

**Investigating tree growth responses to drought, temperature,
and precipitation among *Betula papyrifera*, *Betula
alleghaniensis*, *Pinus resinosa*, and *Tsuga canadensis***



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ABSTRACT:

In order to examine differences between early and late successional trees responses to climate change, we took cores and environmental data (pH, soil moisture, DBH, and ambient temperature) from four species of trees in northern Wisconsin: paper birch (*Betula papyrifera*) and red pine (*Pinus resinosa*) as early successional trees, and yellow birch (*Betula alleghaniensis*), and eastern hemlock (*Tsuga canadensis*) as late successional trees. Using Coorecorder, Cdendro, Cofecha, and R and Rstudio (specifically the dplR package), growth data from each core was extracted, detrended, averaged, and compiled into single chronologies for each species. These chronologies were then regressed against climate data from Wisconsin using the month of May as a representative of each year (since this month was found to demonstrate highest sensitivity between growth and climate in most each stand, and used to visualize the different conditions in which each species lives. Stand characteristics were examined using one-way ANOVAs when normally distributed and Kruskal-Wallis tests when not. Growth in both paper birch and red pine, early successional trees, appeared to be sensitive to drought and demonstrated negative trends as drought increased; only paper birch was found to be negatively sensitive to annual maximum temperatures. No other species appeared to be affected by climate factors. Paper birch also demonstrated the lowest average DBH measurements, suggesting that there is a relationship between tree size and sensitivity to climate; hemlock, one of the late successional trees, was found to have the lowest stand temperature, suggesting that microclimate may contribute to neutralizing the effects of climate on trees. Ultimately, our study didn't confirm our hypotheses, demonstrating that much more work should be done to demystify the relationships between successional status and response to climate change.

Keywords: succession, *Betula papyrifera*, *Pinus resinosa*, *Tsuga canadensis*, *Betula alleghaniensis*, climate change, drought resistance

INTRODUCTION:

Rapid climate change over the past decades has led to a number of environmental changes across the world (Parry et al., 2007). Along with these shifts come several challenges; for one, species acclimated to specific environmental conditions cannot simply readjust their biology to accommodate new conditions—rather, the process of adaptation takes a very long time and likely only occurs in some species, not all. Thus, there is the possibility, and even high probability, of many species going extinct over the next few decades as the climate and conditions continue to drastically change (Thomas et al., 2004).

Our flora's response to changing environments further compounds the climate issue—it is true that some plant species are able to deal well with a small rise in temperature (Berry and Bjorkman, 1980), but there is sufficient evidence to show that large changes in temperature can

actually be irreversibly destructive to a great majority of plants (Mora et al., 2015). Determining different species responses to changes in temperature is critical for planning and combating the challenges that we will face over the coming years.

Precipitation, too, is crucial to the growth and maintenance of plant life. As temperatures increase, rates of evaporation of water are increased; with these higher rates of evaporation comes an increased severity of precipitation events when they occur (Trenberth, 2011). Altered precipitation regimes also serve as harbingers of increased future drought severity, which may have consequences for species survival and distribution (Allen et al., 2010). Some plant species can deal with drought better than others; for example, Ponce-Campos et al. (2013) indicate that there are many plants with high water-usage efficiency indices across all biomes; this means that they are able to withstand longer periods of drought stress as if they were always meant to. However, some species that depend on a constantly hydric environment may be susceptible to increased drought mortality, adding to the growing list of casualties (Allen and Breshears, 1998).

Specifically, the American Midwest faces a significant increase in drought intensity in the near future, creating major challenges not only for industry, but also for species conservation (Niyogi and Mishra, 2013). In order to protect these organisms that are at risk, we must examine their ecology to see where the risk truly lies. To be able to conserve varieties of species, it is critical to examine the mechanisms of diversity. A dominant driver of species diversity in ecosystems is succession; across different successional environments, species of flora and fauna are distributed according to the resources available and type of environment. Climate change may affect each stage of succession and the species that occur there in different ways, and occurrences such as drought, fire, and severe weather are only some of the dangers that will plague forests in the near future (Dale, 2001).

Early and late successional species have been shown to deal with climate factors in different ways. Generally, early successional species are more resistant to severe periods of drought and temperature (Dreyer et al., 1993), while late successional species aren't as tolerant of extreme droughts and temperatures (Bazzaz, 1979). This difference is the result of the characteristics of the different environments. Early successional sites tend to be drier than later successional sites (Olson, 1958) due to higher temperatures. Macronutrient concentration in soil

also has been demonstrated to increase as succession progresses (Goudie, 1989). The pH of the soil, in contrast, has been shown to decrease and become more acidic as the ecosystem ages (Olson, 1958). These discrepancies across status are important to consider in studies relating climate to organismal success, as they may help explain why some species are either better or more poorly adapted to changes in climate.

Another category of interest when studying trees is tree type; either deciduous or evergreen. These two types of trees have different specialties, notably their strategies for dealing with harsh temperature and limited resources. Givnish (2002) noted that deciduous trees tend to be more drought resistant due to their strategy of leaf loss under stressful conditions, while evergreen trees tend to inhabit areas of more consistent ambient conditions. It is possible that as the climate continues to change, so too could the distribution of each of these types of trees, altering not only the distribution of these species, but also the composition of entire land areas too.

In order to better understand how drought will affect different plant species endemic to the Northwoods, the boreal forest in North America that covers land from Wisconsin to Maine, we will examine four species of deciduous and evergreen trees endemic to the area: red pine (*Pinus resinosa*) and paper birch (*Betula papyrifera*) will represent early succession, while eastern hemlock (*Tsuga canadensis*) and yellow birch (*Betula alleghaniensis*) will demonstrate late succession (UNDERC East, 2017). Specifically, tree core samples will be used to determine average tree growth per year, which will help determine sensitivity to temperature, precipitation, and drought indices from the time period of 1940 to 2016 (Intergovernmental Panel on Climate Change, 2014).

Overall, this study hopes to delineate the relationship (or lack thereof) between climate factors (temperature, precipitation, and drought) and annual tree growth. We predict that our early successional deciduous species will exhibit the strongest responses to annual highest drought indices, lowest minimum temperatures, highest maximum temperatures, and highest total precipitation values. We also predict that pH and temperature will be lower in late successional areas than early successional areas, but moisture content in the soils and tree diameter at breast height (DBH) will be greater in late successional areas.

MATERIALS & METHODS:

Research Area

We conducted research for this project at the University of Notre Dame Environmental Research Center (UNDERC) near Land O'Lakes, Wisconsin on the Wisconsin-Michigan border. Much of the Northwoods was logged for human land use from the mid-1800s until the 1930s, altering the overall composition of the forests and creating environments for a variety of plants of all successional type to inhabit (Rhemtulla et al., 2007).

Study Organisms

Red pine (*Pinus resinosa*), paper birch (*Betula papyrifera*), Eastern hemlock (*Tsuga canadensis*) and yellow birch (*Betula alleghaniensis*) are all endemic to the Northwoods. Both red pine and paper birch were chosen to be early successional models, while eastern hemlock and yellow birch represented late successional species. The selection of an evergreen (red pine and hemlock) and a deciduous species (paper and yellow birch) within each successional status also allowed for the variation between tree type to be examined.

Experimental Design

Using a tree species distribution map of the UNDERC property, we chose four stands (one stand per species) from which to take core samples (Figure 1). Two tree cores of 5.15 mm were taken from ten trees of each species, yielding a total of 80 samples (Cook and Blasings, 1987). Coring procedure followed Stokes and Smiley (1968). Tree specimens were selected based on their health, size (greater than 15 cm in diameter), and location. Rather than chose only those trees close to the forest edge, conscious selection of specimens both close to the road and deep within the forest was implemented so as to obtain a more holistic view of the stand's dynamics. When possible, trees on slopes were avoided due to the presence of reaction wood, which is grown in order to provide extra support on inclines and can make cores difficult to read (Speer, 2010). A standard coring height of chest-level was set, and cores were taken taken at 90°

to one another. After removal from the spoon, the cores were stored in plastic straws to preserve shape and integrity of the cores, especially if they were fragmented upon extraction.

To characterize each stand, a Kestrel 3000 Wind and Humidity Meter was used to take temperature at breast height at each tree. Soil and pH measurements were taken from the soil at the base of each tree using a Kelway Soil pH and Moisture Meter. Finally, diameter at breast height (DBH) was recorded for each tree using DBH tape.

In order to measure each core, the specimens were dried in the oven at 50°C for 48 hours, glued onto wooden platforms, dried again for 24 hours, and then sanded using both electric and hand sanders to better expose the rings. Prior to measurement, the cores were visually cross dated using a light microscope. Once preliminary dating had been completed, we scanned the cores into a computer equipped with CooRecorder and CDendro software (Larsson, 2014), used to create growth increment files and individual tree chronologies, respectively.

Extraction of Growth Indices and Statistical Analysis

To cross-date the measurements, the information obtained from Cdendro was compiled into a singular data file for each species using a script in RStudio available on github (https://github.com/Kah5/crossdating/blob/master/R/individual_to_site_RWL.R). Each file was run through the Cofecha crossdating program (Holmes, 2000). Crossdating within the species was necessary for checking the measured dates and allowed for more accurate analysis. If there were specimens that still did not cross date well after repeated examination at all or had significant portions missing, they were excluded so as to eliminate any confounding samples. In the end, 18 hemlock cores, 10 yellow birch cores, 16 red pine cores, and 11 paper birch cores went on to be detrended.

Detrending was done using the Friedman detrending technique in RStudio (https://github.com/Kah5/TreeRings/blob/master/R/dplR_detrend.R) and the dplR package (Bunn, 2010). This step allowed for the removal of growth trends specific to age, disturbances, and canopy position (Stokes and Smiley, 1968). For each species of tree, a master chronology was constructed by taking information from each individual core and compiling it into an average trend.

Pearson's r correlation were run on detrended annual growth rate and monthly Palmer Drought Severity Index (PDSI) values, monthly total precipitation values (in centimeters), and monthly minimum and maximum temperature values (in degrees celsius) to determine which months were strongly linked to tree growth in the region. All climate data came from the NOAA National Climate Data Center records for the state of Wisconsin. For both drought indices and total precipitation, the month that corresponds to the highest positive correlation value was chosen, as both drought severity and growth relationships and precipitation levels and growth relationships were found to be directly proportional. Conversely, for temperature, the month that showed correlations that were the most negative were examined, as higher temperatures can lead to stunted tree growth. From there, a linear regression was used to model the relationship between detrended growth chronologies and climate for each species. We compared soil moisture, temperature, and DBH measurements across all species using a series of one-way ANOVAs in order to characterize possible differences between sites that may affect growth patterns. R and RStudio were used along with the *dlpR* package to run and generate the analyses and figures.

RESULTS:

Correlation Results

To determine which monthly climate indices are strongly correlated with tree growth in the time frame previously mentioned (1940-2016), we used Pearson's r correlation. Since they were only meant to be preliminary analyses used on the master chronology developed and climate, these correlations don't have error bars. For both drought and precipitation index (Figure 2 and 3), the month of highest positive correlation or majority of the species was May. As far as minimum and maximum monthly temperatures (Figure 4 and Figure 5, respectively), the lowest correlation (most negative) seemed to be in the month of May as well. Overall, the correlation coefficients were very low, so for both consistency and convenience, the month of May was chosen to represent each year for the regression analysis.

PDSI /Precipitation Regressions

The relationship between PDSI and growth (Figure 6) was found to be directly proportional and significant only in paper birch ($R^2 = 0.1491$, $y = 0.03456(x) + 0.96396$, $p = 0.0005223$) and red pine ($R^2 = 0.06398$, $y = 0.013116(x) + 0.988380$, $p = 0.0265$), both of which displayed positive slopes. While yellow birch and hemlock had nonsignificant results, their trend line slopes were also generally positive. The relationship between annual total precipitation (in centimeters) and growth was actually found to be nonsignificant in all species (Figure 7). Again, despite nonsignificance, all species displayed positive slopes on all trend lines.

Temperature Regressions

Annual minimum temperatures (in degrees celsius) versus detrended growth indices was found overall to have no significant relationships with any of the species studied (Figure 8). Still, hemlock demonstrated a positive slope while red pine, paper birch and yellow birch displayed negative slopes. For maximum annual temperature relationship with growth (Figure 9), only paper birch was found to have a significant negative trendline ($p = 0.01595$) that fit a small portion of its data ($R^2 = 0.075$, $y = -0.022898(x) + 1.392522$). All other species were found to have non significant, negative slopes.

Stand Characteristics

Results from the stand data (Figure 10) indicated that neither average pH (ranged from 5.8 to 6.5) nor moisture content (ranged from 30 to 70 percent) were found to be normal (Shapiro-Wilk: $p = 0.01699$ and $p = 0.02056$, respectively), so Kruskal-Wallis tests were run after the ANOVA. Still, neither pH nor moisture content were found to be significantly different ($p = 0.4245$ and $p = 0.6145$). Conversely, both average DBH ($p = 0.0000587$) and average temperature ($p = 6.51e-12$) were found to be significantly different and normal (Shapiro-Wilk: $p = 0.8747$ and $p = 0.3787$, respectively) with yellow birch having the highest average DBH of 45.05 cm (compared to that of hemlock with 44.52 cm, red pine with 42.82 cm, and paper birch with 25.69 cm), and paper birch having the highest average temperature of 26.78 °C (compared to that of red pine with 26.27 °C, yellow birch with 25.8 °C, and hemlock with 23.17 °C).

Further analysis on DBH via Tukey's HSD revealed that Paper Birch significantly differed from hemlock, red pine, and yellow birch. Tukey's HSD performed on temperature revealed that hemlock significantly differed from paper birch, red pine, and yellow birch.

DISCUSSION

The results indicated that the majority of our hypotheses were not supported. For one, it appears that there is no relationship between drought severity and hemlock growth or yellow birch. In other words, late successional trees in this study seemed to demonstrate growth patterns that were not sensitive to climate. Additionally, the same can be said for all species when looking at total precipitation levels, and minimum temperatures. For maximum temperatures, it would appear that yellow birch, hemlock, and red pine all demonstrated growth patterns that were not affected by ambient temperatures. However, we observed significant slopes in paper birch trees and red pine trees, both early successional trees, when comparing their respective growth rates to drought indices. Though the trend lines didn't explain much of the data, the significance of the positive slopes suggests that early successional trees are, in fact, sensitive to periods of severe drought and may not grow as well. Also, paper birch trees appeared to have a significant negative relationship with maximum temperatures, meaning that hotter temperatures yielded lower overall growth.

These findings are especially intriguing, as the exact opposite was hypothesized. The fact that late successional species seemed to be unphased by drastic climate factors while early successional species seem to be sensitive to extreme drought and temperatures presents an unusual perspective on these species and their relationships with their environs. If we examine our findings from the climate relationships in light of differences in stand level characteristics, we can get a more detailed explanation of our observations. The DBH measurements proved to significantly differ among species with paper birch having the lowest average DBH overall. Perhaps, paper birch trees are more sensitive to severe droughts because of their smaller DBH, a factor that could affect the tree's ability to store water. Wang & Letchford (1998) noted that under low-water, low-nitrogen conditions, photosynthesis rates in paper birch trees was about

45% lower than at high-water, high-nitrogen concentrations. Whether this is true under low water conditions only and in the area we studied is unknown, but should be area of future study.

Taking into account the significantly lower temperatures found in the hemlock stand than the other stands, it is also a possibility that microclimates may be quite instrumental in influencing growth in trees. As Kjelgren and Clark (1992) demonstrated, microclimates have the ability to dramatically alter growth in trees; whether exposed to more mild temperatures or more extreme ones as a result of surroundings rather than climate can mean the difference between stunted growth or success. We noted that paper birch tree growth exhibited negative responses to higher temperatures, and this could be due to the stand experiencing high temperatures in may, rather than the climate. As a contrast, the hemlock stand appeared to have the lowest average temperature and elicited no growth response to extreme temperatures. Thus, the microclimate created by larger hemlock trees could have a greater influence on the stand's productivity than the macroclimate of the region.

Since climate appears to have little effect on late successional tree growth, a good parameter to expand upon in the future would growth releases in trees, as this is indicative of stand dynamics. We decided to have a look at our chronologies to see if any stands exhibited a great deal of releases, a period of growth that is 1.5 times more than the previous decade, and we were able to find evidence of numerous stand changes in the hemlock stand (Table 1), and. Since this wasn't originally a part of the study, no statistical analysis was performed on the release data, rendering any claims made refutable. Still, examining releases is a successful method by which to learn more about a particular stand, so future studies may consider incorporating this characteristic.

Overall, this study leaves many questions regarding the relationship between succession and climate. The apparent lack of sensitivity to climate found in late successional trees is contradictory to the findings of Bazzaz (1979); similarly, the apparent sensitivity of early successional trees to climate conflicts with the work of Dreyer et al. (1993). Future work should be directed toward exploring these findings in greater detail so as to discern the true relationships between climate and growth. Also, it may be highly beneficial to have a better understanding of whether macro- or microclimate and DBH are indeed responsible for affecting the growth

patterns of some trees, as they found to be in this study. These studies should be done before any future attempts to mitigate climate change can be implemented, as their results could change the way we view both the effects of climate change on trees, and how trees respond to these changes. Ultimately, the scope of these studies should not remain constrained to several stands located in close proximity to one another; expanding the study area to look at different forests in the Northwoods or even the Midwest as a whole.

FIGURES

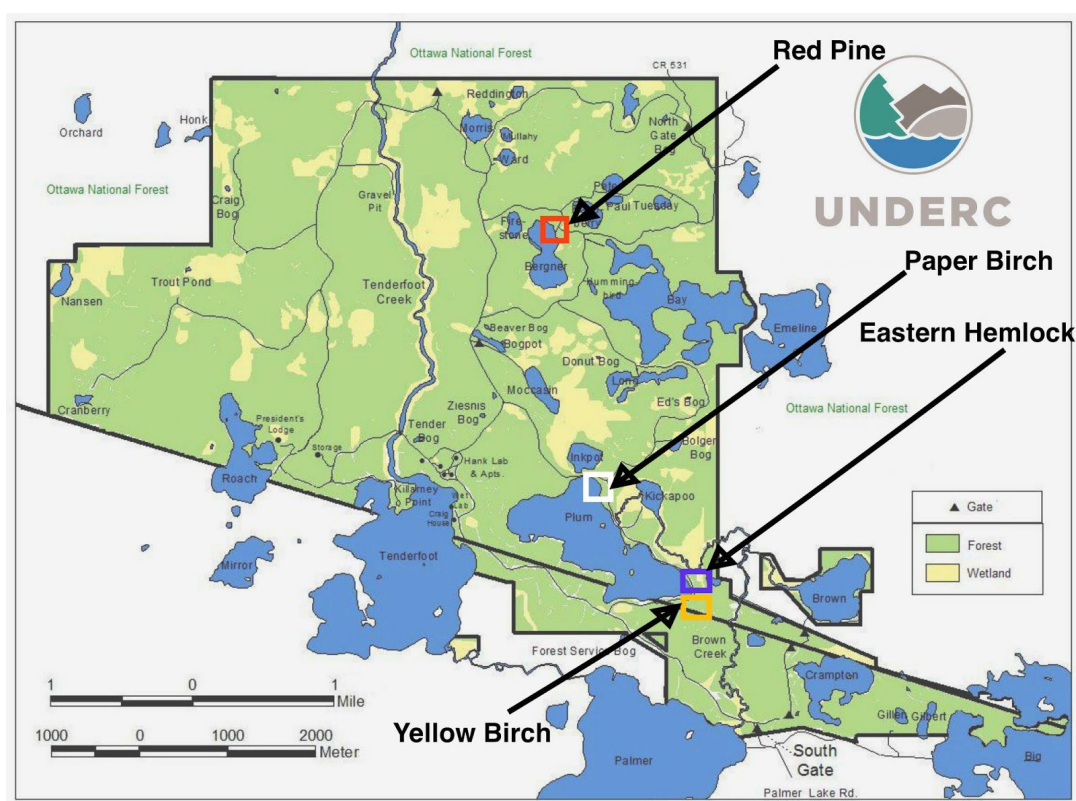


Figure 1. Map of the UNDERC property and stand locations. Each stand was chosen based on its composition. The northernmost stand was located near Bergner Lake and was dominated by red pine, while the paper birch, and yellow birch and hemlock stands were located on the northern and eastern sides of Plum Lake, respectively.

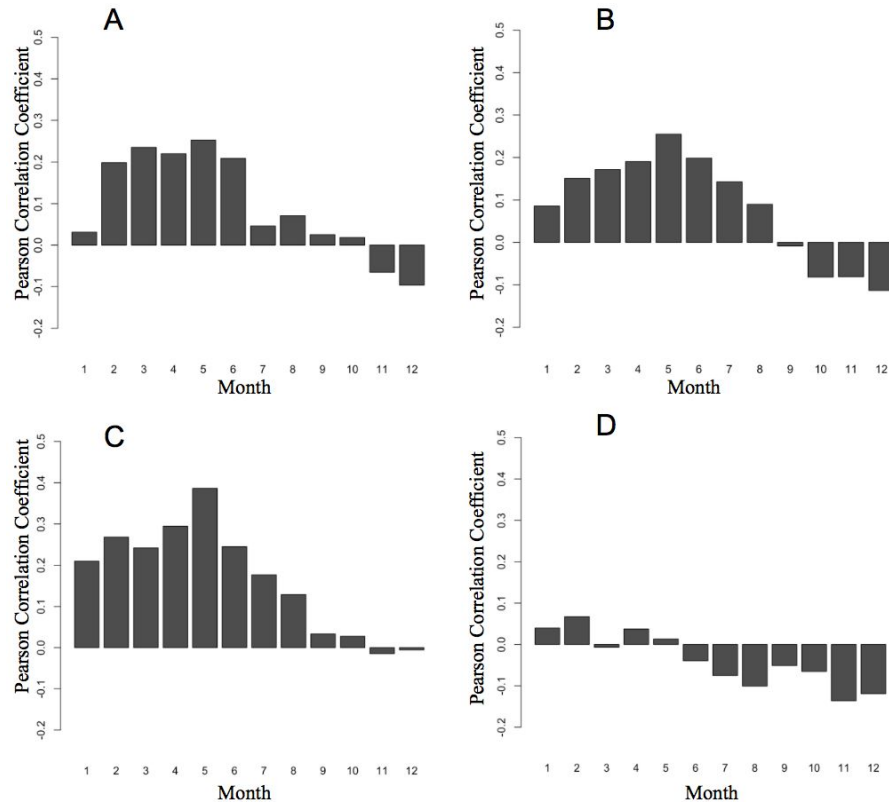


Figure 2. Correlation between monthly PDSI (1940-2016) and detrended growth indices generated from a single chronology for red pine (A), yellow birch (B), paper birch (C), eastern hemlock (D). The month of May (month 5) represents the highest positive correlation for all but one species, and was thus used as representative of the each year in the regression.

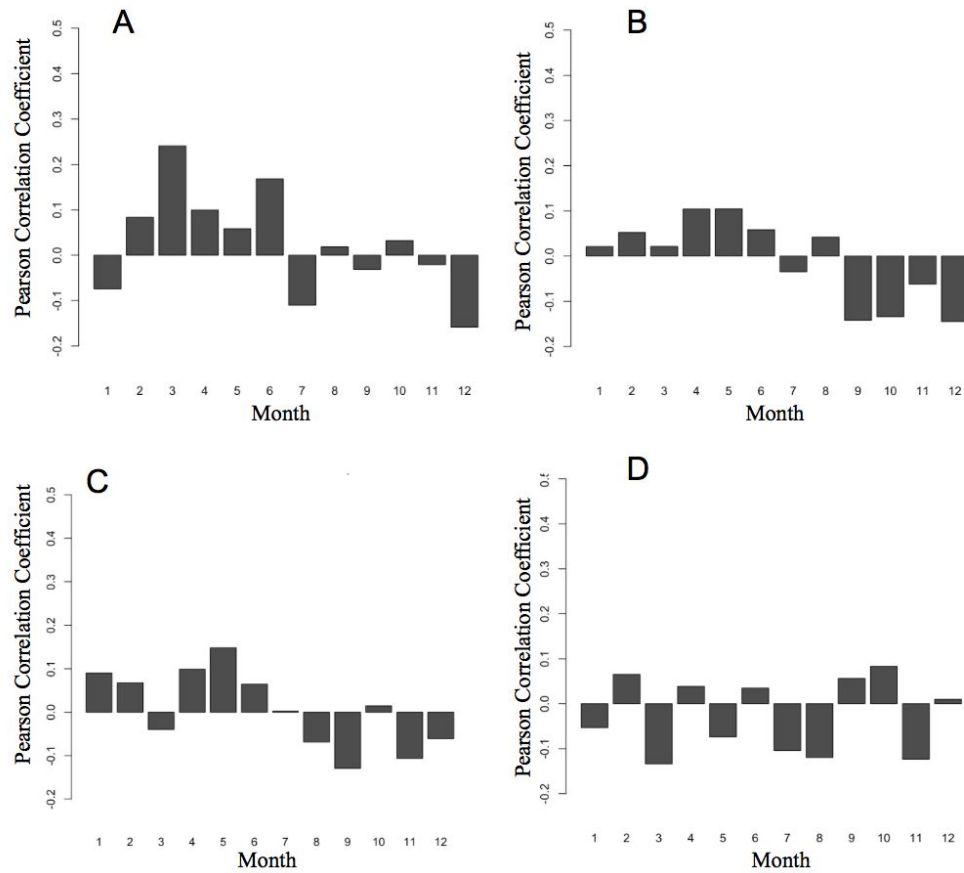


Figure 3. Correlation between monthly precipitation in centimeters (1940-2016) and detrended growth indices generated from a single chronology for red pine (A), yellow birch (B), paper birch (C), eastern hemlock (D). The month of May (month 5) represents the highest positive correlation for paper and yellow birch and thus used as representative of the each year in the regression for consistency.

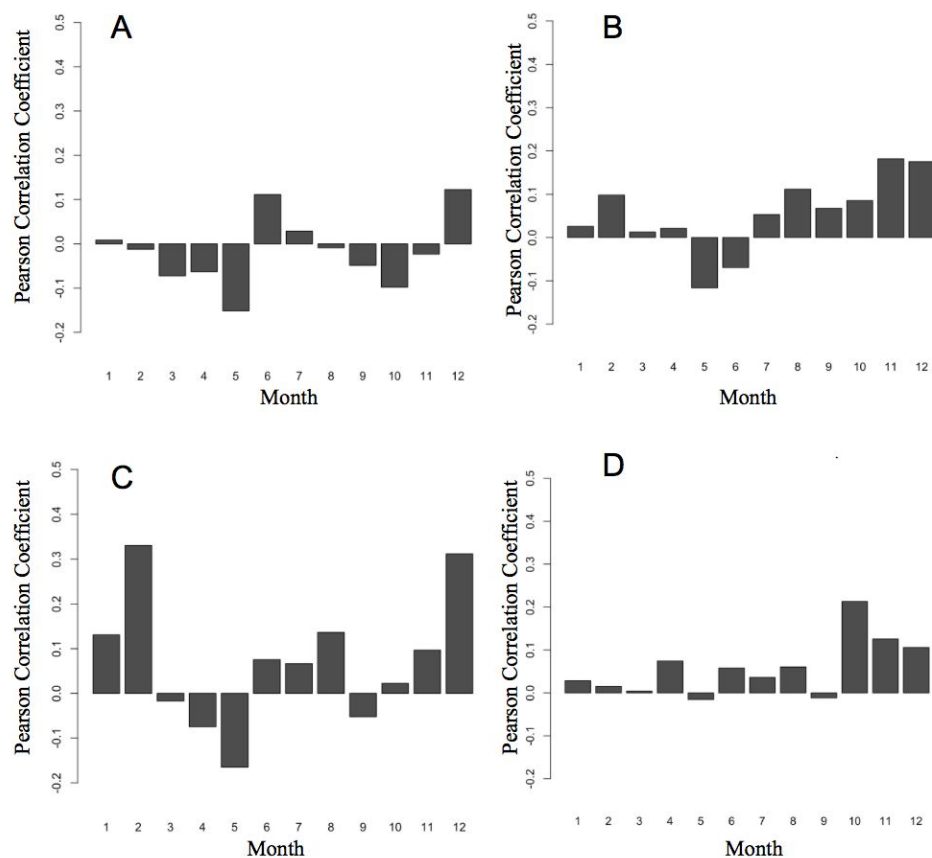


Figure 4. Correlation between minimum monthly temperature in degrees celsius (1940-2016) and detrended growth indices generated from a single chronology for red pine (A), yellow birch (B), paper birch (C), eastern hemlock (D). The month of May (month 5) represents the highest negative correlation for all but one species, and was thus used as representative of the each year in the regression.

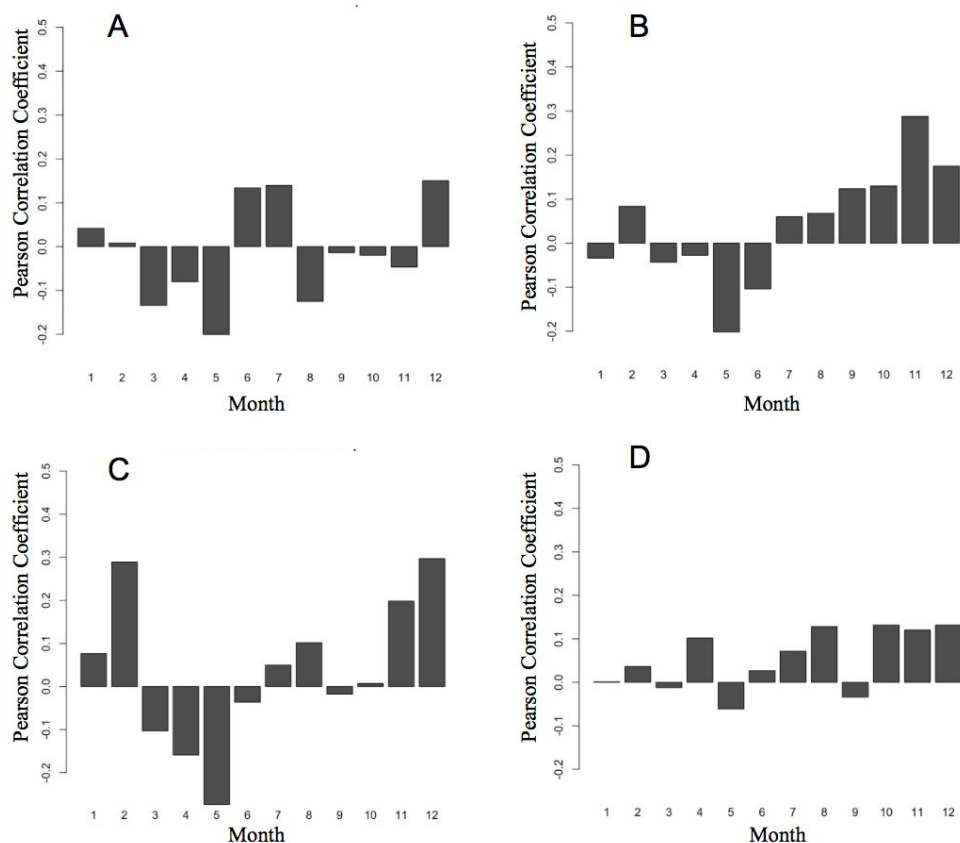


Figure 5. Correlation between maximum monthly temperature in degrees celsius (1940-2016) and detrended growth indices generated from a single chronology for red pine (A), yellow birch (B), paper birch (C), eastern hemlock (D). The month of May (month 5) represents the highest negative correlation for all but one species, and was thus used as representative of the each year in the regression.

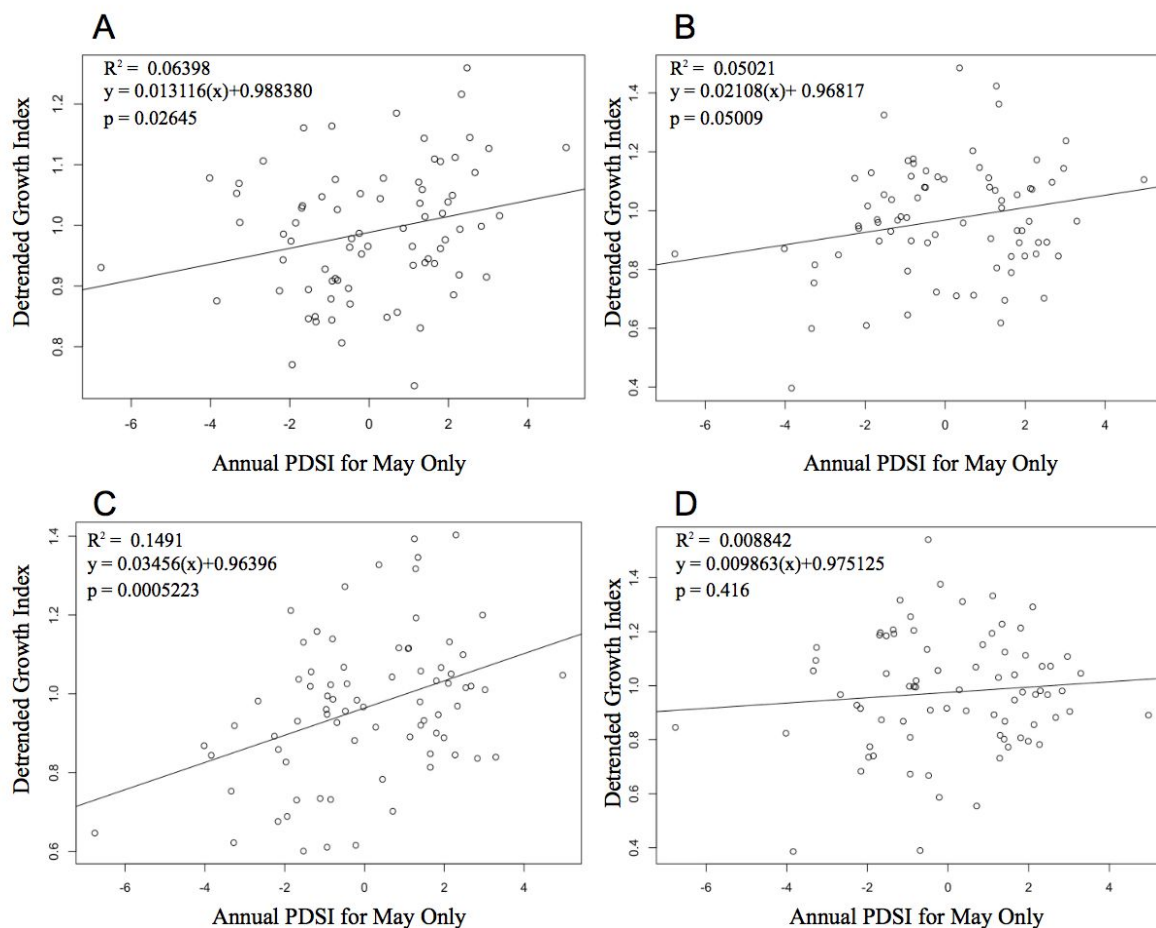


Figure 6. Relationship between annual PDSI (using the data from May only) and detrended growth indices for red pine (A), yellow birch (B), paper birch (C), eastern hemlock (D) from 1940 to 2016. Paper birch ($p = 0.0005223$) and red pine (0.0265) were found to have significant trend lines with positive slopes ($R^2 = 0.1491$ and $R^2 = 0.06398$, respectively), while yellow birch and hemlock had nonsignificant trend lines.

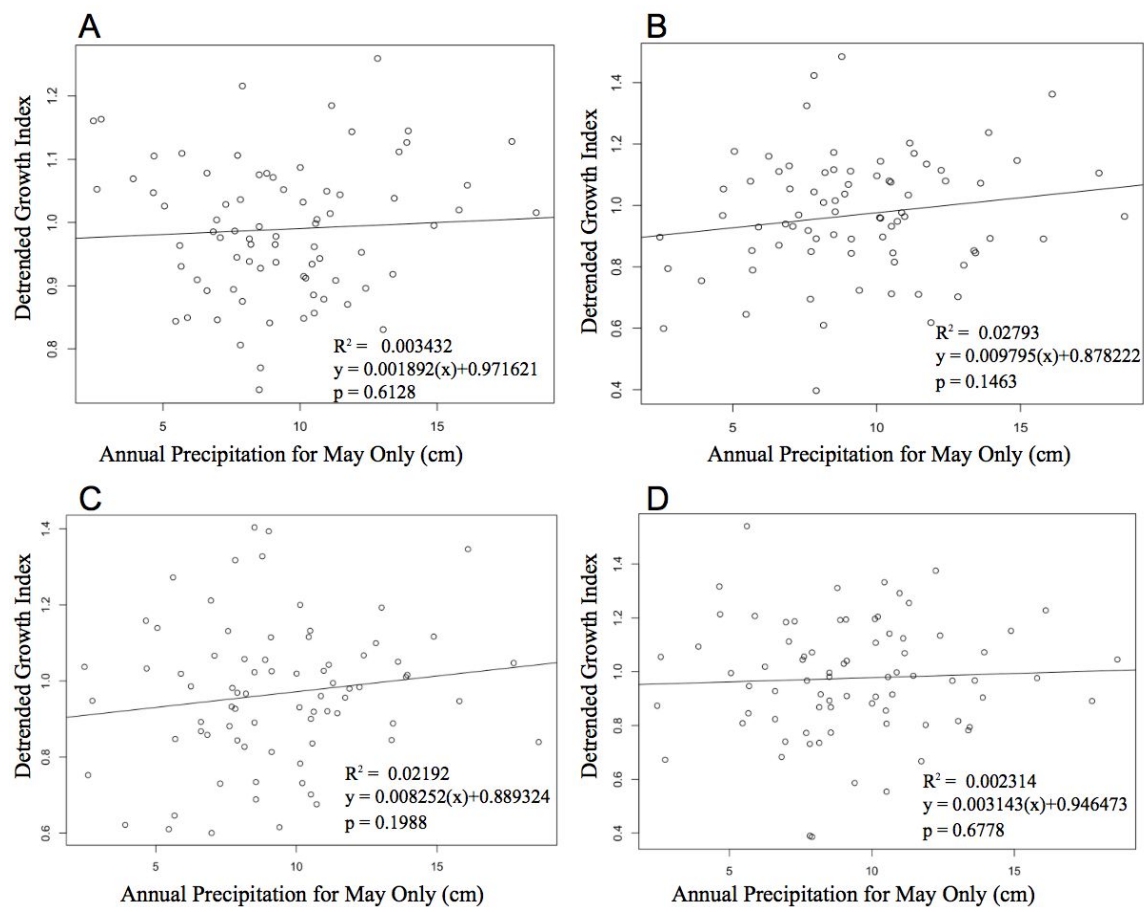


Figure 7. Relationship between annual total precipitation in centimeters (for May only) and detrended growth indices for red pine (A), yellow birch (B), paper birch (C), eastern hemlock (D) from 1940 to 2016. No species was found to have a significant trend line.

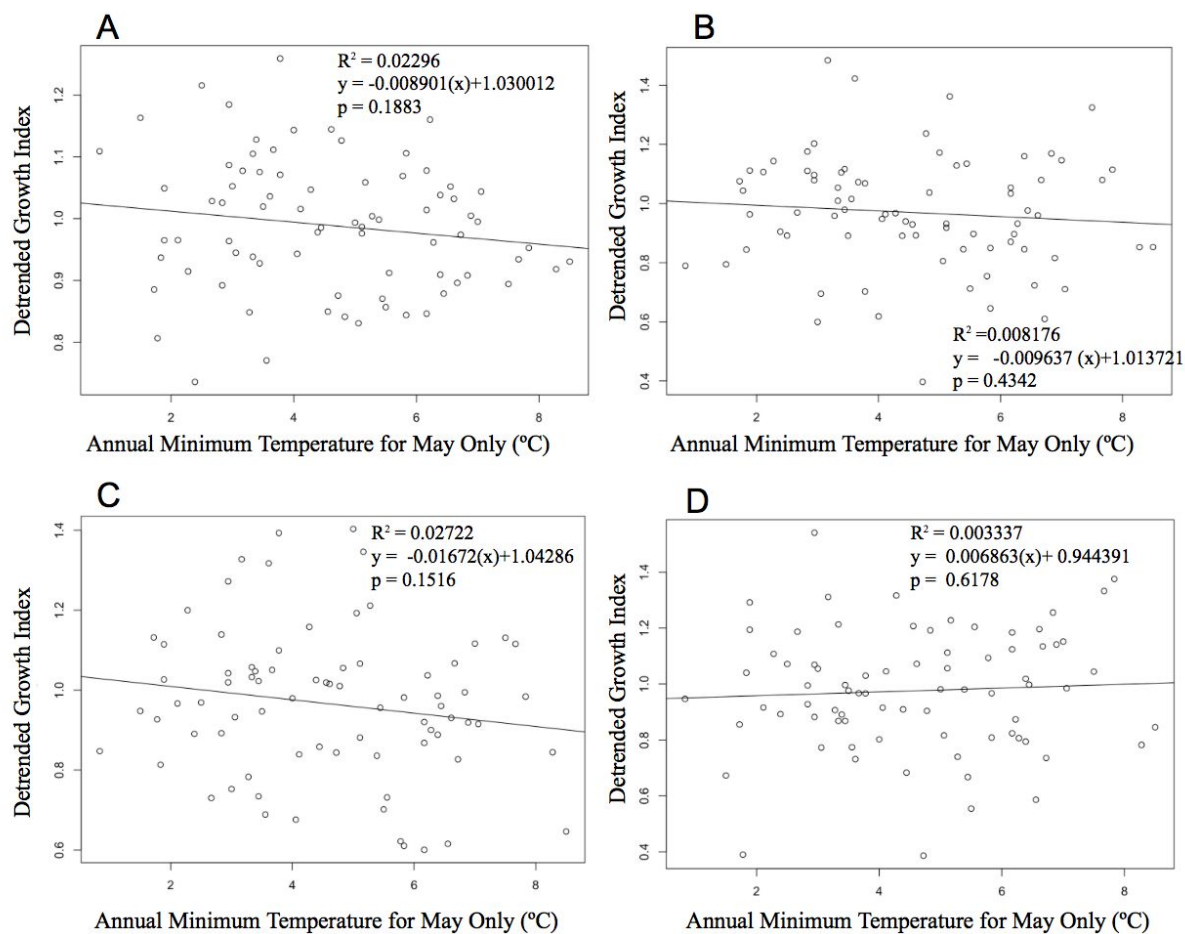


Figure 8. Relationship between annual minimum temperatures in degrees celsius (for May only) and detrended growth indices for red pine (A), yellow birch (B), paper birch (C), eastern hemlock (D) from 1940 to 2016. No species was found to have a significant trend line.

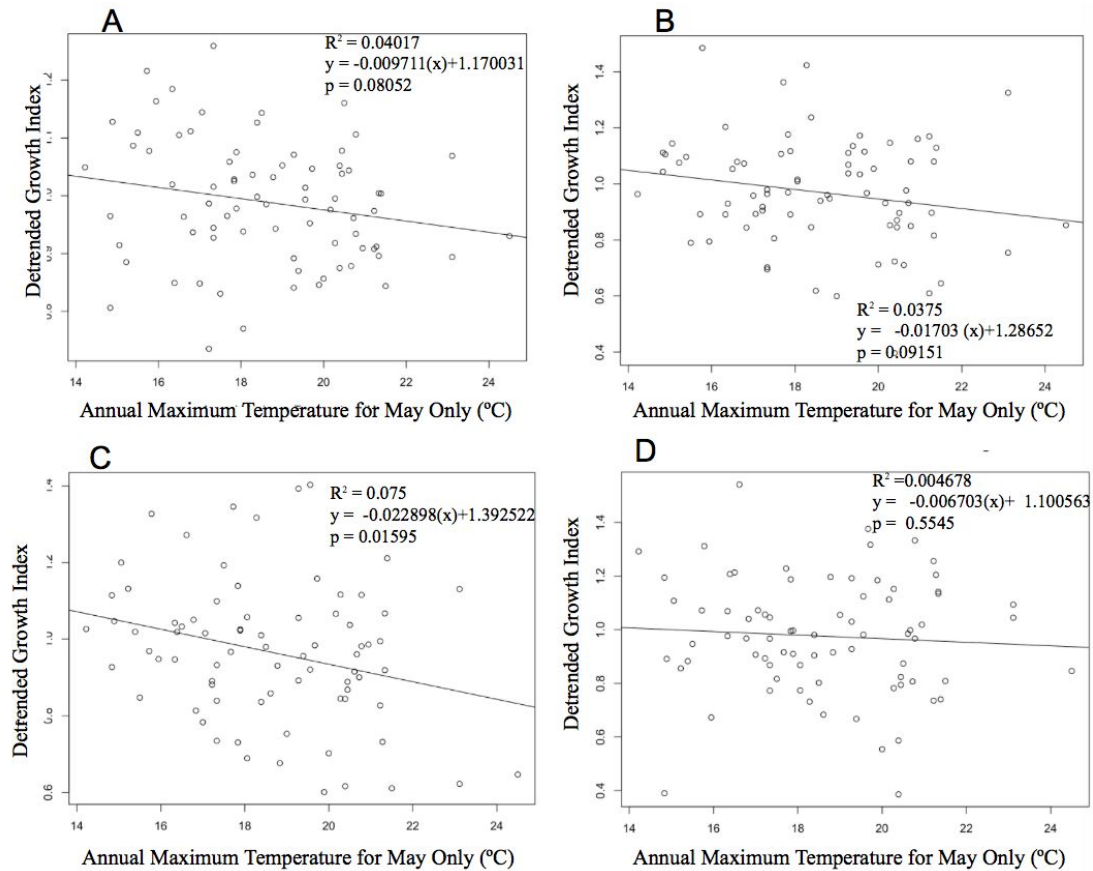


Figure 9. Relationship between annual maximum temperatures in degrees celsius (for May only) and detrended growth indices for red pine (A), yellow birch (B), paper birch (C), eastern hemlock (D) from 1940 to 2016. Only paper birch was found to have a significant trendline ($p = 0.01595$) that fit a small portion of its data ($R^2 = 0.075$), while all other species were found to have non significant trend lines.

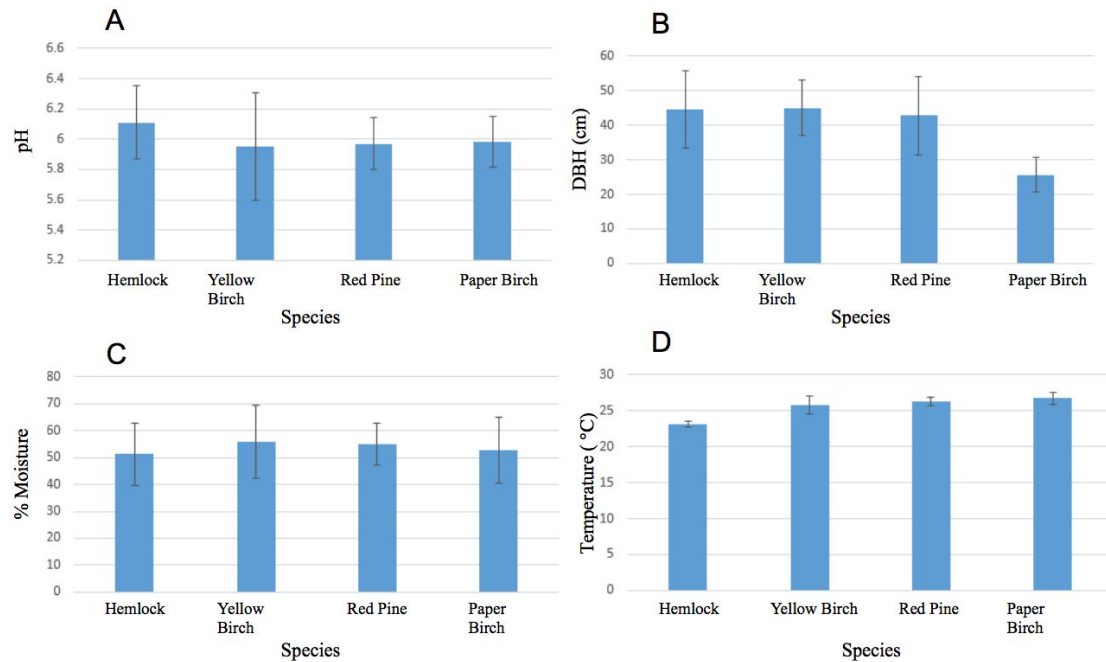


Figure 10. One-way ANOVAs on average pH (A), DBH in centimeters (B), percent moisture content (C), and temperature in degrees celsius (D) across species with standard deviations. Neither pH nor moisture content were found to be normal (Shapiro-Wilk: $p = 0.01699$ and $p = 0.02056$, respectively), so Kruskal-Wallis tests were run after the ANOVA. Still, neither pH nor moisture content were found to be significant ($p = 0.4245$ and $p = 0.6145$). Conversely, both DBH ($p = 0.0000587$) and temperature ($p = 6.51e-12$) were found to be significantly different and normal (Shapiro-Wilk: $p = 0.8747$ and $p = 0.3787$, respectively). Further analysis on DBH via Tukey's HSD revealed that Paper Birch significantly differed from Hemlock, Red Pine, and Yellow Birch. Tukey's HSD performed on temperature revealed that Hemlock significantly differed from Paper Birch, Red Pine, and Yellow Birch.

Table 1. Number of trees per species with releases in years between 1940 and 2016. The number in each box corresponds to the number of individual specimens with releases in that year and from that species. Empty boxes have no specimens with releases in the corresponding year.

Release Year	Number of Eastern Hemlock Individuals	Number of Yellow Birch Individuals	Number of Paper Birch Individuals	Number of Red Pine Individuals

1940	1			
1945	1			
1950		1		
1951		2		
1952	2			
1954	3	1		
1957	1			
1958	2			
1972			1	
1975			1	
1977			2	
1986	1			
1992			1	
1998				1

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least, I would like to extend my gratitude to Kelly Heilman for her incredible patience and help throughout the summer as the best mentor of the program. As I like to say, we are only as strong as those who stand behind us; thank you to all who stood behind me.

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