Historical growth response of black and white spruce trees to temperature, precipitation, and Eastern spruce budworm

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Abstract

Climate change has serious implications for forests, with the potential to completely alter forest composition and the ecosystems within forests. Rising temperatures and more unpredictable precipitation patterns affect various tree species differently; direct changes in the growth or health of trees are possible, as are changes in the dynamics of insects with tree hosts. In this study, a dendroecological analysis of black spruce (*Picea mariana*) and white spruce (*Picea glauca*) in Michigan's Upper Peninsula explored the relationship between growth and several predictor variables. These variables include temperature, precipitation, and Eastern spruce budworm activity, as well as the interactions among them. Spruce tree growth in the area suffers under higher average growing season temperatures, while spruce budworm activity in Michigan declines as a result of higher average winter temperatures. Though determining the exact response of spruce trees to climate change is difficult because of the vast number of variables, the results of this study suggest that rising temperatures could depress both spruce growth and the damage caused by spruce budworm.

Keywords: white spruce, black spruce, dendrology, temperature, precipitation, Eastern spruce budworm, climate change

Introduction

Climate change is causing significant shifts in temperature and precipitation patterns around the world. Increased atmospheric concentrations of carbon dioxide and methane are creating a greenhouse gas effect that has elevated the average global temperature and will continue to do so. Rising temperatures are likely to result in a greater frequency of warm days, heat waves, heavy precipitation events, and areas of drought (IPCC 2007).

Increased atmospheric CO_2 concentrations as a result of climate change may encourage vegetation growth in forests by increasing photosynthesis and carbon assimilation. However, higher temperatures and altered precipitation patterns may cause heat and water stress mortality in some species, while droughts could increase susceptibility to insects (Bachelet et. al. 2003, Hanson and Weltzin 2000; Farquhar et al. 1980). Possible ecosystem disruption from climate change may counteract any positive forest growth effects (Warren et. al. 2011). The Midwest region of the United States in particular has recently faced increased flooding and extreme precipitation events that will continue as a consequence of climate change (Pryor et. al. 2014). Some species, such as paper birch (*Betula papyrifera*), black ash (*Fraxinus nigra*), various aspens (*Populus* spp.), butternut (*Juglans cinerea*), balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and eastern hemlock (*Tsuga canadensis*) might decline, while other species, such as silver maples (*Acer saccharinum*) and various oak species (*Quercus* spp.) could proliferate under these new conditions in the Midwest. The exact consequences of climate change on each species, however, are still uncertain (Hellmann et al. 2010).

More frequent droughts, combined with higher temperatures, have the potential to cause more rapid and widespread tree mortality than droughts in the early twentieth century. This rapid mortality has many implications for ecosystems and surrounding landscapes, including reduced carbon storage, greater erosion, and diminished food sources for various organisms (Breshears et. al. 2005). Data suggests that climate change and all of its associated effects could be contributing to increased tree mortality, although a direct causal relationship is difficult to prove (Allen et al. 2010).

Spruce trees (*Picea* spp.) in particular have shown sensitivity to climate change variables. For example, the combination of soil and atmospheric drought with higher temperatures in the western United States and Belarus has intensified stress and mortality rates in various types of spruce trees (Mildrexler et al. 2016, Kharuk et al. 2016). Both black (*Picea mariana*) and white spruce (*Picea glauca*) seem to suffer under higher temperatures. Black spruce growth, as measured in ring widths, tends to have a negative correlation with temperature (Hoffer and Tardif 2009). Under heat stress, white spruce recovery declines, while needle damage increases; preconditioning white spruce to the heat by previously acclimating them to higher temperatures beforehand, however, helps mitigate the resulting damage (Bigras 2000). In the future, preconditioning could possibly protect spruce trees if they are able to develop a tolerance to higher temperatures resulting from climate change.

As aforementioned, climate change's effects on precipitation are difficult to predict. Since spruce trees tend to grow in mesic to hydric environments, precipitation would not likely limit their growth. In fact, past research indicates that the correlation between drought stress in white spruce and the combination of temperature and precipitation is no stronger than the correlation between drought stress and temperature alone. Thus, temperature appears to be a highly important predictor in drought stress of white spruce, while precipitation is less so (Barber et al. 2000).

Not only will climate change affect tree growth, but it may also change the severity and frequency of insect outbreaks. For example, drought and higher temperatures may expose trees to more insect damage, either by encouraging population growth of some insect species or by making trees more vulnerable. The exact outcome depends on the particular species. Conifers in the West, in New Jersey, and in boreal forests are suffering severe damage from increasingly frequent and severe bark beetle (*Dendroctonus* spp.) outbreaks, likely due to higher temperatures (Weed et. al. 2013).

The Eastern spruce budworm (*Choristneura fumiferana*) historically follows a pattern of outbreaks, normally occurring every 30 to 40 years (Rauchfuss and Ziegler 2011). Though normally considered a pest, the spruce budworm may offer ecological benefits by optimizing the amount of primary production in the forests; feedback from the budworm to the host trees and the ecosystem releases nutrients into the system and eliminates weaker trees, creating an environment more conducive to growth (Mattson and Addy 1975). The eastern spruce budworm primarily feeds on balsam fir and black, white, and red spruce trees; spruce trees are affected more heavily in stands mixed with balsam fir than in pure spruce stands (Kucera and Orr). Data about the effect of climate change on budworm outbreaks is inconclusive, but insects are strongly affected by changes in temperature and precipitation. Some outbreaks are associated with cool falls, warm winters, and warm, dry summers in the years preceding the outbreak (Greenbank 1956; Ives 1974). More recent data, however, suggests outbreaks are more likely after wet conditions in spring and early summer (Rauchfuss et al. 2009). Survival rates might decline from life cycle timing disruption, or survival could increase because of warmer, drier conditions that favor larval growth (Rauchfuss and Ziegler 2011).

The previous information prompts several important questions. How has spruce tree growth responded to the interaction of temperature, precipitation, and insect outbreaks in the past? Has there been a significant decline in growth, as measured in a spruce tree ring analysis, during drought or insect outbreak years? Is there a relationship between spruce budworm activity and temperature or precipitation? This study sought to address these relationships through a dendroecological analysis of black and white spruce tree rings. I hypothesized that the tree rings of spruce trees would reveal significantly slower growth rates during (1) years with high spruce budworm activity, (2) years with low spring and summer precipitation, and (3) years with high growing season temperatures. Furthermore, I hypothesized that (4) greater spruce budworm activity will likely occur in years with heavier spring and summer precipitation and in years with warmer average winter temperatures.

Methods

Study Site

Research was conducted at the University of Notre Dame Environmental Research Center (UNDERC), located in Land O' Lakes, Wisconsin, on the border of Wisconsin and the Upper Peninsula of Michigan. The eastern deciduous forest in this region is mainly composed of both hardwood and conifer stands, including sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*) and red pine (*Pinus resinosa*).

Experimental Design

I cored 7 black spruce and 18 white spruce trees, for a total of 25 trees, from four sites around the UNDERC property. A sample size of 20 to 30 trees is usually sufficient for dendroecological analysis (Cook and Blasings 1987). Sites were located across the property and selected based on the availability of healthy, adequately-sized spruce trees (Figure 1). I sampled five to seven trees, with a minimum diameter breast height (1.2 m) of 25 cm, at each site. Selected trees occurred in mesic to slightly hydric environments, as is typical of spruce trees.

One core was extracted from each sample tree, at a point where there were no branches to interfere with the uniformity of the rings. Trees were cored between a height of 80 and 120 cm. A standard coring height was not necessary because the cores were not analyzed to determine the age of the trees. Cores were then dried for 1 to 2 days on wooden boards at room temperature, mounted with glue, and then sanded with 100 and 150 grit sandpaper. I measured ring widths under a microscope, using a millimeter ruler, counting the outermost ring as 2016, and progressively assigning the previous year to the next inner ring.

The National Oceanic and Atmospheric Administration (NOAA) provided historic temperature and precipitation data for the North Central Wisconsin region and for the state of Michigan (NOAA 2016). I also obtained information about the annual extent of spruce budworm damage from the United States Department of Agriculture Forest Service's Forest Health Protection Mapping and Reporting Tools on their website (USDA Forest Service 2016). Acreages for Michigan state are from 1997 to 2015, and acreages for Gogebic County (UNDERC location in Michigan's Upper Peninsula) are from 2011 to 2015.

Statistical Methods

Trees from the same site were cross dated by graphing each tree's annual growth and ensuring that notably large or small growth years aligned for similar trees, as sometimes there are false or absent rings. Cross dating prevents single inaccuracies from misaligning data for the remaining years (Heikkenen 1984).

Black spruce growth data was not normally distributed (Shapiro-Wilk, $W = 0.947$, $p = 0.005$), so a Wilcoxon signed rank test verified no significant difference between the growth of black and white spruce trees. Therefore, the growth of both species were averaged together for further statistical tests. Replicated simple linear regressions and Pearson correlations were used to analyze the relationships between several predictor variables and each site's average annual growth. These predictor variables include same-year growing season (May to August) precipitation, previous-year growing season precipitation, same-year average maximum growing season temperature, and same-year average growing season temperature. After these tests were performed for each site, they were also performed with the average values for all samples together.

In order to test spruce budworm damage, regressions determined the relationship between acres of spruce budworm damage in Michigan and tree growth and also the acres of damage in Gogebic County and tree growth. Regressions were also used to test the relationships between acres of damage in Michigan and various environmental factors, as well as the relationships between acres of damage in Gogebic County and various environmental factors. These factors include growing season average temperature and total precipitation, previous growing season total precipitation, average temperature of the prior winter (December to March), and the average temperature of the next previous winter.

A regression was also used to determine the trend of growing season average temperature over time. The ANOVA residuals were not normally distributed (Shapiro-Wilk, W = 0.983, P = 0.436), so a Kruskal Wallis test and a post-hoc Tukey and Nemenyi test with a Tukey distribution revealed significant differences among average tree ring widths each decade. All of the statistics were performed in the statistical program, RStudio (RStudio Team 2015).

Results

The growth of black spruce and white spruce did not significantly differ (Wilcoxon signed rank, V = 1194.5, p = 0.427), so ring widths of both species were averaged together for further tests. Average growing season (May to August) temperature negatively correlated with the average growth of all trees sampled (Pearson correlation, r = -0.272, df = 70, t = -2.369, p = 0.021). Further, each year from 1944 to 2015, the average growing season temperature has increased by an average of 0.024°F, though time explained less than 10% of the variation in temperature ($R^2 = 0.092$, df = 70, $F_{1,70} = 7.109$, p = 0.010). Total current growing season precipitation did not have a significant correlation with average tree growth (Pearson correlation,

$r = 0.166$, $t = 1.413$, $df = 70$, $p = 0.162$). There also was no significant correlation between the previous growing season’s total precipitation and average tree growth (Pearson correlation, $r = 0.131$, $t = 1.106$, $df = 70$, $p = 0.273$).

Although there was no relationship between the recent annual acreage of spruce budworm damage in Gogebic County and average annual tree growth in recent years ($R^2 = 0.154$, $df = 3$, $F_{1,3} = 0.545$, $p = 0.514$), there was a significant negative relationship between annual acreage of statewide Michigan spruce budworm damage and recent annual tree growth ($R^2 = 0.365$, $df = 17$, $F_{1,17} = 9.781$, $p = 0.006$). For every additional acre of spruce budworm damage in Michigan, the ring width of spruce trees at UNDERC declined by 3.093×10^{-6} mm, on average ($p = 0.006$). However, an interesting result to note is the lack of a relationship between acres of damage in Michigan and annual growth of trees at the southeast site ($R^2 = 0.026$, $df = 17$, $p = 0.511$). Growth at each of the other sites–central ($R^2 = 0.246$, $df = 17$, $F_{1,17} = 5.552$, $p = 0.031$), west ($R^2 = 0.422$, $df = 17$, $F_{1,17} = 12.430$, $p = 0.003$), and north ($R^2 = 0.364$, $df = 17$, $F_{1,17} = 9.732$, $p = 0.006$)–had a significant negative relationship with acres of spruce budworm damage in Michigan. From 1997 to 2015 in Michigan, increased average temperatures during the immediately prior winter ($R^2 = 0.213$, $df = 17$, $F_{1,17} = 4.595$, $p = 0.047$) and the next previous winter ($R^2 = 0.223$, $df = 17$, $F_{1,17} = 4.883$, $p = 0.041$) have been associated with decreased acreage of spruce budworm damage.

Average growth among decades has been variable ($\chi^2 = 60.482$, $df = 7$, $p < 0.001$). By far, the greatest average period of growth was during the 1950s (4.2 mm +/- 0.132) and the 1960s (4.3 mm +/- 0.093). Average growth has been slowest during the 2000s (1.5 mm +/- 0.121) and 2010s (0.8 mm +/- 0.124). See Table 1 for all average annual growth measurements.

Discussion

Growth of spruce trees sampled on the UNDERC property has been on the decline in recent years (Figure 2). Data from this study suggest two main variables are responsible for the suppressed growth: temperature and spruce budworm activity. The first possible explanation is higher temperatures. Average growing season temperatures in north central Wisconsin have increased over time at an alarming rate (Figure 3). From 1944 to 2015, the average growing season temperature has increased by 0.024°F on average; over the past 70 years, this has likely accumulated to an average total increase of 1.68°F. The negative relationship between average growing season temperature and mean annual ring width prompts further discussion and suggests that spruce may not be well acclimated to temperature increases (Figure 4). The combination of these trends is particularly troubling for its implications in the future. As climate change continues to cause a global temperature rise, spruce trees could be at risk. Previous studies show that white spruce trees suffer significantly more damage when placed under heat stress than under normal conditions and do not recover well from heat stress, although preconditioning could help mitigate damage (Bigras 2000).

Average growth of spruce trees at UNDERC was not significantly associated with precipitation. As discussed earlier, the exact changes in precipitation in this region of the United States are difficult to predict. However, the spruce trees sampled here will likely tolerate a relatively wide range of precipitation levels because each of the samples was located in a mesic to hydric site. Previous studies have suggested that days with precipitation is probably not a limiting factor for growth in moist environments. In fact, more days with precipitation each year could indicate increased total cloud cover time. This, in turn, would slow growth rates by reducing total active photosynthetic time throughout the year (Soulé 2011).

Another main concern and second possible explanation for growth declines in spruce trees is the spruce budworm. *C. fumiferana* is known to defoliate spruce trees, and data also indicates a negative relationship between average ring widths and annual acres of spruce budworm damage in Michigan (Figure 5). As the annual damaged acreage in Michigan increased, the average ring width of spruce trees at UNDERC declined. This relationship held true for the average growth of all samples, as well as each of the sites, except for the southeast site. Perhaps the close proximity of a large lake slowed the spread of the spruce budworm by blocking their advance. Or, since the growing conditions around Plum Lake are favorable, the trees there may have become more robust, and therefore more resilient to insect damage.

In recent years, the combination of higher average growing season temperatures and beginning of a spruce budworm outbreak have likely caused the growth suppression in spruce trees at UNDERC. This relationship must be considered in the context of the data. Ring widths are used as a proxy for health and growth, and acres of damage are not cumulative from one year to the next. Consequently, acres damaged in one year will also be counted in the next year if they are still damaged. Unfortunately, the data from the USDA Forest Service is for recent years only. There is little historic data about spruce budworm in Michigan’s Upper Peninsula, although reports do mention an outbreak through the end of the 1960s to the beginning of the 1980s, and an outbreak beginning in 2015 (Michigan Department of Natural Resources 2015). Spruce trees at UNDERC do show significantly lower average growth during the 1970s, 1980s, 2000s, and 2010s than during the 1950s and 1960s, perhaps from the spruce budworm. Although determining the precise reason why growth was suppressed during these decades is beyond the scope of this study, the data gathered here creates speculation that the spruce budworm outbreak extended onto the UNDERC property. It possibly caused the decline during the 1970s and 1980s, and the combination of an outbreak and higher temperatures might have caused the decline in spruce growth since the beginning of the 21st century (Figure 6).

As mentioned earlier, the relationship between climate and the severity of spruce budworm outbreaks is unclear. Previous studies have suggested a positive association between warm prior winters and spruce budworm outbreaks (Greenbank 1956; Ives 1974). However, more recent models predict that warmer winter temperatures could increase winter mortality of *C. fumiferana* larvae. Data on Michigan suggest that increased average temperatures in prior winters is actually associated with decreased annual spruce budworm damage acreage (Figures 7 & 8). This model suggests that many other variables, including elevation, atmospheric conditions, and host-plant distribution, will also alter spruce budworm populations in North America as climate change continues (Régnière et al. 2012).

The results of this study prompt more questions for future studies at UNDERC. Exploring the effects of climate change on other tree species would be pertinent in order to develop a better understanding of how the forest composition will change in the future. As forest composition changes, the ecosystems that depend on the forest will undoubtedly change as well (Aitken et al. 2008). While hardwood trees are generally more resilient to climate change, coniferous trees face a greater risk of decline from climate change (Hamann and Wang 2006). Other factors also contribute to spruce growth, including atmospheric composition (i.e. concentrations of certain gases or pollutants), elevation, growing environment, competition, tree age, and acidic deposition, each of which might be affected by climate change (Cook and Blasings 1987; Soulé 2011).

Overall, determining the exact cause of growth trends in trees is difficult so specifically testing my hypotheses was challenging. However, the data collected in this study and many others present interesting relationships and trends that should be explored and studied in more detail to understand the trees' responses to environmental, as well as intrinsic (age, species, size, etc.), factors. In turn, these data and conjectures arising from them might offer us an idea of how climate change will affect both individual trees and the entire forest composition at UNDERC in the future.

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Tables

Table 1. Mean annual growth and standard error of all samples for each decade.

Decade	**Growth +/- Standard Error (mm)**
2010s	0.8 mm +/- 0.124
2000s	1.5 mm +/- 0.121
1990s	2.3 mm +/- 0.056
1980s	2.3 mm +/- 0.046
1970s	3.1 mm +/- 0.204
1960s	4.3 mm +/- 0.093
1950s	4.2 mm +/- 0.132
1940s	1.9 mm +/- 0.359

Figures

Figure 1. Map of the University of Notre Dame Environmental Research Center. Each tree sampled is marked with a red diamond. Each site is circled in red. The sites are referred to as north, west, central, and southeast, referring to the cardinal direction of their location.

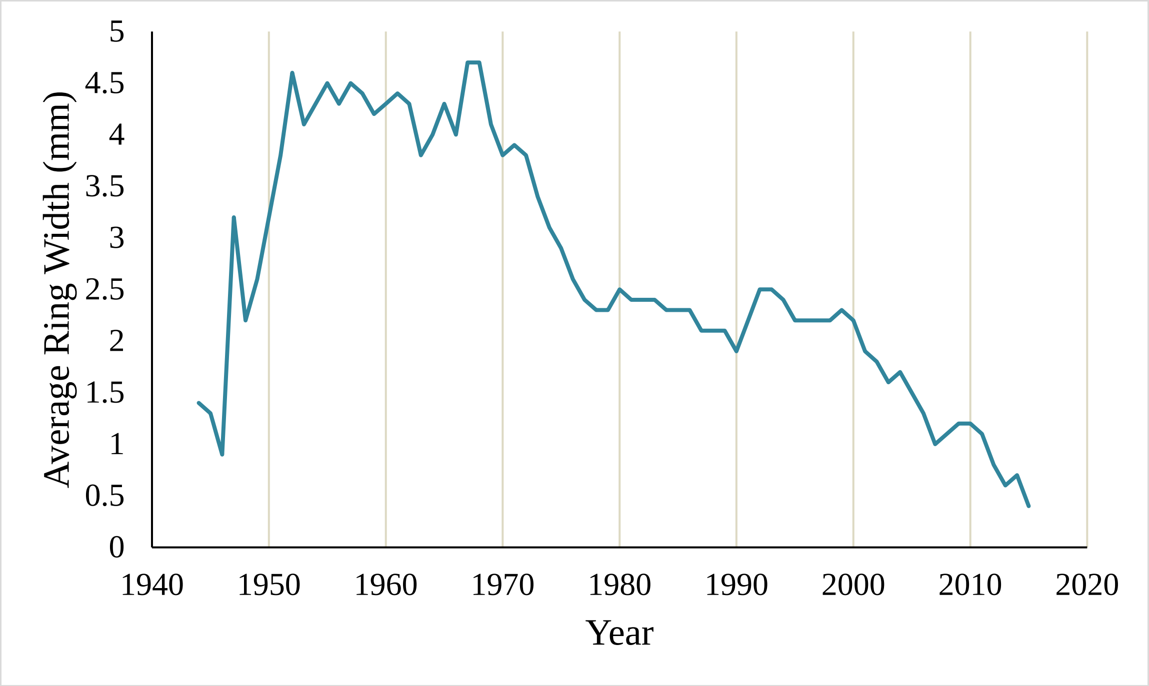

Figure 2. Average ring width of black and white spruce at all UNDERC sites for each year from 1944 to 2015. Growth in recent years shows a negative trend.

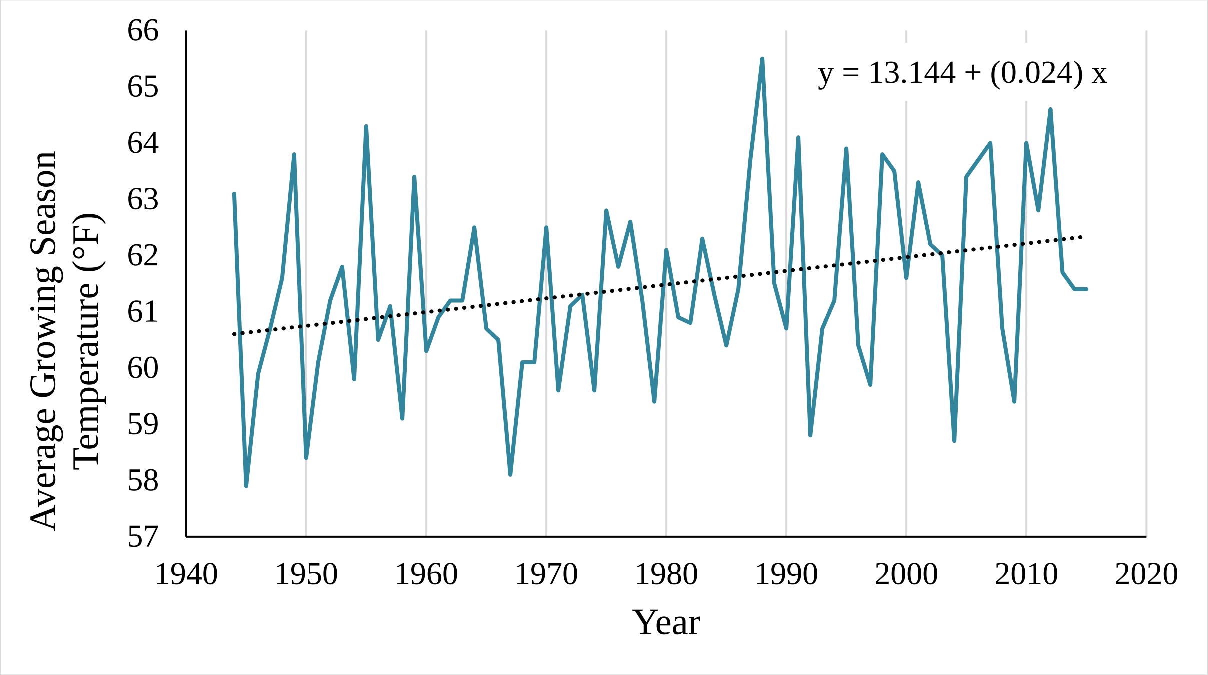

Figure 3. Average growing season (May to August) temperature in North Central Wisconsin from 1944 to 2015. A regression indicated that temperature has risen an average of 0.024°F each year ($R^2 = 0.092$, df = 70, $F_{1,70} = 7.109$, $p = 0.010$).

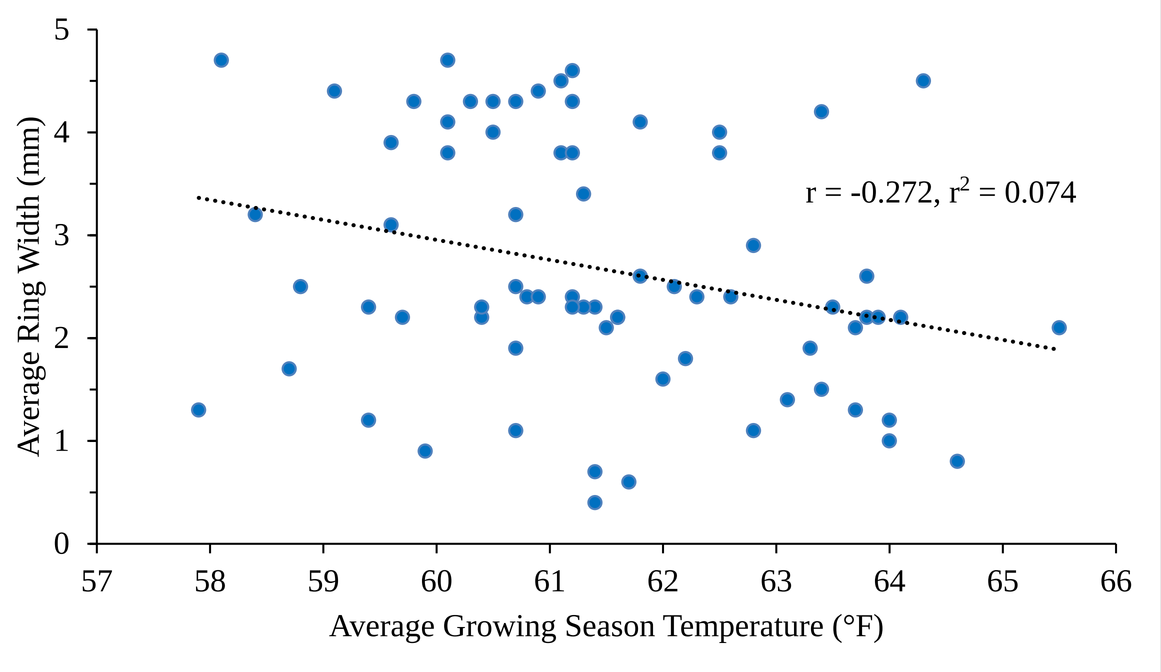

Figure 4. Relationship between average growing season temperature (°F) in North Central Wisconsin and the average annual ring width of all samples. A Pearson test indicated a negative correlation indicates that as average growing season temperature rises, the average annual growth of spruce trees at UNDERC declines ($r = -0.272$, $df = 70$, $t = -2.369$, $p = 0.021$).

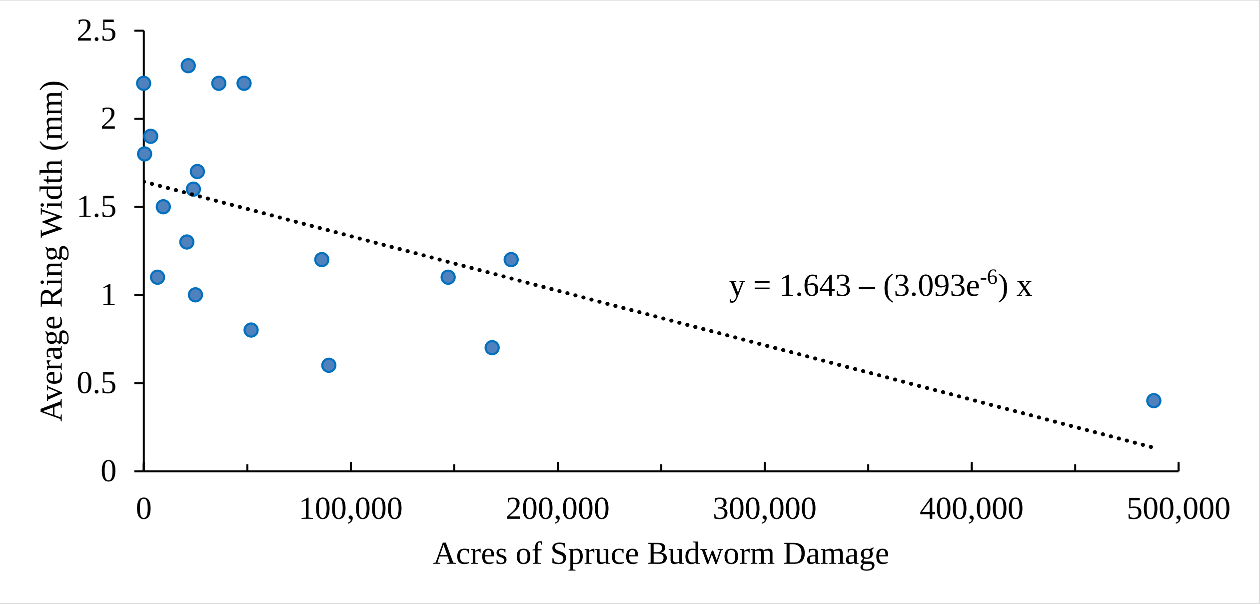

Figure 5. Acres of spruce budworm damage in Michigan from 1997 to 2015 and its effect on average ring widths of sampled trees. A regression indicated a negative linear trend between number of damaged acres and the average ring widths of spruce trees at UNDERC ($R^2 = 0.365$, $df = 17$, $F_{1,17} = 9.781$, $p = 0.006$).

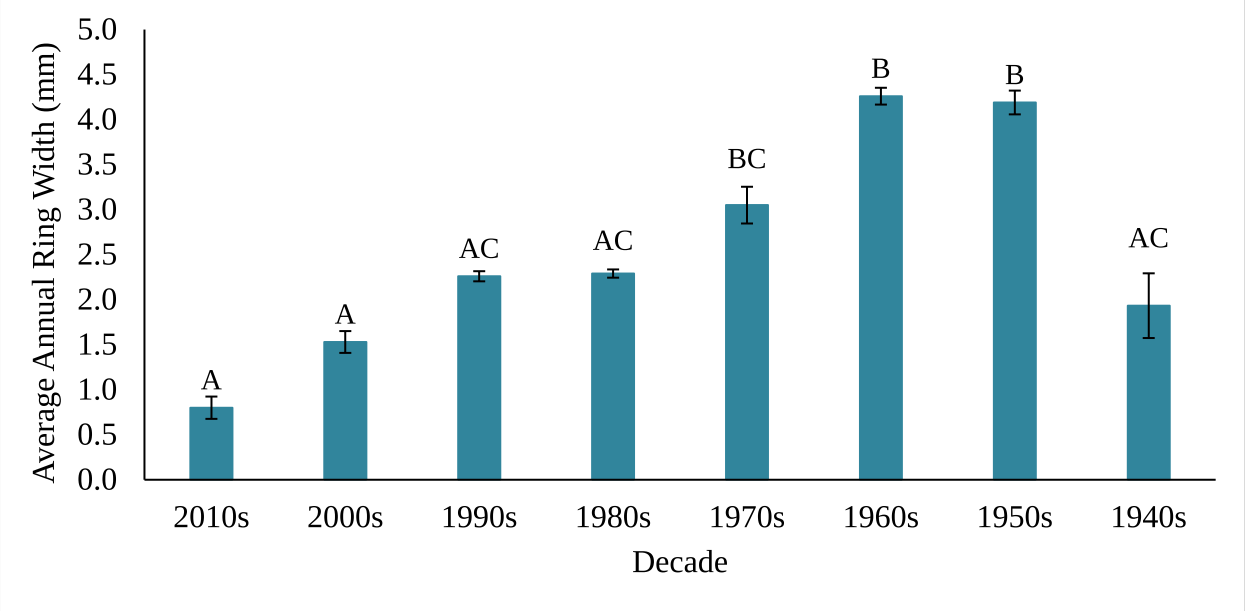

Figure 6. Average annual tree ring widths of all samples each decade. Shared letters indicate no significant difference between average annual ring widths ($\chi^2 = 60.482$, df = 7, $p < 0.001$).

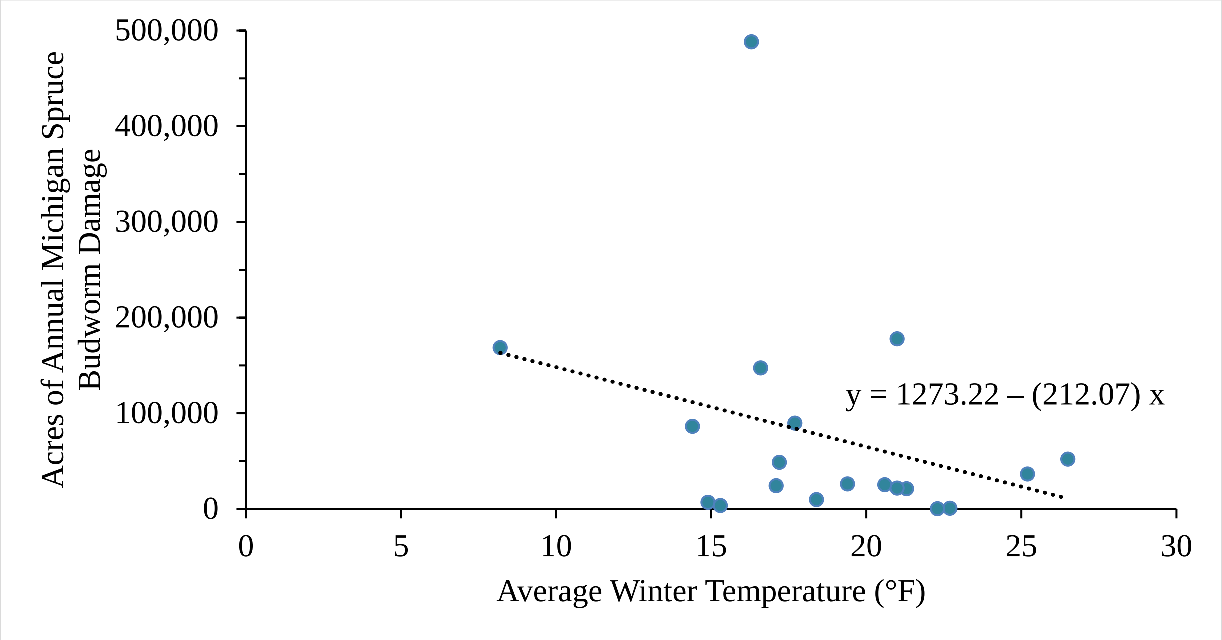

Figure 7. The relationship between average statewide winter (December to March of same year) temperature in Michigan and the acres of spruce budworm damage in Michigan since 1997. A regression indicated that as average winter temperature in Michigan increased, the acres of annual spruce budworm damage decreased ($R^2 = 0.213$, df = 17, $F_{1,17} = 4.595$, $p = 0.047$).

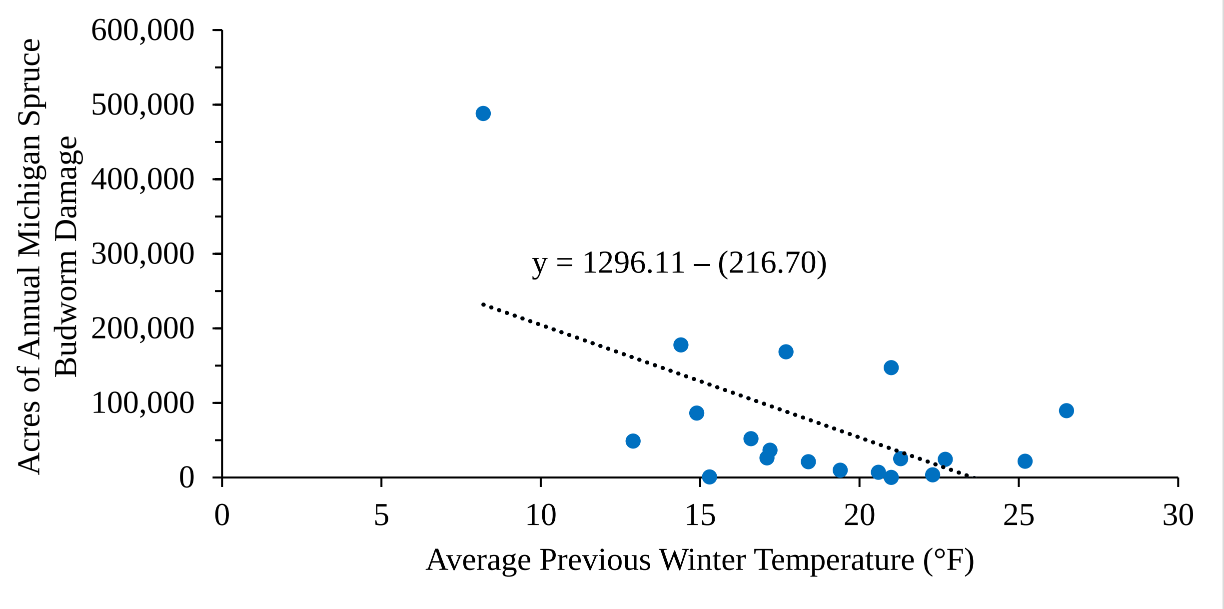

Figure 8. The relationship between average statewide previous winter (December to March of the previous year) temperature in Michigan and the acres of spruce budworm damage in Michigan since 1997. A regression indicated that as the average previous winter temperature increased, the acres of annual spruce budworm damage in Michigan decreased ($R^2 = 0.223$, df = 17, $F_{1,17} = 4.883$, $p = 0.041$).