	42.0 (11.8)	1.7 (0)	15.9 (10.8)	-
	<b>Basal Area (m<sup>2</sup>/ha)</b>	0.6 (0.4)	-	9.7 (2.7)	-	10.2 (0)	37.0 (0.4)	2.2 (0)	4.8 (3.8)	-
<b>B) Red maple</b>	<b>DBH (cm)</b>	-	10.6 (1.2)	26 (19.5)	14.5 (3.9)	14.6 (4.3)	8.3 (1.4)	5.2 (0)	8.3 (1.1)	6.5 (0)
	<b>Basal Area (m<sup>2</sup>/ha)</b>	-	3.2 (0.3)	49.4 (10.5)	8.8 (0.9)	3.5 (0.9)	1 (0.2)	0.4 (0)	1 (0.2)	0.3 (0)
<b>C) Black cherry</b>	<b>DBH (cm)</b>	10.5 (4.5)	5.7 (0)	-	11.9 (0)	15.1 (5.7)	7.9 (1.5)	-	9.5 (7.1)	9.1 (2.8)
	<b>Basal Area (m<sup>2</sup>/ha)</b>	1.6 (0.2)	0.3 (0)	-	1.1 (0)	1(0)	1 (0.3)	-	2.4 (0)	1.4 (0.5)

Note: "-" indicates that none of that species was identified in that particular stand. The standard deviation of the DBH and basal area are provided in parentheses

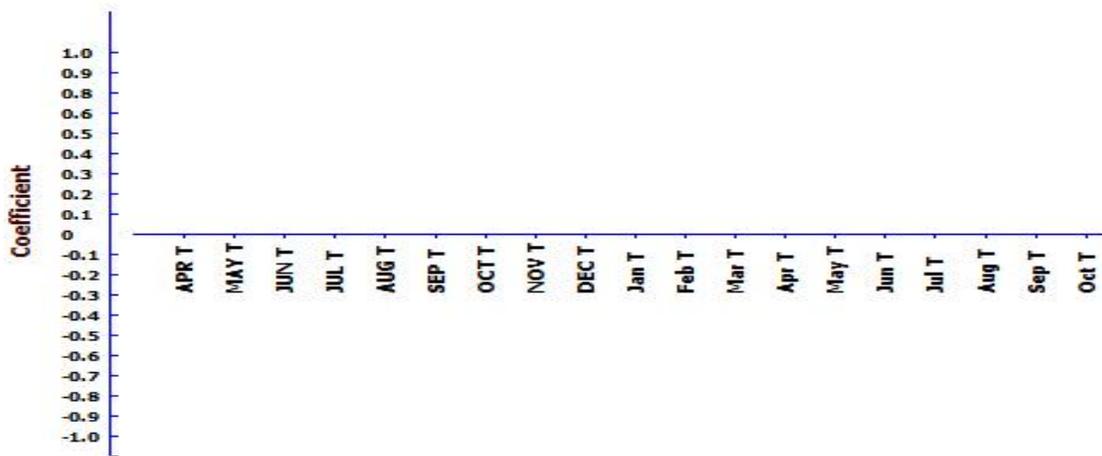
**Table 2. General statistics of the standard chronology of white oak, red maple and black cherry**

Chronology Statistic	White Oak	Red Maple	Black Cherry
Sample Size (No. trees)	6	13	5
Mean Sensitivity	0.214	0.222	0.196
Standard Deviation	0.240	0.264	0.236

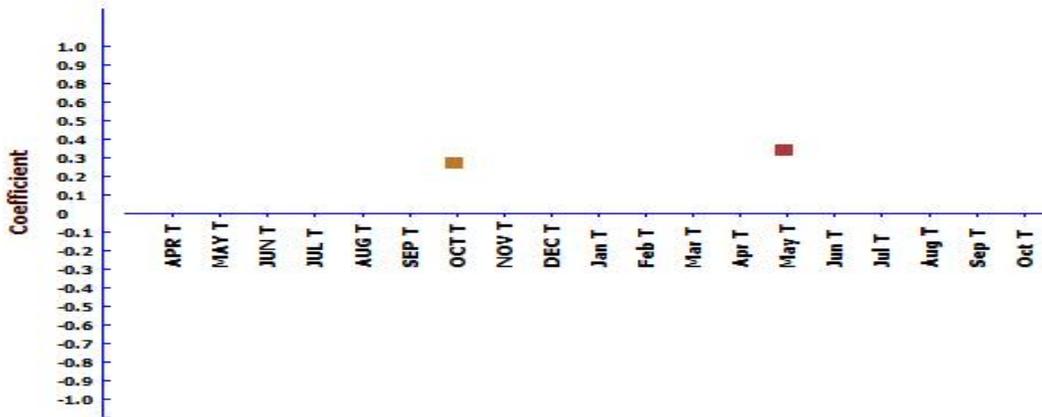


**Fig. 2. Standardized ring width chronologies for white oak (WO), red maple (RM), and black cherry (BC) in the MacCreedy Reserve from 1946 to 2009**

**(A) White Oak**



**(B) Red Maple**



(C) Black Cherry

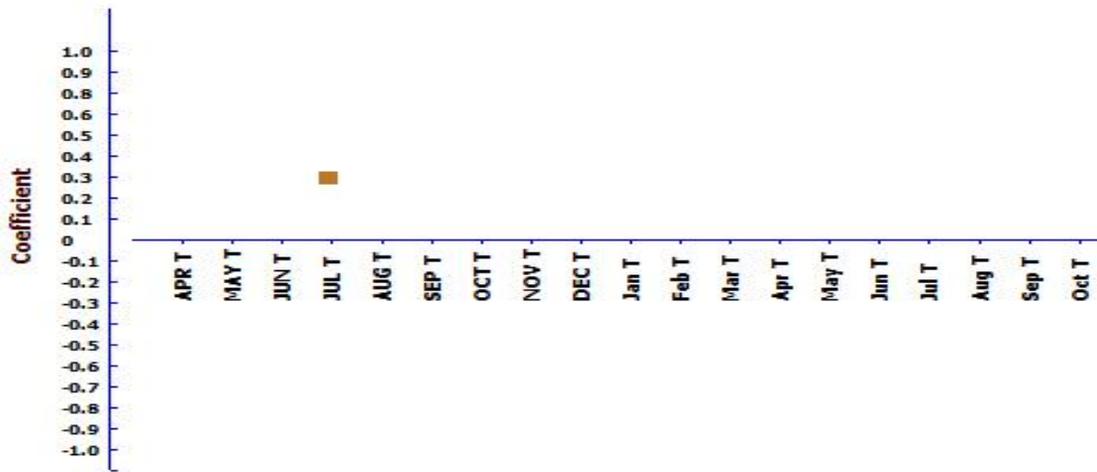
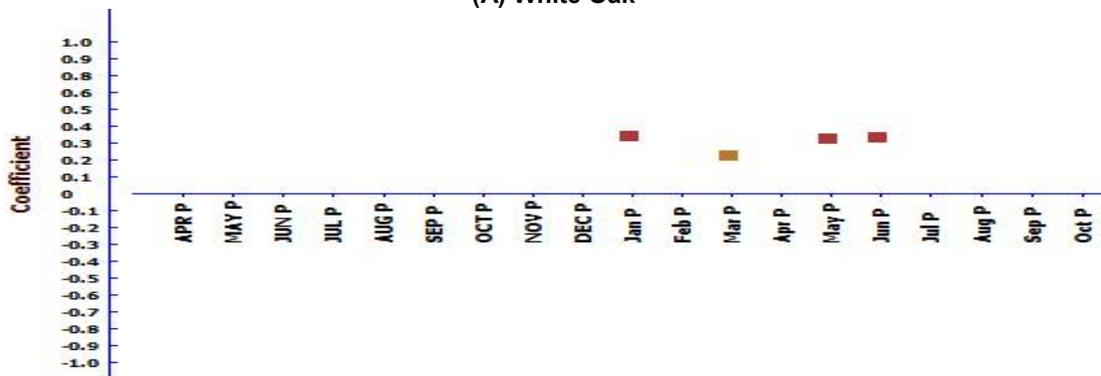
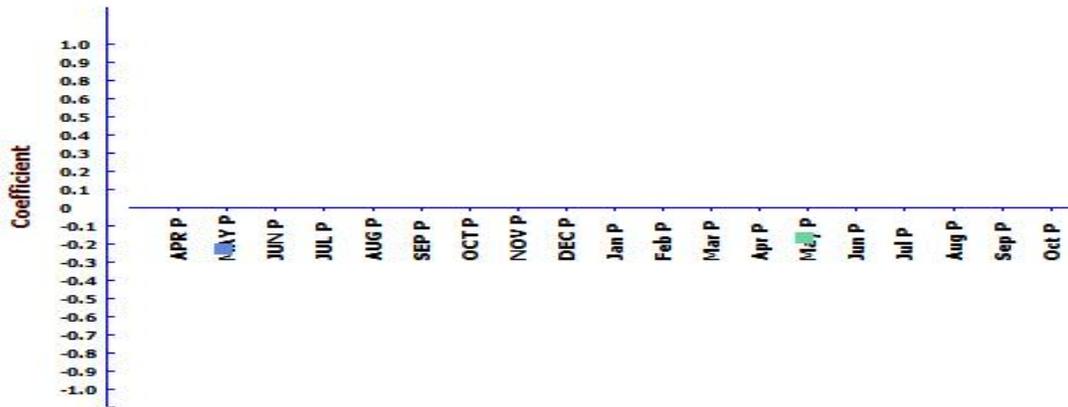


Fig. 3. Monthly correlations between mean temperature and radial growth of (A) white oak, (B) red maple, and (C) black cherry in the MacCready Reserve based on climate from 1928 to 2009, 1946 to 2009, and 1966 to 2009 respectively. Analysis begins in April of the previous year until October of the current year

(A) White Oak



(B) Red Maple



(C) Black Cherry

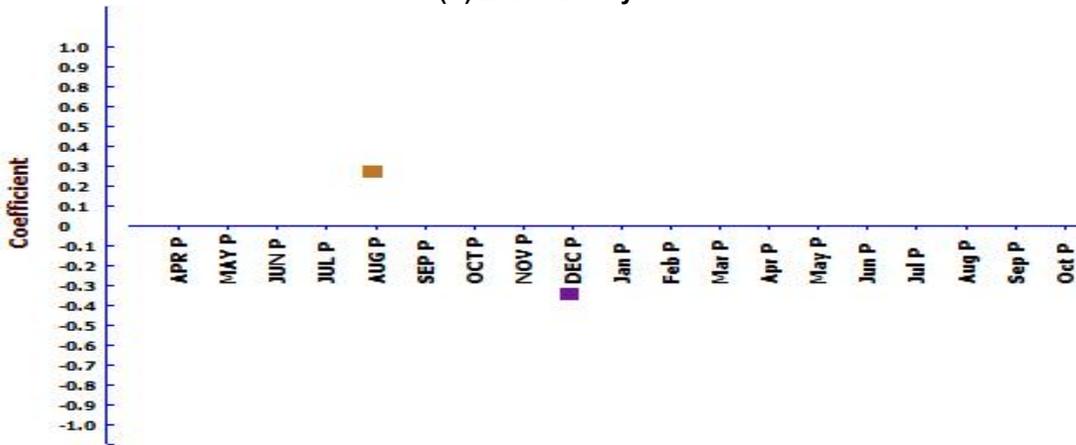
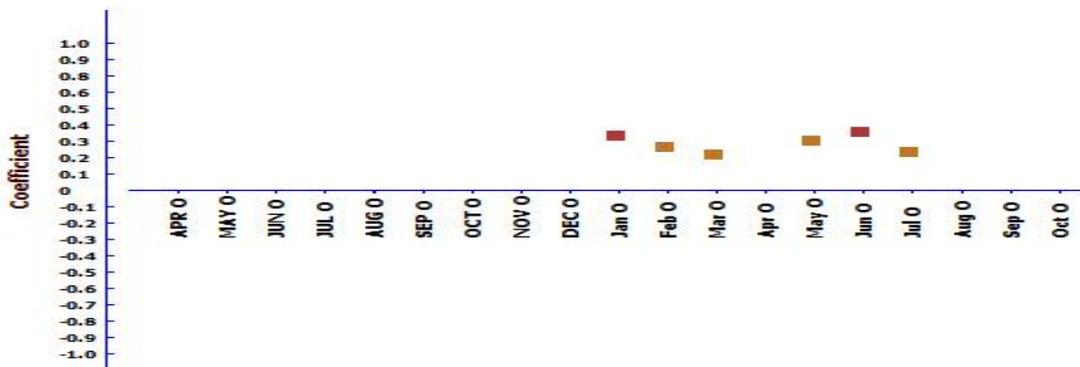
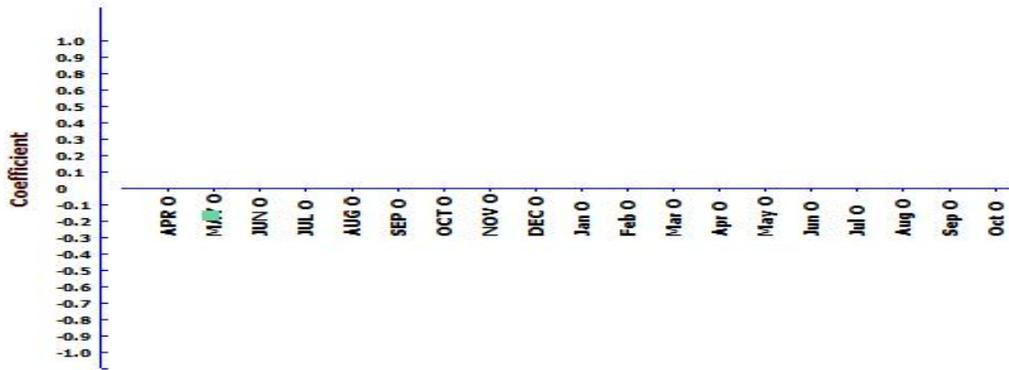


Fig. 4. Monthly correlations between total precipitation and radial growth of (A) white oak, (B) red maple, and (C) black cherry in the MacCreedy Reserve based on climate from 1928 to 2009, 1946 to 2009, and 1966 to 2009 respectively. Analysis begins in April of the previous year until October of the current year

(A) White Oak



(B) Red Maple



(C) Black Cherry

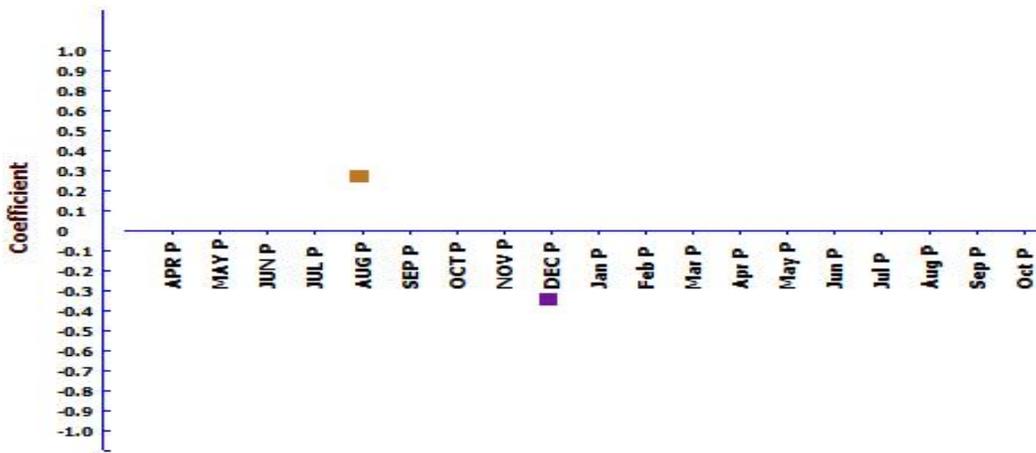
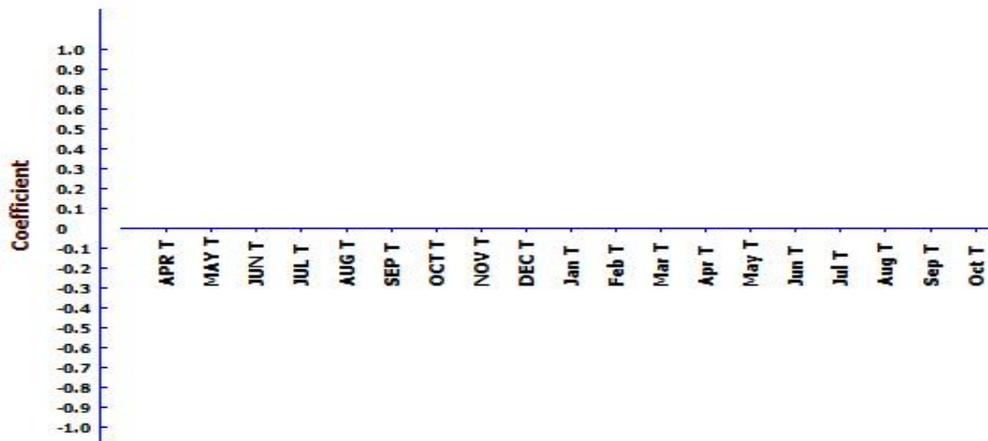


Fig. 5. Monthly correlations between total climatic moisture index and radial growth of (A) white oak, (B) red maple, and (C) black cherry in the MacCreedy Reserve based on climate from 1928 to 2009, 1946 to 2009, and 1966 to 2009 respectively. Analysis begins in April of the previous year until October of the current year

(A) White Oak – Red Maple Competition Ratio



(B) White Oak – Black Cherry Competition Ratio

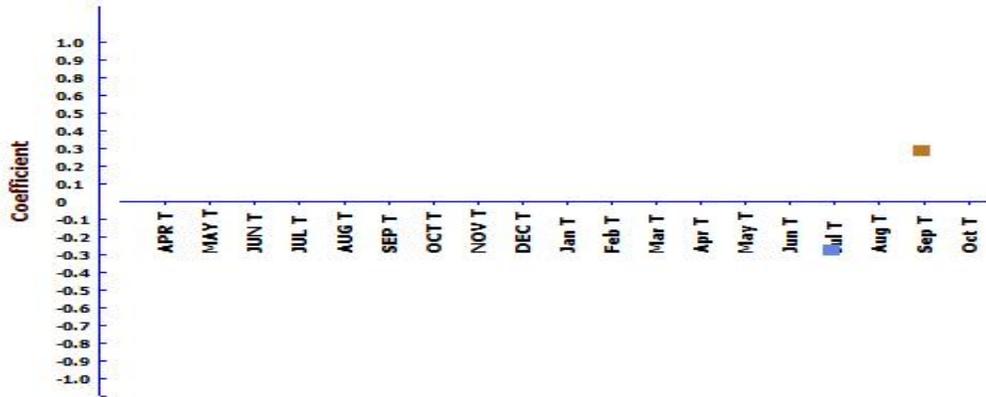
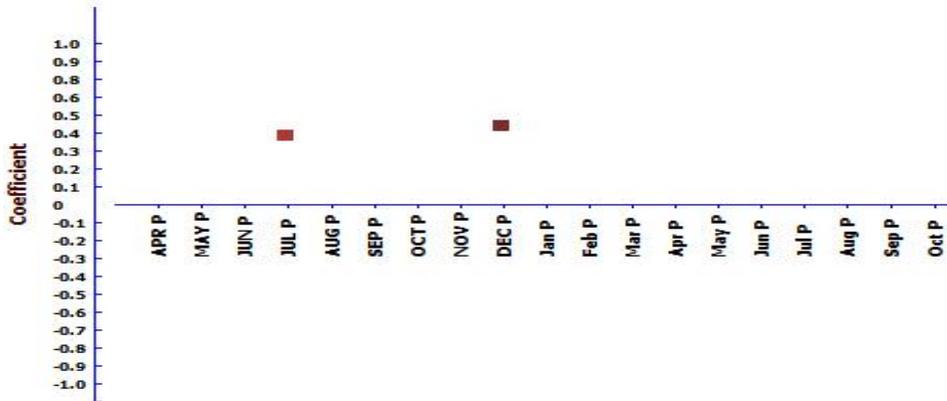


Fig. 6. Competition ratio response to mean temperature by species. Positive relationship indicates that conditions favored white oak growth, whilst negative relationship indicates that conditions favored competitor species growth

(A) White Oak – Red Maple Competition Ratio



(B) White Oak – Black Cherry Competition Ratio

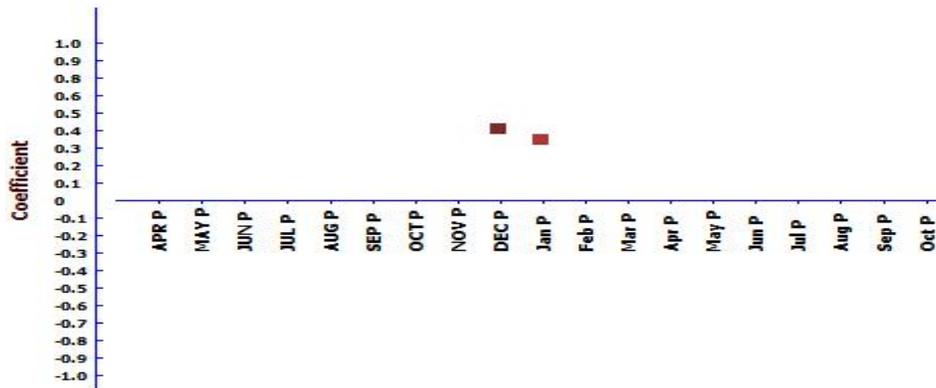
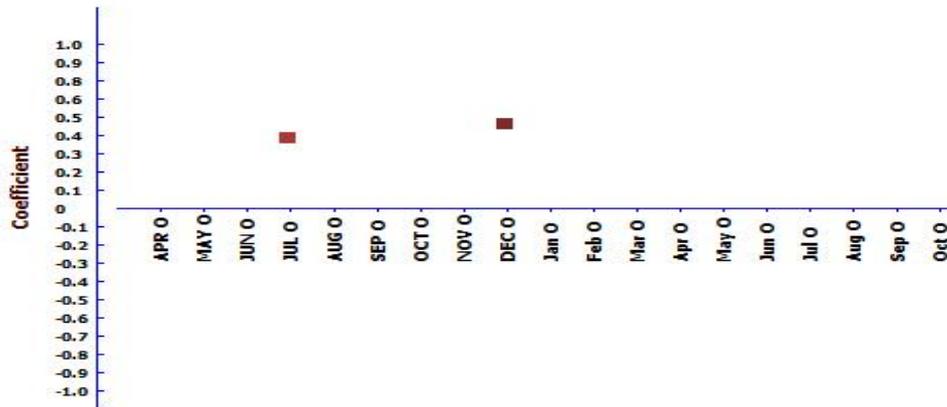
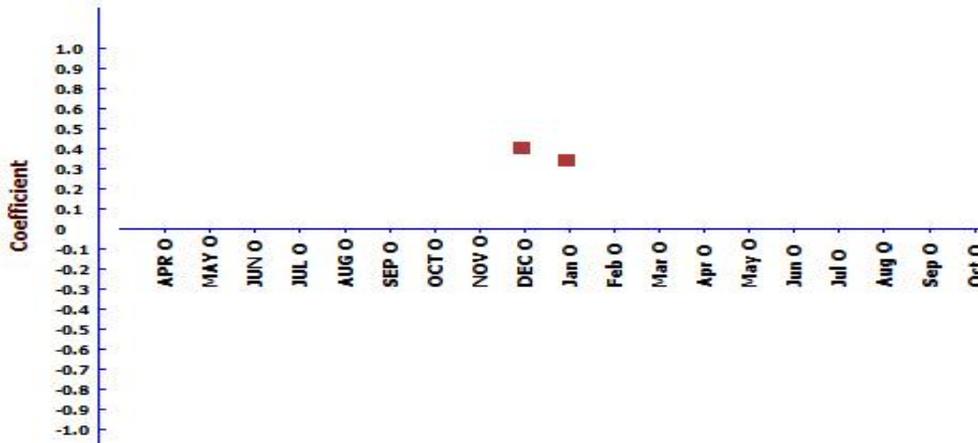


Fig. 7. Competition ratio response to total precipitation by species. Positive relationship indicates that conditions favored white oak growth, whilst negative relationship indicates that conditions favored competitor species growth

(A) White Oak – Red Maple Competition Ratio



(B) White Oak – Black Cherry Competition Ratio



**Fig. 8. Competition ratio response to climate moisture index by species. Positive relationship indicates that conditions favored white oak growth, whilst negative relationship indicates that conditions favored competitor species growth**

## 4. DISCUSSION

### 4.1 Tree-Ring Chronologies

The ARSTAN results indicated that the mean sensitivity and standard deviation of the three species were high and closely related, indicating their high growth sensitivity to climate. The three species (white oak, red maple, and black cherry) showed similarities and variations in their radial increment patterns. The sharp decline in radial growth recorded in this study in early to mid 1960s and late 1980s have also been reported in other dendrochronological studies for white oak [21,27] and red maple [28] in the United States. These pronounced declines in tree growth in the specified years have been associated with low precipitation [28] and seed production [29]. The recovery, however, following the decline is associated with the increased precipitation in the

early 1970s and 1980s, as well as the mid 1980s and 2000s, which is in line with findings reported elsewhere [5,21,28].

Even though radial increment reduced in the late 1980s in all the three species, however, red maple and black cherry exhibited above average growth in those years compared to white oak that experienced below average growth. The greatest reduction in growth experienced by white oak signifies its competitive disadvantage to red maple and black cherry. Climatic conditions such as precipitation and drought severity have the potential to ultimately act as limiting factors even in mixed mesophytic forests and limit the physiological activity of white oak [21]. White oak has adaptations for drought and fire but grows rather slowly when overtopped by other competitors [30]. Red maple and black cherry are reported to have an advantage over oaks due to

their greater morphological and physiological plasticity, and the potential to respond more speedily to changing environmental conditions [31].

#### **4.2 Responses to Precipitation and Climate Moisture Index (CMI)**

The significant positive relationship between the radial growth of white oak and monthly precipitation in January, March, May, and June of the current year means that precipitation in winter, spring, and summer is beneficial for radial growth of white oak, as well as an indication that drought stress reduces growth. Similar pattern and rationale apply for the correlation between the radial growth of white oak and climate moisture index (CMI). The positive relationship between the radial increment of the analyzed white oak and spring and summer precipitation/CMI suggests their vulnerability to moisture deficit during the vegetation period. This observation is confirmed by Rubino & McCarthy [21] that the growth of white oak is positively dominated by precipitation, especially from May to July. The results are also consistent with that of Leblanc & Terrell [32] who in an analysis of 128 white oak sites distributed across the eastern USA, detected that white oak was particularly sensitive to water balance in the early growing season (May to July) in the year when the annual ring is formed. The authors observed that June conditions had the most spatially consistent correlation with radial growth. Similarly, Jacobi & Tainter [33] found that May and June precipitation were positively associated with growth rate of white oak in South Carolina, USA. The dependence of oak growth on summer precipitation has been reported in several different studies in Europe; for instance, Rozas [34] reported a positive correlation of June precipitation and increment of Spanish oaks in northern Spain. In the study by Rozas [34], no correlation was found between precipitation and radial increment of white oak in the prior year. This was somewhat consistent with the study by Leblanc & Terrell [32], where little evidence was found that white oak radial growth was correlated with climate during the early growing season of the year prior to annual ring formation. Even correlations of white oak with variables for late summer-early autumn of the prior year in that study that showed significance were not for all the sites.

Radial growth of red maple was negatively correlated with precipitation in May of both

previous and current year, which is contrary to the findings by Hart et al. [35], where a significant positive correlation between standard chronology of red maple and precipitation was documented. It is speculated that the negative correlations between radial growth of red maple and precipitation in May of the previous and current year in this study might be due to the influence of storm-induced wind that could cause canopy damage. This would cause reduction in radial growth, as resource allocation would be prioritized to repair the damaged crown [5,36,37]. This same reasoning applies to the negative correlation observed between radial growth of red maple and climate moisture index in May of the previous year.

Radial increment of black cherry was positively correlated with late summer (August) precipitation and climate moisture index in the year prior to annual ring formation. The results suggest that in the year of bud formation, the end of growing season condition prior to ring formation contributes to photosynthetic reserves for the subsequent growing season [38]. This prerequisite factor was pronounced in the strong positive correlation with previous August precipitation and climate moisture index. The negative response of black cherry radial growth to December precipitation could be attributed to several mechanisms. Excessive snow can increase mechanical loads on crowns and lead to crown breakage which in turn leads to growth allocation priority to crown repair over radial growth [39].

#### **4.3 Responses to Temperature**

The analysis indicated that white oak radial growth showed no response to temperature in the past and current year. The ring growth of red maple was positively related to mean temperature of the previous October and current May. This explains that warmth during the spring and autumn is very important for red maple growth in the MR. The result is somewhat consistent with a study conducted by Hart et al. [35], where a significant positive relationship was found between the standard chronology of red maple and minimum temperature for the previous October. In addition, the radial growth of black cherry was positively correlated with previous July temperature. According to Grace et al. [40], in the absence of water stress, and with more or less continuous availability of nutrients, it is expected that the growth rate of woody plants in mountainous or other cold environments will

respond markedly to temperature. A warm early season (as observed in previous July in black cherry) would favor leaf growth as well as bud initiation for the following year's leaves [41]. No previous studies have conducted radial growth-climate relationship for black cherry in oak savanna ecosystems.

#### 4.4 Climate and Competition Interactions

The analysis of the interactive effects of temperature and competition in this study showed a neutral effect on white oak and red maple. This finding is presumed to be induced by extreme temperature and competitive conditions as well as high winds associated with storm events characteristic of Michigan springs and summers [42]. Black cherry had better growth performance over white oak in summer of the current year. This goes to confirm the findings by Abrams [30] that even though white oaks are noted to have a suite of ecophysiological adaptations for drought and fire, but not for effectively competing in closed forest understory dominated by shade-tolerant species. Preserving low competition levels through thinning could reduce the negative impacts of increasing temperatures on white oak productivity in oak savannas.

Precipitation and climate moisture index in July and December of the previous year and January of the current year favored white oak over competing red maple and black cherry. The marked radial growth of white oak with total monthly precipitation in December of the past year is consistent with the study by Rubino & McCarthy [21] and Robertson [43] where they observed significant positive correlation in white oak annual growth with total monthly precipitation in December of the prior year. High precipitation in the winter enhances growth in the following year by providing soil moisture when cambial activity commences in the spring [43]. Generally, the findings from the climate-competition interactive effects suggest that white oak had greater radial growth associated with more moisture and precipitation, cooler summer and winters, and warmer autumn than the competitors.

Responses of the species to temperature and precipitation deviated from the expectations of this study. It was hypothesized that competitors will grow better when conditions are favorable, whereas the focal tree will outgrow the competitors during stressful growing conditions

(e.g. drought). This anomaly is presumed to be caused by the anisohydric behavior of white oak and isohydric behavior of red maple and black cherry [44]. Isohydric species close their stomata more rapidly when they experience water stress and thus regulate their stomatal conductance to conserve minimum water potential within a relatively narrow range and so are able to reduce the risk of damaging xylem cavitation driven by extreme tension in trees' hydraulic system. Anisohydric species, on the other hand, keep their stomata open and photosynthetic rates high for longer periods, even in the presence of decreasing leaf water potential. The high risk-taking behavior of anisohydric species could be beneficial when water is abundant but stand a greater danger during intense drought conditions [26,44,45]. This contrasting behavior of the focal tree and the competitors is assumed to have triggered the higher growth response of white oak to precipitation and relatively less growth with temperature.

#### 5. CONCLUSION

Climate (temperature and precipitation, in this case) has the potential to positively and negatively affect tree growth and productivity. Findings from this study indicate that precipitation in winter, spring, and summer is beneficial for radial growth of white oak. The negative correlation of red maple radial growth with precipitation in the previous and current May is speculated to be possibly due to damaging winds (characteristic of Michigan) that could cause canopy destruction, and in effect resource allocation was prioritized to repair the damaged crown. Inasmuch as precipitation in winter, spring, and summer is favorable for tree growth, too much of it could lead to waterlogging and root suffocation and consequent growth reduction, which was confirmed by negative black cherry growth correlation with precipitation and climate moisture index. The study also showed that warmth during the spring and autumn periods is vital for red maple growth in the MacCreedy Reserve. Comparison of ring width chronologies of the different tree species depicted that even though growth generally reduced during stressful climate conditions (e.g. drought), red maple and black cherry, however, had competitive advantage over white oak.

White oak is relatively more resilient to drought stress than red maple and black cherry due to its ecophysiological adaptations but tends to grow rather slower when in competitive co-habitation

with these shade tolerant and fire sensitive competitor species. These findings postulate that if fire suppression continues unrestricted, together with other biotic and abiotic factors responsible for the current decline of oak savanna communities, there would be a successional trend away from oak dominance towards a future of red maple dominance. This postulation can be addressed in future field studies, especially ones incorporating restoration techniques such as prescribed burning and mechanical thinning [46] and spatially explicit models [47]. Understanding the degree of impact of competitor species (e.g. red maple and black cherry) on oak productivity is imperative to oak savanna restoration success [48]. Overall, this study has shown that temperature and precipitation play key roles in tree productivity and thus climatic sensitivity should be incorporated in the restoration of oak savanna ecosystems.

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## COMPETING INTERESTS

Authors have declared that no competing interests exist.

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