

Climate change and edaphic conditions: predicting future growth of a critical boreal tree species - Jack Pine (*Pinus banksiana*)

By Caleb McCollum

A thesis submitted
in partial fulfillment of the requirements
for the degree of Master of Science
(Environment and Sustainability)
at the University of Michigan
April 2019

Faculty advisor(s):
Dr. Inés Ibáñez, Associate Professor
Dr. Donald R. Zak, Professor

Abstract

Global climate predictions anticipate increased temperature, variable total precipitation, as well as a greater number and intensity of severe precipitation events. Deepening our understanding of the complex relationships between climatic factors, tree growth, and edaphic conditions is key for predicting future suitable habitat for environmentally and economically salient tree species. Jack Pine (*Pinus banksiana*) provide crucial structural habitat and are an important species for timber production in the Upper Midwest. Jack Pine habitat ranges across extremes of an edaphic gradient. However, little is known about how these differing conditions influence growth performance as a function of oscillating climate. In this study, I assessed the effect of climatic variability on the growth of trees under different edaphic conditions (two sites with dry soils and one site with wet soils). Using tree core increments from three forest sites in Michigan's northern lower peninsula, tree growth was analyzed as a function of climate, age, and prior growth using a hierarchical Bayesian framework. As expected, trees in the wet soils had the highest growth rates. Individuals in all sites responded positively to increased spring temperature, whereas those in the wet site showed the highest response to increased summer precipitation. However, under predicted drier conditions the growth response in the wet site was expected to decline by 33%, while those in the two drier sites were expected to decline by 2 and 19%, equalizing growth rates across all three sites. Further, the decline in growth associated with drier summers will exceed any benefits conferred by warmer spring temperatures in the wet site. Sites near bogs and intermittent wetlands are currently associated with high growth performance. However, under the forecasted climate for the region, trees growing in these sites will likely lose their advantage.

Acknowledgements

This work would not have been possible without the patient and sage advice from my adviser, Dr. Inés Ibáñez. It has been a truly rewarding experience to be a part of the lab and learn from your example and experience. I would also like to thank my thesis committee member, Dr. Don Zak, for taking the time to provide key insight for the improvement of this manuscript as well as being a constant source of wisdom and kindness. Members of the Global Change Ecology Lab: Kirk Acharya, Dan Katz, Edie Juno, Gwen Keller, Ben Lee, Lais Petri, Sam Schaffer-Morrison, and Jordan Tourville were a source of constant encouragement, insight, and laughter. Mr. Mike Ravesi and Mrs. Susan Thiel from the Camp Grayling Natural Resources Office and the Michigan Department of Natural Resources, respectively, were points of expert knowledge and guided my interests to the right locations around Grayling, Michigan. Finally, my wife, Cari, and our son, Evan, provided daily encouragement and purpose throughout this process.

Table of Contents

Abstract.....	ii
Acknowledgements.....	iii
List of Tables and Figures.....	v
Introduction.....	1
Methods.....	3
<i>Study area and site selection</i>	3
<i>Field and laboratory methods</i>	4
<i>Climate data and analysis</i>	6
Results.....	7
<i>Effects of diameter and previous years' growth on radial growth</i>	8
<i>Effects of climate variables on radial growth</i>	8
<i>Growth simulations</i>	8
Discussion.....	9
Tables and Figures.....	14
Literature Cited.....	21
Supplemental Information.....	27

List of Tables

Table 1: List of forest sites sampled. Sampling sites were assessed and data collected in May and August 2018. Variable means and SD are reported.

List of Figures

Figure 1: Location of the study area with selected forest sites within Crawford County, Michigan. The broader range of Jack Pine (*Pinus banksiana*) is highlighted in green (Little 1971).

Figure 2: Average growth for each tree per year within the three studied forest sites. Individuals in the BOG site had the highest observed growth rates indicating higher overall productivity.

Figure 3: Model results, goodness of fit (R^2), comparing predicted vs observed growth.

Figure 4: Parameter estimates (mean \pm 95% CI) for the growth model showing the effects of April temperature and July PDSI on the growth of individuals within each of the three forest stands. Letters indicate statistically different coefficients between stands. Credible intervals that do not cross zero are considered statistically significant (shown with an asterisk).

Figure 5: Simulations of radial tree growth (mean - solid lines, and 95% predicted interval - dashed lines) under three fixed April temperatures (low: 1.5°C, medium: 7°C, and high: 14°C) and a gradient of July moisture (moist-to-dry) measured by July PDSI. Simulations showed that growth rates were negatively affected in all three stands under drier conditions, but more substantially in the BOG site (~32.8%) as opposed to the DRY 1 and DRY 2 sites (~2.4 and 18.9%, respectively).

Figure 6: Simulations of radial tree growth (mean - solid lines, and 95% predicted interval - dashed lines) under three fixed July PDSI values (moist: 3.0, intermediate: -1.0, and dry: -5.5) and a gradient of April temperature (cold-to-warm). Increasing April temperatures partially mediate the effect of drier July conditions.

Introduction

Global climate patterns are changing at an unprecedented rate (IPCC 2014). Future predictions call for higher average temperatures, more variable and erratic total precipitation, and an increase in the number and intensity of severe precipitation events (IPCC 2014). As climate generally becomes warmer, broad expectations are that organisms will migrate to higher latitudes and elevations (Parmesan 2006; Parmesan and Yohe 2003). In the past, climatic shifts occurred at rates that allowed evolutionary adaptation and migration processes to take place among tree species (Davis and Shaw 2001). However, contemporary changes in climate present new challenges as current changes may be occurring too quickly for many tree species to effectively migrate and/or adapt (Aitken et al. 2008). Thus, understanding how tree populations will respond *in situ* to future conditions will be essential to assess their performance. From a management perspective, understanding population level responses to forecasted climatic conditions across local environmental gradients can be invaluable for informing efforts aimed at maximizing tree growth.

Investigating how the relationship between tree growth and local environmental conditions may change in the near future is particularly relevant for tree species of marked ecological and/or economical relevance. Given the long life-span of trees, information about their future performance can assist with the development of sound conservation or sustainable management plans. Suitable habitat for tree species is determined by a complex combination of abiotic factors and biotic interactions. Because of this complexity, substantial variation and non-uniformity in tree performance have been consistently shown across many species' local ranges. However, a comprehensive understanding for how local abiotic factors influence tree growth rates and how that translates to population performance in the face of extreme climate conditions is lacking (Huang et al. 2010; Wilmking et al. 2004).

The link between climate and tree growth has been strongly established within the field of dendroclimatology, and individual and population responses to fluctuating local climatic conditions have been used to highlight the influence climate has on growth (Barnes and Wagner 1981; Fritts 1976). Climate, specifically precipitation and temperature, largely determines the length of the growing season and the availability of key resources, influencing individual

performance, and ultimately, the range of a particular species. Other physical factors including soils, elevation, aspect, and slope shape that performance and determine the outcome at the local level (Barnes and Wagner 1981; MacArthur 1972). Accounting for site conditions and/or site quality substantially explicates varying growth responses when assessing productivity as a function of climatic variables (Forrester et al. 2013; Mina et al. 2018). In one modeling study, assessing edaphic and topographic factors allowed researchers to predict species range almost as well as solely using climatic factors (Beauregard and de Blois 2014). Additionally, the authors found that models using both edaphic and climate factors were generally the most accurate for predicting species distributions, and they highlighted an additional constraint for estimating species range shifts under projected climate conditions (Beauregard and de Blois 2014).

My study species, Jack Pine (*Pinus banksiana*), is an ecologically and economically important boreal species that is ubiquitous throughout central, northern, and southeastern Canada with a southern range limit in the northern United States, specifically around the Great Lakes and in northern Maine (Barnes and Wagner 1981; Elias 1980; Subedi and Sharma 2013). *P. banksiana* is an early successional species, largely defined by its fast growth, shade intolerance, and relatively short lifespan (60-80 years). Young *P. banksiana* stands in the Northern Lower Peninsula of Michigan, the focal area for this study, provide critical nesting habitat for the endangered Kirtland's Warbler (*Setophaga kirtlandii*) (Benzie 1977; Cayford and McRae 1983). Further, wood production substantially contributes to Michigan's economy, employing approximately 25,000 workers with a valued output of over \$7 billion. More specifically, *P. banksiana* accounted for just under 21 million cubic feet of roundwood production, and approximately 8% of saw logs in 2008 (Haugen et al. 2014). Although *P. banksiana* is a critical tree species for ecosystems and the timber industry in this area, little is known about how environmental factors influence its growth sensitivity as a function of oscillating climatic conditions.

While it is widely established that *P. banksiana* typically grows in pure, even-aged stands on extensively well-drained loamy-sands, it perhaps has a wider range than originally thought (Rudolph and Laidly 1990; Yarranton and Yarranton 1975). More recent studies show that *P. banksiana* are often found growing on various soil types where competitor species struggle to survive (Barton and Grenier 2008; Rudolph and Laidly 1990). For example, individuals and populations have been documented on saturated organic soils in bogs and peatlands in southeastern

Quebec (Pellerin and Lavoie 2003). Again, in Maine and notably atypical for *P. banksiana*, populations have been inventoried at both extremes of the moisture gradient: on sandy, well-drained thin soils and in coastal bogs and wetlands (Barton and Grenier 2008).

The objective of this study is to assess the effect of climatic conditions, specifically in drought years, on the growth and performance of *P. banksiana* stands growing under different edaphic conditions in Michigan's northern lower peninsula. The following specific questions are addressed: 1) what dynamics differentiate *P. banksiana* stands growing near bogs and intermittent wetlands from stands located on well-drained sandy soils? 2) Do populations of *P. banksiana* growing in bogs and intermittent wetlands perform better than those located on extensively drained sandy sites in years with extreme climatic fluctuations, *i.e.*, drought? In order to better inform management decisions for preserving critical habitats that rely on the long-term success of *P. banksiana* populations, we addressed the following questions: 3) how would the future growth of individuals be affected under each of these conditions? 4) Should *P. banksiana* continue to be planted in all these sites in the future? Answers to these questions will shed light about how sensitive *P. banksiana* are to extreme climatic conditions, and allow for more accurate predictions of performance under anticipated shifts in climate.

Methods

Study Area and Site Selection

The study area is located in the center of Michigan's northern lower peninsula, USA (Figure 1; 44.6614° N, 84.7148° W). The area's soils are predominantly well-drained sandy outwash plains, resulting from Pleistocene glaciation which ended approximately 14,000 years ago (Barnes and Wagner 1981). Annual precipitation varies between 770-850 mm, most of which falls between May and October (Barnes and Wagner 1981; U.S. Climate Data 2018). Mean winter (January) and summer (July) temperatures are -8.5 °C and 19.3 °C, respectively (U.S. Climate Data 2018). The particular area of interest is generally considered a pine community; the dry-to-mesic sites are largely dominated by red and white pine (*Pinus resinosa* and *Pinus strobus*) and oaks (*Quercus*), while the extremely dry and excessively drained sites are dominated by Jack Pine (*Pinus banksiana*) (Barnes and Wagner 1981).

Because *P. banksiana* is fire adapted and short lived, Michigan land managers typically simulate stand replacement through clearcutting and/or controlled burns, and then trench and replant from nursery stock on a 50 to 70-year cycle. This allows for the management of both in-demand wood products and for the critical natural habitat *P. banksiana* stands provide (DNR 2016). Forest sites were selected from an assortment of these types of stands which contain pure, even-aged *P. banksiana* growing under similar conditions of light, density, elevation, and approximate age, but that differed in their edaphic conditions. Using the Michigan Department of Natural Resources (DNR) open source Geographic Information System (GIS), 24 forest stands were initially identified on the Camp Grayling National Guard Military Reservation that fit the environmental criteria listed above. Three of these were eventually selected as the final study sites (Table 1) (DNR 2018).

The three stands are within an area that is co-monitored by the Camp Grayling Environmental Resources Office and the Michigan Department of Natural Resources (DNR) with extensive records of past treatments, natural and anthropogenic disturbances, and original seeding events maintained by the latter. All three stands have similar canopy cover, which was used as a proxy for assessing light availability, density, approximate age, and are composed of pure, even-aged *P. banksiana*. The first stand, BOG (44.6781° N, 84.7689° W; 350 m elevation; Stand 20 designation from the Michigan Department of Natural Resources (DNR)) was planted in 1979 (DNR 2018) and is located along the edge of an intermittent wetland/bog. The second stand DRY1 (44.7342° N, 84.5086° W; Stand 29 in DNR records) and the third stand, DRY2 (44.7503° N, 84.5669° W; Stand 36 in DNR records) are located on sandy well drained uplands at an elevation of approximately 369-375 m, both dry stands were recorded as being naturally regenerated in 1976 and 1968, respectively (DNR 2018).

Field and Laboratory Methods

Field work was completed in May and August, 2018. During the initial visit in May, the descriptive information gathered from the DNR website that was used to select the sites was verified using field expedient methods. First, five 10-m x 10-m plots were randomly established within each of the three stands, and diameter at breast height (DBH 1.37m) was measured for all live trees. The measurements were tallied and averaged to determine the mean basal area of each

respective stand. Canopy cover was estimated using the CanopyApp, an iPhone application developed by the University of New Hampshire and available from the Apple app store (University of New Hampshire 2018). Mean soil moisture content was measured for the sites using a Spectrum Technologies FieldScout TDR 300 soil moisture meter. Site level soil moisture was determined by recording values at 1.5 m in each cardinal direction from each tree and then averaging the values. Soil moisture was assessed during the initial data collection in May and again at the end of August in order to compare moisture levels across sites between the beginning and end of one growing season.

Thirty dominant or co-dominant individuals were identified in each of the three stands. DBH and Geographic Position System (GPS) coordinates, using a Garmin Foretrex 301 GPS device, were recorded. Two tree cores, one from the north and one from the south side, were extracted at breast height (1.37m) from each of the 30 trees on each site using a 4.3mm Haglof increment borer. After the 180 total increment cores, 60 from each site, were extracted they were stored in paper straws and transported to the University of Michigan - Ann Arbor where they were dried for a minimum of 24 hours.

Standard methods for preparing tree increment cores were used (Phipps 1985; Stokes and Smiley 1968), beginning by gluing each core to a pre-cut mount and then sanding it with increasing grit sandpaper (P150, P320, P600) to achieve a smooth, flat surface to make it easier to measure the annual growth rings. The cores were scanned using an Epson Expression graphic arts flatbed scanner at 1200 dpi resolution. The annual ring widths (mm) were then measured using two complementary programs. First, the scanned image files were measured in CooRecorder (version 9.3.1) and translated into ring width files to be cross-dated. Both cores per tree and all the cores within a site were graphically and statistically cross-dated in CDendro (Version 9.3.1) (Larsson 2018). Cross-dating was confirmed using the statistical quality control program COFECHA (Grissino-Mayer 2001; Holmes 1983). Twenty-five total cores were either broken, damaged, or were unable to be accurately cross-dated and were discarded. After being cross-dated, north and south ring width measurements were averaged to determine annual radial growth for each tree.

Climate Data and Analysis

Climate data, including average monthly temperature and total precipitation from 1972 to present, was retrieved from the National Oceanic and Atmospheric Administration (NOAA) weather station (GHCND: USC00203391), located in Grayling, Michigan (NOAA 2018a). Palmer Drought Severity Index (PDSI) data was retrieved from the NOAA divisional time series from 1972 to present (NOAA 2018b). Annual growth rates for each tree were examined with monthly average temperature, total precipitation, and PDSI data in order to determine which monthly climate variables were the most correlated with growth. During preliminary analysis, multiple combinations of spring (April and May) temperature, summer (June and July) precipitation and PDSI, and fall (September and October) temperature, precipitation, and PDSI, and lag effects were assessed which indicated that the best fit occurred with April temperature and July PDSI from the current year. The natural log of diameter was included in the analysis to account for growth variation as a function of size (age) (Cook et al. 1990; Fritts 1976). Because growth and climatic conditions from previous years can affect current growth through lag effects (Ogle et al. 2015; Peltier et al. 2016), the effect from each of the previous two years (weighted per year) was also included in the model (Ibáñez et al. 2018). Each tree's response was analyzed to account for tree random effects in order to capture variation from individual interactions (competition, facilitation, and genetic differences etc.). Edaphic conditions were then factored into the model by estimating all parameters at the stand level.

Growth increments for tree i in year y ($G_{i,y}$) were modeled using a normal likelihood:

$$\text{Growth}_{i,y} \sim \text{Normal}(G_{i,y}, \sigma^2)$$

with process model:

$$G_{i,y} = \alpha_i + \beta_1 \cdot \ln(\text{dbh}_{(i,y)}) + \beta_2 \cdot (\omega_{1\text{stand}(i)} \cdot \text{growth}_{(i,y-1)} + \omega_{2\text{stand}(i)} \cdot \text{growth}_{(i,y-2)}) + \beta_3 \cdot \text{AprilTemp}_y + \beta_4 \cdot \text{JulyPDSI}_y$$

Because the variance of the growth data changed with diameter, I estimated the variance of the model (σ^2) as a function of DBH with the following parameter model: ($\sigma_{i,y} = a_{\text{stand}(i)} + b_{\text{stand}(i)} \cdot \ln(\text{dbh}_{i,y})$) (Lines et al. 2012). A Bayesian framework was used to estimate parameter values (see

Appendix S2 for code); parameters in the process model were estimated at the individual level, and these values were then estimated for stand level hyper-parameters, $\alpha_i \sim \text{Normal}(A_{\text{stand}(i)}, \sigma_{\alpha_{\text{stand}(i)}}^2)$, $\beta_i^* \sim \text{Normal}(B_{\text{stand}(i)}^*, \sigma_{\beta_{\text{stand}(i)}^*}^2)$. Finally, non-informative prior distributions were used to estimate the stand level parameters: $\omega_{\text{stand}}^* \sim \text{Dirichlet}(1)$, A^* and $b^* \sim \text{Normal}(0, 0.0001)$, $a^* \sim \text{LogNormal}(1, 0.001)$, $1/\sigma^{*2} \sim \text{gamma}(0.0001, 0.0001)$.

Future performance was estimated using the output of the hierarchical model, *i.e.*, parameter means, variances and covariances, to simulate growth rates for each stand. Growth was forecasted under combinations of increasing April temperatures (from 1.5°C to 14°C; reflecting the range of values in the data) and of July moisture conditions (PDSI from -5.5 to 3; range observed in the data).

Analysis was conducted using OpenBUGS (version 3.2.3, Lunn et al. 2009) running three chains of a Markov Chain Monte Carlo simulation for 150,000 iterations. Once convergence was reached, chains were run for 50,000 iterations more to estimate posterior parameter means, standard deviations, and 95% credible intervals.

Results

Descriptive information collected from the DNR's GIS website, including canopy cover, stand density, and soil moisture were confirmed through field measurements. Canopy cover and basal area were approximately the same across all three sites (Table 1). The BOG site had more variable soil moisture ranging from 18.8% in May to 4.03% in August. Soil moisture was more consistent in the other two stands, ranging in DRY 1 from 10.7% in May to 6.7% in August and 3% in August in DRY 2 (Table 1). I was unable to collect soil moisture measurements at DRY 2 in May due to restricted access on military training land.

A total of 90 trees were sampled, thirty from each site, and 155 of the 180 increment cores collected were used in the final analysis. Average tree diameter ranged from 16.2 to 21.4 cm; individuals in the BOG site being both the largest and youngest (mean \pm SD in Table 1; Figure 2). The final model fit (R^2 representing goodness of fit between observed and predicted data) was 0.70 (Figure 3). Parameter estimates and descriptions are displayed in Appendix S1.

Effects of diameter and previous years' growth on radial growth

As expected, increasing diameter had a statistically significant negative effect on the growth of all individuals in each of the three stands, recorded as -0.27 and -0.59 in DRY 1 and DRY 2, and -3.61 in the BOG (parameter β_1 ; Appendix S1). Previous years' growth had a significantly positive effect on the current year growth, recorded as 0.41 in the BOG, and 0.75 and 0.58 in DRY 1 and DRY2 (parameter β_2 ; Appendix S1). Growth during the previous year had the strongest effect on the current year growth, ranging from 0.81 in DRY 2 to 0.96 in DRY 1 (parameter ω_1 ; Appendix S1).

Effects of climate variables on radial growth

Increasing temperature in April had a statistically significant positive effect on the growth of individuals in all three forest sites, ranging from 0.04 in DRY 1 to 0.07 in the BOG (parameter β_3 ; Figure 4; Appendix S1). Increasing summer moisture, measured by July PDSI, had a statistically significant positive effect on the growth of individuals in the BOG and DRY 2, recorded as 0.07 and 0.04, but was not significant in DRY 1, recorded as 0.004 (parameter β_4 ; Figure 4; Appendix S1).

Growth simulations

The growth simulations show that individuals in all three stands positively respond to warmer April temperatures, with growth being consistently higher in the BOG site. Further, while growth is negatively impacted in all three sites by drought conditions, the effect is the most pronounced in the BOG. Growth in DRY 1 and DRY 2 is predicted to decline by 2 and 19%, respectively, while growth in the BOG is predicted to decline by 33% under the anticipated drier conditions (Figure 5). The second simulation confirmed that increasing April temperatures somewhat mediate the effect of drier July conditions. The growth rate decline between the moist and dry July scenarios was 7% less in the BOG at the highest April temperature, whereas the difference in the two DRY sites was 1 and 5%. This highlights that while the effect of dryer conditions is slightly more pronounced at lower temperatures, the effect of moisture is still the most distinct in the BOG (Figure 6).

Discussion

Global warming is rapidly changing the conditions under which plants are growing. As tree populations cope with these changes, understanding how plant growth may be differently impacted across areas in the landscape becomes critical for assessing future productivity and well-being of the affected species. In this study, I determined how climatic shifts may affect growth in even-aged *P. banksiana* stands differing in their edaphic conditions. Individuals in all of the sites responded positively to increased April temperature while those in the wet site showed the highest positive response to increased July moisture. As expected, average growth rates were highest in the wet site, indicating higher productivity under these conditions (Figure 2). However, the simulations also showed that under predicted drier summer conditions the growth response in the wet site could rapidly decline, curtailing any benefits conferred by warmer spring temperatures. Sites near bogs and intermittent wetlands are currently associated with high growth performance, but trees growing in these sites will likely lose their advantage under future predicted shifts in regional climate.

As with most tree species, growth rates of *P. banksiana* can be strongly influenced by the availability of soil resources (Green and Grigal 1979; Hamilton and Krause 1985). My results revealed this trend in these sites. Individuals in the BOG had the largest average diameter by age, indicating consistently higher growth rates and overall productivity (Figure 2). The oldest individuals, in DRY 2, are just slightly smaller than those in the BOG, which is approximately 10 years younger, whereas those in DRY 1 are the smallest albeit almost the same age. This indicates a gradient of productivity driven by site-specific access to additional resources which may be best explained by moisture availability during the growing season. Soil moisture has been shown to be a relatively accurate variable for predicting *P. banksiana* population productivity (Beland and Bergeron 1996); and, as my results show, it is essential for categorizing growth variation between these forest stands.

Accounting for age and lag effects of previous growth are also critical variables in categorizing tree growth; these two factors contribute substantially to a tree's physiological growth limits (Anderegg et al. 2015; Carrer et al. 2004; Szeicz and MacDonald 1994, 1995). Results from this analysis showed that increasing diameter had a statistically significant negative effect on the

growth of all individuals. This follows the well-established pattern that as trees age (increase in size) they allocate more energy towards storage and maintenance than to growth which can be represented linearly by log transforming the diameter (Cook et al. 1990). The positive trend shown from previous year's growth illustrates how growth performance along consecutive years are related and should be included in tree growth models (Ibáñez et al. 2018). In this case, the positive association is likely a reflection of differential growth rates among trees, while the negative associations shown in other studies (Ogle et al. 2015; Peltier et al. 2016) are likely linked to the depletion of resources; *i.e.*, after a year of high growth trees lack enough stored resources for extensive growth in the following year.

Temperature is an important component for tree growth as it is a principal mediator for photosynthetic capacity (Berry and Bjorkman 1980). A positive response to increasing April temperatures was observed across all stands, which follows previous findings indicating that warmer spring temperatures correspond with a longer growing season and result in higher radial growth of *P. banksiana* (Genries et al. 2012; Subedi and Sharma 2013). Further, conifer species are likely better suited to take advantage of warmer conditions in the spring due to their evergreen foliage which allows for additional photosynthetic activity (Graumlich 1993). Although the responses were not statistically different, the slightly higher growth response in the BOG may be indicative of spring water constraints in the two dry sites, even in lieu of water availability from snowmelt. The region's sandy soils drain rapidly and store relatively little water for advantageous plant growth. Although moisture levels in the BOG fluctuate widely over the growing season, they are much higher in the spring, a result of recent snowmelt accumulation and possibly lower drainage (Table 1). As April temperatures increase, these trees are potentially better situated to take advantage of the additional moisture. Our soil moisture measures were limited to two discrete times during one growing season and could be much improved by continuous monitoring over multiple growing seasons in order to more accurately detail the moisture environment trees are experiencing throughout the season.

Water availability is crucial for the growth and performance of trees, although specific thresholds vary by species. Contrary to expectations, there was a mixed growth response to increasing summer moisture, measured by July PDSI. Because of the typically well-drained sandy conditions that *P. banksiana* are found, we decided to use PDSI as a measure of relative moisture

as it accounts for both temperature and precipitation (Palmer 1965). Growth in the BOG site was positively affected by increasing moisture, whereas the responses in the two dry sites varied between being positive, but less strong than the BOG, and not significant (Figure 4). It may seem surprising that a stronger, uniformly positive response to increased summer moisture is not present given that water availability can limit tree growth (Brzostek et al. 2014). But, a relatively weak signal between growing season moisture and *P. banksiana* growth has been proposed and reported on multiple occasions (Despland and Houle, 1997; Dietrich et al. 2016; Hofgaard et al. 1999; Huang et al. 2010). However, the responses along the temperate-boreal boundary can range widely across a gradient of interacting effects between temperature and moisture availability (Foster et al. 2016).

Identifying the growth response to fluctuating climatic conditions was the main goal of this study and allowed us to gather the information necessary to predict growth performance under future conditions. Climate in our study area is predicted to change in the future; expectations being that spring temperatures will increase between 0.9 - 3.3°C, with more variable summer moisture conditions, ranging from slightly wet to extremely dry (Handler et al. 2014). The simulations we ran with the predicted conditions showed a slight decline in growth in the two DRY sites and a substantial decline in the BOG site. While individuals in the BOG are currently experiencing higher growth performance, our predictions show that they may be most affected under future drought conditions.

Local adaptations to drought have been explained within wide-ranging species by wood hydraulic traits and stomatal regulation, a combination of which elucidate the variation recorded in drought responses of a related conifer - *Pinus contorta* – as a function of latitude and local conditions (Isaac-Renton et al. 2018; O'Neill et al. 2008). The individuals examined during this study were either planted (BOG) or naturally regenerated (DRY sites), thus we are not assuming adaptation, but rather, acclimation to the conditions that the trees are growing under (Peltier and Ibáñez 2015; Tjoelker et al. 2009). Most likely, individuals in the two DRY sites have acclimated to their drier locations. Due to the excessively drained sandy soils and similar climate, the recorded responses may be attributed to stomatal regulation, explaining the lower productivity in those sites (Isaac-Renton et al. 2018). Perhaps then, the more interesting result is the dynamic response to summer moisture in the BOG; where individuals take opportunistic advantage of higher moisture

during critical periods, but are also strongly affected by drought conditions. This may also partially explain the faster growth rates and larger, albeit younger, individuals observed on that site. Further investigation of xylem cellular structure, stomatal regulation, and measured performance of *P. banksiana* under controlled experimental transplant conditions would more clearly determine the physiological mechanisms driving variation between sites. Trees planted at the DRY sites, are likely to be growing under chronically sub-optimal soil moisture conditions, and their growth rates are adjusted to this water scarcity. Hence, the moisture variability between years is less palpable in their growth rates, as these are always low.

This response is consistent with the explanation concerning the lower growth of individuals in the two dry sites. Similar results show that acclimation to drought stress may indicate higher drought tolerance but lower overall productivity (Montwé et al. 2016). Our predictions indicate that under anticipated drought conditions, acclimated individuals in the two dry sites will continue assimilating carbon at approximately the same rate as a result of adequate stomatal regulation. Contrarily, individuals in the BOG will experience a growth rate decline, equalizing rates with the dry sites, as a plastic response to restricted water availability. However, our simulations may have underestimated this effect as the duration of drought could have an even more pronounced negative impact on unacclimated individuals, depleting stored carbohydrates to maintain growth to the detriment of long-term survival (Mitchell et al. 2013). For managers, available sites near bogs and intermittent wetlands in Michigan's northern lower peninsula will likely benefit growth yields for *P. banksiana* stands in the short term. While growth in these sites will continue to be as high or higher than those in the drier areas, we expect that the benefits gained from moister locations to quickly decline under predicted drier conditions.

Understanding the physical factors that most substantially influence a tree population's sensitivity to climate fluctuations is particularly important for the development of effective management strategies for economically and environmentally important tree species. Answers to our proposed questions seek to shed light about the long-term sustainability of *P. banksiana* populations and associated communities. Both Kirtland Warbler habitat and the lumber industry in the region rely on the successful and continual growth of *P. banksiana*. Managers seeking short term yield benefits may consider available sites near bogs and intermittent wetlands, but if outputs are based on current growth performance, the long-term success of such decisions is questionable

due to expected future conditions of summer moisture. Further, induced stress as a result of increased temperature and drier conditions has been shown to alter carbon dynamics and exacerbate the effects of drought (Adams et al. 2009). These unforeseen changes in the physiological response of trees, as well as the possible alteration of community composition, could have long-term negative impacts on this system and, therefore, highlight a need for future research. Site-specific conditions and season-specific climate predictions provide critical insight into the growth performance of *P. banksiana*, but understanding the distribution and diversity of physiological response and genetic adaptation to drought may provide a more comprehensive understanding of realistic limits, and species resilience, under prolonged drought conditions.

Table 1: List of forest sites sampled. Sampling sites were assessed and data collected in May and August 2018. Variable means and SD are reported.

Site	DNR Forest Stand	Latitude/ Longitude	Origin Year	BA (100m ²)	Elevation (m)	Average Diameter	Canopy Cover (%)	Moisture (%)	
								May	August
BOG	20	44.6781° N 84.7689° W	1979	228.3	350-354	21.4 ± 2.2	52.9 ± 12.6	18.8 ± 9.4	4.03 ± 0.95
DRY 1	29	44.7342° N 84.5086° W	1968	319.7	368-375	16.2 ± 2.2	52.0 ± 9.9	10.7 ± 2.1	6.7 ± 1.4
DRY 2	63	44.7503° N 84.5669° W	1976	242.5	375-378	20.1 ± 1.8	54.3 ± 9.4		3.05 ± 0.63

Figure 1: Location of the study area with selected forest sites within Crawford County, Michigan. The broader range of Jack Pine (*Pinus banksiana*) is highlighted in green (Little 1971).

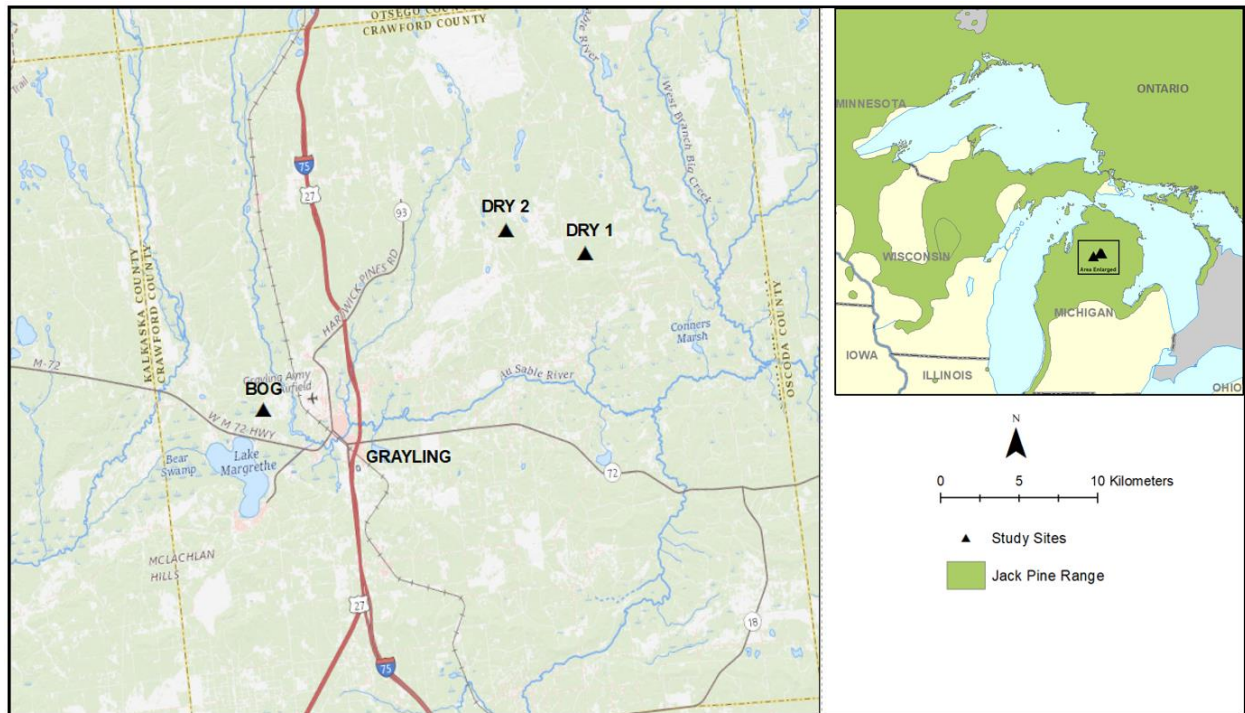


Figure 2: Average growth for each tree per year within the three studied forest sites. Individuals in the BOG site had the highest observed growth rates indicating higher overall productivity.

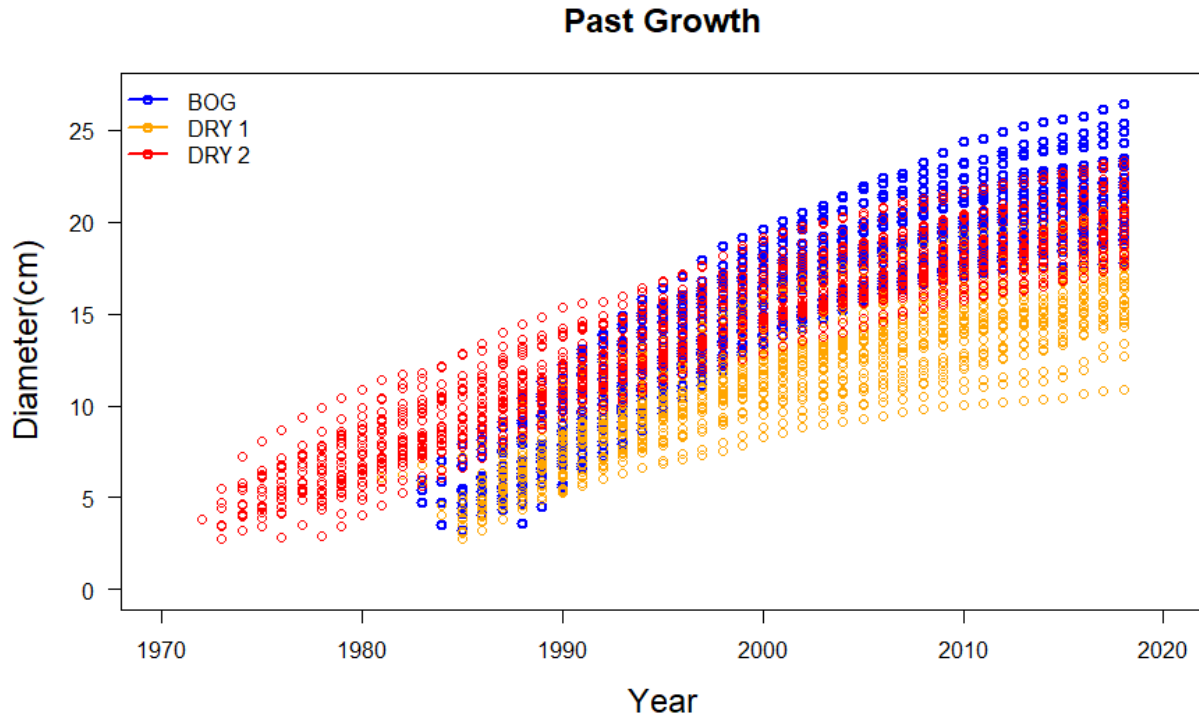


Figure 3: Model results, goodness of fit (R^2), comparing predicted vs observed growth.

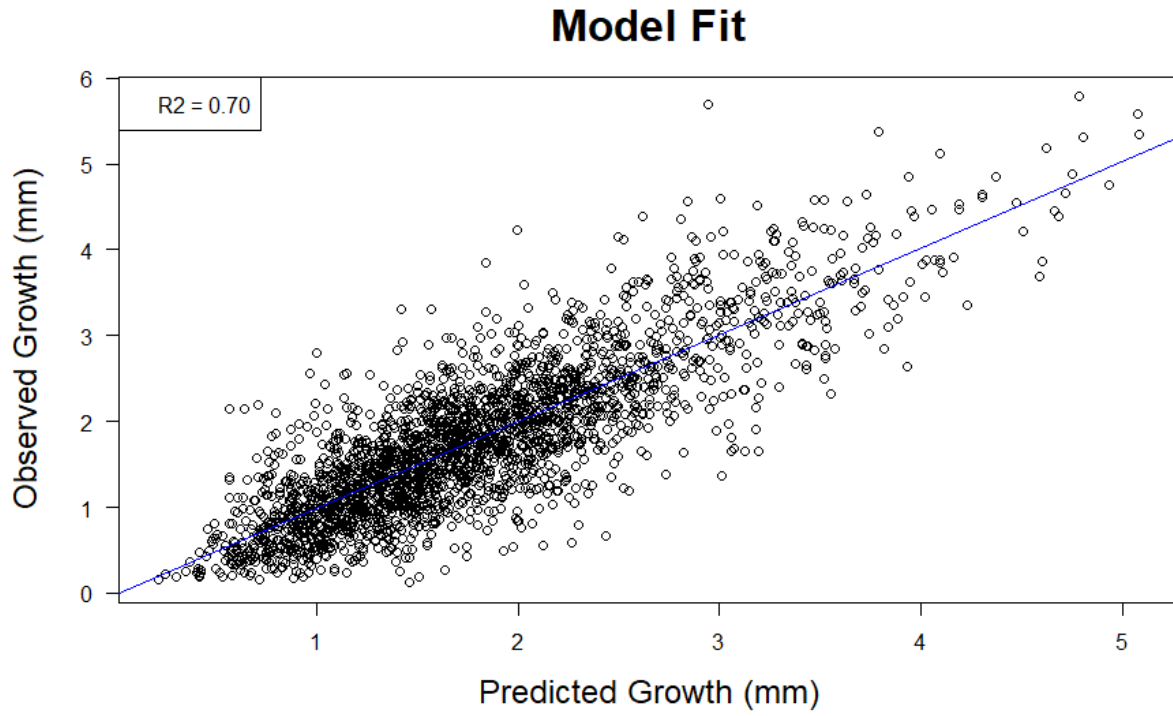


Figure 4: Parameter estimates (mean \pm 95% CI) for the growth model showing the effects of April temperature and July PDSI on the growth of individuals within each of the three forest stands. Letters indicate statistically different coefficients between stands. Credible intervals that do not cross zero are considered statistically significant (shown with an asterisk).

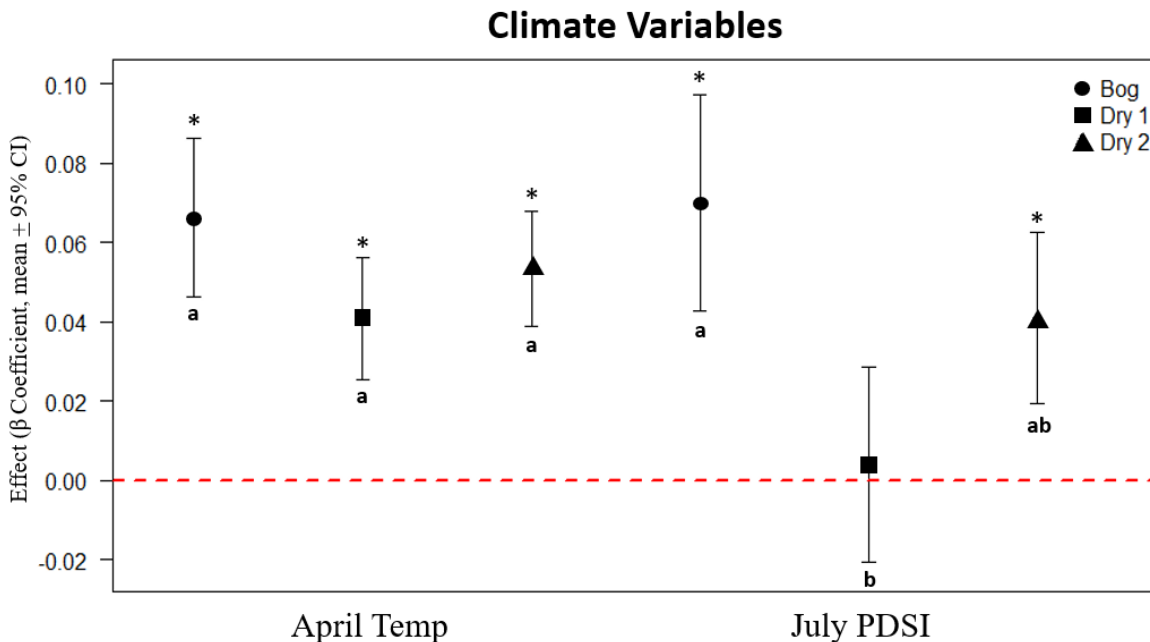


Figure 5: Simulations of radial tree growth (mean - solid lines, and 95% predicted interval - dashed lines) under three fixed April temperatures (low: 1.5°C, medium: 7°C, and high: 14°C) and a gradient of July moisture (moist-to-dry) measured by July PDSI. Simulations showed that growth rates were negatively affected in all three stands under drier conditions, but more substantially in the BOG site (~32.8%) as opposed to the DRY 1 and DRY 2 sites (~2.4 and 18.9%, respectively).

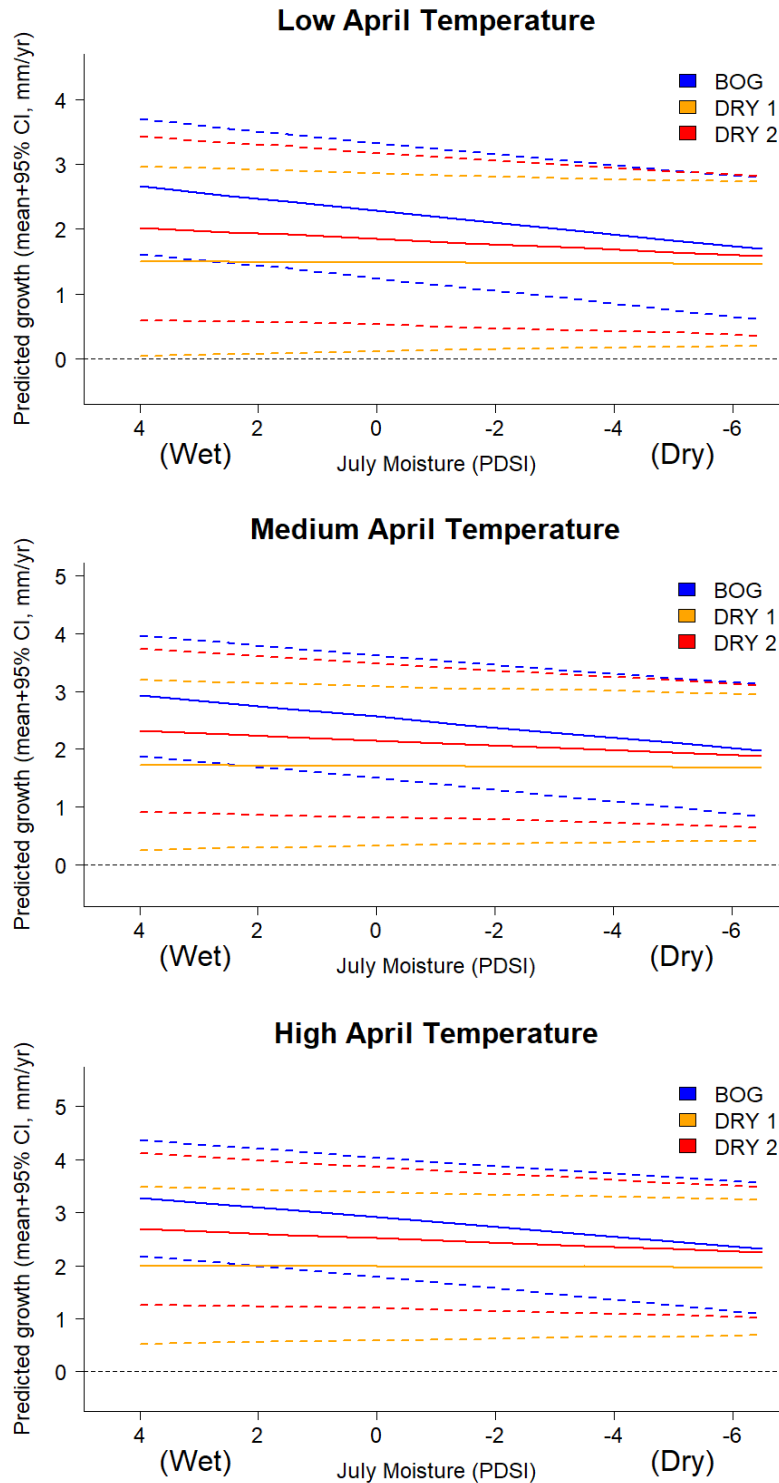
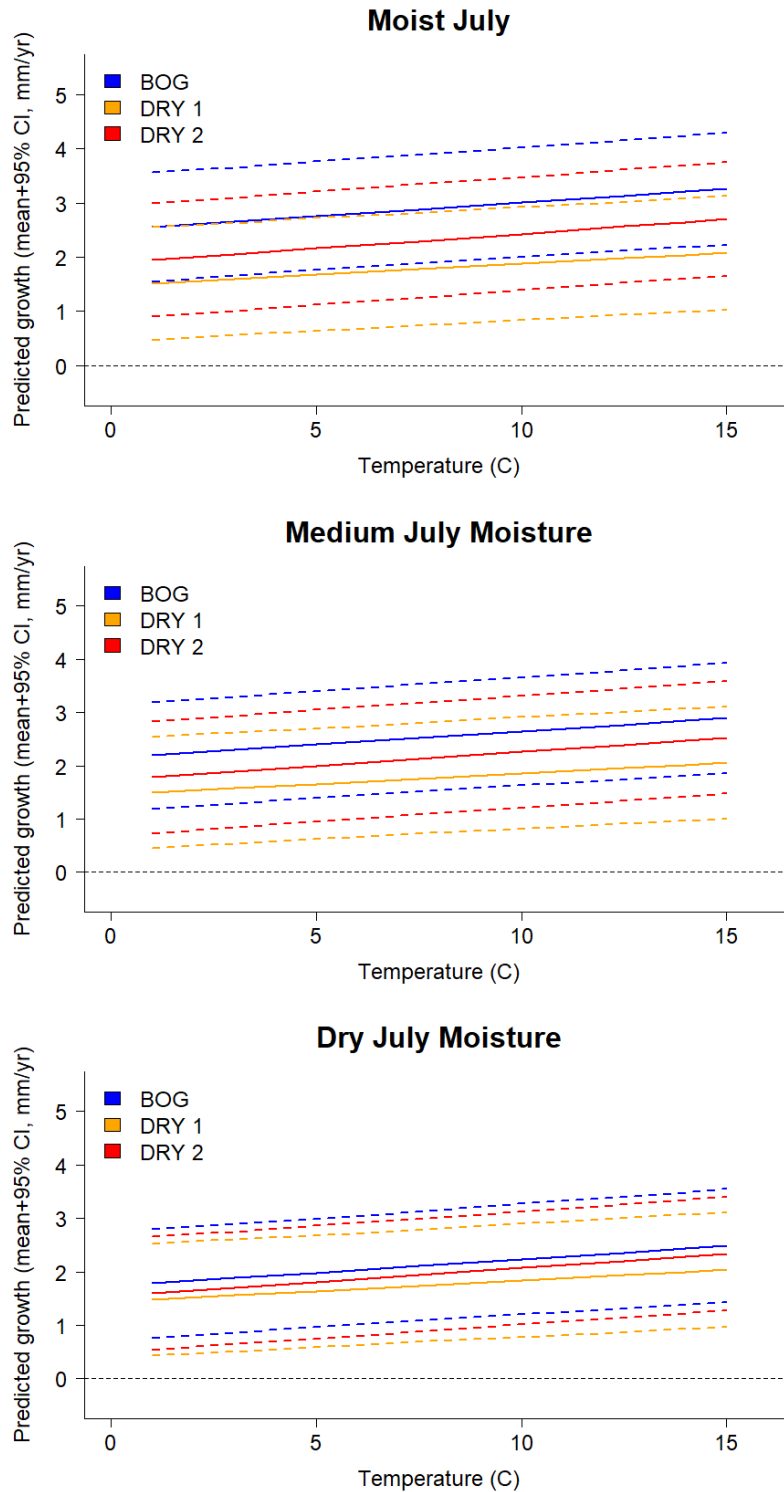


Figure 6: Simulations of radial tree growth (mean - solid lines, and 95% predicted interval - dashed lines) under three fixed July PDSI values (moist: 3.0, intermediate: -1.0, and dry: -5.5) and a gradient of April temperature (cold-to-warm). Increasing April temperatures partially mediate the effect of drier July conditions.



Literature Cited

- Adams, H. D., Guardiola-Claramonte, M., Barron-Gafford, G. A., Villegas, J. C., Breshears, D. D., Zou, C. B., Troch, P.A., Huxman, T. E. (2009). Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *PNAS* 106(17), 7063–7066.
- Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T., & Curtis-McLane, S. (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, 1(1), 95–111.
- Anderegg, W. R. L., Ziaco, E., Litvak, M., Shevliakova, E., Camarero, J. J., Shaw, J. D., Schwalm, C., Biondi, F., Koch, G., Ogle, K., Wolf, A., Pacala, S., Williams, A. P. (2015). Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, 349(6247), 528–532.
- Barnes, B.V., & Wagner, W.H. 1981. Michigan Trees: A guide to the Trees of Michigan and the Great Lakes Region. University of Michigan Press, Ann Arbor, Michigan.
- Barton, A. M., & Grenier, D. J. (2008). Dynamics of Jack Pine at the southern range boundary in downeast Maine. *Canadian Journal of Forest Research*, 38(4), 733–743.
- Beauregard, F., & De Blois, S. (2014). Beyond a climate-centric view of plant distribution: Edaphic variables add value to distribution models. *PLoS ONE*, 9(3).
- Beland, M., & Bergeron, Y. (1996). Height growth of jack pine (*Pinus banksiana*) in relation to site types in boreal forests of Abitibi, Quebec. *Canadian Journal of Forest Research*, 26, 2170–2179.
- Benzie, J.W. 1977. Mangers' handbook for jack pine in the north central states, *US For. Serv., Tech. Rep. NC-23*. 18 pp.
- Berry, J., & Bjorkman, O. (1980). Photosynthetic Response and Adaptation to Temperature in Higher Plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, 31(1), 491–543.
- Brzostek, E. R., Dragoni, D., Schmid, H. P., Rahman, A. F., Sims, D., Wayson, C. A., Johnson, D. J., Phillips, R. P. (2014). Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. *Global Change Biology*, 20(8), 2531–2539.
- Carrer, M., & Urbinati, C. (2004). Age-Dependent Tree-Ring Growth Responses to Climate in *Larix decidua* and *Pinus cembra*. *Ecology*, 85(3), 730–740.
- Cayford, J.H., & McRae, D.J. 1983. The role of fire in jack pine forests. In *The role of fire in northern circumpolar ecosystems*. Edited by R.S. Wein and D.A. McLean. John Wiley and Sons, New York. pp. 183-199.

- Cook, E., Briffa, K., Shiyatov, S., Mazepa, V., & Jones, P.D. 1990. Data Analysis. In E.R. Cook, L.A. Kairiukstis (Ed.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. (pp. 97-153). Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Davis, M. B., & Shaw, R. G. (2001). Range Shifts and Adaptive Responses to Quaternary Climate Change. *Science*, 292(5517), 673–679.
- Department of Natural Resources (DNR). (2016). Fire, jack pine and aspen – understanding a historic relationship. Retrieved from https://www.michigan.gov/dnr/0,4570,7-350-79137_79770_79873_80003-385756--,00.html
- Department of Natural Resources (DNR). (2018). Michigan State Forest Covertypes. Retrieved from <https://gis-midnr.opendata.arcgis.com/datasets/michigan-state-forest-covertypes>.
- Despland, E., & Houle, G. (1997). Climate Influences on Growth and Reproduction of *Pinus banksiana* (Pinaceae) at the Limit of the Species Distribution in Eastern North America. *American Journal of Botany*, 84(7), 928–937.
- Dietrich, R., Bell, F. W., Silva, L. C. R., Cecile, A., Horwath, W. R., & Anand, M. (2016). Climatic sensitivity, water-use efficiency, and growth decline in boreal jack pine (*Pinus banksiana*) forests in Northern Ontario. *Journal of Geophysical Research: Biogeosciences*, 121(10), 2761–2774.
- Elias, T.S. 1980. *The Complete Trees of North America: Field Guide and Natural History*. Van Nostrand Reinhold Company, New York, New York.
- Forrester, D. I., Kohnle, U., Albrecht, A. T., & Bauhus, J. (2013). Complementarity in mixed-species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand density. *Forest Ecology and Management*, 304, 233–242.
- Foster, J. R., Finley, A. O., D'Amato, A. W., Bradford, J. B., & Banerjee, S. (2016). Predicting tree biomass growth in the temperate-boreal ecotone: Is tree size, age, competition, or climate response most important? *Global Change Biology*, 22(6), 2138–2151.
- Fritts, H.C. 1976. *Tree Rings and Climate*. Academic Press, New York, New York.
- Genries, A., Drobyshev, I., & Bergeron, Y. (2012). Growth-climate response of Jack pine on clay soils in northeastern Canada. *Dendrochronologia*, 30(2), 127–136.
- Graumlich, L. J. (1993). Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. *Canadian Journal of Forest Research*, 23(2), 133–143.
- Green, D.C., and Grigal, D.F. (1979). Jack pine biomass accretion on shallow and deep soils in Minnesota. *Soil Science Society of America Journal*. 43, 133-1237.

- Grissino-Mayer, H. D. (2001). Evaluating Crossdating Accuracy: A Manual and Tutorial for the Computer Program COFECHA. *Tree-Ring Research*, 57(2), 205–221.
- Hamilton, W. N., & Krause, H. H. (1985). Relationship between jack pine growth and site variables in New Brunswick plantations. *Canadian Journal of Forest Research*, 15, 922–926.
- Handler, S., et al. 2014. Michigan Forest Ecosystem Vulnerability Assessment and Synthesis: A report from the Northwoods Climate Change Response Framework. General Technical Report NRS-129. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.
- Haugen, D.E., Walters, B.F., Piva, R.J., Neumann, D. 2014. Michigan timber industry—an assessment of timber product output and use, 2008. Resour. Bull. NRS-93. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 67 p.
- Hofgaard, A., Tardif, J., & Bergeron, Y. (1999). Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. *Canadian Journal of Forest Research*, 29(9), 1333–1346.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43:69-78.
- Huang, J. A., Tardif, J. C., Bergeron, Y., Denneler, B., Berninger, F., & Girardin, M. P. (2010). Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Global Change Biology*, 16(2), 711–731.
- Ibáñez, I., Zak, D. R., Burton, A. J., & Pregitzer, K. S. (2018). Anthropogenic nitrogen deposition ameliorates the decline in tree growth caused by a drier climate. *Ecology*, 99(2), 411–420.
- IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups, I, II, and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland.
- Isaac-Renton, M., Montwé, D., Hamann, A., Spiecker, H., Cherubini, P., & Treydte, K. (2018). Northern forest tree populations are physiologically maladapted to drought. *Nature Communications*, 9(1), 1–9.
- Larsson, L. A. 2018. Cybis CooRecorder v9.3.1, Cybis CDendro v9.3.1. Cybis Elektronik and Data AB, Saltsjobaden, Sweden. Retrieved from www.cybis.se/forfun/dendro/index.htm.

- Lines, E. R., Zavala, M. A., Purves, D. W., & Coomes, D. A. (2012). Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. *Global Ecology and Biogeography*, 21, 1017–1028.
- Little, E.L. 1971. Atlas of United States Trees: conifers and important hardwoods. U.S. Department of Agriculture, Washington, D.C., Miscellaneous Publication No. 1146.
- Lunn, D., Spiegelhalter, D., Thomas, A., & Best, N. (2009). The BUGS project: Evolutions, critique and future directions. *Statistics in Medicine*, 28(25), 3049–3067.
- MacArthur, R. H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Princeton University Press, Princeton, New Jersey.
- Mina, M., Huber, M. O., Forrester, D. I., Thürig, E., & Rohner, B. (2018). Multiple factors modulate tree growth complementarity in Central European mixed forests. *Journal of Ecology*, 106(3), 1106–1119.
- Mitchell, P. J., O’Grady, A. P., Tissue, D. T., White, D. A., Ottenschlaeger, M. L., & Pinkard, E. A. (2013). Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. *New Phytologist*, 197(3), 862–872.
- Montwé, D., Isaac-Renton, M., Hamann, A., & Spiecker, H. (2016). Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north. *Global Change Biology*, 22(2), 806–815.
- NOAA National Centers for Environmental Information, Climate Data Online: Station Details published May 2018, retrieved on October 7, 2018 from <https://www.ncdc.noaa.gov/cdo-web/datasets/GSOM/stations/GHCND:USC00203391/detail>.
- NOAA National Centers for Environmental information, Climate at a Glance: Divisional Time Series, published December 2018, retrieved on January 30, 2019 from <https://www.ncdc.noaa.gov/cag/>.
- Ogle, K., Barber, Jarrett, J., Barron-gafford, G. A., Young, J. M., Huxman, T. E., Loik, M. E., & Tissue, D. T. (2015). Quantifying ecological memory in plant and ecosystem processes. *Ecology Letters*, 18(3), 221–235.
- O’Neill, G. A. O., Hamann, A., & Wang, T. (2008). Accounting for population variation improves estimates of the impact of climate change on species’ growth and distribution. *Journal of Applied Ecology*, 45(4), 1040–1049.
- Palmer, W. United States Department of Commerce. 1965. *Meteorological Drought* (Research Paper No. 45). Washington D.C., USA: Office of Climatology, U.S. Weather Bureau.

- Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 37(1), 637–669.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37–42.
- Pellerin, S., & Lavoie, C. (2003). Recent expansion of jack pine in peatlands of southeastern Québec: A paleoecological study. *Ecoscience*, 10(2), 247–257.
- Peltier, D. M. P., Fell, M., & Ogle, K. (2016). Legacy effects of drought in the southwestern United States: A multi-species synthesis. *Ecological Monographs*, 86(3), 312–326.
- Peltier, D. M. P., & Ibáñez, I. (2015). Patterns and variability in seedling carbon assimilation: Implications for tree recruitment under climate change. *Tree Physiology*, 35, 71–85.
- Phipps, R. L., 1985. Collecting, preparing, crossdating, and measuring tree increment cores. *USDI Geological Survey. Water Res. Invest. Rep.* 85-4148.
- Rudolph, T.D., & Laidly, P.R. 1990. *Pinus banksiana* Lamb. (jack pine). In *Silvics of North America I. Conifers*. Edited by R.M. Burns and B.H. Honkala. *USDA For. Serv. Agric. Handb.* 654. pp. 280-293.
- Szeicz, J. M., & MacDonald, G. M. (1994). Age-dependent tree-ring growth responses of subarctic white spruce to climate. *Canadian Journal of Forest Research*, 24(1), 120–132.
- Szeicz, J. M., & MacDonald, G. M. (1995). Dendroclimatic Reconstruction of Summer Temperatures in Northwestern Canada since A.D. 1638 Based on Age-Dependent Modeling. *Quaternary Research*, 44(2), 257–266.
- Stokes, M.A., & Smiley, T. L. 1968. *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago, Illinois.
- Subedi, N., & Sharma, M. (2013). Climate-diameter growth relationships of black spruce and jack pine trees in boreal Ontario, Canada. *Global Change Biology*, 19(2), 505–516.
- Tjoelker, M. G., Oleksyn, J., Lorenc-Plucinska, G., & Reich, P. B. (2009). Acclimation of respiratory temperature responses in northern and southern populations of *Pinus banksiana*. *New Phytologist*, 181(1), 218–229.
- U.S. Climate Data. (2018). *Temperature – Precipitation – Sunshine – Snowfall*. Retrieved from <https://www.usclimatedata.com/climate/grayling/michigan/united-states/usmi0349/2018/1>.
- Wilmking, M., Juday, G. P., Barber, V. A., & Zald, H. S. J. (2004). Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology*, 10(10), 1724–1736.

Yarranton, M., & Yarranton, G. A. (1975). Demography of a jack pine stand. *Canadian Journal of Botany*, 53(3), 310–314.

University of New Hampshire. (2018). CanopyApp (1.0.3) [Mobile application software]. Retrieved from <https://itunes.apple.com/us/app/canopyapp/id926943048?mt=8>.

Supplemental Information

S1: Posterior parameter estimates, mean \pm SD and 95% credible intervals (CI)

Parameter	BOG	DRY 1	DRY 2
A: Intersect of model	11.19 \pm 1.3 (8.94, 13.5)	0.87 \pm 0.23 (0.38,1.26)	2.0 \pm 0.28 (1.39, 2.52)
β_1 : effect of Size on Growth (log)	-3.61 \pm 0.41 (-4.35, -2.89)	-0.27 \pm 0.08 (-0.42, -0.09)	-0.59 \pm 0.09 (-0.75, -0.40)
β_2 : lag effects of previous growth	0.41 \pm 0.05 (0.29, 0.52)	0.75 \pm 0.03 (0.7,0.8)	0.58 \pm 0.04 (0.51, 0.65)
β_3 : effect of April temperature	0.07 \pm 0.01 (0.05, 0.09)	0.04 \pm 0.01 (0.03,0.06)	0.05 \pm 0.007 (0.04, 0.07)
β_4 : effect of July PDSI	0.07 \pm 0.01 (0.04, 0.09)	0.004 \pm 0.01 (-0.02,0.03)	0.04 \pm 0.01 (0.02, 0.06)
a : Intercept of standard deviation model (log)	0.15 \pm 0.18 (7.8E-06, 0.58)	0.28 \pm 0.12 (5.91E-04,0.51)	0.92 \pm 0.12 (0.69, 1.16)
b : effect of diameter on SD	0.02 \pm 0.06 (-0.13, 0.08)	-0.01 \pm 0.05 (-0.1,0.1)	-0.24 \pm 0.04 (-0.33, -0.16)
ω_1 : weighted lag effect of growth (y-1)	0.9 \pm 0.06 (0.77, 0.99)	0.96 \pm 0.03 (0.9, 1.0)	0.81 \pm 0.05 (0.71, 0.91)
ω_2 : weighted lag effect of growth (y-2)	0.1 \pm 0.06 (0.005,0.23)	0.03 \pm 0.03 (0.002, 0.1)	0.19 \pm 0.05 (0.09, 0.29)

Results in bold indicate statistically significant covariate effects (95% CI does not intersect with zero)

S2: OpenBUGS Code

```

model{
for(i in 1:86){
  for(y in (beg[i]+2):46){

    rg[i,y]~dnorm(R[i,y],tau0[i,y])#likelihood
    rg.h[i,y]~dnorm(R[i,y],tau0[i,y])#predictions

    R[i,y]<-alpha[i]+beta [1,i]*log(dbh[i,y])+beta[2,i]*(wG[stand[i],1]*rg[i,y-
1]+wG[stand[i],2]*rg[i,y-2])+beta[3,i]*Apriltemp[y]+beta[4,i]*Julypdsi[y]

tau0[i,y]<-1/var0[i,y]
var0[i,y]<-a[stand[i]]+b[stand[i]]*log(dbh[i,y])
}

alpha[i]~dnorm(A[stand[i]],tau[1,stand[i]])
for(k in 1:4){
beta[k,i]~dnorm(B[k,stand[i]],tau[k+1,stand[i]])
}

}

#priors
for(i in 1:3){
A[i]~dnorm(0,0.0001)
a[i]~dlnorm(1,0.001)
b[i]~dnorm(0,0.0001)
for(k in 1:5){tau[k,i]~dgamma(0.0001,0.0001)
var[k,i]<-1/tau[k,i]
}

for(k in 1:4){B[k,i]~dnorm(0,0.0001) }
wG[i,1:2]~ddirich(wGm[i,])

for(k in 1:2){
wGm[i,k]<-1
}
}

}#end model

```